Branching out: A comparative analysis of demographic determinants of mammalian speciation

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Preface

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text.

It is not substantially the same as any work that has already been submitted before for any degree or other qualification except as declared in the preface and specified in the text.

It does not exceed the prescribed word limit of 80,000 words for the Archaeology and Anthropology Degree Committee.

Summary

Mammalian speciation is not usually an instantaneous event. It is a protracted process, the course and outcome of which is determined by the interaction between demographic and genetic processes. These demographic processes include the formation of population isolates and the persistence of these isolates. The role and regulators of the demographic determinants of speciation have received some empirical attention, but mostly across birds and squamates. The point of this thesis is to ask what factors regulate the demographic determinants of speciation in mammals, and how these relationships shape macroevolutionary patterns of speciation and species richness.

The thesis is divided into two sections that approach the question from different angles. The first is focused on extant mammals and uses subspecies as a proxy for population isolates to ask how ecological factors (1) regulate population isolate formation and (2) mediate the evolutionary trajectory of these isolates. In taking this approach, this section also sheds new light on the debated evolutionary 'role' of subspecies in mammals.

The second section focuses on a particular subgroup of mammals as a case study: hominins. Hominin speciation rate is calculated across three phylogenies based on different taxonomic approaches. I then test whether climate, time, and interspecific competition explains variation in these rates, and so ask what abiotic or biotic factors determined hominin speciation. Differences between results obtained across more and less inclusive ("lumping" and "splitting", respectively) phylogenies are then used to link these results to the main question in the thesis. It is suggested that taxa in "split" taxonomies are populations of taxa in "lumped" taxonomies, so that determinants of speciation on "split" taxonomies represent determinants of population isolate formation, and those of speciation on "lumped" taxonomies represent determinants of the rate at which those isolates become detached from the rest of the species.

Mammalian population isolate formation provides the raw material for speciation, and the rate at which it occurs is regulated by barriers in the landscape, the level of habitat fragmentation, and climate variability. Speciation is the road less travelled for most mammalian subspecies: and general determinants of the evolutionary trajectory of a mammalian population isolate include ecological substrate and metapopulation niche availability. Across all mammals, terrestrial population isolates become species less often than their non-terrestrial equivalents; and this pattern holds up in hominins. Patterns found

across hominins suggest that the probability of a population isolate becoming a novel species can also be determined by whether or not species-level niche space is saturated.

An important bridge between population isolate formation and speciation in mammals is the length of population isolate persistence: extended persistence, rather than extending the time it takes to become a full species, increases speciation rate. Again, abiotic factors—particularly climate and possibly habitat fragmentation—are important determinants of this process. Of interest here is the contradicting effects of these abiotic factors: habitat fragmentation promotes population isolate formation across mammals, but it can also curtail how long these isolates persist for. In hominins, a previously unknown role for climate is in mediating the link between intraspecific processes and speciation: the results suggest that longer-term persistence of populations necessary for these to split from the rest of the species tended to occur in more stable climates.

Macroevolutionary patterns of mammalian species richness are the cumulative outcome of the balance between population isolate formation and persistence over time: and including demographic determinants of speciation rate in evolutionary models can provide novel insights into why, and how, mammalian species form.

Acknowledgements

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I first heard about a “Robert Foley” from Alex Wilshaw, whose encouragement and support during my undergraduate degree and subsequent PhD application is largely to blame for this thesis. I owe him very much. Some blame is also to be apportioned to Ms. Freitas, my high school biology teacher, whose enthusiasm, unassailable kindness, and belief in her students was a very big reason I felt like I was allowed to—and in fact, that I *should*—follow my interests and stay forever curious at university. This is where it led!

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This thesis is dedicated to my friend Silvia Hogg (1960-2020).

Table of contents

List of figures

List of tables

1 Introduction

1.1 Introduction

How and why species form is a principal question in evolutionary biology. Speciation can be studied at microevolutionary and macroevolutionary scales, with the former focused on the mechanics of the process, and the latter asking what explains variation in speciation rates, and consequently in patterns of species diversity. Within the metaphorical phylogeny of approaches to studying the origin of species, the microevolutionary clade is decidedly unbalanced, with a skew towards examining how and why speciation happens through the lens of reproductive isolation (reviewed in Harvey, Singhal, & Rabosky, 2019). Indeed, examining the genetic correlates of reproductive isolation is the central focus of the two microevolutionary future research areas outlined by the Marie Curie SPECIATION Network (Butlin et al. 2012). Research emphasis on reproductive isolation stems from the central role this process occupies in the Biological Species Concept (Mayr 1942); and it can also occupy an important position as the final stage of speciation in hierarchical species concepts such as the General Lineage Concept (de Queiroz 1998). The breaking down of gene flow is usually the final, and therefore critical, threshold in speciation: but intraspecific population-level processes, and the biotic and abiotic factors controlling them, must play major roles, at least in part by regulating whether or not it is possible for this genetic threshold to be reached. Across mammals, speciation tends to be a protracted process, with the cessation of gene flow between incipient taxa arising relatively gradually (Coyne 1998; Harvey, Singhal, and Rabosky 2019; Rosindell et al. 2010). There are exceptions to this rule (Arnold and Meyer 2006; Burrell et al. 2009), but these are comparatively rare: and what this means is that although speciation is ultimately a genetic process, intraspecific population-level dynamics must play a major role in facilitating it.

These intraspecific processes are what Harvey et al (2019) collectively refer to as "demographic processes"—this phrasing is adopted in this thesis—and they include, first, the formation of population isolates between which reproductive isolation may arise, and second, the persistence of these isolates for a sufficient amount of time for this to happen. These processes have enjoyed some empirical attention across vertebrate clades, but there has been an emphasis on exploring them in birds and squamates (Claramunt et al. 2012; Weeks and Claramunt 2014; Phillimore et al. 2007). The point of this thesis, in the broadest terms, is to

ask how these comparatively underexplored demographic processes operate to control speciation across mammals, and what abiotic and biotic factors regulate these processes.

1.2 What is speciation?

'Speciation', in this thesis, refers to Simpson's (1944) branching mode of evolution, or Vrba's (1993) 'speciation': that is, the process by which lineages split to form new species, regardless of whether or not the ancestral population persists after the speciation event (see Figure 1-1). It excludes gradual change within a species without such splits (Simpson's phyletic change or Vrba's phyletic evolution). Speciation, as it is used here, is thus synonymous with cladogenesis (Allmon 2017), and refers to the overall process by which new species form through the splitting of lineages.

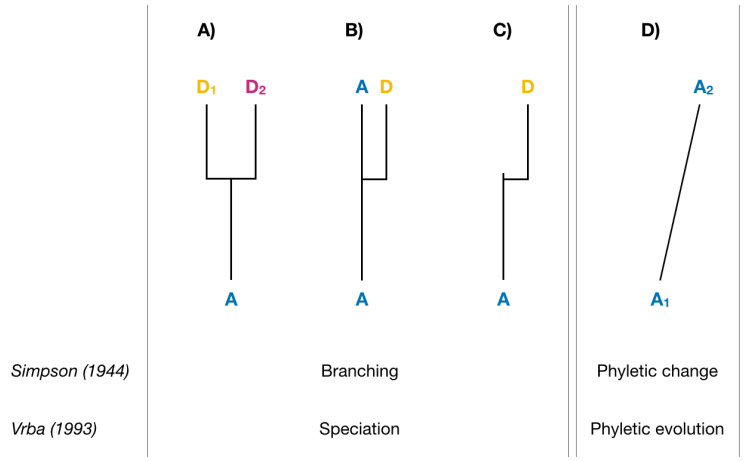


Figure 1-1: Definition of process terms

Figure adapted from Figure 1 in Vrba (1993). A) An ancestral species, A, splits into two new species, D_1 and D_2. A goes extinct in this scenario. B) A new species, D, splits from its ancestral form, A, which persists. C) As in B), but the ancestral species goes extinct soon after D splits from it. D) A_1 evolves, without a splitting event, into A_2. Scenarios A), B), and C) are called 'branching' in Simpson (1944) and 'speciation' in Vrba (1993). Scenario D) is not included as a speciation or cladogenetic event here.

1.3 Demographic determinants of speciation

What is implicit in an emphasis on the role of demographic processes in speciation is the idea that populations are the 'raw material' of speciation: and this is certainly not new. It can, maybe unsurprisingly, be traced back at least to Darwin (1859), who suggested that the production of 'varieties' and species are linked. Mayr (1982) extended this line of reasoning to consider subspecies formation the second of five stages in avian speciation. The evolutionary role of populations implied by these theoretical models means factors regulating their formation and subsequent evolutionary trajectory are important elements in the answer

to how and why species form, but they have remained underexplored relative to the genetic architecture of reproductive isolation. Reproductive isolation is key to two of the three core future speciation research areas described by the Marie Curie SPECIATION Network (Butlin et al. 2012); and in a more recent review of papers published between 2008 and 2018, Harvey et al (2019) illustrate a clear asymmetry between research focus on demographic factors versus reproductive isolation and speciation genetics. Further, in many modern microevolutionary models of speciation, demographic elements are only explicitly included in restricted ways: only a single population splitting event is typically assumed (e.g. Nosil and Flaxman 2011), and population size is often also included as a parameter in theoretical models.

That there is an emphasis on reproductive isolation is not to say, however, that no work has been devoted to the relationship between population isolate formation and persistence and speciation at all. Early work focused on the link between populations and adaptive change within species. Wright's (1931) 'shifting balance' model of evolution, for example, relies critically on the subdivision of species into populations. In brief, the model suggests the effect of genetic drift is greater within semi-isolated and small populations, resulting in quicker exploration of genotypic space; and migrants from populations on the highest fitness peaks cause other populations to also move towards these peaks. Although there is some experimental evidence to support parts of Wright's model (Wade and Goodnight 1991), it is heavily criticised on theoretical and empirical grounds (Coyne 1998). In the second half of the last century, population isolation became more explicitly linked to speciation through the idea of species selection on traits predisposing species to forming population isolates. Paleontological work on marine invertebrates was taken to suggest that larval dispersal mode was subject to species selection, with sessile larvae increasing the probability of population isolate formation and consequently speciation (Hansen 1983; Jablonski 1986). More recently, demographic controls on speciation have been explored through both simulations (Rangel et al. 2018) and empirical work, predominantly across birds and lizards (Harvey, Singhal, and Rabosky 2019; Haskell and Adhikari 2009; Singhal et al. 2018).

Simulations explore the relationship between demographic processes and speciation by asking how hypothetical determinants of population isolate formation or persistence affect the probability of species formation. An important salvo in favour of the idea that demographic processes are key in species formation was fired by Gavrilets (2000), whose metapopulation simulation suggested an unambiguously positive relationship between population persistence and speciation. Subsequent work (often based on the Gavrilets model) has suggested that dispersal rates are negatively associated with speciation rate, because it precludes genetic

differentiation between populations (Birand, Vose, and Gavrilets 2012); but other work has suggested this relationship is positive when new and isolated geographic space is more easily colonised (Rangel et al. 2018). In addition, habitat heterogeneity and fragmentation have been invoked as factors promoting population divergence and therefore speciation (Aguilée et al. 2018). Results from simulation work, in sum, point towards an important role for demographic processes in speciation: empirical work is needed to clarify what this role is, whether this role is constant across taxa and through time, and what abiotic and biotic factors are important controls of these processes.

Recent empirical work has typically tested the hypothesis of a causal relationship between the rate of population isolate formation and speciation across avian and squamate clades by taking a comparative approach. The appeal of interspecific comparisons in a phylogenetic framework, which is also the approach adopted here for mammals, is that they can provide robust tests of the association between intraspecific demographic processes and macroevolution. The results from empirical studies align with those from simulation work in that they provide support for either a positive relationship between population isolation rate and speciation rate, or the role of hypothesised promotors of population isolation rate and speciation rate. Regarding the former, for example, Harvey et al. (2017) find a positive relationship between rates of population genetic differentiation and speciation rates in New World birds, and Haskell & Adhikari (2009) show subspecies richness is positively correlated with species richness across avian genera. Regarding the latter, dispersal ability has been focused on as potential determinants of population isolate formation rate and thus speciation. Dispersal ability has been shown to correlate positively with avian speciation rate (Phillimore et al. 2006), but other work has recovered a negative relationship (Claramunt et al. 2012; Weeks and Claramunt 2014).

Population persistence, by contrast, has received less empirical attention than population isolate formation across extant taxa (Dynesius and Jansson 2014). This is primarily because it is difficult to measure population loss without a fossil record or detailed natural history records. The importance of population persistence, however, can be inferred from a common pattern across the tree of life: asymmetrical rates of population isolate formation and speciation, with the former exceeding the latter (Rosenblum et al. 2012).

Despite the growing attention given to demographic controls on speciation outlined above, the unknowns far outnumber what is currently known about their role and determinants, and this is particularly true in mammals.

1.4 Approach and structure of the thesis

This thesis is a response to this comparative dearth, and its principal aim is to test hypotheses about the of role and determinants of demographic processes in mammalian speciation. It is divided into two sections that approach the problem from different angles. Section A is focused on extant mammals, takes a comparative phylogenetic approach, and uses subspecies as a proxy for population isolates to ask how ecological factors (1) regulate population isolate formation and (2) mediate the relationship between population isolates, after their formation, and future species. In taking this approach, this section also sheds new light on the contentious evolutionary 'role' of subspecies in mammals.

Section B, in contrast, focuses on a particular subgroup of mammals: hominins. The fossil record for our lineage is comparatively rich and well-studied, making it an ideal clade with which to explore the roles of demographic determinants of speciation. Hominin speciation and what determines it has long been of interest to paleoanthropologists, but most, if not all, approaches to date have relied on first appearance dates (FADs) of fossils alone without taking into account phylogenetic relationships, and consequently, hominin speciation rate has never been directly measured. FADs are also determined by taxonomic practice, which is notoriously controversial in paleoanthropology. In this section, I address these problems by directly measuring, for the first time, hominin speciation rates across three phylogenies based on different taxonomic approaches. I test longstanding assumptions about the role of climate in hominin speciation by asking whether these rates correlate with climatic variables; but also ask whether interspecific competition might have determined speciation rates. To link these analyses back to the question of demographic determinants of speciation, I suggest a framework with which to interpret results obtained from "splitting" (less inclusive) and "lumping" (more inclusive) taxonomies, in order to explore the shifting roles of various abiotic and biotic factors across the hominin speciation process.

With the exception of introductory chapters for each section and the methods chapter for Section B, each chapter is written as a stand-alone analysis of a specific question within the general theme of the thesis. To relate the results from each chapter back to this overall theme, however, they are contextualised in a metapopulation model of speciation at the end of each section. This also means results from Sections A and B can be compared within a central framework—even though methodologies differ between the sections—and this is done in the concluding chapter.

Section A: Speciation in extant mammals

2 Introduction to Section A: Speciation in extant mammals

2.1 Introduction

Why so many rodents, and so few elephants? The uneven distribution of species richness across the mammal tree must ultimately reflect different rates of speciation and extinction along its branches: the focus of this thesis, however, is speciation in particular. Explaining variation in speciation rates is a central theme in mammalian evolutionary biology, and is very often approached from a macroevolutionary perspective by exploring correlates of speciation rates calculated across phylogenies or inferred from fossil data. A non-exhaustive list of determinants of mammalian speciation rate includes heritable characters such as body size (Gittleman and Purvis 1998; Isaac et al. 2005), life history (Cardillo, Huxtable, and Bromham 2003), ecological factors (Upham, Esselstyn, and Jetz 2019), and latitude (Weir and Schluter 2007). What is common to these studies is the use of species as the most basic unit: if the tree of life is visualised instead as coral, most comparative work focuses on the shape of the carbonate skeleton.

Here, the question is approached by looking within the structure instead. That is, this section is centred on exploring the link between intraspecific demographic processes and speciation in extant mammals, by using subspecies and species, respectively, as proxies for these processes.

First, the history and application of subspecies and species concepts is discussed in Chapter 3; and the case is made that subspecies, existing at the locus of tension between intraspecific processes and speciation, represent useful taxonomic units for inclusion in evolutionary models.

Two themes are the focus of the subsequent three chapters:

1. Chapter 4: Exploring abiotic and biotic determinants of the strength of the correlation between generic species richness and average subspecies richness across all mammals, and placing these results in broader vertebrate context;
2. Chapters 5 and 6: Exploring ways to calculate elements of subspecies diversification rate, and asking what abiotic and biotic factors correlate with variation in these rates.

Chapter 4, as it appears in this thesis, is published as a research article in Proceedings of the Royal Society B (van Holstein and Foley 2020). Chapter 5 focuses on subspeciation rates across all mammals, and asks whether it correlates with extinction risk. Chapter 6 is a continuation of Chapter 5, but also explores subspecies "death" rates—which comprises extinction and resorption back into the general gene pool of the species. Chapter 6 is restricted to primates because they are comparatively well-studied, both from a taxonomic and biogeographic perspective; and the generalizability of these results to all mammals is discussed. Chapters 4, 5, and 6 are stand-alone analyses of the determinants of the evolutionary relationship between mammalian subspecies and species, but the results are contextualised in a metapopulation model of speciation in Chapter 6 to set out the broader implications of the results for the question of how demographic processes relate to speciation.

2.2 Microevolution and macroevolution in mammals

By exploring how demographic processes within species relate to the splitting of species in mammals, this section has some bearing on one of the biggest challenges in mammalian evolutionary biology: linking microevolution to macroevolution. Microevolution can be taken rather loosely as referring to within-species processes—usually adaptation; and macroevolution as the appearance of new species and divisions above the species level (sensu Reznick and Ricklefs 2009).

Within mammals, as in most clades, microevolutionary processes and macroevolutionary patterns as defined by Reznick & Ricklefs (2009) are usually treated separately, with the former examined by explaining phenotypic change within single species, and with the latter being the focus of comparative paleontological and phylogenetic work. That is not to say they cannot be considered together: Uyeda and colleagues (2011), for example, combine body size data across micro- and macroevolutionary timescales to show that in mammals, birds, and squamates, within-species phenotypic change can be rapid, but is bounded before 1 Myr of existence; and that divergence in body size only starts accumulating after this point. To explain this pattern, they invoke Futuyma's (1987, 2010) ephemeral divergence model, which suggests that adaptive changes at the scale of populations do not often leave macroevolutionary signatures because these changes are not adaptive across the entire range of the species. In this model, only two putatively rare events may result in local adaptation scaling up to species-wide changes in phenotype: a shift in adaptive optimum across the species' entire range, or range contraction. A major point to make in relation to the focus on

speciation in this thesis is that Uyeda et al. (2011) do not evaluate whether or not speciation can explain the observed jumps in divergence after 1 Myr.

Here, in contrast to most work dealing with the relationship between microevolution and macroevolution in mammals, the microevolutionary element is not explicitly evolutionary change in a key phenotypic trait. Rather, it is intraspecific population splitting. Since subspecies should capture statistically significant breaks in phenotype across a species' range (reviewed in detail in Chapter 3), intraspecific morphological evolution is implicitly included here; but characters between which mammalian subspecies differ will not be the same across taxa. The link with macroevolution—that is, the appearance of novel species—is the question of the role of these populations in the speciation process, and what mediates the relationship between population and novel species. Mammalian subspecies have, to the best of my knowledge, not been used to explore the relationship between microevolution and macroevolution in this way before.

3 Species and subspecies

3.1 Introduction

Section A examines factors mediating the relationship between intraspecific and macroevolutionary splitting by using subspecies and species, respectively, as proxies for these processes. Neither the meaning of the terms 'species' and 'subspecies', nor the means by which these are applied to identify these taxonomic units, have been consistent across time and disciplines. At the core of the problem lies the difficulty in imposing discrete categories onto a continuous process. This chapter outlines the history and application of species and subspecies concepts, sets out how they are defined in the rest of this section, and makes the case that they can be viewed, rather than discrete and unrelated categories, as stages across an evolutionary continuum.

3.2 Species

'Species' can refer to two things: first, the species *category* or *rank* (that is, the entire class of units known as species and how to identify units within it), and second, specific species *taxa* (that is, specific units within this category, e.g. *Homo sapiens* or *Cavia porcellus*). The former, in particular, has long been the subject of debate: post-Darwinian definitions of the species category comprise more than 30 distinct concepts (Zachos 2016), each emphasizing different diagnostic features. This sub-section begins with an outline of the history of both the species category and species taxon definitions, followed by a discussion of the practical problems inconsistent taxonomic practice raises for the methodology of subsequent chapters.

3.2.1 Application through time

'Species' was not an exclusively biological concept until around the 19th century. The idea that things, both biological and non-biological, can be classified into definable types or categories of entities has a long philosophical history with roots in Platonic and Aristotelian thinking. Plato and Aristotle both sought, in the broadest terms, to classify things by defining their 'essences'. Aristotle referred to "eidos" (species) in both his biological and logical works. Aristotelian philosophy formed the bedrock of much Medieval thought, and, during this time, 'species' continued to be applied to classify biological and non-biological things alike. Wilkins (2009) suggests that the first definition of 'species' in an exclusively biological context was published in 1686 by John Ray, an English naturalist: but 'species' continued to

include nonliving objects until the 19th century: indeed, Linnaeus classified minerals alongside plants and animals in his Systema Naturae.

3.2.2 A *very* brief history of the species taxon

The species taxon is an individual unit of the species category: for example, the specific ape lineage known as *Homo sapiens*. It is now widely accepted that species taxa are logical individuals: that is, spatiotemporally delimited entities (Ghiselin 1997). Until Ghiselin's suggestion that species taxa are logical individuals, however, they were widely conceived of as a class. If species taxa are classes, there are essential properties that are necessary and sufficient for elements (that is, individuals in a species) to be considered members of the class. Conversely, if species taxa are logical individuals, they are historical entities with spatial and temporal restrictions: no essential properties are needed to define it, and crucially, they have a start and end point. Therefore, even if an identical species taxon replaces it after its death, these are two separate logical entities. As an example, if a population of hominins physically and genetically indistinguishable from Neanderthals evolved on Mars, it would be considered the same class as *Homo neanderthalensis,* but not the same logical individual.

3.2.3 The species category

The species category is a rank in the taxonomic hierarchy; it outlines the characteristics species taxa share that mark them as members of the category.

3.2.3.1 In the classificatory hierarchy

The species category was a relative term in classical and early modern scholarship, unlike the fixed rank it occupies today. This is best illustrated by what became known in the Middle Ages as Porphyry's tree (Figure 3-1), a nested classificatory hierarchy by the 3rd century Greek neoplatonist philosopher Porphyry. The tree comprises a hierarchy of dichotomous divisions where all levels (except the highest and lowest) are 'genus' to the level below it, and all levels are 'species' to that above it. In contrast, the species category occupies an absolute rank in Linnaeus' Systema Naturae, first published in 1735. His taxonomic hierarchy comprised five levels, with species occupying the lowest; this system, of course, is still in use today with additional ranks above and below the species level.

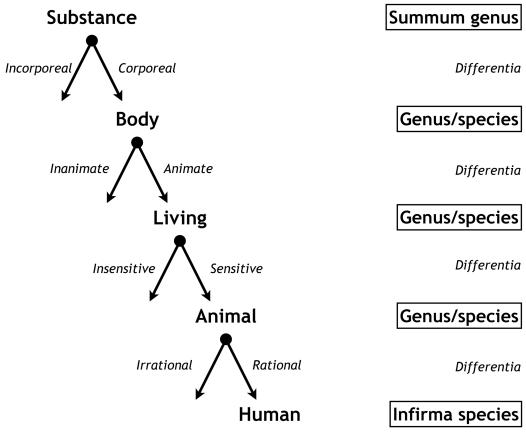


Figure 3-1: Porphyry's tree

Porphyry's tree, with a classification of humans to illustrate its use. Each level of classification is 'genus' to the level below it and 'species' to the level above it, except for the highest and lowest levels, which are the summum genus and infirma species respectively. Classification proceeds dichotomously: each genus is split up into species according to a 'differentia' with two options. Figure adapted from Fig 2.1 in (Zachos 2016)

3.2.3.2 Approaches to defining the species category: essentialist versus population thinking

Modern species definitions—of which there are at least 30 (Zachos 2016)—are attempts to define the species category. Despite this diversity, they are all based on population thinking (Mayr 1959). This approach is characterised by a belief that the 'type' (that is, the average) is an abstraction: only variation is real and measurable. The traditional interpretation of the history of species category definitions is a clear dichotomy: before Darwin, the standard approach to classification was essentialism, and Darwin revolutionized taxonomy by pioneering population thinking (Winsor 2003). In the essentialist approach, species are conceived of as Platonic types with necessary and sufficient properties that defined them. Thus, the 'type', defined by properties that must always be present, is real, and variations around it are illusions. The established view holds that the "stranglehold" of essentialism produced "two thousand years of stasis" in taxonomic practice and evolutionary theory (Hull 1965), principally because it does not allow essential characters to vary in a population while evolution by natural selection requires them to. This view has been increasingly successfully challenged on the basis of two arguments: first, that the practice of pre-Darwinian taxonomy was not restricted to an essentialist paradigm (even if taxonomists adhered to an essentialist worldview in theory); and second, that essentialism was not the sole theoretical approach to taxonomy, and other species taxon concepts emphasizing genealogy rather than essential defining features were in use before Darwin.

Regarding the first argument, Winsor (2003) makes the case that the pre-Darwinian practice of classifying organisms more frequently followed a polythetic approach, in which species were delineated according to common but not essential shared features. The method of "exemplars", for example, defined groups with reference to a 'typical' member, analogous in some ways to today's type specimens; potential members of the group were then compared to the typical member and excluded if they were distinct enough. Classification was largely pragmatic in practice and taxonomists acknowledged problematic 'fuzzy boundaries' between groups in nature. Even if early taxonomists *theoretically* conceived of species in an essentialist paradigm, this did not necessarily inform classification in *practice*.

That is not to say that an essentialist theoretical conception of species was universal, however. Wilkins (2009) claims a "generative" conception of species, which emphasized common descent rather than the need to exhibit essential and sufficient features, was actually the most commonly used species definition. There are numerous examples to support his case, including the first species definition in a purely biological context by John Ray ("…No matter what variations…if they spring from the seed of one and the same, they are accidental variations" (Ray, 1686 quoted in Zachos (2016)), and Kant's (1775) assertion that "In the animal kingdom the division of nature into… species is grounded on the general law of reproduction" (p.11). Regarding Linnaeus, commonly conceived of as the archetypical essentialist, Richards (2010) writes that "if he was an essentialist, it was of a genealogical kind. Essences were passed on in reproduction via the transmission of medullar matter…" (p.58). There were, of course, pre-Darwinian theoretical essentialists alongside those who prioritized descent, but the variety of early species concepts has been severely underestimated in the traditional account.

At the very least, then, the view that Darwin liberated biology from the shackles of essentialism by promoting 'population thinking' underestimates the variety of species definitions in use in pre-Darwinian times; a shared feature of many early species definitions emphasizes shared descent and genealogy. It is likely that many early taxonomists employed more pragmatic definitions in the actual practice of classifying organisms. Darwin, by contrast, never produced a clear species definition and his view on species remains debated (Zachos 2016). Darwin's contribution to species definitions is not so much that he revolutionized taxonomy, but rather that he altered the fundamental framework in which species were interpreted. More specifically, the relationships between organisms classified in the pre-Darwinian Linnaean system are now understood in terms of shared descent—and this was Darwin's key contribution.

3.2.3.3 Approaches to defining the species category: evolutionary species versus taxonomic species

An important distinction is that between evolutionary and taxonomic species (Endler 1989). Evolutionary species are lineages that undergo evolution; taxonomic species are species as delimited by taxonomists, using one of the ~30 species concepts. Ideally, these two are equivalent; but taxonomic species represent approximations of evolutionary species in reality. The key issue preventing unambiguous synonymy of the two is that evolution is a continuous process, while taxonomy is discrete and occurs at a single point in time.

3.2.3.4 Modern species concepts

The ~30 species concepts in the literature can be classified in various ways. The first is splitting concepts into those based on processes and those based on pattern. This thesis is divided into two sections, with the first focused on extant taxa defined by relevant authorities in Wilson & Reeder's Mammal Species of the World (2005), and the second on extinct hominins. Extant species tend to be identified based on process-based species definitions, and since the implied processes (i.e. mate recognition and reproductive isolation) cannot be observed in the fossil record, pattern-based concepts tend to be applied to fossil taxa. Consequently, Section A primarily relies on process-based species definitions, while Section B makes use of pattern-based concepts.

The second approach to classifying species concepts is a functional hierarchy, comprising a primary or ontological concept which defines what species really are, and secondary concepts, which are operational definitions—that is, those that can be used in practice to identify individual species (Mayden 1997). In Mayden's view, the primary species concept is the Evolutionary Species Concept (Simpson 1951): species, then, are independent lineages with their own historical fate. All other species concepts, in this classification, are simply ways to identify such a lineage.

A variant of the hierarchical approach to species concepts was advanced as the "General Lineage Concept" by de Queiroz (1998). His model forms the foundation of the framework advanced to interpret results in Section B. The essence of de Queiroz's argument is that species are lineages (mirroring Mayden's (1997) emphasis on the Evolutionary Species Concept), and that, because speciation is a protracted process, different species concepts can be thought of as representing different stages in this process (see Figure 3-2). For example, morphological differences between species (as emphasized in the Morphological Species

Concept (Cronquist 1978), may arise before they are reproductively isolated (Biological Species Concept (Mayr 1942)).

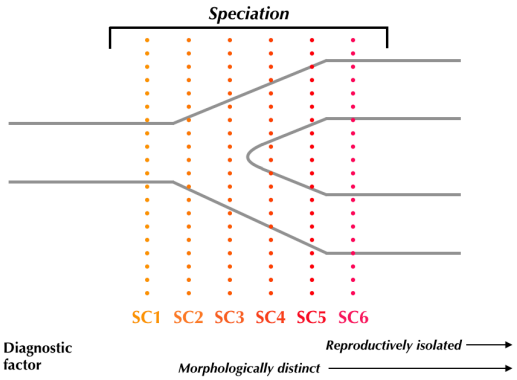


Figure 3-2: The General Lineage Concept

Adapted from Fig. 5.4 in de Queiroz (1998). SC denotes "species concept"; please note that the inclusion of only six species concepts is arbitrary. Speciation is a protracted process, illustrated by the black bar; species concepts place emphasis on different biological stages that species undergo during the process of speciation. For example, morphological differences between species (Morphological Species Concept), represented by SC4, may arise before they are reproductively isolated (Biological Species Concept), at SC6.

3.2.3.5 Apples and oranges

An important point in the sub-section on the species category is that, at least in modern usage, the species category occupies a fixed position in the classificatory hierarchy; and subsequent chapters in this section certainly assume this is true. Whether or not taxonomic practice across disciplines and taxa do actually consistently identify groups occupying this specific objective level as "species" remains an important unanswered question. A particular problem here, especially if applied non-randomly across a dataset, is taxonomic "inflation" (Isaac, Mallet, and Mace 2004), which broadly refers to a recent shift from the application of the Biological Species Concept (BSC), which emphasizes reproductive isolation, to the widespread use of the Phylogenetic Species Concept (PSC), which conceives of species as "diagnosable clusters…within which there is a parental pattern of ancestry and descent" (Cracraft 1983). This commonly results in subspecies being lifted to species status: a recent example is that of the elevation of two subspecies of *Thrachypithecus phayrei* to species status (Roos et al. 2020). Inconsistent taxonomic practice, regardless of whether or not it is appropriate or biologically justifiable, evidently presents a problem for the analyses in subsequent chapters. I account for it in Chapter 4 by modelling the potential impact of taxonomically non-random "inflation" and asking how likely it was that the observed pattern is the result of "inflation", and in Chapter 5 by repeating all analyses on an extremely conservatively "non-inflated"

subset of the data (which excluded all species that were 1) named after 1980 (since the PSC became more widely applied after 1980 (Isaac, Mallet, and Mace 2004)) and/or 2) have, irrespective of when it was reclassified as a species, at any point been considered a subspecies of another species).

3.3 Subspecies

The existence of an objective taxonomic rank of 'species' itself is almost universally accepted, while its definition remains debated because of the sheer number of formal concepts advanced in the literature. By contrast, the subspecies rank is contentious for precisely the opposite reason: there is a single explicit definition, but inconsistent application thereof has led to the objective reality and usefulness of the subspecific taxonomic rank being questioned. In this sub-section, I make the case that revising subspecies designations in light of genetic data should not result in the invalidation of the concept as a whole, and that subspecies, existing at the locus of tension between microevolution and macroevolution, represent useful taxonomic units for inclusion in evolutionary models.

3.3.1 What are subspecies, and how do they relate to species?

Subspecies are fairly universally defined in practice as geographically non-overlapping, phenotypically distinct, reproductively non-isolated units within species (Patten 2010; Patten and Remsen 2017; Patten and Unitt 2002; Phillimore and Owens 2006).

These requirements are clearly descriptive, but some quantitative guidelines exist. The geographical element is far easiest to measure—subspecies cannot be sympatric. The most common statistical approach to subspecific recognition pertains to morphology, and is known as the "75% rule". It states that "a population is given subspecific status [if] at least 75 per cent of the individuals comprising it [are]… separable from 99+ per cent of the individuals of all other populations of the same species (Amadon 1949, p.251). The application of this rule discerns phenotypically distinct clusters, and when correctly applied, produces results where <5% of individuals in one subspecies overlap phenotypically with 99% of individuals in the other (Pimentel 1959). In terms of which phenotypic characters are best suited to proper subspecies identification, Skalski et al. (2008)illustrate that clinally varying traits are least appropriate. This is because subspecies, by definition, need to be phenotypically distinct, so appropriate characters should capture 'breaks' in phenotype. Patten (2010) suggests the following general hierarchy: pattern > colour = shape > size. In other words, pattern is less likely to vary clinally than size in most animals.

The question of how to genetically identify subspecies is more contentious. Most recent molecular work (Burbrink, Lawson, and Slowinski 2000; Cronin et al. 2015; Zink 2004)

requires subspecies to be monophyletic in order to qualify as 'good' phylogenetic clusters, but this patently ignores the expectation that subspecies are not reproductively isolated from each other. Indeed, this is the point Edwards and Patten (Edwards 2009; Patten 2010) make. A summary of their arguments is that monophyly is not a suitable criterion for subspecies delimitation on two counts. First, monophyly is affected by processes such as founder effects and sampling error, so is not a reliable indicator of the independent evolutionary history and reproductive isolation being hunted for in subspecies (or species) delimitation. Second, even if monophyly were a good indicator of reproductive isolation, such a threshold is not what subspecies should have attained: if a population satisfies the two other requirements of the subspecies definition– that is, it is phenotypically distinct and occupies a unique range – and has ceased to interbreed with other members of the species, it constitutes a full species under the Biological Species Concept.

This point is significant for the question of how subspecies relate to species, because it means that subspecies, when properly identified, are precursors to BSC species. The relationship between the BSC and the subspecies definition is illustrated in Panel A of Figure 3-3. If 'species', in the BSC sense, and subspecies, as defined above, are essentially stages in a continuum of genetic differentiation, it is tempting to conceive of subspecies as incipient species (e.g. Zink 2004). This is an inaccurate generalisation. Under models of allopatric speciation, the formation of subspecies is a stage through which species must pass (Mayr, 1940), but this does not mean that every subspecies will inevitably become a species: subspecies can be re-absorbed into larger undifferentiated populations of individuals of the same species through persistent interbreeding. When they do represent incipient species, however, they fit into de Queiroz's (1998) General Lineage Concept of species (see Figure 3-2) as a distinct stage of speciation. Thus, de Queiroz's framework represents a logical way to integrate species and subspecies concepts.

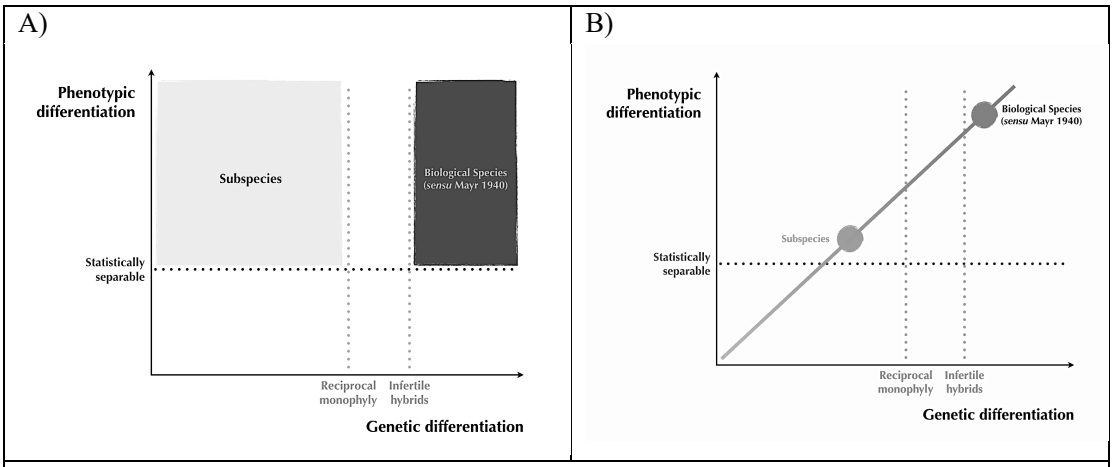


Figure 3-3: Where do subspecies fit?

Both panels ignore the first defining feature of subspecies, geographic isolation, as it is relatively more straightforward to ascertain whether or not populations achieve this in practice, and the relationship between phenotypic and genetic differentiation between subspecies has historically been more difficult to resolve. Panel A shows the definition of subspecies relative to the BSC: both require statistically separable phenotypic clusters, and the two taxonomic ranks differ solely in the degree of genetic differentiation achieved by the two (or more) groups of individuals. Panel B shows a potential evolutionary relationship between allopatric subspecies and full species, with the blue line representing the process of speciation. It is important to note that the evolution of subspecies into full species does not need to be realized in every case: subspecies are not the same thing as incipient species, because they do not invariably evolve into species, but on the other hand the formation of subspecies does constitute a stage in allopatric speciation.

The tension between subspecific persistence, resorption, and evolution into a new species makes the subspecific unit an interesting, useful, and underexplored link between splitting at the microevolutionary—that is, within-species—level and that at the macroevolutionary level—speciation. How do abiotic and biotic factors influence whether subspecies persist indefinitely, are resorbed into the general species gene pool, or become fully differentiated species; and do these factors operate in the same way across taxa? This question has received little empirical attention, particularly so in mammals. In birds, the focus has primarily been on explaining low phylogenetic signal in subspecies richness (Phillimore et al. 2007) —that is, exploring non-phylogenetic correlates of subspecific splitting, not what happens to them after they have formed. That some bird species show a preference for subspecies-specific song (Nelson 2000) can suggest communicative signals play a role in maintaining subspecies boundaries. Finally, and in line with the point that subspecies can be used in evolutionary models to explore the relationship between within-species splitting and speciation, Haskell & Adhikari (2009) demonstrate a general correlation between avian generic species richness and subspecific richness, and take this to suggest the rate of subspecies formation and speciation are linked.

3.3.2 Application of subspecies definition

The definition of subspecies has remained relatively constant through its history, but its application has been somewhat inconsistent. This inconsistency has resulted in major questioning of the validity of the rank.

The first mention of subspecies purportedly dates to 1844 in an ornithological context (quoted in Patten, 2010), and it became a widely used taxonomic rank in the late 1800s and early 1900s. It thus has a far shorter history than the species rank. Many subspecies diagnoses from the era of its initial application were arbitrary, based on trivial (and not necessarily statistically significant) morphological differences, and small sample sizes. Early criticisms of the ranks' biological validity have rested on the allegation that this definition has not been rigorously applied, leaving subspecies designations mostly arbitrary (Wilson and Brown 1953). The subspecies rank has recently come under fire again, this time with salvos from molecular phylogenetic approaches: many authors have concluded that the subspecies unit is biologically invalid because subspecies are not reciprocally monophyletic (Cronin et al. 2015; Zink 2004). Such criticisms are flawed in two respects. First, they conflate revisions of the application of a taxonomic unit's definition with the validity of that taxonomic unit. Revising traditional subspecies designations in light of genetic data should not equate to the invalidation of the concept as a whole. Second, the expectation that subspecies should be reciprocally monophyletic itself is at odds with the concept of subspecies: if there was no gene flow between phenotypically distinct populations, they classify as species under the BSC—as discussed above.

At a basic level, work is needed to clarify the expected degree of genetic differentiation between subspecies, and how (and in which parts of the genome) to measure it. In tandem, areas of tension between subspecies' phenotypic and genetic divergence need resolving: at present, for example, the genetic foundations of phenotypic differences between subspecies remain mostly unclear. Patten (2010) and Patten & Remsen (2017) suggest some statistical avenues that might prove profitable, although they admit realistically that "currently, we lack the tools to do so properly" (ibid, p.463). Underlying this are unresolved questions about the general relationships between genotype, phenotype, and local conditions over different time scales: again, more empirical work is needed.

However, the genetic component of the subspecies definition is only one of three diagnostic features. This means that, despite unanswered questions about the genetic bases of subspecific splitting, the subspecies rank is a useful taxonomic unit—both for cataloguing biological diversity, and also for use within evolutionary biology. Subspecies sit at the point of tension

between within-species population splits and speciation, and they can therefore be important units with which to answer what factors mediate the relationship between lineage splitting at microevolutionary and macroevolutionary scales.

3.3.3 Taxonomy used in Section A

The taxonomy used in this section is Wilson and Reeder's (2005) third edition of *Mammal Species of the World* (MSW3). The full list of species and subspecies richness is presented in Appendix 1. The MSW3 does not differ fundamentally from alternative authorities, such as the IUCN Red List: in fact, the default taxonomy for the Red List is MSW3 (IUCN 2019). The Red List departs from MSW3 only in well-justified cases, such as when a novel species is introduced in a peer-reviewed journal or other authoritative taxonomic work, and so the major difference between the two authorities is that the Red List is more species-rich than MSW3. A comparison of the total number of mammal species included in MSW3, the IUCN Red List at the start of this project (2017), and one of the most recent new mammalian taxonomies, that of Upham et al. (2019), is presented in Table 3-1. The 2017 edition of the Red List comprised 5,488 mammal species, a ~1% increase from MSW3; and the Upham et al. (2019) taxonomy included 5,804 species, a ~7% increase from MSW3.

Table 3-1: Comparison of taxonomic authorities

	MSW3 (2005)	**IUCN (2017)**	**Upham et al. (2019)** (modified IUCN + new species)
Extant species	5,416	5,488	5,804
% increase from MSW3		~1%	~7%

MSW3, rather than alternative authorities, was used in this section for the following reasons. The growth of mammalian species numbers since 2005 is principally the result of a shift from the application of the Biological Species Concept (BSC) to the Phylogenetic Species Concept (PSC), the adoption of which commonly results in the "inflation" of subspecies to species (Isaac et al. 2004; Gippoliti and Groves 2013). This is not necessarily a misguided or inappropriate shift: what species 'are', after all, remains debated, and what is happening is simply the increasingly widespread adoption of a different, but not 'wrong', species concept. However, when contextualised in the General Lineage Concept of species (see Figure 3-2 and 3-3), PSC species sit somewhere between subspecies and BSC species, which most closely represent the end stage of speciation out of all species concepts. This is a problem for this section, which uses (1) subspecies as a proxy for isolated populations within species, and (2) species as the end product of the process of speciation. The use of subspecific richness in PSC-based taxonomies as proxies for population isolates is likely to underestimate the

number of these isolates, because subspecies are commonly elevated to species status under the PSC; and moreover, species defined on the basis of the PSC do not actually represent the end stage of speciation they are used as a proxy for in this section. Further, Isaac et al. (2004) made the case that the shift from BSC to PSC is not happening uniformly across vertebrates, which means that the taxonomy of some mammalian clades still predominantly follows the BSC while others, such as Primates, follow the PSC. This is a problem because this section assumes that 'species' and 'subspecies' sit at the same positions along the speciation trajectory across all mammals. Inconsistent application of the PSC across the sample violates this assumption. The bottom line, then, is that the species and subspecies included in the 2005 MSW3 likely approximate the evolutionary units they are used as proxies for in this section more closely than those in more recently revised mammal taxonomies.

4 Ecological substrate and the evolutionary continuum between subspecies and species

Note: *This chapter has been published as van Holstein and Foley (2020). The text has had minor stylistic edits to fit the style of this thesis, but otherwise this is the published form. LVH conceived of the study, designed the analytical methods, collected the data, carried out the analysis, co-interpreted the results and wrote the paper; RAF co-interpreted the results and edited the manuscript.*

4.1 Introduction

Speciation across all forms of life is usually the process by which intraspecific population divergence culminates in sufficient discontinuity between populations to establish them on independent evolutionary trajectories. This process may be initiated by phenotypic differentiation, geographic isolation, or both (Harvey et al. 2017). Given the link between intraspecific population divergence and speciation, it follows that rates of population divergence and patterns of species richness should be linked, and consequently, that taxonomic richness should be correlated between the species and subspecies levels. Darwin predicted such an association, hypothesizing that lineages comprising more species would "oftener present varieties" (Darwin 1859), or in other words, comprise more distinct populations, than less species-rich lineages. An association between dynamics of divergence at and below the species level, however, is not a given: intraspecific populations may be too ephemeral for their origination to be linked to speciation (Harvey et al. 2017), and other intraspecific processes such as population persistence or degree and nature of reproductive isolation between populations may affect patterns of species richness more (Dynesius and Jansson 2014). Nonetheless, in a sample of 173 bird species, rates of population divergence were shown to correlate positively with speciation rates, and there also seems to be a latitudinal effect on the strength of this association with at- and below-species processes being more tightly linked in tropical lineages (Harvey et al. 2017).

Estimating rates of population divergence requires high-coverage genetic data and multiple samples per species, which are currently unavailable for most animal taxa. Insofar as subspecies represent spatially and phenotypically distinct populations within species (Patten 2010) they can be used as a proxy for the product of intraspecific population divergence. Whether subspecies tend to represent 'incipient' species, and that average subspecies richness (hereafter "S-SR") and species richness ("SR") should thus be correlated, remains unresolved.

Mayr (1982), for example, conceived of the formation of subspecies as the second of five stages of speciation in birds, while Zink (2004) made the contrasting case that avian subspecies nomenclature does not capture 'real' (that is, monophyletic) evolutionary units within species. In birds, however, SR and mean S-SR do correlate positively with a Kendall's tau of 0.23 (Haskell and Adhikari 2009).

While the relationship between subspecies richness and higher taxonomic levels has received some attention among birds (Harvey et al. 2017; Zink 2004; Haskell and Adhikari 2009), much less is known about this in mammals. Here, I test Darwin's prediction of a correlation between SR and S-SR in mammals, and, using avian studies as context, consider the effect of environmental substrate by comparing terrestrial and non-terrestrial mammals. I use multi-predictor phylogenetic regressions to test whether the relationship between S-SR and SR differs significantly depending on environmental substrate, latitude, or both. Finally, as it might be expected that range size is a key predictor of subspecies richness, I examine the relationship between subspecies richness and species range size.

4.2 Materials and methods

4.2.1 Data collection

The number of subspecies per species for all mammals was extracted from Wilson and Reeder's Mammal Species of the World (Wilson and Reeder 2005). I separated mammals into two groups based on environmental substrate; non-terrestrial mammals were the Orders Chiroptera, Cetacea and Sirenia, and Families Otariidae, Odobenidae, and Phocidae. Species per genus and mean number of subspecies per species were calculated in R 4.01 (R Development Core Team 2016). All further analyses were conducted in R. Species range data (total extent of species range (km^2)) and median latitude were obtained from the PanTHERIA database (Jones et al. 2009). Range data were not available for aquatic mammals. Tropical genera were defined as those with median latitude between 23.5°N and 23.5°S; temperate genera as those above 23.5°N and below 23.5°S.

4.2.2 Phylogenetic signal

I calculated Blomberg's K and Pagel's λ for generic average S-SR using the "phylosig" function in phytools (Revell 2012) on 50 genus-level trees randomly sampled from Upham et al's (Upham, Esselstyn, and Jetz 2019) posterior sample. I generated these trees by using the online Vertlife subsetting tool to produce trees with one species per genus, which avoids topological issues arising from any generic paraphyly. Supplemental analyses on the behaviour of Blomberg's K and Pagel's λ, given the right-skewed and long-tailed distribution

of trait values, were carried out by simulating different data distributions and calculating Blomberg's K and Pagel's λ (see Appendix 2-Supplementary Materials and Methods).

4.2.3 Species and genus "ages"

As significantly different average species or genus ages between the two groups might affect patterns of subspecies richness, I compared the distributions of terrestrial versus non-terrestrial species and genus branch lengths (as a proxy for taxon "age") with Wilcoxon rank sum tests.

To obtain species "ages", I extracted branch lengths from the MCC DNA-only node-dated tree from (Upham, Esselstyn, and Jetz 2019) using the "edge.length" command in phytools. I created a MCC genus-level tree from the species-level MCC tree using the "drop.tip" command in phytools, leaving only one tip per genus, and extracted branch lengths in the same way as for the species-level tree.

4.2.4 Correlations between species richness and subspecies richness

I calculated Kendall's tau between SR and S-SR. Kendall's tau was chosen to place the results for mammals in avian context: Haskell & Adhikari (2009) calculate Kendall's tau for the same variables across birds. Next, I ran phylogenetic regressions incorporating S-SR, ecological substrate, latitude, and species range on the 50 trees using the PGLS function in caper (David et al. 2018). SR, S-SR, and species range (km^2) were log transformed in all models. I optimized kappa and lambda branch length transformations (i.e. kappa="ML", lambda="ML") because AIC scores for models with these transformations suggested these performed best out of all combinations of transformations (see Appendix 2- Table 17-1). Categorical predictors were coded as binary factors: for environmental substrate, these were "non-terrestrial" and "terrestrial"; for latitude, these were "tropical" and "temperate". To test whether these categorical predictors interacted meaningfully with S-SR to predict SR, I compared three linear models:

1.	***Simple:***	$y = \beta_0 + \beta_1 x + \varepsilon$	*Equation 4-1*
2.	***Variable intercept:***	$y = \beta_0 + \beta_1 x + \beta_2 x + \varepsilon$	*Equation 4-2*
3.	***Interaction:***	$y = \beta_0 + \beta_1 x + \beta_2 x + \beta_1 \beta_2 x + \varepsilon$	*Equation 4-3*

where y is SR, *x* is S-SR, and ß$_2$ is the categorical predictor of interest. The significance of the addition of the variable intercept (Model 2), and the interaction term (Model 3) was assessed by an ANOVA. Finally, I ran a model in which latitude and environmental substrate were

allowed to interact, to ask whether the relationship between SR and S-SR is mediated by latitude and substrate.

The same format was followed to explore the relationship between species' range size and mean S-SR, and whether this relationship is affected by ecological substrate. The categories of environmental substrate were "terrestrial" and "powered flight" in this analysis, as no aquatic range data were available.

4.2.5 Testing for statistical artefacts

To confirm whether changes in statistical significance of correlations between species richness and subspecies richness are not simply a statistical artifact of subdividing a larger dataset, I took 10,000 random samples of 270 genera (since the non-terrestrial sample comprises 266 genera) from the data and calculated (1) Kendall's tau between species richness and average subspecies richness and (2) *p*-values for these correlation coefficients.

4.3 Results

4.3.1 Species richness and mean subspecies richness

Mammalian genera (n=1251) comprise, on average, 4.4 species. Terrestrial mammalian genera (n=985) tend to contain fewer species than non-terrestrial ones, but contain more subspecies per species (see

Table 4-1).

Table 4-1: Summary of results

	Mean species richness	**Mean subspecies richness**	**Kendall's *tau***
All mammals	4.4	1.9	**0.15** ***
Terrestrial	4.3	1.9	**0.11** ***
Non-terrestrial	4.7	1.8	**0.31** ***

*** = $p<0.001$

4.3.2 Phylogenetic signal

Median Blomberg's K for the 50 trees was 0.09 (with *p*-values above and below 0.05), while that of Pagel's λ was 0.64 (all $p<0.05$) (see Appendix 2 - Figure 17-1). Given that Pagel's λ was significant in all cases, I took into account phylogenetic structure in subsequent analyses by running phylogenetic regressions.

4.3.3 Clade "ages"

Wilcoxon rank sum test with continuity correction indicated no difference between distributions of genus branch length between terrestrial and non-terrestrial groups (p=0.33), and the same result was obtained for species (p=0.38). Further analyses were therefore performed without correcting for clade "age".

4.3.4 Effect of environmental substrate on the relationship between species richness and subspecies richness

SR and mean S-SR are positively correlated in mammals as a whole, but there is major scatter around this trend (Kendall's tau=0.15, 2-sided p<0.001). Terrestrial mammals alone exhibit a weaker, but still positive, correlation (tau=0.11, 2-sided p<0.001). In non-terrestrial mammals, the relationship is stronger: more speciose genera tend to have species with a higher number of mean subspecies (tau=0.31, 2-sided p<0.001). ANOVAs showed the addition of the interaction term was significant (p<0.05) in all 50 phylogenetic regressions (see Appendix 2- Figure 17-2): that is, a model with an interaction term explained more of the variance in average subspecies richness than the two other models. In addition, the interaction term was significant (p<0.05) in the interaction model itself in all 50 phylogenetic regressions. To illustrate the difference in slopes between terrestrial and non-terrestrial groups, the phylogenetic regression on the first of the 50 trees is plotted in Figure 4-1a.

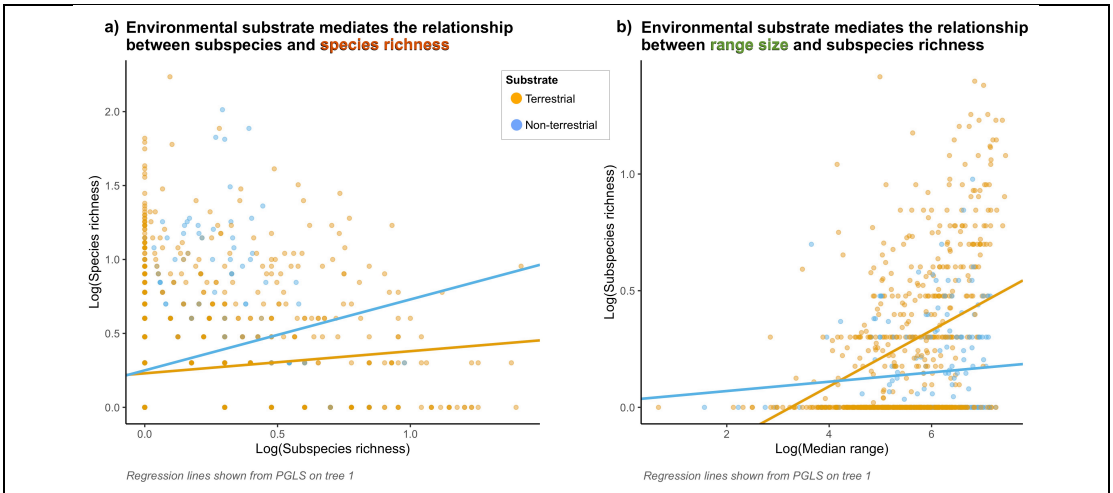


Figure 4-1: Environmental substrate influences dynamics of diversification at two taxonomic levels

A) shows the results from a phylogenetic regression on the first of the 50 trees between species richness (SR) and subspecies richness (S-SR), where slope and intercept were allowed to vary depending on substrate. The interaction between S-SR and substrate was found to be statistically significant, implying substrate mediates the relationship between average S-SR and SR in mammals. B) shows the results from a phylogenetic regression on the same tree between median species range and S-SR, where slope and intercept were allowed to vary depending on substrate. Again, the interaction term was found to be significant, implying substrate mediates the relationship between range size and S-SR within mammalian species.

4.3.5 The effect of latitude

No significant correlation between SR and mean S-SR was found in temperate mammals. In tropical mammals, there is a significant positive correlation (Kendall's tau=0.11, 2-sided $p<0.05$). Phylogenetic regressions in which the intercept or intercept and slope were allowed to vary based on latitude were non-significant. Models in which the relationship between SR and S-SR was mediated by latitude and substrate together was not significant overall, and no two-way interaction terms were significant either.

4.3.6 Species ranges and mean subspecies richness

In all mammals, the number of subspecies per species increases with species range (km^2) (tau=0.32, 2-sided $p<0.001$). When compared by ecological substrate, the correlation is very similar between terrestrial mammals and bats. In terrestrial mammals, tau=0.32 (2-sided $p<0.001$), while that in bats is very slightly weaker (tau=0.30, 2-sided $p<0.001$).

The interaction term between median range size and ecological substrate was significant ($p<0.05$) in all phylogenetic regressions (see Appendix 2- Figure 17-2). ANOVAs showed the addition of the interaction term was significant ($p<0.05$). The regression on the first of the 50 trees is plotted in Figure 4-1b.

4.3.7 Testing for statistical artefacts

In the 10,000 randomised subsets, an increase in correlation coefficient to 0.31 (the observed Kendall's tau for non-terrestrial taxa) did not occur, implying it is extremely unlikely that the increase I report occurred as a consequence of subsetting the dataset. All values of tau above 0.09 yielded significant p-values ($p<0.05$). These results are shown in Figure 4-2.

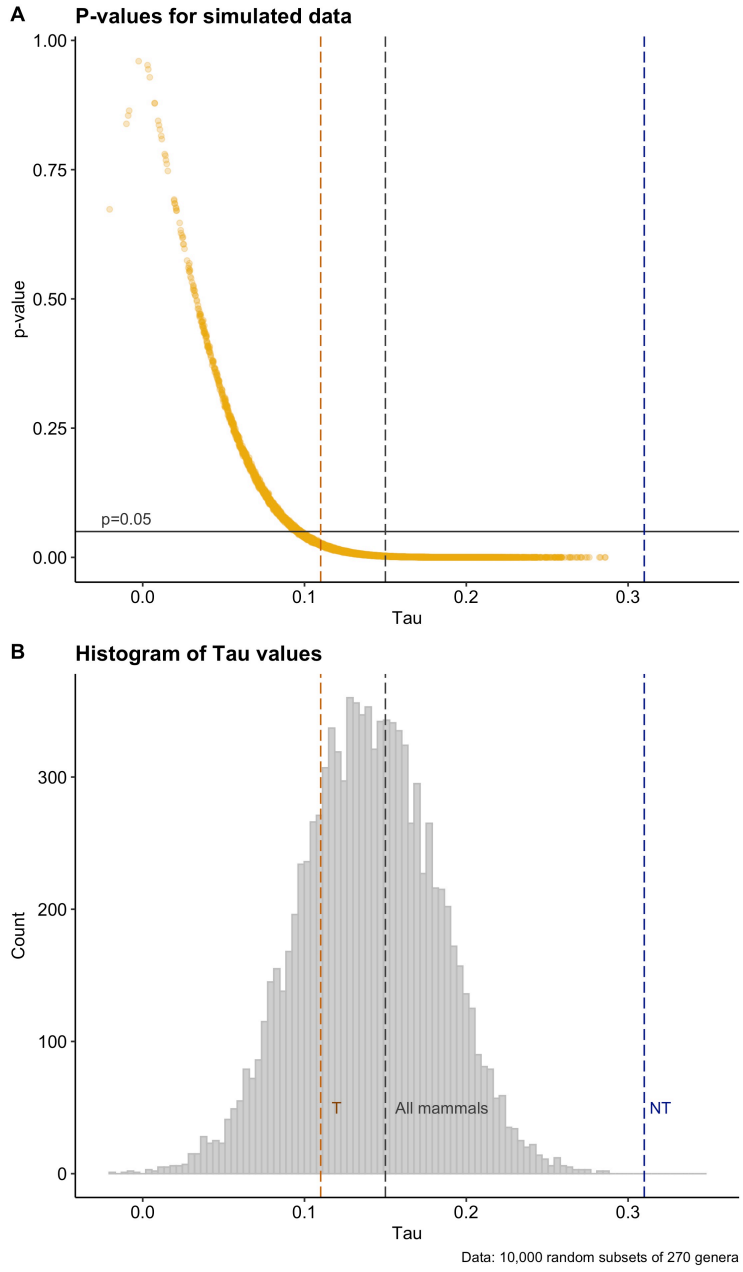


Figure 4-2: Results of randomly subsetting the dataset 10,000 times

A) *p*-values for Kendall's tau correlation between species and average subspecies richness in random subsets of 270 genera. B) Histogram of Kendall's tau values for the same random subsets of 270 genera. Blue dashed line marked "NT": Kendall's tau for non-terrestrial mammals. Orange dashed line marked "T": Kendall's tau for terrestrial mammals. Grey dashed line: Kendall's tau for all mammals.

4.4 Discussion

SR and S-SR are positively related across all mammals, but the strength of this relationship is mediated by environmental substrate, with a stronger correlation in non-terrestrial mammals. This result generally supports the hypothesis that if the permeable phenotypic or geographic boundaries between intraspecific populations are evolutionary faultlines along which speciation is generally more likely to occur, then intraspecific diversity and species diversity

should be linked. Darwin's expectation that more speciose genera also comprise more subspecies on average is met, but there is considerable scatter around this trend.

The findings can be compared with those reported for birds; the relationship between SR and S-SR in all mammals is much weaker, with Kendall's tau being 0.15, than that reported for birds, with a tau of 0.23 (Haskell and Adhikari 2009). However, most birds are non-terrestrial, and when mammals are separated into terrestrial and non-terrestrial groups, non-terrestrial mammals have a substantially higher correlation coefficient (Kendall's tau=0.31) than both terrestrial mammals (at 0.11) and birds. The difference in correlation strength between the two groups of mammals, and terrestrial mammals and birds, implies the relationship between SR and S-SR is mediated by terrestriality. To test whether an interaction between terrestriality and S-SR is statistically significant, I compared three phylogenetic regressions (see Methods). The interaction term between ecological substrate and S-SR was significant ($p<0.05$) in all phylogenetic regressions, and ANOVAs confirmed the interaction model explained more of the variance in SR than the two other models. The interaction model is shown in Figure 4-1; the steeper slope of the non-terrestrial group compared to that of the terrestrial group illustrates that, for an equal increase in S-SR, SR increases more in non-terrestrial habitats than terrestrial ones. It is possible that the conclusion that SR and S-SR are more tightly linked in non-terrestrial taxa is specious if an increase in correlation strength from 0.15 to 0.31 is the consequence of subsetting a larger dataset, but such an increase did not occur in 10,000 random subsets of 270 genera (see Figure 4-2). These results suggest that ecological substrate mediates the relationship between S-SR and SR in mammals—and more specifically, that terrestrial habitats might play a role in decoupling otherwise linked dynamics of diversity across the taxonomic hierarchy.

This is consistent with a scenario in which processes shaping terrestrial unit richness (that is, unit birth and death) are more influenced by physical barriers or ecological heterogeneity than those processes in non-terrestrial taxa. Alternatively, ecological features determine the dynamics of diversification in the same way in the two groups, and the pattern is the consequence of terrestrial habitats containing more physical barriers and ecological heterogeneity in the first place (Grosberg, Vermeij, and Wainwright 2012). In both cases, two patterns should be evident: the relationship between S-SR and range size should be stronger in terrestrial taxa than in non-terrestrial taxa, and S-SR and SR should be more weakly correlated in terrestrial taxa than in non-terrestrial taxa. This model is illustrated in Figure 4-3.

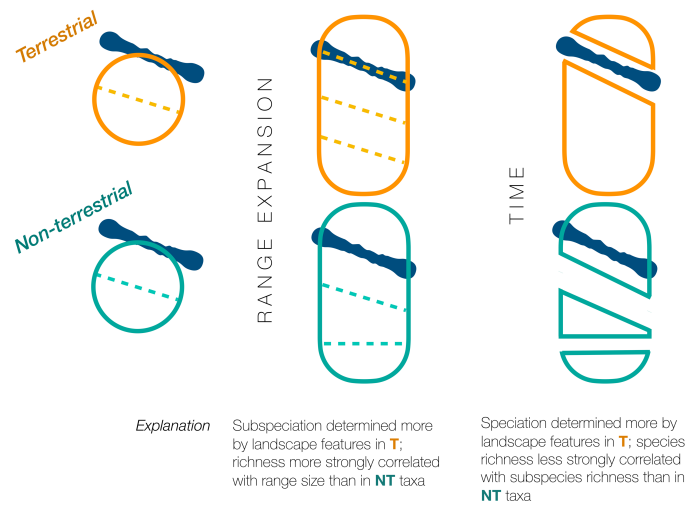


Figure 4-3: Terrestrial habitats affect dynamics of diversification across two taxonomic levels more than non-terrestrial habitats

Both terrestrial and non-terrestrial species begin with two subspecies, the permeable boundary between which is indicated with a dotted line. Following range expansion over the physical barrier (solid bar), the terrestrial species comprises four subspecies; subspecies formation is more tightly linked to local variation in landscape. By contrast, the non-terrestrial species now only comprises three subspecies, because it can maintain genetic unity over the physical barrier more easily. Given sufficient time, the barrier between the four subspecies in the terrestrial species impedes gene flow and the species gives rise to two new species. In the non-terrestrial species, the same physical barrier is not a barrier to gene flow, and the inherent boundaries between subspecies become the evolutionary faultlines along which new species are formed.

Indeed, the correlation between species range and S-SR is somewhat stronger in terrestrial mammals (0.32) than those with powered flight (0.30). I compared three linear models, run on the 50 trees, in which average subspecies richness was predicted by median species range size. The interaction term was significant in the third model across all trees, and ANOVAs confirmed the inclusion of the interaction term explained significantly more of the variance in S-SR. The prediction that species range should exert a stronger effect on S-SR in terrestrial taxa is met: the differences in terrestrial versus non-terrestrial slopes, illustrated in Figure 4-1, indicate that S-SR increases more with equal range expansions in terrestrial mammals than non-terrestrial mammals. These results are concordant with a model in which unit birth and death are more affected by ecological constraints in terrestrial habitats at two taxonomic levels. At smaller timescales, the formation of subspecies in terrestrial mammals is related more strongly to range size—in the model, this is explained by subspecies formation being more tightly linked to local variation in the landscape. By contrast, either because of greater dispersal capacity or because they are not exposed to as many physical constraints within ranges in the first place (Grosberg, Vermeij, and Wainwright 2012), non-terrestrial taxa are able to maintain genetic unity over greater distances or (if present) over the same physical

barrier; subspecies diversification is, consequently, less determined by physical constraints. Over greater timescales, a predominance of classic vicariant speciation (Mayr 1982a), in which physical barriers impede gene flow and daughter species form along these barriers, is consistent with a weaker relationship between S-SR and SR in terrestrial taxa. In non-terrestrial species, equivalent physical barriers are less common or do not restrict gene flow to the same extent, and permeable boundaries between subspecies become the evolutionary faultlines along which new species are formed.

This model implies two key points, the first of which is a strong relationship between dispersal ability and diversification. Dispersal ability is a strong predictor of avian species diversification rates (Phillimore and Owens 2006; Claramunt et al. 2012) and recently dispersed mammalian groups tend to contain more species than their sister clades in ancestral regions (Kisel et al. 2011). However, no work to date has directly compared terrestrial and non-terrestrial mammalian dispersal ability and its relationship to diversification: this remains to be explored.

A second implication is that subspecies might represent different evolutionary units in different mammalian taxa, and particularly depending on ecological substrate. In non-terrestrial taxa, as in birds, subspecies might be best conceived of as more often representing incipient species than in terrestrial taxa. Greater correlations between SR and S-SR suggest speciation occurs along the phenotypic or geographic boundaries between subspecies more often in these clades. By contrast, terrestrial mammalian subspecies might more often be distinct but ephemeral populations, and play a less pronounced role in speciation. It is important to emphasize that, even if 'species' in the Biological Species Concept (BSC) sense and subspecies are stages in a continuum of genetic differentiation and the formation of subspecies is a stage through which species must pass, not every subspecies will inevitably become a species; subspecies can be re-absorbed into larger undifferentiated populations of individuals of the same species through persistent interbreeding.

It may be the case that correlated SR and S-SR diversity is explained by heritable factors influencing their diversification (Kisel et al. 2011), in which case phylogenetic signal in one or both should be high. Consistently significant and high values for Pagel's λ in S-SR, and the fact that subspecies richness is not predicted by species' branch lengths, suggest that this may be the case. If heritable diversification at both levels alone explains the correlation between SR and S-SR, subspecies and species do not necessarily represent stages on an evolutionary continuum, as I suggest in the model. The heritability of diversification rate and subspecies diverging over time to become BSC species, however, are not mutually exclusive scenarios,

and it seems reasonable to expect overlap between them. For example, subspeciation rate, or factors influencing subspeciation, might be heritable, and lineages which inherited a high rate of subspeciation would, if subspecies represent incipient species, consequently comprise more species.

In terms of phylogenetic signal, the degree of asymmetry in the distributions of K and λ is unexpected, even if they measure different things (K being a measure of the partitioning of variance of the trait across clades and λ being a measure of covariance among species). Given the complex relationship between evolutionary process and phylogenetic signal (Revell, Harmon, and Collar 2008), I am hesitant to use the asymmetry in these measures to infer information about the process of inheritance of subspeciation rate or factors influencing subspeciation in the sample. Instead, supplemental analyses (Appendix 2-Supplementary Materials and Methods) show that the unusual distribution of trait values—right skewed with a heavy tail—can explain the consistent difference between K and λ.

A major assumption is that taxonomists consistently define mammalian subspecies and species according to the same criteria across taxa and through time. Taxonomic practice is variable across taxa when it comes to species and subspecies ranks (Agapow et al. 2004). Biased departures from consistency confound the comparative analysis, because error resulting from species uncertainty will be non-randomly distributed through the dataset. A shift from relatively universal use of the BSC towards application of the phylogenetic species concept (PSC) in some groups further precludes accurate comparisons of species and subspecies richness between groups, because the PSC inflates subspecies under the BSC to full species status and consequently recognises around 48% more species (Agapow et al. 2004). Taxonomic inflation should reduce correlations between SR and S-SR, and could explain the reduction in correlation strength in terrestrial mammals if the PSC is more routinely applied in this group. I explored the degree to which these confounding variables would affect the results and conclusions and simulated the effect of different inflation regimes on correlation strength (see Appendix 2- Testing the effect of taxonomic inflation). Reductions in correlation strength were only observed when taxonomic inflation was extreme – that is, all subspecies in most species in a genus were inflated to species status. In the contrasting regime, where only one subspecies was elevated to species status in a genus, correlation strength increased. The light inflation scenario is probably a more accurate approximation of the cumulative effect of no taxonomic inflation in some taxa and a moderate amount in others. If this is the case, the reduction in correlation strength in terrestrial mammals is unlikely to be the consequence of a greater degree of taxonomic inflation in this group than in the non-terrestrial group. Moreover, and in agreement with the simulation,

correlation strength was reduced to tau=0.09 (two-sided $p<0.001$) when I calculated the terrestrial Kendall correlation without Primates, the most heavily "taxonomically inflated" clade of the last two decades (Agapow et al. 2004). Finally, given that there is potentially less consistent taxonomic practice or less frequent equivalence between phylogenetic structure and subspecies nomenclature in mammals than in birds, it is interesting that the correlation between species and subspecies richness is far stronger in non-terrestrial mammals than those in birds.

Ultimately, one of the biggest challenges in evolutionary biology is linking microevolutionary processes to macroevolutionary patterns. This chapter sheds some new light on the factors mediating the relationship between population-level processes and speciation in mammals, and shows that the pathway from subspecies to species is environmentally contingent. In short, these results suggest that the dynamics of diversification of terrestrial mammals are more affected by physical barriers or ecological heterogeneity than those of non-terrestrial mammals, at two evolutionary levels. An implication of this model is that the evolutionary relationship between subspecies and species might, as a rule of thumb, differ between mammalian taxa, and be weakened in terrestrial habitats. This conclusion generates a number of testable hypotheses that should form the basis of future work. In particular, this study should encourage the exploration of the influence of substrate and other environmental parameters on speciation trajectories and probabilities, and consider these with more fine-grained taxonomic units and ecological categories.

4.5 Conclusion

Darwin proposed that lineages with higher diversification rates should evidence this capacity at both the species and subspecies level, a view consistent with population-level processes being integral drivers of speciation. I show this hypothesis is weakly supported in mammals as a whole, but when taxa are separated by ecological substrate, non-terrestrial groups show much stronger correlations between taxonomic richness at the two levels than terrestrial mammals do. As these processes also appear more tightly coupled in birds, I suggested fundamental factors unique to terrestrial habitats, such as increased exposure to ecological or physical barriers, increasingly become the causal drivers of divergence at two levels. These results imply that the evolutionary relationship between subspecies and species might differ between mammalian taxa, and that this relationship is mediated significantly by ecological substrate.

5 Subspeciation and habitat fragmentation

5.1 Introduction

In the absence of subspecies-level phylogenies, the toolkit for asking what causes subspecies diversification across mammals remains restricted to inferences based on macroevolutionary patterns, such as those explored in the previous chapter. In response, Chapters 5 and 6 explore two ways to calculate the rate at which subspecies form.

Since subspecies represent the raw material for full speciation—in Mayr's (1982b) view, all species were once subspecies of a parent species—the question of which biotic and abiotic factors determine the rates of the processes that comprise subspecies diversification is an important element in the link between microevolution and macroevolution. Diversification at the species level is equal to species formation—speciation—minus species disappearance—extinction. Subspecies, however, can disappear through an additional process for which the underlying causes need not be the same as for extinction: reabsorption into the general gene pool of the species it belongs to. Species- and subspecies-level diversification rates, consequently, are not completely analogous, with diversification rate at the subspecies level being the net outcome of 'subspeciation' rate minus subspecies extinction and subspecies reabsorption.

In the absence of a subspecies-level phylogeny for mammals, almost no empirical work has focused on directly calculating the clade's subspecies-level diversification rates, and instead, subspecies richness is usually treated as a trait by including it as the dependent variable in phylogenetic regressions (Botero et al. 2013). Here, I focus on one element of subspecific diversification: subspecies formation, or subspeciation. I isolate the subspeciation rate component of diversification by assuming an exponential pure birth process:

$$SSR = \frac{\ln(\rho)}{\alpha} \qquad \textit{Equation 5-1}$$

where SSR = subspeciation rate, ρ = subspecies richness, and α = species "age", following Phillimore (2010).

If subspecies represent an incipient stage of speciation, there should be a positive relationship between subspeciation rate and speciation rate. I test this prediction by running a phylogenetic

regression between SSR and a species-specific measure of speciation rate, Jetz et al's (2012) "tip DR", across all mammals. The first question in this chapter, then, is: is there a relationship between subspeciation rate and speciation rate in mammals?

Subspecies richness across mammals is strongly predicted by geographic range size, as shown in the previous chapter, suggesting a role for biogeographic factors in shaping subspeciation rate. Of these factors, a major potential correlate of subspeciation rate is habitat fragmentation, here defined as the breaking apart of habitat as in Fahrig (2003), for the simple reason that it increases the probability of genetic isolation of populations (Tocheri et al. 2016). Since a major factor underlying IUCN Red List classifications is habitat fragmentation (IUCN Standards and Committee 2019), I use these classifications as a proxy for the level of habitat fragmentation, and so test the hypothesised relationship between SSR and habitat fragmentation in mammals. The second question in this chapter is, therefore: does increased extinction risk, as a proxy for habitat fragmentation, correlate with higher subspeciation rates across all mammals?

As discussed in Chapter 3, subspeciation rate can be affected by taxonomic "inflation", in which the application of the phylogenetic species concept (PSC) elevates subspecies to species status (Isaac, Mallet, and Mace 2004), so for this reason I make use of Wilson and Reeder's Mammal Species of the World (2005), which predates some recent application of the PSC, and I repeated the above analyses with an extremely conservatively defined "non-inflated" subsample to ask whether the patterns persist when "inflation" is controlled for.

5.2 Materials and Methods

5.2.1 Data collection

All analyses were conducted in R 4.01 (R Development Core Team 2016). Raw subspecies richness data were extracted from Wilson and Reeder's Mammal Species of the World (Wilson and Reeder 2005).

IUCN classifications for all mammal species were obtained from the IUCN Red List (IUCN 2019). I classified species into three groups of increasing immediate likelihood of extinction: 'Least Concern' (LC), 'Vulnerable/Near Threatened' (V/NT), and 'Endangered/Critically Endangered' (EN/CR).

Analyses across all mammals were run on the MCC DNA-only node-dated tree from (Upham, Esselstyn, and Jetz 2019). For each species, I calculated Jetz et al's (2012) tip DR, a tip-specific measure of speciation rate:

$$DR = \frac{1}{\sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}}} \qquad \textit{Equation 5-2}$$

where DR is tip DR for species i, N_i is the number of edges between species i and the root, and l is the length of edge j (with j=1 being the edge closest to the extant tip).

For each species, I also calculated its terminal branch length, using the "edge.length" command in the phytools package (Revell 2012) as a proxy for its "age". In the absence of a subspecies-level tree for mammals, I calculated subspeciation rate (SSR) as

$$SSR = \frac{\ln(\rho)}{\alpha} \qquad \textit{Equation 5-3}$$

where ρ = subspecies richness, and α = species "age".

5.2.2 Subspeciation rate and speciation rate

To explore whether subspeciation can be thought of as a very early stage of speciation—and consequently, whether subspecies richness can be used as an indicator of future speciation dynamics—I ran a phylogenetic generalized least squares (GLS) in the nlme package (Pinheiro et al. 2020) of subspeciation rate, SSR, against speciation rate, DR.

5.2.3 Does subspeciation rate differ between three groups of increasing conservation concern?

To compare subspecies diversification rate between the three groups, I ran the following phylogenetic GLS regression using the nlme package:

$$SSR \sim group \qquad \textit{Equation 5-4}$$

where *SSR* is subspeciation rate. The phylogenetic correlation structure of residual error (i.e. the variance-covariance matrix) was accounted for in the nlme "correlation" argument. The model assumed a Brownian motion model for residual error structure, following previous work (Harvey and Rabosky 2018).

5.2.4 Correcting for phylogenetic "inflation"

I repeated the above analyses with an extremely conservatively defined non-inflated subsample. To obtain the non-inflated subsample, I obtained 1) authority and 2) IUCN taxonomic notes on all mammal species from (IUCN 2019) and removed all species that were 1) named after 1980 (since the phylogenetic species concept (PSC), which commonly inflates subspecies to species status, became more widely applied after 1980 (Isaac et al. 2004)) and/or 2) have, irrespective of when it was reclassified as a species, at any point been considered a subspecies of another species.

5.3 Results

5.3.1 The relationship between subspeciation rate and speciation rate in mammals

Tip DR, a species-specific measure of speciation rate, and SSR, subspeciation rate, are positively correlated (see Figure 5-1). DR was a significant predictor of SSR in the model run on the whole dataset as well as that with potentially "inflated" species removed (in both cases, $p<0.05$). The intercept of the model is -0.05, and the slope of the model is 0.95, suggesting a near one-to-one relationship between DR and SSR. When potentially "inflated" species are removed, the slope of the model is 0.99.

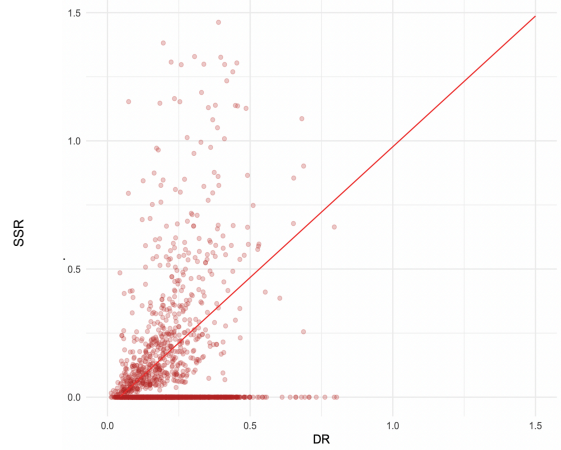


Figure 5-1: The relationship between speciation rate and subspeciation rate in mammals

Figure shows tip DR (a species-specific measure of speciation rate) plotted against subspeciation rate (SSR) across all mammals. Regression line is from the phylogenetic GLS on the whole dataset.

5.3.2 Is subspeciation rate significantly different in endangered/critically endangered taxa?

Mean subspeciation rate across all mammals was 0.14 in the whole dataset; this increased to 0.18 in the non-inflated subsample. Mean subspeciation rate for the three groups across the whole dataset and non-inflated subsample are presented in Table 5-1.

Level of conservation concern was a significant predictor of subspeciation rate across mammals, in both the whole dataset and the non-inflated dataset. In both datasets, endangered and critically endangered species have a significantly higher SSR than either vulnerable/near threatened taxa or those classified as being of least concern.

Table 5-1: Results from phylogenetic GLS: mean subspeciation rates across groups of differing conservation concern

	Whole	Non-inflated
Endangered/critically endangered	0.33	0.37
Vulnerable/near threatened	0.12**	0.00**
Least concern	0.14**	0.00**

Baseline group: endangered/critically endangered. Significance levels indicate whether or not group of interest differs significantly from endangered/critically endangered group in the variable of interest.

** $p<0.05$; ** $p<0.001$*

5.4 Discussion

Mammalian subspeciation rate (SSR), calculated as an exponential pure-birth process, correlates positively with both speciation rate and increasing IUCN extinction risk. The former strengthens the case that subspecies and species exist on an evolutionary continuum; and the latter, taken together with this inferred evolutionary relationship between subspecies and species, suggests that factors underlying heightened extinction risk, such as habitat fragmentation, can be the context for future speciation—but only if given sufficient time.

The statistically significant and positive relationship between SSR and speciation rate (tip DR) in both the complete dataset and the conservatively defined "non-inflated" subsample fits the expectation set out in Chapter 3—that the subspecies stage can be thought of as an early, but reversible, stage of speciation. Even if not all subspecies become fully diverged new species, all species must have initially been subspecies of a parent species, for however long or short a period (Mayr 1982b). Consequently, as a general rule, lineages producing subspecies at higher rates should split into new species faster than lineages that tend to produce subspecies at slower rates. The suggested relationship between the specific measures of speciation and subspeciation rate used here is illustrated in Figure 5-2. Species-specific speciation rate, or tip DR, is based on 1) the number of splitting events and 2) internode distances from the root to the tip of a phylogeny, with emphasis on those closer to the present (Jetz et al. 2012; Title and Rabosky 2019). In other words, tip DR is an estimate of the splitting history along a specific phylogenetic branch: and this history can be thought of as the aggregate of recurrent full subspeciation-speciation cycles (that is, subspeciation followed by

successful divergence from the rest of the gene pool). Present subspeciation rate, by extension, must correlate positively with future speciation.

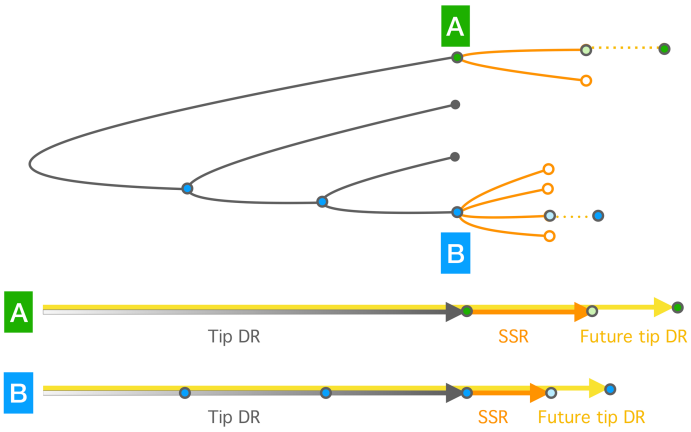


Figure 5-2: The relationship between tip DR and SSR

Species are denoted by circles filled with darker colours; subspecies with lighter colours. Tip DR uses the number of splitting events and internode distances from the root to the tip of a phylogeny, with emphasis on those closer to the present, to calculate species-specific speciation rate. Consequently, species B has a higher tip DR than species A. It has also produced more subspecies over a shorter period of time than species A, and so has higher SSR. Given the correlation between SSR and DR, a higher rate of future DR is predicted for this species.

Across all mammals, tip DR and SSR do not just correlate positively—the relationship is nearly one-to-one, with the slope of the phylogenetic regression being 0.95 across the complete dataset, and 0.99 across the "non-inflated" subsample. Since tip DR measures the number of species produced per million years, and SSR the number of subspecies produced per million years, this result suggests that there is an almost one-to-one relationship between mammalian subspecies and species—or in other words, mammalian subspecies tend to turn into fully diverged species.

This is the average trend across all mammals, but there is considerable and likely biologically meaningful variation around it (see Figure 5-1). Many mammalian taxa comprise no subspecies at all, and their SSR is therefore 0; and many of those who do have more subspecies than the model predicts based on tip DR. That is, for subspecies-comprising taxa, subspeciation rate exceeds speciation rate. To the best of my knowledge, this has not been shown previously in mammals, but does mirror the pattern found across birds: avian subspeciation rate was found to be 30-40 times higher than speciation rate (Martin and Tewksbury 2008; Phillimore et al. 2007). Subspeciation rate exceeding speciation rate means that speciation is initiated far more often than it is completed, and this raises questions about

why some subspecies ‘make it’ and others do not. The results from the previous chapter pointed towards an important role for ecology in mediating this relationship in mammals, but there are many other hypothetical correlates of subspecific persistence and the completion of speciation (Dynesius and Jansson 2014). Given the difficulty in studying population persistence in extant animals—rates of population extinction are hard to measure without a fossil record—these questions are probably better suited to fossil-based approaches, or work on specific species or groups of species for which detailed natural history records are available.

The variability around the general relationship between SSR and DR suggests there is an important role for factors other than inherited or inherent splitting rates in determining variation in SSR across mammals. One potential factor is habitat fragmentation—that is, the breaking apart of suitable habitats—given the obvious link between geographical isolation and independent evolutionary trajectories (Fahrig 2003; Larison et al. 2021; Mayr 1982a), of which subspecies represent an early stage.

The results presented in this chapter show that endangered and critically endangered mammal species tend to have significantly higher SSR than species classified as being of least concern, vulnerable, or near threatened. This can be taken as general support for the hypothesis that habitat fragmentation should lead to subspecies formation, but it is not an explicit test of the relationship. IUCN category assessments are based on five criteria (IUCN Standards and Committee 2019): population size reduction, small geographic range size and fragmentation of habitat, small population size and fragmentation, very small population or restricted distribution, and quantitative analysis of extinction risk. One of the five criteria, then, is a direct measure of habitat fragmentation; and the remaining four have been shown to be the direct consequence of this process. For example, higher subspeciation rates in endangered taxa may also result from an inverse relationship between (effective) population size and the speed of speciation (and by extension, subspeciation) (Charlesworth 2009; Gillespie 2001), so that the smaller population sizes that define them as endangered predispose them to population isolation, and thus subspeciation. However, population fragmentation and size reduction is often the direct result of habitat fragmentation (Fahrig 2003; Keyghobadi 2007; Larison et al. 2021; Templeton et al. 1990). Further, small population size may, after a critical population size threshold is passed, preclude species from forming novel subspecies at all—either because the species occupies too small a geographical range, or because there is not enough genetic diversity to produce the necessary phenotypic breaks between populations for them to qualify as ‘good’ subspecies.

Out of the IUCN criteria, then, the most plausible link between the level of conservation concern and subspeciation rates is habitat fragmentation. Subspecies, of course, are not only geographically isolated populations, but must also be phenotypically distinct from the rest of the species; and habitat fragmentation may determine the rate at which *both* of these criteria are met. Habitat fragmentation directly severs populations geographically from the rest of the species. The consequence of this severing is reduced genetic connectivity, and possibly even total isolation from the rest of the gene pool, as well a smaller effective population size, resulting in increased rates at which morphological, genetic, or behavioural differences can arise between the isolated population and the rest of the species.

Higher subspeciation rates in endangered and critically endangered taxa, whose habitats are on the whole expected to be more fragmented than non-endangered taxa, aligns with previous work showing that intraspecific divergence is positively correlated with habitat heterogeneity in terrestrial mammals (Botero et al. 2013), although this paper did not measure subspeciation directly and instead used subspecies richness as the predictor variable. Testing whether the relationship between present-day habitat fragmentation and subspeciation rate suggested by these data holds using different measures of habitat fragmentation is a clear direction for future work.

A major assumption, however, is that the habitat fragmentation measured in the IUCN criteria occurred in tandem with the formation of extant subspecies, so that species exposed to higher rates of this habitat fragmentation, and which are therefore classed as being at higher risk of extinction in the IUCN classification, also formed subspecies at concomitantly higher rates. The alternative scenario is that many cases of subspecies formation predate the habitat fragmentation measured in the IUCN criteria. For example, *Pan troglodytes troglodytes and P. t. verus*, Central and Western chimpanzees respectively, are estimated to have diverged around 420,000 years ago (Won and Hey 2004). If this is the case, then the results presented here suggest that higher subspeciation rates might *predispose* species to present-day extinction risk. If taxa are more likely to produce geographically isolated, phenotypically distinct populations because of intrinsic characteristics such as dispersal ability (Rangel et al. 2018), then these taxa may disproportionately put at risk of extinction in the present-day pulse of anthropogenic climate and habitat change. If so, this brings to the fore the importance of considering the intrinsic and extrinsic determinants of subspecies formation in conservation planning.

However, there are also examples of much more recent subspecific divergence events. Some tiger (*Panthera tigris*) subspecies diverged from each other around 9,000 years ago

(Armstrong et al. 2021), and the divergence between some Eurasian red fox (*Vulpes vulpes*) subspecies occurred less than 1,000 years ago (Kutschera et al. 2013). Distinguishing between subspeciation-first or IUCN habitat fragmentation-first models is difficult to do in the absence of a mammalian subspecies-level phylogeny and detailed, species-specific reconstructions of the long-term trends in the availability and level of fragmentation of suitable habitats. It might be the case, for example, that the present-day patterns of habitat loss and fragmentation captured in the IUCN criteria are the continuation of longer-term Holocene trends (Ambrose and Sikes 1991; De Bruyn et al. 2009). If so, the IUCN habitat fragmentation-first model holds for taxa in which subspecies formation happened relatively recently, while it does not for taxa with older subspecies. This does not rule out an important role for habitat fragmentation in these taxa, however: a recurring pattern in published work on the comparatively few taxa in which subspecific divergence times have been explicitly estimated is that these divergence events are nearly always linked to episodes of climate change and attendant habitat turnover and the formation of boundaries within species' ranges (Won and Hey 2004; Davison et al. 2011; Armstrong et al. 2021). For example, chimpanzee subspecies splits are attributed to the fragmentation of suitable habitat by river barriers (Won and Hey 2004).

What can be said with certainty based on these results is that species at higher risk of extinction have significantly higher subspeciation rates than those at lower levels of risk. The data used here do not allow a distinction to be made between alternative explanations for this pattern. It could be the case that higher subspeciation rates predispose species to extinction risk, but it might also be the case that the causes of present-day extinction risk, such as habitat fragmentation, are also the determinants of subspeciation. The case for an important role for habitat fragmentation, however, is still strong: in taxa in which subspecific divergence is known to have occurred before the habitat fragmentation trends of which IUCN criteria are a good measure, these divergence events are nearly always dated to periods in which suitable habitat was breaking up (Won and Hey 2004; Davison et al. 2011; Armstrong et al. 2021). Finally, these two alternative explanations are not mutually exclusive, and it is to be expected that the exact biogeographical history of subspecific divergence is species-specific, and therefore varies across mammals.

Combining the results for the two main questions in this chapter has implications for the conservation of biodiversity. If the relationship between subspeciation rate and future speciation rates holds, *and* if higher subspeciation rates in many endangered taxa are the result of the microevolutionary correlates of present-day extinction risk such as habitat fragmentation, then the results suggest that the correlates of extinction risk are providing the

context for future speciation. This is a conclusion concordant with models of allopatric speciation (Mayr 1982a). This result might seem a hopeful one, because it means taxa at risk of extinction might produce new biodiversity, but it is not. For subspecies to represent a store of potential future biodiversity, these distinct populations require evolutionary timescales and ecological stability that is not guaranteed.

A final key point to make here is that higher SSR in higher-risk taxa does not simply have to reflect higher real subspeciation rates alone. SSR is a simple measure of a complex process: and, most importantly, does not account for subspecies extinction or resorption rates, since it is based on a pure-birth model. It may be the case, then, that real subspeciation rates between the high-risk and lower-risk groups are similar, with lower subspecies extinction/resorption rates resulting in higher observed SSR in high-risk taxa. If so, these results would point towards a possible role for habitat fragmentation in subspecific persistence rather than subspecies formation. This sets out two clear directions for future work: first, asking whether a pure birth or birth-death model (Nee, May, and Harvey 1994) best explains variation in subspecies richness across mammals and then testing whether the relationship between subspeciation rate and extinction risk holds; and second, pursuing finer-grained species-specific analyses of the dynamics and correlates of subspecies formation, persistence, resorption, and extinction.

5.5 Conclusion

Across all mammals, subspeciation can be thought of as an early but reversible stage of speciation. Subspeciation rate correlates positively with extinction risk: endangered and critically endangered taxa, whose habitats are on the whole expected to be more fragmented than non-endangered taxa, produce subspecies at higher rates than non-endangered taxa. A disconnect between subspeciation and speciation rates points towards an important role for subspecific persistence in determining whether or not speciation is completed. A more comprehensive understanding of the evolutionary dynamics of mammalian subspecies is important for the conservation of evolutionary potential.

6 Subspecific diversification across primate evolutionary history

6.1 Introduction

6.1.1 Introduction

This chapter is a continuation of Chapter 5, in that it is concerned with estimating the tempo of subspecific diversification. One point raised in Chapter 5 was that even if a pure-birth model can explain extant subspecies richness across mammals, subspecies diversification is the outcome of subspeciation minus subspecific "extinction"—a process that includes extinction as well as resorption back into the general gene pool of the species. In response, here, I fit subspecies birth-death models to estimate subspecific diversification rate regimes and major shifts in these regimes. I restrict this analysis to the Order Primates because it is a comparatively well-studied clade, both from a taxonomic and biogeographic perspective. Regarding the former, this means it is likely that taxonomic approaches are at least more homogenous across the clade than they might be across all mammals, and I use the latter to suggest hypotheses about the relationship between primate subspecies diversification rates and possible determinants of these processes.

6.1.2 Primate subspeciation

Primate subspecies have not escaped the attention of evolutionary biologists. In general, explorations of the evolutionary biology of primate subspecies have focused on specific primate clades: for example, by testing whether catarrhine subspecies richness is predicted by range size or body mass (Elton and Dunn 2015), or elucidating the principal axes of subspecific morphological variation in baboons and guenons and so shedding light on which traits are involved in the early stages of divergence (Elton, Dunn, and Cardini 2010; Dunn, Cardini, and Elton 2013). Important promotors of catarrhine subspecies richness include large range size and possibly higher levels of habitat fragmentation (Elton and Dunn 2015). To the best of my knowledge, however, a reconstruction of subspecies diversification rate evolution has not been attempted across the whole Order Primates. In addition to reconstructing the history of subspecies diversification rate regimes, the approach taken in this chapter can be taken as a test of the associations found within smaller clades: if range size or habitat fragmentation are important determinants of primate subspecies diversification, and thus of subspecies richness, there should be a signal of this across the entire clade.

6.2 Materials and methods

6.2.1 Data collection and taxonomy

Raw subspecies richness data were extracted from Wilson and Reeder's Mammal Species of the World (Wilson and Reeder 2005). The analysis was first run on 100 randomly sampled primate phylogenies from the posterior distribution of Upham et al.'s (2019) mammal phylogeny, so that the frequency of shifts in "subspeciation rate" could be calculated as a measure of confidence.

6.2.2 Analyses

The analyses were conducted in R 4.01 (R Development Core Team 2016). Since subspecific phylogenetic relationships are unresolved across most primate species, I used the "multiMEDUSA" function in the MEDUSA package (Brown 2013) to estimate subspecies-level diversification rates across the 100 primate phylogenies from Upham et al. (2019). multiMEDUSA estimates diversification rate (i.e. birth minus death rate) regimes and shifts in these regimes across phylogenies that can include unresolved clades, for which subclade taxonomic richness is input in the "richness" argument. MEDUSA first calculates the AIC score of a maximum likelihood birth-death rate regime, without shifts in this regime, based on a phylogeny and taxonomic data (the age and subclade richness of a tip). It then fits a series of models of increasing complexity, involving shifts in rate regimes, and stops when improvement in AIC score is <4 (Alfaro et al. 2009). I estimated the frequency and timing of shifts in subspecies diversification rate across the 100 primate trees by inputting species' subspecies richness into the "richness" argument. All other options were kept at their default settings. From the MEDUSA birth and death rate outputs, I calculated relative extinction rate of primate subspecies as a measure of their persistence.

6.3 Results

Figure 6-1 shows median estimated subspecies diversification rates, and the frequencies and timing of shifts in these rates across the 100 primate trees from Upham et al. (2019), plotted on the maximum clade credibility (MCC) consensus tree from Upham et al. (2019). Note that this tree is for display only; it contains DNA-missing species that randomly vary in topological position within reasonable taxonomic constraints (genus or family) across the posterior distribution of trees. The analysis was purposefully run across 100 randomly sampled trees to take into account this topological uncertainty. Across these 100 trees, a 3-shift regime was best supported in more than 50% of the trees. Background birth, death, and relative extinction rates, as well as those of the three clades that are characterised by significant shifts in these rates, are presented in Table 6-1. The background rate of primate

subspecific diversification is marked by high turnover and a low overall tempo of subspecific diversification, with death rate 98% of the birth rate.

Table 6-1: Subspecies diversification rate regimes in primates estimated by MEDUSA across the 100 primate trees from Upham et al. (2019)

Rate regime	Birth rate	Death rate	Relative extinction
Background	*0.59*	*0.58*	*98%*
1) Simiiformes	0.93	0.85	91%
2) Cercopithecidae[1]	0.73	0.34	47%
3) Lepilemuridae + Cheirogaleidae	0.50	0.25	50%

[1]The indentation of the table shows the nested structure of these shifts in rates: shifts in the Cercopithecidae are relative to those inferred across all Simiiformes.

In the haplorhine clade, there are two increases in subspecific diversification rate: first, in the Simiiformes, which represents a shift from the background rate for all primates, and second, in the Cercopithecidae, which is a shift from the rate in Simiiformes. The shift in Simiiformes is underlain by increases in birth and death rates, with a net decrease in relative extinction rate: subspecific turnover thus happens at a slower pace. The shift in the Cercopithecidae is underlain by a decrease in birth rate relative to that of all Simiiformes; but also a decrease in death rate: and consequently, it has a much lower relative rate of extinction. In the Cercopithecidae, then, subspecific turnover happens much more slowly than across the rest of the primate tree.

In the strepsirrhine clade, there is one increase in subspecific diversification rate relative to the inferred background rates: within the Lepilemuridae + Cheirogalidae clade. This shift is caused by a decrease in both birth and death rates, and a concomitant lowering of the relative extinction rate. As in the haplorhine clade, then, this shift is underlain by a slowing down of subspecific turnover.

Overall, the lowest estimated subspecies diversification rates are found within strepshirrines, with the exception of the Lepilemuridae and Cheirogaleidae, and within platyrrhines. The highest estimated subspecies diversification rates are found within the Cercopithecinae.

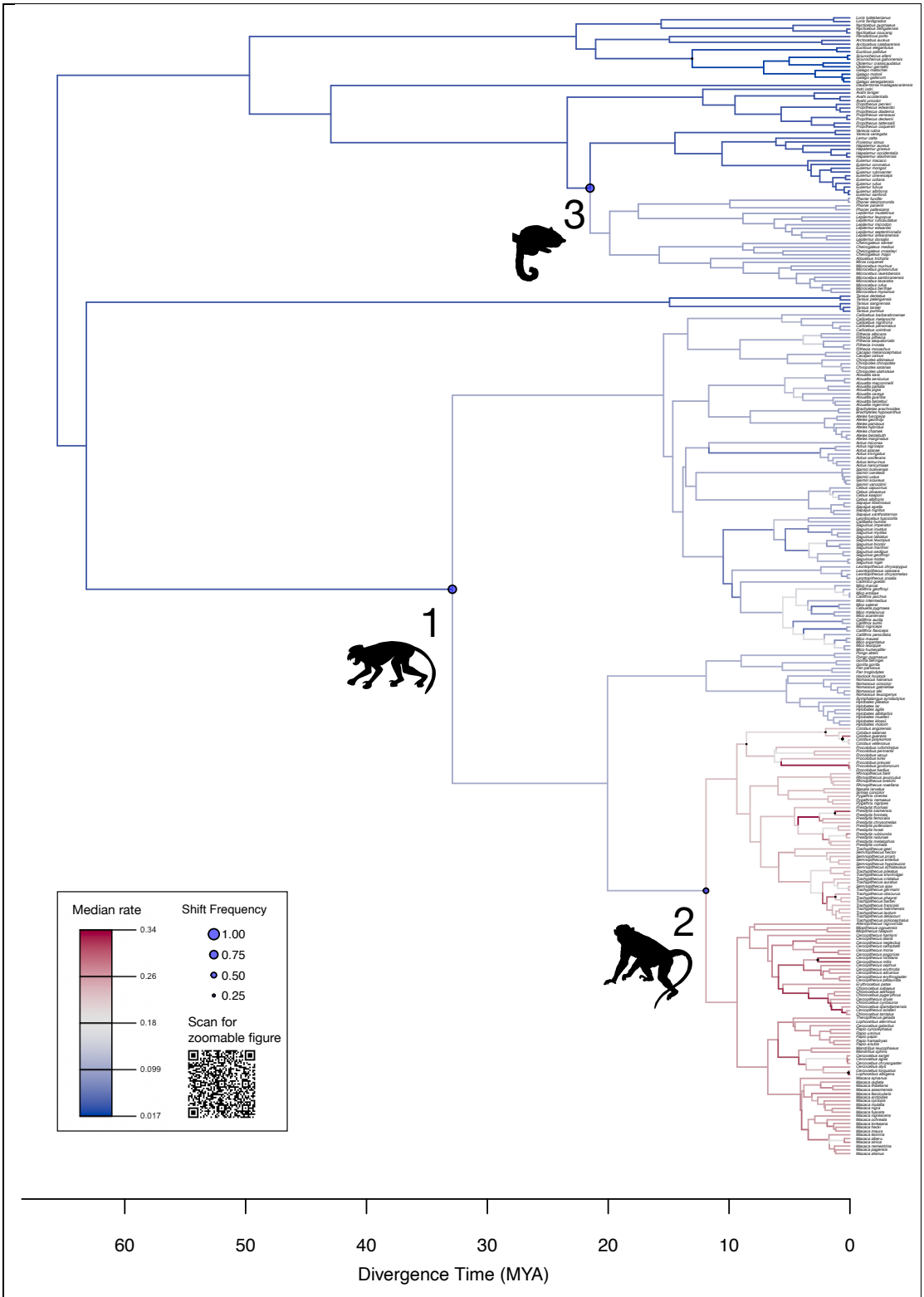


Figure 6-1: Shifts in primate subspecies diversification rate

Figure shows median estimated diversification rate, as well as the timing and frequency of shifts in this rate, across 100 primate trees. QR code links to zoomable figure.

6.4 Discussion

The MEDUSA analysis revealed two key evolutionary trends in primate subspecific diversification rate. First, the background tempo of subspecific diversification is marked by a high level of turnover: subspecific extinction and resorption happens at 98% the rate of subspecific formation. Second, there is strong support—that is, the patterns are replicated across more than 50% of the 100 Upham et al. (2019) phylogenies—for three shifts from this background rate, in Simiiformes, the Lepilemuridae + Cheirogaleidae clade, and in the Cercopithecidae. These shifts correspond to increases in subspecies diversification rate relative to the background rate in the case of the Simiiformes and Lepilemuridae + Cheirogaleidae clade, and relative to the regime in Simiiformes in the case of the Cercopithecidae. All three cases are underlain by decreases in the rate of subspecific turnover: that is, subspecies persist for longer after they are formed. It is probable that there are multiple biotic and abiotic determinants of subspecific persistence in primates that interact to produce the patterns reported here.

MEDUSA has not been used to estimate subspecies diversification rate before (Brown 2020) and its application to these data is therefore entirely experimental. MEDUSA estimates diversification rate regimes and shifts in these regimes based on phylogenies and taxonomic data—clade age and subclade taxonomic richness. Species diversification rates can thus, for example, be estimated from a genus-level tree. Alfaro et al. (2009) use MEDUSA to estimate species diversification rate regimes across jawed vertebrates using a phylogeny with 47 tips, representing 47 major jawed vertebrate clades. The ability to calculate diversification rates for unresolved clades is an attractive one for the question at hand, since the phylogenetic relationships among primate subspecies are unresolved for most primate taxa. The application of MEDUSA to the question of subspecies diversification rates derives from the idea that a species-level phylogeny shows the aggregate of recurrent successful subspeciation-speciation cycles through time, comparable in a sense to the largest Russian doll that contains ever-smaller analogues inside. In other words, the evolutionary link between subspecies and species means a species-level phylogeny must contain information about subspeciation minus subspecies extinction and/or resorption rates. The degree to which this method is successful at recovering real subspecies diversification rates must ultimately depend on the strength of the correlation between (1) subspeciation and speciation, and (2) subspecies extinction/resorption rates and species extinction rates. It is probable that the strength of this correlation depends on a number of factors, some of which were discussed in the previous chapter. Regarding the relationship between subspeciation and speciation rates, Figure 5-1 illustrated that this relationship is positive across mammals when subspeciation rate is calculated based on a pure birth model—but that there is, nonetheless, variation around this general relationship. When

the regression between tip DR and SSR performed in Chapter 5 is restricted to primates, the relationship between DR and SSR is no different to that found across all mammals (intercept=-0.04, slope=0.95, $p<0.001$). The relationship between species extinction rate and subspecies extinction and resorption rates is more difficult to explicitly test; detailed reconstruction of subspecific extinction patterns of extant and recently extinct taxa for which comprehensive natural histories are available would be of particular interest here.

Even if the strength of the relationship between subspecies and species diversification rates remains an open question, that it exists is both theoretically expected and empirically indirectly supported (Botero et al. 2013; Haskell and Adhikari 2009; van Holstein and Foley 2020).What follows, therefore, is a discussion of both the trends in inferred subspecies diversification rates across primates and potential correlates of these trends.

The overall trend in subspecific diversification across primate evolutionary history is of increasing diversification rates and decreasing relative extinction rates. The first major shift from the inferred background rate is found for Simiiformes—the anthropoids, which include the apes and New and Old World monkeys. This clade is characterised by increased subspecific birth *and* death rates relative to the background rate that characterises tarsiers and most strepsirrhines, a concomitant increase in subspecific diversification rate, and a decrease in relative subspecific extinction rate from 98% to 91%. Compared to tarsiers and strepsirrhines, anthropoids produce subspecies at higher rates, and, on average, these then persist for longer periods of time. What this means is that higher speciation rates in extant anthropoids compared to the rest of the primate tree (Upham, Esselstyn, and Jetz 2019) can be explained by significant differences in demographic processes controlling speciation.

More specifically, anthropoid speciation rate is higher than that of strepsirrhines and tarsiers because of the combination of higher rates of subspecies formation rates *and* their longer persistence. Higher rates of subspeciation result in more ‘raw material’ for speciation; extended persistence makes it possible for these populations to accrue sufficient genetic isolation from the rest of the gene pool to complete the speciation process. The evolutionary success of the anthropoid radiation can thus be recast—perhaps somewhat prosaically—as the numeric outcome of a shift in the rates of subspecies formation and persistence.

Less prosaic are the questions these results raise about the determinants of anthropoid speciation: why are anthropoid subspecies produced at higher rates, and why do they persist for longer periods of time? In the present, of course, a major difference between anthropoids and most non-anthropoids is in their geographical distribution—most strepshirrines are found

on Madagascar—and given the positive relationship between subspecific richness and range size found for all mammals in Chapter 4, and for catarrhines by Elton & Dunn (2015), a restricted range must place limits on subspecies production. In this way, these results show that range size is a significant predictor of subspecific diversification across all primates. The timing of this shift, however, is much further back in time than the present, at a time when prosimians were found throughout Asia, North America, and Europe (Fleagle 2013), and this suggests that fundamentally different subspecific rate regimes, correlating with higher speciation rates in anthropoids, might have contributed to the replacement of this lineage by anthropoids. A possible correlate are ecological and climatic factors: Elton & Dunn (2015) suggest a potential role for habitat fragmentation in promoting subspeciation, and the anthropoid radiation coincides with a general trend towards cooler temperatures, increased climatic fluctuation, and consequent habitat turnover and fragmentation (Zachos, Dickens, and Zeebe 2008). This suggests that the relationship between ecological variability, and both subspecies formation and subspecies persistence fundamentally differed between anthropoids on the one hand, and the ancestors of tarsiers and strepsirrhines on the other. Ecological generalists are expected to cope better with environmental instability and habitat fragmentation (Day, Hua, and Bromham 2016; Dennis et al. 2011); and it might also be the case that anthropoids had higher dispersal abilities than did the non-anthropoids, thus increasing the rate of subspecies formation, and consequently speciation. These hypotheses should be tested in future work.

Next, the results point towards a significant shift, in the Cercopithecidae or Old World Monkeys, from the rate regime that characterises all Simiiformes. This shift is characterised by a decrease in inferred birth rate offset by decreased relative extinction rate, so that the Old World Monkeys have the highest inferred subspecies diversification rates across the whole primate tree. In other words, Old World monkey subspecies are produced at slower rates than they are in other anthropoids, but they also persist for the longest periods of time. This pattern provides an interesting test of hypothesised determinants of primate subspecies formation: these factors must dampen subspecies formation in non-anthropoids, promote it in anthropoids with the exception of Old World Monkeys, and, relative to those anthropoids, dampen them again in the Old World Monkeys. An interaction between range size and dispersal ability might be a good starting point: larger ranges include more subspeciation-promoting environmental variability, while dispersal ability has been shown to reduce subspeciation rate as populations are better able to maintain genetic connectivity (Aguilée et al. 2018). Anthropoids tend to have larger ranges than prosimians (Fleagle 2013); and within anthropoids, cercopithecine monkeys are able to maintain high dispersal ability across fragmented habitats (Albert et al. 2014).

Old World monkeys generally have higher speciation rates than the rest of the anthropoids (median tip DR in OWM: 0.40; in other anthropoids: 0.34; 2-tailed t-test $p<0.05$), so these results emphasize the importance of subspecific persistence as a regulator of speciation. Explanations for differences between speciation rates in anthropoids then need to be sought, at least in large part, in the determinants of subspecific persistence. A comparison between New and Old World monkeys (NWM and OWM, respectively) can shed some light on this question. The difference in subspecific persistence between these clades may be related to habitat fragmentation: both groups comprise ecological specialists and generalists, a range of body masses, and locomotor behaviours (Fleagle 2013), but the degree of habitat fragmentation estimated by Crooks et al. (2017) across the geographical distribution of OWM is higher than that across the NWM range (see Figure 6-2). NWM taxa are mostly concentrated in the Amazon basin (Vallejos-Garrido et al. 2017), an area with the lowest levels of habitat fragmentation; OWM taxa are distributed across regions comprising both low and very high levels of habitat fragmentation. An additional clue—although it is an indirect proxy for habitat fragmentation, as discussed above—is the difference in the number of endangered taxa between the two groups: 38% of OWM species are presently classed as endangered or critically endangered, and the same is true for only 23% of NWM (IUCN 2019). Taken together, these patterns point towards a potentially positive relationship between subspecific persistence and habitat fragmentation in anthropoids: the more fragmentation, the longer subspecies persist; and, subsequently, the higher the chance of achieving full reproductive isolation.

Within the Cercopithecidae family, the Cercopithecinae have higher inferred subspecies diversification rates than do the Colobinae. In the case of African Cercopithecidae monkeys, the division between Cercopithecinae and Colobinae generally overlaps with the geographical distribution of habitat fragmentation. African colobines are found in the sub-Saharan forested regions Crooks et al. (2017) characterise as having low degrees of habitat fragmentation, while the widespread distribution of African cercopithecines includes more regions with high fragmentation levels. Beyond Africa, however, this correlation does not hold up: both groups are found in areas of generally high habitat fragmentation in Asia. Further, a major argument against a key role for fragmented habitats in shaping the difference between colobine and cercopithecine SDRs can be made based on the exceptional habitat disturbance tolerance of the latter: even in highly degraded habitats, many cercopithecine monkeys maintain high dispersal ability (Albert et al. 2014). This can result in lower subspecies birth rates as the required isolation of populations is precluded; but simulation work has also recovered a positive relationship between dispersal and population isolate formation, because it allows

new and isolated geographic space to be more easily colonised (Rangel et al. 2018). Many alternative correlates of subspecies diversification rate may be suggested based on the division between the Colobinae and Cercopithecinae, including ecological strategy (with the former being relatively specialized and the latter relatively generalized (Codron et al. 2008; Wrangham, Conklin-Brittain, and Hunt 1998) and locomotor behaviour (with the former generally arboreal and the latter generally terrestrial (Fleagle 2013). These hypothesised correlates can be explicitly tested in future work.

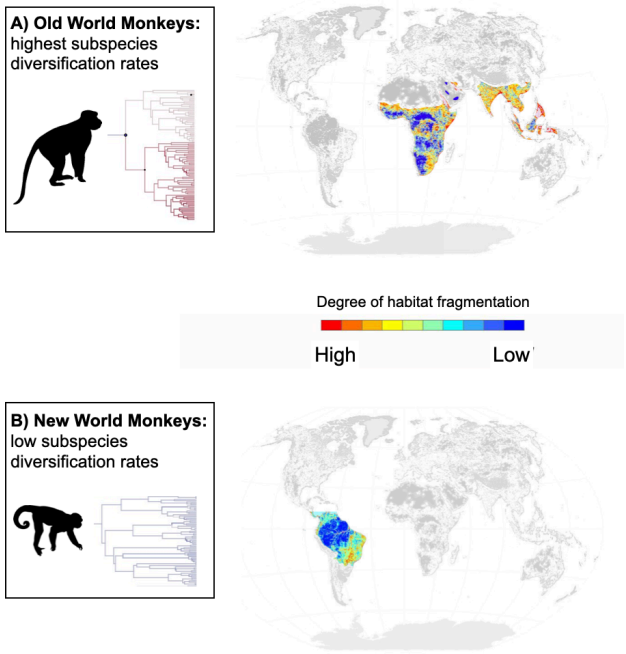


Figure 6-2: Geographical distribution of habitat fragmentation and inferred subspecies diversification rates in Old World monkeys and New World monkeys

Figure shows the degree of habitat fragmentation, taken from Crooks et al. (2017) across the geographical distribution of A) the Old World monkeys (family Cercopithecidae), and B) the New World monkeys (parvorder Platyrrhini).

The final significant jump in subspecies diversification rate relative to the background tempo was found for the Lepilemuridae (sportive lemurs) + Cheirogaleidae (dwarf and mouse lemurs) clade. This increase is underlain by a slight reduction in subspecies birth rate offset by a reduction in relative extinction rate from 98% to 50%. Speciation rates in this clade are higher than in other strepsirrhines who are characterised by the background rate (median tip DR in Lepilemuridae + Cheirogaleidae: 0.29; in other strepsirrhines: 0.23; 2-tailed t-test $p<0.05$), so again, subspecific persistence emerges as an important determinant of speciation rate. This shift is not obviously linked to the distribution of habitat fragmentation, or indeed to habitat at all, because the geographical distributions of the sportive, dwarf, and mouse

lemur clade overlaps almost entirely with that of clades characterised by the background rate. It may be the case that, instead, differential abilities to maintain genetic connectivity across abiotic barriers underlie the difference in inferred subspecific persistence between sportive lemurs and other strepsirrhines. Craul et al. (2007), for example, invoke rivers as major factors promoting sportive lemur population splitting, while this signal is not as strong in the Lemuridae (Blair et al. 2013; Markolf and Kappeler 2013). In other words, these patterns suggest abiotic barriers do not preclude true lemur subspecies from being resorbed back into the general gene pool of their parental species as much as they do in sportive lemurs. In mouse and dwarf lemurs, a group characterised by many cases of cryptic speciation and sympatry (Poelstra et al. 2020), potential correlates of increased subspecies persistence relative to those found in Lemuridae are rapid evolution of male advertisement calls, which differ significantly between mouse lemur species (Braune, Schmidt, and Zimmermann 2008), and evolutionary lability in the timing of reproduction, which also differs strongly between sympatric taxa (Rina Evasoa et al. 2018). Such behavioural differences may serve to enforce emerging reproductive barriers between subspecies and thus facilitate subspecific persistence.

6.5 Conclusion

In summary, the history of primate subspecific diversification is characterised by high background turnover and an evolutionary trend towards longer subspecific persistence. Across the primate tree, subspecific persistence emerges as an important determinant of speciation rates, with the two positively related: longer persistence correlates with higher speciation rates. This is an interesting result, because it suggests that, rather than extending the "waiting time" to speciation (Gavrilets 2000), extended subspecies persistence increases the likelihood that reproductive isolation is reached, and that full speciation occurs.

Comparative approaches to explaining variation in primate speciation rate and species richness typically take the approach of asking whether heritable traits, such as body mass, correlate with speciation rate (Matthews et al. 2011). These results suggest that reframing this question as a search for the determinants of subspecies persistence can provide a more detailed understanding of the dynamics of primate speciation. So, instead of only asking whether locomotor behaviour correlates with primate speciation rate, the relationship between subspecific persistence and locomotion, ecology, and dispersal capacity should be explored. Again, these are hypotheses best suited for detailed work on single species or groups of species.

Macroevolutionary patterns in primate evolutionary history can also be recast as the outcome of shifting balances between subspecies origination and extinction. The success of the anthropoid radiation can be attributed to a combination of increased rates of subspeciation and longer subspecific persistence. This means that explaining the divergent evolutionary histories of anthropoids and other primates requires elucidation of the determinants of both of these processes. Within anthropoids, higher speciation rates in OWMs are due in large part to the lowest relative subspecies extinction rates found across primates. Taking biogeographic patterns of habitat fragmentation together with this result points towards a potentially positive relationship between habitat fragmentation and subspecies persistence in anthropoids; explicitly testing this hypothesised association is a clear direction for future research. The shift in subspecies diversification rate in the sportive, dwarf, and mouse lemur clade, underlain in large part by a decreased relative extinction rate relative to the background rate, can potentially be linked to a more limited ability to maintain genetic connectivity over abiotic barriers; but other behavioural correlates of this pattern can also be invoked. It is likely that there are multiple biotic and abiotic determinants of subspecific persistence in primates in addition to habitat fragmentation, and that they interact to produce the patterns reported here.

Finally, to what extent these results are representative of the pattern across mammals is a major unanswered question, and one that can be answered in future by extending the method to the mammal phylogeny. The case against primate exceptionalism can be made based on the fact that the inferred importance of subspecific persistence in determining primate speciation is exactly what is expected based on the disconnect between mammalian speciation and subspeciation rates. Primates do not always toe the mammalian evolutionary line, however: as an Order they are characterised by, for example, significantly higher rates of speciation than all other mammalian genera (Upham, Esselstyn, and Jetz 2019), and are also generally more gregarious and encephalised than most mammals are (Fleagle 2013). The former is of most immediate interest here: if demographic controls on speciation operate in the same way across mammals, the results from this chapter mean higher rates of subspecific turnover are expected in most mammalian lineages. Since the results from analyses across all mammals suggest subspecies represent a store of future biodiversity, the hypothesised ephemerality of most mammalian subspecies is of significant concern for conservation efforts.

7 Speciation in extant mammals

7.1 A metapopulation model of mammalian speciation

Reproductive isolation has long reigned supreme the realm of speciation. There is a skew towards answering the question of why and how species form by empirically examining why and how groups stop exchanging genes. This section, by contrast, approached the question by examining factors mediating the relationship between cladogenesis at microevolutionary and macroevolutionary scales, using subspecies and species, respectively, as proxies for these processes. In doing so, the focus is shifted from an emphasis on the (genetic) correlates of reproductive isolation to one which includes spatial and demographic processes as key determinants of speciation.

The approach taken here is easily embedded in the metapopulation model of speciation described by Harvey, Singhal, and Rabosky (2019), and doing so provides a useful framework for comparing the results for extant mammals from this section and extinct hominins from the next. Harvey et al. (2019) base their model on the metapopulation conception of species most commonly used in community ecology (Gotelli 1991; Holt and Keitt 2000; Levin 1995; Levins 1969). They define a species as a metapopulation: a collection of semi-isolated populations exhibiting partial demographic independence from each other. In asking how and why speciation takes place, they highlight the roles of spatially explicit factors underlying the origin and evolutionary trajectory of these interspecific populations. More specifically, given the evolutionary link between populations and future species, (1) population isolate formation, (2) population isolate persistence, and (3) ecological differentiation between populations are crucial determinants of speciation—in addition to (4) the evolution of reproductive isolation. Figure 7-1 is a simple illustration of the relationship between these process in a metapopulation speciation model. Processes (2), (3), and (4) are not chronological, and interactions between them are expected: for example, ecological differentiation between populations likely contributes to the evolution of full reproductive isolation.

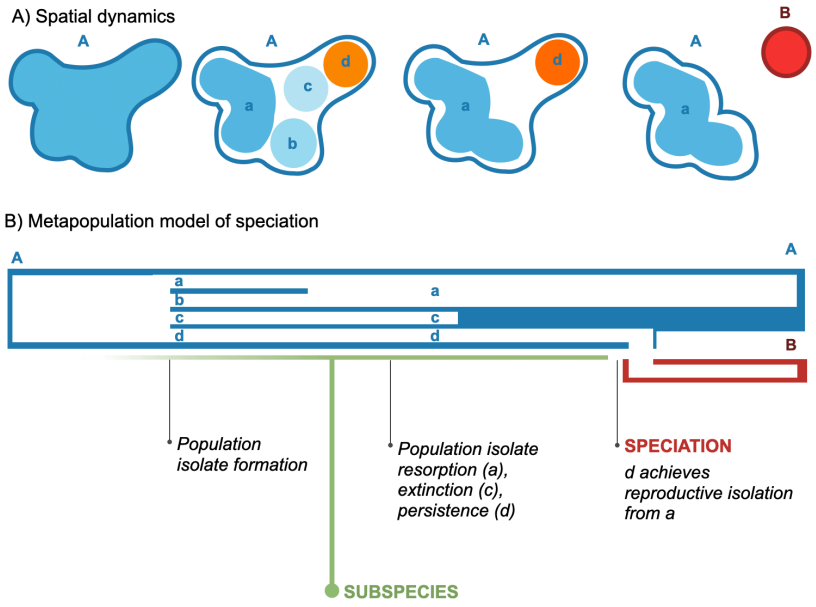


Figure 7-1: Speciation in a metapopulation framework

A) shows the spatial dimension of a hypothetical speciation event, in which species—or metapopulations—are denoted by capital letters, and populations by lowercase letters. B) tracks the relationships between populations through time. Metapopulation "A" starts off as an undifferentiated group, which splits into four semi-independent population isolates (*a, b, c*, and *d*). There are three key evolutionary trajectories that these population isolates may follow after they form: population isolate persistence, ecological differentiation, and the evolution of reproductive isolation. *b* is resorbed into the gene pool of *a,* and *c* goes extinct (i.e. both do not persist over time), while *a* and *d* persist over time. *d* differentiates from *a* in key ecological traits, indicated by the colour difference between it and the other populations. Over time, this process results in *d* achieving reproductive isolation from *a*, and so a novel species or metapopulation, B, is recognised. The relationship between "populations", as defined here, and subspecies is indicated in green: subspecific status entails a degree of morphological and possibly genetic differentiation that a population does not need to have, so subspecies can be thought of as populations further along an evolutionary trajectory.

Although subspecies are not mentioned at all in the Harvey et al. (2019) paper, I suggest they are very good approximations of the semi-isolated populations the metapopulation model is based on, being spatially, morphologically, and potentially genetically distinct groups within species. A distinct advantage of taking subspecies and Harvey et al's (2019) populations as broadly synonymous is that data on subspecies richness are available for most extant taxa, so making comparative work across large groups of taxa possible. "Populations", of course, are not exactly synonymous with subspecies: populations are so broadly defined in the Harvey et al. (2019) model that any degree of spatial population structure qualifies as metapopulation structure. A major difference between populations and subspecies, then, is that populations, in this definition, do not need to be morphologically distinct from each other to the degree subspecies do (at least theoretically). Given the evolutionary relationship between subspecies and species implied by the results presented in this section, it makes sense to think of

populations and subspecies in a similar way, with subspecies being populations slightly further along an evolutionary trajectory, having accumulated more morphological differentiation (see Figure 7-1 for an illustration of this relationship). Enduring debates about baboon taxonomy illustrate the evolutionary continuity between populations, subspecies, and species: population structure exists within the six recognised *Papio hamadryas* subspecies (Rogers 2009), and in turn, there exists sufficient behavioural and morphological variation between these subspecies that many researchers consider them full species (Jolly 1993; Newman, Jolly, and Rogers 2004). The time it takes for sufficient morphological differentiation to accumulate for a population to be considered a subspecies likely depends on interactions between a number of biotic and abiotic factors, including (but clearly not limited to) genetic diversity, the strength of local selective pressures, dispersal ability, phenotypic and behavioural plasticity, and life history traits.

Treating "populations" and subspecies as broadly analogous within a metapopulation model of speciation, finally, provides a flexible framework for comparing results from Section A and Section B. If the recognition of species and subspecies can be difficult in extant taxa for which genetic, behavioural, morphological, and geographical data are available, it is even more challenging in the hominin fossil record. Hominin species diversity remains a contentious question, with data limited to hard tissues and low sample sizes, and enduring debates about the degree of morphological variation acceptable within hominin taxa (White 2003; Wood and Boyle 2016). The question of subspecies richness across hominin taxa has received much less empirical attention, primarily because low sample sizes are even more of a problem here. Elton & Dunn (2015), in one of the few explicit discussions of subspecific differentiation in hominins, use the relationship between subspecies richness and range size in extant catarrhines to estimate that *Australopithecus afarensis* and *Paranthropus boisei* likely comprised subspecies, but acknowledge the difficulties posed by fossil data. The existence of semi-isolated populations within species is practically universal in mammals (Harrison and Taylor 1997) and hominins are likely no exception (Scerri et al. 2018). In most cases, however, the limitations of the (hominin) fossil record preclude robust assessment of whether or not such populations were characterised by the necessary degree of morphological, geographical, and possibly genetic patterns of discontinuity between populations for them to be considered full subspecies. In other words, differentiating between full subspecies and less diverged populations requires larger sample sizes, better preservation, and higher-resolution reconstructions of populations' geographical and temporal distributions. Given this uncertainty, it makes more sense to discuss results between the two sections of this thesis in terms of metapopulations and "populations"—an umbrella term that includes full subspecies as well as less morphologically diverged groups.

What follows is a summary of the principal conclusions of this section in the context of the metapopulation model.

7.2 Results across extant mammals in the context of the metapopulation model

7.2.1 Ecological substrate and the evolutionary continuum of subspecies and species

1. Across mammalian genera, there is a weakly positive correlation between species richness and average population richness: in other words, species within genera with higher species richness generally tend to comprise more populations, but there is considerable variation around this trend. When separated by environmental substrate, however, this relationship is much stronger in non-terrestrial taxa than it is for terrestrial taxa or for mammals as a whole. Species' range size, further, has a stronger effect on average population richness in terrestrial taxa than in non-terrestrial taxa. Taken together, these results suggest that the pathway from population to novel species is environmentally contingent—and in particular, that ecological substrate is an important rate-limiting determinant of (1) population isolate formation and (2) the transition from population isolate to novel species.
2. Regarding the first, the results are concordant with a model in which population isolate formation is more tightly linked to the presence or absence of abiotic barriers within the landscape in terrestrial taxa. By contrast, either because of greater dispersal capacity or because they are not exposed to as many physical constraints within ranges in the first place, non-terrestrial taxa are able to maintain genetic unity over greater distances *or* (if present) over the same physical barriers; population isolate formation is, consequently, less determined by physical constraints.
3. Regarding the second, the results point towards a more decoupled evolutionary relationship between populations and novel species in terrestrial habitats. In the context of the metapopulation model, the implication is that the evolutionary trajectory of a terrestrial population is less likely than that of a non-terrestrial population to culminate in sufficient discontinuity between it and the rest of its specific gene pool for it to be considered a novel species. Which of the three interrelated processes that determine the evolutionary trajectory of a population—isolate persistence, ecological differentiation, and the establishment of reproductive isolation—is involved here is difficult to say based on these data alone, especially since the expectation is that interactions between these processes are the norm. This provides a clear agenda for future work, to which detailed work on single species or groups of species is probably best suited.

7.2.2 Subspecies diversification rate, speciation, and habitat fragmentation

1. Across all mammals, population isolate formation is an early but reversible stage of speciation. The implication is that population persistence is an important factor controlling mammalian speciation in addition to population isolate formation, and this is supported by two key results from this chapter. First, for mammalian species that comprise subspecies, the rate at which these morphologically diverged population isolates form tends to exceed speciation rate, suggesting not all population isolates 'make it'. Second, when subspecific birth and death rates are explicitly calculated across primates, clades with the highest speciation rates are characterised by the lowest rates of population isolate turnover and longest population isolate persistence. Both results align with the decoupled relationship between populations and novel species in terrestrial habitats found in chapter 4, as most mammals (including primates) were classified as 'terrestrial'.
2. Reframing explanations of variation in primate speciation rate in terms of the demographic controls on speciation will provide a much more detailed understanding of the dynamics of primate speciation, and also produces novel insights into primate evolutionary history. The diversification of primate population isolates is characterised by high background turnover, and an evolutionary trend towards extended population isolate persistence. The success of the anthropoid radiation can be attributed to a combination of increased rates of population isolate formation *and* longer isolate persistence. Work explaining the divergent evolutionary histories of anthropoids and other primates might benefit, therefore, by being framed as a search for the determinants of both processes. Within anthropoids, higher speciation rates in Old World monkeys are due in part to the lowest relative population isolate extinction rates found across primates. Taking biogeographic patterns of habitat fragmentation together with this result points towards a potentially positive relationship between habitat fragmentation and isolate persistence in anthropoids; explicitly testing this hypothesised association is a clear direction for future research. Whether or not these patterns are representative of those across all mammals, finally, and thus whether variation in population isolate persistence underlies much of the variation in mammalian speciation rate, is an open question: but the concordance between the patterns seen in primates and the general mammalian asymmetry between subspeciation rate and speciation rate suggests this is probably the case.
3. Both population isolate formation and persistence can be linked to habitat fragmentation, but this relationship is probably mediated by other factors, such as ecological strategy and dispersal ability. Across all mammals, population isolate formation is positively predicted by extinction risk, which is generally underpinned

by habitat fragmentation. Although it is not an explicit test of the relationship, there is also a potentially positive relationship between habitat fragmentation and subspecies persistence in anthropoids.

7.3 Summary and future directions

A particular advantage of comparative work across a large number of taxa is that it can provide a robust test of the hypothesised relationship between, first, demographic processes and speciation, and second, the abiotic and biotic determinants mediating this relationship. In the briefest terms, the results from this chapter can be summarised as showing that population-level splitting and population persistence are determinants of macroevolutionary patterns of species richness in mammals; and that ecology emerges as an important factor regulating this relationship. So, why so many rodents and so few elephants? The results presented here suggest that, at least in part, this must be because the possibility for elephant speciation is truncated by demographic processes.

Mammals are relatively underrepresented in comparative work on demographic determinants of speciation: the vertebrate spotlight has fallen in particular on avian clades (Harvey et al. 2017; Claramunt et al. 2012; Phillimore et al. 2007; Harvey, Singhal, and Rabosky 2019). The results across mammals align with general patterns found across other vertebrates: population isolate formation is a determinant of speciation (shown for birds in Haskell and Adhikari (2009)), population isolate formation outpaces speciation (shown for birds in (Phillimore et al. (2007)) and, in line with this result, population isolate persistence is an important control on speciation. The results from chapter 4, however, suggest that the mammalian relationship between population isolates and novel species might be decoupled relative to that in birds, and this is echoed in the inferred importance of population persistence in determining primate speciation. This makes further elucidation of the factors controlling population isolate persistence in mammals an important area for future research on mammalian speciation.

Important methodological limitations, unanswered questions resulting from these limitations, and potential future directions for each analysis were discussed in detail in the relevant chapters. Regarding the section as a whole, however, a major point to make is that comparative phylogenetic work is complementary to detailed work on single species or smaller groups of species, and that this is a key way in which most of the hypotheses generated by the results in this section can be tested in future work. Of the two demographic processes discussed in this section, population isolate persistence is more difficult to study in large groups of extant taxa than population formation; and here, work on extant species for

which there are detailed natural histories and comparative work incorporating fossil data will be of particular interest. The next section takes this approach, by exploring the relationship between intraspecific processes and speciation in hominins.

Population isolate persistence is the scaffolding for the cessation of gene flow that ultimately determines the trajectory of speciation. The metapopulation model explicitly hypothesises that population persistence, ecological differentiation, and reproductive isolation should coevolve: so exploring the relationship between demographic processes and the genetics of speciation in mammals is another area of significant interest in future work.

The inferred ephemerality of subspecies in more slowly speciating prosimian primates, finally, is of considerable conservation concern. The results from both chapters imply the relationship between subspecific persistence and speciation should hold across mammals, and this means most mammalian subspecies do not have extended lifespans. These future research directions are not solely of theoretical interest, then: a more comprehensive understanding of the evolutionary dynamics of mammalian subspecies will have important implications for the conservation of evolutionary potential.

Section B: Speciation in extinct hominins

8 Introduction to Section B: Speciation in extinct hominins

8.1 Introduction

The present section is focused on a particular clade of mammals: our own. The hominin fossil record is comparatively rich and well-studied, making it an excellent candidate for a case study about the demographic determinants of speciation in mammals. Human evolutionary studies has historically operated in a state of splendid isolation from evolutionary biology—the affiliation of the author (Department of Archaeology) is a case in point—but here, hominins are considered 'just' a clade within mammals. The case against hominin exceptionalism has been made by, for example, Vrba (1993), who noted similarities in timing of evolutionary turnover between hominins and bovids; as well as authors using cercopithecids as models for human evolution (summarised in Elton (2006)).

This section is principally concerned with testing longstanding hypotheses about the role of biotic and abiotic determinants of hominin speciation, but the results are linked back to the overall question of how demographic determinants of speciation operate in mammals. I do so by suggesting a framework within which to reconcile results obtained from "splitting" (less inclusive) and "lumping" (more inclusive) taxonomies in order to shed light on the determinants of various thresholds in the protracted process of speciation: in the briefest terms, taxa in "split" taxonomies can be taken as populations of taxa in "lumped" taxonomies.

There are three key questions, some with sub-questions, on which this section is centered:

1. What are the basic patterns of hominin speciation?
    a. Did speciation rates vary between genera?
    b. Was hominin speciation rate time-dependent?
2. Was hominin speciation climate-dependent?
    a. To what extent was hominin speciation determined by climatic variability or general trends in climate?
    b. Across which timescales was hominin speciation determined by any climatic variable?
3. What was the role of interspecific competition between hominin species in hominin speciation?

The first two questions have long been the focus of much work in palaeoanthropology (Kimbel 1995; Vrba 1993; Potts 1998a, 2013; Shultz and Maslin 2013), while the latter has received less explicit attention. Previous work regarding each of these three main questions is summarized and discussed in more detail in the subsequent chapters that deal with them specifically. However, most, if not all, approaches to date have relied on first appearance dates (FADs) alone without taking into account phylogenetic relationships, and consequently, hominin speciation rate has never been directly measured. Simply put, FADs are not speciation events; there is likely to be variation around the time lag between a speciation event and a species' FAD determined by factors entirely unrelated to the process of interest, such as the availability of suitable rock exposure, and present-day collection effort (Maxwell et al. 2018b). Dating error further confounds attempts to establish causal links between extrinsic causes and species formation. FADs, finally, are entirely determined by taxonomic practice inasmuch as the identification of species in the fossil record is dependent on the range of morphological variation considered acceptable for a species (Wood and Boyle 2016): the larger this range, the lower the inferred 'rate' of speciation. In this section, I address most of these problems by directly measuring, for the first time, hominin speciation rates.

To take into account different approaches to hominin taxonomy, I apply the method across three hominin phylogenies, and ask how abiotic factors—climate and time—and biotic factors—interspecific competition—correlate with speciation rates. I describe a framework with which to interpret differences between 'splitting' and 'lumping' approaches to hominin taxonomy. Crucially, in this framework, these differences can be used to examine how relationships between abiotic and biotic factors and speciation shift across stages of the hominin speciation process, and thus shed new light on the relationship between intraspecific processes and speciation.

As in the previous section, each chapter—with the exception of Chapter 9, which details the materials and methods for this section as a whole, because the methods used to answer each chapter's questions is the same across the section—is written as a stand-alone answer to a particular question. Results from this section are then contextualized in the metapopulation model introduced in Chapter 7, in order to set out the broader implications of this section for the question of the role of demographic processes in mammalian speciation.

8.2 Microevolution and macroevolution in hominins

Microevolutionary processes and macroevolutionary patterns are usually treated separately in human evolutionary studies: the former is typically only examined by quantifying and

explaining phenotypic change within single species (Kimbel et al. 2006; Martin et al. 2020), and regarding the latter, questions are usually restricted to exploring hypotheses about the temporal distribution of speciation (Foley 2016; Wood and Boyle 2016). Here, the focus is on the relationship between these two levels—and more specifically, on exploring how biotic and abiotic causal factors mediated this relationship.

To date, the relationship between microevolution and macroevolution across the hominin clade as a whole has received almost no explicit and empirical attention—no doubt in large part due to enduring taxonomic debates. Within the framework of the previous section, in which the micro-macroevolutionary relationship was examined by asking how recurrent episodes of subspecific diversification scale up to speciation in extant mammals, it is the 'micro' level that is particularly difficult to reconstruct within hominins. Even so, Elton and Dunn (2015), in one of the very few explicit examinations of population structure within hominin species, suggest that subspecific diversity was probable in at least three (*Australopithecus afarensis, Australopithecus africanus, Paranthropus boisei*) and possibly four (the previous three and *Paranthropus robustus*) African taxa. Even if difficult to reconstruct, then, Elton and Dunn's (2015) results suggest population splitting below the species level occurred in hominins and can be reconstructed. The key question here is: what factors mediated how this process scaled up to macroevolutionary patterns of speciation?

8.3 Splitting and speciation

This section uses Jetz et al's (2012) "tip DR" as a measure of speciation rate. Although the measure is more thoroughly described and discussed in Chapter 9, it is important to emphasize here that its use implies a specific evolutionary process. Tip DR is a tip-specific measure (and therefore usually a species-specific measure): it comprises both the number of splits from tip to root along the tip's branch and the time between these splits. It has been shown to estimate real speciation rate (rather than diversification rate; i.e. speciation minus extinction) in simulation studies (Jetz et al. 2012; Title and Rabosky 2019).

Here, then, 'speciation' is restricted to Simpson's (1944) branching mode of evolution, or Vrba's (1993) speciation: that is, 'speciation' refers to the process by which lineages split to form new species, regardless of whether or not the ancestral population persists after the speciation event (see Figure 8-1). It excludes gradual change within a species without such splits (Simpson's (1944) phyletic change or Vrba's (1993) phyletic evolution).

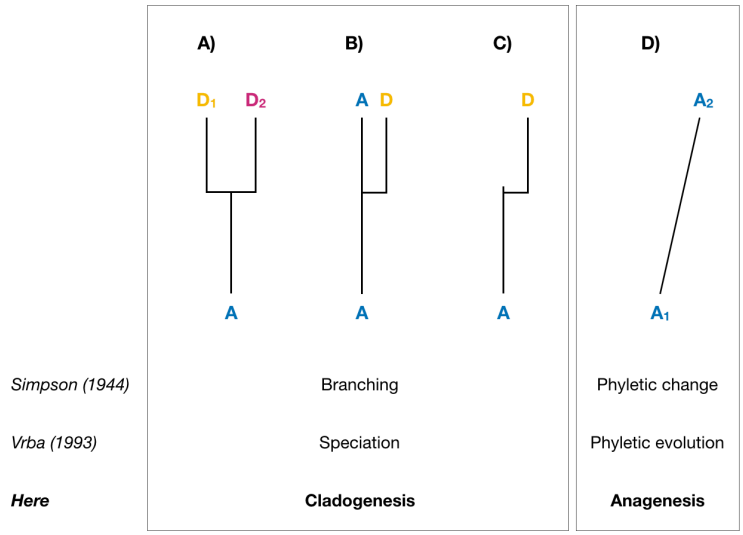


Figure 8-1: Definition of process terms in this section

Figure adapted from Figure 1 in (Vrba, 1993). A) An ancestral species, A, splits into two new species, D1 and D2. A goes extinct in this scenario. B) A new species, D, splits from its ancestral form, A, which persists. C) As in B), but the ancestral species goes extinct soon after D splits from it. D) A1 evolves, without a splitting event, into A2. Scenarios A), B), and C) are called 'branching' in Simpson (1944) 'speciation' in Vrba (1993) and usually referred to as 'cladogenesis' in this section. Scenario D) is not included as a speciation or cladogenetic event here.

Speciation is thus synonymous with cladogenesis (Allmon 2017) as it is throughout this thesis, and refers to the overall process by which new species form through the splitting of lineages. In this section, however, I give preference to the terms 'rate of cladogenesis' or 'splitting rate' when referring to tip DR for two reasons: first, for clarity—tip DR is based specifically on splitting events, while speciation has multiple meanings across the literature—and second, because I calculate tip DR across multiple phylogenies that differ in their definition of species. 'Speciation' across one phylogeny is therefore not equivalent to 'speciation' across another. The framework within which these disparate approaches are reconciled to provide a coherent picture of the entire process of speciation is described below.

8.4 A species by any other name

Hominin taxonomy is notoriously controversial. Prevailing approaches can, broadly speaking, be dichotomized into 'lumpers' and 'splitters': through the lens of the former, the hominin fossil record comprises ~15 species at present, while an extreme "splitting" approach would recognise upwards of 30 species (Wood and Boyle 2016). The two schools of thought actually approach the hominin fossil record with the same conceptual foundation—that species are autapomorphic groups—but differ, at a superficial level, in the range of

intraspecific morphological variation they accept. ‘Lumpers’, for example, make the case that the hypodigms of ‘split’ taxa are too narrow and overlap too much for them to be considered distinct species (White 2003; White et al. 2009; Lordkipanidze et al. 2013).

At a more fundamental level, however, differences between these schools of thought arise from the problem of studying a temporally extended process with no clear start or end points. The complex and reticulated genetic histories of Late Pleistocene hominins (Posth et al. 2017; Reich et al. 2010; Green et al. 2010) illustrate the complexity and drawn-out nature of speciation. As a result, I suggest that more and less speciose hominin taxonomies can be placed in a framework similar to de Queiroz’s (1998) “General Lineage Concept” of species, in which differences between species concepts are reconciled by making the argument that each concept simply emphasizes a different stage of the overall speciation process (see Figure 8-2A). In a similar way, ‘lumpers’ and ‘splitters’ differ in their emphasis on different thresholds within the speciation process as the point at which a species can be recognized (see Figure 8-2B). While neither approach explicitly state the species concept they use, a ‘splitting’ taxonomy effectively adheres to the Evolutionary Species Concept (Wiley 1981): from this perspective, the potential for a distinct “historical fate” (sensu Wiley (1981)), for which morphological autapomorphies are a proxy, is considered sufficient for a population to attain species status. Morphological overlap with other species is not an issue: what matters is the unique evolutionary trajectory implied by autapomorphies. In a more ‘lumped’ taxonomy, populations are required to have reached a greater degree of morphological divergence, in addition to autapomorphies, to be considered species. Crucially, given that the degree of overlap in populations’ trait distributions is expected to grow smaller over the time as they split (see Figure 8-2B), the degree of morphological differentiation required by ‘splitters’ is probably achieved earlier in the speciation process (see Figure 8-2B). In temporal terms, then, the model advanced here suggests that ‘splitters’ recognize and name units at earlier stages of the process, while ‘lumpers’ recognize and name later stages of speciation. Given its emphasis on different thresholds in a complex process, the model described here will be referred to as the “threshold model” in the following chapters.

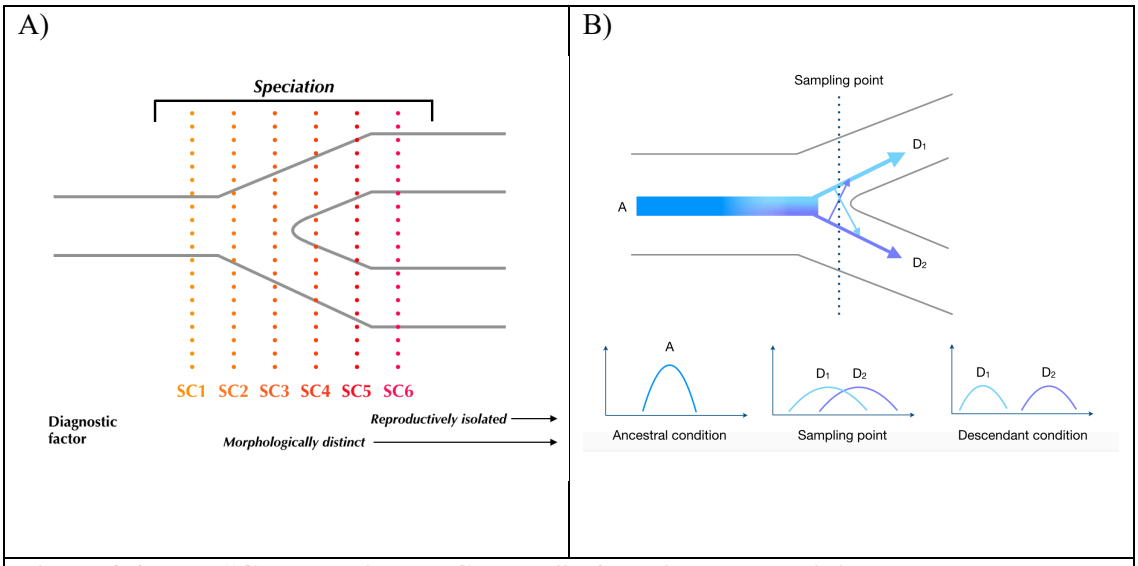


Figure 8-2: The "General Lineage Concept" of species and hominin taxonomy

A) Adapted from Fig. 5.4 in de Queiroz (1998).SC denotes "species concept"; note that the inclusion of only six species concepts is arbitrary. Speciation is a protracted process, illustrated by the black bar; species concepts place emphasis on different biological thresholds that taxa may pass through during the process of speciation. For example, morphological differences between species (Morphological Species Concept), here represented by SC4, may arise before they are reproductively isolated (Biological Species Concept), at SC6.
B) In a similar way, the difference between 'lumping' and 'splitting' hominin taxonomy can be conceived of as emphasizing different thresholds in the protracted process of speciation: a 'splitting' taxonomy considers the potential for a distinct "historical fate", captured in a number of autapomorphies, sufficient for species designation, while a 'lumped' approach requires a much greater degree of morphological divergence between 'species'. Thus, at the sampling point, a 'splitting' approach might recognize two species: the two groups have started on their own evolutionary trajectories. By contrast, a 'lumping' approach considers the degree of overlap between the hypodigms of the groups too large for them to be considered species, and recognizes only one species. The effect on a phylogeny is that a 'splitting' phylogeny is effectively a tree of incipient species, and a 'lumping' phylogeny shows relationships between species that have crossed more thresholds of the speciation process.

What this means for the questions at hand is that the relationship between tip DR and abiotic or biotic factors on speciose 'splitting' phylogenies and species-poor 'lumping' phylogenies might capture the changing roles of these factors through the various stages of hominin speciation. Speciose phylogenies capture an earlier phase—a complex one, in which populations are beginning to diverge, evolve autapomorphies, and start out on distinct evolutionary trajectories, but can probably still interbreed and be resorbed into the gene pool of their parental species. Tip DRs on speciose phylogenies therefore represent, in this framework, the splitting rates of lineages beginning to diverge in terms of their evolutionary trajectories. Whether or not one considers these species "real" species, then, matters less than the recognition that they represent an early stage of a complex process. The argument in the previous section was that the formation of population isolates represents such an early and

reversible stage of speciation in mammals: and therefore, the units recognized on species-rich phylogenies can be thought of as distinct populations within taxa recognized on species-poor phylogenies. Whether or not these distinct populations can be considered full subspecies in all cases is difficult to say with much certainty given low sample sizes and a geographic bias towards particular fossil-bearing deposits across Africa. For this reason, I describe taxa recognized on "splitting" phylogenies simply as taxa that have reached early stages of speciation, not as subspecies.

Species-poor phylogenies capture later or final phases of speciation, at which point diverging populations have become firmly established on their evolutionary trajectories, boundaries between species are well established, and consequently they have probably stopped exchanging genes. As such, tip DR on these phylogenies captures the rate at which reproductively isolated groups, or at least groups with firmly established and differentiated evolutionary trajectories, split.

Although the correlation between morphological divergence and stage of speciation upon which the threshold model is based probably generally holds true, speciation is by no means always marked by morphological differentiation between daughter species (Tattersall 1993). The model would utterly fail to recognize or include cryptic speciation (Bickford et al. 2007; Giraldo et al. 2008; Roux et al. 2016) and speciation accompanied by morphological divergence in characters that do not fossilise—and the only consolation is that this problem is not a limitation of specifically this model, but a practically unsurmountable problem to all fields dealing primarily with fossil evidence.

In sum, the threshold model described here suggests that associations between biotic or abiotic factors and tip DR on speciose phylogenies can reveal initial causes of intraspecific divergence, while those on species-poor phylogenies probably contain signals of the relationship between these factors and the final stages of speciation, in which boundaries between novel species are cemented.

8.5 List of terminology in Section B

In summary,

- Speciation: The splitting of an ancestral species to form two new species. Synonymous with cladogenesis.
- Tip DR: Splitting rate. Across speciose phylogenies, I take tip DR to measure the splitting rate of less morphologically diverged, incipient species, and it can therefore be conceived of as a proxy for the rate at which

speciation is initiated. Across species-poor phylogenies, tip DR probably measures the rate at which reproductively isolated groups – or at least groups with firmly established and differentiated evolutionary trajectories – split.

9 Materials and methods for Section B

9.1 Data collection

9.1.1 Phylogenies

Hominin taxonomy is notoriously disputed. In light of this, analyses in this section were performed on three phylogenies to compare and contrast the effect of different phylogenetic hypotheses on the strength and direction of correlations between speciation rate, climate, and diversity.

The first phylogeny (hereafter called the "Parins-Fukuchi et al. phylogeny" or "Parins phylogeny" on figures) is the phylogeny with the best Akaike information criterion (AIC) score from Parins-Fukuchi et al. (2019). This phylogeny is based on the same dataset as the phylogeny published by Dembo et al. (2016), but, in contrast to the latter, Parins-Fukuchi et al. (2019) combined probabilistic models of morphological evolution and fossil preservation to recover anagenetic as well as cladogenetic relationships between hominin species. Consequently, the phylogeny incorporates ancestor-descendant relationships broadly accepted based on morphological evidence alone (for example, between *Australopithecus anamensis* and *Australopithecus afarensis* (Kimbel et al. 2006); although there is now evidence to suggest these species overlapped temporally and spatially (Haile-Selassie et al. 2019)).

I removed *Homo floresiensis* from the Parins-Fukuchi et al. phylogeny using the "dropTip" function in the phytools package (Revell 2012) for three key reasons. First, and most importantly, the species occupies an unexpectedly long branch given its geologic sampling age, with a 2.5-million year period before its FAD. Although Parins-Fukuchi et al. (2019) do not report confidence estimates, this unexpectedly long unsampled period suggests a large potential for error around the topological placement of the *Homo floresiensis* branching event. Indeed, the branching event inferred in this phylogeny occurs around 0.7 million years before the oldest branching events inferred, using cladistic methods, across the published literature (Argue et al. 2009). A further argument for the removal of *Homo floresiensis* is that its phylogenetic affinities remain an open question (Collard and Wood 2015), and, given the importance of recovering the true topology of the hominin tree for the accuracy of the method described below, I erred on the side of caution by only including branches which are relatively well supported by the fossil record. That is, given that the measure of speciation rate employed here—Jetz et al's (2012) tip DR—is based on the number and timing of

branching events for individual tips, erroneous placement of a branching event can have large effects on the results. Finally, including the *floresiensis* branch (especially in the context of the lack of empirical support for the placement of the branching event) in estimates of diversity well before its geologic sampling age is potentially misleading.

The second phylogeny is based on the Parins-Fukuchi et al. phylogeny, but with alterations so as to approximate a most inclusive, 'lumping' taxonomy – in other words, to make it the least speciose phylogeny possible given current evidence. To do so, I removed temporally overlapping species for which Wood & Boyle classify the confidence that these are indeed separate taxa as "low" (Wood and Boyle 2016), using the "dropTip" function in the phytools package (Revell 2012). These taxa were *Homo erectus (Georgian)* and *Homo erectus (African)*; these are therefore collapsed into a single taxon, *Homo erectus (sensu lato)*. I also collapsed *Paranthropus aethiopicus* and *Paranthropus boisei* into a single lineage to account for perspectives that these taxa belong to a single hypodigm, *P. boisei sensu lato* (Wood and Constantino, 2007). This phylogeny is presented in Figure 9-1.

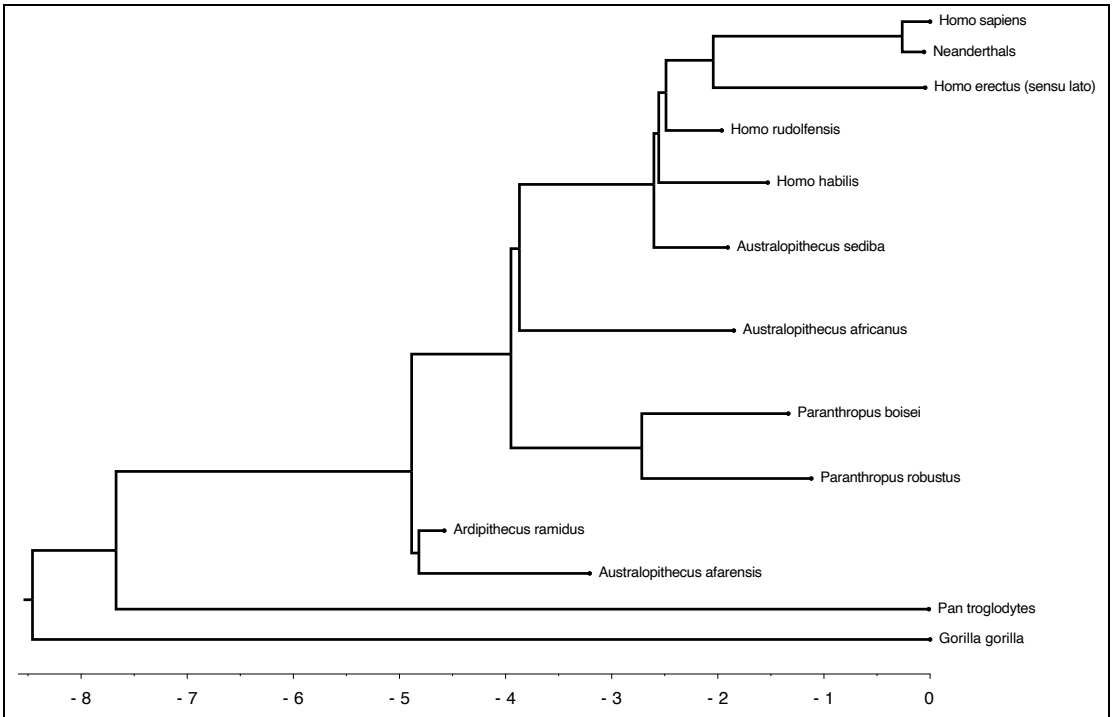


Figure 9-1: The least speciose, 'high certainty' Parins-Fukuchi phylogeny

This is the least speciose phylogeny used in this section, constructed by removing the taxa for which Wood & Boyle (2016) classify the likelihood of them being separate, distinct species as "low" from the phylogeny with the highest AIC score reported in Parins-Fukuchi et al. (2019). This phylogeny, then, represents a 'lumping' approach to hominin taxonomy.

The third, and most speciose, phylogeny (see Figure 9-2) is a novel composite tree for which the principal aim was to include more taxa currently recognized in a "splitting" framework. Since "split" taxa are not as well represented by fossils than "lumped" taxa, this phylogeny was based on a combination of published cladograms, each focusing on particular time periods, and aDNA estimates of split times between *Homo sapiens,* Neanderthals, and Denisovans. The full list of sources is given in Appendix 3. Time ranges of most of the taxa were sourced from Wood and Boyle (2016), supplemented in some cases by more recent dates. As first appearance dates (FADs) for taxa the cladograms suggest as sister clades seldom matched, a 'speciation time' of 200,000 years was added to the date of the youngest FAD to estimate split times. This is Rosenzweig's (1995) estimate of average time for species differentiation to occur among mammals.

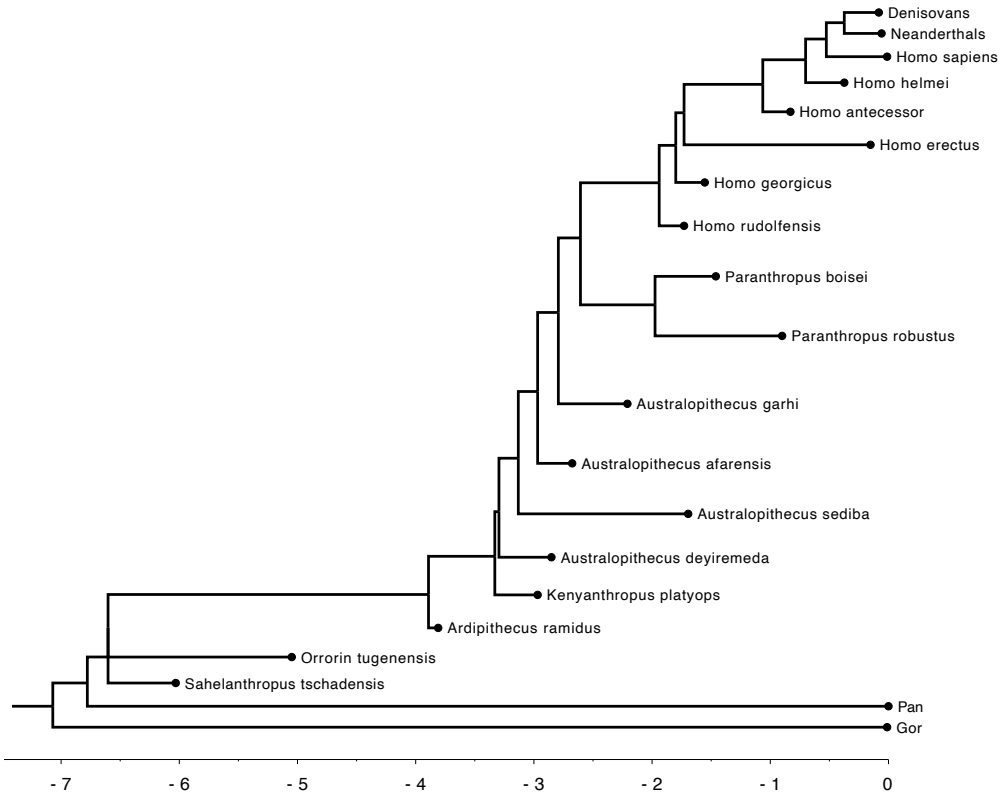


Figure 9-2: The most speciose 'composite' phylogeny

This is the most speciose phylogeny used in this section, constructed based on a combination of published cladograms, each focusing on particular time periods, and aDNA estimates of split times between *Homo sapiens*, Neanderthals, and Denisovans. This phylogeny, then, represents an extreme 'splitting' approach to hominin taxonomy.

9.1.2 Calculating speciation rate

The data collection methods described in sections 9.1.2, 9.1.3, and 9.1.4 were repeated for all three phylogenies.

I sliced the phylogeny rootwards at intervals of 0.5 million years using the "timeSliceTree" function in the paleotree package (Bapst 2012) in R. The only exception to these 0.5-million-year intervals was that we replaced the tree at 0 mya (i.e. the present), in which only *Homo sapiens* is extant, with one at 0.2 mya. For every extant tip on each resulting phylogeny, I calculated Jetz et al's (2012) tip DR:

$$DR = \frac{1}{\sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}}} \qquad \textit{Equation 9-1}$$

where DR is tip DR for species i, N_i is the number of edges between species i and the root, and l is the length of edge j (with j=1 being the edge closest to the extant tip).

Tip DR is a species-specific measure of the number of splitting events (captured in N_i) and time between them (captured in l) from root to tip. It has been shown to estimate true speciation rate (rather than diversification rate, i.e. speciation minus extinction) in simulations (Jetz et al. 2012; Title and Rabosky 2019). The measure places greater emphasis on splitting events closer to the present, weighing each edge length between cladogenesis down by $\frac{1}{2^{j-1}}$, and is therefore described as a measure of "instantaneous" speciation rate (Upham, Esselstyn, and Jetz 2019).

What this means for the analysis here, for example, is that DR of *Paranthropus boisei* at 2 mya includes information about its DR at 3 mya, but places emphasis on speciation events closest to 2 mya. Time intervals between measuring points, then, need to be balanced between resolution and the amount of new information captured in each measurement. That is, intervals 'too' close together will add little in the way of new information – for example, measurements taken 10,000 years apart would not differ by much on average, given that there are unlikely to be splitting events every 10,000 years (Rosenzweig 1995; Uyeda et al. 2011). Indeed, in a sample of birds and mammals, estimates of split times between extant sister species ranged from a mean of 3.4 mya in the tropics to ~1 mya at higher latitudes (Weir and Schluter 2007). The choice of 0.5-million-year intervals between measuring points, then, was based on the probability of capturing at least one splitting event, on average, between measuring points, so that each additional measurement across a branch would meaningfully capture new information.

Some tips on the newly created phylogenies do not correspond directly to named, or indeed sampled, species. For example, the ancestral hominin population that gave rise to all *Paranthropus* species (whatever their underlying phylogenetic relationships) is not known from fossils, but exists on the phylogeny and is therefore included in the analyses. I categorized each unsampled tip as belonging to the genus of its next named descendant supplied by the "timeSliceTree" function.

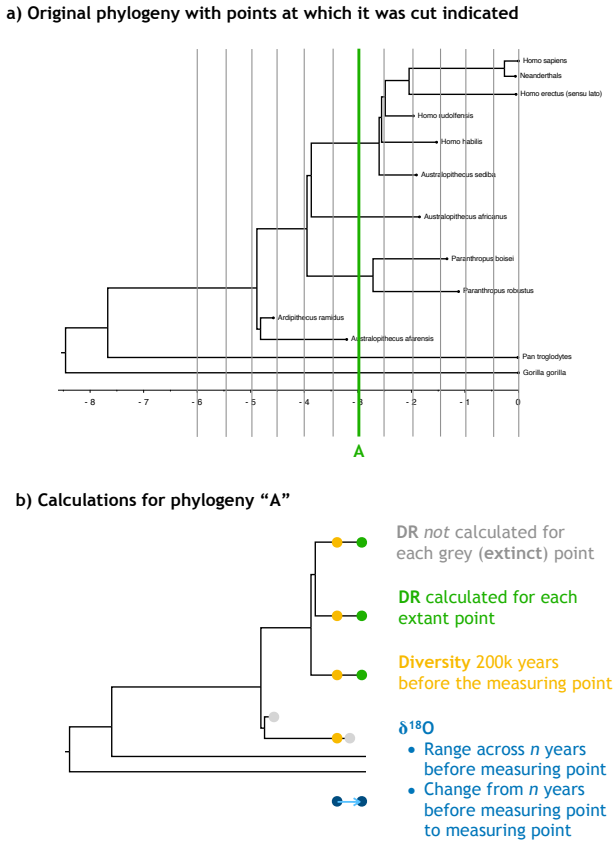


Figure 9-3: Methodology of Section B

The original phylogeny was sliced at 0.5-million-year intervals towards the root to produce new phylogenies—e.g. the original phylogeny in a) is sliced at the 3 Ma mark to produce phylogeny A, shown in b). The "present" on phylogeny A is thus the 3 Ma measuring point on the original phylogeny. For phylogeny A, the variables illustrated in b) were calculated for the 200k year interval before the "present"; this was repeated for the climate variables at 500k and 100k year interval before the "present".

9.1.3 Diversity and measures of climate

On each resulting phylogeny, I recorded the number of extant species at 200k years before the present using the "getExtant" function in the phytools package (Revell 2012). The reason this time range was chosen was based on the expectation that there should be a time lag between cause and effect. The 'present' on each resulting phylogeny, of course, is each 0.5-million-year measuring point on the original phylogeny (see Figure 9-3), so hereafter I simply refer to the numbers of extant species as species density at 200k years before the measuring point.

In addition to asking what the effect of overall diversity is on splitting rate variation, I ask whether non-isolated species, whose range overlapped with that of one or more other hominin, have slower splitting rates than isolated taxa. I classified taxa into "non-isolated" and "isolated" by adopting Wood and Boyle's (2016) division of taxa into "sympatric" and "non-sympatric" respectively. Thus, each data point that corresponds to a sampled and named species in Wood and Boyle (2016) was classified as "non-isolated" when Wood and Boyle (2016) record it as "sympatric" with at least one other hominin taxon at that time. When a data point was unsampled or not named (in the case of a branch being somewhat longer than the physically sampled timespan of the species, for instance), the categorization of the next named and sampled descendant was adopted.

I calculated climate variables across three ranges: 100k, 200k, and 500k years before each measuring point. $\delta^{18}O$ data, as a proxy for climate conditions (Potts 1998a) were sourced from Lisiecki and Raymo (2005). $\delta^{18}O$ data is a general proxy for climate, estimating both global temperature and ocean ice volume (Potts 1998a).

In Chapter 11, I examine the two key hypotheses that suggest a role for climate change as a driver of hominin cladogenesis. These hypotheses are Potts' (Potts 1996a, 1998b, 2013; Potts and Faith 2015) "Variability Selection Hypothesis" (VSH), and Vrba's (1985a, 1985b, 1993) "Turnover Pulse Hypothesis" (TPH). Both hypotheses are introduced in more detail in Chapter 11. In brief, the VSH suggests that hominin speciation should occur at higher rates in periods of climatic variability. To test the VSH, I calculated the range of $\delta^{18}O$ (hereafter simply "$\delta^{18}O$ range") across the three time periods before each measuring point as a proxy for relative climatic variability.

The TPH suggests that changes in temperature, rather than climatic variability, determined hominin speciation. I tested two versions of the TPH: first, using models which included information about the direction of change, and second, using models which only took into account the absolute amount of change. For the first approach, I calculated the difference between mean $\delta^{18}O$ in the 100k-year bin starting with the measuring point, and 1) mean $\delta^{18}O$ in the preceding 100k-year bin, 2) mean $\delta^{18}O$ in the bin starting 200k years before the measuring point, and 3) mean $\delta^{18}O$ in the bin starting 500k years before the measuring point. For the second approach, I used the absolute value of the previously calculated change in mean $\delta^{18}O$ values.

9.1.4 Time

Speciation rate cannot be directly regressed against time, given that it already includes a time component, so instead I asked whether speciation rates before and after peak diversity of 1) the clade as a whole and 2) each genus differ significantly. To do so, I plotted lineage-through-time (LTT) plots for the whole clade and for each genus, and classified tip DRs *before* the peak as "before peak" and those *after* the peak as "after peak" (see Figure 9-4).

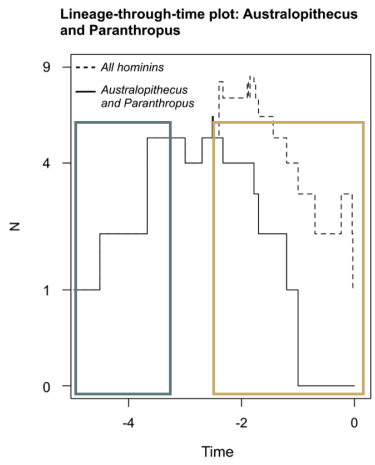


Figure 9-4: Methodology to compare speciation rates before and after peak diversity

Diversity is the outcome of speciation minus extinction: therefore, it is possible that the reduction in diversity seen after its peak is merely the outcome of an increase in extinction rate rather than a decrease in speciation rate. To ask whether speciation rate was slower at the 'end' of a lineage's lifespan than at the 'beginning', I compared speciation rates before peak diversity (in grey) to those after peak diversity (in gold).

9.2 Analyses

9.2.1 Time dependence (Chapter 10)

These, and all further analyses, were performed in R 4.01 (R Development Core Team 2016). To compare speciation rate before and after peak diversity at the level of the entire hominin clade, I ran the following phylogenetic GLS:

$$DR \sim TP \qquad \textit{Equation 9-2}$$

where *DR* is tip DR for a given tip and *TP* is time period, a binary variable (before and after peak).

In this model, and all subsequent models, the phylogenetic correlation structure of residual error (i.e. the variance-covariance matrix) was accounted for in the nlme "correlation" argument. All models assumed a Brownian motion model for residual error structure,

following previous work on regressions including speciation rates (Freckleton, Phillimore, and Pagel 2008; Jetz et al. 2012; Harvey and Rabosky 2018). Non-contemporaneity of tips was represented in the nlme argument "weights".

To compare speciation rate before and after peak diversity for each genus, I ran the following phylogenetic generalized least squares (GLS) regression:

$$DR \sim TP \times genus \qquad \textit{Equation 9-3}$$

where *DR* is tip DR for a given tip and *TP* is time period, a binary variable (before and after peak).

9.2.2 Climate and cladogenesis (Chapter 11)

To test at which timescale the VSH and TPH operate to affect tip DR in the hominin clade, I ran the following phylogenetic generalized least squares (GLS) regressions using the nlme package (Pinheiro et al. 2020) for each time range (i.e. 100k, 200k, and 500k years before measuring points):

$$DR = V_{time} \qquad \textit{Equation 9-4}$$

where *DR* is tip DR for a given tip and V_{time} is the variable of interest at a given time point (in the case of the VSH, $\delta^{18}O$ range, and in the case of the TPH, the actual and absolute differences in mean $\delta^{18}O$).

For all variables of interest (i.e. $\delta^{18}O$ range, difference in mean $\delta^{18}O$, and absolute difference in mean $\delta^{18}O$), I compared significant models using their AIC values and Cox and Snell's (1989) pseudo-R^2 to ask which model, and thus which time range, best predicts hominin tip DR. The use of AIC in comparing non-nested models is an area of debate, with Ripley (2004) arguing that a nested assumption is important in order to keep the variance of the AIC estimator low. However, Akaike's original paper makes no assumption about models being nested, Burnham & Anderson (2002) argue in favour of the approach, and the normalizing constant is the same across the models under consideration. Here, in any case, the model with lowest AIC *and* highest pseudo-R^2 was chosen as the best model.

I repeated the analyses described above to test at which timescale the VSH and TPH operate to affect tip DR within hominin genera, running the following phylogenetic GLS:

$$DR = V_{time} \times genus \qquad \textit{Equation 9-5}$$

9.2.3 Diversity and cladogenesis (Chapter 12)

I tested the relationship between diversity 200k years before the measuring point and DR for the clade as a whole (as in Equation 9-4, where *V* is diversity). Next, I repeated this procedure for the relationship between diversity and DR for each genus (as in Equation 9-5, where *V* is diversity).

To compare speciation rates between "non-isolated" taxa and "isolated" taxa at the level of the entire hominin clade, I ran the following phylogenetic GLS:

$$DR \sim I \qquad \textit{Equation 9-6}$$

where *DR* is tip DR for a given tip and *I* is a binary variable ("non-isolated" and "isolated").

To compare speciation rates between "sympatric" taxa and those not classified as "sympatric" for each genus, I ran the following phylogenetic generalized least squares (GLS) regression:

$$DR \sim I \times genus \qquad \textit{Equation 9-7}$$

where *DR* is tip DR for a given tip and *I* is a binary variable ("non-isolated" and "isolated").

9.2.4 Testing the performance of the approach

To test how often my approach yields false positive relationships between speciation rate and diversity, I simulated 1000 constant-rate birth-death trees and repeated the analyses for overall diversity described above in section 9.2.3.

10 Basic patterns of hominin cladogenesis

10.1 Background

10.1.1 Introduction

Across the tree of life, speciation and extinction rates vary across space and through time (Rabosky 2014). The clearest evidence of these rate heterogeneities are enormous differences in species richness between extant clades. Despite hominin taxonomy being notoriously unresolved, a generally agreed upon pattern is that *Paranthropus*, with 3 species, is a less speciose clade than *Australopithecus* or *Homo*; and, potentially, that *Australopithecus*, comprising ~7 species in a "splitting" approach, is a less speciose clade than *Homo*, which comprises ~14 species in the same framework (Wood and Boyle 2016). To date, the only work to have estimated hominin speciation rate (Bokma, van den Brink, and Stadler 2012) did so by assuming speciation rate to have been constant across the entire clade. The first question I examine in this chapter is whether differences in species richness between hominin genera is the consequence of significantly different splitting rates. This need not be the case, as Bokma et al. (2012) assumed, since species richness is the outcome of diversification – that is, speciation minus extinction – rather than speciation alone. That is, a less speciose lineage can have the same speciation rate as a more speciose lineage, with different extinction rates underlying their different species richness. The major question underlying this chapter's first focus, then, is really whether or not hominin genera differed fundamentally from each other in terms of their speciation rates.

A recurrent pattern in speciation rate variation within lineages, reported for extant bird genera (Phillimore and Price 2008), some extant mammalian lineages (Upham, Esselstyn, and Jetz 2019), and other clades (e.g. extant reptiles (Alencar et al. 2016)), is a slowdown in speciation rates over time. This pattern is frequently interpreted as a signal of an inverse relationship between species density and speciation rate (Moen and Morlon 2014). Put simply: the more extant and closely related species, the less probable future speciation becomes, and as a result, speciation rate slows down over time. The most common explanation for this relationship, although other causes have been proposed (Moen and Morlon 2014), is that competition for limited resources and niches places caps on clade expansion. Here, the second question I am interested in testing in this chapter, as a foundation for exploring potential biotic determinants of hominin speciation in Chapter 12, is whether or not this general vertebrate pattern also characterised hominin evolution. Was hominin speciation time-dependent?

Previous work has suggested that the first appearance dates (FADs) of hominin species are correlated with—and probably caused by—climatic events at global and local scales (Potts 1998a; Shultz and Maslin 2013; Potts and Faith 2015). Such 'extrinsic' models leave less room for increasing interspecific competition limiting speciation rate over time, and, as such, produce no *a priori* expectations regarding time-based slowdowns. Others have observed that hominin species do not appear in any markedly clumped pattern from around 5 million years ago onwards (Foley 2016; Wood and Boyle 2016), implying, potentially in contrast to a pure climate model, that hominin speciation is characterised by regularity. Again, these interpretations of the fossil record suggest speciation rate did not slow down over time. Finally, characterisations of hominin evolution as a series of adaptive radiations (Foley 2003, 2013) do implicitly suggest speciation rate should be temporally variable, but whether or not a slowdown actually happened was not explicitly tested in these papers.

10.1.2 Terminology

A more in-depth introduction to terminology used in this Section is offered in Chapter 8. "Speciation", here, refers to the complex and temporally extended process of lineage splitting. Because I measure tip DR across multiple phylogenies that differ in their definition of species, I refer to tip DR calculated across phylogenies simply as "splitting rate". The model, described in Chapter 8, which is put forward as a way to reconcile differences between phylogenies based on different taxonomic practices, is referred to as the threshold model of hominin speciation. In brief, it suggests that phylogenies based on more species-rich 'splitting' taxonomy show relationships between incipiently diverging lineages, and thus in effect capture an early stage of speciation. Less speciose 'lumping' taxonomies recognize more highly morphologically diverged groups—lineages which have probably reached later stages of speciation—and phylogenies that are based on these thus capture the cumulative effect of the cladogenesis, extinction, and persistence of lineages recognized at earlier stages of speciation.

10.1.3 Materials and methods

The full method for this section is described in Chapter 9. In brief, the analyses were run on three phylogenies to account for different approaches to hominin taxonomy: 1) the phylogeny with the lowest AIC score published by Parins-Fukuchi et al. (2019), 2) a "high certainty" version of this phylogeny, with species Wood and Boyle (2016) have "low" confidence in treating as distinct taxa removed, and 3) a composite phylogeny based on a review of the literature on hominin cladograms at the time of writing. Mean DR across the whole phylogeny was calculated in R 4.01 (R Development Core Team 2016). To ask whether average DR differed significantly between genera, I ran phylogenetic generalized least

squares (GLS) regressions using the "nlme" package (Pinheiro et al. 2020) with *Homo* as a baseline. To ask whether tip DRs varied across time, I compared tip DR before peak diversity to those after peak diversity for the clade as a whole, and for each genus separately, using phylogenetic GLS regressions.

10.2 Results

10.2.1 Parins-Fukuchi phylogenies

The results from models run on the original Parins-Fukuchi phylogeny are presented in Table 10-1, and the lineage-through-time (LTT) plot for the whole clade on this phylogeny is shown in Figure 10-1A.

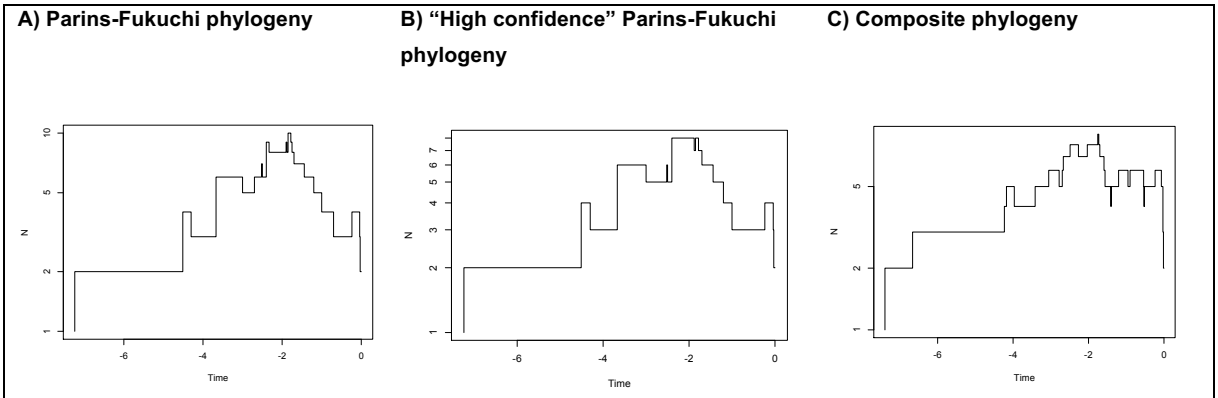


Figure 10-1: Lineage-through-time plots for the three phylogenies

A) Lineage-through-time (LTT) plot for the original Parins-Fukuchi et al. phylogeny. The *y*-axis, *N*, was log-transformed, so that diversification rate is equal to the slope. Note that lineage diversity includes *Pan troglodytes* to root the tree; hominin diversity, then, is equal to *N*-1. B) as A), but for the "high confidence" Parins-Fukuchi phylogeny; C) as A), but for the composite phylogeny. For all three phylogenies, DR after peak diversity was not significantly slower than DR before peak diversity, implying an increase in extinction rate explains the fall in diversity after the peak.

Table 10-1: Results from phylogenetic GLS across the Parins-Fukuchi phylogeny

	Average DR		**Slowdown over time?**	
Clade-level	**0.75**		**No** "After" peak relative to "before" peak: -0.05 (p=0.61)	
Genus-level	**No sig. differences between genera**		**Variable**	
	Homo	0.75	*Homo*	-0.33 (p<0.001)
	Australopithecus	0.74 (p=0.84)	*Australopithecus*	-0.31 (p<0.001)
	Paranthropus	0.76 (p=0.76)	*Paranthropus*	-0.25 (p=0.106)

Across the original Parins-Fukuchi phylogeny, average DR is 0.75. DR does not significantly differ between genera. *Paranthropus* is the only genus not to show the expected slowdown in

splitting rate after its peak diversity, while *Homo* and *Australopithecus* show significant slowdowns in splitting rate before and after peak diversity. Across all hominins, the expected slowdown is not found: there is no significant difference between before- and after-peak diversity splitting rates.

The results from models run on the "high certainty" Parins-Fukuchi phylogeny are presented in Table 10-2, and the LTT plot for the whole clade on this phylogeny is shown in Figure 10-1B.

Table 10-2: Results from phylogenetic GLS across the "high certainty" Parins-Fukuchi phylogeny

	Average DR		**Slowdown over time?**	
Clade-level	**0.69**		**No** "After" peak relative to "before" peak: -0.04 (p=0.64)	
Genus-level	**No sig. differences between genera**		**Yes**	
	Homo:	0.73	*Homo*	-0.23 (p<0.05)
	Australopithecus:	0.90 (p=0.19)	*Australopithecus*	-0.25 (p<0.05)
	Paranthropus	0.53 (p=0.20)	*Paranthropus*	-0.22 (p<0.05)

Across the "high certainty" Parins-Fukuchi phylogeny, average DR is 0.69. DR does not significantly differ between genera. All three genera show the expected slowdown in splitting rate after their peak diversity. Across all hominins, the expected slowdown is not found: there is no significant difference between before- and after-peak diversity splitting rates.

10.2.2 Composite phylogeny

The results from models run on the composite phylogeny are presented in Table 10-3, and the LTT plot for the whole clade on this phylogeny is shown in Figure 10-1C. LTT plots per genus on this phylogeny are shown in Figure 10-2.

Table 10-3: Results from phylogenetic GLS across the composite phylogeny

	Average DR		**Slowdown over time?**	
Clade-level	**0.81**		**No** "After" peak relative to "before" peak: +0.02 (p=0.76)	
Genus-level	**Significant differences between genera**		**Variable**	
	Homo:	0.92	*Homo:*	-0.01 (p=0.84)
	Australopithecus:	0.79 (p<0.05)	*Australopithecus*:	-0.10 (p=0.24)
	Paranthropus:	0.62 (p<0.001)	*Paranthropus*:	-0.20 (p<0.05)

Across the whole composite phylogeny, average DR is 0.81. DR differs significantly between genera, with *Homo* having the highest splitting rate (DR=0.92), and *Paranthropus* the lowest (DR=0.62). *Paranthropus* is the only genus to show the expected slowdown in splitting rate after its peak diversity, while *Homo* and *Australopithecus* show no significant difference in splitting rate before and after peak diversity. Across all hominins, the expected slowdown is also not found: there is no significant difference between before- and after-peak splitting rates.

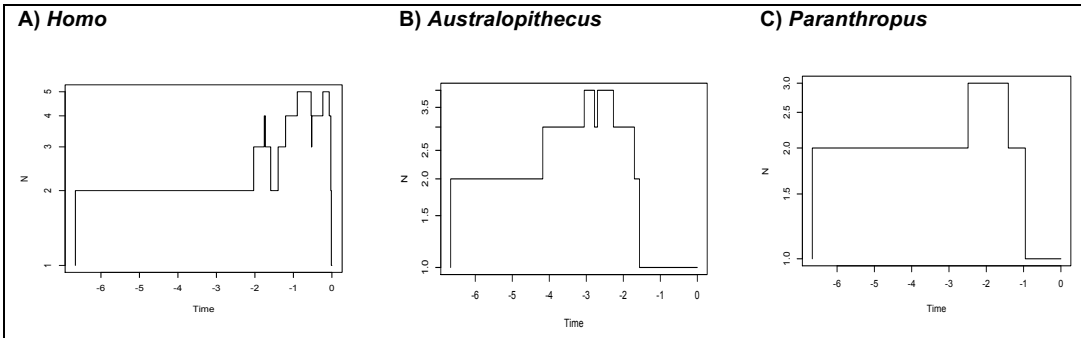


Figure 10-2: Lineage-through-time plots for the three genera on the composite phylogeny

A) Lineage-through-time (LTT) plot for *Homo*. The *y*-axis, *N*, was log-transformed, so that diversification rate is equal to the slope. Note that lineage diversity includes *Pan troglodytes* to root the tree; hominin diversity, then, is equal to *N*-1. B) as A), but for *Australopithecus*; C) as A), but for *Paranthropus*.

10.3 Discussion

The main, and probably unsurprising, point to emerge from these analyses is that different hominin phylogenies are characterised by different patterns of cladogenesis. The clearest way in which they differ is in their average DR: across more speciose phylogenies, splitting rate is higher than across less species-rich phylogenies (0.81 across the most speciose composite phylogeny; 0.75 across the Parins-Fukuchi phylogeny; and 0.69 across the least species-rich "high confidence" Parins-Fukuchi phylogeny). When viewed through the lens of the threshold framework, this implies incipient species were formed at higher rates than more morphologically differentiated species. This means that not all taxa recognized at earlier stages of speciation survived as independent units for sufficiently long periods of time to reach later stages of speciation. An illustration of this dynamic is the combination of autapomorphies suggesting separate evolutionary trajectories (Tattersall 2007), reticulated genetic histories suggesting the speciation threshold described by the Biological Species Concept had not quite been reached (Krause et al. 2010; Prufer et al. 2014), and eventual extinction of Neanderthals and Denisovans. If taxa recognized on "splitting" taxonomies represent diverging populations within larger hypodigms recognized on "lumping"

taxonomies, the implication of these results is that the splitting of these more morphologically diverged taxa is decoupled, to some degree, from intraspecific population splitting. Consequently, as was found within mammals in the previous section, there is a role for other factors mediating the relationship between processes at the level of intraspecific populations and divergence at higher taxonomic levels.

Interestingly, even the estimate for splitting rate across the least speciose phylogeny used here (0.69 species per million years) is notably higher than that (0.46 species per million years) obtained by Bokma and colleagues (2012). Their approach reconstructed speciation and extinction rates probabilistically, given the time since the split from the panin lineage and the number of extant hominins alive today. The results presented here, then, suggest that even in the most conservative taxonomic framework, hominin cladogenesis occurred at rates higher than expected from a theoretical perspective.

One pattern is common to all three phylogenies: across the whole clade, splitting rate is not significantly slower after peak diversity than before peak diversity. In the context of the threshold model, this implies that the rate at which speciation was initiated (captured on the more speciose phylogenies) did not differ pre- and post-peak, and neither did the rate at which differences between incipient species became cemented and more pronounced (captured on less speciose phylogenies).

This is not what is expected. Slowdowns in rates of cladogenesis have been found across the tree of life: they are common across extant birds, reptiles, and mammals (Phillimore and Price 2008; Rabosky and Lovette 2008; Etienne et al. 2012; Moen and Morlon 2014). The hominin lineage, then, is comparatively unusual in this respect. LTT plots for all three phylogenies, shown in Figure 10-1, show a slowdown in diversification rate—the slope—after peak diversity, and from this it follows that the cause of shrinking diversity in the later stages of hominin evolution is the outcome solely of increasing extinction rates, not decreasing rates of cladogenesis. In other words, post-peak hominins essentially had the same chance of splitting as they did before peak diversity, but cladogenesis was outpaced by increasing extinction rates to produce a net decrease in taxic diversity. Post-peak diversity extinctions tend to be linked to climate in the literature: for example, Louys & Roberts (2020) linked Quaternary changes in habitat distribution, particularly the disappearance of savannahs, to large-scale extinction events of megafauna and hominins in Southeast Asia; Grove (2012) found a possible relationship between obliquity cycles and hominin extinction after 1.5 Ma; and Foley (1994) made the case that the primary way in which climate influenced hominin evolution across the entire clade was through extinction, not speciation. Whether or not climate explains

the post-peak increases in extinction rate relative to that before the peak inferred here, however, cannot be concluded based on the data presented here.

The expected pattern of splitting rate slowdowns is almost always interpreted as the consequence of negative density-dependent cladogenesis (Moen and Morlon 2014), and the most commonly invoked—although not often explicitly tested—causal link between density-dependence and cladogenesis is niche differentiation. In this model, cladogenesis is regulated by ecological opportunity. Available niches become occupied by closely related species as a clade grows; when they are (nearly) all occupied, an ecological limit is reached, and cladogenesis slows down (Schluter 1996; Gavrilets and Vose 2005) so that a stable level of taxic diversity is maintained. If these associations hold, the implications for hominins, which do not show such a slowdown across the three trees, is that an ecological limit to taxic diversity was never reached. This pattern is independent of taxonomic practice. There are a number of explanations, which are not mutually exclusive, for the pattern. First, the upturn in extinction rate, implied by the combination of temporally stable splitting rates and decreasing diversity after the peak, could have prevented the lineage from reaching an ecological limit, or might have obscured the signal of diversity stability if the limit was reached. Second, whether or not ecological 'limits' are ever reached is a major problem in evolutionary biology: first, a 'maximum' number of niches is difficult to ascertain, and second, there is some evidence that equilibrium diversity tends to be below ecological maxima (Rabosky 2013; Moen and Morlon 2014). Third, it could be the case that it makes no sense to think of ecological 'limits' for the clade as a whole because it comprises multiple adaptive grades (Foley 2016) and an intercontinental distribution; and, as a result, signals of density-dependent cladogenesis within smaller geographical ranges or adaptive grades would be obscured at this scale.

In the third scenario, in which a signal of slowdowns is obscured at the level of the clade as a whole, within-genus slowdowns in cladogenesis are expected. This requires, of course, that hominin genera represent distinct adaptive grades. There is strong support for *Homo* occupying a distinct adaptive grade that was different to that of earlier hominins (Collard and Wood 2015; Foley 2016). By contrast, the isotopic evidence that *Paranthropus* and *Australopithecus* occupy distinct adaptive grades is less clear (Faith and Wood, in prep.; Sponheimer et al. 2013). Despite the somewhat ambiguous isotopic evidence, *Paranthropus* and *Australopithecus* cranial gross morphology does imply significantly different ecological strategies (Wood and Constantino 2007), and *Paranthropus* is routinely found to be a monophyletic clade, implying a separate evolutionary trajectory to *Australopithecus*, in

cladistic studies (Kimbel, Rak, and Johanson 2004; Wood and Constantino 2007) as well as on the three phylogenies used here.

The three phylogenies differ in the signals of time-dependence they contain at the scale of genera. Across the more speciose Parins-Fukuchi et al. phylogeny, only *Paranthropus* does not show a slowdown; and across the less speciose "high confidence" Parins-Fukuchi tree, all three genera have significantly slower DR after peak diversity. Save in the case of *Parathropus* on the Parins-Fukuchi et al. phylogeny, falling taxic diversity within genera after peak diversity, then, was at least in part the consequence of reduced rates of cladogenesis. The role extinction played in falling diversity is less clear. Taken together within the framework of the threshold model, these results suggest that the rate at which more morphologically diverged taxa arose slowed down after peak diversity within each genus.

A possible implication of these within-genus patterns, at both taxonomic scales represented by the two phylogenies, and thus potentially at both stages of speciation, is that biotic competition for finite niche space may have operated to constrain cladogenesis. This follows models suggested on the bases of data from extant lineages (McPeek 2008; Phillimore and Price 2008; Rabosky and Lovette 2008). If it was indeed competition for niches, functionally relevant ecological diversification is expected to accompany speciation. Although interspecific variation in ecologically relevant traits (e.g. diet (Sponheimer et al. 2013) and dentition (Wood and Boyle 2016)) has been described for all three genera, it is difficult to explicitly link these to well-defined ecological niches because environmental reconstructions are presently relatively coarse (Foley 2013). The strongest support for the niche differentiation model probably comes from *Paranthropus*: carbon isotope signatures of *P. boisei* and *P. robustus* are suggestive of major differences in dietary strategy, with *boisei* consuming a significantly larger proportion of C4 plants (Cerling et al. 2011), the two species lived in distinct regions of Africa without known sympatry, and there is some evidence that derived features of *boisei'*s masticatory apparatus were specifically adapted to a relatively committed C4-based grazing niche (Faith and Wood, in prep.). Overall, however, the evidence for ecological niche differentiation regulating speciation within both genera is relatively weak. Still, at a grander analytical scale, the case can be made that the division of (most) pre-*Homo* hominins into *Paranthropus* and *Australopithecus* does capture the two fundamental niches available to early hominins—postcranial robusticity and megadonty on the one hand, and less specialized masticatory apparatus and a mixed locomotor strategy on the other—and that, once these niches were occupied, speciation was restricted.

An alternative explanation, which does not require the phenotypic specialization implied by the niche differentiation model, is that slowdowns in splitting rate can occur as a result of two processes determined by geography. First, geographical range partitioning: if the overall geographic range a clade occupies is bounded, strong slowdowns in speciation rate are expected over time as the range is subdivided over successive speciation events (Pigot et al. 2010; Moen and Morlon 2014). Second, peripatric speciation, in which a larger-ranged species produces a number of small-ranged species at its periphery, can produce splitting rate slowdowns (Pigot et al. 2010). In the light of ambiguous phenotype-environment correlations, a minimum of 25 cases of hominin sympatry in a 'splitting' framework (Wood and Boyle 2016), and recent work suggesting even more instances of temporal and geographical overlap (Haile-Selassie et al. 2019), geographical models are strong contenders to explain slowdowns in rates of cladogenesis within hominin genera.

A final explanation for slower rates of cladogenesis after peak diversity, of course, is a purely climatic model. If, as much recent work (Potts 1998a; Grove 2011, 2012; Shultz and Maslin 2013; Lupien et al. 2020) suggests, hominin cladogenesis was determined by particular climate events, the cessation or absence of them can explain slowdowns. Differentiating between the three (non-mutually exclusive) explanations cannot be done solely on the basis of the analyses presented in this chapter; but biotic competition and abiotic climate models are tested in subsequent chapters.

In contrast to patterns found across the two Parins-Fukuchi phylogenies, only splitting rate in *Paranthropus* slows down on the most speciose composite phylogeny. Within the other two genera, DR is *not* significantly slower after peak diversity compared to that before. Again, in contrast to the pattern expected based on extant comparators, stable splitting rates in *Homo* are combined with a hint of the attainment and maintenance of a diversity equilibrium: *Homo* diversity remains relatively constant, cycling between 3 and 4 species from 1.5 Ma to just before the present. In extant lineages, diversity equilibria are usually the consequence of a slowdown in the rate of cladogenesis as niches are filled (Phillimore and Price 2008). If the ecological model holds, meaning there was a limit to the number of niches available to *Homo,* the result across the composite tree is suggestive of recurrent and dynamic turnover of incipient lineages in our genus. As before, no conclusions about the root cause of this pattern can be drawn from the data presented here, but biotic and abiotic causal models are tested in the following chapters.

Finally, the question of whether hominin genera differed in their rates of cladogenesis remains, and the answer is that results vary across phylogenies. Across the Parins-Fukuchi et

al. phylogenies—both the original and the "high confidence" versions—the three genera do not have significantly different DR. On these phylogenies, then, asymmetrical taxic richness is not the product of fundamentally different rates at which lineages split. In the context of the threshold model, these results suggest genera did not differ in the rate at which earlier lineage splitting occurred, nor the rate at which more morphologically differentiated groups were formed from lineages that survived for long enough to accrue greater levels of morphological divergence. Across the composite phylogeny, however, genera *did* differ significantly from each other: cladogenesis in *Homo*, here, occurs at a significantly higher rate than that in *Australopithecus* and *Paranthropus*. If the composite phylogeny is taken as a phylogeny representing relationships between units recognized at very early stages of speciation in the threshold model, the conclusion that the rate at which this occurred in *Homo* is significantly higher than that in its predecessors can be drawn. The implication, if the model holds, is that there must also have been a correspondingly high rate at which these incipiently diverging groups went extinct, because the rate at which more morphologically diverged taxa formed is no different in *Homo* than *Australopithecus* or *Paranthropus*.

In the context of the threshold model, the key point that stands out is the differences in patterns at the earliest stages of speciation, represented by the most speciose composite phylogeny, and later stages of speciation, captured in phylogenies showing relationships between more diverged groups. Genus A in Figure 10-3 shows such a scenario; it is characterised by a higher rate of turnover on the phylogeny comprising more exclusive, 'split' taxa, than on the phylogeny comprising more inclusive, 'lumped' taxa. In both *Homo* and *Australopithecus,* DR is not significantly slower after peak diversity on the 'split' composite phylogeny, while it is for both genera on the more 'lumped' Parins-Fukuchi et al. phylogenies.

Taken within the threshold model, these results suggest incipient lineages possibly experienced more evolutionary turnover than more morphologically diverged groups within *Homo* and *Australopithecus*.

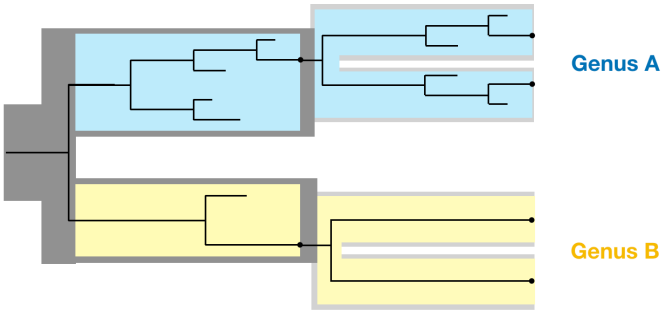


Figure 10-3: Differences in rates of cladogenesis across two approaches to taxonomy

Phylogeny in black represents relationships between 'split' species; these represent, in reality, lineages that are diverging early on in the speciation process. Genus A, in blue, experiences a significantly higher rate of turnover at this level than Genus B, in yellow. However, when it comes to more morphologically diverged taxa (that is, lineages that have reached later stages of speciation), represented by the dots, the two genera produce them at the same rate: the first splitting event at this level is indicated by the dark grey bars, and the second splitting event by the light grey bars.

Finally, *Homo* emerges as a somewhat different genus to both *Australopithecus* and *Paranthropus* in terms of the lineage splitting that comprises the earlier stages of speciation. Across the composite phylogeny, it is characterised by significantly higher DR than *Australopithecus* and *Paranthropus*, an absence of a slowdown in DR after it reaches peak diversity (although it shares this with *Australopithecus*), and the potential attainment and maintenance of a diversity equilibrium. These patterns suggest a dynamic pattern of lineage turnover with higher rates of production *and* extinction than that which characterised its predecessors. *Homo* is no different to *Australopithecus* and *Paranthropus*, however, in the cladogenetic patterns it evidences across less speciose phylogenies. In the context of the model, this suggests it is specifically the earlier stages of speciation that were more dynamic and comprised higher rates of turnover in *Homo* than in the other genera. This is visualized in the difference between Genus A and Genus B on Figure 10-3.

10.4 Conclusion

Taken together, these results are suggestive of a number of interesting and underexplored processes that shaped basic patterns of hominin cladogenesis. First, at the level of the clade as a whole, falling taxic diversity after peak diversity was probably the consequence of higher rates of extinction, rather than slowdowns in cladogenesis. This pattern holds across all three phylogenies, suggesting, when viewed through the lens of the threshold model, that splitting rates of both incipient and more differentiated groups remained constant before and after peak

diversity. The absence of a splitting rate slowdown across the whole clade is probably the result of signals being lost at this scale, since within-genus cladogenesis *is* time-dependent across both Parins-Fukuchi et al. phylogenies. Finally, and perhaps most importantly, the temporal patterns found for *Australopithecus* and *Homo* on the composite phylogeny are different to those found for each genus on the Parins-Fukuchi et al. phylogenies, suggesting that the formation of incipient lineages was characterised by more turnover than that of more morphologically diverged groups in these genera. The implication, then, is that the relationship between incipiently diverging lineages and more morphologically diverged taxa that contain them is mediated by biotic or abiotic factors—or both.

11 Climate and hominin cladogenesis

11.1 Background

11.1.1 Introduction

Hominin evolution has long been examined through a "Court Jester" (Barnosky 1999) lens: that is, climate is frequently invoked as an explanation for the first appearances of novel traits, and of novel hominin taxa. The exact role the Court Jester has been hypothesised to play in shaping hominin evolution has varied. The roots of this kind of thinking extend back to Dart's (1953) "Savannah Hypothesis", where the transition from ancestral to derived hominin was initiated by expanding savannah ecosystems; this model dominated paleoanthropological narratives until at least the 1980s (Potts 1998a). Woodlands and forests, in contrast, were invoked as the setting for early hominin evolution by Rayner et al. (1993). De Menocal (1995) suggested that selection for arid-adapted traits shaped hominin evolution. In addition to a general relationship between climate and patterns of hominin macroevolution, the appearance of nearly every hominin autapomorphy has been linked to the expansion or contraction of particular habitats: for example, encephalised brains (Shultz and Maslin 2013; Shultz, Nelson, and Dunbar 2012), bipedalism (Potts 1996b; Senut et al. 2018), and lithic technology (Grove 2011). Here, I examine the two key hypotheses that focus not on how specific habitats may have selected for particular adaptive traits in hominins, but rather those that suggest a role for climate change as a driver of hominin cladogenesis. These hypotheses are Potts' (Potts 1996a, 1998b, 2013; Potts and Faith 2015) "Variability Selection Hypothesis" (VSH), and Vrba's (1985a, 1985b, 1993) "Turnover Pulse Hypothesis" (TPH). Both hypotheses share a focus on particular episodes of hominin cladogenesis—but here, the original hypotheses are interpreted more broadly to ask whether the pattern they predict extends to the clade as a whole. Despite a long history of paleoanthropological attention, two fundamental questions remain for the two hypotheses:

1. Is variation in the *rate* of cladogenesis, not just first appearance dates (FADs) of fossil species, predicted by climate change (as in the TPH) or climate variability (as in the VSH)?
2. At what time scale do these models operate?

The difference between FADs and the rate of cladogenesis was discussed in more detail in Chapter 9, but FADs, of course, are not speciation events, and are simply a proxy for the rate of cladogenesis. Their temporal distribution can be determined by factors quite unrelated to

climate, such as sampling bias (Maxwell et al. 2018b). The relationship between climate and rates of cladogenesis—for which FADs are used as a proxy—therefore remains open to question.

The second question, regarding the time scale at which these climatic factors are expected to affect hominin cladogenesis, has never been explicitly tested. Most work has only tested time lags of 100k years between a climate event and possible evolutionary consequences (Kimbel 1995; Vrba 1995; Grove 2012); but this might be too short a time scale to pick up associations between climate and cladogenesis given ~1-million-year estimates for the average time between divergence events in mammals (Uyeda et al. 2011).

11.1.2 Terminology

A more in-depth introduction to terminology used in this Section is offered in Chapter 8. "Speciation", here, refers to the complex and temporally extended process of lineage splitting. Because I measure tip DR across multiple phylogenies that differ in their definition of species, I refer to tip DR calculated across phylogenies simply as "splitting rate". The model, described in Chapter 8, which is put forward as a way to reconcile differences between phylogenies based on different taxonomic practices, is referred to as the "threshold model" of hominin speciation. In brief, it suggests that phylogenies based on more species-rich 'splitting' taxonomy show relationships between incipiently diverging lineages, and thus probably tend to capture relationships between taxa that can be considered representatives of an early stage of speciation. Less speciose 'lumping' taxonomies recognize more highly morphologically diverged groups, and thus probably lineages which have effectively reached later stages of speciation; and phylogenies that are based on these thus capture the cumulative outcome of the cladogenesis, extinction, and persistence of incipiently diverging lineages.

11.1.3 Variability Selection Hypothesis

Potts' (Potts 1996a, 1998b, 2013; Potts and Faith 2015) "Variability Selection Hypothesis" (VSH) suggests that major instances of hominin adaptive evolution – including key episodes of cladogenesis – were the result of increasingly greater climate variability. Such variability corresponded to "inconsistencies" (Potts 1998a, p.112) in selective environments over time, resulting in the appearance of increasingly ecologically generalized hominin species in the late Pliocene and early Pleistocene. The patterns predicted by Potts' model—that is, of generalist species emerging at times of ecological instability – are found across the hominin fossil record (Potts and Faith 2015; Roberts and Stewart 2018), and the model has held up across different approaches to measuring climatic variability (Trauth et al. 2007; Grove 2012; Lupien et al. 2020).

The original hypothesis, which suggests a specific link between the relative evolutionary success of ecological generalists and climatic instability, is extended here to a more general, ecologically non-specific model: that hominin cladogenesis should be linked to climatic instability. Potts' description of the hypothesis does, implicitly, suggest this to have been the case (e.g. Figure "Variability selection in a Mendelian population" in Potts (1996a)). In this generalized statement of the hypothesis, the expected link between climatic variability and cladogenesis is the product of habitat fragmentation (Rosenzweig 1995): the more variability, the more fragmentation, and thus a greater likelihood of allopatric speciation.

The generalized extension of Potts' model, hereafter referred to as the "VSH", is tested by asking whether larger ranges of $\delta^{18}O$ (as a proxy for relative climatic variability) in the 100k, 200k, and 500k-year periods before each measuring point correlate with higher rates of cladogenesis. The expected patterns for the VSH are presented in Table 11-1. In terms of the time scale across which the VSH is expected to affect hominin evolution, Potts expected specific adaptations to reflect long-term environmental dynamics, but he makes no explicit reference to the exact time scale of causality.

Table 11-1: Expected patterns for the VSH

		VSH
Clade-level	Timescale	Previous work has mostly assumed 100kyr
	Correlation	Positive: more variability should correlate with higher rates of cladogenesis
Genus-level	Timescale	Previous work has mostly assumed 100kyr
	Correlation	Positive: more variability should correlate with higher rates of cladogenesis

11.1.4 Turnover Pulse Hypothesis

In Vrba's (1985a, 1985b, 1993) "Turnover Pulse Hypothesis" (TPH), the initiation of all species turnover—including speciation—is ultimately the consequence of changes in the physical environment. The major way in which this hypothesis differs from the VSH is that it is non-oscillatory changes in the physical environment that are envisaged as the primary cause of speciation. In the most extreme interpretation of the TPH, speciation should not occur in times of climatic stability. Although Vrba allows a role for biotic competition in shaping selective environments, and biotic factors can thus cause speciation, she makes the case that the ultimate cause of biotic competition is changes in the physical environment (Vrba 1993).

This general statement of the hypothesis (hereafter referred to as the "general TPH") does not include specific predictions about the direction of change (i.e. that it should be cooling or warming climates that promote splitting) and rates of cladogenesis. It is tested here, in a broad interpretation of the hypothesis, by asking what effect absolute change in mean $\delta^{18}O$ values have on hominin splitting rate. In other words, do bigger changes in mean $\delta^{18}O$ correlate with higher rates of cladogenesis than smaller changes in mean $\delta^{18}O$?

For hominins specifically, the TPH has been invoked as an explanation for the relationship between marked temperature decline and an inferred event of major turnover of hominin species between 2.7 and 2.5 Ma, which coincides with the appearance of the genus *Homo* (Vrba 1985a, 1995). The hypothesis has received mixed empirical support. Vrba's evidence in its favour was based on similarities in the timing of events between the hominin and bovid fossil records (Vrba 1985a, 1995). By contrast, White (1995) did not find evidence of a major turnover of hominin species at the relevant time, although this may be due, in part, to his inclusive taxonomic approach (White 2003). Behrensmeyer et al. (1997), similarly, found no evidence of a turnover pulse in the Turkana Basin and Ethiopia between 2.8 and 2.5 Ma, but show that a pulse of significant faunal turnover occurred later, between 2.5 and 1.8 Ma. Bobe et al. (2002) suggested that the TPH operated at a smaller scale in the late Pliocene Omo mammal community: not at the scale of species, but rather at the scale of populations.

In summary, while Vrba's original model invoking the TPH at a specific period in human evolution is not well supported by the hominin fossil record, there is some evidence that significant cooling events did determine hominin cladogenesis—either at different time periods, or at different taxonomic scales. I therefore extend her original hypothesis, hereafter referred to as "TPH in hominins", to the rest of the clade and test it by asking whether increases in mean $\delta^{18}O$—a proxy for decreasing temperature (Potts 1998a)—correlate with increased rates of cladogenesis. Thus: do cooling events correlate with higher rates of cladogenesis in hominins? Foley (1994) failed to find a significant relationship between hominin speciation and climate change – but again, this was based on FADs rather than rates of cladogenesis calculated across a phylogeny.

The expected patterns for the two variants of the TPH are presented in Table 11-2.

Table 11-2: Expected patterns for the TPH

		TPH – hominins	TPH - general
Clade-level	Timescale	Previous work has mostly assumed 100kyr	Previous work has mostly assumed 100kyr
	Correlation	Positive: shifts to colder climates promote cladogenesis	Positive: greater change should correlate with higher rates of cladogenesis
Genus-level	Timescale	Previous work has mostly assumed 100kyr	Previous work has mostly assumed 100kyr
	Correlation	Positive: shifts to colder climates promote cladogenesis. Vrba expected this pattern especially in *Homo*	Positive: greater change should correlate with higher rates of cladogenesis

11.1.5 Materials and methods

The full method for this section is described in Chapter 9. In brief, phylogenetic generalised least squares (GLS) regressions including DR and the climate variable of interest were run on three phylogenies to account for different approaches to hominin taxonomy: 1) the phylogeny with the lowest AIC score published by Parins-Fukuchi et al. (2019), 2) a "high certainty" version of this phylogeny, with species Wood and Boyle (2016) have "low" confidence in treating as distinct taxa removed, and 3) a composite phylogeny based on a review of the literature on hominin cladograms at the time of writing. $\delta^{18}O$ data were sourced from Lisiecki and Raymo (2005). To test the VSH, I calculated the range of $\delta^{18}O$ (hereafter simply "$\delta^{18}O$ range") in the 100k, 200k, and 500k-year periods before each measuring point as a proxy for relative climatic variability. For the hominin-specific variant of the TPH, I calculated the difference between mean $\delta^{18}O$ in the 100k-year bin starting with the measuring point, and 1) mean $\delta^{18}O$ in the preceding 100k-year bin, 2) mean $\delta^{18}O$ in the bin starting 200k years before the measuring point, and 3) mean $\delta^{18}O$ in the bin starting 500k years before the measuring point. For the general statement of the VSH, I used the absolute value of the previously calculated change in mean $\delta^{18}O$ values. Figures 11-1, 11-2, and 11-3 show the least and most speciose phylogenies ("high certainty" and composite, respectively) and climate data for the three hypotheses across the three timescales.

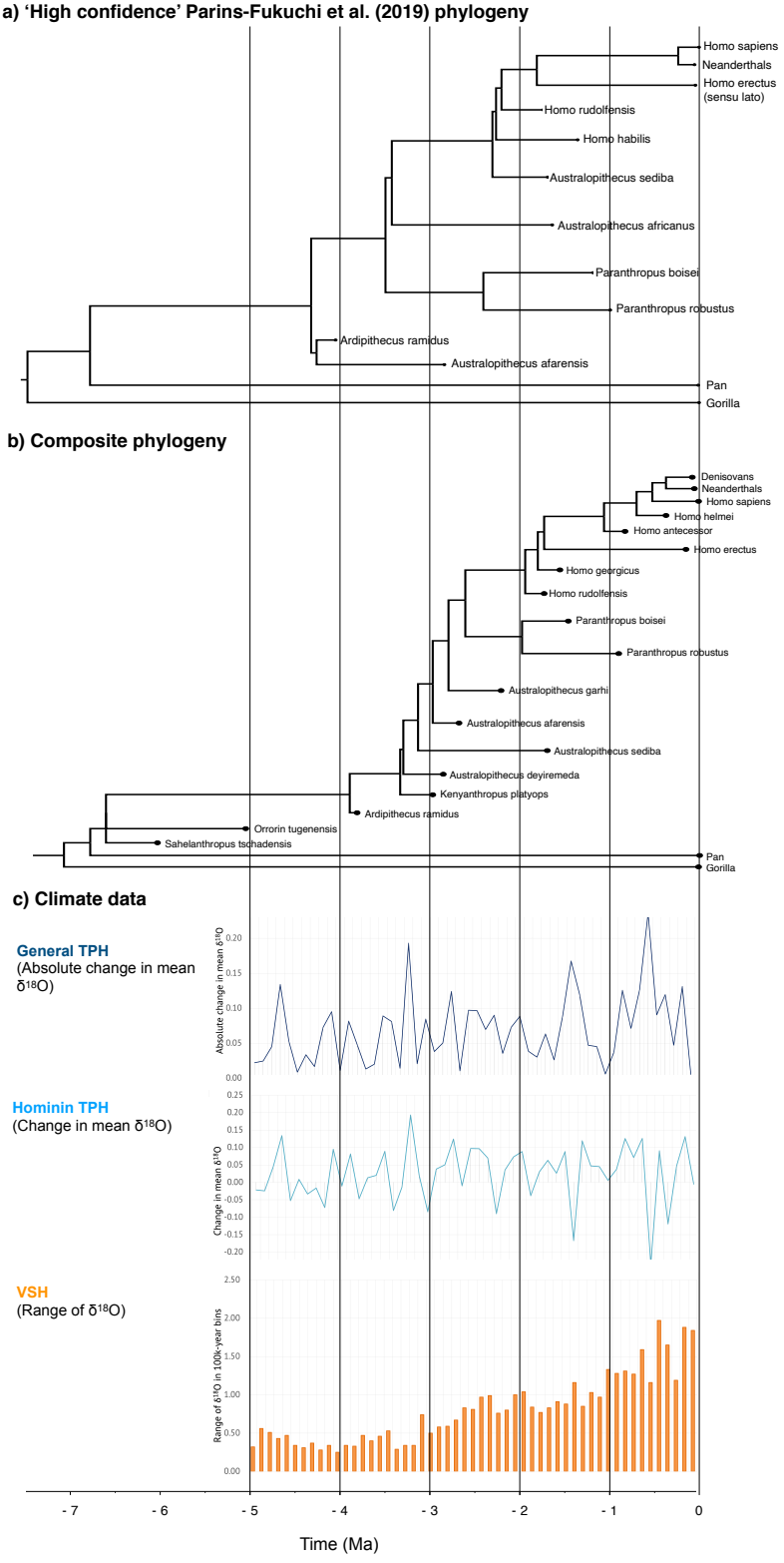


Figure 11-1: Phylogenies and climate data for 100k-year intervals

a) shows the least speciose 'high confidence' Parins phylogeny used in this chapter; b) shows the most speciose composite phylogeny used in this chapter; c) shows $\delta^{18}O$ data across 100k-year intervals for each of the three hypotheses tested in this chapter.

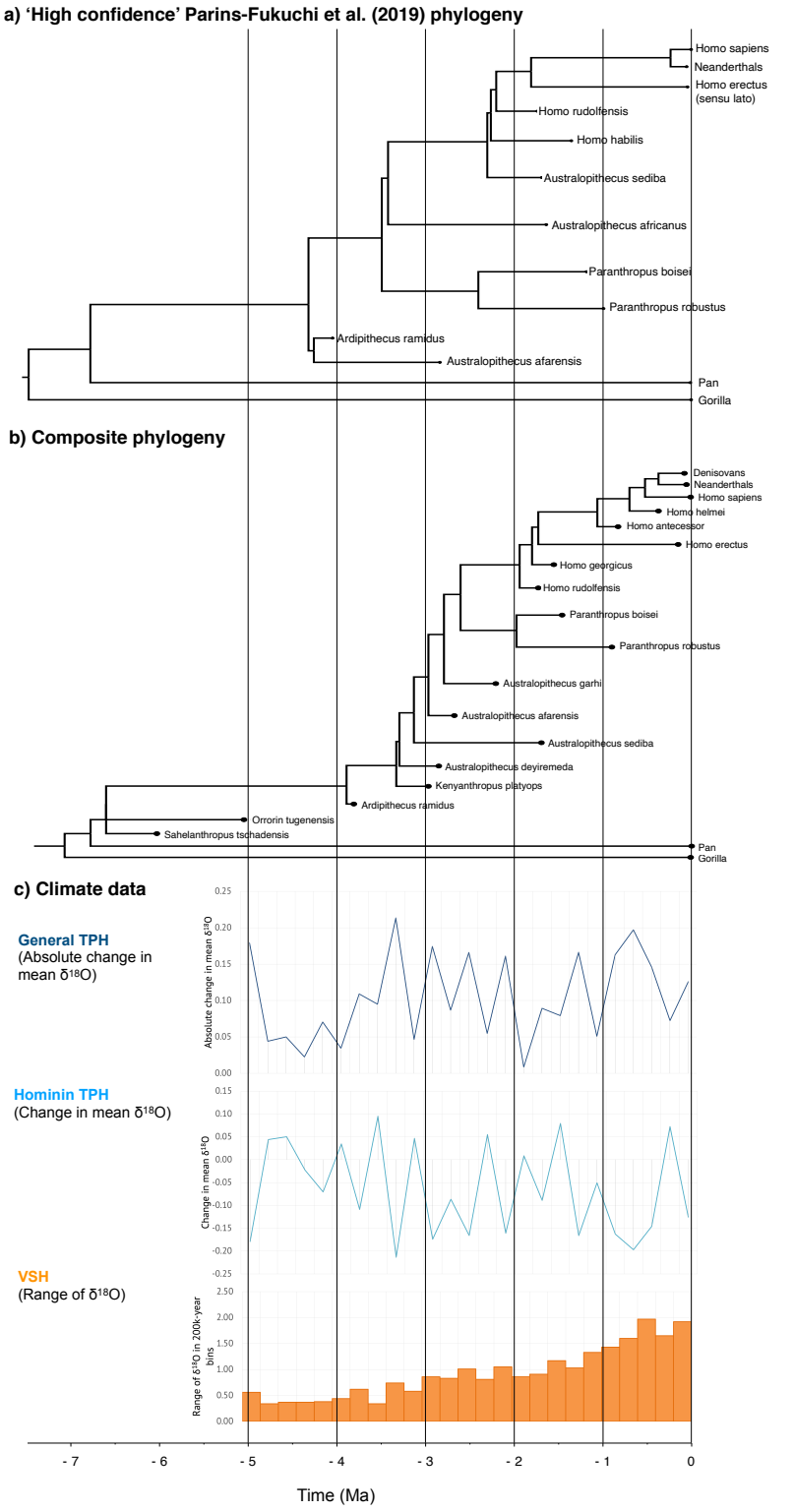


Figure 11-2: Phylogenies and climate data for 200k-year intervals

a) shows the least speciose 'high confidence' Parins phylogeny used in this chapter; b) shows the most speciose composite phylogeny used in this chapter; c) shows $\delta^{18}O$ data across 200k-year intervals for each of the three hypotheses tested in this chapter.

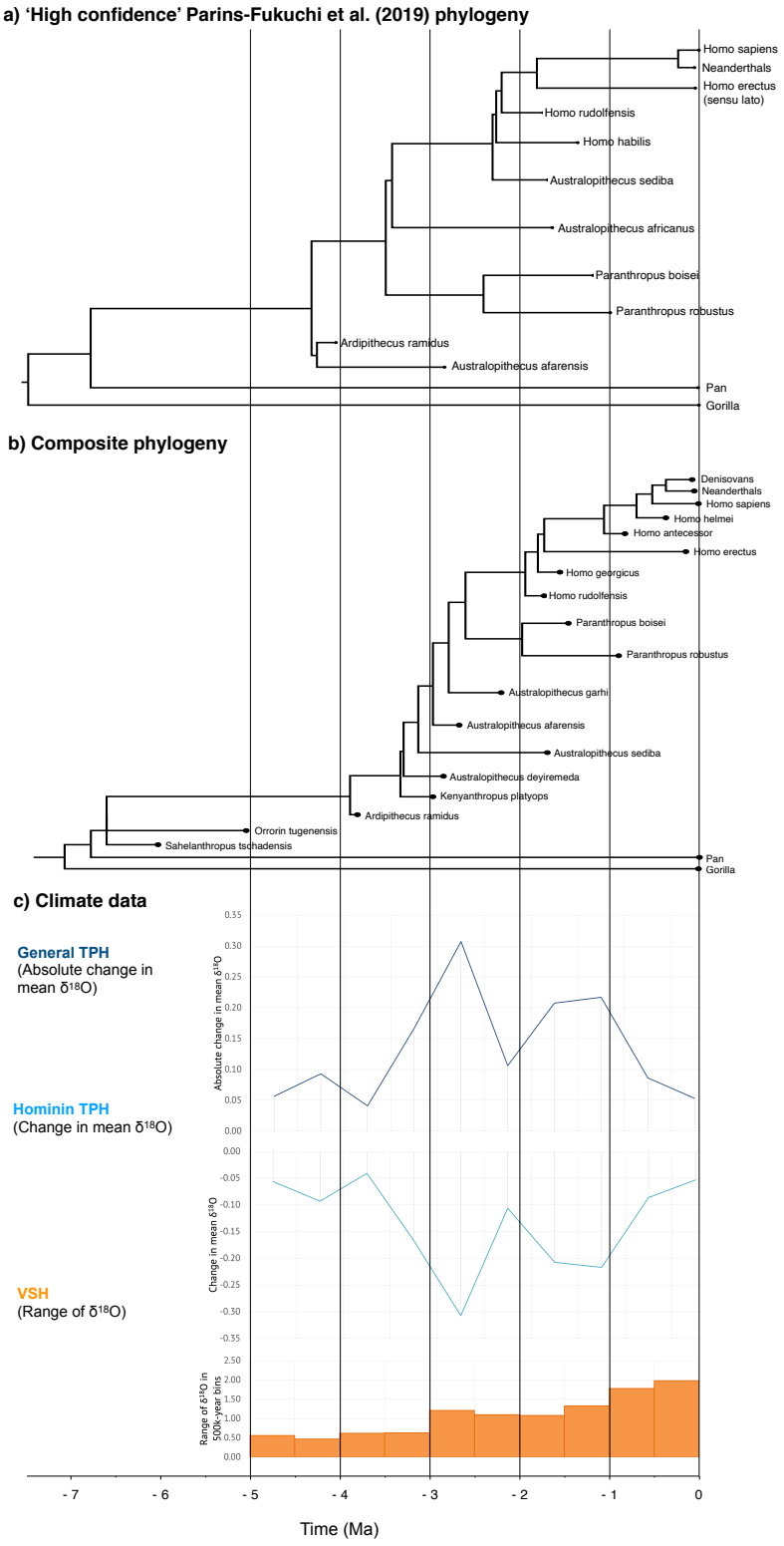


Figure 11-3: Phylogenies and climate data for 500k-year intervals

a) shows the least speciose 'high confidence' Parins phylogeny used in this chapter; b) shows the most speciose composite phylogeny used in this chapter; c) shows $\delta^{18}O$ data across 500k-year intervals for each of the three hypotheses tested in this chapter.

11.2 Results

11.2.1 Parins-Fukuchi phylogenies

For the whole phylogeny, full model outputs, as well as Cox & Snell's (1989) pseudo-R^2, AIC score, and likelihood-ratio test p-values are reported in Appendix 4 Tables 1-6. The results are summarized in Table 11-3.

Table 11-3: Summary of results from phylogenetic GLS across the Parins-Fukuchi phylogeny

		VSH	TPH – hominins	TPH - general
Clade-level	Timescale	100k	*n.s.*	*n.s.*
	Correlation	Negative	*n.s.*	*n.s.*
Genus-level	Timescale	100k	100k	*(200k/500k)*[1]
	Correlation	Variable	Variable	Variable

[1]Time scale across which climate operated to influence cladogenesis ambiguous

11.2.1.1 VSH

At the level of the whole clade, $\delta^{18}O$ range across the 100k years before each measuring point (hereafter "bmp") best predicts hominin tip DR. The slope term in the 100k-year bmp model is shown in Figure 11-4: in contrast to the expected pattern, the relationship between $\delta^{18}O$ range and hominin cladogenesis is negative, meaning DR decreases as $\delta^{18}O$ range increases.

When the relationship between DR and $\delta^{18}O$ range was allowed to vary by genus, tip DR was again best predicted by $\delta^{18}O$ range across the 100k years bmp. The negative relationship between $\delta^{18}O$ range and DR found for the whole clade is also found within each genus, but there is considerable uncertainty around parameter estimates for *Australopithecus* and *Paranthropus*, for both of which the 95% confidence interval (CI) overlaps with 0 (see Figure 11-4).

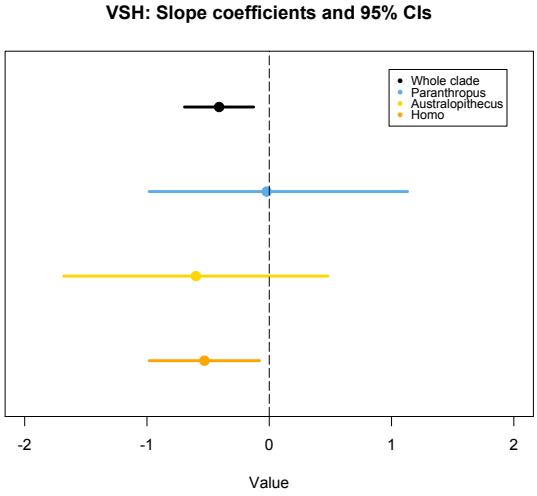


Figure 11-4: Variability Selection Hypothesis: slope coefficients and 95% CIs on the original Parins-Fukuchi et al. phylogeny

Figure shows slope term coefficient and 95% confidence intervals around the parameter estimate for 1) the 100 bmp model for the clade as a whole (in black), and 2) the 100 bmp model in which slope was allowed to vary by genus (in colour).

11.2.1.2 Hominin TPH

At the level of the whole clade, change in mean $\delta^{18}O$ values did not significantly predict hominin DR across any time range.

When the relationship between mean $\delta^{18}O$ change and DR was allowed to vary by genus, the change from mean $\delta^{18}O$ in the 100-200k year bin bmp to mean $\delta^{18}O$ in the 0-100k year bin bmp best predicts DR. Within each genus, then, the TPH operates on a similarly short timescale as the VSH. The slope terms for each genus in this model are shown in Figure 11-5. The direction of the relationship between change in mean $\delta^{18}O$ and DR varied by genus (see Figure 11-5): in *Homo*, the relationship is positive, with shifts from lower mean $\delta^{18}O$ to higher mean $\delta^{18}O$ increasing speciation rate. The 95% CI for the slope term in *Paranthropus* is wide, overlaps with that of *Homo*, and overlaps with 0. This uncertainty is most probably the result of low sample size, or simply evidence of climate change having no effect on *Paranthropus* DR. *Australopithecus*, however, has a significantly different relationship between mean $\delta^{18}O$ change and DR compared to *Homo.* In *Australopithecus*, shifts from higher mean $\delta^{18}O$ values to lower mean $\delta^{18}O$ values increases DR: thus, splitting rate is higher when climate shifts to hotter temperatures.

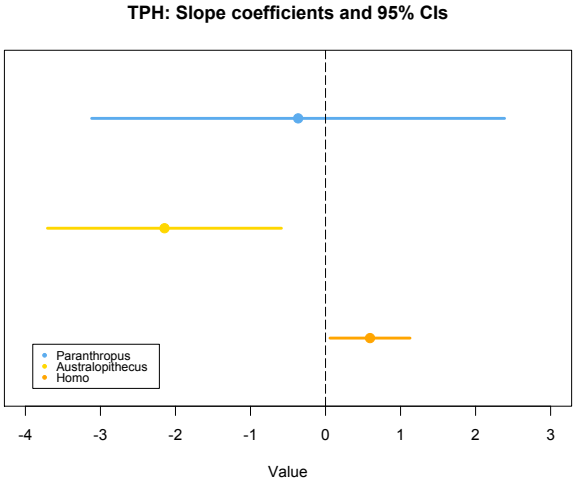


Figure 11-5: Hominin Turnover Pulse Hypothesis: slope coefficients and 95% CIs on the original Parins-Fukuchi et al. phylogeny

Figure shows slope term coefficient and 95% confidence intervals around the parameter estimate for the 100k year bmp model in which slope was allowed to vary by genus. There is considerable uncertainty around the slope parameter estimate for *Paranthropus*, while *Homo* and *Australopithecus* differ significantly: in *Homo*, shifts to colder temperatures promote splitting, while the opposite pattern is true for *Australopithecus*.

11.2.1.3 General TPH

At the level of the whole clade, absolute change in mean $\delta^{18}O$ did not significantly predict hominin DR at any timescale. The time scale across which climate operated to influence genus-specific cladogenesis was ambiguous: the model including change from the 500-600k year bmp bin to the 0-100k year bmp bin has a higher pseudo-R^2 (of 0.35), but higher AIC (-17.6), while the model including change from the 200-300k year bmp bin to the 0-100k year bmp bin has a lower pseudo-R^2 (of 0.32), but lower AIC (-18.9). However, the results, at least in terms of the direction of the relationship between DR and change in mean $\delta^{18}O$ within each genus, are the same across each model (see Figure 11-6). The direction of the relationship between change in mean $\delta^{18}O$ and DR varied by genus (see Figure 11-6): in *Homo*, a greater difference between mean $\delta^{18}O$ values increases speciation rate. Again, there is considerable uncertainty around the *Paranthropus* slope parameter estimate and its slope is not significantly different to that of *Homo* in the models. *Australopithecus*, however, shows the generally opposite pattern to that found in *Homo* – but its 95% CI does overlap with 0. In *Australopithecus*, there is some evidence that a greater difference between mean $\delta^{18}O$ values slows speciation rate down.

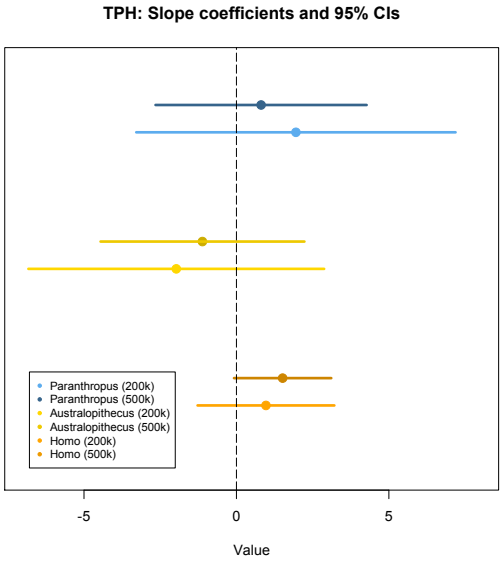


Figure 11-6: General Turnover Pulse Hypothesis: slope coefficients and 95% CIs on the original Parins-Fukuchi et al. phylogeny

Figure shows slope term coefficient and 95% confidence intervals around the slope parameter estimate for two models: one including change in mean $\delta^{18}O$ from the 200-300k year bmp bin to the 0-100k year bmp bin ("200k"), and one including change in mean $\delta^{18}O$ from the 500-600k year bmp bin to the 0-100k year bmp bin ("500k"). There is considerable uncertainty around the slope parameter estimates for all three genera. Uncertainty notwithstanding, *Homo* and *Australopithecus* differ in the general pattern they show: in *Homo*, greater changes in temperature promote splitting, while the opposite pattern is true for *Australopithecus*.

11.2.1.4 Results from the "high certainty" Parins-Fukuchi phylogeny

For the high certainty phylogeny, full model outputs, as well as Cox & Snell's (1989) pseudo-R^2, AIC scores, and likelihood-ratio test *p*-values are reported in Appendix 4 Tables 7-12. The results are summarized in Table 11-4.

Table 11-4: Summary of results from phylogenetic GLS across the "high certainty" Parins-Fukuchi phylogeny

		VSH	TPH – hominins	TPH - general
Clade-level	Timescale	100k	500k	*n.s.*
	Correlation	Negative	Negative	*n.s.*
Genus-level	Timescale	*(100k/500k)*[1]	100k	500k
	Correlation	Variable	Variable	Variable

[1]Time scale across which climate operated to influence cladogenesis ambiguous

The removal of Boyle & Wood's (2016) "low certainty" species did not change the direction of the relationship between DR and any variable at the level of genera, so no plots were made for these models. Across this phylogeny, the time scale across which climate variability operated to influence DR was ambiguous, but the direction of inferred relationships was the same across both time scales. On this phylogeny, the time scale across which the magnitude

of changes in temperature operates to influence DR—in other words, the general TPH—is more certain than across the original Parins-Fukuchi phylogeny: 500k years.

The major difference between the original Parins-Fukuchi phylogeny and the "high certainty" phylogeny is that changes in temperature correlate with DR across the whole clade, when there was no significant relationship between the two on the original phylogeny. Across the clade as a whole, DR increases when mean temperature increases from the 500-600 year bmp bin to the 0-100 year bmp bin (slope term coefficient: -0.629 (95% CI: -1.076 — -0.182), $p<0.01$).

11.2.2 Composite phylogeny

For the composite phylogeny, full model outputs, as well as Cox & Snell's (1989) pseudo-R^2, AIC scores, and likelihood-ratio test *p*-values are reported in Appendix 4 Tables 13-18. The results are summarized in Table 11-5.

Table 11-5: Summary of results from phylogenetic GLS across the composite phylogeny

		VSH	TPH – hominins	TPH - general
Clade-level	Timescale	500k	*n.s*	*n.s*
	Correlation	Positive	*n.s.*	*n.s.*
Genus-level	Timescale	*(100k/500k)*[1]	*(100k/500k)* [1]	*(200k/500k)*[1]
	Correlation	Variable[2]	Variable	Positive[2]

[1]Time scale across which climate operated to influence cladogenesis ambiguous
[2]Models were significant overall but no slope terms were significant

11.2.2.1 VSH

At the level of the whole clade, $\delta^{18}O$ range across the 500k years bmp best predicts hominin tip DR: the data thus suggest that, across this phylogeny, the effect of climatic variability operates at relatively long timescales to influence hominin cladogenesis. The slope term coefficient estimate for the VSH model at the 500k-year scale is shown in Figure 11-7: it suggests that the relationship between $\delta^{18}O$ range and hominin cladogenesis is positive, with increasing DR as $\delta^{18}O$ range increases.

The time scale across which climate variability operated to influence genus-specific cladogenesis was ambiguous: the model including variability across 500k years bmp has a higher pseudo-R^2 (of 0.49), but higher AIC (-10.37), while the model including variability across 100k years bmp has a lower pseudo-R^2 (of 0.48), but lower AIC (-10.71). However, the results, at least in terms of the direction of the relationship between DR and $\delta^{18}O$ range within each genus, are the same across each model (see Figure 11-7). Both models suggest

variable relationships between $\delta^{18}O$ range and DR across genera, with no relationship in *Homo*, a negative relationship in *Paranthropus* (although its CI overlaps with 0), and a positive relationship in *Australopithecus (*although its CI, too, overlaps with 0) (see Figure 11-7). There is sufficient uncertainty around parameter estimates that slope coefficients were non-significant in both models : thus, while the model was significant overall, suggesting a better fit than a null model, the data do not allow confident conclusions to be made regarding the exact direction of the relationship within the three genera.

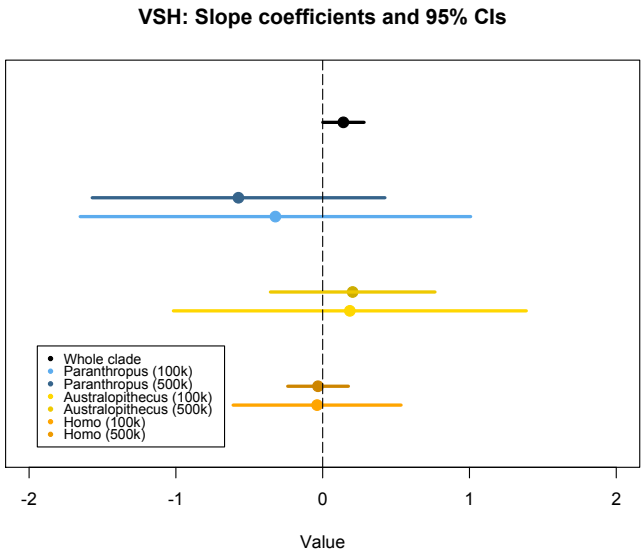


Figure 11-7: Variability Selection Hypothesis: slope coefficients and 95% CIs on the composite phylogeny

Figure shows slope term coefficient and 95% confidence intervals around the slope parameter estimate for two models: one including variability across 100k years bmp ("100k"), and one including variability across 500k years bmp (500k). There is considerable uncertainty around the slope parameter estimates for all three genera, and 95% CIs overlap with 0 in all cases. In *Homo*, there is no relationship between climate variability and DR, while it positively correlates with DR in *Australopithecus*, and negatively correlates with DR in *Paranthropus*.

11.2.2.2 Hominin TPH

At the level of the whole clade, change in mean $\delta^{18}O$ values did not predict hominin DR across any time range.

The time scale across which changes in temperature operated to influence genus-specific cladogenesis was ambiguous: the model including change from the 500-600k year bmp bin to the 0-100k year bmp bin has a higher pseudo-R^2 (of 0.55), but higher AIC (-17.90), while the model including change from the 100-200k year bmp bin to the 0-100k year bmp bin has a lower pseudo-R^2 (of 0.53), but lower AIC (-20.29). However, the results, at least in terms of

the direction of the relationship between DR and change in mean $\delta^{18}O$ within each genus, are the same across each model (see Figure 11-8). The direction of the relationship between change in mean $\delta^{18}O$ and DR was broadly positive in *Paranthropus* and *Australopithecus* (see Figure 11-8) – that is, shifts from lower mean $\delta^{18}O$ to higher mean $\delta^{18}O$ increase speciation rate – but 95% CIs overlapped with 0 in all cases. In *Homo*, there is no relationship between change in mean $\delta^{18}O$ and DR.

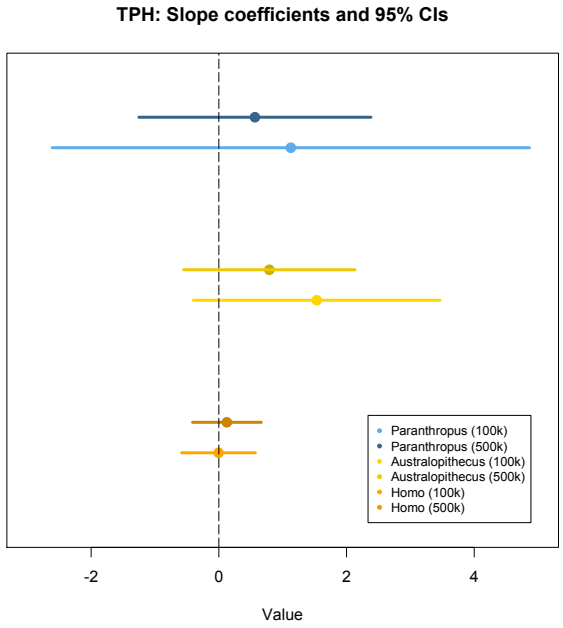


Figure 11-8: Hominin Turnover Pulse Hypothesis: slope coefficients and 95% CIs on the composite phylogeny

Figure shows slope term coefficient and 95% confidence intervals around the slope parameter estimate for two models: one including change in mean $\delta^{18}O$ from the 100-200k year bmp bin to the 0-100k year bmp bin ("100k"), and one including change in mean $\delta^{18}O$ from the 500-600k year bmp bin to the 0-100k year bmp bin ("500k"). There is considerable uncertainty around the slope parameter estimates for all three genera. The direction of the relationship between change in mean $\delta^{18}O$ and DR was broadly positive in *Paranthropus* and *Australopithecus* – that is, shifts from lower mean $\delta^{18}O$ to higher mean $\delta^{18}O$ increase speciation rate, while in *Homo*, there is no relationship between change in mean $\delta^{18}O$ and DR.

11.2.2.3 General TPH

At the level of the whole clade, absolute change in mean $\delta^{18}O$ did not correlate significantly with hominin DR at any timescale.

The time scale across which changing climate operated to influence genus-specific cladogenesis was ambiguous: the model including change from the 500-600k year bmp bin to the 0-100k year bmp bin has a higher pseudo-R^2 (of 0.54), but higher AIC (-18.76), while the

model including change from the 200-300k year bmp bin to the 0-100k year bmp bin has a lower pseudo-R^2 (of 0.50), but lower AIC (-19.64). However, the results, at least in terms of the direction of the relationship between DR and change in mean $\delta^{18}O$ within each genus, are the same across each model (see Figure 11-9). The direction of the relationship between change in mean $\delta^{18}O$ and DR was broadly positive in each of the three genera (see in Figure 11-9) – that is, a greater difference between mean $\delta^{18}O$ values increases speciation rate – but again, there is considerable uncertainty around parameter estimates.

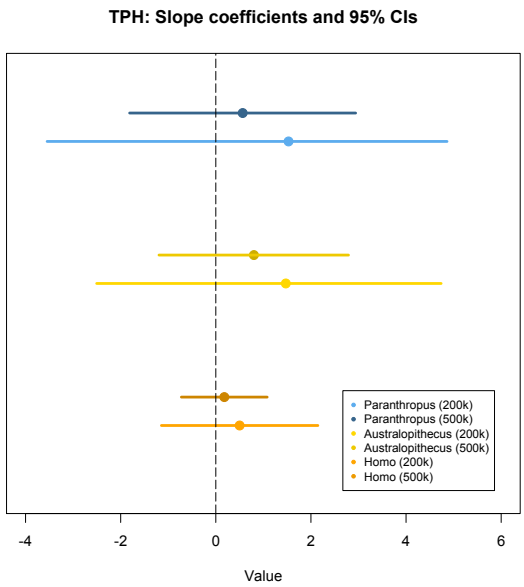


Figure 11-9: General Turnover Pulse Hypothesis: slope coefficients and 95% CIs on the composite phylogeny

Figure shows slope term coefficient and 95% confidence intervals around the slope parameter estimate for two models: one including change in mean $\delta^{18}O$ from the 200-300k year bmp bin to the 0-100k year bmp bin ("200k"), and one including change in mean $\delta^{18}O$ from the 500-600k year bmp bin to the 0-100k year bmp bin ("500k"). There is considerable uncertainty around the slope parameter estimates for all three genera. The direction of the relationship between change in mean $\delta^{18}O$ and DR was broadly positive in all three genera, meaning greater shifts in mean $\delta^{18}O$ increase speciation rate.

11.3 Discussion

The most obvious signal in these results is the lack of a consistent relationship between climate and variation in the rate of hominin cladogenesis. Climate and hominin cladogenesis are related in more complex, diffuse, and potentially nonlinear ways than previous work has assumed.

Regarding the relationship between intraspecific processes and speciation, the results suggest that, across hominins as a whole, the results suggest longer-term persistence of incipient

species necessary for these to accrue sufficient morphological divergence from their parent taxa tended to occur in more stable climates. Thus, a previously unknown way in which climate determined hominin speciation is by mediating the link between intraspecific demographic processes and speciation.

This is the general pattern: but there are some interesting indications that there is a difference between *Homo* and *Australopithecus* in the link between intraspecific population-level processes and speciation. The results suggest that climate-mediated incipient lineage persistence was a less important link between the splitting of smaller groups within larger hypodigms and the splitting of these larger hypodigms in *Homo*. To arrive at this conclusion, I first examine the results for each hypothesis separately before discussing them together.

11.3.1 Variability Selection Hypothesis

The expected pattern in the generalized extension of Potts' model was a positive correlation between $\delta^{18}O$ range and the rate of cladogenesis, resulting from habitat fragmentation and consequent allopatric speciation. The data support the VSH in the sense that models including climate variability were significant overall, but the general relationship between climate variability and cladogenesis is rather diffuse, with specific terms within the models often non-significant. When significant, the relationship between variability and cladogenesis is often in the opposite direction to that expected. The time scale across which the VSH operates was, in many cases, ambiguous.

Regardless of the specific direction of the relationship, all models were significant. Overall, then, $\delta^{18}O$ range predicts the rate of hominin cladogenesis at both 1) the scale of the clade as a whole *and* 2) at the level of genera, across all three phylogenies. A summary of results for the VSH across the three phylogenies is presented in
Table 11-6.

Table 11-6: Summary of results from phylogenetic GLS: VSH

Threshold model:		← More 'split'		More 'lumped' →
		Composite tree	**Parins-Fukuchi et al**	**"High confidence" Parins-Fukuchi et al**
Clade-level	Timescale	500k	100k	100k
	Correlation	Positive	Negative	Negative
Genus-level	Timescale	*(100k/500k)*[1]	100k	*(100k/500k)*[1]
	Correlation	Variable[2]	Variable	Variable[2]

[1]Time scale across which climate variability operated to influence cladogenesis ambiguous
[2]Models were significant overall, but no slope terms were significant

Across the Parins-Fukuchi phylogeny, first, $\delta^{18}O$ range across the 100k years bmp best predicts hominin tip DR at both the clade and genus level. These data thus suggest climatic variability influences hominin cladogenesis at relatively short timescales. In contrast to the expected pattern, the way in which greater degrees of variability influence cladogenesis is by tempering it: across the clade as a whole, there is a negative relationship between $\delta^{18}O$ range and the rate of cladogenesis. At the level of genera, in both *Homo* and *Australopithecus*, the inferred relationship is negative; in *Paranthropus*, the regression slope is close to 0, and there is a large amount of uncertainty around this slope. The general pattern across hominin genera, then, is similar to that seen at the level of the clade as a whole.

There are a number of potential reasons for the results' divergence from the expected pattern. The first of these is that $\delta^{18}O$ range might not accurately capture the climatic variability the model invokes as a potential cause of cladogenesis. $\delta^{18}O$ is a proxy for ocean ice volume and temperature, and these might decoupled from terrestrial conditions (DeMenocal, Ruddiman, and Pokras 1993); future work will benefit from a multivariate approach that includes other measures of climate, like Aeolian dust percentage (DeMenocal 1995). The range of $\delta^{18}O$, moreover, is a simple proxy for climatic variability: future directions might include further measures derived from $\delta^{18}O$ data, such as the eccentricity, obliquity, and precession components of climate that interact to create fluctuations in insolation (Grove 2012). Further, the changes in terrestrial habitat in response to the changes in climate indicated by $\delta^{18}O$ can differ between habitats; and, since this analysis is conducted at the level of the whole hominin clade, which comprises multiple adaptive grades (Foley 2016) and an intercontinental distribution, signals of habitat fragmentation leading to cladogenesis are possibly obscured at this scale. That the genus-level analyses—insofar as these might capture the relationship between climatic variability and cladogenesis within more specific ecologies (Collard and Wood 2015)—across this phylogeny returned the same broadly negative relationship, however, suggests this final point might not fully explain the disparity between expected and observed patterns.

Methodological limitations aside, the pattern potentially points to an ecological scenario. Potts' (1996a) original model, of course, suggested a relationship between climate variability and selection for ecological generalism in *Homo*. It could be the case that generalists and specialists respond differently to climatic instability and resulting habitat fragmentation (Foley 1994; Wells and Stock 2007; Dennis et al. 2011; Vamosi et al. 2014; Day, Hua, and Bromham 2016), with generalists less likely to speciate in response to habitat change. This fits the "buffering" model proposed for the genus *Homo*, in which phenotypic plasticity and

cultural behaviour buffered the genome from selection as ranges expanded (Wells and Stock 2007). The negative relationship between climatic variability and rates of cladogenesis reported here for *Homo* might therefore be the macroevolutionary outcome of Potts' original hypothesis.

However, exactly how geographical range affects generalist versus specialist speciation varies across lineages (Day, Hua, and Bromham 2016) and remains an open question—the answer to which probably lies partly in models acknowledging that a species might be a "specialist" along one axis and a "generalist" along another (Vamosi et al. 2014). If *Australopithecus* is reconstructed as comprising more ecologically specialized taxa than *Homo*—evidence for this comes in the form of, for example, *Homo erectus'* eurytopic distribution relative to that of most australopith taxa (Rightmire 2001)—the results presented here suggest that hominin specialists *and* generalists responded in the same way to climatic variability. That is: in both *Australopithecus* and *Homo,* the more climate varied, the lower the rates of cladogenesis.

Results across the "high confidence" Parins-Fukuchi phylogeny were broadly similar to those across the original Parins-Fukuchi phylogeny, with the exception that the time scale across which the VSH potentially operates was ambiguous. Although both the model across 100k years bmp and the model across 500k bmp years were significant overall, no slope terms were significant in either—suggesting a diffuse effect of climatic variability on cladogenesis within genera at best, and certainly not one with a clear direction nor time scale.

Results across the most speciose composite tree show a very different pattern to those across both Parins-Fukuchi phylogenies. Here, for the clade as a whole, $\delta^{18}O$ range across the 500k year bmp best explains variation in the rate of cladogenesis. Thus, the results across the composite tree suggest the VSH operates across longer timescales than previous work (e.g. Foley 1994; Grove 2012) has assumed. In other words, hominin cladogenesis across this phylogeny is best explained by climate variability across relatively long time scales. A major consideration, in addition to the methodological limitations described above, is the possibility that $\delta^{18}O$ range over longer time scales might be a less accurate measure of climatic variability than short time scales; and this sets a clear direction for future work. As suggested above, the analyses presented here should be repeated using further climate proxies derived from $\delta^{18}O$ records (e.g.(Grove 2012)) and other paleoenvironmental data (e.g. (DeMenocal 1995)).

Methodological considerations notwithstanding, Potts (1996a, 1998a) suggested it was long-term, rather than short-term, climatic variability that selected for generalist traits: so the signal

of a longer-term relationship between climate and cladogenesis is perhaps not surprising. The positive direction of the relationship across the clade as a whole, too, is unsurprising in light of previous work: for example, fossil and archaeological evidence points towards a concentration of evolutionary events during intervals of greater climatic instability in the Turkana basin (Lupien et al. 2018, 2020).

When it comes to the genus level, the time scale across which the VSH potentially operates was ambiguous. The 100k and 500k years bmp models were significant overall, but no slope terms were significant in either—and just like the results across the "high confidence" Parins-Fukuchi phylogeny, this probably suggests at a diffuse effect of climatic variability on cladogenesis within genera.

One final point is deserving of discussion: in both the 100k and 500k year bmp models, the slope terms for *Homo* were extremely close to 0—that is, $\delta^{18}O$ range does not correlate, at all, with variation in the rate of *Homo* cladogenesis. Taken together with the intrinsically higher rate of cladogenesis in *Homo* across the composite tree reported in Chapter 9, these results point towards a decoupling of the relationship between climatic variability and cladogenesis in *Homo*: that is, at this taxonomic level, the rate of cladogenesis in *Homo* was intrinsically higher than that of *Australopithecus*, and variation in *Homo* cladogenetic rate was independent of climatic variability. The case must be made, however, that even if *variation* in *Homo* cladogenesis is not explained by $\delta^{18}O$ range—which is what the models reported here test—the higher rate of cladogenesis seen across the composite phylogeny in *Homo* overall could be the consequence of greater average climatic variability in the Pleistocene. In other words, *Homo* probably experienced higher rates of incipient lineage production and likely turnover than its predecessors, in part because these lineages evolved in the context of greater climatic variability than did its predecessors. The relationship between climate variability and variation in rates of cladogenesis need not be linear, implying that after a critical level of variability is reached, a high level of turnover of incipient lineages occurs regardless of further increases in climate variability. Indeed, the Pleistocene is characterised by comparatively greater climatic oscillations than the Pliocene (Potts 1998a; Lisiecki and Raymo 2005).

How, then, did climate variability-determined smaller-scale turnover within hominin genera (captured on the composite phylogeny) scale up to larger-scale patterns of cladogenesis (captured on the Parins-Fukuchi trees)? It is difficult to comment with much certainty about the implied time scales across which the VSH operates in the context of the threshold model. It is probable that the proxy for climate variability used is a poorer estimate of variability over

longer time scales than shorter time scales, so the signal of a longer-term effect can be inaccurate. Where time scales were ambiguous, however, the implied directions—even though there is uncertainty around the parameter estimates—of the effect of climate variability on cladogenesis were the same, so these can be discussed with more confidence. The clearest result is that, across the hominin lineage as a whole, cladogenesis of incipient lineages (represented on the composite phylogeny) is positively related to $\delta^{18}O$ range. The implication of the results in the threshold model is that increased climatic fluctuation promoted the formation of incipient lineages—probably through the fragmentation of habitats and consequent splitting of populations. In this way, these results mirror those from Chapter 5, in which it was shown that extant mammalian subspecies formation is linked to habitat fragmentation.

By contrast, the formation of more differentiated groups (captured on the Parins-Fukuchi et al. phylogenies) is negatively correlated with climatic variability. This scenario is illustrated in Figure 11-10. In brief, splitting of incipient lineages tends to occur when there is high climatic variability, but these lineages are not recognized as separate species in more inclusive taxonomies. The required degree of morphological differentiation between incipient lineages for them to be considered separate taxa on ‘lumping’ phylogenies is only attained after some time of turnover of incipient lineages. This point is reached when incipient lineages have some time to persist and fully develop their own evolutionary trajectories, of which there is a higher chance when climate is relatively more stable. The formation of more morphologically differentiated lineages is negatively related to climate variability.

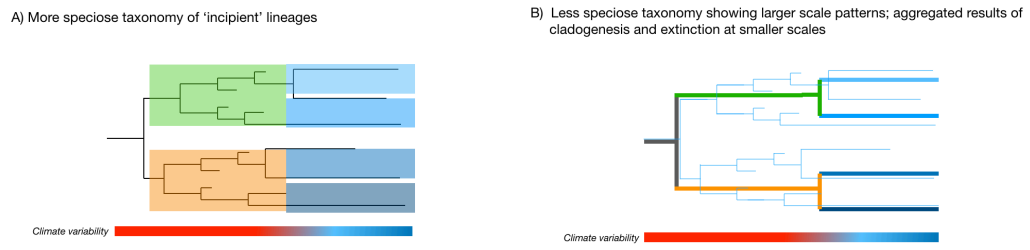


Figure 11-10: VSH results in the context of the threshold model

A) Shows a phylogeny based on a less inclusive 'splitting' taxonomy in black, imposed on hypodigms of a 'lumped' taxonomy. Lineage splitting rate on this phylogeny is higher when climate is more variable (in warmer colours) than when it is more stable (in cooler colours). Lineage splitting in the context of high climate variability on this phylogeny occurs 'within' the hypodigm of 'lumped' species. Sufficient levels of morphological differentiation for these lineages to be registered as separate species on the lumped phylogeny are achieved later, shown by the colour block changes on A) and the splitting events on the corresponding phylogeny in B). The attainment of such morphological disparity might be related to the time an incipient lineage persists as an independent lineage: and, given the positive relationship between incipient lineages' cladogenesis and climate variability, this might usually only occur when climate is relatively more stable. Thus, the formation of more differentiated lineages, as captured on the phylogeny in B), is negatively related to climate variability.

There are differences between *Australopithecus* and *Homo* in the regulation of incipient lineage splitting by climate variability. The evidence that *Paranthropus* differs from either genus is weaker, as there is much uncertainty around its slope parameters (probably due to low sample sizes). This difference is that, in *Homo*, $\delta^{18}O$ range does not correlate with variation in the rate of cladogenesis of incipient lineages, while it correlates positively with that in *Australopithecus*. It is possible that the relationship between climate variability and variation in rates of cladogenesis was not linear, meaning that a sufficient level of variability was reached in *Homo* to ensure a relatively high turnover of incipient lineages regardless of variation in $\delta^{18}O$ range. This model is illustrated in Figure 11-11.

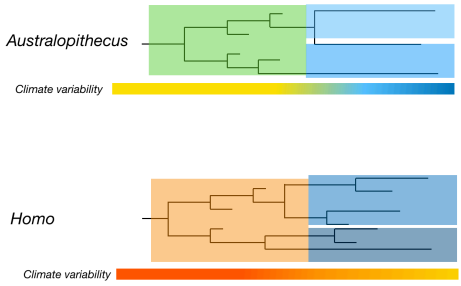


Figure 11-11: Differences in the operation of the VSH between *Australopithecus* and *Homo*

Figure shows phylogenies based on a less inclusive 'splitting' taxonomy in black, imposed on hypodigms of a 'lumped' taxonomy. Climate variability is indicated on the bar below each phylogeny: warmer colours indicate higher levels of variability; cooler colours indicate lower levels of variability. In *Australopithecus*, early lineage splitting is positively related to climate variability. In *Homo*, however, average climate variability is sufficiently high to ensure a high rate of incipient lineage cladogenesis regardless of the level of variability of climate: and, although the relatively higher rate of cladogenesis at this level is thus potentially the product of higher levels of average climate variability, *variation* in cladogenesis at this taxonomic scale is decoupled from variation in climate.

However, despite some clear trends, there is much uncertainty around many parameter estimates in the models, implying a considerable degree of variation around these trends. Taken together, the results across all three trees point to a complex, diffuse, and potentially nonlinear relationship between climatic variability and rates of cladogenesis in hominins.

11.3.2 Turnover Pulse Hypothesis

11.3.2.1 General statement of the TPH

In the generalized version of the TPH tested here, relatively large changes in mean $\delta^{18}O$ should be accompanied by increased rates of cladogenesis, and vice versa. Indeed, in the most extreme interpretation of the TPH, cladogenesis should not occur when the physical environment does not change. Overall, the data presented here indicate little support for this model—the only case where changes in mean $\delta^{18}O$ correlate positively with cladogenesis is found at the level of genera on the composite tree. The clearest signal, found across all three trees, is that across the hominin clade as a whole changes in mean $\delta^{18}O$ do not correlate with cladogenesis. Results for the general TPH are summarized in Table 11-7.

Table 11-7: Summary of results from phylogenetic GLS: general TPH

Threshold model		← More 'split'		More 'lumped' →
		Composite tree	**Parins-Fukuchi et al**	**"High confidence" Parins-Fukuchi et al**
Clade-level	Timescale	*n.s*	*n.s.*	*n.s.*
	Correlation	*n.s.*	*n.s.*	*n.s.*
Genus-level	Timescale	*(200k/500k)*[1]	*(200k/500k)*[1]	500k
	Correlation	Positive[2]	Variable	Variable

[1]Time scale across which climate change operated to influence cladogenesis ambiguous
[2]Models were significant overall, but no slope terms were significant

In line with previous work, which has called into question the presence of a specific "pulsed" turnover of hominin species between 2.8 and 2.5 Ma (White 1995; Behrensmeyer et al. 1997; Bobe, Behrensmeyer, and Chapman 2002), I do not find evidence for a general relationship between change in mean $\delta^{18}O$ and hominin cladogenesis across any time span or any of the three phylogenies. In other words: these data suggest cladogenesis occurred independently of change in mean $\delta^{18}O$ across the history of the hominin clade. Clearly, this does not imply climate and hominin cladogenesis were unrelated—indeed, the results discussed above suggest a link between climatic variability and cladogenesis, even if the link itself was diffuse and variable across taxa. The major point here, though, is that these results suggest hominin evolutionary history was determined more by climatic variability than changes in average climate. This result is consistent with Foley's (1994) failure to find a relationship between cladogenesis and climate change in hominins, and also with work done on other clades (Bobe, Behrensmeyer, and Chapman 2002; Faith and Behrensmeyer 2013), which suggested that changing climate results in turnover at more local, population scales rather than at the scale of species.

In the context of the threshold model, the phylogeny that comes closest to capturing such a scale, although it still captures relationships between taxa at a higher taxonomic level than that of populations suggested by previous work (Bobe, Behrensmeyer, and Chapman 2002), is the composite tree. In line with those previous conclusions, it does carry a signal of a positive relationship between change in mean $\delta^{18}O$ and cladogenesis at the level of genera. However, as in many of the results for the VSH, this signal is weak: models were significant overall, but there is a great degree of uncertainty around parameter estimates for the slopes, and no slope terms were significant. The time scale across which change in mean $\delta^{18}O$ had the greatest effect on the rate of cladogenesis, too, is ambiguous. The general pattern in both the 200k and 500k year bmp models, although the relationship is certainly not strong, is that all three genera show a positive relationship between mean $\delta^{18}O$ change and splitting rate. Thus, there is a weak signal that greater changes in mean $\delta^{18}O$ were followed by higher rates of

cladogenesis. The exact way changing climate operated to regulate cladogenesis within these genera is hard to say based on these data, as benthic $\delta^{18}O$ is a general proxy for climate, estimating both global temperature and ocean ice volume (Potts 1998a), and it is unlikely that different habitats respond in the same way to the same average change in climate. The models show, then, that despite occupying divergent niches, habitats, and ranges, the splitting rate of incipient lineages was probably determined by climate change in the same way in all three genera.

On the Parins-Fukuchi phylogenies, again, the data point to a diffuse effect of climate change on cladogenesis within hominin genera at best. Across both Parins-Fukuchi phylogenies, the slope parameter for *Homo* is nonsignificant: factors other than changing climate probably determined variation in the rates of splitting within *Homo. Australopithecus* shows a statistically significant negative correlation between change in mean $\delta^{18}O$ and the rate of cladogenesis on the original Parins-Fukuchi phylogeny, but the time scale across which change in mean $\delta^{18}O$ had the biggest effect is ambiguous. On the least speciose "high certainty" Parins-Fukuchi phylogeny, however, this relationship disappears. Taken within the context of the threshold model, this suggests that, in *Australopithecus*, reaching a moderate degree of morphological differentiation was more probable in times of less climate change, but that reaching a high level of morphological differentiation was decoupled from the amount of change in climate. Finally, in *Paranthropus,* the only significant relationship between cladogenesis and change in mean $\delta^{18}O$ was found on the least speciose "high certainty" Parins-Fukuchi phylogeny, where the relationship was positive. The implication, here, is that the attainment of a sufficiently high level of morphological divergence between paranthropine taxa for them to be recognized as separate species within 'lumping' taxonomies was most probable in times of climate change. One of the principal ecological differences between the two terminal paranthropine taxa on the "high confidence" Parins-Fukuchi phylogeny, *Paranthropus boisei* and *Paranthropus robustus,* is their inferred dietary strategies (Faith and Wood, in prep.; Cerling et al. 2011; Sponheimer et al. 2013), and diet is certainly a potential way in which climate change could have shaped cladogenesis in this clade. Geography is another, possibly stronger, contender for the link between climate and cladogenesis: *boisei* is an East African taxon, while *robustus* has been found in Southern Africa. The data suggest changing climate could have influenced the geographical distribution of suitable habitats for their shared ancestral population, leading to the splitting of the two lineages.

11.3.2.2 Hominin-specific TPH

Vrba (1995) suggested a causal relationship between marked temperature decline and an event of major turnover of hominin species between 2.7 and 2.5 Ma, which coincided with the appearance of the genus *Homo*. Here, I tested a more general version of this temperature-specific model by asking what the relationship between the rate of cladogenesis and directional change in mean $\delta^{18}O$ is in hominins. The expected pattern, then, was that shifts to colder climates, indicated by positive change in mean $\delta^{18}O$, should correlate with higher rates of cladogenesis. I find almost no evidence that this was the case in hominins, at any taxonomic level. Overall, the main pattern to emerge across all three phylogenies is at most a very weak relationship between change in temperature and splitting rate. At the level of the clade as a whole, there was no relationship between temperature change and the rate of cladogenesis on the composite and original Parins-Fukuchi phylogeny across any time scale; and the negative relationship between temperature change and cladogenesis on the "high confidence" Parins-Fukuchi phylogeny was most likely driven by the statistically significant relationship between temperature and cladogenesis in *Australopithecus* on this tree. Most slope parameter estimates, even in models that were statistically significant overall, were nonsignificant, with large 95% confidence intervals around them. The only genus in which there was consistently a significant relationship between change in mean $\delta^{18}O$ and the rate of cladogenesis was *Australopithecus*. Results for the hominin-specific TPH are summarized in Table 11-8.

Table 11-8: Summary of results from phylogenetic GLS: hominin TPH

Threshold model		← More 'split'		More 'lumped' →
		Composite tree	**Parins-Fukuchi et al**	**"High confidence" Parins-Fukuchi et al**
Clade-level	Timescale	*n.s*	*n.s.*	500k
	Correlation	*n.s.*	*n.s.*	Negative
Genus-level	Timescale	*(100k/500k)* [1]	100k	100k
	Correlation	Variable	Variable	Variable

[1]Time scale across which climate variability operated to influence cladogenesis ambiguous

Australopithecus showed a statistically significant negative relationship between temperature and cladogenesis on both Parins-Fukuchi trees, meaning it experienced higher rates of cladogenesis when climate shifted to warmer temperatures, and lower rates of cladogenesis when this shift was towards colder temperatures. By contrast, on the composite tree, its rate of cladogenesis was positively related to increases in mean $\delta^{18}O$. Taken within the context of the threshold model, these results suggest that the splitting of incipient lineages within *Australopithecus* taxa tended to occur in periods where climate cooled—in line with the

prevailing idea that early hominin evolution occurred as a result of cooling and increasing aridity (Dart 1953; DeMenocal 1995). The time scale across which cooling had the greatest effect on cladogenesis on this phylogeny was ambiguous—but, in any case, the correlation in *Australopithecus* was positive in both the 100k and 500k year bmp models. The persistence of these incipient lineages for a long enough time for them to accrue sufficient morphological differences for them to be classified as separate species in a 'lumping' taxonomy, then, was more likely in periods of warming.

In *Paranthropus,* there is so much uncertainty around parameter estimates that no slope terms were significant in any model. This points to one of two possibilities: either there was a role for changes in temperature in shaping paranthropine cladogenesis and sample sizes are simply too low to clarify how it did; or that changes in temperature did not affect cladogenesis in this group. Given the generally weak relationship between temperature shifts and cladogenesis in the rest of the hominins, it is probable that the latter scenario was the case.

The pattern for *Homo* is very different to that seen in *Australopithecus*. The differences between these two genera are illustrated in Figure 11-12. In *Homo*, directional temperature change did not correlate, across either of the potential time scales, with the rate of cladogenesis across the most speciose composite tree. In the context of the threshold model, this implies variation in the rate of splitting of incipient evolutionary lineages in *Homo* was decoupled from changes in temperature. There is a possibility that, in a similar way to the relationship between climatic variability and splitting of evolutionarily incipient lineages, a nonlinear relationship between changes in temperature and cladogenesis regulated hominin splitting rates. The absence of a significant relationship between changes in mean $\delta^{18}O$ cladogenesis in *Homo* on the composite tree might indicate that a critical threshold, ensuring a higher rate of cladogenesis regardless of variation beyond that threshold, was reached in *Homo*. The Pleistocene, of course, is marked by comparatively colder average temperatures than the Pliocene (Potts 1998a; Lisiecki and Raymo 2005). In this way, Vrba's general point still holds: colder Pleistocene climates were associated with major turnover in hominins: not by initiating a pulsed turnover, as, indeed, others have argued (White 1995; Bobe, Behrensmeyer, and Chapman 2002), but rather by setting a higher average *rate* of production and possibly turnover at a particular taxonomic scale. At a higher taxonomic scale (across the original Parins-Fukuchi tree) a contrasting pattern was found: there is a statistically significant positive relationship between splitting rate in *Homo* and change in mean $\delta^{18}O$ across the 100k years bmp. In other words, the cooler climate became, the higher the rate of cladogenesis at this scale. Although the relationship between change in mean $\delta^{18}O$ and the rate of *Homo* cladogenesis was positive on the "high confidence" Parins-Fukuchi tree as well,

there is a sufficiently great 95% confidence interval around the parameter estimate to make the slope term nonsignificant. In general, though, the pattern suggested by these data is that, in *Homo*, variation in splitting rate between evolutionarily incipient lineages was unaffected by changing temperatures; but that the appearance of more morphologically differentiated lineages tended to happen as a consequence of shifts to cooler climates.

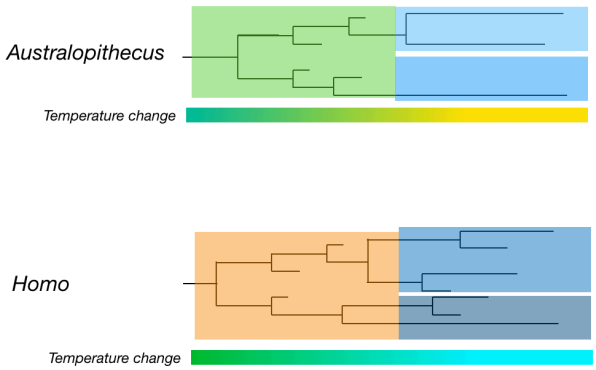


Figure 11-12: Differences in the operation of the hominin-specific TPH between *Australopithecus* and *Homo*

Figure shows phylogenies based on a less inclusive 'splitting' taxonomy in black, imposed on hypodigms of a 'lumped' taxonomy. Temperature change is indicated on the bar below each phylogeny: warmer colours indicate shifts to warmer temperatures; cooler colours indicate shifts to cooler climates. In *Australopithecus*, splitting of incipient evolutionary lineages is negatively related to temperature: that is, it experienced higher rates of cladogenesis when climate shifted to colder temperatures. When temperatures shifted to warmer temperatures, however, these incipient evolutionary lineages could persist for sufficient lengths of time to accumulate the morphological divergence necessary for them to be recognized as separate species on a 'lumped' taxonomy, indicated by the shift from green to blue 'lumped' hypodigms. In *Homo*, by contrast, average temperature is sufficiently low to ensure a high rate of incipient lineage cladogenesis regardless of shifts in temperature: so although the relatively higher rate of cladogenesis at this level is potentially the product of cooler average temperatures, *variation* in cladogenesis at this taxonomic scale is decoupled from variation in temperature. The appearance of more morphologically differentiated lineages tended to happen as a consequence of shifts to cooler climates in *Homo*, indicated by the shift from orange to blue 'lumped' hypodigms.

11.4 Summary and conclusion

11.4.1 Was hominin cladogenesis regulated by climate – and if so, how?

Overall, relationships between climatic variables and hominin cladogenesis at any scale were rather diffuse; the implications of this conclusion are that, firstly, the relationship between climate and hominin cladogenesis is not a simple one, nor consistent through time or across

taxa, and secondly, that much variation in splitting rates remains unexplained by variation in climate.

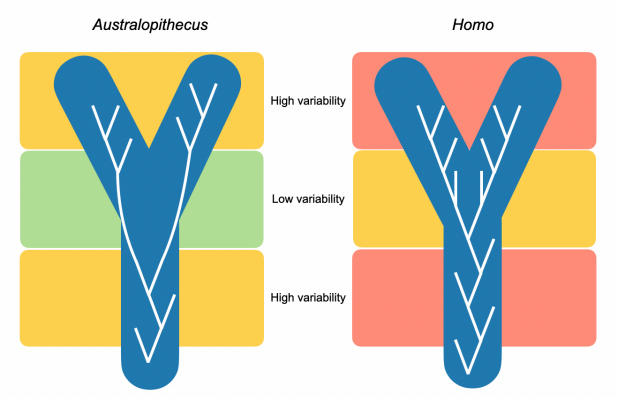
There is stronger support for a role of climatic variability, as predicted by the Variability Selection Hypothesis (Potts 1996b, 1998b), than general temperature trends in determining hominin cladogenesis, suggesting habitat fragmentation as a potentially important factor in lineage splitting.

Uncertainty around parameter estimates notwithstanding, the results reported here are suggestive of a previously unknown way in which climate determined hominin speciation. In the context of the threshold model, the data suggest that splitting of evolutionarily incipient lineages in hominins tends to occur when there is high climatic variability. The point at which these incipient lineages then attain sufficient morphological divergence for them to be recognized as separate taxa on 'lumping' phylogenies tends to be reached only when the incipient lineages have time to persist and fully develop their own evolutionary trajectories, of which there is a higher chance when climate is relatively more stable.

There are differences between *Homo* and *Australopithecus* in how climate determined speciation, however. In *Australopithecus*, general temperature trends also mediate incipient lineage persistence and thus speciation, with extended persistence in periods of warming. So: in *Australopithecus,* incipient lineages were produced at higher rates in periods of variability and cooling, and these lineages tended to have time to accrue sufficient morphological differences to be registered as novel taxa on "lumped" phylogenies in periods of stability and warming. These patterns are illustrated in Figure 11-13.

The pattern for *Homo* is comparatively different to that of the rest of its clade: its evolution happened during sufficient level of climatic variability and cooling to ensure a higher rate of incipient lineage turnover, regardless of variation in either climate variable. In *Homo,* climate possibly decoupled relationship between the splitting of incipient lineages and the splitting of more morphologically diverged taxa. The pattern for *Homo* suggests the effect of climate on speciation, then, is potentially nonlinear. *Homo* produced more morphologically diverged taxa in a contrasting way to *Australopithecus*, namely during periods of cooling. In summary: in *Homo*, climate possibly decoupled the relationship between the splitting of less and more morphologically diverged taxa by increasing the rate of incipient lineage turnover; and morphologically diverged members of *Homo* tended to appear during times of stability and cooling.

A)



B)

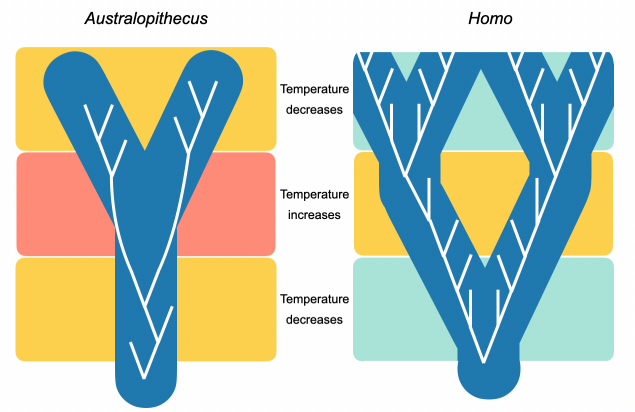


Figure 11-13: Splitting, at two levels, mediated by climate

In both A) and B), dark blue outline represents a 'lumping' phylogeny; white lines represent 'splitting' phylogenies. A) shows the relationship between climate variability and splitting rates on lumping and splitting phylogenies in *Australopithecus* and *Homo*. This is the general pattern; but it must be noted that the inferred relationships are weak. In *Australopithecus*, splitting on the 'lumped' phylogeny occurs when evolutionarily incipient lineages have the opportunity to persist and develop as separate evolutionary units, and this tends to occur in times of less climate variability. In *Homo*, there is a higher rate of splitting of evolutionarily incipient lineages – potentially due to higher average levels of climatic variability than *Australopithecus* experienced – and variation in this splitting rate is unrelated to climatic variability. Despite this, *Homo* does produce more morphologically diverged taxa in a similar way to *Australopithecus*, namely during periods of less climatic variability. B) shows the relationship between temperature change and splitting rates on lumping and splitting phylogenies in *Australopithecus* and *Homo*. Again, these relationships are often only very weak, and with large 95% CIs around their reconstructed direction; but this is the general pattern. In *Australopithecus*, splitting on the 'lumped' phylogeny occurs in periods of warming, when incipiently diverging lineages have time to persist and develop as separate evolutionary units. In *Homo*, there is a higher rate of splitting of evolutionarily incipient lineages – potentially due to colder average climate than *Australopithecus* experienced – and variation in this splitting rate is unrelated to variability in temperature. *Homo* produced more morphologically diverged taxa in a contrasting way to *Australopithecus*, namely during periods of cooling.

11.4.2 Over which time scale do these variables affect speciation?

The time scales over which different aspects of climate operated to influence hominin cladogenesis are ambiguous, but this is unsurprising given the generally weak, often genus-specific relationship between climate and splitting rates. In light of the complexity of this relationship, the time scale across which different elements of climate affected hominin cladogenesis must have varied between taxa and between habitats.

12 Competition and hominin cladogenesis

12.1 Background

12.1.1 Introduction

In the metaphorical battle for evolutionary causality, the Court Jester (Barnosky 1999) can be pitted against the Red Queen (Van Valen 1973). From the Court Jester perspective, the primary causes of evolutionary change are environmental factors, while that role is fulfilled by interspecific competition in Red Queen models. Research interest in these two competing models, or indeed their interaction, has been surprisingly asymmetrical in palaeoanthropology: human evolution has almost exclusively been examined through a Court Jester lens, and popular narratives of human evolution are undeniably oriented almost exclusively around climate. The effect of interspecific competition on hominin evolution was the focus of several papers in the 1980s and 1990s, but these were primarily concerned with reconstructing the ecological dynamics of competition between hominins and nonhominin carnivores or primates competing for access to resources (Brantingham 1998; Foley 1984, 1987; King 1976; Stiner 2002). Brantingham (1998), for example, reconstructed Plio-Pleistocene hominins as ecologically 'in between' top predators and confrontational scavengers; and Stiner (2002) made the case that *Homo* developed a unique predator-prey relationship as a consequence of coevolution with other large predators. Recently, empirical interest in interspecific competition between hominin taxa was revived by Schroer & Wood (2015), who showed that "sympatry" between *Homo* and *Paranthropus*, insofar as it can be reconstructed from the fossil record, contributed to their diverging mandibular fourth premolar sizes.

What these approaches share, however, is a focus on linking particular cases of competition to specific adaptive traits—not a general relationship between the intensity of interspecific competition (with any species) and hominin speciation. Indeed, this has received almost no empirical attention; and neither has the more specific case of interspecific competition between hominins.

Chapters 10 and 11, however, suggest and leave room for a role for interspecific competition between hominin species, respectively. In Chapter 9, it was shown that splitting rates in *Australopithecus, Paranthropus*, and *Homo* are significantly slower after peak diversity within each genus across the Parins-Fukuchi et al. trees. Slowdowns in splitting rates of

extant clades are usually interpreted as the consequence of negatively "density"-dependent cladogenesis (Phillimore and Price 2008; Rabosky and Lovette 2008; Rabosky 2013; Moen and Morlon 2014): in this model, increasing species "density" (or in other words, the total number of closely related species) as a clade expands results in higher levels of interspecific competition, restricting further speciation. Next, the results discussed in Chapter 10 suggested that, on the whole, climate variables correlated only weakly with hominin splitting rates across all phylogenies; and that the direction and magnitude of these correlations were certainly not consistent across taxa, nor through time. As a result, a large proportion of variation in the rate of cladogenesis across hominins is left unexplained – particularly that of *Homo* on the most speciose composite phylogeny, which did not show statistically significant relationships with any climate variable across any timescale.

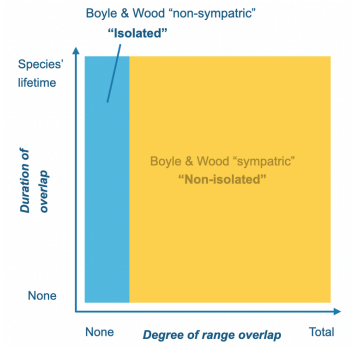


Figure 12-1: The degrees of geographical and temporal association of "isolated" and "non-isolated" taxa

Taxa defined here as "isolated" are taxa that show no evidence of range overlap with any other hominin taxon. The "non-isolated" category, however, comprises a large amount of variation in the geographic degree of range overlap taxa experienced, and the duration of this overlap.

The Red Queen, then, may yet have the last word. Here, I test whether interspecific competition between hominin species regulated speciation rates in the lineage as a whole, and within *Australopithecus, Paranthropus,* and *Homo* separately. One key question, of course, is the geographic scale at which such competition is expected to have taken place; and I focus on two. First, I ask whether or not splitting rates differ significantly between "non-isolated" taxa, whose reconstructed range overlapped with that of one or more other hominin, and "isolated" taxa, whose range did not overlap with that of any other. Taxon categorisations are presented in Table 16. Wood and Boyle (2016) classified taxa I here refer to as "non-isolated" as "sympatric"; and the reason that I do not follow their terminology is because "sympatry" implies a very specific set of conditions which are difficult to reconstruct based on fossil data. Figure 12-1 shows the degrees of temporal and geographical association of taxa that fall in either category: non-isolated taxa are those reconstructed to have shared some portion of their range with at least one other hominin taxon. It is assumed that taxa classified as non-isolated were synchronous, but Figure 12-1 shows that there is a possibility that this was not the case. This is simply due to the nature of the evidence: major problems in reconstructing fossil species' synchrony derive from, for example, time-averaging of fossil sites (Maxwell et al. 2018).

Table 12-1: Taxon categorisations

Taxon[1]	Category	Overlapping taxa and time interval in which overlap occurred[2]
Australopithecus anamensis	Non-isolated	*Ardipithecus ramidus* (5-4 Ma)
Australopithecus afarensis	Non-isolated	*Australopithecus deyiremeda* (4-3 Ma)
Australopithecus africanus	Isolated	
Australopithecus sediba	Non-isolated	*Homo erectus (sensu lato)/Homo ergaster* (2-1.5 Ma)
Australopithecus garhi	Isolated	
Australopithecus deyiremeda	Non-isolated	Burtele foot, *Australopithecus afarensis* (4-3 Ma)
Paranthropus aethiopicus	Isolated	
Paranthropus boisei	Non-isolated	*Homo habilis* (2.5-2 Ma), *Homo rudolfensis* (2.5-2 Ma), *Homo erectus (sensu lato)/Homo ergaster* (2-1.5 Ma)
Paranthropus robustus	Isolated	
Homo habilis	Non-isolated	*Paranthropus boisei* (2.5-2 Ma), *Homo rudolfensis* (2.5-1.5 Ma), *Homo erectus (sensu lato)/Homo ergaster* (2-1.5 Ma)
Homo rudolfensis	Non-isolated	*Paranthropus boisei* (2.5-2 Ma), *Homo habilis* (2.5-1.5 Ma), *Homo erectus (sensu lato)/Homo ergaster* (2-1.5 Ma)
Homo erectus (sensu lato)	Non-isolated	*Paranthropus boisei* (2-1 Ma), *Homo habilis* (2-1 Ma), *Homo rudolfensis* (2-1 Ma), *Australopithecus sediba* (2-1.5 Ma), *Homo heidelbergensis* (1-0.25 Ma), *Homo helmei* (1-0.25 Ma), *Homo sapiens* (0.25 Ma-present), Denisovans (0.25 Ma-present)
Homo erectus (sensu stricto)	Non-isolated	*Homo heidelbergensis* (1-0.25 Ma), *Homo sapiens* (0.25 Ma-present), Denisovans (0.25 Ma-present)
Homo ergaster	Non-isolated	*Paranthropus boisei* (2-1 Ma), *Homo habilis* (2-1 Ma), *Homo rudolfensis* (2-1 Ma), *Australopithecus sediba* (2-1.5 Ma), *Homo helmei* (1-0.25 Ma)
Homo georgicus	Isolated	
Homo heidelbergensis	Non-isolated	*Homo erectus (sensu lato)/Homo erectus (sensu stricto)* (1-0.25 Ma), *Homo sapiens** (0.25 Ma-present), Neanderthals* (0.25 Ma-present)
Homo antecessor	Isolated	
Homo helmei	Non-isolated	*Homo erectus (sensu lato)/Homo ergaster* (1-0.25 Ma)
Neanderthals	Non-isolated	*Homo sapiens* (0.25 Ma-present), Denisovans (0.25 Ma-present)
Denisovans	Non-isolated	*Homo sapiens* (0.25 Ma-present), Denisovans (0.25 Ma-present), *Homo erectus (sensu lato)/Homo erectus (sensu stricto)* (0.25 Ma-present)
Homo sapiens	Non-isolated	Neanderthals (0.25 Ma-present), Denisovans (0.25 Ma-present), *Homo erectus (sensu lato)/Homo erectus (sensu stricto)* (0.25 Ma-present)

[1]This is the total list of taxa; not every phylogeny includes all taxa. Ancestral taxa, when unsampled, do not appear in this list but were included in these analyses. Ancestral taxa were classified as either non-isolated or isolated depending on the status of their next named descendant.
[2]Modified from Wood and Boyle (2016). Time interval in which overlap occurred need not be the actual time range of overlap; these are merely the time intervals Wood and Boyle (2016) employ to assess taxic diversity.

The second geographic scale is larger: I ask whether the total number of extant hominin taxa 200k years before each measuring point ("bmp") correlates with splitting rate. Here, I do not refer to the number of extant taxa as species "density", as some earlier zoological papers (Phillimore and Price 2008; Rabosky and Lovette 2008) have done, but rather as "diversity",

as is typical in human evolutionary studies and more recent zoological papers (Rabosky 2013; Wood and Boyle 2016).

These scales capture different types of interspecific competition. "Non-isolated" taxa competed for resources in overlapping ranges. The size of range overlap as a percentage of total range is difficult to reconstruct based on fossil data, and so is the length of time in which taxa shared geographic space (see Figure 12-1). In any case, the expected outcome competition in cases of range overlap is niche differentiation (Weir and Mursleen 2013). If the general pattern of negative diversity-dependent cladogenesis found in extant clades (Moen and Morlon 2014) holds, splitting rates should be significantly slower in non-isolated taxa as ecological saturation restricts further cladogenesis; but the opposite pattern might be expected if interspecific competition promoted splitting into more ecologically specialised or geographically smaller-ranged species.

At the second, larger geographic scale, the emphasis is shifted to larger-scale evolutionary processes. At this scale, diversity-dependence would reflect the partitioning of biogeographical space (Price and Kirkpatrick 2009; Pigot and Tobias 2013) and interspecific competition has been invoked as a major cause of ecological and evolutionarily stable boundaries between species' ranges (Case et al. 2005; Price and Kirkpatrick 2009). The baseline expectation for hominins, based on patterns reported for extant vertebrates (Phillimore and Price 2008; Rabosky and Lovette 2008), is that cladogenesis should be negatively diversity-dependent: but only across the phylogenies and scales where slowdowns in splitting rate were observed in the analyses presented in Chapter 10. So, for the clade as a whole, no diversity-dependence is expected across any phylogeny; and within genera, negative diversity-dependence is only expected for all three genera across both Parins-Fukuchi phylogenies.

12.1.2 Terminology

A more in-depth introduction to terminology used in this section was offered in Chapter 8. "Sympatric" taxa are those that meet two criteria: they have fossil representatives found in the same locality as one or more different hominin taxa, and they are reconstructed as being contemporaneous with these taxa. "Speciation" refers to the complex and temporally extended process of lineage splitting. Because tip DR is measured across multiple phylogenies that differ in their definition of species, I refer to tip DR calculated across phylogenies simply as "splitting rate" or the "rate of cladogenesis".

The model, described in Chapter 8, which is put forward as a way to reconcile differences between phylogenies based on different taxonomic practices, is referred to as the "threshold model" of hominin speciation. In brief, it suggests that phylogenies based on more species-rich 'splitting' taxonomy show relationships between incipiently diverging lineages, and thus in effect capture an early stage of speciation. Less speciose 'lumping' taxonomies recognize more highly diverged groups – lineages which have effectively reached later stages of speciation – and phylogenies that are based on these thus capture the cumulative outcome of the cladogenesis, extinction, and persistence of incipiently diverging lineages.

12.1.3 Materials and methods

The full method for this section is described in Materials and methods for Section B. In brief, phylogenetic generalised least squares (GLS) regressions were run, using the "nlme" package (Pinheiro et al. 2019) on three phylogenies to account for different approaches to hominin taxonomy: 1) the phylogeny with the lowest AIC score published by Parins-Fukuchi et al. (2019), 2) a "high certainty" version of this phylogeny, with species Wood and Boyle (2016) have "low" confidence in treating as distinct taxa removed, and 3) a composite phylogeny based on a review of the literature on hominin cladistics at the time of writing. To ask whether DR differs significantly between cases of hominin isolation and cases of non-isolation, I compared non-isolated DRs to isolated DRs for the clade as a whole, and for each genus separately, using phylogenetic GLS regressions. To ask whether DR is diversity-dependent, I ran phylogenetic GLS regressions in which DR was predicted by hominin diversity 200k years bmp; to ask whether this relationship differed between genera, I ran this model again but allowed the slope and intercept to vary by genus. In this regression, *Homo* was used as the baseline. The approach was repeated on 1000 simulated constant-birth phylogenies to test the accuracy of the method.

12.2 Results

12.2.1 Parins-Fukuchi phylogenies

12.2.1.1 Original Parins-Fukuchi phylogeny

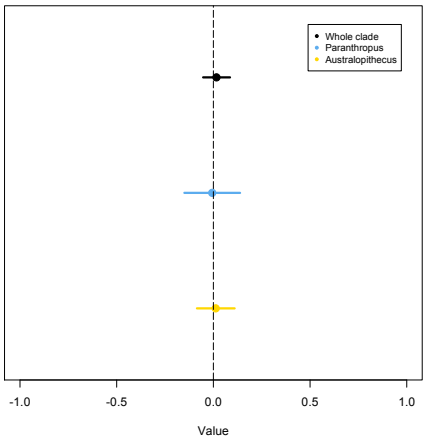
The results from analyses run across the original Parins-Fukuchi et al. phylogeny are presented in Table 12-2 and Figure 12-2.

Table 12-2: Results from phylogenetic GLS on original Parins-Fukuchi phylogeny

	Slower in non-isolated taxa?		Diversity	
Clade-level	**No** (0.01, p=0.65)		**No relationship** (-0.02, p=0.34)	
Genus-level	**No**		**Variable**	
	Homo	NA[1]	*Homo*	0.14 (p<0.05)
	Australopithecus[1]	0.01 (p=0.80)	*Australopithecus*	-0.08 (p<0.001)
	Paranthropus	0.00 (p=0.94)	*Paranthropus*	-0.09 (p<0.001)

[1]All species non-isolated

A) Difference in DR between isolated taxa and non-isolated taxa



B) The effect of diversity on DR

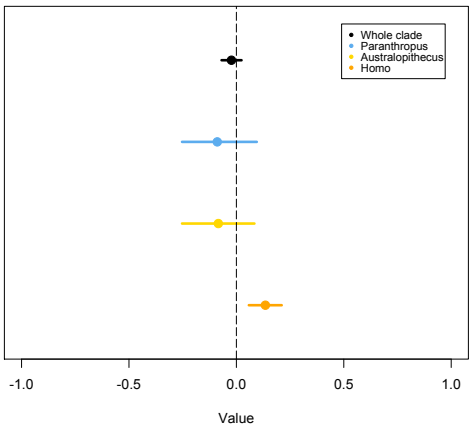


Figure 12-2: The effect of interspecific competition on DR on the original Parins-Fukuchi et al. phylogeny

A) Figure shows the difference in DR of taxa that were non-isolated compared to taxa that were, and 95% confidence intervals around the parameter estimate. All species of *Homo* included on this tree were non-isolated, so there is no estimate for *Homo*. Across the clade as a whole, and within *Paranthropus* and *Australopithecus*, DR in non-isolated taxa is not significantly different to DR of those that were. B) Figure shows the slope term and 95% confidence intervals around the parameter estimate for the model in which hominin DR across the clade as a whole was predicted by overall hominin diversity 200k years before measuring points (in black), and slope terms and 95% confidence intervals around the parameter estimate for each genus for the model in which the relationship between diversity and DR was allowed to vary by genus. *Homo* DR is statistically significantly related to overall hominin diversity: in this genus, DR increases when diversity increases. The relationships between DR and diversity in *Paranthropus* and *Australopithecus* were significantly different to that of *Homo* – and the slope estimates for both suggest DR negatively correlates with diversity – but the 95% confidence interval overlaps with 0 for both genera.

There is no significant difference between DR in non-isolated taxa and DR in isolated taxa across the clade as a whole, nor within genera. As expected, based on the lack of a slowdown in DR after peak diversity reported in Chapter 9, there is no statistically significant relationship between DR and hominin diversity at 200k years bmp for the clade as a whole. Again as expected based on the pattern of slowing DR post-peak diversity reported in Chapter 9, *Paranthropus* and *Australopithecus* are characterised by negatively density-dependent DR: DR slows as diversity increases. The 95% CI around the slope parameter estimate, for both genera, overlaps with 0, but in any case, *Paranthropus* and *Australopithecus'* relationship between DR and diversity is statistically significantly different to that seen in *Homo.* Indeed, the pattern is reversed in *Homo*: in our genus, DR is positively predicted by diversity – in other words, the more species, the higher splitting rates.

Finally, the effect of only *Homo* diversity on *Homo* DR was significant, and positive (slope coefficient of the model: 0.173, $p<0.05$).

12.2.1.2 "High certainty" Parins-Fukuchi phylogeny

The results from analyses run across the "high certainty" Parins-Fukuchi et al. phylogeny are presented in Table 12-3 and Figure 12-3. The exact same patterns as reported above for the original Parins-Fukuchi et al. tree were found across this phylogeny: there is no significant difference between DR in non-isolated and isolated taxa at any level, and there is no statistically significant relationship between diversity and DR at the level of the clade as a whole. *Homo*, again, shows positive diversity-dependence, and this relationship was significantly different to that in *Australopithecus* and *Paranthropus.*

Finally, the effect of only *Homo* diversity on *Homo* DR was not significant (slope coefficient of the model: 0.036, $p=0.56$).

Table 12-3: Results from phylogenetic GLS on the "high certainty" Parins-Fukuchi phylogeny

	Slower in non-isolated taxa?		**Diversity**	
Clade-level	**No** (0.00, $p=0.95$)		**No relationship** (-0.01, $p=0.46$)	
Genus-level	**No**		**Variable**	
	Homo	NA[1]	*Homo*	0.09 ($p<0.001$)
	Australopithecus	-0.03 ($p=0.60$)	*Australopithecus*	-0.08 ($p<0.001$)
	Paranthropus	0.00 ($p= 0.92$)	*Paranthropus*	-0.02 ($p<0.05$)

[1]All species non-isolated

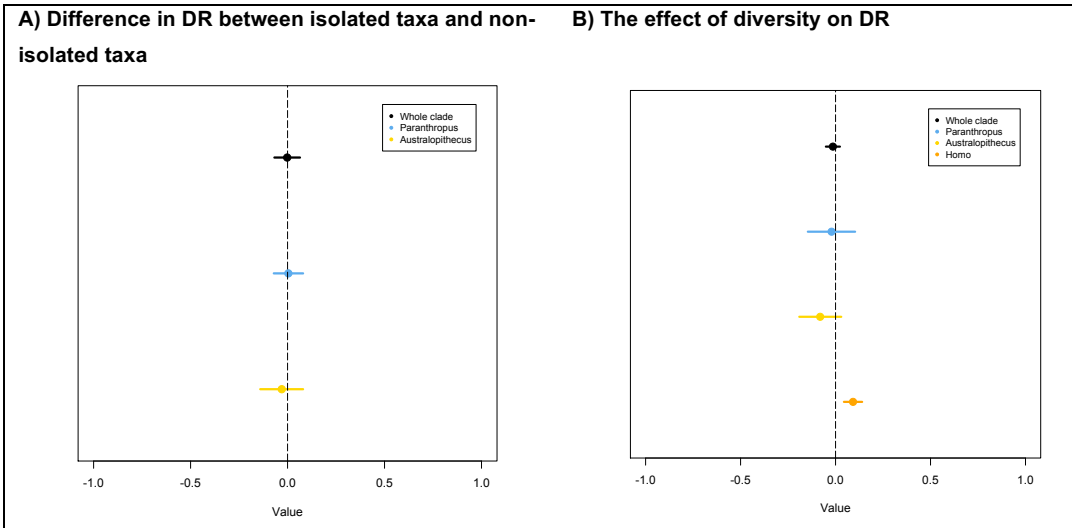


Figure 12-3: The effect of interspecific competition on DR on the "high confidence" Parins-Fukuchi et al. phylogeny

A) Figure shows the difference in DR of taxa that were non-isolated compared to taxa that were, and 95% confidence intervals around the parameter estimate. All species of *Homo* included on this tree were non-isolated, so there is no estimate for *Homo*. Across the clade as a whole, and within *Paranthropus* and *Australopithecus*, DR in non-isolated taxa is not significantly different to DR of those that were. B) Figure shows the slope term and 95% confidence intervals around the parameter estimate for the model in which hominin DR across the clade as a whole was predicted by overall hominin diversity 200k years before measuring points (in black), and slope terms and 95% confidence intervals around the parameter estimate for each genus for the model in which the relationship between diversity and DR was allowed to vary by genus. *Homo* DR is statistically significantly related to overall hominin diversity: in this genus, DR increases when diversity increases. The relationships between DR and diversity in *Paranthropus* and *Australopithecus* were significantly different to that of *Homo* – the slope estimates for both suggest DR negatively correlates with diversity – but the 95% confidence interval overlaps with 0 for both genera.

12.2.2 Composite phylogeny

The results from analyses run across the composite phylogeny are presented in Table 12-4 and Figure 12-4.

There is no significant difference between DR of non-isolated taxa and that of isolated taxa across the clade as a whole, but it is significantly slower in non-isolated australopiths. For the other two genera, there is no significant difference between DR of non-isolated taxa and that of isolated taxa. As expected based on patterns reported in Chapter 9–that is, the lack of a slowdown in DR after peak diversity across the clade as a whole and within each genus–there is no statistically significant relationship between DR and hominin diversity at 200k years bmp at any scale.

Table 12-4: Results from phylogenetic GLS on the composite phylogeny

	Slower in non-isolated taxa?		Diversity	
Clade-level	**No** (0.05, p=0.45)		**No relationship** (-0.01, p=0.70)	
Genus-level	**Variable**		**No relationship**	
	Homo	-0.02 (p=0.9)	*Homo*	0.01 (p=0.79)
	Australopithecus[1]	-0.21 (p<0.05)	*Australopithecus*	0.00 (p=0.83)
	Paranthropus	0.02 (p=0.84)	*Paranthropus*	-0.03 (p=0.56)

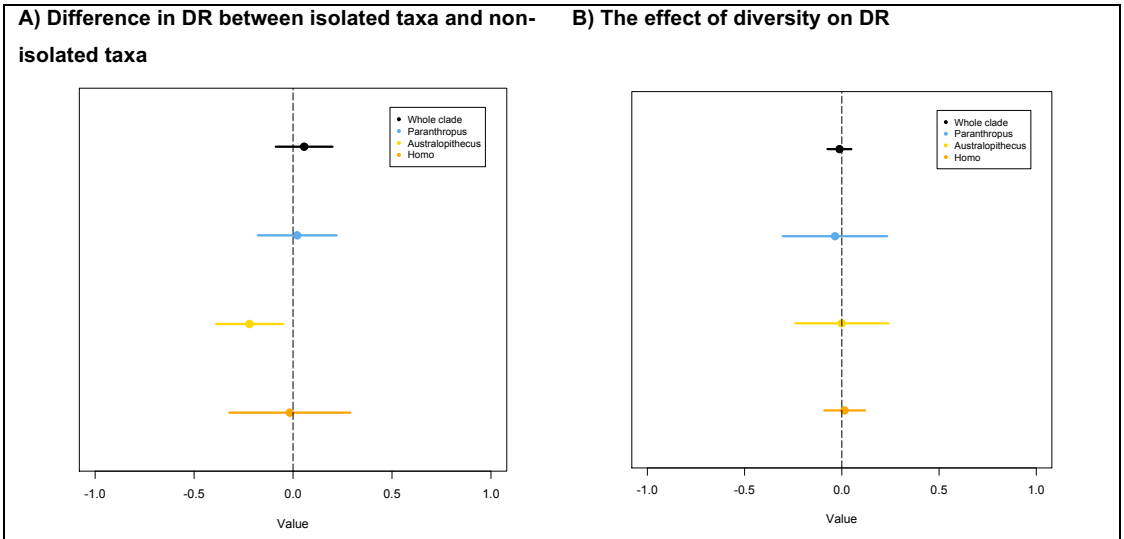


Figure 12-4: The effect of interspecific competition on DR on the composite phylogeny

A) Figure shows the difference in DR of taxa that were non-isolated compared to taxa that were, and 95% confidence intervals around the parameter estimate. Across the clade as a whole, and within *Paranthropus* and *Homo*, DR in non-isolated taxa is not significantly different to DR in isolated taxa. In *Australopithecus*, however, non-isolated species have significantly lower DR than species which did not overlap geographically with others. B) Figure shows the slope term and 95% confidence intervals around the parameter estimate for the model in which hominin DR across the clade as a whole was predicted by overall hominin diversity 200k years before measuring points (in black), and slope terms and 95% confidence intervals around the parameter estimate for each genus for the model in which the relationship between diversity and DR was allowed to vary by genus. DR is not statistically significantly related to overall diversity at any taxonomic scale.

12.2.3 The performance of the diversity approach

Across the 1000 simulated trees, there was a statistically significant relationship between DR and diversity on 39 phylogenetic GLS regressions, meaning the method has a false positive rate of ~4%. The direction of all false-positive relationships was negative.

12.3 Discussion

The principal results of this chapter are, first, that range overlap did not tend to slow hominin cladogenesis down; but second, that cladogenesis within individual genera *was* determined by the overall number of hominin taxa. Taken together, these results are concordant with a model in which the principal way interspecific competition shaped hominin cladogenesis was through competition for biogeographic space. Before discussing the results of analyses at both geographic scales together to come to this conclusion, the questions of the differences between splitting in isolation versus non-isolation and splitting across a larger geographic scale are discussed separately.

12.3.1 Splitting where ranges overlap

Splitting rates of taxa whose range overlapped with that of at least one other taxon, in most cases, did not differ significantly from splitting rates of taxa whose ranges did not. This is true for the clade as a whole across all three phylogenies, and within genera for the two variants of the Parins-Fukuchi et al. phylogenies. The implication, then, is that cladogenesis was equally likely to occur across a given period of time in cases where the ranges of hominin taxa overlapped with those of any number of other taxa as in cases whether they did not.

The taxa here classified as overlapping temporally and geographically with at least one other hominin taxon were those Boyle and Wood (2016) go as far as to classify as “sympatric”: and if, in most cases, the degree of geographical and temporal overlap was large or total, these results are surprising in the context of the inferred rarity of true sympatric speciation across mammalian evolutionary history. The long-held view, championed by Mayr (1963), was that true sympatric speciation is theoretically unlikely and empirically unsupported. On the basis of a growing body of empirical evidence and simulation studies, it is now broadly accepted that speciation in sympatry is theoretically plausible in particular contexts (Orr and Orr 1996) and that it has occurred in nature (Dieckmann and Doebeli 1999; Via 2001; Bolnick and Fitzpatrick 2007). Despite this shift, the consensus is that sympatric speciation is comparatively rare, and that speciation usually occurs in allopatry. Wood and Boyle (2016), however, identify at least 25 cases of “sympatry” in a speciose taxonomic framework, and although this could simply be evidence either of speciation in sympatry or of Mayr’s model of secondary contact (Mayr 1963), the data presented here show that the rates of splitting did not differ between cases where ranges overlapped and where they did not.

A major question remains: to what degree did ranges of non-isolated taxa overlap? This question is difficult to answer given limitations of the evidence, the most difficult of which to

overcome are uncertainty around date estimates, preservation bias, and time-averaging of fossil sites (Maxwell et al. 2018a). Fossil species' ranges, further, are difficult to reconstruct (MacDonald, Smaers, and Steele 2015), and this means that the degree of range overlap between putatively "sympatric" taxa cannot easily be reconstructed either. From a comparative perspective, however, it is not completely unlikely that at least some hominin species were sympatric, or at least shared a proportion of their range for some time. For example, there are at least 673 species-pairs of extant sympatric primates globally (Schreier et al. 2009); in Africa, sympatric guenons associate in mixed-species groups (Cords 1990); and terrestrial baboons and patas monkeys coexist and compete where their habitats meet (Crook and Aldrich-Blake 1968).

Based on the fossil record, there are two relatively strong cases for hominin sympatry, or at least temporally sustained and geographically substantial overlap: first, that of *Paranthropus boisei, Homo habilis, Homo rudolfensis, and Homo ergaster* at Koobi Fora (Spoor et al. 2007); and second, that of *Australopithecus afarensis* and *Australopithecus deyiremeda* at Woranso-Mille (Haile-Selassie, Melillo, and Su 2016). The geographical extent and duration of inferred range overlap of taxa in the Middle and Late Pleistocene was probably less constant through time and space as a consequence of dynamic range expansions and contractions in climatically variable settings (Potts 2013). Further, as species' range sizes increased, the evolutionary pressure exerted by a taxon with which it overlapped spatially and temporally might be relatively smaller than that exerted on each other by taxa within smaller, more completely overlapping ranges. Thus, overlap between *Homo erectus* (sensu lato) and *Homo heidelbergensis*, even if sustained, probably did not exert the same evolutionary pressure as did the overlap between *Paranthropus boisei*, *Homo habilis, Homo rudolfensis*, and *Homo ergaster* in Turkana. However, the general trend is of range size increases in all hominin taxa (Foley 2016), so it is possible that the proportion of range overlap remained relatively steady throughout human evolution. Finally, occasional sympatry of *Homo sapiens*, *Homo neanderthalensis*, and the Denisovans is betrayed by their genomes (Reich et al. 2010; Posth et al. 2017): but again, the degree to which their ranges overlapped probably varied over time.

If the majority of non-isolated hominin taxa did indeed overlap spatially and temporally to the degrees implied by "sympatry", and this remains a big and presently unclarifiable "if", theoretical models suggest that a specific set of conditions must have shaped many hominin splitting events in order for sympatric splitting to have occurred sufficiently frequently to produce the pattern reported here. In simulation studies, sympatric speciation is facilitated by intense disruptive selection, or direct selection on reproductive traits and mate choice, but

most likely both (Bolnick and Fitzpatrick 2007). Previous work has suggested the strength of these types of selection would have had to be strong in order to overcome the neutralizing effects of random mating and consequent genetic recombination (Gavrilets 2005). Sexually selected traits, of course, tend not to fossilize; nor do behavioural patterns like assortative mating. However, disruptive selection is likely to have been ecological (Levene 1953; Gavrilets 2006; Bolnick and Fitzpatrick 2007), and this might be captured in fossil material. A global review of extant sympatric primates suggested that the primary type of niche separation was dietary (Schreier et al. 2009). Of the two locations at which there is relatively strong evidence for sympatry—Koobi Fora in East Africa and Woranso-Mille in Ethiopia—the strongest evidence for disruptive selection is character displacement in mandibular premolar morphology of *Homo* and *Paranthropus* in East Africa (Schroer and Wood 2015). By contrast, in the same location, there is little fossil evidence for intense ecological disruptive selection between the taxa belonging to the genus *Homo: Homo habilis, H. rudolfensis,* and *H. ergaster* have reduced postcanine teeth, and are reconstructed as ecological generalists (Wood and Strait 2004; Elton 2006). The same is true of *Australopithecus afarensis* and *Australopithecus deyiremeda* at Woranso-Mille (Ungar 2004; Levina et al. 2015; Haile-Selassie, Melillo, and Su 2016). It might be the case that these taxa avoided direct competition through such generalism (Elton 2006), but the point is that their common ancestor is unlikely to have split in true sympatry based on this evidence.

Linking autapomorphic dietary traits to specified ecological niches, however, is challenging, so there is a chance disruptive selection had occurred at these sites. This difficulty derives part from the fact environmental reconstructions are relatively coarse (Foley 2013), and in part because 'niches' are not easily defined in the first place (Poisot et al. 2011; Vamosi et al. 2014). Improved environmental reconstructions of localities in which hominin species were sympatric can offer a way forward in this regard. At a larger scale, the case could be made that *Australopithecus* and *Paranthropus* occupy the two fundamental dietary niches available to early hominins—megadonty on the one hand, and smaller dentition on the other. However, this may be an overly simplified interpretation: the carbon isotope signatures of *P. boisei* and *P. robustus* suggest at potentially major differences in dietary strategy, with *boisei* consuming a significantly larger proportion of C4 plants (Faith and Wood, in prep.; Cerling et al. 2011). The overall point, though, is that it is unclear whether dietary specialization was the primary way in which the disruptive selection, implied by theoretical models as a likely shaper of hominin splitting events, operated.

A second way in which extant sympatric primates partition ecological niche space is through locomotor and postural differentiation (Youlatos 1999); and the early hominin fossil record

does suggest at considerable interspecific diversity in this regard (Ward 2002; DeSilva et al. 2013; Rein et al. 2017; Georgiou et al. 2020). It is unclear whether divergent selection on locomotor traits underlay the cladogenesis of taxa at Koobi Fora and Woranso-Mille, however. At the former, all members of *Homo* were obligate bipeds; but there is evidence that *Paranthropus boisei* incorporated an element of arboreality in its locomotor repertoire (Domínguez-Rodrigo et al. 2013). At the latter, since there is no postcranial material unambiguously associated with *Australopithecus deyiremeda*, it is impossible to say at present whether it differed markedly from *Australopithecus afarensis*. Moving beyond these two cases, mosaics of locomotor traits in pre-*Homo* species, and the variable locomotor behaviours implied by these morphologies, are invariably attributed exclusively to climate change and resulting habitat fragmentation (e.g. Foley (2016)); but the implication of the results presented here is that this need not be the only cause. Rather, the inferred prevalence of splitting in non-isolation can be taken to suggest that divergent locomotive behaviours was the product of disruptive selection when ranges overlapped. Of course, disruptive selection and selection for novel locomotive behaviours in changing environments are not mutually exclusive scenarios; and these probably interacted.

However, the reality is that the geographical and temporal degree to which the ranges of most non-isolated taxa overlapped remains uncertain. Instead of hominin evolution being characterised by a frequency of sympatric speciation that is largely unexpected for mammals (Fitzpatrick and Turelli 2006), the more likely scenario is that the lack of a signal of slower cladogenesis in cases of range overlap is because the degree of overlap was too small, on average, to affect cladogenesis in the expected way. Similarly, it is also possible that non-isolated taxa did not overlap temporally for sufficiently long periods of time for the expected evolutionary consequences. It may be the case that cladogenesis occurred in sympatry at Koobi Fora and Woranso-Mille, and that the signal of this process is diluted by the inclusion of less fully overlapping taxa in the non-isolated group: but unfortunately, the nature of the fossil record means much further improvement in the resolution required to resolve the problem is unlikely.

The single clade in which splitting rates are significantly slower when ranges were shared with other hominins is *Australopithecus,* and only on the composite phylogeny. It might be the case, then, that in *Australopithecus*, the zone of overlap between ranges tended to be larger, or that their ranges often overlapped completely. In a general way, slower cladogenesis when ranges overlapped can be taken as support, albeit indirect and weak, for the view that sympatric speciation is uncommon (Mayr 1963), or even theoretically impossible (Felsenstein 1981), in nature. When ranges overlap, the result suggests, australopith cladogenesis is

essentially less likely than when they do not. This result also aligns, broadly, with models of ecologically-driven cladogenesis in which splitting rate slows when ecological niches are filled (Rabosky 2013), and also with previous simulation studies suggesting cladogenesis in sympatry can be "extremely" slow if there is a high cost to assortative mating (Bolnick 2004). Whether the pattern reported here for *Australopithecus* is the consequence of the ecological, genetic, or behavioural factors that have been implicated in slowing down the rate of splitting in sympatry in extant animals cannot be clarified based on these data alone; but the ecological hypothesis should certainly be empirically tested with fossil data in the future. If the saturation (or near-saturation) of ecological niches restricted cladogenesis in *Australopithecus* species that overlapped spatially with other hominins, these species should show strong phenotype-environment correlations (Schluter 1996), but, as discussed above, the evidence for this in terms of dietary specialization is weak. The strongest evidence, perhaps, is the inferred differences in broad dietary niches of *Australopithecus* and *Paranthropus.* In relation to the patterns reported here for *Australopithecus*, however, it is difficult to argue that the saturation of these two broad niches restricted cladogenesis because there is no clear evidence of sympatry between taxa belonging to these two genera (Wood and Boyle 2016), and the pattern is not found for *Paranthropus*. It might be the case that, instead of dietary niches, the saturation of locomotor or postural niches in sympatry restricted early lineage divergence in *Australopithecus*. However, as with the evidence for dietary adaptations, variation in suites of locomotor traits is difficult to link to clearly defined niches with any certainty. Phylogenetic data alone cannot definitively distinguish between locomotor or dietary niche partitioning, but the pattern reported here can be taken as the foundation for future directions exploring the ecological factors regulating splitting rates in *Australopithecus*.

What remains to be explained is why *Australopithecus'* splitting rate is slower in in non-isolated taxa on the most speciose composite tree, and not so on the two less speciose Parins-Fukuchi phylogenies. In the context of the threshold model, the implication of these results is that the splitting of lineages early on in the process of speciation was slower when these lineages overlapped spatially with other hominins—or in other words, that incipient lineages formed more frequently across a given period of time when parent taxa were geographically isolated. The formation of more morphologically differentiated taxa when parent taxa overlapped spatially with another taxon, however, occurred at the same rate as that when parent taxa were isolated. If the geography of cladogenesis was broadly the same at both levels of taxonomy (i.e. if morphologically inclusive taxa on 'lumped' phylogenies *and* the split lineages they comprise are all either isolated or non-isolated), then these results suggest, potentially, that splitting events of incipient lineages were decoupled from splitting events of more morphologically diverged lineages in isolation (see Figure 12-5). In other words, the

rate at which incipient lineages are able to form in isolation often exceeds the time required for the degree of morphological differentiation required for a split to be recorded on a 'lumped' phylogeny to accrue; or, perhaps more simply, in isolation there is less competitive pressure to diverge from a sister taxon morphologically. This aligns, broadly, with empirical data from birds (e.g. (Dong et al. 2020)), which suggests that secondary contact following allopatric divergence accelerates morphological differentiation.

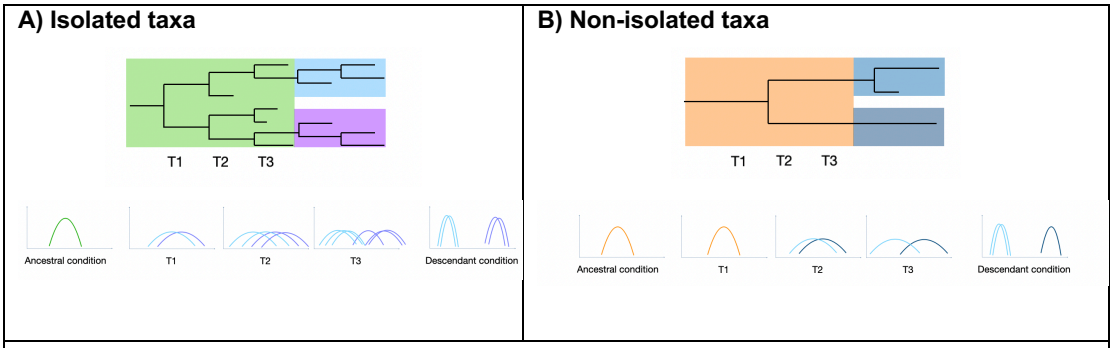


Figure 12-5: *Australopithecus* cladogenesis in isolation and non-isolation

Figure shows a phylogeny based on a less inclusive 'splitting' taxonomy in black, imposed on hypodigms of a 'lumped' taxonomy. The rate of lineage splitting is higher, here, when parent taxa are isolated, shown in A); in other words, DR is significantly slower in non-isolated taxa, shown in B). However, on phylogenies based on more inclusive 'lumping' taxonomies, there is no difference between DR in non-isolated and isolated taxa. Thus, the rate at which sufficient levels of morphological differentiation for lineages to be registered as separate species on the 'lumped' phylogeny is the same in non-isolation and in isolation. This might imply that splitting events of incipient lineages were decoupled from splitting events of more morphologically diverged lineages in isolation: in the figure, this is captured by the difference in the number of splits on the speciose phylogeny relative to the number of splits on the lumped phylogeny. In non-isolation, there is only one split at both levels. In other words, the rate at which incipient lineages are able to form in isolation often exceeds the time required for the degree of morphological differentiation required for a split to be recorded on a 'lumped' phylogeny to accrue; or, perhaps more simply, in isolation there is less competitive pressure to diverge from a sister taxon morphologically.

The overall pattern, in sum, is that hominin splitting rates were no slower in non-isolated taxa than in isolated taxa, save one exception. If, on average, non-isolated taxa shared a large proportion of their range, theoretical models imply there are two conditions which must have played important roles in hominin splitting events: intense disruptive selection, or direct selection on reproductive traits and mate choice, or both. However, given limitations of the fossil record, the degree of range overlap of hominin taxa is difficult to reconstruct; and it is probable that the results are the outcome of non-isolated taxa generally not overlapping spatially, or temporally, or both, sufficiently for the predicted pattern of splitting rate slowdowns to emerge.

12.3.2 Diversity-dependent cladogenesis?

When it comes to the question of the effect of overall hominin diversity on the rate of cladogenesis, the Red Queen does what is expected of her. That is, hypotheses based on the fundamental patterns of cladogenesis reported in Chapter 9 were supported by these data—with one exception: the patterns found for the genus *Homo*.

These expectations were, first, that there should be no diversity-dependence for the clade as a whole across any phylogeny, because there is no signal that splitting rates slowed down after peak diversity at this level; and second, that all three genera should show negative diversity-dependence across the Parins-Fukuchi phylogenies, because here they *do* show splitting rate slowdowns. For the clade as a whole, the prediction is met: there is no statistically significant relationship between overall hominin diversity 200k years before measuring points across any phylogeny.

On both Parins-Fukuchi et al. trees, splitting in *Australopithecus, Paranthropus,* and *Homo* was regulated by hominin diversity. The method has a false positive rate of ~4% on simulated phylogenies, suggesting these results can be treated with relative confidence. Surprisingly, the direction of the relationship between speciation and hominin diversity in *Homo* is the reverse of that in *Australopithecus* and *Paranthropus*. Contrary to speciation rates in these genera, which slow down as the number of (potentially) competing species grows, speciation rate *increases* as a function of diversity in *Homo*. The contrast between *Homo* and the two older genera explains the loss of a signal of diversity-dependence when hominins are pooled across the two Parins-Fukuchi et al. phylogenies.

Across the Parins-Fukuchi et al. trees, *Australopithecus* and *Paranthropus* DR is negatively related to general hominin diversity. That is, in phylogenetic GLS regressions of DR predicted by diversity, the slope term for these two genera is negative – although in all cases, the 95% confidence interval does overlap with 0, suggesting the effect is relatively weak. What the models are unequivocal about is that the pattern found for *Australopithecus* and *Paranthropus* is different to that found for *Homo,* in which DR is positively related to diversity. The overall patterns in *Australopithecus* and *Paranthropus*, then, are that across the Parins-Fukuchi et al. trees splitting rates slow down as a function of time (as reported in Chapter 9), and probably also as a function of the overall number of species.

Slowdowns in speciation rates are common across birds, reptiles, and mammals (Phillimore and Price 2008; Rabosky and Lovette 2008; Etienne and Haegeman 2012; Moen and Morlon 2014), and these clades almost always also show negative diversity-dependent speciation

(Moen and Morlon 2014). The most commonly invoked – although not often explicitly tested– causal link between negative diversity-dependence and speciation rate slowdowns is niche differentiation. In this model, speciation is regulated by ecological opportunity. Available niches become occupied by closely related species as a clade grows; when they are (nearly) all occupied, an ecological limit is reached, and speciation rate slows down (Schluter 1996; Gavrilets and Vose 2005). This model is nearly synonymous with adaptive radiation, with the only difference being that speciation must occur rapidly at the beginning of an adaptive radiation (Schluter 1996). Slowdowns in speciation rate can also occur as a result of diversity-dependent speciation without the phenotypic specialisation implied by the niche differentiation model: if the overall geographic range a clade occupies is bounded, strong slowdowns in speciation rate are expected over time as the range is subdivided over successive speciation events (Pigot et al. 2010; Moen and Morlon 2014). At the scale of this analysis, of course, this range is (primarily East and South) Africa before c. 1.8 Ma, and it is extended to Eurasia afterwards. Distinguishing between niche differentiation and geographic partitioning scenarios requires the presence (in the case of the former) or absence (in the case of the latter) of phenotype-environment correlations: as discussed above, the evidence for explicit links between phenotype and niche is weak in terms of diet and locomotion – but this could simply be the consequence of relatively coarse environmental and dietary reconstructions. The geography of hominin splitting was discussed more fully above: but the major point is that it is difficult to reconstruct with any certainty. In sum: splitting in *Australopithecus* and *Paranthropus* was probably regulated by the number of other competing hominin taxa: but whether the cap on clade expansion was an ecological or geographic one is unclear.

*Homo'*s pattern of positive diversity-dependent speciation on the Parins-Fukuchi et al. trees is unexpected, not least because it evidently sets it apart, in macroevolutionary terms, from its hominin relatives. Casting the comparative net a little wider, positive diversity-dependence is not what is expected based on *Homo*'s slowdown in speciation rate over time. Slowdowns in speciation rate in other animals are habitually taken as evidence for negative diversity-dependent speciation dynamics (Moen and Morlon 2014); the results for *Homo* illustrate that this link is not a given. The question, of course, becomes: why and how was *Homo* able to escape the limits on cladogenesis imposed by closely related and competing species that shaped, to a degree, cladogenesis in *Paranthropus* and *Australopithecus* – and, perhaps even more intriguingly, how did the presence of other taxa act as a promotor, rather than a prohibitor, of cladogenesis? The first question rests on a major assumption: that *Homo* directly competed with other hominin taxa for the same ecological niches or geographical space. Competition for ecological niches, again, is difficult to ascertain with real certainty;

but there is some indirect evidence that this was the case. Schroer & Wood (2015), for example, found evidence of character displacement between early *Homo* and *Paranthropus* in mandibular premolar morphology. Regarding geographical space, the evidence is even stronger: late members of *Australopithecus* and *Paranthropus* occupied the same areas as early members of *Homo* (Domínguez-Rodrigo et al. 2013).

There are three ways in which *Homo* could have escaped the checks on speciation imposed by the interspecific competition it thus presumably also faced, thereby reversing the species-splitting relationship: by outcompeting *Australopithecus* and *Paranthropus* for ecological niche space, by actively carving out new niche space, or by expanding its range. The latter it did – but only really after *Australopithecus* and *Paranthropus* became extinct. Regarding the first two options, a key way in which *Homo* was likely able to outcompete other species *or* access new ecological niche space in saturated evolutionary environments was through technology. That is, technology might either have allowed *Homo* to compete for the same resources more efficiently, or it may have been the case that repeated innovations in lithic technology made possible the extraction of novel resources from the environment (Bird and O'Connell 2006; Blumenschine and Pobiner 2007). Of course, lithic technology predates *Homo* (Harmand et al. 2015), but what can be said with some certainty is that *Australopithecus* and *Paranthropus* did not rely on stone tool technology to the same degree as did *Homo*.

If competing for the same niches as *Paranthropus* and *Australopithecus* – and indeed, outcompeting them – explains the positive relationship found between DR and species diversity for *Homo*, this raises an important point: that the emergence of *Homo* contributed to their extinction. In this model, *Homo* effectively replaces its predecessors and fills the broad ecological niches these occupied. The advantage of this model is that it explains why there is no signal of diversity-dependence *or* a slowdown in cladogenesis after peak diversity for hominins as a whole; but on the other hand, the effect of climatic change on these dynamics cannot be discounted on the basis of these data. Indeed, these results can also be interpreted in the context of "Court Jester" models – in which case there need not have been direct competition for the same niches, as changes in climate with which the emergence of *Homo* overlaps remodelled the ecological landscape (Vrba 1993). However, when the evidence for competition between *Homo* and *Paranthropus* (Schroer and Wood 2015) is combined with the prevalence of overlap in ranges between early *Homo* and late *Australopithecus* and *Paranthropus* (Domínguez-Rodrigo et al. 2013), the degree of ecological remodelling required for a complete non-overlap of niches, the results presented here, and the generally weak signal of an impact of climate on hominin cladogenesis discussed in Chapter 10, there is

a strong case to be made that competition between *Homo* and its predecessors shaped, at least to some degree, their patterns of cladogenesis.

The suggestion that a possible response to competition was the active creation of new niche space through technological innovation stands in stark contrast to Wolpoff's single species hypothesis (Wolpoff 1971), which held that hominin "culture" precluded cladogenesis. Instead, if members of *Homo* used it to access novel niches, these results suggest that cultural behaviour in *Homo* enabled cladogenesis. The idea that niche construction (Odling-Smee, Laland, and Feldman 2013) has played an important role in human evolution is not new; but it tends to be discussed in terms of a smaller-scale phenomenon – namely, gene-culture coevolution. If it was indeed technological behaviour that explains the patterns reported here, culture fundamentally affected evolution at much larger scales as well: it reversed a macroevolutionary relationship between cladogenesis and the number of species occupying given niches that has been documented in diverse clades across the tree of life.

One question remains for the Parins-Fukuchi et al. phylogenies: was it only competition with *Australopithecus* and *Paranthropus* that drove the pattern in *Homo*, or also competition between members of *Homo*? To answer this question, I repeated the analysis on both Parins-Fukuchi trees but using the number of only *Homo* taxa alive 200k years before each measuring point. On the original Parins-Fukuchi et al. tree, there was a positive relationship between *Homo* DR and the diversity of *Homo* species (slope parameter: 0.173, $p<0.05$); but on the "high certainty" Parins-Fukuchi et al. tree, there was no relationship (slope parameter: 0.036, $p=0.56$). In the context of the threshold model, then, the emergence of the most morphologically diverged forms of *Homo* was determined not by competition with other, equally diverged *Homo* taxa – only competition with late *Australopithecus* and *Paranthropus*. The pattern on the original Parins-Fukuchi phylogeny, however, is that competition between species of *Homo* did still play a role in cladogenesis.

On the composite phylogeny, as was expected based on the absence of a slowdown in DR after peak diversity in *Homo* and *Australopithecus*, there is no statistically significant correlation between hominin diversity and DR. Although *Paranthropus*' DR was significantly slower after peak diversity on this phylogeny, it, too, is not characterised by a significant correlation between diversity and splitting rate – again, then, time-dependent cladogenesis does not necessarily go hand-in-hand with diversity-dependence, as much previous work in extant clades has assumed (Phillimore and Price 2008). In summary, early lineage splitting was not curtailed by the number of putatively competing lineages at this level. There are a number of explanations for this pattern in an ecological framework. The first is that a pattern

of diversity-dependence is only expected if there is a relatively consistent taxon-niche correlation – that is, that each new taxon occupies a specific niche. It may well be the case that the incipiently diverging lineages captured on this phylogeny did not differ sufficiently from closely related taxa to meet this requirement. This point is relatively well-supported by the fossil record: for example, there is little evidence that the diverse Middle Pleistocene members of *Homo* recognized at this taxonomic level (i.e. *Homo helmei, Homo antecessor, Homo heidelbergensis*) are ecologically extremely differentiated (Pearson 2013). In the absence of niche differentiation at this level, competition between taxa could still affect cladogenesis through the partitioning of geographic space; that is, taxa could exclude each other from specific ranges – but these results suggest that this was not the case either. The second explanation is that these incipient lineages did occupy distinct niches, but that there was no ecological limit to the number of taxic diversity at this level; or, if there was, that this limit was never reached. Whether or not ecological 'limits' are ever reached is an unanswered in evolutionary biology, however: a 'maximum' number of niches is difficult to determine (Rabosky 2013; Moen and Morlon 2014).

In sum, in the context of the threshold model, the results suggest that it was only relatively more morphologically diverged taxa that affected each other's cladogenesis: across the composite tree, there were no statistically significant correlations between diversity and DR at any level. This is most probably because incipiently diverging lineages occupied very similar ecological niches, so that the presence of one does not necessarily imply the occupation of a niche. It could also be because, at this level, there was no ecological limit to taxic diversity, or if there was, that this limit was never reached. On the two Parins-Fukuchi et al. phylogenies, however, cladogenesis in all three genera was regulated by the diversity of other hominin species competing for ecological niche space, geographical space, or both: but surprisingly, the pattern seen in *Homo* is the reverse of that seen in *Australopithecus* and *Paranthropus*. In these two genera, the more extant taxa, the slower cladogenesis—and although the ecological niche versus geographic partitioning models cannot be distinguished between using the data presented here, this implies that competition between hominin taxa shaped their cladogenesis, as expected. The *positive* relationship between species diversity and cladogenesis in *Homo* reveals that, rather than restricting cladogenesis as they did in *Australopithecus* and *Paranthropus*, competing species were a pressure for *Homo* to diversify.

12.3.3 Synthesis and summary

In the briefest terms, the key results of this chapter are, first, that range overlap—the size of which is difficult to reconstruct based on fossil data—did not tend to slow hominin cladogenesis down; but second, that cladogenesis within individual genera *was* determined by the overall number of hominin taxa.

Taken together, these results can be interpreted as the product of hominin taxa principally affecting each other's cladogenesis through the saturation of geographic space. Figure 12-6 illustrates this model. It assumes the geographical space into which hominin taxa could speciate was bounded, but its area can theoretically be as large as all terrestrial habitats available to hominins. Within this bounded space, there is a limit to the number of hominin ranges, each occupiable by one taxon alone: when there is unoccupied space, splitting is possible into it, and when all or most viable ranges are occupied, splitting rate is constrained. Thus, the more taxa, the more geographical space is occupied, and splitting rate slows concomitantly. This pattern is indeed found for *Australopithecus* and *Paranthropus* on the Parins-Fukuchi et al. phylogenies, although the signal is somewhat weak.

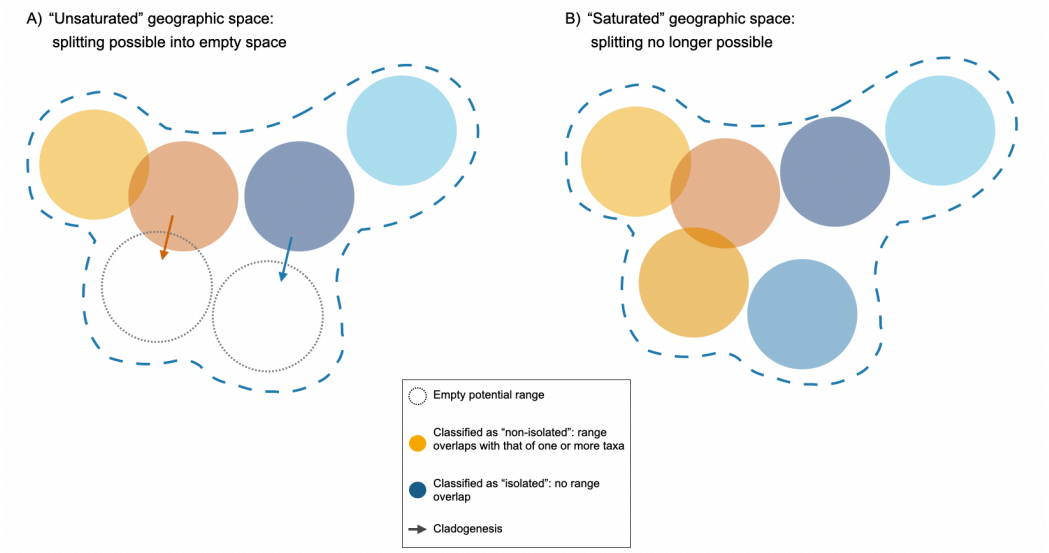


Figure 12-6: The saturation of geographic space controlling hominin cladogenesis

Within bounded geographical space, there is a maximum limit to the number of taxa whose ranges can exist within it. In this figure, there is a maximum of six taxa. The results from this chapter suggest the availability of geographic space was the primary determinant of hominin splitting rate, not range overlap: thus, both non-isolated taxa (that is, their range overlapped with that of one or more hominin taxon) and isolated taxa (whose ranges did not overlap with those of any other hominin) have the same rate of cladogenesis across the time period from A) to B).

On the same phylogenies, *Homo* is characterised by the opposite pattern: splitting rate is higher when there are more extant taxa. In this model, this pattern is explained by the emergence of *Homo* happening in the context of competition for space already saturated by *Australopithecus* and *Paranthropus*. The competition implied here does not necessarily imply direct competition for ecological niches, as it might be the case that *Homo* made available new ecological niche space within biogeographically saturated environments; but there is some indirect evidence (e.g. Schroer and Wood (2015)) that direct competition for dietary resources between *Homo* and *Paranthropus* resulted in dental character displacement. An alternative explanation, still concordant with the model, is that the bounded space which placed caps on clade expansion in *Australopithecus* and *Paranthropus* did not contain *Homo* in the same way: this is supported by *Homo*'s cosmopolitan distribution. *Homo* is, by all accounts, an evolutionarily odd genus, at least in terms of its autapomorphies: its members had unexpectedly large brain sizes for mammals and primates of their size (Aiello and Wheeler 1995), they relied far more heavily on manufactured tools for extractive foraging than any extant animal (Sanz, Call, and Boesch 2013), and were the first in hominin evolution to range intercontinentally (Carotenuto et al. 2016). What has received far less attention is the question of whether its speciation dynamics are equally unusual in comparative context: and although the data presented here do not permit the disentangling of exactly *why* the caps on splitting in *Australopithecus* and *Paranthropus* did not shape splitting in *Homo* in the same way, the results presented here suggest these dynamics were indeed unusual.

In this model, the availability of geographic space is the primary determinant of splitting rate, not range overlap—as suggested by the data. It is entirely possible, and indeed predicted by models that link interspecific competition with range sizes and distributions (Case et al. 2005; Price and Kirkpatrick 2009), that zones of overlap between competing taxa comprise a relatively small proportion of their overall ranges, so that direct competition for resources in overlapping ranges was a negligible element of the overall selective pressures experienced by hominin taxa. The alternative, of course, is that ranges of non-isolated taxa *did* overlap substantially, both spatially and temporally, but that this overlap did not restrict the rate of cladogenesis in sympatry. If so, competition for biogeographic niche space can remain the principal determinant of splitting rate, as suggested by the results for overall diversity (see Figure 12-7): and this implies some key differences between ecological strategies of lineages that tended to split in allopatry versus those that tended to split in true sympatry. More specifically, as discussed above, splitting in sympatry is theoretically only possible in cases of intense disruptive selection, or direct selection on reproductive traits and mate choice, or both. The consequent expectation is that taxa that speciated in sympatry should show stronger environment-phenotype correlations than those that speciated without geographical overlap.

The geographic pattern of diversification implied by the lack of a significant difference between rates of cladogenesis in isolation and non-isolation is probably somewhat different to that when non-isolated taxa do not share significant portions of their ranges: the isolated lineage is then more likely to colonize a larger proportion of the overall bounded geographical space (see Figure 12-7). The limitations of the fossil record are such that exact range sizes *and* the degree of spatial overlap between hominin taxa will probably remain ambiguous, however.

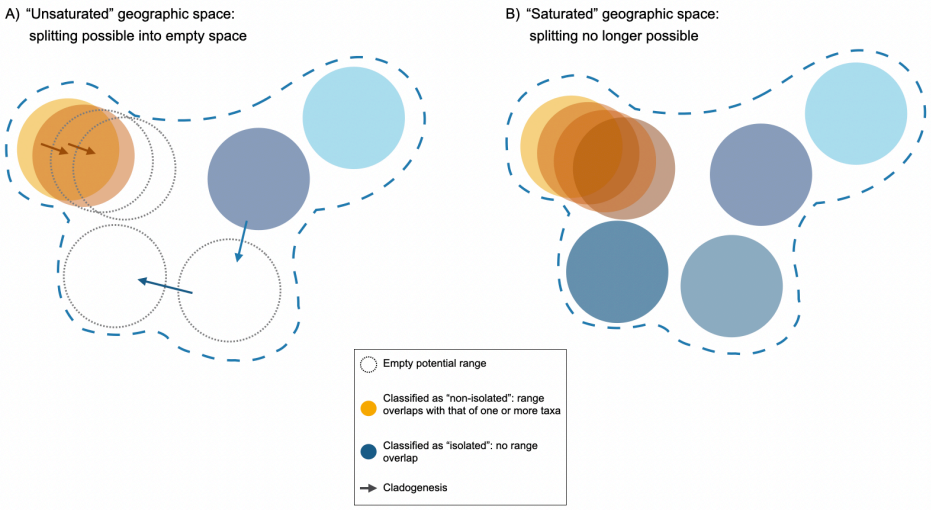


Figure 12-7: The saturation of geographic space controlling hominin cladogenesis in cases where non-isolated taxa share large portions of their ranges

As in Figure 5, there is a maximum limit to the number of taxa whose ranges can exist within a bounded area. Here, however, non-isolated taxa *do* overlap spatially to large degrees. The consequent geographic pattern of diversification implied by the lack of a significant difference between rates of cladogenesis in non-isolated taxa and isolated taxa is different to that when non-isolated taxa do not share significant portions of their ranges: here, the isolated lineage colonises a larger proportion of the overall bounded geographical space.

The combination of results presented here can thus be interpreted as a signal that there was a limit to the number of hominin taxa within bounded geographical space—and since this analysis included all hominin taxa, this bounded space probably refers to all areas habitable to hominins. The question then becomes: is there evidence for such limits in extant taxa, and what set these limits? Regarding the former, Rabosky (2009) made the case that the lack of a relationship between clade age and diversity, found across many higher taxa and timescales, is the outcome of ecological limits on diversity. Rabosky's argument for ecological limits to species richness is evidently indirect, however, and has been criticized on these grounds by Wiens and Dykhuizen (Wiens and Dykhuizen 2011). Direct evidence for caps on diversity is difficult to come by, in part because it is unclear at which geographic scale such limits should exist (Cornell 1993). Some direct evidence that, at least for some clades and in certain

geographical cases, limits to diversity do exist comes from community compositions of anoles on the Greater Antilles: although the islands comprise different faunas at the species level, communities are ecologically extremely similar, suggesting a ceiling to the number of ecomorphs a bounded area can support (Losos et al. 1998). Case et al. (2005) speculate that communities of land birds on either side of Wallace's line are stable represent alternative stable states, resisting colonization by other taxa as a consequence of ecological saturation. Theoretical models, further, also predict limits to species richness: although interestingly, this is only true in the context of biotic interactions, including interspecific competition for niche space (MacArthur, Diamond, and Karr 1972; Cornell and Lawton 1992; Cornell 1993). In sum, then, there is some evidence from extant taxa that limits to diversity exist in some cases, and these cases align with predictions from theory. That is, extant cases arise from ecological limits: there is a set maximum number of ecological niches within bounded space. Within hominins, as discussed above, unambiguous links between phenotype and niche are difficult to establish—although this can simply be the consequence of relatively coarse environmental reconstructions. The point, then, is that limits to diversity do seem to exist in nature, although direct evidence is hard to come by; that these limits tend to be linked to caps on the number of ecological niches within bounded space; and that it is ambiguous whether such limits operated to produce the patterns reported here, because phenotype-niche correlations are difficult to reconstruct based on fossil evidence.

A different limit to the number of taxa, alluded to in the descriptions of the model advanced above, is that there is a spatial control on diversity. A common pattern across vertebrates is that species have spatially confined geographical distributions and that closely related taxa have only small zones of overlap between them (Case et al. 2005): it follows that, if species' range sizes and the degree to which they overlap with those of competitors are controlled by biotic or abiotic factors, these factors also produce a limit to the number of ranges that can fit within bounded space. These ranges need not overlap with specific ecological niches. The most obvious controls on species' range sizes and distributions are abiotic barriers such as mountain ranges and coastlines: Lynch Alfaro et al. (2015), for example, make the case that the distribution of *Lagothrix* was determined during its radiation by the Amazon and Tapajós Rivers, and the Andes. Abiotic barriers, however, do not necessarily set a limit to the number of ranges within an area; and it might indeed be the case, as it was for *Lagothrix*, that abiotic barriers set the physical bounds of the area within which hominins diversified. Theoretical work derived from Lotka-Volterra equations has shown that, instead of abiotic factors, interspecific competition can set ecologically and evolutionarily stable range limits in various ways (MacLean and Holt 1979; Roughgarden 1979; Holt and Keitt 2000; Price and Kirkpatrick 2009). For example, Roughgarden (1979) demonstrated that, in the case of an

environmental gradient along which two species' carrying capacities varied inversely (that is, for the first taxon, the highest carrying capacity is possible at one end of the gradient while the opposite is true for the second taxon), competition in the region of overlap would lead to defined range boundaries. Further, MacLean and Holt (1979) showed that in the case of two taxa whose interspecific and intraspecific competition intensity are equal, the species with the higher carrying capacity will exclude the other, so range limits are set where ranking of either taxon's carrying capacity changes. Theoretical models also predict varying degrees of range intersection based on the strength of interspecific competition, spatial starting conditions, environmental heterogeneity, and other factors (e.g. Case et al. 2005): thus, interspecific competition setting a limit to the number of taxa within an area leaves room for variation in the level of range overlap.

This makes for a dynamic model relating interspecific competition to hominin cladogenesis, in which interactions between hominin taxa determine the cap on taxic richness, and thus future cladogenesis, within an area. What is particularly attractive about this model is, firstly, that it does not necessarily invoke only niche-based limits on speciation, for which there is not much obvious evidence in hominin phenotypes: but does not preclude such processes *a priori* either. Secondly, it is to be expected that this maximum number of taxa was not static over evolutionary time as community compositions changed; and this goes some way to explain why the signal for *Paranthropus* and *Australopithecus* was somewhat weak, with 95% CIs overlapping with 0.

Finally, taken within the threshold model and the geographic model described above, the disparity in signals of diversity-dependence between the speciose composite phylogeny and the less speciose Parins-Fukuchi et al. phylogenies suggest that there was no limit to the number of taxa at the scale captured by the composite phylogeny—or, more probably, that this limit was not reached (see Figure 12-8). Thus, the splitting of more exclusively defined populations within larger hypodigms, captured on the composite phylogeny and Parins-Fukuchi et al. phylogenies respectively, could be constrained by the diversity of other taxa at this level; but the results suggest a sufficient level of saturation might not have been reached. Consequently, the splitting of populations at the incipient stages of speciation was not constrained by the taxic diversity at this level.

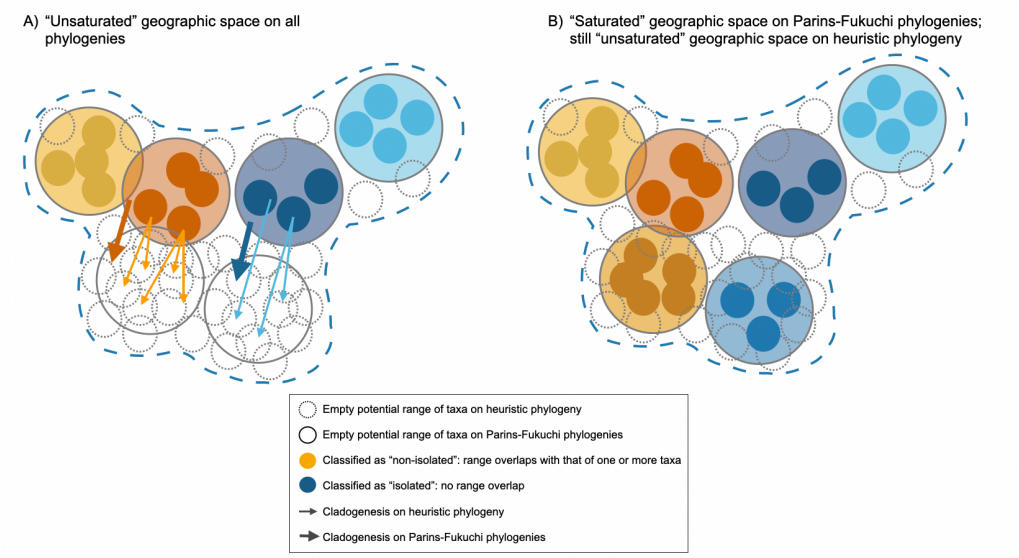


Figure 12-8: The saturation of geographic space controlling hominin cladogenesis at different levels of taxonomy

Within bounded geographical space, there is a maximum limit to the number of taxa whose ranges can exist within it; and this is the case for both more and less inclusive taxonomies indicated with solid lines and dashed lines respectively. Although the maximum number of taxa is reached for the more inclusive taxonomies in B), and splitting rate is consequently restrained, this is not the case for taxa defined in less inclusive taxonomies: thus, these can still split into new geographical space in B).

12.4 Conclusion

In sum, there are two key results in this chapter: first, range overlap did not tend to slow hominin cladogenesis down; and second, cladogenesis within individual genera was determined by the overall number of hominin taxa, although *Homo* was characterised by the opposite pattern to that seen in *Australopithecus* and *Paranthropus*. These results, taken together, are concordant with a model in which hominins primarily shaped each other's cladogenesis through competition for geographic space, and not through competition for the same resources within an extensively overlapping range. I suggested that, within bounded space, there was a limit to the number of ranges, each occupiable by a single hominin taxon. This limit might be explicitly ecological, as it is in some extant communities in which there seems to be a limit to the number of niches within bounded space; or it might arise from interspecific competition in other ways. Splitting is possible so long as there is unoccupied space, and when all or most viable ranges are occupied, splitting rate is constrained, resulting in negative diversity-dependent cladogenesis. This pattern is indeed found for *Australopithecus* and *Paranthropus* on the Parins-Fukuchi et al. phylogenies, although the signal is somewhat weak: this is possibly because the maximum number of taxa was not static over evolutionary time as community compositions changed. On the same phylogenies, *Homo* is characterised by the opposite pattern: splitting rate is higher when there are more extant

taxa. In this model, this pattern is explained by the emergence of *Homo* happening in the context of competition with *Australopithecus* and *Paranthropus* for space already saturated. Although the data presented here do not shed light on how *Homo* was able to outcompete other species *or* access new ecological niche space in saturated evolutionary environments, a compelling case can be made that this was made possible through technology. That is, technology might either have allowed *Homo* to compete for the same resources more efficiently, or it may have been the case that repeated innovations in lithic technology made possible the extraction of novel resources from the environment. Whatever the underlying process, these results suggest *Homo* was characterised by comparatively unusual and unexpected dynamics of cladogenesis of morphologically diverged taxa.

13 Speciation in extinct hominins

13.1 A metapopulation model of hominin speciation and its determinants

13.1.1 Review of the threshold model

Speciation is a temporally extended process initiated by the formation of population isolates within species, and generally culminating in the establishment of reproductive isolation and morphological differences between these isolates. The fundamental question on which this section was centered was how biotic (interspecific competition) and abiotic (time and climate) factors influenced hominin population splitting at various stages of speciation, and crucially, how these factors mediate the relationship between these stages.

I put forward the idea that, rather than representing irreconcilably disparate approaches to hominin taxonomy, "split" and "lumped" interpretations of the hominin fossil record can be used as tools to answer this question. "Split" taxonomies recognize splits between less morphologically diverged taxa, while "lumped" taxonomies name more morphologically diverged taxa. Phylogenies based on "split" taxonomies can therefore be used to ask what factors influence the rate of less morphologically diverged lineages, while those based on "lumped" taxonomies can be used to ask how these same factors determine the rate at which these lineages accrued sufficient morphological divergence to be recognized as separate taxa within this framework.

The degree to which the stages captured by these taxonomies approximate the key stages of speciation described above (that is, its initiation through population isolate formation; and a much later stage at which the process nears its end) depends entirely upon the degree to which morphological differences accrue over the course of speciation, and this is by no means consistent across time, taxa, or space. For example, it is unlikely modern chimpanzees and bonobos would be recognized as separate taxa on a "lumped" phylogeny, even though they are considered genetically diverged, separate species (Prüfer et al. 2012). This is the reason that, throughout this section, I referred to taxa on "lumped" phylogenies as more morphologically diverged taxa, rather than simply as fully diverged species. The model, further, is limited in that it ignores cryptic speciation as well as speciation involving morphological divergence in characters that do not fossilize. The model is, ultimately, purely based on morphology and therefore only captures one dimension of speciation: but this remains, unfortunately, a limitation of the fossil record rather than a failing of the model

specifically.

13.1.2 The link with a metapopulation model

The link between the threshold model and the metapopulation model of speciation introduced in Chapter 7 is fairly instinctive: taxa recognized on "split" taxonomies represent independent populations within metapopulations, which are recognized as species on "lumped" taxonomies. This is illustrated in Figure 13-1. Correlations between abiotic and biotic factors and cladogenesis on the composite tree, then, shed light on the factors that affect the rate at which population isolates are formed within metapopulations, while correlations between the same factors and cladogenesis on the Parins-Fukuchi et al. trees shed light on how these factors determine the rate at which these isolates become morphologically distinct from its parent metapopulation, and speciation is completed. The limitations of the threshold model derived from its use of only morphological data are, of course, transferred to the metapopulation model of hominin splitting: that is, it relies on the critical assumption that morphological divergence accompanies speciation, and will fail to include instances of speciation involving non-fossilised morphological change and cryptic speciation.

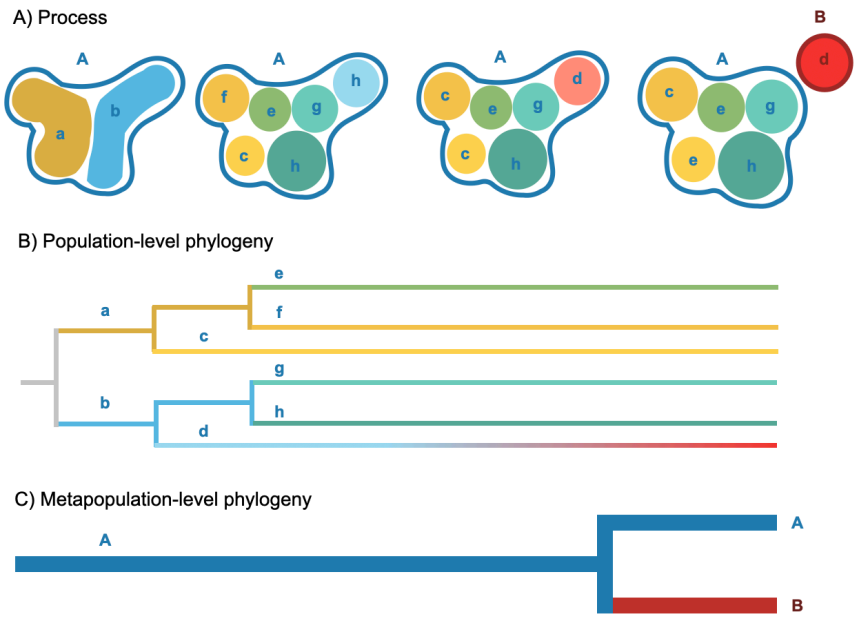


Figure 13-1: A metapopulation model of hominin splitting

A) shows the geography of speciation; B) shows this process on phylogeny at the level of populations; C) shows this process on a metapopulation phylogeny. Metapopulations are denoted labelled with capital letters; populations within them with lowercase letters. Metapopulation A initially comprises two populations (a and b), which each split into three further populations (a into c, e, and f; and b into d, g, and h). Only population d accrues enough morphological differences for it to be recognized as a new metapopulation, B.

What follows is a summary of the principal conclusions from each chapter in this section in the context of the metapopulation model.

13.2 Section B results in the context of the metapopulation model

13.2.1 What are the basic patterns of hominin cladogenesis?

1. Average splitting rates of metapopulations do not differ significantly between *Australopithecus, Paranthropus,* and *Homo*. The rates at which populations split does differ significantly between the three genera, however, with *Homo*'s rates significantly higher than those of its two predecessors. Taken together, these results suggest that within *Homo* metapopulations, distinct populations formed more frequently but that this did not scale up to a higher rate of metapopulation splitting: thus, these data suggest that in *Homo*, population splitting is more decoupled from metapopulation splitting than it is in *Australopithecus* and *Paranthropus*.
2. Across the hominin clade as a whole, splitting rates of metapopulations *and* populations are not significantly slower after peak diversity than before peak diversity. This is not what is expected: slowdowns in splitting rates have been found across the tree of life, and are usually explained as the consequence of niche-based caps on taxic diversity (Moen and Morlon 2014). The most likely explanation for the absence of this pattern across all hominins is that caps on taxonomic diversity are found within adaptive grades, so that, for example, competition for a restricted number of niches occurs mostly between species within the same genus.
3. The three phylogenies differ in the signals of time-dependence they contain at the scale of genera. The general pattern is that metapopulation splitting occurs significantly more slowly after peak diversity within genera: so, within adaptive grades, splitting rate slows down over time, and this is consistent with limits on niche availability. Population splitting, however, does not slow down over time. Thus, these data suggest that, within genera, population splitting became decoupled from metapopulation splitting over time. It might be the case that the evolutionary trajectory of a population is limited by metapopulation-level, or species-level niche availability.

13.2.2 Was hominin speciation climate-dependent?

1. The clearest signal in these results was the lack of a consistent relationship between climate and variation in splitting rate. The results suggest climate and hominin splitting were related in more complex, diffuse, and potentially nonlinear ways than previous work, based on first appearance dates (FADs) as proxies for speciation, has

concluded. The time range across which climate tended to operate to influence cladogenesis was also unclear.

2. Signals were thus diffuse: but taken together, the data across the clade as a whole more strongly support a relationship between climatic variability and hominin cladogenesis (as in the Variability Selection Hypothesis (Potts 1998a)) than a consistent role for changes in temperature in determining splitting (as in the Turnover Pulse Hypothesis (Vrba 1985b)).
3. The link between climate and human evolution tends to be approached in terms of climate-based selection for hominin autapomorphies (e.g. (Shultz and Maslin 2013; Potts 1998b; Grove 2011)). The results presented here suggest the role of climate might, in addition, be as a determinant of population-level processes and how these relate to metapopulation-level splitting. Across the clade as a whole, population splitting rate slowed—that is, populations persisted for longer periods of time—in times of less climate variability, while the relationship between metapopulation splitting and climate stability was inverted. This suggests the longer-term persistence of populations necessary for these to split from the rest of the metapopulation tended to occur in more stable climates.
4. This was the pattern for the clade as a whole; but *Homo* and *Australopithecus* differed in the exact way climate mediated the link between population-level processes and metapopulation-level patterns. In *Australopithecus*, general temperature trends also have an effect, with extended population persistence and metapopulation splitting happening at higher rates during periods of warming. In *Australopithecus,* then, populations tended to be produced in periods of variability and cooling, and these split from the rest of the metapopulation in periods of stability and warming. In *Homo*, however, variation in the rate of population splitting in this genus was unrelated to any climate variable. This probably reflects a nonlinear relationship between climate and population splitting, with a sufficient level of variability and cooling being reached in *Homo* to ensure a higher population turnover regardless of variation in either climate variable. Climate possibly contributed to the decoupled relationship between population and metapopulation splitting in our genus. Climate did potentially play a role in metapopulation splitting in *Homo*: the cooler and more stable climate became, the higher the rate of cladogenesis at this scale; but this relationship was not driven by a relationship between climate and population-level processes.

13.2.3 What was the role of interspecific competition between hominin species in hominin speciation?

1. Splitting rates of taxa whose range overlapped with that of one or more other hominin taxa were no different to splitting rates of isolated taxa. This was true for metapopulations and populations alike, and suggests competition for resources in areas of range overlap did not tend to slow splitting rate down. If, on average, non-isolated taxa shared a large proportion of their range, intense disruptive selection, direct selection on reproductive traits and mate choice, or both must have played important roles in hominin cladogenesis. However, the degree of range overlap of hominin taxa is difficult to reconstruct based on fossil evidence; and it is probable that the results are the outcome of non-isolated taxa generally not overlapping sufficiently in spatial or temporal terms—or both.
2. Within genera, metapopulation splitting rate was regulated by the overall number of extant metapopulations, while population splitting rate was not determined by the diversity of extant populations. The direction of the relationship between diversity and metapopulation splitting rate was significantly different in *Homo* than in its predecessors, which followed the pattern seen in many vertebrate clades. In *Australopithecus* and *Paranthropus*, as in birds, reptiles, and other mammals, metapopulation splitting rate slowed as a function of increasing diversity, meaning cladogenesis was regulated by competition for ecological or geographical space. In *Homo*, by contrast, metapopulation splitting rate is higher when there are more extant taxa. It is possible *Homo* competed with *Australopithecus* and *Paranthropus* for space already saturated, and, although the data presented here do not shed light on how *Homo* was able to outcompete other species *or* access new ecological niche space in saturated evolutionary environments, a case can be made that either was possible through technology. Regarding population splitting rate, the lack of a signal that population diversity restricted population splitting implies that at this level, there was no competitive limit to taxic diversity; or if there was, that this limit was never reached.
3. Taken together, these results are concordant with a model in which hominin metapopulations primarily shaped each other's cladogenesis through competition for geographic space, and not through competition for the same resources within an extensively overlapping range. In this model, there is a limit to the number of ranges, each occupiable by a single hominin taxon. This limit might be explicitly ecological, or it might arise from interspecific competition setting the boundaries between ranges. Metapopulation splitting is possible into unoccupied space but is constrained when all or most viable ranges are occupied, resulting in negative diversity-dependent

cladogenesis. This pattern is indeed found for *Australopithecus* and *Paranthropus,* while *Homo* shows positive diversity-dependent metapopulation splitting because it outcompetes *Australopithecus* and *Paranthropus* for space already saturated.

13.3 Nothing but mammals

The hominin apple did not fall far from the mammalian phylogeny: the majority of the patterns reported in this section are exactly those expected based on those reported for mammals, and indeed other vertebrates. Chapter 4 showed the link between subspecies and species is decoupled in terrestrial mammals relative to those in non-terrestrial mammals. Although *Australopithecus* and *Paranthropus* would not fall into that non-terrestrial group, the general pattern found across all mammals holds up in hominins: *Homo,* whose population-level splitting appears more decoupled from metapopulation-level splitting than that of its predecessors, led a more exclusively terrestrial existence than *Australopithecus* and *Paranthropus* (Georgiou et al. 2020; Rein et al. 2017; Ward 2002). Further, at the metapopulation level, slowdowns in splitting rates are observed over time: this pattern is found across vertebrate clades (Moen and Morlon 2014). *Australopithecus* and *Paranthropus,* moreover, follow the vertebrate rule book to the letter, and are characterised by negative diversity-dependent metapopulation splitting dynamics. Finally, the positive relationship between climate variability and population-level splitting is echoed in the relationship between habitat fragmentation and subspecies formation in all mammals suggested in Chapter 5.

Speciation in *Homo,* however, is characterised by two surprising patterns in comparative context. First, *Homo* did not have significantly slower splitting rates than the other two genera across the metapopulation phylogenies while its population-level splitting happened at a higher tempo than that of *Australopithecus* and *Paranthropus*. Results in Chapter 6 suggested that in primates, higher rates of population isolate formation correlated with higher speciation rates; so the pattern for *Homo* is unexpected. Second, *Homo* is characterised by the opposite pattern of diversity-dependent metapopulation splitting to that expected based on results across vertebrates (Moen and Morlon 2014): splitting rate is higher when there are more extant taxa. It is unclear, based on these data, exactly how *Homo* was able to outcompete other hominin species *or* access new ecological niche space in saturated evolutionary environments. In any case, these results suggest speciation dynamics of our genus were comparatively unusual—when it comes to *Homo*, we might be looking more at oranges than at apples.

13.4 Open questions and future directions

This section represents a shift away from the conventional use of FADs to explore determinants of hominin speciation, and aside from the results described above, it contributes a methodological foundation for future work. This future work falls broadly into three categories: first, clarifying elements of the theoretical model upon which interpretations are based; second, the application of the method to different potential correlates of hominin cladogenesis; and third, the testing of hypotheses, derived from the results presented in this section, using other methods.

The relationship between morphological change and speciation thresholds remains an important open question. There is evidence that the rate of morphological evolution and the rate of speciation are correlated (Rabosky et al. 2013); but what would be particularly useful here is an explicit comparative analysis of the degree and type of morphological divergence between the units known as "populations" in the metapopulation model and "less diverged taxa" in the threshold model, and "metapopulations" or "more diverged taxa" in mammals, and primates specifically.

The lack of support for a consistent role for climate in hominin cladogenesis across the clade is somewhat surprising given results from previous work, based on FADs, which generally support very strong and consistent links between speciation events and climate variables (Grove 2012; Lupien et al. 2020). This suggests at the limitations of using FADs to explore the determinants of hominin speciation—fossil appearances, after all, are not speciation events, nor are their temporal distributions determined by speciation rate alone—but the climate proxies used here are relatively coarse. Future work, then, should make use of a multivariate approach that includes other measures of climate, like Aeolian dust percentage (DeMenocal 1995), as well as further measures derived from $\delta^{18}O$ data, such as the eccentricity, obliquity, and precession components of climate that interact to create fluctuations in insolation (Grove 2012). Further, there are a number of variables previous work has implied as important determinants of splitting rates: these include range size (Dynesius and Jansson 2014), body size (Isaac et al. 2005), and ecological strategy (Day, Hua, and Bromham 2016). The method used here can be used to test the relationship between splitting rate and any variable for which there is sufficient data in hominins.

The results presented in this section can be used to generate testable hypotheses that can form the basis of future work. First, taken together, results in Chapters 11 and 12 raise an interesting possibility: that the role of climate on hominin cladogenesis was relatively indirect, operating through determining hominin range size and setting the taxic limits

implied by results in Chapter 12. There are many ways in which climate can set or change range limits of extant taxa (Gaston 2009; Van Der Putten, Macel, and Visser 2010), so reconstructions of hominin species' geographical responses to environmental change are needed to explore this idea. Second, a major point in Chapter 12 was the possibility that the unusual and unexpected positive relationship between metapopulation splitting rate and metapopulation diversity in *Homo* was the result of *Homo* outcompeting *Australopithecus* and *Paranthropus* for already saturated ecological or geographic space using technology. The hypothesised relationship between technology, interspecific competition, and splitting rate can be tested: for example, rates of local technological innovation should increase as a function of local species diversity.

14 Summary and Conclusion

14.1 Demographic determinants of mammalian speciation

This thesis comprised six stand-alone chapters that each explored a specific question about the relationship between intraspecific population-level processes and speciation. Chapters 7 and 12 summarised results from these chapters in the context of a metapopulation model of speciation for extant mammals and extinct hominins, respectively. What follows, here, is a discussion of the major conclusions that can be drawn from the combination of results from both sections.

1. Population isolate formation provides the raw material for speciation in mammals; population-level splitting is principally determined by abiotic, not biotic factors; and these factors include barriers in the landscape, habitat fragmentation, and climate variability.

Across all extant mammals, there is a weakly positive correlation between generic species richness and average subspecies richness, and there is a significant and nearly one-to-one relationship between subspeciation rate, calculated as a pure-birth process, and speciation rate. Both results point towards subspecies—morphologically differentiated population isolates—existing on an evolutionary continuum with species. This relationship aligns with theoretical expectations (Gavrilets 2000; Harvey, Singhal, and Rabosky 2019; Rosenblum et al. 2012) as well as general patterns found across avian clades (Haskell and Adhikari 2009; Phillimore et al. 2007). The reality and consequent theoretical relevance of mammalian subspecies has been questioned (Cronin et al. 2015; Larison et al. 2021) but these results suggest that mammalian subspecies can, in general terms, be thought of as incipient species. This is theoretically and practically relevant: they can be incorporated in evolutionary models as proxies for population-level processes, and they also represent a store of future biodiversity for conservation purposes. Taxonomic revision based on new molecular data will only improve the resolution of evolutionary models incorporating subspecies.

Population isolate formation, then, is the sine qua non of mammalian speciation: but what factors control the rate at which this happens? Taken together, the results suggest that these factors tend to be abiotic rather than biotic. First, population richness is more strongly

predicted by species' range size in terrestrial taxa than in non-terrestrial taxa; and given that population connectivity of terrestrial taxa is more likely to be restricted by abiotic barriers, this points towards their role in shaping population splitting. This point is supported by the positive relationship found between subspeciation rate and extinction risk across all mammals: mammalian species at higher risk of extinction—which is generally underpinned by, or at least strongly correlates with, habitat fragmentation—produce subspecies at higher rates. This has clear significance for the conservation of evolutionary potential. Habitat fragmentation might also be linked to shifts in primate subspeciation rate over primate evolutionary history, but this association was not explicitly tested. Finally, within hominins, population-level splitting rates were not regulated by biotic competition—population splitting rates did not correlate with populations diversity—but in *Australopithecus*, population splitting rates correlated with climate: populations isolate formation occurred at higher rates in periods of high climate variability and periods of cooling. Climate variability and cooling are key determinants of habitat heterogeneity and fragmentation: so, taken together, the results presented in this thesis indicate a key role for abiotic factors in shaping mammalian population isolate formation.

2. Not all population isolates become species; general determinants of the evolutionary trajectory of a mammalian population isolate include ecology and metapopulation niche availability.

Although all population isolates can become species, speciation is the road less travelled by for most mammalian population isolates. The wide range of variation around the positive relationship between subspeciation rate and speciation rate, and especially the fact that in taxa that comprise subspecies, subspeciation rate usually outpaces speciation rate, point directly towards the ephemerality of most mammalian population isolates. In primates, moreover, the tempo of background subspecific diversification is marked by a very high rate of turnover, with subspecies death rate 98% of birth rate.

So, what has made all the difference? Ecological substrate and metapopulation niche availability appear general mediators of the relationship between population isolate and novel species. First, the relationship between generic species richness and average subspecies richness across all mammals is significantly stronger in non-terrestrial taxa than in terrestrial taxa. Taken together with patterns found across birds, in which the relationship between generic species and average subspecies richness is also strong (Haskell and Adhikari 2009), this suggests terrestrial population isolates become species less often than their non-terrestrial

equivalents. Rather interesting is the fact that this pattern is also found in hominins: in *Homo*, population splitting is more decoupled from metapopulation splitting than it is in *Australopithecus* and *Paranthropus. Homo* is characterised by fully bipedal locomotion (Harcourt-Smith and Aiello 2004) and thus terrestrial existence, while *Australopithecus* and *Paranthropus* retained adaptations for arboreality and likely exhibited a combination of arboreal and terrestrial locomotion (Georgiou et al. 2020; Rein et al. 2017; Ward 2002). Second, patterns found across hominins suggest that the probability of a population isolate becoming a novel species can be determined by whether or not species-level niche space is saturated. Within hominin genera—which are generally taken as representing distinct adaptive grades—metapopulation splitting occurs significantly more slowly after peak diversity, consistent with niche-based caps on species diversity (Moen and Morlon 2014). By contrast, population splitting does not slow down over time: population splitting becomes decoupled from metapopulation splitting as metapopulation-level niche space is saturated.

3. Population isolate persistence is an important control of mammalian speciation; extended population isolate persistence is positively related to speciation rate; and abiotic factors are important controls of this process.

An important determinant of whether or not a population isolate becomes reproductively isolated from its parental species, and thus of speciation, is how long it persists for. The importance of population isolate persistence is implicitly shown in the asymmetry between subspeciation rate and speciation rate across all mammals, with subspeciation rate outpacing speciation rate in taxa that comprise subspecies: more subspecies are produced than turn into species. It is explicitly shown in the pattern of subspecific diversification rate variation across the primate tree: primate clades with the highest speciation rates are characterised by the lowest rates of population isolate turnover and longest population isolate persistence. Rather than extending the "waiting time" to speciation (Gavrilets 2000), then, extended subspecies persistence results in higher speciation rates in primates.

In hominins, climatic stability promotes population persistence, although the signal is weak and the effect of climate on splitting rates was generally diffuse. Across the clade as a whole, population splitting rate slowed—that is, they persisted for longer periods of time—in times of less climate variability, while the relationship between metapopulation splitting and climate stability was inverted. The longer-term persistence of populations necessary for these to split from the rest of the metapopulation tended to occur in more stable climates. Whether or not this relationship between climatic stability and population persistence holds across all

mammals can be tested by extending the method to other fossil clades. If it does, the generally positive relationship between climatic variability and habitat fragmentation (Ackerly et al. 2010; Malhi et al. 2020) points towards the contradicting effects of these abiotic factors: on the one hand, fragmentation promotes population isolate formation in mammals, but on the other, the pattern found across hominins suggests it then reduces the tenure of these population isolates. This aligns with theoretical predictions (Dynesius and Jansson 2014), and is of concern for conservation efforts.

Although this is the general pattern, there is some variation between hominin genera. In *Australopithecus*, general temperature trends also mediate population persistence and thus speciation: persistence was extended in periods of warming. The specific pattern for our genus, *Homo*, is comparatively different to that of the rest of its clade: its evolution was marked by a sufficient level of climatic variability and cooling to ensure a higher rate of population production and possibly turnover, regardless of variation in either climate variable. In *Homo*, then, climate possibly contributed to the decoupled relationship between population and metapopulation splitting rates.

Climate, ecological substrate, and niche availability most probably interact to regulate demographic determinants of speciation: changing climate affects the distribution of abiotic barriers within landscapes, habitat heterogeneity, and ecological niche space, for example (Sinervo et al. 2010; Vrba 1993; Wiens et al. 2009). The combination of these results across extant and extinct mammals, then, suggests the pathway from population to species is complex, and that population persistence is mediated by likely interrelated abiotic factors.

4. Macroevolutionary patterns of species richness can be explained in terms of demographic processes.

Variation in speciation rate and macroevolutionary patterns of species richness are the cumulative outcome of demographic processes over time. This is most clearly seen in the results obtained for primates. The diversification of primate population isolates is characterised by high background rates of turnover, and an evolutionary trend towards extended population isolate persistence. Primate evolutionary history can be recast as the outcome of shifting balances between subspecies origination and extinction. For example, the success of the anthropoid radiation can be explained by a combination of increased rates of subspeciation and longer subspecific persistence. This means that explaining the divergent evolutionary histories of anthropoids and other primates requires elucidation of the

determinants of both of these processes. Within anthropoids, higher speciation rates in Old World monkeys are due in large part to the lowest relative population isolate extinction rates found across primates. Taking biogeographic patterns of habitat fragmentation together with this result points towards a potentially positive relationship between habitat fragmentation and isolate persistence in anthropoids; explicitly testing this hypothesised association is a clear direction for future research. Whether or not these patterns are representative of those across all mammals is an open question: but the concordance between the patterns seen in primates and the general mammalian asymmetry between subspeciation rate and speciation rate suggests this is probably the case.

14.2 Demographic processes and genetics

Across mammals—and indeed most vertebrates—speciation is a protracted process, with the cessation of gene flow between incipient taxa arising relatively gradually (Coyne 1998; Harvey, Singhal, and Rabosky 2019; Rosindell et al. 2010). Although there are exceptions to this rule (Arnold and Meyer 2006; Burrell et al. 2009), these are rare: and this means a particular condition—incipient species' extended isolation—must usually be met in order for gene flow to cease entirely, and for speciation to occur. This is where demographic processes become controls on speciation. The relative importance of demographic processes, then, is ultimately dependent on the genetic mechanisms of speciation: population isolate formation and persistence are likely to be less crucial stages of speciation if genetic isolation can happen instantaneously through, for example, polyploidy (Wood et al. 2009) or gene transposition (Masly et al. 2006). Demographic processes are therefore probably less important determinants of speciation in unicellular organisms, plants, and non-vertebrates than they are in mammals.

Speciation cannot be completely understood through an exclusively demographic lens; but neither is the picture complete if the genetic component is considered in isolation. Demographic and genetic processes are tightly linked, and interact to determine whether or not, and how quickly, speciation happens. This thesis implicitly emphasized one causal direction: that of population-level processes making the genetic component of speciation possible. That is, population isolate formation detaches a group from the rest of the gene pool, making it possible for processes such as drift and selection to ultimately sever the unit from its parent species if the population isolate persists for a sufficient amount of time. But it takes two to tango: and examining the relationship in the other direction is an important and complementary approach to the one taken here. It might be expected, for example, that the overall level of genetic diversity within a species is a major determinant of whether or not a

population isolate becomes a new species, regardless of the length of its persistence. Dispersal has a genetic basis in many organisms (Saastamoinen et al. 2018), furthermore, and has been shown to affect the rate at which population isolates form.

14.3 Conclusion

Speciation is one of multiple evolutionary trajectories an intraspecific population can take. To ask why a species formed is to ask why a particular population formed, why it persisted and became reproductively isolated from the rest of its parental species, and, equally importantly, why others did not. Taking this 'inside out' approach to speciation exposes the value of exploring demographic processes and their determinants for the question of how and why species form. In mammals, population isolate formation provides the raw material for speciation, and it is determined principally by abiotic, not biotic, factors. These include barriers in the landscape, habitat fragmentation, and climate variability. Although they can, not all mammalian population isolates become new species: and general determinants of the evolutionary trajectory of a mammalian population isolate include ecology and metapopulation niche availability. An important bridge between population isolate formation and speciation in mammals is the length of population isolate persistence: extended persistence increases speciation rate. Again, abiotic factors—particularly climate and possibly habitat fragmentation—are important determinants. Of interest here is the contradicting effects of these abiotic factors: habitat fragmentation promotes population isolate formation, but it can also curtail how long these isolates persist for. Macroevolutionary patterns of mammalian species richness are the cumulative outcome of the balance between population isolate formation and persistence over time: and including demographic determinants of speciation in evolutionary models can thus provide important insights into why, and how, mammalian species form.

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Appendices

16 Appendix 1: List of mammal species and subspecies richness

Family	Genus	Species	Number of subspecies
Tachyglossidae	Tachyglossus	aculeatus	5
Tachyglossidae	Zaglossus	attenboroughi	0
Tachyglossidae	Zaglossus	bartoni	4
Tachyglossidae	Zaglossus	bruijni	0
Ornithorhynchidae	Ornithorhynchus	anatinus	0
Didelphidae	Caluromys	derbianus	6
Didelphidae	Caluromys	lanatus	6
Didelphidae	Caluromys	philander	4
Didelphidae	Caluromysiops	irrupta	0
Didelphidae	Glironia	venusta	0
Didelphidae	Chironectes	minimus	4
Didelphidae	Didelphis	albiventris	0
Didelphidae	Didelphis	aurita	0
Didelphidae	Didelphis	imperfecta	0
Didelphidae	Didelphis	marsupialis	2
Didelphidae	Didelphis	pernigra	0
Didelphidae	Didelphis	virginiana	4
Didelphidae	Gracilinanus	aceramarcae	0
Didelphidae	Gracilinanus	agilis	0
Didelphidae	Gracilinanus	agricolai	0
Didelphidae	Gracilinanus	dryas	0
Didelphidae	Gracilinanus	emiliae	0
Didelphidae	Gracilinanus	formosus	0
Didelphidae	Gracilinanus	ignitus	0
Didelphidae	Gracilinanus	marica	0
Didelphidae	Gracilinanus	microtarsus	2
Didelphidae	Hyladelphys	kalinowskii	0
Didelphidae	Lestodelphys	halli	0
Didelphidae	Lutreolina	crassicaudata	2
Didelphidae	Marmosa	andersoni	0
Didelphidae	Marmosa	lepida	0
Didelphidae	Marmosa	mexicana	3
Didelphidae	Marmosa	murina	0
Didelphidae	Marmosa	quichua	0
Didelphidae	Marmosa	robinsoni	8
Didelphidae	Marmosa	rubra	0

Didelphidae	Marmosa	tyleriana	0
Didelphidae	Marmosa	xerophila	0
Didelphidae	Marmosops	bishopi	0
Didelphidae	Marmosops	cracens	0
Didelphidae	Marmosops	dorothea	0
Didelphidae	Marmosops	fuscatus	3
Didelphidae	Marmosops	handleyi	0
Didelphidae	Marmosops	impavidus	0
Didelphidae	Marmosops	incanus	0
Didelphidae	Marmosops	invictus	0
Didelphidae	Marmosops	juninensis	0
Didelphidae	Marmosops	neblina	0
Didelphidae	Marmosops	noctivagus	0
Didelphidae	Marmosops	parvidens	0
Didelphidae	Marmosops	paulensis	0
Didelphidae	Marmosops	pinheiroi	0
Didelphidae	Metachirus	nudicaudatus	5
Didelphidae	Micoureus	alstoni	0
Didelphidae	Micoureus	constantiae	0
Didelphidae	Micoureus	demerarae	5
Didelphidae	Micoureus	paraguayanus	2
Didelphidae	Micoureus	phaeus	0
Didelphidae	Micoureus	regina	3
Didelphidae	Monodelphis	adusta	0
Didelphidae	Monodelphis	americana	0
Didelphidae	Monodelphis	brevicaudata	0
Didelphidae	Monodelphis	dimidiata	0
Didelphidae	Monodelphis	domestica	0
Didelphidae	Monodelphis	emiliae	0
Didelphidae	Monodelphis	glirina	0
Didelphidae	Monodelphis	iheringi	0
Didelphidae	Monodelphis	kunsi	0
Didelphidae	Monodelphis	maraxina	0
Didelphidae	Monodelphis	osgoodi	0
Didelphidae	Monodelphis	palliolata	0
Didelphidae	Monodelphis	rubida	0
Didelphidae	Monodelphis	scalops	0
Didelphidae	Monodelphis	sorex	0
Didelphidae	Monodelphis	theresa	0
Didelphidae	Monodelphis	umbristriata	0
Didelphidae	Monodelphis	unistriata	0
Didelphidae	Philander	andersoni	0

Didelphidae	Philander	frenatus	0
Didelphidae	Philander	mcilhennyi	0
Didelphidae	Philander	opossum	4
Didelphidae	Thylamys	cinderella	0
Didelphidae	Thylamys	elegans	0
Didelphidae	Thylamys	karimii	0
Didelphidae	Thylamys	macrurus	0
Didelphidae	Thylamys	pallidior	0
Didelphidae	Thylamys	pusillus	0
Didelphidae	Thylamys	sponsorius	0
Didelphidae	Thylamys	tatei	0
Didelphidae	Thylamys	velutinus	0
Didelphidae	Thylamys	venustus	0
Didelphidae	Tlacuatzin	canescens	2
Caenolestidae	Caenolestes	caniventer	0
Caenolestidae	Caenolestes	condorensis	0
Caenolestidae	Caenolestes	convelatus	2
Caenolestidae	Caenolestes	fuliginosus	3
Caenolestidae	Lestoros	inca	0
Caenolestidae	Rhyncholestes	raphanurus	2
Microbiotheriidae	Dromiciops	gliroides	0
Notoryctidae	Notoryctes	caurinus	0
Notoryctidae	Notoryctes	typhlops	0
Thylacinidae	Thylacinus	cynocephalus	0
Myrmecobiidae	Myrmecobius	fasciatus	2
Dasyuridae	Dasycercus	cristicauda	0
Dasyuridae	Dasykaluta	rosamondae	0
Dasyuridae	Dasyuroides	byrnei	0
Dasyuridae	Dasyurus	albopunctatus	0
Dasyuridae	Dasyurus	geoffroii	0
Dasyuridae	Dasyurus	hallucatus	0
Dasyuridae	Dasyurus	maculatus	0
Dasyuridae	Dasyurus	spartacus	0
Dasyuridae	Dasyurus	viverrinus	0
Dasyuridae	Myoictis	melas	0
Dasyuridae	Myoictis	wallacii	0
Dasyuridae	Neophascogale	lorentzi	0
Dasyuridae	Parantechinus	apicalis	0
Dasyuridae	Phascolosorex	doriae	0
Dasyuridae	Phascolosorex	dorsalis	3
Dasyuridae	Pseudantechinus	bilarni	0
Dasyuridae	Pseudantechinus	macdonnellensis	0

Dasyuridae	Pseudantechinus	mimulus	0
Dasyuridae	Pseudantechinus	ningbing	0
Dasyuridae	Pseudantechinus	roryi	0
Dasyuridae	Pseudantechinus	woolleyae	0
Dasyuridae	Sarcophilus	harrisii	2
Dasyuridae	Antechinus	adustus	0
Dasyuridae	Antechinus	agilis	0
Dasyuridae	Antechinus	bellus	0
Dasyuridae	Antechinus	flavipes	2
Dasyuridae	Antechinus	godmani	0
Dasyuridae	Antechinus	leo	0
Dasyuridae	Antechinus	minimus	0
Dasyuridae	Antechinus	stuartii	0
Dasyuridae	Antechinus	subtropicus	0
Dasyuridae	Antechinus	swainsonii	0
Dasyuridae	Micromurexia	habbema	0
Dasyuridae	Murexechinus	melanurus	0
Dasyuridae	Murexia	longicaudata	0
Dasyuridae	Paramurexia	rothschildi	0
Dasyuridae	Phascomurexia	naso	0
Dasyuridae	Phascogale	calura	0
Dasyuridae	Phascogale	tapoatafa	0
Dasyuridae	Antechinomys	laniger	0
Dasyuridae	Ningaui	ridei	0
Dasyuridae	Ningaui	timealeyi	0
Dasyuridae	Ningaui	yvonnae	0
Dasyuridae	Sminthopsis	aitkeni	0
Dasyuridae	Sminthopsis	archeri	0
Dasyuridae	Sminthopsis	bindi	0
Dasyuridae	Sminthopsis	boullangerensis	0
Dasyuridae	Sminthopsis	butleri	0
Dasyuridae	Sminthopsis	crassicaudata	0
Dasyuridae	Sminthopsis	dolichura	0
Dasyuridae	Sminthopsis	douglasi	0
Dasyuridae	Sminthopsis	fuliginosus	0
Dasyuridae	Sminthopsis	gilberti	0
Dasyuridae	Sminthopsis	granulipes	0
Dasyuridae	Sminthopsis	griseoventer	0
Dasyuridae	Sminthopsis	hirtipes	0
Dasyuridae	Sminthopsis	leucopus	0
Dasyuridae	Sminthopsis	longicaudata	0
Dasyuridae	Sminthopsis	macroura	0

Dasyuridae	Sminthopsis	murina	0
Dasyuridae	Sminthopsis	ooldea	0
Dasyuridae	Sminthopsis	psammophila	0
Dasyuridae	Sminthopsis	virginiae	3
Dasyuridae	Sminthopsis	youngsoni	0
Dasyuridae	Planigale	gilesi	0
Dasyuridae	Planigale	ingrami	3
Dasyuridae	Planigale	maculata	2
Dasyuridae	Planigale	novaeguineae	0
Dasyuridae	Planigale	tenuirostris	0
Thylacomyidae	Macrotis	lagotis	0
Thylacomyidae	Macrotis	leucura	0
Chaeropodidae	Chaeropus	ecaudatus	0
Peramelidae	Isoodon	auratus	3
Peramelidae	Isoodon	macrourus	2
Peramelidae	Isoodon	obesulus	2
Peramelidae	Perameles	bougainville	0
Peramelidae	Perameles	eremiana	0
Peramelidae	Perameles	gunnii	0
Peramelidae	Perameles	nasuta	0
Peramelidae	Peroryctes	broadbenti	0
Peramelidae	Peroryctes	raffrayana	2
Peramelidae	Echymipera	clara	0
Peramelidae	Echymipera	davidi	0
Peramelidae	Echymipera	echinista	0
Peramelidae	Echymipera	kalubu	4
Peramelidae	Echymipera	rufescens	2
Peramelidae	Microperoryctes	longicauda	3
Peramelidae	Microperoryctes	murina	0
Peramelidae	Microperoryctes	papuensis	0
Peramelidae	Rhynchomeles	prattorum	0
Phascolarctidae	Phascolarctos	cinereus	0
Vombatidae	Lasiorhinus	krefftii	3
Vombatidae	Lasiorhinus	latifrons	0
Vombatidae	Vombatus	ursinus	0
Burramyidae	Burramys	parvus	0
Burramyidae	Cercartetus	caudatus	2
Burramyidae	Cercartetus	concinnus	2
Burramyidae	Cercartetus	lepidus	0
Burramyidae	Cercartetus	nanus	2
Phalangeridae	Ailurops	melanotis	0
Phalangeridae	Ailurops	ursinus	4

Phalangeridae	Phalanger	alexandrae	0
Phalangeridae	Phalanger	carmelitae	2
Phalangeridae	Phalanger	gymnotis	2
Phalangeridae	Phalanger	intercastellanus	0
Phalangeridae	Phalanger	lullulae	0
Phalangeridae	Phalanger	matabiru	0
Phalangeridae	Phalanger	matanim	0
Phalangeridae	Phalanger	mimicus	2
Phalangeridae	Phalanger	orientalis	2
Phalangeridae	Phalanger	ornatus	0
Phalangeridae	Phalanger	rothschildi	0
Phalangeridae	Phalanger	sericeus	2
Phalangeridae	Phalanger	vestitus	0
Phalangeridae	Spilocuscus	kraemeri	0
Phalangeridae	Spilocuscus	maculatus	4
Phalangeridae	Spilocuscus	papuensis	0
Phalangeridae	Spilocuscus	rufoniger	0
Phalangeridae	Strigocuscus	celebensis	3
Phalangeridae	Strigocuscus	pelengensis	2
Phalangeridae	Trichosurus	arnhemensis	0
Phalangeridae	Trichosurus	caninus	0
Phalangeridae	Trichosurus	cunninghami	0
Phalangeridae	Trichosurus	johnstonii	0
Phalangeridae	Trichosurus	vulpecula	0
Phalangeridae	Wyulda	squamicaudata	0
Pseudocheiridae	Hemibelideus	lemuroides	0
Pseudocheiridae	Petauroides	volans	2
Pseudocheiridae	Petropseudes	dahli	0
Pseudocheiridae	Pseudocheirus	peregrinus	4
Pseudocheiridae	Pseudochirulus	canescens	5
Pseudocheiridae	Pseudochirulus	caroli	2
Pseudocheiridae	Pseudochirulus	cinereus	0
Pseudocheiridae	Pseudochirulus	forbesi	0
Pseudocheiridae	Pseudochirulus	herbertensis	0
Pseudocheiridae	Pseudochirulus	larvatus	0
Pseudocheiridae	Pseudochirulus	mayeri	0
Pseudocheiridae	Pseudochirulus	schlegeli	0
Pseudocheiridae	Pseudochirops	albertisii	3
Pseudocheiridae	Pseudochirops	archeri	0
Pseudocheiridae	Pseudochirops	corinnae	3
Pseudocheiridae	Pseudochirops	coronatus	0
Pseudocheiridae	Pseudochirops	cupreus	0

Petauridae	Dactylopsila	megalura	0
Petauridae	Dactylopsila	palpator	0
Petauridae	Dactylopsila	tatei	0
Petauridae	Dactylopsila	trivirgata	4
Petauridae	Gymnobelideus	leadbeateri	0
Petauridae	Petaurus	abidi	0
Petauridae	Petaurus	australis	2
Petauridae	Petaurus	biacensis	0
Petauridae	Petaurus	breviceps	4
Petauridae	Petaurus	gracilis	0
Petauridae	Petaurus	norfolcensis	0
Tarsipedidae	Tarsipes	rostratus	0
Acrobatidae	Acrobates	pygmaeus	0
Acrobatidae	Distoechurus	pennatus	0
Hypsiprymnodontidae	Hypsiprymnodon	moschatus	0
Potoroidae	Aepyprymnus	rufescens	0
Potoroidae	Bettongia	gaimardi	0
Potoroidae	Bettongia	lesueur	0
Potoroidae	Bettongia	penicillata	0
Potoroidae	Bettongia	tropica	0
Potoroidae	Caloprymnus	campestris	0
Potoroidae	Potorous	gilbertii	0
Potoroidae	Potorous	longipes	0
Potoroidae	Potorous	platyops	0
Potoroidae	Potorous	tridactylus	2
Macropodidae	Lagostrophus	fasciatus	2
Macropodidae	Dendrolagus	bennettianus	0
Macropodidae	Dendrolagus	dorianus	3
Macropodidae	Dendrolagus	goodfellowi	2
Macropodidae	Dendrolagus	inustus	2
Macropodidae	Dendrolagus	lumholtzi	0
Macropodidae	Dendrolagus	matschiei	0
Macropodidae	Dendrolagus	mbaiso	0
Macropodidae	Dendrolagus	pulcherrimus	0
Macropodidae	Dendrolagus	scottae	0
Macropodidae	Dendrolagus	spadix	0
Macropodidae	Dendrolagus	stellarum	0
Macropodidae	Dendrolagus	ursinus	0
Macropodidae	Dorcopsis	atrata	0
Macropodidae	Dorcopsis	hageni	0
Macropodidae	Dorcopsis	luctuosa	2
Macropodidae	Dorcopsis	muelleri	4

Macropodidae	Dorcopsulus	macleayi	0
Macropodidae	Dorcopsulus	vanheurni	0
Macropodidae	Lagorchestes	asomatus	0
Macropodidae	Lagorchestes	conspicillatus	0
Macropodidae	Lagorchestes	hirsutus	0
Macropodidae	Lagorchestes	leporides	0
Macropodidae	Macropus	agilis	4
Macropodidae	Macropus	antilopinus	0
Macropodidae	Macropus	bernardus	0
Macropodidae	Macropus	dorsalis	0
Macropodidae	Macropus	eugenii	0
Macropodidae	Macropus	fuliginosus	3
Macropodidae	Macropus	giganteus	2
Macropodidae	Macropus	greyi	0
Macropodidae	Macropus	irma	0
Macropodidae	Macropus	parma	0
Macropodidae	Macropus	parryi	0
Macropodidae	Macropus	robustus	4
Macropodidae	Macropus	rufogriseus	3
Macropodidae	Macropus	rufus	0
Macropodidae	Onychogalea	fraenata	0
Macropodidae	Onychogalea	lunata	0
Macropodidae	Onychogalea	unguifera	0
Macropodidae	Petrogale	assimilis	0
Macropodidae	Petrogale	brachyotis	0
Macropodidae	Petrogale	burbidgei	0
Macropodidae	Petrogale	coenensis	0
Macropodidae	Petrogale	concinna	0
Macropodidae	Petrogale	godmani	0
Macropodidae	Petrogale	herberti	0
Macropodidae	Petrogale	inornata	0
Macropodidae	Petrogale	lateralis	3
Macropodidae	Petrogale	mareeba	0
Macropodidae	Petrogale	penicillata	0
Macropodidae	Petrogale	persephone	0
Macropodidae	Petrogale	purpureicollis	0
Macropodidae	Petrogale	rothschildi	0
Macropodidae	Petrogale	sharmani	0
Macropodidae	Petrogale	xanthopus	2
Macropodidae	Setonix	brachyurus	0
Macropodidae	Thylogale	billardierii	0
Macropodidae	Thylogale	browni	0

Macropodidae	Thylogale	brunii	0
Macropodidae	Thylogale	calabyi	0
Macropodidae	Thylogale	lanatus	0
Macropodidae	Thylogale	stigmatica	4
Macropodidae	Thylogale	thetis	0
Macropodidae	Wallabia	bicolor	0
Tenrecidae	Geogale	aurita	2
Tenrecidae	Limnogale	mergulus	0
Tenrecidae	Microgale	brevicaudata	0
Tenrecidae	Microgale	cowani	0
Tenrecidae	Microgale	dobsoni	0
Tenrecidae	Microgale	drouhardi	0
Tenrecidae	Microgale	dryas	0
Tenrecidae	Microgale	fotsifotsy	0
Tenrecidae	Microgale	gracilis	0
Tenrecidae	Microgale	gymnorhyncha	0
Tenrecidae	Microgale	longicaudata	0
Tenrecidae	Microgale	monticola	0
Tenrecidae	Microgale	nasoloi	0
Tenrecidae	Microgale	parvula	0
Tenrecidae	Microgale	principula	0
Tenrecidae	Microgale	pusilla	0
Tenrecidae	Microgale	soricoides	0
Tenrecidae	Microgale	taiva	0
Tenrecidae	Microgale	talazaci	0
Tenrecidae	Microgale	thomasi	0
Tenrecidae	Oryzorictes	hova	0
Tenrecidae	Oryzorictes	tetradactylus	0
Tenrecidae	Micropotamogale	lamottei	0
Tenrecidae	Micropotamogale	ruwenzorii	0
Tenrecidae	Potamogale	velox	0
Tenrecidae	Echinops	telfairi	0
Tenrecidae	Hemicentetes	nigriceps	0
Tenrecidae	Hemicentetes	semispinosus	0
Tenrecidae	Setifer	setosus	0
Tenrecidae	Tenrec	ecaudatus	0
Chrysochloridae	Carpitalpa	arendsi	0
Chrysochloridae	Chlorotalpa	duthieae	0
Chrysochloridae	Chlorotalpa	sclateri	4
Chrysochloridae	Chrysochloris	asiatica	0
Chrysochloridae	Chrysochloris	stuhlmanni	3
Chrysochloridae	Chrysochloris	visagiei	0

Chrysochloridae	Chrysospalax	trevelyani	0
Chrysochloridae	Chrysospalax	villosus	6
Chrysochloridae	Cryptochloris	wintoni	0
Chrysochloridae	Cryptochloris	zyli	0
Chrysochloridae	Eremitalpa	granti	2
Chrysochloridae	Amblysomus	corriae	2
Chrysochloridae	Amblysomus	hottentotus	5
Chrysochloridae	Amblysomus	marleyi	0
Chrysochloridae	Amblysomus	robustus	0
Chrysochloridae	Amblysomus	septentrionalis	0
Chrysochloridae	Calcochloris	leucorhinus	2
Chrysochloridae	Calcochloris	obtusirostris	3
Chrysochloridae	Calcochloris	tytonis	0
Chrysochloridae	Neamblysomus	gunningi	0
Chrysochloridae	Neamblysomus	julianae	0
Macroscelididae	Elephantulus	brachyrhynchus	0
Macroscelididae	Elephantulus	edwardii	0
Macroscelididae	Elephantulus	fuscipes	0
Macroscelididae	Elephantulus	fuscus	0
Macroscelididae	Elephantulus	intufi	0
Macroscelididae	Elephantulus	myurus	0
Macroscelididae	Elephantulus	revoili	0
Macroscelididae	Elephantulus	rozeti	2
Macroscelididae	Elephantulus	rufescens	6
Macroscelididae	Elephantulus	rupestris	0
Macroscelididae	Macroscelides	proboscideus	2
Macroscelididae	Petrodromus	tetradactylus	9
Macroscelididae	Rhynchocyon	chrysopygus	0
Macroscelididae	Rhynchocyon	cirnei	6
Macroscelididae	Rhynchocyon	petersi	2
Orycteropodidae	Orycteropus	afer	17
Procaviidae	Dendrohyrax	arboreus	0
Procaviidae	Dendrohyrax	dorsalis	6
Procaviidae	Heterohyrax	brucei	25
Procaviidae	Procavia	capensis	17
Elephantidae	Elephas	maximus	3
Elephantidae	Loxodonta	africana	0
Elephantidae	Loxodonta	cyclotis	0
Dugongidae	Dugong	dugon	0
Dugongidae	Hydrodamalis	gigas	0
Trichechidae	Trichechus	inunguis	0
Trichechidae	Trichechus	manatus	0

Trichechidae	Trichechus	senegalensis	0
Dasypodidae	Dasypus	hybridus	0
Dasypodidae	Dasypus	kappleri	2
Dasypodidae	Dasypus	novemcinctus	6
Dasypodidae	Dasypus	pilosus	0
Dasypodidae	Dasypus	sabanicola	0
Dasypodidae	Dasypus	septemcinctus	0
Dasypodidae	Dasypus	yepesi	0
Dasypodidae	Calyptophractus	retusus	0
Dasypodidae	Chaetophractus	nationi	0
Dasypodidae	Chaetophractus	vellerosus	2
Dasypodidae	Chaetophractus	villosus	0
Dasypodidae	Chlamyphorus	truncatus	0
Dasypodidae	Euphractus	sexcinctus	5
Dasypodidae	Zaedyus	pichiy	2
Dasypodidae	Cabassous	centralis	0
Dasypodidae	Cabassous	chacoensis	0
Dasypodidae	Cabassous	tatouay	0
Dasypodidae	Cabassous	unicinctus	2
Dasypodidae	Priodontes	maximus	0
Dasypodidae	Tolypeutes	matacus	0
Dasypodidae	Tolypeutes	tricinctus	0
Bradypodidae	Bradypus	pygmaeus	0
Bradypodidae	Bradypus	torquatus	0
Bradypodidae	Bradypus	tridactylus	0
Bradypodidae	Bradypus	variegatus	7
Megalonychidae	Choloepus	didactylus	0
Megalonychidae	Choloepus	hoffmanni	5
Cyclopedidae	Cyclopes	didactylus	7
Myrmecophagidae	Myrmecophaga	tridactyla	3
Myrmecophagidae	Tamandua	mexicana	4
Myrmecophagidae	Tamandua	tetradactyla	4
Tupaiidae	Anathana	ellioti	0
Tupaiidae	Dendrogale	melanura	2
Tupaiidae	Dendrogale	murina	0
Tupaiidae	Tupaia	belangeri	2
Tupaiidae	Tupaia	chrysogaster	0
Tupaiidae	Tupaia	dorsalis	0
Tupaiidae	Tupaia	glis	0
Tupaiidae	Tupaia	gracilis	3
Tupaiidae	Tupaia	javanica	0
Tupaiidae	Tupaia	longipes	2

Tupaiidae	Tupaia	minor	4
Tupaiidae	Tupaia	moellendorffi	3
Tupaiidae	Tupaia	montana	2
Tupaiidae	Tupaia	nicobarica	2
Tupaiidae	Tupaia	palawanensis	0
Tupaiidae	Tupaia	picta	2
Tupaiidae	Tupaia	splendidula	5
Tupaiidae	Tupaia	tana	15
Tupaiidae	Urogale	everetti	0
Ptilocercidae	Ptilocercus	lowii	2
Cynocephalidae	Cynocephalus	volans	0
Cynocephalidae	Galeopterus	variegates	0
Cheirogaleidae	Allocebus	trichotis	0
Cheirogaleidae	Cheirogaleus	adipicaudatus	0
Cheirogaleidae	Cheirogaleus	crossleyi	0
Cheirogaleidae	Cheirogaleus	major	0
Cheirogaleidae	Cheirogaleus	medius	0
Cheirogaleidae	Cheirogaleus	minusculus	0
Cheirogaleidae	Cheirogaleus	ravus	0
Cheirogaleidae	Cheirogaleus	sibreei	0
Cheirogaleidae	Microcebus	berthae	0
Cheirogaleidae	Microcebus	griseorufus	0
Cheirogaleidae	Microcebus	murinus	0
Cheirogaleidae	Microcebus	myoxinus	0
Cheirogaleidae	Microcebus	ravelobensis	0
Cheirogaleidae	Microcebus	rufus	0
Cheirogaleidae	Microcebus	sambiranensis	0
Cheirogaleidae	Microcebus	tavaratra	0
Cheirogaleidae	Mirza	coquereli	0
Cheirogaleidae	Phaner	electromontis	0
Cheirogaleidae	Phaner	furcifer	0
Cheirogaleidae	Phaner	pallescens	0
Cheirogaleidae	Phaner	parienti	0
Lemuridae	Eulemur	albifrons	0
Lemuridae	Eulemur	albocollaris	0
Lemuridae	Eulemur	cinereiceps	0
Lemuridae	Eulemur	collaris	0
Lemuridae	Eulemur	coronatus	0
Lemuridae	Eulemur	fulvus	0
Lemuridae	Eulemur	macaco	2
Lemuridae	Eulemur	mongoz	0
Lemuridae	Eulemur	rubriventer	0

Lemuridae	Eulemur	rufus	0
Lemuridae	Eulemur	sanfordi	0
Lemuridae	Hapalemur	alaotrensis	0
Lemuridae	Hapalemur	aureus	0
Lemuridae	Hapalemur	griseus	2
Lemuridae	Hapalemur	occidentalis	0
Lemuridae	Lemur	catta	0
Lemuridae	Prolemur	simus	0
Lemuridae	Varecia	rubra	0
Lemuridae	Varecia	variegata	3
Lepilemuridae	Lepilemur	ankaranensis	0
Lepilemuridae	Lepilemur	dorsalis	0
Lepilemuridae	Lepilemur	edwardsi	0
Lepilemuridae	Lepilemur	leucopus	0
Lepilemuridae	Lepilemur	microdon	0
Lepilemuridae	Lepilemur	mustelinus	0
Lepilemuridae	Lepilemur	ruficaudatus	0
Lepilemuridae	Lepilemur	septentrionalis	0
Indridae	Avahi	laniger	0
Indridae	Avahi	occidentalis	0
Indridae	Avahi	unicolor	0
Indridae	Indri	indri	2
Indridae	Propithecus	coquereli	0
Indridae	Propithecus	deckenii	2
Indridae	Propithecus	diadema	2
Indridae	Propithecus	edwardsi	0
Indridae	Propithecus	perrieri	0
Indridae	Propithecus	tattersalli	0
Indridae	Propithecus	verreauxi	0
Daubentoniidae	Daubentonia	madagascariensis	0
Lorisidae	Arctocebus	aureus	0
Lorisidae	Arctocebus	calabarensis	0
Lorisidae	Loris	lydekkerianus	4
Lorisidae	Loris	tardigradus	0
Lorisidae	Nycticebus	bengalensis	0
Lorisidae	Nycticebus	coucang	3
Lorisidae	Nycticebus	pygmaeus	0
Lorisidae	Perodicticus	potto	3
Lorisidae	Pseudopotto	martini	0
Galagidae	Euoticus	elegantulus	0
Galagidae	Euoticus	pallidus	2
Galagidae	Galago	alleni	0

Galagidae	Galago	cameronensis	0
Galagidae	Galago	demidoff	0
Galagidae	Galago	gabonensis	0
Galagidae	Galago	gallarum	0
Galagidae	Galago	granti	0
Galagidae	Galago	matschiei	0
Galagidae	Galago	moholi	0
Galagidae	Galago	nyasae	0
Galagidae	Galago	orinus	0
Galagidae	Galago	rondoensis	0
Galagidae	Galago	senegalensis	4
Galagidae	Galago	thomasi	0
Galagidae	Galago	zanzibaricus	0
Galagidae	Otolemur	crassicaudatus	2
Galagidae	Otolemur	garnettii	4
Galagidae	Otolemur	monteiri	2
Tarsiidae	Tarsius	bancanus	3
Tarsiidae	Tarsius	dentatus	0
Tarsiidae	Tarsius	pelengensis	0
Tarsiidae	Tarsius	pumilus	0
Tarsiidae	Tarsius	sangirensis	0
Tarsiidae	Tarsius	syrichta	0
Tarsiidae	Tarsius	tarsier	0
Cebidae	Callimico	goeldii	0
Cebidae	Callithrix	acariensis	0
Cebidae	Callithrix	argentata	0
Cebidae	Callithrix	aurita	0
Cebidae	Callithrix	chrysoleuca	0
Cebidae	Callithrix	emiliae	0
Cebidae	Callithrix	flaviceps	0
Cebidae	Callithrix	geoffroyi	0
Cebidae	Callithrix	humeralifera	0
Cebidae	Callithrix	humilis	0
Cebidae	Callithrix	intermedia	0
Cebidae	Callithrix	jacchus	0
Cebidae	Callithrix	kuhlii	0
Cebidae	Callithrix	leucippe	0
Cebidae	Callithrix	manicorensis	0
Cebidae	Callithrix	marcai	0
Cebidae	Callithrix	mauesi	0
Cebidae	Callithrix	melanura	0
Cebidae	Callithrix	nigriceps	0

Cebidae	Callithrix	penicillata	0
Cebidae	Callithrix	pygmaea	2
Cebidae	Callithrix	saterei	0
Cebidae	Leontopithecus	caissara	0
Cebidae	Leontopithecus	chrysomelas	0
Cebidae	Leontopithecus	chrysopygus	0
Cebidae	Leontopithecus	rosalia	0
Cebidae	Saguinus	bicolor	0
Cebidae	Saguinus	fuscicollis	10
Cebidae	Saguinus	geoffroyi	0
Cebidae	Saguinus	graellsi	0
Cebidae	Saguinus	imperator	2
Cebidae	Saguinus	inustus	0
Cebidae	Saguinus	labiatus	3
Cebidae	Saguinus	leucopus	0
Cebidae	Saguinus	martinsi	2
Cebidae	Saguinus	melanoleucus	0
Cebidae	Saguinus	midas	0
Cebidae	Saguinus	mystax	2
Cebidae	Saguinus	niger	0
Cebidae	Saguinus	nigricollis	2
Cebidae	Saguinus	oedipus	0
Cebidae	Saguinus	pileatus	0
Cebidae	Saguinus	tripartitus	0
Cebidae	Cebus	albifrons	6
Cebidae	Cebus	apella	6
Cebidae	Cebus	capucinus	0
Cebidae	Cebus	kaapori	0
Cebidae	Cebus	libidinosus	4
Cebidae	Cebus	nigritus	3
Cebidae	Cebus	olivaceus	0
Cebidae	Cebus	xanthosternos	0
Cebidae	Saimiri	boliviensis	2
Cebidae	Saimiri	oerstedii	2
Cebidae	Saimiri	sciureus	4
Cebidae	Saimiri	ustus	0
Cebidae	Saimiri	vanzolinii	0
Aotidae	Aotus	azarae	3
Aotidae	Aotus	hershkovitzi	0
Aotidae	Aotus	lemurinus	4
Aotidae	Aotus	miconax	0
Aotidae	Aotus	nancymaae	0

Aotidae	Aotus	nigriceps	0
Aotidae	Aotus	trivirgatus	0
Aotidae	Aotus	vociferans	0
Pitheciidae	Callicebus	baptista	0
Pitheciidae	Callicebus	barbarabrownae	0
Pitheciidae	Callicebus	bernhardi	0
Pitheciidae	Callicebus	brunneus	0
Pitheciidae	Callicebus	caligatus	0
Pitheciidae	Callicebus	cinerascens	0
Pitheciidae	Callicebus	coimbrai	0
Pitheciidae	Callicebus	cupreus	0
Pitheciidae	Callicebus	discolor	0
Pitheciidae	Callicebus	donacophilus	0
Pitheciidae	Callicebus	dubius	0
Pitheciidae	Callicebus	hoffmannsi	0
Pitheciidae	Callicebus	lucifer	0
Pitheciidae	Callicebus	lugens	0
Pitheciidae	Callicebus	medemi	0
Pitheciidae	Callicebus	melanochir	0
Pitheciidae	Callicebus	modestus	0
Pitheciidae	Callicebus	moloch	0
Pitheciidae	Callicebus	nigrifrons	0
Pitheciidae	Callicebus	oenanthe	0
Pitheciidae	Callicebus	olallae	0
Pitheciidae	Callicebus	ornatus	0
Pitheciidae	Callicebus	pallescens	0
Pitheciidae	Callicebus	personatus	0
Pitheciidae	Callicebus	purinus	0
Pitheciidae	Callicebus	regulus	0
Pitheciidae	Callicebus	stephennashi	0
Pitheciidae	Callicebus	torquatus	0
Pitheciidae	Cacajao	calvus	4
Pitheciidae	Cacajao	melanocephalus	0
Pitheciidae	Chiropotes	albinasus	0
Pitheciidae	Chiropotes	chiropotes	0
Pitheciidae	Chiropotes	israelita	0
Pitheciidae	Chiropotes	satanas	0
Pitheciidae	Chiropotes	utahickae	0
Pitheciidae	Pithecia	aequatorialis	0
Pitheciidae	Pithecia	albicans	0
Pitheciidae	Pithecia	irrorata	0
Pitheciidae	Pithecia	monachus	2

Pitheciidae	Pithecia	pithecia	2
Atelidae	Alouatta	belzebul	0
Atelidae	Alouatta	caraya	0
Atelidae	Alouatta	coibensis	2
Atelidae	Alouatta	guariba	2
Atelidae	Alouatta	macconnelli	0
Atelidae	Alouatta	nigerrima	0
Atelidae	Alouatta	palliata	0
Atelidae	Alouatta	pigra	0
Atelidae	Alouatta	sara	0
Atelidae	Alouatta	seniculus	3
Atelidae	Ateles	belzebuth	0
Atelidae	Ateles	chamek	0
Atelidae	Ateles	fusciceps	2
Atelidae	Ateles	geoffroyi	5
Atelidae	Ateles	hybridus	0
Atelidae	Ateles	marginatus	0
Atelidae	Ateles	paniscus	0
Atelidae	Brachyteles	arachnoides	0
Atelidae	Brachyteles	hypoxanthus	0
Atelidae	Lagothrix	cana	2
Atelidae	Lagothrix	lagotricha	0
Atelidae	Lagothrix	lugens	0
Atelidae	Lagothrix	poeppigii	0
Atelidae	Oreonax	flavicauda	0
Cercopithecidae	Allenopithecus	nigroviridis	0
Cercopithecidae	Cercocebus	agilis	0
Cercopithecidae	Cercocebus	atys	2
Cercopithecidae	Cercocebus	chrysogaster	0
Cercopithecidae	Cercocebus	galeritus	0
Cercopithecidae	Cercocebus	sanjei	0
Cercopithecidae	Cercocebus	torquatus	0
Cercopithecidae	Cercopithecus	albogularis	12
Cercopithecidae	Cercopithecus	ascanius	5
Cercopithecidae	Cercopithecus	campbelli	0
Cercopithecidae	Cercopithecus	cephus	3
Cercopithecidae	Cercopithecus	denti	0
Cercopithecidae	Cercopithecus	diana	0
Cercopithecidae	Cercopithecus	doggetti	0
Cercopithecidae	Cercopithecus	dryas	0
Cercopithecidae	Cercopithecus	erythrogaster	2
Cercopithecidae	Cercopithecus	erythrotis	2

Cercopithecidae	Cercopithecus	hamlyni	2
Cercopithecidae	Cercopithecus	kandti	0
Cercopithecidae	Cercopithecus	lhoesti	0
Cercopithecidae	Cercopithecus	lowei	0
Cercopithecidae	Cercopithecus	mitis	6
Cercopithecidae	Cercopithecus	mona	0
Cercopithecidae	Cercopithecus	neglectus	0
Cercopithecidae	Cercopithecus	nictitans	2
Cercopithecidae	Cercopithecus	petaurista	2
Cercopithecidae	Cercopithecus	pogonias	4
Cercopithecidae	Cercopithecus	preussi	2
Cercopithecidae	Cercopithecus	roloway	0
Cercopithecidae	Cercopithecus	sclateri	0
Cercopithecidae	Cercopithecus	solatus	0
Cercopithecidae	Cercopithecus	wolfi	2
Cercopithecidae	Chlorocebus	aethiops	0
Cercopithecidae	Chlorocebus	cynosuros	0
Cercopithecidae	Chlorocebus	djamdjamensis	0
Cercopithecidae	Chlorocebus	pygerythrus	5
Cercopithecidae	Chlorocebus	sabaeus	0
Cercopithecidae	Chlorocebus	tantalus	3
Cercopithecidae	Erythrocebus	patas	0
Cercopithecidae	Lophocebus	albigena	3
Cercopithecidae	Lophocebus	aterrimus	0
Cercopithecidae	Lophocebus	opdenboschi	0
Cercopithecidae	Macaca	arctoides	0
Cercopithecidae	Macaca	assamensis	2
Cercopithecidae	Macaca	cyclopis	0
Cercopithecidae	Macaca	fascicularis	10
Cercopithecidae	Macaca	fuscata	2
Cercopithecidae	Macaca	hecki	0
Cercopithecidae	Macaca	leonina	0
Cercopithecidae	Macaca	maura	0
Cercopithecidae	Macaca	mulatta	0
Cercopithecidae	Macaca	nemestrina	0
Cercopithecidae	Macaca	nigra	0
Cercopithecidae	Macaca	nigrescens	0
Cercopithecidae	Macaca	ochreata	2
Cercopithecidae	Macaca	pagensis	0
Cercopithecidae	Macaca	radiata	0
Cercopithecidae	Macaca	siberu	0
Cercopithecidae	Macaca	silenus	0

Cercopithecidae	Macaca	sinica	2
Cercopithecidae	Macaca	sylvanus	0
Cercopithecidae	Macaca	thibetana	4
Cercopithecidae	Macaca	tonkeana	0
Cercopithecidae	Mandrillus	leucophaeus	2
Cercopithecidae	Mandrillus	sphinx	0
Cercopithecidae	Miopithecus	ogouensis	0
Cercopithecidae	Miopithecus	talapoin	0
Cercopithecidae	Papio	anubis	0
Cercopithecidae	Papio	cynocephalus	3
Cercopithecidae	Papio	hamadryas	0
Cercopithecidae	Papio	papio	0
Cercopithecidae	Papio	ursinus	3
Cercopithecidae	Theropithecus	gelada	2
Cercopithecidae	Colobus	angolensis	6
Cercopithecidae	Colobus	guereza	7
Cercopithecidae	Colobus	polykomos	0
Cercopithecidae	Colobus	satanas	2
Cercopithecidae	Colobus	vellerosus	0
Cercopithecidae	Nasalis	larvatus	0
Cercopithecidae	Piliocolobus	badius	3
Cercopithecidae	Piliocolobus	foai	5
Cercopithecidae	Piliocolobus	gordonorum	0
Cercopithecidae	Piliocolobus	kirkii	0
Cercopithecidae	Piliocolobus	pennantii	3
Cercopithecidae	Piliocolobus	preussi	0
Cercopithecidae	Piliocolobus	rufomitratus	0
Cercopithecidae	Piliocolobus	tephrosceles	0
Cercopithecidae	Piliocolobus	tholloni	0
Cercopithecidae	Presbytis	chrysomelas	2
Cercopithecidae	Presbytis	comata	2
Cercopithecidae	Presbytis	femoralis	3
Cercopithecidae	Presbytis	frontata	0
Cercopithecidae	Presbytis	hosei	4
Cercopithecidae	Presbytis	melalophos	4
Cercopithecidae	Presbytis	natunae	0
Cercopithecidae	Presbytis	potenziani	2
Cercopithecidae	Presbytis	rubicunda	5
Cercopithecidae	Presbytis	siamensis	4
Cercopithecidae	Presbytis	thomasi	0
Cercopithecidae	Procolobus	verus	0
Cercopithecidae	Pygathrix	cinerea	0

Cercopithecidae	Pygathrix	nemaeus	0
Cercopithecidae	Pygathrix	nigripes	0
Cercopithecidae	Rhinopithecus	avunculus	0
Cercopithecidae	Rhinopithecus	bieti	0
Cercopithecidae	Rhinopithecus	brelichi	0
Cercopithecidae	Rhinopithecus	roxellana	3
Cercopithecidae	Semnopithecus	ajax	0
Cercopithecidae	Semnopithecus	dussumieri	0
Cercopithecidae	Semnopithecus	entellus	0
Cercopithecidae	Semnopithecus	hector	0
Cercopithecidae	Semnopithecus	hypoleucos	0
Cercopithecidae	Semnopithecus	priam	0
Cercopithecidae	Semnopithecus	schistaceus	0
Cercopithecidae	Simias	concolor	0
Cercopithecidae	Trachypithecus	auratus	2
Cercopithecidae	Trachypithecus	barbei	0
Cercopithecidae	Trachypithecus	cristatus	2
Cercopithecidae	Trachypithecus	delacouri	0
Cercopithecidae	Trachypithecus	ebenus	0
Cercopithecidae	Trachypithecus	francoisi	0
Cercopithecidae	Trachypithecus	geei	2
Cercopithecidae	Trachypithecus	germaini	2
Cercopithecidae	Trachypithecus	hatinhensis	0
Cercopithecidae	Trachypithecus	johnii	0
Cercopithecidae	Trachypithecus	laotum	0
Cercopithecidae	Trachypithecus	obscurus	7
Cercopithecidae	Trachypithecus	phayrei	3
Cercopithecidae	Trachypithecus	pileatus	4
Cercopithecidae	Trachypithecus	poliocephalus	2
Cercopithecidae	Trachypithecus	shortridgei	0
Cercopithecidae	Trachypithecus	vetulus	4
Hylobatidae	Bunopithecus	hoolock	2
Hylobatidae	Hylobates	agilis	0
Hylobatidae	Hylobates	albibarbis	0
Hylobatidae	Hylobates	klossii	0
Hylobatidae	Hylobates	lar	5
Hylobatidae	Hylobates	moloch	0
Hylobatidae	Hylobates	muelleri	3
Hylobatidae	Hylobates	pileatus	0
Hylobatidae	Nomascus	concolor	5
Hylobatidae	Nomascus	gabriellae	0
Hylobatidae	Nomascus	hainanus	0

Hylobatidae	Nomascus	leucogenys	0
Hylobatidae	Nomascus	siki	0
Hylobatidae	Symphalangus	syndactylus	0
Hominidae	Gorilla	beringei	2
Hominidae	Gorilla	gorilla	2
Hominidae	Homo	sapiens	0
Hominidae	Pan	paniscus	0
Hominidae	Pan	troglodytes	4
Hominidae	Pongo	abelii	0
Hominidae	Pongo	pygmaeus	3
Aplodontiidae	Aplodontia	rufa	7
Sciuridae	Ratufa	affinis	9
Sciuridae	Ratufa	bicolor	10
Sciuridae	Ratufa	indica	4
Sciuridae	Ratufa	macroura	3
Sciuridae	Sciurillus	pusillus	3
Sciuridae	Microsciurus	alfari	6
Sciuridae	Microsciurus	flaviventer	8
Sciuridae	Microsciurus	mimulus	3
Sciuridae	Microsciurus	santanderensis	0
Sciuridae	Rheithrosciurus	macrotis	0
Sciuridae	Sciurus	aberti	6
Sciuridae	Sciurus	aestuans	10
Sciuridae	Sciurus	alleni	0
Sciuridae	Sciurus	anomalus	3
Sciuridae	Sciurus	arizonensis	3
Sciuridae	Sciurus	aureogaster	2
Sciuridae	Sciurus	carolinensis	5
Sciuridae	Sciurus	colliaei	4
Sciuridae	Sciurus	deppei	5
Sciuridae	Sciurus	flammifer	0
Sciuridae	Sciurus	gilvigularis	2
Sciuridae	Sciurus	granatensis	32
Sciuridae	Sciurus	griseus	3
Sciuridae	Sciurus	ignitus	5
Sciuridae	Sciurus	igniventris	2
Sciuridae	Sciurus	lis	0
Sciuridae	Sciurus	nayaritensis	3
Sciuridae	Sciurus	niger	10
Sciuridae	Sciurus	oculatus	3
Sciuridae	Sciurus	pucheranii	3
Sciuridae	Sciurus	pyrrhinus	0

Sciuridae	Sciurus	richmondi	0
Sciuridae	Sciurus	sanborni	0
Sciuridae	Sciurus	spadiceus	3
Sciuridae	Sciurus	stramineus	0
Sciuridae	Sciurus	variegatoides	15
Sciuridae	Sciurus	vulgaris	23
Sciuridae	Sciurus	yucatanensis	3
Sciuridae	Syntheosciurus	brochus	0
Sciuridae	Tamiasciurus	douglasii	2
Sciuridae	Tamiasciurus	hudsonicus	24
Sciuridae	Tamiasciurus	mearnsi	0
Sciuridae	Aeretes	melanopterus	2
Sciuridae	Aeromys	tephromelas	2
Sciuridae	Aeromys	thomasi	0
Sciuridae	Belomys	pearsonii	2
Sciuridae	Biswamoyopterus	biswasi	0
Sciuridae	Eoglaucomys	fimbriatus	2
Sciuridae	Eupetaurus	cinereus	0
Sciuridae	Glaucomys	sabrinus	25
Sciuridae	Glaucomys	volans	11
Sciuridae	Hylopetes	alboniger	3
Sciuridae	Hylopetes	bartelsi	0
Sciuridae	Hylopetes	lepidus	0
Sciuridae	Hylopetes	nigripes	2
Sciuridae	Hylopetes	phayrei	2
Sciuridae	Hylopetes	platyurus	0
Sciuridae	Hylopetes	sipora	0
Sciuridae	Hylopetes	spadiceus	2
Sciuridae	Hylopetes	winstoni	0
Sciuridae	Iomys	horsfieldii	4
Sciuridae	Iomys	sipora	0
Sciuridae	Petaurillus	emiliae	0
Sciuridae	Petaurillus	hosei	0
Sciuridae	Petaurillus	kinlochii	0
Sciuridae	Petaurista	alborufus	5
Sciuridae	Petaurista	elegans	7
Sciuridae	Petaurista	leucogenys	4
Sciuridae	Petaurista	magnificus	0
Sciuridae	Petaurista	nobilis	2
Sciuridae	Petaurista	petaurista	18
Sciuridae	Petaurista	philippensis	7
Sciuridae	Petaurista	xanthotis	0

Sciuridae	Petinomys	crinitus	0
Sciuridae	Petinomys	fuscocapillus	0
Sciuridae	Petinomys	genibarbis	0
Sciuridae	Petinomys	hageni	0
Sciuridae	Petinomys	lugens	0
Sciuridae	Petinomys	mindanensis	0
Sciuridae	Petinomys	sagitta	0
Sciuridae	Petinomys	setosus	0
Sciuridae	Petinomys	vordermanni	0
Sciuridae	Pteromys	momonga	0
Sciuridae	Pteromys	volans	4
Sciuridae	Pteromyscus	pulverulentus	2
Sciuridae	Trogopterus	xanthipes	0
Sciuridae	Callosciurus	adamsi	0
Sciuridae	Callosciurus	albescens	0
Sciuridae	Callosciurus	baluensis	0
Sciuridae	Callosciurus	caniceps	6
Sciuridae	Callosciurus	erythraeus	26
Sciuridae	Callosciurus	finlaysonii	16
Sciuridae	Callosciurus	inornatus	0
Sciuridae	Callosciurus	melanogaster	3
Sciuridae	Callosciurus	nigrovittatus	4
Sciuridae	Callosciurus	notatus	5
Sciuridae	Callosciurus	orestes	0
Sciuridae	Callosciurus	phayrei	0
Sciuridae	Callosciurus	prevostii	6
Sciuridae	Callosciurus	pygerythrus	7
Sciuridae	Callosciurus	quinquestriatus	2
Sciuridae	Dremomys	everetti	0
Sciuridae	Dremomys	gularis	0
Sciuridae	Dremomys	lokriah	5
Sciuridae	Dremomys	pernyi	6
Sciuridae	Dremomys	pyrrhomerus	2
Sciuridae	Dremomys	rufigenis	5
Sciuridae	Exilisciurus	concinnus	0
Sciuridae	Exilisciurus	exilis	0
Sciuridae	Exilisciurus	whiteheadi	0
Sciuridae	Funambulus	layardi	2
Sciuridae	Funambulus	palmarum	3
Sciuridae	Funambulus	pennantii	2
Sciuridae	Funambulus	sublineatus	2
Sciuridae	Funambulus	tristriatus	2

Sciuridae	Glyphotes	simus	0
Sciuridae	Hyosciurus	heinrichi	0
Sciuridae	Hyosciurus	ileile	0
Sciuridae	Lariscus	hosei	0
Sciuridae	Lariscus	insignis	5
Sciuridae	Lariscus	niobe	2
Sciuridae	Lariscus	obscurus	3
Sciuridae	Menetes	berdmorei	7
Sciuridae	Nannosciurus	melanotis	4
Sciuridae	Prosciurillus	abstrusus	0
Sciuridae	Prosciurillus	leucomus	4
Sciuridae	Prosciurillus	murinus	3
Sciuridae	Prosciurillus	rosenbergii	0
Sciuridae	Prosciurillus	weberi	0
Sciuridae	Rhinosciurus	laticaudatus	3
Sciuridae	Rubrisciurus	rubriventer	0
Sciuridae	Sundasciurus	brookei	0
Sciuridae	Sundasciurus	davensis	0
Sciuridae	Sundasciurus	fraterculus	0
Sciuridae	Sundasciurus	hippurus	5
Sciuridae	Sundasciurus	hoogstraali	0
Sciuridae	Sundasciurus	jentinki	0
Sciuridae	Sundasciurus	juvencus	0
Sciuridae	Sundasciurus	lowii	7
Sciuridae	Sundasciurus	mindanensis	0
Sciuridae	Sundasciurus	moellendorffi	0
Sciuridae	Sundasciurus	philippinensis	0
Sciuridae	Sundasciurus	rabori	0
Sciuridae	Sundasciurus	samarensis	0
Sciuridae	Sundasciurus	steerii	0
Sciuridae	Sundasciurus	tenuis	5
Sciuridae	Tamiops	mcclellandii	6
Sciuridae	Tamiops	maritimus	4
Sciuridae	Tamiops	rodolphii	2
Sciuridae	Tamiops	swinhoei	4
Sciuridae	Atlantoxerus	getulus	0
Sciuridae	Spermophilopsis	leptodactylus	3
Sciuridae	Xerus	erythropus	6
Sciuridae	Xerus	inauris	0
Sciuridae	Xerus	princeps	0
Sciuridae	Xerus	rutilus	8
Sciuridae	Epixerus	ebii	3

Sciuridae	Funisciurus	anerythrus	4
Sciuridae	Funisciurus	bayonii	0
Sciuridae	Funisciurus	carruthersi	4
Sciuridae	Funisciurus	congicus	0
Sciuridae	Funisciurus	isabella	2
Sciuridae	Funisciurus	lemniscatus	2
Sciuridae	Funisciurus	leucogenys	3
Sciuridae	Funisciurus	pyrropus	9
Sciuridae	Funisciurus	substriatus	0
Sciuridae	Heliosciurus	gambianus	16
Sciuridae	Heliosciurus	mutabilis	5
Sciuridae	Heliosciurus	punctatus	2
Sciuridae	Heliosciurus	rufobrachium	22
Sciuridae	Heliosciurus	ruwenzorii	4
Sciuridae	Heliosciurus	undulatus	0
Sciuridae	Myosciurus	pumilio	0
Sciuridae	Paraxerus	alexandri	0
Sciuridae	Paraxerus	boehmi	4
Sciuridae	Paraxerus	cepapi	10
Sciuridae	Paraxerus	cooperi	0
Sciuridae	Paraxerus	flavovittis	4
Sciuridae	Paraxerus	lucifer	0
Sciuridae	Paraxerus	ochraceus	8
Sciuridae	Paraxerus	palliatus	7
Sciuridae	Paraxerus	poensis	0
Sciuridae	Paraxerus	vexillarius	2
Sciuridae	Paraxerus	vincenti	0
Sciuridae	Protoxerus	aubinnii	2
Sciuridae	Protoxerus	stangeri	12
Sciuridae	Ammospermophilus	harrisii	2
Sciuridae	Ammospermophilus	insularis	0
Sciuridae	Ammospermophilus	interpres	0
Sciuridae	Ammospermophilus	leucurus	9
Sciuridae	Ammospermophilus	nelsoni	0
Sciuridae	Cynomys	gunnisoni	2
Sciuridae	Cynomys	leucurus	0
Sciuridae	Cynomys	ludovicianus	2
Sciuridae	Cynomys	mexicanus	0
Sciuridae	Cynomys	parvidens	0
Sciuridae	Marmota	baibacina	3
Sciuridae	Marmota	bobak	2
Sciuridae	Marmota	broweri	0

Sciuridae	Marmota	caligata	3
Sciuridae	Marmota	camtschatica	3
Sciuridae	Marmota	caudata	3
Sciuridae	Marmota	flaviventris	7
Sciuridae	Marmota	himalayana	2
Sciuridae	Marmota	marmota	2
Sciuridae	Marmota	menzbieri	2
Sciuridae	Marmota	monax	4
Sciuridae	Marmota	olympus	0
Sciuridae	Marmota	sibirica	2
Sciuridae	Marmota	vancouverensis	0
Sciuridae	Sciurotamias	davidianus	2
Sciuridae	Sciurotamias	forresti	0
Sciuridae	Spermophilus	adocetus	2
Sciuridae	Spermophilus	alashanicus	0
Sciuridae	Spermophilus	annulatus	2
Sciuridae	Spermophilus	armatus	0
Sciuridae	Spermophilus	atricapillus	0
Sciuridae	Spermophilus	beecheyi	8
Sciuridae	Spermophilus	beldingi	3
Sciuridae	Spermophilus	brevicauda	0
Sciuridae	Spermophilus	brunneus	0
Sciuridae	Spermophilus	canus	0
Sciuridae	Spermophilus	citellus	4
Sciuridae	Spermophilus	columbianus	2
Sciuridae	Spermophilus	dauricus	0
Sciuridae	Spermophilus	elegans	3
Sciuridae	Spermophilus	erythrogenys	0
Sciuridae	Spermophilus	franklinii	0
Sciuridae	Spermophilus	fulvus	3
Sciuridae	Spermophilus	lateralis	13
Sciuridae	Spermophilus	madrensis	0
Sciuridae	Spermophilus	major	0
Sciuridae	Spermophilus	mexicanus	2
Sciuridae	Spermophilus	mohavensis	0
Sciuridae	Spermophilus	mollis	3
Sciuridae	Spermophilus	musicus	0
Sciuridae	Spermophilus	pallidicauda	0
Sciuridae	Spermophilus	parryii	10
Sciuridae	Spermophilus	perotensis	0
Sciuridae	Spermophilus	pygmaeus	4
Sciuridae	Spermophilus	ralli	0

Sciuridae	Spermophilus	relictus	0
Sciuridae	Spermophilus	richardsonii	0
Sciuridae	Spermophilus	saturatus	0
Sciuridae	Spermophilus	spilosoma	13
Sciuridae	Spermophilus	suslicus	3
Sciuridae	Spermophilus	tereticaudus	4
Sciuridae	Spermophilus	townsendii	2
Sciuridae	Spermophilus	tridecemlineatus	10
Sciuridae	Spermophilus	undulatus	6
Sciuridae	Spermophilus	variegatus	8
Sciuridae	Spermophilus	washingtoni	0
Sciuridae	Spermophilus	xanthoprymnus	0
Sciuridae	Tamias	alpinus	0
Sciuridae	Tamias	amoenus	14
Sciuridae	Tamias	bulleri	0
Sciuridae	Tamias	canipes	2
Sciuridae	Tamias	cinereicollis	2
Sciuridae	Tamias	dorsalis	6
Sciuridae	Tamias	durangae	0
Sciuridae	Tamias	merriami	3
Sciuridae	Tamias	minimus	18
Sciuridae	Tamias	obscurus	3
Sciuridae	Tamias	ochrogenys	0
Sciuridae	Tamias	palmeri	0
Sciuridae	Tamias	panamintinus	2
Sciuridae	Tamias	quadrimaculatus	0
Sciuridae	Tamias	quadrivittatus	0
Sciuridae	Tamias	ruficaudus	2
Sciuridae	Tamias	rufus	0
Sciuridae	Tamias	senex	2
Sciuridae	Tamias	sibiricus	9
Sciuridae	Tamias	siskiyou	2
Sciuridae	Tamias	sonomae	2
Sciuridae	Tamias	speciosus	4
Sciuridae	Tamias	striatus	11
Sciuridae	Tamias	townsendii	2
Sciuridae	Tamias	umbrinus	7
Gliridae	Graphiurus	angolensis	0
Gliridae	Graphiurus	christyi	0
Gliridae	Graphiurus	crassicaudatus	0
Gliridae	Graphiurus	johnstoni	0
Gliridae	Graphiurus	kelleni	0

Gliridae	Graphiurus	lorraineus	0
Gliridae	Graphiurus	microtis	0
Gliridae	Graphiurus	monardi	0
Gliridae	Graphiurus	murinus	0
Gliridae	Graphiurus	nagtglasii	0
Gliridae	Graphiurus	ocularis	0
Gliridae	Graphiurus	platyops	0
Gliridae	Graphiurus	rupicola	0
Gliridae	Graphiurus	surdus	0
Gliridae	Chaetocauda	sichuanensis	0
Gliridae	Dryomys	laniger	0
Gliridae	Dryomys	niethammeri	0
Gliridae	Dryomys	nitedula	0
Gliridae	Eliomys	melanurus	0
Gliridae	Eliomys	munbyanus	0
Gliridae	Eliomys	quercinus	0
Gliridae	Muscardinus	avellanarius	0
Gliridae	Myomimus	personatus	0
Gliridae	Myomimus	roachi	0
Gliridae	Myomimus	setzeri	0
Gliridae	Selevinia	betpakdalaensis	0
Gliridae	Glirulus	japonicus	0
Gliridae	Glis	glis	0
Castoridae	Castor	canadensis	0
Castoridae	Castor	fiber	0
Heteromyidae	Dipodomys	agilis	2
Heteromyidae	Dipodomys	californicus	3
Heteromyidae	Dipodomys	compactus	2
Heteromyidae	Dipodomys	deserti	4
Heteromyidae	Dipodomys	elator	0
Heteromyidae	Dipodomys	gravipes	0
Heteromyidae	Dipodomys	heermanni	9
Heteromyidae	Dipodomys	ingens	0
Heteromyidae	Dipodomys	merriami	19
Heteromyidae	Dipodomys	microps	13
Heteromyidae	Dipodomys	nelsoni	0
Heteromyidae	Dipodomys	nitratoides	3
Heteromyidae	Dipodomys	ordii	32
Heteromyidae	Dipodomys	panamintinus	5
Heteromyidae	Dipodomys	phillipsii	4
Heteromyidae	Dipodomys	simulans	2
Heteromyidae	Dipodomys	spectabilis	6

Heteromyidae	Dipodomys	stephensi	0
Heteromyidae	Dipodomys	venustus	3
Heteromyidae	Microdipodops	megacephalus	13
Heteromyidae	Microdipodops	pallidus	5
Heteromyidae	Heteromys	anomalus	4
Heteromyidae	Heteromys	australis	3
Heteromyidae	Heteromys	desmarestianus	12
Heteromyidae	Heteromys	gaumeri	0
Heteromyidae	Heteromys	nelsoni	0
Heteromyidae	Heteromys	oasicus	0
Heteromyidae	Heteromys	oresterus	0
Heteromyidae	Heteromys	teleus	0
Heteromyidae	Liomys	adspersus	0
Heteromyidae	Liomys	irroratus	7
Heteromyidae	Liomys	pictus	4
Heteromyidae	Liomys	salvini	3
Heteromyidae	Liomys	spectabilis	0
Heteromyidae	Chaetodipus	arenarius	11
Heteromyidae	Chaetodipus	artus	0
Heteromyidae	Chaetodipus	baileyi	2
Heteromyidae	Chaetodipus	californicus	8
Heteromyidae	Chaetodipus	dalquesti	0
Heteromyidae	Chaetodipus	eremicus	2
Heteromyidae	Chaetodipus	fallax	6
Heteromyidae	Chaetodipus	formosus	7
Heteromyidae	Chaetodipus	goldmani	0
Heteromyidae	Chaetodipus	hispidus	4
Heteromyidae	Chaetodipus	intermedius	8
Heteromyidae	Chaetodipus	lineatus	0
Heteromyidae	Chaetodipus	nelsoni	2
Heteromyidae	Chaetodipus	penicillatus	6
Heteromyidae	Chaetodipus	pernix	2
Heteromyidae	Chaetodipus	rudinoris	6
Heteromyidae	Chaetodipus	spinatus	18
Heteromyidae	Perognathus	alticolus	2
Heteromyidae	Perognathus	amplus	4
Heteromyidae	Perognathus	fasciatus	2
Heteromyidae	Perognathus	flavescens	8
Heteromyidae	Perognathus	flavus	14
Heteromyidae	Perognathus	inornatus	3
Heteromyidae	Perognathus	longimembris	16
Heteromyidae	Perognathus	merriami	2

Heteromyidae	Perognathus	parvus	12
Geomyidae	Cratogeomys	castanops	18
Geomyidae	Cratogeomys	goldmani	7
Geomyidae	Cratogeomys	fumosus	0
Geomyidae	Cratogeomys	gymnurus	4
Geomyidae	Cratogeomys	merriami	7
Geomyidae	Cratogeomys	neglectus	0
Geomyidae	Cratogeomys	tylorhinus	6
Geomyidae	Cratogeomys	zinseri	0
Geomyidae	Geomys	attwateri	2
Geomyidae	Geomys	arenarius	2
Geomyidae	Geomys	breviceps	2
Geomyidae	Geomys	bursarius	10
Geomyidae	Geomys	knoxjonesi	0
Geomyidae	Geomys	personatus	7
Geomyidae	Geomys	pinetis	6
Geomyidae	Geomys	texensis	3
Geomyidae	Geomys	tropicalis	0
Geomyidae	Orthogeomys	cavator	3
Geomyidae	Orthogeomys	cherriei	3
Geomyidae	Orthogeomys	cuniculus	0
Geomyidae	Orthogeomys	dariensis	0
Geomyidae	Orthogeomys	grandis	16
Geomyidae	Orthogeomys	heterodus	3
Geomyidae	Orthogeomys	hispidus	12
Geomyidae	Orthogeomys	lanius	0
Geomyidae	Orthogeomys	matagalpae	0
Geomyidae	Orthogeomys	thaeleri	0
Geomyidae	Orthogeomys	underwoodi	0
Geomyidae	Pappogeomys	alcorni	0
Geomyidae	Pappogeomys	bulleri	8
Geomyidae	Thomomys	bottae	133
Geomyidae	Thomomys	bulbivorus	0
Geomyidae	Thomomys	clusius	0
Geomyidae	Thomomys	idahoensis	3
Geomyidae	Thomomys	mazama	15
Geomyidae	Thomomys	monticola	0
Geomyidae	Thomomys	talpoides	54
Geomyidae	Thomomys	townsendii	2
Geomyidae	Thomomys	umbrinus	25
Geomyidae	Zygogeomys	trichopus	0
Dipodidae	Allactaga	balikunica	0

Dipodidae	Allactaga	bullata	0
Dipodidae	Allactaga	elater	0
Dipodidae	Allactaga	euphratica	0
Dipodidae	Allactaga	firouzi	0
Dipodidae	Allactaga	hotsoni	0
Dipodidae	Allactaga	major	0
Dipodidae	Allactaga	severtzovi	0
Dipodidae	Allactaga	sibirica	0
Dipodidae	Allactaga	tetradactyla	0
Dipodidae	Allactaga	vinogradovi	0
Dipodidae	Allactaga	williamsi	0
Dipodidae	Allactodipus	bobrinskii	0
Dipodidae	Pygeretmus	platyurus	0
Dipodidae	Pygeretmus	pumilio	0
Dipodidae	Pygeretmus	shitkovi	0
Dipodidae	Cardiocranius	paradoxus	0
Dipodidae	Salpingotulus	michaelis	0
Dipodidae	Salpingotus	crassicauda	0
Dipodidae	Salpingotus	heptneri	0
Dipodidae	Salpingotus	kozlovi	0
Dipodidae	Salpingotus	pallidus	0
Dipodidae	Salpingotus	thomasi	0
Dipodidae	Dipus	sagitta	0
Dipodidae	Eremodipus	lichtensteini	0
Dipodidae	Jaculus	blanfordi	0
Dipodidae	Jaculus	jaculus	0
Dipodidae	Jaculus	orientalis	0
Dipodidae	Paradipus	ctenodactylus	0
Dipodidae	Stylodipus	andrewsi	0
Dipodidae	Stylodipus	sungorus	0
Dipodidae	Stylodipus	telum	0
Dipodidae	Euchoreutes	naso	0
Dipodidae	Sicista	armenica	0
Dipodidae	Sicista	betulina	0
Dipodidae	Sicista	caucasica	0
Dipodidae	Sicista	caudata	0
Dipodidae	Sicista	concolor	0
Dipodidae	Sicista	kazbegica	0
Dipodidae	Sicista	kluchorica	0
Dipodidae	Sicista	napaea	0
Dipodidae	Sicista	pseudonapaea	0
Dipodidae	Sicista	severtzovi	0

Dipodidae	Sicista	strandi	0
Dipodidae	Sicista	subtilis	0
Dipodidae	Sicista	tianshanica	0
Dipodidae	Eozapus	setchuanus	0
Dipodidae	Napaeozapus	insignis	0
Dipodidae	Zapus	hudsonius	0
Dipodidae	Zapus	princeps	0
Dipodidae	Zapus	trinotatus	0
Platacanthomyidae	Platacanthomys	lasiurus	0
Platacanthomyidae	Typhlomys	cinereus	0
Spalacidae	Eospalax	fontanierii	0
Spalacidae	Eospalax	rothschildi	0
Spalacidae	Eospalax	smithii	0
Spalacidae	Myospalax	aspalax	0
Spalacidae	Myospalax	myospalax	0
Spalacidae	Myospalax	psilurus	0
Spalacidae	Cannomys	badius	0
Spalacidae	Rhizomys	pruinosus	0
Spalacidae	Rhizomys	sinensis	0
Spalacidae	Rhizomys	sumatrensis	0
Spalacidae	Spalax	arenarius	0
Spalacidae	Spalax	carmeli	0
Spalacidae	Spalax	ehrenbergi	0
Spalacidae	Spalax	galili	0
Spalacidae	Spalax	giganteus	0
Spalacidae	Spalax	golani	0
Spalacidae	Spalax	graecus	0
Spalacidae	Spalax	judaei	0
Spalacidae	Spalax	leucodon	0
Spalacidae	Spalax	microphthalmus	0
Spalacidae	Spalax	nehringi	0
Spalacidae	Spalax	uralensis	0
Spalacidae	Spalax	zemni	0
Spalacidae	Tachyoryctes	ankoliae	0
Spalacidae	Tachyoryctes	annectens	0
Spalacidae	Tachyoryctes	audax	0
Spalacidae	Tachyoryctes	daemon	0
Spalacidae	Tachyoryctes	ibeanus	0
Spalacidae	Tachyoryctes	macrocephalus	0
Spalacidae	Tachyoryctes	naivashae	0
Spalacidae	Tachyoryctes	rex	0
Spalacidae	Tachyoryctes	ruandae	0

Spalacidae	Tachyoryctes	ruddi	0
Spalacidae	Tachyoryctes	spalacinus	0
Spalacidae	Tachyoryctes	splendens	0
Spalacidae	Tachyoryctes	storeyi	0
Calomyscidae	Calomyscus	bailwardi	0
Calomyscidae	Calomyscus	baluchi	0
Calomyscidae	Calomyscus	elburzensis	0
Calomyscidae	Calomyscus	grandis	0
Calomyscidae	Calomyscus	hotsoni	0
Calomyscidae	Calomyscus	mystax	0
Calomyscidae	Calomyscus	tsolovi	0
Calomyscidae	Calomyscus	urartensis	0
Nesomyidae	Beamys	hindei	0
Nesomyidae	Beamys	major	0
Nesomyidae	Cricetomys	ansorgei	0
Nesomyidae	Cricetomys	emini	0
Nesomyidae	Cricetomys	gambianus	0
Nesomyidae	Cricetomys	kivuensis	0
Nesomyidae	Saccostomus	campestris	0
Nesomyidae	Saccostomus	mearnsi	0
Nesomyidae	Delanymys	brooksi	0
Nesomyidae	Dendromus	insignis	0
Nesomyidae	Dendromus	kahuziensis	0
Nesomyidae	Dendromus	leucostomus	0
Nesomyidae	Dendromus	lovati	0
Nesomyidae	Dendromus	melanotis	0
Nesomyidae	Dendromus	mesomelas	0
Nesomyidae	Dendromus	messorius	0
Nesomyidae	Dendromus	mystacalis	0
Nesomyidae	Dendromus	nyasae	0
Nesomyidae	Dendromus	nyikae	0
Nesomyidae	Dendromus	oreas	0
Nesomyidae	Dendromus	vernayi	0
Nesomyidae	Dendroprionomys	rousseloti	0
Nesomyidae	Malacothrix	typica	0
Nesomyidae	Megadendromus	nikolausi	0
Nesomyidae	Prionomys	batesi	0
Nesomyidae	Steatomys	bocagei	0
Nesomyidae	Steatomys	caurinus	0
Nesomyidae	Steatomys	cuppedius	0
Nesomyidae	Steatomys	jacksoni	0
Nesomyidae	Steatomys	krebsii	0

Nesomyidae	Steatomys	opimus	0
Nesomyidae	Steatomys	parvus	0
Nesomyidae	Steatomys	pratensis	0
Nesomyidae	Mystromys	albicaudatus	0
Nesomyidae	Brachytarsomys	albicauda	0
Nesomyidae	Brachytarsomys	villosa	0
Nesomyidae	Brachyuromys	betsileoensis	0
Nesomyidae	Brachyuromys	ramirohitra	0
Nesomyidae	Eliurus	antsingy	0
Nesomyidae	Eliurus	ellermani	0
Nesomyidae	Eliurus	grandidieri	0
Nesomyidae	Eliurus	majori	0
Nesomyidae	Eliurus	minor	0
Nesomyidae	Eliurus	myoxinus	0
Nesomyidae	Eliurus	penicillatus	0
Nesomyidae	Eliurus	petteri	0
Nesomyidae	Eliurus	tanala	0
Nesomyidae	Eliurus	webbi	0
Nesomyidae	Gymnuromys	roberti	0
Nesomyidae	Hypogeomys	antimena	0
Nesomyidae	Macrotarsomys	bastardi	0
Nesomyidae	Macrotarsomys	ingens	0
Nesomyidae	Monticolomys	koopmani	0
Nesomyidae	Nesomys	audeberti	0
Nesomyidae	Nesomys	lambertoni	0
Nesomyidae	Nesomys	rufus	0
Nesomyidae	Voalavo	gymnocaudus	0
Nesomyidae	Petromyscus	barbouri	0
Nesomyidae	Petromyscus	collinus	0
Nesomyidae	Petromyscus	monticularis	0
Nesomyidae	Petromyscus	shortridgei	0
Cricetidae	Alticola	albicaudus	0
Cricetidae	Alticola	argentatus	0
Cricetidae	Alticola	barakshin	0
Cricetidae	Alticola	lemminus	0
Cricetidae	Alticola	macrotis	0
Cricetidae	Alticola	montosa	0
Cricetidae	Alticola	olchonensis	0
Cricetidae	Alticola	roylei	0
Cricetidae	Alticola	semicanus	0
Cricetidae	Alticola	stoliczkanus	0
Cricetidae	Alticola	strelzowi	0

Cricetidae	Alticola	tuvinicus	0
Cricetidae	Arborimus	albipes	0
Cricetidae	Arborimus	longicaudus	0
Cricetidae	Arborimus	pomo	0
Cricetidae	Arvicola	amphibius	0
Cricetidae	Arvicola	sapidus	0
Cricetidae	Arvicola	scherman	0
Cricetidae	Blanfordimys	afghanus	0
Cricetidae	Blanfordimys	bucharensis	0
Cricetidae	Caryomys	eva	0
Cricetidae	Caryomys	inez	0
Cricetidae	Chionomys	gud	0
Cricetidae	Chionomys	nivalis	0
Cricetidae	Chionomys	roberti	0
Cricetidae	Dicrostonyx	groenlandicus	0
Cricetidae	Dicrostonyx	hudsonius	0
Cricetidae	Dicrostonyx	nelsoni	0
Cricetidae	Dicrostonyx	nunatakensis	0
Cricetidae	Dicrostonyx	richardsoni	0
Cricetidae	Dicrostonyx	torquatus	0
Cricetidae	Dicrostonyx	unalascensis	0
Cricetidae	Dicrostonyx	vinogradovi	0
Cricetidae	Dinaromys	bogdanovi	0
Cricetidae	Ellobius	alaicus	0
Cricetidae	Ellobius	fuscocapillus	0
Cricetidae	Ellobius	lutescens	0
Cricetidae	Ellobius	talpinus	0
Cricetidae	Ellobius	tancrei	0
Cricetidae	Eolagurus	luteus	0
Cricetidae	Eolagurus	przewalskii	0
Cricetidae	Eothenomys	cachinus	0
Cricetidae	Eothenomys	chinensis	0
Cricetidae	Eothenomys	custos	0
Cricetidae	Eothenomys	melanogaster	0
Cricetidae	Eothenomys	miletus	0
Cricetidae	Eothenomys	olitor	0
Cricetidae	Eothenomys	proditor	0
Cricetidae	Eothenomys	wardi	0
Cricetidae	Hyperacrius	fertilis	0
Cricetidae	Hyperacrius	wynnei	0
Cricetidae	Lagurus	lagurus	0
Cricetidae	Lasiopodomys	brandtii	0

Cricetidae	Lasiopodomys	fuscus	0
Cricetidae	Lasiopodomys	mandarinus	0
Cricetidae	Lemmiscus	curtatus	0
Cricetidae	Lemmus	amurensis	0
Cricetidae	Lemmus	lemmus	0
Cricetidae	Lemmus	portenkoi	0
Cricetidae	Lemmus	sibiricus	0
Cricetidae	Lemmus	trimucronatus	0
Cricetidae	Microtus	abbreviatus	0
Cricetidae	Microtus	agrestis	0
Cricetidae	Microtus	anatolicus	0
Cricetidae	Microtus	arvalis	0
Cricetidae	Microtus	bavaricus	0
Cricetidae	Microtus	brachycercus	0
Cricetidae	Microtus	breweri	0
Cricetidae	Microtus	cabrerae	0
Cricetidae	Microtus	californicus	0
Cricetidae	Microtus	canicaudus	0
Cricetidae	Microtus	chrotorrhinus	0
Cricetidae	Microtus	clarkei	0
Cricetidae	Microtus	daghestanicus	0
Cricetidae	Microtus	dogramacii	0
Cricetidae	Microtus	duodecimcostatus	0
Cricetidae	Microtus	evoronensis	0
Cricetidae	Microtus	felteni	0
Cricetidae	Microtus	fortis	0
Cricetidae	Microtus	gerbei	0
Cricetidae	Microtus	gregalis	0
Cricetidae	Microtus	guatemalensis	0
Cricetidae	Microtus	guentheri	0
Cricetidae	Microtus	ilaeus	0
Cricetidae	Microtus	irani	0
Cricetidae	Microtus	kikuchii	0
Cricetidae	Microtus	levis	0
Cricetidae	Microtus	liechtensteini	0
Cricetidae	Microtus	limnophilus	0
Cricetidae	Microtus	longicaudus	0
Cricetidae	Microtus	lusitanicus	0
Cricetidae	Microtus	majori	0
Cricetidae	Microtus	maximowiczii	0
Cricetidae	Microtus	mexicanus	0
Cricetidae	Microtus	middendorffii	0

Cricetidae	Microtus	miurus	0
Cricetidae	Microtus	mongolicus	0
Cricetidae	Microtus	montanus	0
Cricetidae	Microtus	montebelli	0
Cricetidae	Microtus	mujanensis	0
Cricetidae	Microtus	multiplex	0
Cricetidae	Microtus	oaxacensis	0
Cricetidae	Microtus	ochrogaster	0
Cricetidae	Microtus	oeconomus	0
Cricetidae	Microtus	oregoni	0
Cricetidae	Microtus	paradoxus	0
Cricetidae	Microtus	pennsylvanicus	0
Cricetidae	Microtus	pinetorum	0
Cricetidae	Microtus	qazvinensis	0
Cricetidae	Microtus	quasiater	0
Cricetidae	Microtus	richardsoni	0
Cricetidae	Microtus	sachalinensis	0
Cricetidae	Microtus	savii	0
Cricetidae	Microtus	schelkovnikovi	0
Cricetidae	Microtus	schidlovskii	0
Cricetidae	Microtus	socialis	0
Cricetidae	Microtus	subterraneus	0
Cricetidae	Microtus	tatricus	0
Cricetidae	Microtus	thomasi	0
Cricetidae	Microtus	townsendii	0
Cricetidae	Microtus	transcaspicus	0
Cricetidae	Microtus	umbrosus	0
Cricetidae	Microtus	xanthognathus	0
Cricetidae	Myodes	andersoni	0
Cricetidae	Myodes	californicus	0
Cricetidae	Myodes	centralis	0
Cricetidae	Myodes	gapperi	0
Cricetidae	Myodes	glareolus	0
Cricetidae	Myodes	imaizumii	0
Cricetidae	Myodes	regulus	0
Cricetidae	Myodes	rex	0
Cricetidae	Myodes	rufocanus	0
Cricetidae	Myodes	rutilus	0
Cricetidae	Myodes	shanseius	0
Cricetidae	Myodes	smithii	0
Cricetidae	Myopus	schisticolor	0
Cricetidae	Neodon	forresti	0

Cricetidae	Neodon	irene	0
Cricetidae	Neodon	juldaschi	0
Cricetidae	Neodon	sikimensis	0
Cricetidae	Neofiber	alleni	0
Cricetidae	Ondatra	zibethicus	0
Cricetidae	Phaiomys	leucurus	0
Cricetidae	Phenacomys	intermedius	0
Cricetidae	Phenacomys	ungava	0
Cricetidae	Proedromys	bedfordi	0
Cricetidae	Prometheomys	schaposchnikowi	0
Cricetidae	Synaptomys	borealis	0
Cricetidae	Synaptomys	cooperi	0
Cricetidae	Volemys	millicens	0
Cricetidae	Volemys	musseri	0
Cricetidae	Allocricetulus	curtatus	0
Cricetidae	Allocricetulus	eversmanni	0
Cricetidae	Cansumys	canus	0
Cricetidae	Cricetulus	alticola	0
Cricetidae	Cricetulus	barabensis	0
Cricetidae	Cricetulus	kamensis	0
Cricetidae	Cricetulus	longicaudatus	0
Cricetidae	Cricetulus	migratorius	0
Cricetidae	Cricetulus	sokolovi	0
Cricetidae	Cricetus	cricetus	0
Cricetidae	Mesocricetus	auratus	0
Cricetidae	Mesocricetus	brandti	0
Cricetidae	Mesocricetus	newtoni	0
Cricetidae	Mesocricetus	raddei	0
Cricetidae	Phodopus	campbelli	0
Cricetidae	Phodopus	roborovskii	0
Cricetidae	Phodopus	sungorus	0
Cricetidae	Tscherskia	triton	0
Cricetidae	Lophiomys	imhausi	0
Cricetidae	Baiomys	musculus	0
Cricetidae	Baiomys	taylori	0
Cricetidae	Habromys	chinanteco	0
Cricetidae	Habromys	delicatulus	0
Cricetidae	Habromys	ixtlani	0
Cricetidae	Habromys	lepturus	0
Cricetidae	Habromys	lophurus	0
Cricetidae	Habromys	simulatus	0
Cricetidae	Hodomys	alleni	0

Cricetidae	Isthmomys	flavidus	0
Cricetidae	Isthmomys	pirrensis	0
Cricetidae	Megadontomys	cryophilus	0
Cricetidae	Megadontomys	nelsoni	0
Cricetidae	Megadontomys	thomasi	0
Cricetidae	Nelsonia	goldmani	0
Cricetidae	Nelsonia	neotomodon	0
Cricetidae	Neotoma	albigula	0
Cricetidae	Neotoma	angustapalata	0
Cricetidae	Neotoma	anthonyi	0
Cricetidae	Neotoma	bryanti	0
Cricetidae	Neotoma	bunkeri	0
Cricetidae	Neotoma	chrysomelas	0
Cricetidae	Neotoma	cinerea	0
Cricetidae	Neotoma	devia	0
Cricetidae	Neotoma	floridana	0
Cricetidae	Neotoma	fuscipes	0
Cricetidae	Neotoma	goldmani	0
Cricetidae	Neotoma	lepida	0
Cricetidae	Neotoma	leucodon	0
Cricetidae	Neotoma	macrotis	0
Cricetidae	Neotoma	magister	0
Cricetidae	Neotoma	martinensis	0
Cricetidae	Neotoma	mexicana	0
Cricetidae	Neotoma	micropus	0
Cricetidae	Neotoma	nelsoni	0
Cricetidae	Neotoma	palatina	0
Cricetidae	Neotoma	phenax	0
Cricetidae	Neotoma	stephensi	0
Cricetidae	Neotomodon	alstoni	0
Cricetidae	Ochrotomys	nuttalli	0
Cricetidae	Onychomys	arenicola	0
Cricetidae	Onychomys	leucogaster	0
Cricetidae	Onychomys	torridus	0
Cricetidae	Osgoodomys	banderanus	0
Cricetidae	Peromyscus	attwateri	0
Cricetidae	Peromyscus	aztecus	0
Cricetidae	Peromyscus	beatae	0
Cricetidae	Peromyscus	boylii	0
Cricetidae	Peromyscus	bullatus	0
Cricetidae	Peromyscus	californicus	0
Cricetidae	Peromyscus	caniceps	0

Cricetidae	Peromyscus	crinitus	0
Cricetidae	Peromyscus	dickeyi	0
Cricetidae	Peromyscus	difficilis	0
Cricetidae	Peromyscus	eremicus	0
Cricetidae	Peromyscus	eva	0
Cricetidae	Peromyscus	fraterculus	0
Cricetidae	Peromyscus	furvus	0
Cricetidae	Peromyscus	gossypinus	0
Cricetidae	Peromyscus	grandis	0
Cricetidae	Peromyscus	gratus	0
Cricetidae	Peromyscus	guardia	0
Cricetidae	Peromyscus	guatemalensis	0
Cricetidae	Peromyscus	gymnotis	0
Cricetidae	Peromyscus	hooperi	0
Cricetidae	Peromyscus	hylocetes	0
Cricetidae	Peromyscus	interparietalis	0
Cricetidae	Peromyscus	keeni	0
Cricetidae	Peromyscus	leucopus	0
Cricetidae	Peromyscus	levipes	0
Cricetidae	Peromyscus	madrensis	0
Cricetidae	Peromyscus	maniculatus	0
Cricetidae	Peromyscus	mayensis	0
Cricetidae	Peromyscus	megalops	0
Cricetidae	Peromyscus	mekisturus	0
Cricetidae	Peromyscus	melanocarpus	0
Cricetidae	Peromyscus	melanophrys	0
Cricetidae	Peromyscus	melanotis	0
Cricetidae	Peromyscus	melanurus	0
Cricetidae	Peromyscus	merriami	0
Cricetidae	Peromyscus	mexicanus	0
Cricetidae	Peromyscus	nasutus	0
Cricetidae	Peromyscus	ochraventer	0
Cricetidae	Peromyscus	pectoralis	0
Cricetidae	Peromyscus	pembertoni	0
Cricetidae	Peromyscus	perfulvus	0
Cricetidae	Peromyscus	polionotus	0
Cricetidae	Peromyscus	polius	0
Cricetidae	Peromyscus	pseudocrinitus	0
Cricetidae	Peromyscus	sagax	0
Cricetidae	Peromyscus	sejugis	0
Cricetidae	Peromyscus	simulus	0
Cricetidae	Peromyscus	slevini	0

Cricetidae	Peromyscus	spicilegus	0
Cricetidae	Peromyscus	stephani	0
Cricetidae	Peromyscus	stirtoni	0
Cricetidae	Peromyscus	truei	0
Cricetidae	Peromyscus	winkelmanni	0
Cricetidae	Peromyscus	yucatanicus	0
Cricetidae	Peromyscus	zarhynchus	0
Cricetidae	Podomys	floridanus	0
Cricetidae	Reithrodontomys	brevirostris	0
Cricetidae	Reithrodontomys	burti	0
Cricetidae	Reithrodontomys	chrysopsis	0
Cricetidae	Reithrodontomys	creper	0
Cricetidae	Reithrodontomys	darienensis	0
Cricetidae	Reithrodontomys	fulvescens	0
Cricetidae	Reithrodontomys	gracilis	0
Cricetidae	Reithrodontomys	hirsutus	0
Cricetidae	Reithrodontomys	humulis	0
Cricetidae	Reithrodontomys	megalotis	0
Cricetidae	Reithrodontomys	mexicanus	0
Cricetidae	Reithrodontomys	microdon	0
Cricetidae	Reithrodontomys	montanus	0
Cricetidae	Reithrodontomys	paradoxus	0
Cricetidae	Reithrodontomys	raviventris	0
Cricetidae	Reithrodontomys	rodriguezi	0
Cricetidae	Reithrodontomys	spectabilis	0
Cricetidae	Reithrodontomys	sumichrasti	0
Cricetidae	Reithrodontomys	tenuirostris	0
Cricetidae	Reithrodontomys	zacatecae	0
Cricetidae	Scotinomys	teguina	0
Cricetidae	Scotinomys	xerampelinus	0
Cricetidae	Xenomys	nelsoni	0
Cricetidae	Abrawayaomys	ruschii	0
Cricetidae	Abrothrix	andinus	0
Cricetidae	Abrothrix	hershkovitzi	0
Cricetidae	Abrothrix	illuteus	0
Cricetidae	Abrothrix	jelskii	0
Cricetidae	Abrothrix	lanosus	0
Cricetidae	Abrothrix	longipilis	0
Cricetidae	Abrothrix	markhami	0
Cricetidae	Abrothrix	olivaceus	0
Cricetidae	Abrothrix	sanborni	0
Cricetidae	Aepeomys	lugens	0

Cricetidae	Aepeomys	reigi	0
Cricetidae	Akodon	aerosus	0
Cricetidae	Akodon	affinis	0
Cricetidae	Akodon	albiventer	0
Cricetidae	Akodon	aliquantulus	0
Cricetidae	Akodon	azarae	0
Cricetidae	Akodon	bogotensis	0
Cricetidae	Akodon	boliviensis	0
Cricetidae	Akodon	budini	0
Cricetidae	Akodon	cursor	0
Cricetidae	Akodon	dayi	0
Cricetidae	Akodon	dolores	0
Cricetidae	Akodon	fumeus	0
Cricetidae	Akodon	iniscatus	0
Cricetidae	Akodon	juninensis	0
Cricetidae	Akodon	kofordi	0
Cricetidae	Akodon	latebricola	0
Cricetidae	Akodon	leucolimnaeus	0
Cricetidae	Akodon	lindberghi	0
Cricetidae	Akodon	lutescens	0
Cricetidae	Akodon	mimus	0
Cricetidae	Akodon	molinae	0
Cricetidae	Akodon	mollis	0
Cricetidae	Akodon	montensis	0
Cricetidae	Akodon	mystax	0
Cricetidae	Akodon	neocenus	0
Cricetidae	Akodon	oenos	0
Cricetidae	Akodon	orophilus	0
Cricetidae	Akodon	paranaensis	0
Cricetidae	Akodon	pervalens	0
Cricetidae	Akodon	reigi	0
Cricetidae	Akodon	sanctipaulensis	0
Cricetidae	Akodon	serrensis	0
Cricetidae	Akodon	siberiae	0
Cricetidae	Akodon	simulator	0
Cricetidae	Akodon	spegazzinii	0
Cricetidae	Akodon	subfuscus	0
Cricetidae	Akodon	surdus	0
Cricetidae	Akodon	sylvanus	0
Cricetidae	Akodon	toba	0
Cricetidae	Akodon	torques	0
Cricetidae	Akodon	varius	0

Cricetidae	Amphinectomys	savamis	0
Cricetidae	Andalgalomys	olrogi	0
Cricetidae	Andalgalomys	pearsoni	0
Cricetidae	Andalgalomys	roigi	0
Cricetidae	Andinomys	edax	0
Cricetidae	Anotomys	leander	0
Cricetidae	Auliscomys	boliviensis	0
Cricetidae	Auliscomys	pictus	0
Cricetidae	Auliscomys	sublimis	0
Cricetidae	Bibimys	chacoensis	0
Cricetidae	Bibimys	labiosus	0
Cricetidae	Bibimys	torresi	0
Cricetidae	Blarinomys	breviceps	0
Cricetidae	Brucepattersonius	albinasus	0
Cricetidae	Brucepattersonius	griserufescens	0
Cricetidae	Brucepattersonius	guarani	0
Cricetidae	Brucepattersonius	igniventris	0
Cricetidae	Brucepattersonius	iheringi	0
Cricetidae	Brucepattersonius	misionensis	0
Cricetidae	Brucepattersonius	paradisus	0
Cricetidae	Brucepattersonius	soricinus	0
Cricetidae	Calomys	boliviae	0
Cricetidae	Calomys	callidus	0
Cricetidae	Calomys	callosus	0
Cricetidae	Calomys	expulsus	0
Cricetidae	Calomys	hummelincki	0
Cricetidae	Calomys	laucha	0
Cricetidae	Calomys	lepidus	0
Cricetidae	Calomys	musculinus	0
Cricetidae	Calomys	sorellus	0
Cricetidae	Calomys	tener	0
Cricetidae	Calomys	tocantinsi	0
Cricetidae	Calomys	venustus	0
Cricetidae	Chelemys	delfini	0
Cricetidae	Chelemys	macronyx	0
Cricetidae	Chelemys	megalonyx	0
Cricetidae	Chibchanomys	orcesi	0
Cricetidae	Chibchanomys	trichotis	0
Cricetidae	Chilomys	instans	0
Cricetidae	Chinchillula	sahamae	0
Cricetidae	Delomys	collinus	0
Cricetidae	Delomys	dorsalis	0

Cricetidae	Delomys	sublineatus	0
Cricetidae	Deltamys	kempi	0
Cricetidae	Eligmodontia	moreni	0
Cricetidae	Eligmodontia	morgani	0
Cricetidae	Eligmodontia	puerulus	0
Cricetidae	Eligmodontia	typus	0
Cricetidae	Euneomys	chinchilloides	0
Cricetidae	Euneomys	fossor	0
Cricetidae	Euneomys	mordax	0
Cricetidae	Euneomys	petersoni	0
Cricetidae	Galenomys	garleppi	0
Cricetidae	Geoxus	valdivianus	0
Cricetidae	Graomys	centralis	0
Cricetidae	Graomys	domorum	0
Cricetidae	Graomys	edithae	0
Cricetidae	Graomys	griseoflavus	0
Cricetidae	Handleyomys	fuscatus	0
Cricetidae	Handleyomys	intectus	0
Cricetidae	Holochilus	brasiliensis	0
Cricetidae	Holochilus	chacarius	0
Cricetidae	Holochilus	sciureus	0
Cricetidae	Ichthyomys	hydrobates	0
Cricetidae	Ichthyomys	pittieri	0
Cricetidae	Ichthyomys	stolzmanni	0
Cricetidae	Ichthyomys	tweedii	0
Cricetidae	Irenomys	tarsalis	0
Cricetidae	Juliomys	pictipes	0
Cricetidae	Juliomys	rimofrons	0
Cricetidae	Juscelinomys	candango	0
Cricetidae	Juscelinomys	guaporensis	0
Cricetidae	Juscelinomys	huanchacae	0
Cricetidae	Kunsia	fronto	0
Cricetidae	Kunsia	tomentosus	0
Cricetidae	Lenoxus	apicalis	0
Cricetidae	Loxodontomys	micropus	0
Cricetidae	Loxodontomys	pikumche	0
Cricetidae	Lundomys	molitor	0
Cricetidae	Megalomys	desmarestii	0
Cricetidae	Megalomys	luciae	0
Cricetidae	Megaoryzomys	curioi	0
Cricetidae	Melanomys	caliginosus	0
Cricetidae	Melanomys	robustulus	0

Cricetidae	Melanomys	zunigae	0
Cricetidae	Microakodontomys	transitorius	0
Cricetidae	Microryzomys	altissimus	0
Cricetidae	Microryzomys	minutus	0
Cricetidae	Neacomys	dubosti	0
Cricetidae	Neacomys	guianae	0
Cricetidae	Neacomys	minutus	0
Cricetidae	Neacomys	musseri	0
Cricetidae	Neacomys	paracou	0
Cricetidae	Neacomys	pictus	0
Cricetidae	Neacomys	spinosus	0
Cricetidae	Neacomys	tenuipes	0
Cricetidae	Necromys	amoenus	0
Cricetidae	Necromys	benefactus	0
Cricetidae	Necromys	lactens	0
Cricetidae	Necromys	lasiurus	0
Cricetidae	Necromys	lenguarum	0
Cricetidae	Necromys	obscurus	0
Cricetidae	Necromys	punctulatus	0
Cricetidae	Necromys	temchuki	0
Cricetidae	Necromys	urichi	0
Cricetidae	Nectomys	apicalis	0
Cricetidae	Nectomys	magdalenae	0
Cricetidae	Nectomys	palmipes	0
Cricetidae	Nectomys	rattus	0
Cricetidae	Nectomys	squamipes	0
Cricetidae	Neotomys	ebriosus	0
Cricetidae	Nesoryzomys	darwini	0
Cricetidae	Nesoryzomys	fernandinae	0
Cricetidae	Nesoryzomys	indefessus	0
Cricetidae	Nesoryzomys	swarthi	0
Cricetidae	Neusticomys	monticolus	0
Cricetidae	Neusticomys	mussoi	0
Cricetidae	Neusticomys	oyapocki	0
Cricetidae	Neusticomys	peruviensis	0
Cricetidae	Neusticomys	venezuelae	0
Cricetidae	Noronhomys	vespuccii	0
Cricetidae	Notiomys	edwardsii	0
Cricetidae	Oecomys	auyantepui	0
Cricetidae	Oecomys	bicolor	0
Cricetidae	Oecomys	catherinae	0
Cricetidae	Oecomys	cleberi	0

Cricetidae	Oecomys	concolor	0
Cricetidae	Oecomys	flavicans	0
Cricetidae	Oecomys	mamorae	0
Cricetidae	Oecomys	paricola	0
Cricetidae	Oecomys	phaeotis	0
Cricetidae	Oecomys	rex	0
Cricetidae	Oecomys	roberti	0
Cricetidae	Oecomys	rutilus	0
Cricetidae	Oecomys	speciosus	0
Cricetidae	Oecomys	superans	0
Cricetidae	Oecomys	trinitatis	0
Cricetidae	Oligoryzomys	andinus	0
Cricetidae	Oligoryzomys	arenalis	0
Cricetidae	Oligoryzomys	brendae	0
Cricetidae	Oligoryzomys	chacoensis	0
Cricetidae	Oligoryzomys	delticola	0
Cricetidae	Oligoryzomys	destructor	0
Cricetidae	Oligoryzomys	eliurus	0
Cricetidae	Oligoryzomys	flavescens	0
Cricetidae	Oligoryzomys	fornesi	0
Cricetidae	Oligoryzomys	fulvescens	0
Cricetidae	Oligoryzomys	griseolus	0
Cricetidae	Oligoryzomys	longicaudatus	0
Cricetidae	Oligoryzomys	magellanicus	0
Cricetidae	Oligoryzomys	microtis	0
Cricetidae	Oligoryzomys	nigripes	0
Cricetidae	Oligoryzomys	stramineus	0
Cricetidae	Oligoryzomys	vegetus	0
Cricetidae	Oligoryzomys	victus	0
Cricetidae	Oryzomys	albigularis	0
Cricetidae	Oryzomys	alfaroi	0
Cricetidae	Oryzomys	angouya	0
Cricetidae	Oryzomys	auriventer	0
Cricetidae	Oryzomys	balneator	0
Cricetidae	Oryzomys	bolivaris	0
Cricetidae	Oryzomys	caracolus	0
Cricetidae	Oryzomys	chapmani	0
Cricetidae	Oryzomys	couesi	0
Cricetidae	Oryzomys	curasoae	0
Cricetidae	Oryzomys	devius	0
Cricetidae	Oryzomys	dimidiatus	0
Cricetidae	Oryzomys	emmonsae	0

Cricetidae	Oryzomys	galapagoensis	0
Cricetidae	Oryzomys	gorgasi	0
Cricetidae	Oryzomys	hammondi	0
Cricetidae	Oryzomys	keaysi	0
Cricetidae	Oryzomys	lamia	0
Cricetidae	Oryzomys	laticeps	0
Cricetidae	Oryzomys	legatus	0
Cricetidae	Oryzomys	levipes	0
Cricetidae	Oryzomys	macconnelli	0
Cricetidae	Oryzomys	maracajuensis	0
Cricetidae	Oryzomys	marinhus	0
Cricetidae	Oryzomys	megacephalus	0
Cricetidae	Oryzomys	melanotis	0
Cricetidae	Oryzomys	meridensis	0
Cricetidae	Oryzomys	nelsoni	0
Cricetidae	Oryzomys	nitidus	0
Cricetidae	Oryzomys	palustris	0
Cricetidae	Oryzomys	perenensis	0
Cricetidae	Oryzomys	polius	0
Cricetidae	Oryzomys	rhabdops	0
Cricetidae	Oryzomys	rostratus	0
Cricetidae	Oryzomys	russatus	0
Cricetidae	Oryzomys	saturatior	0
Cricetidae	Oryzomys	scotti	0
Cricetidae	Oryzomys	seuanezi	0
Cricetidae	Oryzomys	subflavus	0
Cricetidae	Oryzomys	talamancae	0
Cricetidae	Oryzomys	tatei	0
Cricetidae	Oryzomys	xanthaeolus	0
Cricetidae	Oryzomys	yunganus	0
Cricetidae	Oxymycterus	akodontius	0
Cricetidae	Oxymycterus	amazonicus	0
Cricetidae	Oxymycterus	angularis	0
Cricetidae	Oxymycterus	caparoae	0
Cricetidae	Oxymycterus	dasytrichus	0
Cricetidae	Oxymycterus	delator	0
Cricetidae	Oxymycterus	hiska	0
Cricetidae	Oxymycterus	hispidus	0
Cricetidae	Oxymycterus	hucucha	0
Cricetidae	Oxymycterus	inca	0
Cricetidae	Oxymycterus	josei	0
Cricetidae	Oxymycterus	nasutus	0

Cricetidae	Oxymycterus	paramensis	0
Cricetidae	Oxymycterus	quaestor	0
Cricetidae	Oxymycterus	roberti	0
Cricetidae	Oxymycterus	rufus	0
Cricetidae	Paralomys	gerbillus	0
Cricetidae	Pearsonomys	annectens	0
Cricetidae	Phaenomys	ferrugineus	0
Cricetidae	Phyllotis	amicus	0
Cricetidae	Phyllotis	andium	0
Cricetidae	Phyllotis	bonariensis	0
Cricetidae	Phyllotis	caprinus	0
Cricetidae	Phyllotis	darwini	0
Cricetidae	Phyllotis	definitus	0
Cricetidae	Phyllotis	haggardi	0
Cricetidae	Phyllotis	limatus	0
Cricetidae	Phyllotis	magister	0
Cricetidae	Phyllotis	osgoodi	0
Cricetidae	Phyllotis	osilae	0
Cricetidae	Phyllotis	wolffsohni	0
Cricetidae	Phyllotis	xanthopygus	0
Cricetidae	Podoxymys	roraimae	0
Cricetidae	Pseudoryzomys	simplex	0
Cricetidae	Punomys	kofordi	0
Cricetidae	Punomys	lemminus	0
Cricetidae	Reithrodon	auritus	0
Cricetidae	Reithrodon	typicus	0
Cricetidae	Rhagomys	longilingua	0
Cricetidae	Rhagomys	rufescens	0
Cricetidae	Rheomys	mexicanus	0
Cricetidae	Rheomys	raptor	0
Cricetidae	Rheomys	thomasi	0
Cricetidae	Rheomys	underwoodi	0
Cricetidae	Rhipidomys	austrinus	0
Cricetidae	Rhipidomys	caucensis	0
Cricetidae	Rhipidomys	couesi	0
Cricetidae	Rhipidomys	emiliae	0
Cricetidae	Rhipidomys	fulviventer	0
Cricetidae	Rhipidomys	gardneri	0
Cricetidae	Rhipidomys	latimanus	0
Cricetidae	Rhipidomys	leucodactylus	0
Cricetidae	Rhipidomys	macconnelli	0
Cricetidae	Rhipidomys	macrurus	0

Cricetidae	Rhipidomys	mastacalis	0
Cricetidae	Rhipidomys	modicus	0
Cricetidae	Rhipidomys	nitela	0
Cricetidae	Rhipidomys	ochrogaster	0
Cricetidae	Rhipidomys	venezuelae	0
Cricetidae	Rhipidomys	venustus	0
Cricetidae	Rhipidomys	wetzeli	0
Cricetidae	Salinomys	delicatus	0
Cricetidae	Scapteromys	aquaticus	0
Cricetidae	Scapteromys	tumidus	0
Cricetidae	Scolomys	melanops	0
Cricetidae	Scolomys	ucayalensis	0
Cricetidae	Sigmodon	alleni	0
Cricetidae	Sigmodon	alstoni	0
Cricetidae	Sigmodon	arizonae	0
Cricetidae	Sigmodon	fulviventer	0
Cricetidae	Sigmodon	hirsutus	0
Cricetidae	Sigmodon	hispidus	0
Cricetidae	Sigmodon	inopinatus	0
Cricetidae	Sigmodon	leucotis	0
Cricetidae	Sigmodon	mascotensis	0
Cricetidae	Sigmodon	ochrognathus	0
Cricetidae	Sigmodon	peruanus	0
Cricetidae	Sigmodon	planifrons	0
Cricetidae	Sigmodon	toltecus	0
Cricetidae	Sigmodon	zanjonensis	0
Cricetidae	Sigmodontomys	alfari	0
Cricetidae	Sigmodontomys	aphrastus	0
Cricetidae	Tapecomys	primus	0
Cricetidae	Thalpomys	cerradensis	0
Cricetidae	Thalpomys	lasiotis	0
Cricetidae	Thaptomys	nigrita	0
Cricetidae	Thomasomys	apeco	0
Cricetidae	Thomasomys	aureus	0
Cricetidae	Thomasomys	baeops	0
Cricetidae	Thomasomys	bombycinus	0
Cricetidae	Thomasomys	caudivarius	0
Cricetidae	Thomasomys	cinereiventer	0
Cricetidae	Thomasomys	cinereus	0
Cricetidae	Thomasomys	cinnameus	0
Cricetidae	Thomasomys	daphne	0
Cricetidae	Thomasomys	eleusis	0

Cricetidae	Thomasomys	erro	0
Cricetidae	Thomasomys	gracilis	0
Cricetidae	Thomasomys	hudsoni	0
Cricetidae	Thomasomys	hylophilus	0
Cricetidae	Thomasomys	incanus	0
Cricetidae	Thomasomys	ischyrus	0
Cricetidae	Thomasomys	kalinowskii	0
Cricetidae	Thomasomys	ladewi	0
Cricetidae	Thomasomys	laniger	0
Cricetidae	Thomasomys	macrotis	0
Cricetidae	Thomasomys	monochromos	0
Cricetidae	Thomasomys	niveipes	0
Cricetidae	Thomasomys	notatus	0
Cricetidae	Thomasomys	onkiro	0
Cricetidae	Thomasomys	oreas	0
Cricetidae	Thomasomys	paramorum	0
Cricetidae	Thomasomys	popayanus	0
Cricetidae	Thomasomys	praetor	0
Cricetidae	Thomasomys	pyrrhonotus	0
Cricetidae	Thomasomys	rhoadsi	0
Cricetidae	Thomasomys	rosalinda	0
Cricetidae	Thomasomys	silvestris	0
Cricetidae	Thomasomys	taczanowskii	0
Cricetidae	Thomasomys	ucucha	0
Cricetidae	Thomasomys	vestitus	0
Cricetidae	Thomasomys	vulcani	0
Cricetidae	Wiedomys	pyrrhorhinos	0
Cricetidae	Wilfredomys	oenax	0
Cricetidae	Zygodontomys	brevicauda	0
Cricetidae	Zygodontomys	brunneus	0
Cricetidae	Nyctomys	sumichrasti	0
Cricetidae	Otonyctomys	hatti	0
Cricetidae	Ototylomys	phyllotis	0
Cricetidae	Tylomys	bullaris	0
Cricetidae	Tylomys	fulviventer	0
Cricetidae	Tylomys	mirae	0
Cricetidae	Tylomys	nudicaudus	0
Cricetidae	Tylomys	panamensis	0
Cricetidae	Tylomys	tumbalensis	0
Cricetidae	Tylomys	watsoni	0
Muridae	Acomys	airensis	0
Muridae	Acomys	cahirinus	0

Muridae	Acomys	chudeaui	0
Muridae	Acomys	cilicicus	0
Muridae	Acomys	cineraceus	0
Muridae	Acomys	dimidiatus	0
Muridae	Acomys	ignitus	0
Muridae	Acomys	johannis	0
Muridae	Acomys	kempi	0
Muridae	Acomys	louisae	0
Muridae	Acomys	minous	0
Muridae	Acomys	mullah	0
Muridae	Acomys	nesiotes	0
Muridae	Acomys	percivali	0
Muridae	Acomys	russatus	0
Muridae	Acomys	seurati	0
Muridae	Acomys	spinosissimus	0
Muridae	Acomys	subspinosus	0
Muridae	Acomys	wilsoni	0
Muridae	Deomys	ferrugineus	0
Muridae	Lophuromys	aquilus	0
Muridae	Lophuromys	angolensis	0
Muridae	Lophuromys	ansorgei	0
Muridae	Lophuromys	brevicaudus	0
Muridae	Lophuromys	brunneus	0
Muridae	Lophuromys	chrysopus	0
Muridae	Lophuromys	dieterleni	0
Muridae	Lophuromys	dudui	0
Muridae	Lophuromys	eisentrauti	0
Muridae	Lophuromys	flavopunctatus	0
Muridae	Lophuromys	huttereri	0
Muridae	Lophuromys	luteogaster	0
Muridae	Lophuromys	medicaudatus	0
Muridae	Lophuromys	melanonyx	0
Muridae	Lophuromys	nudicaudus	0
Muridae	Lophuromys	rahmi	0
Muridae	Lophuromys	roseveari	0
Muridae	Lophuromys	sikapusi	0
Muridae	Lophuromys	verhageni	0
Muridae	Lophuromys	woosnami	0
Muridae	Lophuromys	zena	0
Muridae	Uranomys	ruddi	0
Muridae	Ammodillus	imbellis	0
Muridae	Brachiones	przewalskii	0

Muridae	Desmodilliscus	braueri	0
Muridae	Desmodillus	auricularis	0
Muridae	Dipodillus	bottai	0
Muridae	Dipodillus	campestris	0
Muridae	Dipodillus	dasyurus	0
Muridae	Dipodillus	harwoodi	0
Muridae	Dipodillus	jamesi	0
Muridae	Dipodillus	lowei	0
Muridae	Dipodillus	mackilligini	0
Muridae	Dipodillus	maghrebi	0
Muridae	Dipodillus	rupicola	0
Muridae	Dipodillus	simoni	0
Muridae	Dipodillus	somalicus	0
Muridae	Dipodillus	stigmonyx	0
Muridae	Dipodillus	zakariai	0
Muridae	Gerbilliscus	afra	0
Muridae	Gerbilliscus	boehmi	0
Muridae	Gerbilliscus	brantsii	0
Muridae	Gerbilliscus	guineae	0
Muridae	Gerbilliscus	inclusus	0
Muridae	Gerbilliscus	kempi	0
Muridae	Gerbilliscus	leucogaster	0
Muridae	Gerbilliscus	nigricaudus	0
Muridae	Gerbilliscus	phillipsi	0
Muridae	Gerbilliscus	robustus	0
Muridae	Gerbilliscus	validus	0
Muridae	Gerbillurus	paeba	0
Muridae	Gerbillurus	setzeri	0
Muridae	Gerbillurus	tytonis	0
Muridae	Gerbillurus	vallinus	0
Muridae	Gerbillus	acticola	0
Muridae	Gerbillus	agag	0
Muridae	Gerbillus	amoenus	0
Muridae	Gerbillus	andersoni	0
Muridae	Gerbillus	aquilus	0
Muridae	Gerbillus	brockmani	0
Muridae	Gerbillus	burtoni	0
Muridae	Gerbillus	cheesmani	0
Muridae	Gerbillus	dongolanus	0
Muridae	Gerbillus	dunni	0
Muridae	Gerbillus	famulus	0
Muridae	Gerbillus	floweri	0

Muridae	Gerbillus	garamantis	0
Muridae	Gerbillus	gerbillus	0
Muridae	Gerbillus	gleadowi	0
Muridae	Gerbillus	grobbeni	0
Muridae	Gerbillus	henleyi	0
Muridae	Gerbillus	hesperinus	0
Muridae	Gerbillus	hoogstraali	0
Muridae	Gerbillus	latastei	0
Muridae	Gerbillus	mauritaniae	0
Muridae	Gerbillus	mesopotamiae	0
Muridae	Gerbillus	muriculus	0
Muridae	Gerbillus	nancillus	0
Muridae	Gerbillus	nanus	0
Muridae	Gerbillus	nigeriae	0
Muridae	Gerbillus	occiduus	0
Muridae	Gerbillus	perpallidus	0
Muridae	Gerbillus	poecilops	0
Muridae	Gerbillus	principulus	0
Muridae	Gerbillus	pulvinatus	0
Muridae	Gerbillus	pusillus	0
Muridae	Gerbillus	pyramidum	0
Muridae	Gerbillus	rosalinda	0
Muridae	Gerbillus	syrticus	0
Muridae	Gerbillus	tarabuli	0
Muridae	Gerbillus	vivax	0
Muridae	Gerbillus	watersi	0
Muridae	Meriones	arimalius	0
Muridae	Meriones	chengi	0
Muridae	Meriones	crassus	0
Muridae	Meriones	dahli	0
Muridae	Meriones	grandis	0
Muridae	Meriones	hurrianae	0
Muridae	Meriones	libycus	0
Muridae	Meriones	meridianus	0
Muridae	Meriones	persicus	0
Muridae	Meriones	rex	0
Muridae	Meriones	sacramenti	0
Muridae	Meriones	shawi	0
Muridae	Meriones	tamariscinus	0
Muridae	Meriones	tristrami	0
Muridae	Meriones	unguiculatus	0
Muridae	Meriones	vinogradovi	0

Muridae	Meriones	zarudnyi	0
Muridae	Microdillus	peeli	0
Muridae	Pachyuromys	duprasi	0
Muridae	Psammomys	obesus	0
Muridae	Psammomys	vexillaris	0
Muridae	Rhombomys	opimus	0
Muridae	Sekeetamys	calurus	0
Muridae	Tatera	indica	0
Muridae	Taterillus	arenarius	0
Muridae	Taterillus	congicus	0
Muridae	Taterillus	emini	0
Muridae	Taterillus	gracilis	0
Muridae	Taterillus	harringtoni	0
Muridae	Taterillus	lacustris	0
Muridae	Taterillus	petteri	0
Muridae	Taterillus	pygargus	0
Muridae	Taterillus	tranieri	0
Muridae	Leimacomys	b¬∏ttneri	0
Muridae	Abditomys	latidens	0
Muridae	Abeomelomys	sevia	0
Muridae	Aethomys	bocagei	0
Muridae	Aethomys	chrysophilus	0
Muridae	Aethomys	hindei	0
Muridae	Aethomys	ineptus	0
Muridae	Aethomys	kaiseri	0
Muridae	Aethomys	nyikae	0
Muridae	Aethomys	silindensis	0
Muridae	Aethomys	stannarius	0
Muridae	Aethomys	thomasi	0
Muridae	Anisomys	imitator	0
Muridae	Anonymomys	mindorensis	0
Muridae	Apodemus	agrarius	0
Muridae	Apodemus	alpicola	0
Muridae	Apodemus	argenteus	0
Muridae	Apodemus	chevrieri	0
Muridae	Apodemus	draco	0
Muridae	Apodemus	epimelas	0
Muridae	Apodemus	flavicollis	0
Muridae	Apodemus	gurkha	0
Muridae	Apodemus	hyrcanicus	0
Muridae	Apodemus	latronum	0
Muridae	Apodemus	mystacinus	0

Muridae	Apodemus	pallipes	0
Muridae	Apodemus	peninsulae	0
Muridae	Apodemus	ponticus	0
Muridae	Apodemus	rusiges	0
Muridae	Apodemus	semotus	0
Muridae	Apodemus	speciosus	0
Muridae	Apodemus	sylvaticus	0
Muridae	Apodemus	uralensis	0
Muridae	Apodemus	witherbyi	0
Muridae	Apomys	abrae	0
Muridae	Apomys	datae	0
Muridae	Apomys	gracilirostris	0
Muridae	Apomys	hylocetes	0
Muridae	Apomys	insignis	0
Muridae	Apomys	littoralis	0
Muridae	Apomys	microdon	0
Muridae	Apomys	musculus	0
Muridae	Apomys	sacobianus	0
Muridae	Archboldomys	luzonensis	0
Muridae	Archboldomys	musseri	0
Muridae	Arvicanthis	abyssinicus	0
Muridae	Arvicanthis	ansorgei	0
Muridae	Arvicanthis	blicki	0
Muridae	Arvicanthis	nairobae	0
Muridae	Arvicanthis	neumanni	0
Muridae	Arvicanthis	niloticus	0
Muridae	Arvicanthis	rufinus	0
Muridae	Bandicota	bengalensis	0
Muridae	Bandicota	indica	0
Muridae	Bandicota	savilei	0
Muridae	Batomys	dentatus	0
Muridae	Batomys	granti	0
Muridae	Batomys	russatus	0
Muridae	Batomys	salomonseni	0
Muridae	Berylmys	berdmorei	0
Muridae	Berylmys	bowersi	0
Muridae	Berylmys	mackenziei	0
Muridae	Berylmys	manipulus	0
Muridae	Bullimus	bagobus	0
Muridae	Bullimus	gamay	0
Muridae	Bullimus	luzonicus	0
Muridae	Bunomys	andrewsi	0

Muridae	Bunomys	chrysocomus	0
Muridae	Bunomys	coelestis	0
Muridae	Bunomys	fratrorum	0
Muridae	Bunomys	penitus	0
Muridae	Bunomys	prolatus	0
Muridae	Carpomys	melanurus	0
Muridae	Carpomys	phaeurus	0
Muridae	Chiromyscus	chiropus	0
Muridae	Chiropodomys	calamianensis	0
Muridae	Chiropodomys	gliroides	0
Muridae	Chiropodomys	karlkoopmani	0
Muridae	Chiropodomys	major	0
Muridae	Chiropodomys	muroides	0
Muridae	Chiropodomys	pusillus	0
Muridae	Chiruromys	forbesi	0
Muridae	Chiruromys	lamia	0
Muridae	Chiruromys	vates	0
Muridae	Chrotomys	gonzalesi	0
Muridae	Chrotomys	mindorensis	0
Muridae	Chrotomys	silaceus	0
Muridae	Chrotomys	whiteheadi	0
Muridae	Coccymys	albidens	0
Muridae	Coccymys	ruemmleri	0
Muridae	Colomys	goslingi	0
Muridae	Conilurus	albipes	0
Muridae	Conilurus	penicillatus	0
Muridae	Coryphomys	buehleri	0
Muridae	Crateromys	australis	0
Muridae	Crateromys	heaneyi	0
Muridae	Crateromys	paulus	0
Muridae	Crateromys	schadenbergi	0
Muridae	Cremnomys	cutchicus	0
Muridae	Cremnomys	elvira	0
Muridae	Crossomys	moncktoni	0
Muridae	Crunomys	celebensis	0
Muridae	Crunomys	fallax	0
Muridae	Crunomys	melanius	0
Muridae	Crunomys	suncoides	0
Muridae	Dacnomys	millardi	0
Muridae	Dasymys	alleni	0
Muridae	Dasymys	cabrali	0
Muridae	Dasymys	foxi	0

Muridae	Dasymys	incomtus	0
Muridae	Dasymys	montanus	0
Muridae	Dasymys	nudipes	0
Muridae	Dasymys	rufulus	0
Muridae	Dasymys	rwandae	0
Muridae	Dasymys	sua	0
Muridae	Dephomys	defua	0
Muridae	Dephomys	eburneae	0
Muridae	Desmomys	harringtoni	0
Muridae	Desmomys	yaldeni	0
Muridae	Diomys	crumpi	0
Muridae	Diplothrix	legata	0
Muridae	Echiothrix	centrosa	0
Muridae	Echiothrix	leucura	0
Muridae	Eropeplus	canus	0
Muridae	Golunda	ellioti	0
Muridae	Grammomys	aridulus	0
Muridae	Grammomys	buntingi	0
Muridae	Grammomys	caniceps	0
Muridae	Grammomys	cometes	0
Muridae	Grammomys	dolichurus	0
Muridae	Grammomys	dryas	0
Muridae	Grammomys	gigas	0
Muridae	Grammomys	ibeanus	0
Muridae	Grammomys	kuru	0
Muridae	Grammomys	macmillani	0
Muridae	Grammomys	minnae	0
Muridae	Grammomys	poensis	0
Muridae	Hadromys	humei	0
Muridae	Hadromys	yunnanensis	0
Muridae	Haeromys	margarettae	0
Muridae	Haeromys	minahassae	0
Muridae	Haeromys	pusillus	0
Muridae	Hapalomys	delacouri	0
Muridae	Hapalomys	longicaudatus	0
Muridae	Heimyscus	fumosus	0
Muridae	Hybomys	badius	0
Muridae	Hybomys	basilii	0
Muridae	Hybomys	lunaris	0
Muridae	Hybomys	planifrons	0
Muridae	Hybomys	trivirgatus	0
Muridae	Hybomys	univittatus	0

Muridae	Hydromys	chrysogaster	0
Muridae	Hydromys	habbema	0
Muridae	Hydromys	hussoni	0
Muridae	Hydromys	neobritannicus	0
Muridae	Hydromys	shawmayeri	0
Muridae	Hylomyscus	aeta	0
Muridae	Hylomyscus	alleni	0
Muridae	Hylomyscus	baeri	0
Muridae	Hylomyscus	carillus	0
Muridae	Hylomyscus	denniae	0
Muridae	Hylomyscus	grandis	0
Muridae	Hylomyscus	parvus	0
Muridae	Hylomyscus	stella	0
Muridae	Hyomys	dammermani	0
Muridae	Hyomys	goliath	0
Muridae	Kadarsanomys	sodyi	0
Muridae	Komodomys	rintjanus	0
Muridae	Lamottemys	okuensis	0
Muridae	Leggadina	forresti	0
Muridae	Leggadina	lakedownensis	0
Muridae	Lemniscomys	barbarus	0
Muridae	Lemniscomys	bellieri	0
Muridae	Lemniscomys	griselda	0
Muridae	Lemniscomys	hoogstraali	0
Muridae	Lemniscomys	linulus	0
Muridae	Lemniscomys	macculus	0
Muridae	Lemniscomys	mittendorfi	0
Muridae	Lemniscomys	rosalia	0
Muridae	Lemniscomys	roseveari	0
Muridae	Lemniscomys	striatus	0
Muridae	Lemniscomys	zebra	0
Muridae	Lenomys	meyeri	0
Muridae	Lenothrix	canus	0
Muridae	Leopoldamys	ciliatus	0
Muridae	Leopoldamys	edwardsi	0
Muridae	Leopoldamys	milleti	0
Muridae	Leopoldamys	neilli	0
Muridae	Leopoldamys	sabanus	0
Muridae	Leopoldamys	siporanus	0
Muridae	Leporillus	apicalis	0
Muridae	Leporillus	conditor	0
Muridae	Leptomys	elegans	0

Muridae	Leptomys	ernstmayri	0
Muridae	Leptomys	signatus	0
Muridae	Limnomys	bryophilus	0
Muridae	Limnomys	sibuanus	0
Muridae	Lorentzimys	nouhuysi	0
Muridae	Macruromys	elegans	0
Muridae	Macruromys	major	0
Muridae	Madromys	blanfordi	0
Muridae	Malacomys	cansdalei	0
Muridae	Malacomys	edwardsi	0
Muridae	Malacomys	longipes	0
Muridae	Mallomys	aroaensis	0
Muridae	Mallomys	gunung	0
Muridae	Mallomys	istapantap	0
Muridae	Mallomys	rothschildi	0
Muridae	Malpaisomys	insularis	0
Muridae	Mammelomys	lanosus	0
Muridae	Mammelomys	rattoides	0
Muridae	Margaretamys	beccarii	0
Muridae	Margaretamys	elegans	0
Muridae	Margaretamys	parvus	0
Muridae	Mastacomys	fuscus	0
Muridae	Mastomys	awashensis	0
Muridae	Mastomys	coucha	0
Muridae	Mastomys	erythroleucus	0
Muridae	Mastomys	huberti	0
Muridae	Mastomys	kollmannspergeri	0
Muridae	Mastomys	natalensis	0
Muridae	Mastomys	pernanus	0
Muridae	Mastomys	shortridgei	0
Muridae	Maxomys	alticola	0
Muridae	Maxomys	baeodon	0
Muridae	Maxomys	bartelsii	0
Muridae	Maxomys	dollmani	0
Muridae	Maxomys	hellwaldii	0
Muridae	Maxomys	hylomyoides	0
Muridae	Maxomys	inas	0
Muridae	Maxomys	inflatus	0
Muridae	Maxomys	moi	0
Muridae	Maxomys	musschenbroekii	0
Muridae	Maxomys	ochraceiventer	0
Muridae	Maxomys	pagensis	0

Muridae	Maxomys	panglima	0
Muridae	Maxomys	rajah	0
Muridae	Maxomys	surifer	0
Muridae	Maxomys	wattsi	0
Muridae	Maxomys	whiteheadi	0
Muridae	Melasmothrix	naso	0
Muridae	Melomys	aerosus	0
Muridae	Melomys	arcium	0
Muridae	Melomys	bannisteri	0
Muridae	Melomys	bougainville	0
Muridae	Melomys	burtoni	0
Muridae	Melomys	capensis	0
Muridae	Melomys	caurinus	0
Muridae	Melomys	cervinipes	0
Muridae	Melomys	cooperae	0
Muridae	Melomys	dollmani	0
Muridae	Melomys	fraterculus	0
Muridae	Melomys	frigicola	0
Muridae	Melomys	fulgens	0
Muridae	Melomys	howi	0
Muridae	Melomys	leucogaster	0
Muridae	Melomys	lutillus	0
Muridae	Melomys	matambuai	0
Muridae	Melomys	obiensis	0
Muridae	Melomys	paveli	0
Muridae	Melomys	rubicola	0
Muridae	Melomys	rufescens	0
Muridae	Melomys	spechti	0
Muridae	Melomys	talaudium	0
Muridae	Mesembriomys	gouldii	0
Muridae	Mesembriomys	macrurus	0
Muridae	Micaelamys	granti	0
Muridae	Micaelamys	namaquensis	0
Muridae	Microhydromys	musseri	0
Muridae	Microhydromys	richardsoni	0
Muridae	Micromys	minutus	0
Muridae	Millardia	gleadowi	0
Muridae	Millardia	kathleenae	0
Muridae	Millardia	kondana	0
Muridae	Millardia	meltada	0
Muridae	Muriculus	imberbis	0
Muridae	Mus	baoulei	0

Muridae	Mus	booduga	0
Muridae	Mus	bufo	0
Muridae	Mus	callewaerti	0
Muridae	Mus	caroli	0
Muridae	Mus	cervicolor	0
Muridae	Mus	cookii	0
Muridae	Mus	crociduroides	0
Muridae	Mus	famulus	0
Muridae	Mus	fernandoni	0
Muridae	Mus	fragilicauda	0
Muridae	Mus	goundae	0
Muridae	Mus	haussa	0
Muridae	Mus	indutus	0
Muridae	Mus	macedonicus	0
Muridae	Mus	mahomet	0
Muridae	Mus	mattheyi	0
Muridae	Mus	mayori	0
Muridae	Mus	minutoides	0
Muridae	Mus	musculoides	0
Muridae	Mus	musculus	5
Muridae	Mus	neavei	0
Muridae	Mus	orangiae	0
Muridae	Mus	oubanguii	0
Muridae	Mus	pahari	0
Muridae	Mus	phillipsi	0
Muridae	Mus	platythrix	0
Muridae	Mus	saxicola	0
Muridae	Mus	setulosus	0
Muridae	Mus	setzeri	0
Muridae	Mus	shortridgei	0
Muridae	Mus	sorella	0
Muridae	Mus	spicilegus	0
Muridae	Mus	spretus	0
Muridae	Mus	tenellus	0
Muridae	Mus	terricolor	0
Muridae	Mus	triton	0
Muridae	Mus	vulcani	0
Muridae	Mylomys	dybowskii	0
Muridae	Mylomys	rex	0
Muridae	Myomyscus	angolensis	0
Muridae	Myomyscus	brockmani	0
Muridae	Myomyscus	verreauxii	0

Muridae	Myomyscus	yemeni	0
Muridae	Nesokia	bunnii	0
Muridae	Nesokia	indica	0
Muridae	Nesoromys	ceramicus	0
Muridae	Nilopegamys	plumbeus	0
Muridae	Niviventer	andersoni	0
Muridae	Niviventer	brahma	0
Muridae	Niviventer	cameroni	0
Muridae	Niviventer	confucianus	0
Muridae	Niviventer	coninga	0
Muridae	Niviventer	cremoriventer	0
Muridae	Niviventer	culturatus	0
Muridae	Niviventer	eha	0
Muridae	Niviventer	excelsior	0
Muridae	Niviventer	fraternus	0
Muridae	Niviventer	fulvescens	0
Muridae	Niviventer	hinpoon	0
Muridae	Niviventer	langbianis	0
Muridae	Niviventer	lepturus	0
Muridae	Niviventer	niviventer	0
Muridae	Niviventer	rapit	0
Muridae	Niviventer	tenaster	0
Muridae	Notomys	alexis	0
Muridae	Notomys	amplus	0
Muridae	Notomys	aquilo	0
Muridae	Notomys	cervinus	0
Muridae	Notomys	fuscus	0
Muridae	Notomys	longicaudatus	0
Muridae	Notomys	macrotis	0
Muridae	Notomys	mitchellii	0
Muridae	Notomys	mordax	0
Muridae	Oenomys	hypoxanthus	0
Muridae	Oenomys	ornatus	0
Muridae	Palawanomys	furvus	0
Muridae	Papagomys	armandvillei	0
Muridae	Papagomys	theodorverhoeveni	0
Muridae	Parahydromys	asper	0
Muridae	Paraleptomys	rufilatus	0
Muridae	Paraleptomys	wilhelmina	0
Muridae	Paramelomys	gressitti	0
Muridae	Paramelomys	levipes	0
Muridae	Paramelomys	lorentzii	0

Muridae	Paramelomys	mollis	0
Muridae	Paramelomys	moncktoni	0
Muridae	Paramelomys	naso	0
Muridae	Paramelomys	platyops	0
Muridae	Paramelomys	rubex	0
Muridae	Paramelomys	steini	0
Muridae	Paruromys	dominator	0
Muridae	Paulamys	naso	0
Muridae	Pelomys	campanae	0
Muridae	Pelomys	fallax	0
Muridae	Pelomys	hopkinsi	0
Muridae	Pelomys	isseli	0
Muridae	Pelomys	minor	0
Muridae	Phloeomys	cumingi	0
Muridae	Phloeomys	pallidus	0
Muridae	Pithecheir	melanurus	0
Muridae	Pithecheir	parvus	0
Muridae	Pithecheirops	otion	0
Muridae	Pogonomelomys	bruijni	0
Muridae	Pogonomelomys	mayeri	0
Muridae	Pogonomys	championi	0
Muridae	Pogonomys	fergussoniensis	0
Muridae	Pogonomys	loriae	0
Muridae	Pogonomys	macrourus	0
Muridae	Pogonomys	sylvestris	0
Muridae	Praomys	daltoni	0
Muridae	Praomys	degraaffi	0
Muridae	Praomys	delectorum	0
Muridae	Praomys	derooi	0
Muridae	Praomys	hartwigi	0
Muridae	Praomys	jacksoni	0
Muridae	Praomys	lukolelae	0
Muridae	Praomys	minor	0
Muridae	Praomys	misonnei	0
Muridae	Praomys	morio	0
Muridae	Praomys	mutoni	0
Muridae	Praomys	obscurus	0
Muridae	Praomys	petteri	0
Muridae	Praomys	rostratus	0
Muridae	Praomys	tullbergi	0
Muridae	Praomys	verschureni	0
Muridae	Protochromys	fellowsi	0

Muridae	Pseudohydromys	ellermani	0
Muridae	Pseudohydromys	fuscus	0
Muridae	Pseudohydromys	murinus	0
Muridae	Pseudohydromys	occidentalis	0
Muridae	Pseudomys	albocinereus	0
Muridae	Pseudomys	apodemoides	0
Muridae	Pseudomys	australis	0
Muridae	Pseudomys	bolami	0
Muridae	Pseudomys	calabyi	0
Muridae	Pseudomys	chapmani	0
Muridae	Pseudomys	delicatulus	0
Muridae	Pseudomys	desertor	0
Muridae	Pseudomys	fieldi	0
Muridae	Pseudomys	fumeus	0
Muridae	Pseudomys	glaucus	0
Muridae	Pseudomys	gouldii	0
Muridae	Pseudomys	gracilicaudatus	0
Muridae	Pseudomys	hermannsburgensis	0
Muridae	Pseudomys	higginsi	0
Muridae	Pseudomys	johnsoni	0
Muridae	Pseudomys	laborifex	0
Muridae	Pseudomys	nanus	0
Muridae	Pseudomys	novaehollandiae	0
Muridae	Pseudomys	occidentalis	0
Muridae	Pseudomys	oralis	0
Muridae	Pseudomys	patrius	0
Muridae	Pseudomys	pilligaensis	0
Muridae	Pseudomys	shortridgei	0
Muridae	Rattus	adustus	0
Muridae	Rattus	andamanensis	0
Muridae	Rattus	annandalei	0
Muridae	Rattus	arfakiensis	0
Muridae	Rattus	argentiventer	0
Muridae	Rattus	arrogans	0
Muridae	Rattus	baluensis	0
Muridae	Rattus	blangorum	0
Muridae	Rattus	bontanus	0
Muridae	Rattus	burrus	0
Muridae	Rattus	colletti	0
Muridae	Rattus	elaphinus	0
Muridae	Rattus	enganus	0
Muridae	Rattus	everetti	0

Muridae	Rattus	exulans	0
Muridae	Rattus	feliceus	0
Muridae	Rattus	fuscipes	0
Muridae	Rattus	giluwensis	0
Muridae	Rattus	hainaldi	0
Muridae	Rattus	hoffmanni	0
Muridae	Rattus	hoogerwerfi	0
Muridae	Rattus	jobiensis	0
Muridae	Rattus	koopmani	0
Muridae	Rattus	korinchi	0
Muridae	Rattus	leucopus	0
Muridae	Rattus	losea	0
Muridae	Rattus	lugens	0
Muridae	Rattus	lutreolus	0
Muridae	Rattus	macleari	0
Muridae	Rattus	marmosurus	0
Muridae	Rattus	mindorensis	0
Muridae	Rattus	mollicomulus	0
Muridae	Rattus	montanus	0
Muridae	Rattus	mordax	0
Muridae	Rattus	morotaiensis	0
Muridae	Rattus	nativitatis	0
Muridae	Rattus	niobe	0
Muridae	Rattus	nitidus	0
Muridae	Rattus	norvegicus	0
Muridae	Rattus	novaeguineae	0
Muridae	Rattus	omichlodes	0
Muridae	Rattus	osgoodi	0
Muridae	Rattus	palmarum	0
Muridae	Rattus	pelurus	0
Muridae	Rattus	pococki	0
Muridae	Rattus	praetor	0
Muridae	Rattus	pyctoris	0
Muridae	Rattus	ranjiniae	0
Muridae	Rattus	rattus	0
Muridae	Rattus	richardsoni	0
Muridae	Rattus	salocco	0
Muridae	Rattus	sanila	0
Muridae	Rattus	satarae	0
Muridae	Rattus	simalurensis	0
Muridae	Rattus	sordidus	0
Muridae	Rattus	steini	0

Muridae	Rattus	stoicus	0
Muridae	Rattus	tanezumi	0
Muridae	Rattus	tawitawiensis	0
Muridae	Rattus	timorensis	0
Muridae	Rattus	tiomanicus	0
Muridae	Rattus	tunneyi	0
Muridae	Rattus	vandeuseni	0
Muridae	Rattus	verecundus	0
Muridae	Rattus	villosissimus	0
Muridae	Rattus	xanthurus	0
Muridae	Rhabdomys	dilectus	0
Muridae	Rhabdomys	pumilio	0
Muridae	Rhagamys	orthodon	0
Muridae	Rhynchomys	isarogensis	0
Muridae	Rhynchomys	soricoides	0
Muridae	Solomys	ponceleti	0
Muridae	Solomys	salamonis	0
Muridae	Solomys	salebrosus	0
Muridae	Solomys	sapientis	0
Muridae	Solomys	spriggsarum	0
Muridae	Sommeromys	macrorhinos	0
Muridae	Spelaeomys	florensis	0
Muridae	Srilankamys	ohiensis	0
Muridae	Stenocephalemys	albipes	0
Muridae	Stenocephalemys	albocaudata	0
Muridae	Stenocephalemys	griseicauda	0
Muridae	Stenocephalemys	ruppi	0
Muridae	Stochomys	longicaudatus	0
Muridae	Sundamys	infraluteus	0
Muridae	Sundamys	maxi	0
Muridae	Sundamys	muelleri	0
Muridae	Taeromys	arcuatus	0
Muridae	Taeromys	callitrichus	0
Muridae	Taeromys	celebensis	0
Muridae	Taeromys	hamatus	0
Muridae	Taeromys	microbullatus	0
Muridae	Taeromys	punicans	0
Muridae	Taeromys	taerae	0
Muridae	Tarsomys	apoensis	0
Muridae	Tarsomys	echinatus	0
Muridae	Tateomys	macrocercus	0
Muridae	Tateomys	rhinogradoides	0

Muridae	Thallomys	loringi	0
Muridae	Thallomys	nigricauda	0
Muridae	Thallomys	paedulcus	0
Muridae	Thallomys	shortridgei	0
Muridae	Thamnomys	kempi	0
Muridae	Thamnomys	major	0
Muridae	Thamnomys	venustus	0
Muridae	Tokudaia	muenninki	0
Muridae	Tokudaia	osimensis	0
Muridae	Tryphomys	adustus	0
Muridae	Uromys	anak	0
Muridae	Uromys	boeadii	0
Muridae	Uromys	caudimaculatus	0
Muridae	Uromys	emmae	0
Muridae	Uromys	hadrourus	0
Muridae	Uromys	imperator	0
Muridae	Uromys	neobritannicus	0
Muridae	Uromys	porculus	0
Muridae	Uromys	rex	0
Muridae	Uromys	siebersi	0
Muridae	Vandeleuria	nilagirica	0
Muridae	Vandeleuria	nolthenii	0
Muridae	Vandeleuria	oleracea	0
Muridae	Vernaya	fulva	0
Muridae	Xenuromys	barbatus	0
Muridae	Xeromys	myoides	0
Muridae	Zelotomys	hildegardeae	0
Muridae	Zelotomys	woosnami	0
Muridae	Zyzomys	argurus	0
Muridae	Zyzomys	maini	0
Muridae	Zyzomys	palatilis	0
Muridae	Zyzomys	pedunculatus	0
Muridae	Zyzomys	woodwardi	0
Muridae	Myotomys	sloggetti	0
Muridae	Myotomys	unisulcatus	0
Muridae	Otomys	anchietae	0
Muridae	Otomys	angoniensis	0
Muridae	Otomys	barbouri	0
Muridae	Otomys	burtoni	0
Muridae	Otomys	cuanzensis	0
Muridae	Otomys	dartmouthi	0
Muridae	Otomys	denti	0

Muridae	Otomys	dollmani	0
Muridae	Otomys	irroratus	0
Muridae	Otomys	jacksoni	0
Muridae	Otomys	lacustris	0
Muridae	Otomys	laminatus	0
Muridae	Otomys	maximus	0
Muridae	Otomys	occidentalis	0
Muridae	Otomys	orestes	0
Muridae	Otomys	saundersiae	0
Muridae	Otomys	tropicalis	0
Muridae	Otomys	typus	0
Muridae	Otomys	uzungwensis	0
Muridae	Parotomys	brantsii	0
Muridae	Parotomys	littledalei	0
Anomaluridae	Anomalurus	beecrofti	0
Anomaluridae	Anomalurus	derbianus	0
Anomaluridae	Anomalurus	pelii	2
Anomaluridae	Anomalurus	pusillus	0
Anomaluridae	Idiurus	macrotis	0
Anomaluridae	Idiurus	zenkeri	0
Anomaluridae	Zenkerella	insignis	0
Pedetidae	Pedetes	capensis	0
Pedetidae	Pedetes	surdaster	0
Ctenodactylidae	Ctenodactylus	gundi	0
Ctenodactylidae	Ctenodactylus	vali	0
Ctenodactylidae	Felovia	vae	0
Ctenodactylidae	Massoutiera	mzabi	0
Ctenodactylidae	Pectinator	spekei	0
Bathyergidae	Bathyergus	janetta	0
Bathyergidae	Bathyergus	suillus	0
Bathyergidae	Cryptomys	amatus	0
Bathyergidae	Cryptomys	anselli	0
Bathyergidae	Cryptomys	bocagei	0
Bathyergidae	Cryptomys	damarensis	0
Bathyergidae	Cryptomys	darlingi	0
Bathyergidae	Cryptomys	foxi	0
Bathyergidae	Cryptomys	hottentotus	3
Bathyergidae	Cryptomys	kafuensis	0
Bathyergidae	Cryptomys	mechowi	2
Bathyergidae	Cryptomys	ochraceocinereus	2
Bathyergidae	Cryptomys	zechi	0
Bathyergidae	Georychus	capensis	0

Bathyergidae	Heliophobius	argenteocinereus	9
Bathyergidae	Heterocephalus	glaber	0
Hystricidae	Atherurus	africanus	0
Hystricidae	Atherurus	macrourus	0
Hystricidae	Hystrix	africaeaustralis	2
Hystricidae	Hystrix	brachyura	5
Hystricidae	Hystrix	crassispinis	0
Hystricidae	Hystrix	cristata	0
Hystricidae	Hystrix	indica	0
Hystricidae	Hystrix	javanica	0
Hystricidae	Hystrix	pumila	0
Hystricidae	Hystrix	sumatrae	0
Hystricidae	Trichys	fasciculata	0
Petromuridae	Petromus	typicus	15
Thryonomyidae	Thryonomys	gregorianus	2
Thryonomyidae	Thryonomys	swinderianus	0
Erethizontidae	Chaetomys	subspinosus	0
Erethizontidae	Coendou	bicolor	4
Erethizontidae	Coendou	nycthemera	0
Erethizontidae	Coendou	prehensilis	0
Erethizontidae	Coendou	rothschildi	0
Erethizontidae	Echinoprocta	rufescens	0
Erethizontidae	Erethizon	dorsata	7
Erethizontidae	Sphiggurus	ichillus	0
Erethizontidae	Sphiggurus	insidiosus	0
Erethizontidae	Sphiggurus	melanurus	0
Erethizontidae	Sphiggurus	mexicanus	3
Erethizontidae	Sphiggurus	pruinosus	0
Erethizontidae	Sphiggurus	roosmalenorum	0
Erethizontidae	Sphiggurus	spinosus	0
Erethizontidae	Sphiggurus	vestitus	0
Erethizontidae	Sphiggurus	villosus	0
Chinchillidae	Chinchilla	chinchilla	2
Chinchillidae	Chinchilla	lanigera	0
Chinchillidae	Lagidium	peruanum	7
Chinchillidae	Lagidium	viscacia	13
Chinchillidae	Lagidium	wolffsohni	0
Chinchillidae	Lagostomus	crassus	0
Chinchillidae	Lagostomus	maximus	3
Dinomyidae	Dinomys	branickii	0
Caviidae	Cavia	aperea	6
Caviidae	Cavia	fulgida	0

Caviidae	Cavia	intermedia	0
Caviidae	Cavia	magna	0
Caviidae	Cavia	porcellus	0
Caviidae	Cavia	tschudii	6
Caviidae	Galea	flavidens	0
Caviidae	Galea	musteloides	5
Caviidae	Galea	spixii	3
Caviidae	Microcavia	australis	3
Caviidae	Microcavia	niata	2
Caviidae	Microcavia	shiptoni	0
Caviidae	Dolichotis	patagonum	2
Caviidae	Dolichotis	salinicola	0
Caviidae	Hydrochoeris	hydrochaeris	0
Caviidae	Hydrochoeris	isthmius	0
Caviidae	Kerodon	acrobata	0
Caviidae	Kerodon	rupestris	0
Dasyproctidae	Dasyprocta	azarae	0
Dasyproctidae	Dasyprocta	coibae	0
Dasyproctidae	Dasyprocta	cristata	0
Dasyproctidae	Dasyprocta	fuliginosa	2
Dasyproctidae	Dasyprocta	guamara	0
Dasyproctidae	Dasyprocta	kalinowskii	0
Dasyproctidae	Dasyprocta	leporina	8
Dasyproctidae	Dasyprocta	mexicana	0
Dasyproctidae	Dasyprocta	prymnolopha	0
Dasyproctidae	Dasyprocta	punctata	19
Dasyproctidae	Dasyprocta	ruatanica	0
Dasyproctidae	Myoprocta	acouchy	0
Dasyproctidae	Myoprocta	pratti	0
Cuniculidae	Cuniculus	paca	5
Cuniculidae	Cuniculus	taczanowskii	0
Ctenomyidae	Ctenomys	argentinus	0
Ctenomyidae	Ctenomys	australis	0
Ctenomyidae	Ctenomys	azarae	0
Ctenomyidae	Ctenomys	bergi	0
Ctenomyidae	Ctenomys	boliviensis	2
Ctenomyidae	Ctenomys	bonettoi	0
Ctenomyidae	Ctenomys	brasiliensis	0
Ctenomyidae	Ctenomys	budini	2
Ctenomyidae	Ctenomys	colburni	0
Ctenomyidae	Ctenomys	coludo	0
Ctenomyidae	Ctenomys	conoveri	0

Ctenomyidae	Ctenomys	coyhaiquensis	0
Ctenomyidae	Ctenomys	dorbignyi	0
Ctenomyidae	Ctenomys	dorsalis	0
Ctenomyidae	Ctenomys	emilianus	0
Ctenomyidae	Ctenomys	famosus	0
Ctenomyidae	Ctenomys	flamarioni	0
Ctenomyidae	Ctenomys	fochi	0
Ctenomyidae	Ctenomys	fodax	0
Ctenomyidae	Ctenomys	frater	2
Ctenomyidae	Ctenomys	fulvus	2
Ctenomyidae	Ctenomys	goodfellowi	0
Ctenomyidae	Ctenomys	haigi	2
Ctenomyidae	Ctenomys	johannis	0
Ctenomyidae	Ctenomys	juris	0
Ctenomyidae	Ctenomys	knighti	0
Ctenomyidae	Ctenomys	lami	0
Ctenomyidae	Ctenomys	latro	0
Ctenomyidae	Ctenomys	leucodon	0
Ctenomyidae	Ctenomys	lewisi	0
Ctenomyidae	Ctenomys	magellanicus	4
Ctenomyidae	Ctenomys	maulinus	2
Ctenomyidae	Ctenomys	mendocinus	0
Ctenomyidae	Ctenomys	minutus	2
Ctenomyidae	Ctenomys	occultus	0
Ctenomyidae	Ctenomys	opimus	3
Ctenomyidae	Ctenomys	osvaldoreigi	0
Ctenomyidae	Ctenomys	pearsoni	0
Ctenomyidae	Ctenomys	perrensi	0
Ctenomyidae	Ctenomys	peruanus	0
Ctenomyidae	Ctenomys	pilarensis	0
Ctenomyidae	Ctenomys	pontifex	0
Ctenomyidae	Ctenomys	porteousi	0
Ctenomyidae	Ctenomys	pundti	0
Ctenomyidae	Ctenomys	rionegrensis	0
Ctenomyidae	Ctenomys	roigi	0
Ctenomyidae	Ctenomys	saltarius	0
Ctenomyidae	Ctenomys	scagliai	0
Ctenomyidae	Ctenomys	sericeus	0
Ctenomyidae	Ctenomys	sociabilis	0
Ctenomyidae	Ctenomys	steinbachi	0
Ctenomyidae	Ctenomys	sylvanus	2
Ctenomyidae	Ctenomys	talarum	4

Ctenomyidae	Ctenomys	torquatus	0
Ctenomyidae	Ctenomys	tuconax	0
Ctenomyidae	Ctenomys	tucumanus	0
Ctenomyidae	Ctenomys	tulduco	0
Ctenomyidae	Ctenomys	validus	0
Ctenomyidae	Ctenomys	viperinus	0
Ctenomyidae	Ctenomys	yolandae	0
Octodontidae	Aconaemys	fuscus	0
Octodontidae	Aconaemys	porteri	0
Octodontidae	Aconaemys	sagei	0
Octodontidae	Octodon	bridgesi	0
Octodontidae	Octodon	degus	0
Octodontidae	Octodon	lunatus	0
Octodontidae	Octodon	pacificus	0
Octodontidae	Octodontomys	gliroides	0
Octodontidae	Octomys	mimax	0
Octodontidae	Pipanacoctomys	aureus	0
Octodontidae	Salinoctomys	loschalchalerosorum	0
Octodontidae	Spalacopus	cyanus	3
Octodontidae	Tympanoctomys	barrerae	0
Abrocomidae	Abrocoma	bennettii	2
Abrocomidae	Abrocoma	boliviensis	0
Abrocomidae	Abrocoma	budini	0
Abrocomidae	Abrocoma	cinerea	0
Abrocomidae	Abrocoma	famatina	0
Abrocomidae	Abrocoma	shistacea	0
Abrocomidae	Abrocoma	uspallata	0
Abrocomidae	Abrocoma	vaccarum	0
Abrocomidae	Cuscomys	ashaninka	0
Abrocomidae	Cuscomys	oblativa	0
Echimyidae	Dactylomys	boliviensis	0
Echimyidae	Dactylomys	dactylinus	3
Echimyidae	Dactylomys	peruanus	0
Echimyidae	Kannabateomys	amblyonyx	2
Echimyidae	Olallamys	albicauda	0
Echimyidae	Olallamys	edax	0
Echimyidae	Callistomys	pictus	0
Echimyidae	Diplomys	caniceps	0
Echimyidae	Diplomys	labilis	0
Echimyidae	Diplomys	rufodorsalis	0
Echimyidae	Echimys	chrysurus	0
Echimyidae	Echimys	saturnus	0

Echimyidae	Echimys	semivillosus	0
Echimyidae	Isothrix	bistriata	2
Echimyidae	Isothrix	negrensis	0
Echimyidae	Isothrix	pagurus	0
Echimyidae	Isothrix	sinnamariensis	0
Echimyidae	Makalata	didelphoides	0
Echimyidae	Makalata	grandis	0
Echimyidae	Makalata	macrura	0
Echimyidae	Makalata	obscura	0
Echimyidae	Makalata	occasius	0
Echimyidae	Makalata	rhipidura	0
Echimyidae	Phyllomys	blainvillii	0
Echimyidae	Phyllomys	brasiliensis	0
Echimyidae	Phyllomys	dasythrix	0
Echimyidae	Phyllomys	kerri	0
Echimyidae	Phyllomys	lamarum	0
Echimyidae	Phyllomys	lundi	0
Echimyidae	Phyllomys	mantiqueirensis	0
Echimyidae	Phyllomys	medius	0
Echimyidae	Phyllomys	nigrispinus	0
Echimyidae	Phyllomys	pattoni	0
Echimyidae	Phyllomys	thomasi	0
Echimyidae	Phyllomys	unicolor	0
Echimyidae	Carterodon	sulcidens	0
Echimyidae	Clyomys	bishopi	0
Echimyidae	Clyomys	laticeps	0
Echimyidae	Euryzygomatomys	spinosus	0
Echimyidae	Hoplomys	gymnurus	0
Echimyidae	Lonchothrix	emiliae	0
Echimyidae	Mesomys	hispidus	0
Echimyidae	Mesomys	leniceps	0
Echimyidae	Mesomys	occultus	0
Echimyidae	Mesomys	stimulax	0
Echimyidae	Proechimys	brevicauda	0
Echimyidae	Proechimys	canicollis	0
Echimyidae	Proechimys	chrysaeolus	0
Echimyidae	Proechimys	cuvieri	0
Echimyidae	Proechimys	decumanus	0
Echimyidae	Proechimys	echinothrix	0
Echimyidae	Proechimys	gardneri	0
Echimyidae	Proechimys	goeldii	0
Echimyidae	Proechimys	guairae	0

Echimyidae	Proechimys	guyannensis	6
Echimyidae	Proechimys	hoplomyoides	0
Echimyidae	Proechimys	kulinae	0
Echimyidae	Proechimys	longicaudatus	0
Echimyidae	Proechimys	magdalenae	0
Echimyidae	Proechimys	mincae	0
Echimyidae	Proechimys	oconnelli	0
Echimyidae	Proechimys	pattoni	0
Echimyidae	Proechimys	poliopus	0
Echimyidae	Proechimys	quadruplicatus	0
Echimyidae	Proechimys	roberti	0
Echimyidae	Proechimys	semispinosus	10
Echimyidae	Proechimys	simonsi	0
Echimyidae	Proechimys	steerei	0
Echimyidae	Proechimys	trinitatus	0
Echimyidae	Proechimys	urichi	0
Echimyidae	Thrichomys	apereoides	2
Echimyidae	Thrichomys	inermis	0
Echimyidae	Thrichomys	pachyurus	0
Echimyidae	Trinomys	albispinus	3
Echimyidae	Trinomys	dimidiatus	0
Echimyidae	Trinomys	eliasi	0
Echimyidae	Trinomys	gratiosus	2
Echimyidae	Trinomys	iheringi	0
Echimyidae	Trinomys	mirapitanga	0
Echimyidae	Trinomys	moojeni	0
Echimyidae	Trinomys	myosuros	0
Echimyidae	Trinomys	paratus	0
Echimyidae	Trinomys	setosus	3
Echimyidae	Trinomys	yonenagae	0
Echimyidae	Boromys	offella	0
Echimyidae	Boromys	torrei	0
Echimyidae	Brotomys	contractus	0
Echimyidae	Brotomys	voratus	0
Echimyidae	Heteropsomys	antillensis	0
Echimyidae	Heteropsomys	insulans	0
Myocastoridae	Myocastor	coypus	4
Capromyidae	Capromys	gundlachianus	0
Capromyidae	Capromys	pilorides	3
Capromyidae	Geocapromys	brownii	0
Capromyidae	Geocapromys	ingrahami	0
Capromyidae	Geocapromys	thoracatus	0

Capromyidae	Mesocapromys	angelcabrerai	0
Capromyidae	Mesocapromys	auritus	0
Capromyidae	Mesocapromys	melanurus	0
Capromyidae	Mesocapromys	nanus	0
Capromyidae	Mesocapromys	sanfelipensis	0
Capromyidae	Mysateles	garridoi	0
Capromyidae	Mysateles	meridionalis	0
Capromyidae	Mysateles	prehensilis	2
Capromyidae	Hexolobodon	phenax	0
Capromyidae	Isolobodon	montanus	0
Capromyidae	Isolobodon	portoricensis	0
Capromyidae	Plagiodontia	aedium	2
Capromyidae	Plagiodontia	araeum	0
Capromyidae	Plagiodontia	ipnaeum	0
Capromyidae	Rhizoplagiodontia	lemkei	0
Heptaxodontidae	Clidomys	osborni	0
Heptaxodontidae	Amblyrhiza	inundata	0
Heptaxodontidae	Elasmodontomys	obliquus	0
Heptaxodontidae	Quemisia	gravis	0
Ochotonidae	Ochotona	alpina	4
Ochotonidae	Ochotona	argentata	0
Ochotonidae	Ochotona	cansus	4
Ochotonidae	Ochotona	collaris	0
Ochotonidae	Ochotona	curzoniae	0
Ochotonidae	Ochotona	dauurica	4
Ochotonidae	Ochotona	erythrotis	0
Ochotonidae	Ochotona	forresti	0
Ochotonidae	Ochotona	gaoligongensis	0
Ochotonidae	Ochotona	gloveri	3
Ochotonidae	Ochotona	himalayana	0
Ochotonidae	Ochotona	hoffmanni	0
Ochotonidae	Ochotona	huangensis	0
Ochotonidae	Ochotona	hyperborea	9
Ochotonidae	Ochotona	iliensis	0
Ochotonidae	Ochotona	koslowi	0
Ochotonidae	Ochotona	ladacensis	0
Ochotonidae	Ochotona	macrotis	5
Ochotonidae	Ochotona	muliensis	0
Ochotonidae	Ochotona	nigritia	0
Ochotonidae	Ochotona	nubrica	2
Ochotonidae	Ochotona	pallasi	4
Ochotonidae	Ochotona	princeps	5

Ochotonidae	Ochotona	pusilla	2
Ochotonidae	Ochotona	roylei	2
Ochotonidae	Ochotona	rufescens	3
Ochotonidae	Ochotona	rutila	0
Ochotonidae	Ochotona	thibetana	5
Ochotonidae	Ochotona	thomasi	0
Ochotonidae	Ochotona	turuchanensis	0
Prolagidae	Prolagus	sardus	0
Leporidae	Brachylagus	idahoensis	0
Leporidae	Bunolagus	monticularis	0
Leporidae	Caprolagus	hispidus	0
Leporidae	Lepus	alleni	2
Leporidae	Lepus	americanus	6
Leporidae	Lepus	arcticus	4
Leporidae	Lepus	brachyurus	4
Leporidae	Lepus	californicus	6
Leporidae	Lepus	callotis	2
Leporidae	Lepus	capensis	12
Leporidae	Lepus	castroviejoi	0
Leporidae	Lepus	comus	0
Leporidae	Lepus	coreanus	0
Leporidae	Lepus	corsicanus	0
Leporidae	Lepus	europaeus	16
Leporidae	Lepus	fagani	0
Leporidae	Lepus	flavigularis	0
Leporidae	Lepus	granatensis	3
Leporidae	Lepus	habessinicus	0
Leporidae	Lepus	hainanus	0
Leporidae	Lepus	insularis	0
Leporidae	Lepus	mandshuricus	0
Leporidae	Lepus	microtis	4
Leporidae	Lepus	nigricollis	7
Leporidae	Lepus	oiostolus	4
Leporidae	Lepus	othus	2
Leporidae	Lepus	peguensis	2
Leporidae	Lepus	saxatilis	2
Leporidae	Lepus	sinensis	3
Leporidae	Lepus	starcki	0
Leporidae	Lepus	tibetanus	5
Leporidae	Lepus	timidus	15
Leporidae	Lepus	tolai	8
Leporidae	Lepus	townsendii	2

Leporidae	Lepus	yarkandensis	0
Leporidae	Nesolagus	netscheri	0
Leporidae	Nesolagus	timminsi	0
Leporidae	Oryctolagus	cuniculus	6
Leporidae	Pentalagus	furnessi	0
Leporidae	Poelagus	marjorita	0
Leporidae	Pronolagus	crassicaudatus	2
Leporidae	Pronolagus	randensis	3
Leporidae	Pronolagus	rupestris	5
Leporidae	Romerolagus	diazi	0
Leporidae	Sylvilagus	aquaticus	2
Leporidae	Sylvilagus	audubonii	7
Leporidae	Sylvilagus	bachmani	6
Leporidae	Sylvilagus	brasiliensis	21
Leporidae	Sylvilagus	cognatus	0
Leporidae	Sylvilagus	cunicularius	2
Leporidae	Sylvilagus	dicei	0
Leporidae	Sylvilagus	floridanus	18
Leporidae	Sylvilagus	graysoni	0
Leporidae	Sylvilagus	insonus	0
Leporidae	Sylvilagus	mansuetus	0
Leporidae	Sylvilagus	nuttallii	3
Leporidae	Sylvilagus	obscurus	0
Leporidae	Sylvilagus	palustris	3
Leporidae	Sylvilagus	robustus	0
Leporidae	Sylvilagus	transitionalis	0
Leporidae	Sylvilagus	varynaensis	0
Erinaceidae	Atelerix	albiventris	0
Erinaceidae	Atelerix	algirus	3
Erinaceidae	Atelerix	frontalis	2
Erinaceidae	Atelerix	sclateri	0
Erinaceidae	Erinaceus	amurensis	0
Erinaceidae	Erinaceus	concolor	3
Erinaceidae	Erinaceus	europaeus	0
Erinaceidae	Erinaceus	roumanicus	5
Erinaceidae	Hemiechinus	auritus	5
Erinaceidae	Hemiechinus	collaris	0
Erinaceidae	Mesechinus	dauuricus	0
Erinaceidae	Mesechinus	hughi	0
Erinaceidae	Paraechinus	aethiopicus	5
Erinaceidae	Paraechinus	hypomelas	5
Erinaceidae	Paraechinus	micropus	0

Erinaceidae	Paraechinus	nudiventris	0
Erinaceidae	Echinosorex	gymnura	2
Erinaceidae	Hylomys	megalotis	0
Erinaceidae	Hylomys	parvus	0
Erinaceidae	Hylomys	suillus	7
Erinaceidae	Neohylomys	hainanensis	0
Erinaceidae	Neotetracus	sinensis	0
Erinaceidae	Podogymnura	aureospinula	0
Erinaceidae	Podogymnura	truei	0
Nesophontidae	Nesophontes	edithae	0
Nesophontidae	Nesophontes	hypomicrus	0
Nesophontidae	Nesophontes	longirostris	0
Nesophontidae	Nesophontes	major	0
Nesophontidae	Nesophontes	micrus	0
Nesophontidae	Nesophontes	paramicrus	0
Nesophontidae	Nesophontes	submicrus	0
Nesophontidae	Nesophontes	superstes	0
Nesophontidae	Nesophontes	zamicrus	0
Solenodontidae	Solenodon	arredondoi	0
Solenodontidae	Solenodon	cubanus	0
Solenodontidae	Solenodon	marcanoi	0
Solenodontidae	Solenodon	paradoxus	2
Soricidae	Crocidura	aleksandrisi	0
Soricidae	Crocidura	allex	0
Soricidae	Crocidura	andamanensis	0
Soricidae	Crocidura	ansellorum	0
Soricidae	Crocidura	arabica	0
Soricidae	Crocidura	arispa	0
Soricidae	Crocidura	armenica	0
Soricidae	Crocidura	attenuata	0
Soricidae	Crocidura	attila	0
Soricidae	Crocidura	baileyi	0
Soricidae	Crocidura	baluensis	0
Soricidae	Crocidura	batesi	0
Soricidae	Crocidura	beatus	0
Soricidae	Crocidura	beccarii	0
Soricidae	Crocidura	bottegi	0
Soricidae	Crocidura	bottegoides	0
Soricidae	Crocidura	brunnea	2
Soricidae	Crocidura	buettikoferi	0
Soricidae	Crocidura	caliginea	0
Soricidae	Crocidura	canariensis	0

Soricidae	Crocidura	caspica	0
Soricidae	Crocidura	cinderella	0
Soricidae	Crocidura	congobelgica	0
Soricidae	Crocidura	crenata	0
Soricidae	Crocidura	crossei	0
Soricidae	Crocidura	cyanea	0
Soricidae	Crocidura	denti	0
Soricidae	Crocidura	desperata	0
Soricidae	Crocidura	dhofarensis	0
Soricidae	Crocidura	dolichura	0
Soricidae	Crocidura	douceti	0
Soricidae	Crocidura	dsinezumi	0
Soricidae	Crocidura	eisentrauti	0
Soricidae	Crocidura	elgonius	0
Soricidae	Crocidura	elongata	0
Soricidae	Crocidura	erica	0
Soricidae	Crocidura	fischeri	0
Soricidae	Crocidura	flavescens	0
Soricidae	Crocidura	floweri	0
Soricidae	Crocidura	foetida	3
Soricidae	Crocidura	foxi	0
Soricidae	Crocidura	fuliginosa	2
Soricidae	Crocidura	fulvastra	0
Soricidae	Crocidura	fumosa	0
Soricidae	Crocidura	fuscomurina	0
Soricidae	Crocidura	glassi	0
Soricidae	Crocidura	gmelini	0
Soricidae	Crocidura	goliath	2
Soricidae	Crocidura	gracilipes	0
Soricidae	Crocidura	grandiceps	0
Soricidae	Crocidura	grandis	0
Soricidae	Crocidura	grassei	0
Soricidae	Crocidura	grayi	0
Soricidae	Crocidura	greenwoodi	0
Soricidae	Crocidura	harenna	0
Soricidae	Crocidura	hildegardeae	0
Soricidae	Crocidura	hilliana	0
Soricidae	Crocidura	hirta	0
Soricidae	Crocidura	hispida	0
Soricidae	Crocidura	horsfieldii	0
Soricidae	Crocidura	hutanis	0
Soricidae	Crocidura	ichnusae	0

Soricidae	Crocidura	indochinensis	0
Soricidae	Crocidura	jacksoni	0
Soricidae	Crocidura	jenkinsi	0
Soricidae	Crocidura	jouvenetae	0
Soricidae	Crocidura	katinka	0
Soricidae	Crocidura	kivuana	0
Soricidae	Crocidura	lamottei	2
Soricidae	Crocidura	lanosa	0
Soricidae	Crocidura	lasiura	0
Soricidae	Crocidura	latona	0
Soricidae	Crocidura	lea	0
Soricidae	Crocidura	lepidura	0
Soricidae	Crocidura	leucodon	0
Soricidae	Crocidura	levicula	0
Soricidae	Crocidura	littoralis	0
Soricidae	Crocidura	longipes	0
Soricidae	Crocidura	lucina	0
Soricidae	Crocidura	ludia	0
Soricidae	Crocidura	luna	0
Soricidae	Crocidura	lusitania	0
Soricidae	Crocidura	macarthuri	0
Soricidae	Crocidura	macmillani	0
Soricidae	Crocidura	macowi	0
Soricidae	Crocidura	malayana	0
Soricidae	Crocidura	manengubae	0
Soricidae	Crocidura	maquassiensis	0
Soricidae	Crocidura	mariquensis	3
Soricidae	Crocidura	maurisca	0
Soricidae	Crocidura	maxi	0
Soricidae	Crocidura	mindorus	0
Soricidae	Crocidura	miya	0
Soricidae	Crocidura	monax	0
Soricidae	Crocidura	monticola	0
Soricidae	Crocidura	montis	0
Soricidae	Crocidura	muricauda	0
Soricidae	Crocidura	musseri	0
Soricidae	Crocidura	mutesae	0
Soricidae	Crocidura	nana	0
Soricidae	Crocidura	nanilla	0
Soricidae	Crocidura	negligens	0
Soricidae	Crocidura	negrina	0
Soricidae	Crocidura	nicobarica	0

Soricidae	Crocidura	nigeriae	0
Soricidae	Crocidura	nigricans	0
Soricidae	Crocidura	nigripes	2
Soricidae	Crocidura	nigrofusca	0
Soricidae	Crocidura	nimbae	0
Soricidae	Crocidura	niobe	0
Soricidae	Crocidura	obscurior	0
Soricidae	Crocidura	olivieri	20
Soricidae	Crocidura	orientalis	2
Soricidae	Crocidura	orii	0
Soricidae	Crocidura	palawanensis	0
Soricidae	Crocidura	paradoxura	0
Soricidae	Crocidura	parvipes	0
Soricidae	Crocidura	pasha	0
Soricidae	Crocidura	pergrisea	0
Soricidae	Crocidura	phaeura	0
Soricidae	Crocidura	picea	0
Soricidae	Crocidura	pitmani	0
Soricidae	Crocidura	planiceps	0
Soricidae	Crocidura	poensis	0
Soricidae	Crocidura	polia	0
Soricidae	Crocidura	pullata	0
Soricidae	Crocidura	raineyi	0
Soricidae	Crocidura	ramona	0
Soricidae	Crocidura	rapax	4
Soricidae	Crocidura	religiosa	0
Soricidae	Crocidura	rhoditis	0
Soricidae	Crocidura	roosevelti	0
Soricidae	Crocidura	russula	6
Soricidae	Crocidura	selina	0
Soricidae	Crocidura	serezkyensis	0
Soricidae	Crocidura	shantungensis	2
Soricidae	Crocidura	sibirica	0
Soricidae	Crocidura	sicula	4
Soricidae	Crocidura	silacea	0
Soricidae	Crocidura	smithii	2
Soricidae	Crocidura	somalica	0
Soricidae	Crocidura	stenocephala	0
Soricidae	Crocidura	suaveolens	0
Soricidae	Crocidura	susiana	0
Soricidae	Crocidura	tanakae	0
Soricidae	Crocidura	tansaniana	0

Soricidae	Crocidura	tarella	0
Soricidae	Crocidura	tarfayensis	0
Soricidae	Crocidura	telfordi	0
Soricidae	Crocidura	tenuis	0
Soricidae	Crocidura	thalia	0
Soricidae	Crocidura	theresae	0
Soricidae	Crocidura	thomensis	0
Soricidae	Crocidura	trichura	0
Soricidae	Crocidura	turba	0
Soricidae	Crocidura	ultima	0
Soricidae	Crocidura	usambarae	0
Soricidae	Crocidura	viaria	0
Soricidae	Crocidura	virgata	0
Soricidae	Crocidura	voi	0
Soricidae	Crocidura	vorax	0
Soricidae	Crocidura	vosmaeri	0
Soricidae	Crocidura	watasei	0
Soricidae	Crocidura	whitakeri	0
Soricidae	Crocidura	wimmeri	0
Soricidae	Crocidura	wuchihensis	0
Soricidae	Crocidura	xantippe	0
Soricidae	Crocidura	yankariensis	0
Soricidae	Crocidura	zaphiri	0
Soricidae	Crocidura	zarudnyi	0
Soricidae	Crocidura	zimmeri	0
Soricidae	Crocidura	zimmermanni	0
Soricidae	Diplomesodon	pulchellum	0
Soricidae	Feroculus	feroculus	0
Soricidae	Paracrocidura	graueri	0
Soricidae	Paracrocidura	maxima	0
Soricidae	Paracrocidura	schoutedeni	0
Soricidae	Ruwenzorisorex	suncoides	0
Soricidae	Scutisorex	somereni	0
Soricidae	Solisorex	pearsoni	0
Soricidae	Suncus	aequatorius	0
Soricidae	Suncus	ater	0
Soricidae	Suncus	dayi	0
Soricidae	Suncus	etruscus	0
Soricidae	Suncus	fellowesgordoni	0
Soricidae	Suncus	hosei	0
Soricidae	Suncus	infinitesimus	0
Soricidae	Suncus	lixus	0

Soricidae	Suncus	madagascariensis	0
Soricidae	Suncus	malayanus	0
Soricidae	Suncus	megalura	0
Soricidae	Suncus	mertensi	0
Soricidae	Suncus	montanus	2
Soricidae	Suncus	murinus	0
Soricidae	Suncus	remyi	0
Soricidae	Suncus	stoliczkanus	0
Soricidae	Suncus	varilla	0
Soricidae	Suncus	zeylanicus	0
Soricidae	Sylvisorex	camerunensis	0
Soricidae	Sylvisorex	granti	2
Soricidae	Sylvisorex	howelli	2
Soricidae	Sylvisorex	isabellae	0
Soricidae	Sylvisorex	johnstoni	0
Soricidae	Sylvisorex	konganensis	0
Soricidae	Sylvisorex	lunaris	0
Soricidae	Sylvisorex	morio	0
Soricidae	Sylvisorex	ollula	0
Soricidae	Sylvisorex	oriundus	0
Soricidae	Sylvisorex	pluvialis	0
Soricidae	Sylvisorex	vulcanorum	0
Soricidae	Congosorex	polli	0
Soricidae	Congosorex	verheyeni	0
Soricidae	Myosorex	babaulti	0
Soricidae	Myosorex	blarina	0
Soricidae	Myosorex	cafer	0
Soricidae	Myosorex	eisentrauti	0
Soricidae	Myosorex	geata	0
Soricidae	Myosorex	kihaulei	0
Soricidae	Myosorex	longicaudatus	2
Soricidae	Myosorex	okuensis	0
Soricidae	Myosorex	rumpii	0
Soricidae	Myosorex	schalleri	0
Soricidae	Myosorex	sclateri	0
Soricidae	Myosorex	tenuis	0
Soricidae	Myosorex	varius	0
Soricidae	Myosorex	zinki	0
Soricidae	Surdisorex	norae	0
Soricidae	Surdisorex	polulus	0
Soricidae	Anourosorex	assamensis	0
Soricidae	Anourosorex	schmidi	0

Soricidae	Anourosorex	squamipes	0
Soricidae	Anourosorex	yamashinai	0
Soricidae	Blarinella	griselda	0
Soricidae	Blarinella	quadraticauda	0
Soricidae	Blarinella	wardi	0
Soricidae	Blarina	brevicauda	11
Soricidae	Blarina	carolinensis	3
Soricidae	Blarina	hylophaga	2
Soricidae	Blarina	peninsulae	0
Soricidae	Cryptotis	alticola	0
Soricidae	Cryptotis	brachyonyx	0
Soricidae	Cryptotis	colombiana	0
Soricidae	Cryptotis	endersi	0
Soricidae	Cryptotis	equatoris	0
Soricidae	Cryptotis	goldmani	2
Soricidae	Cryptotis	goodwini	0
Soricidae	Cryptotis	gracilis	0
Soricidae	Cryptotis	griseoventris	0
Soricidae	Cryptotis	hondurensis	0
Soricidae	Cryptotis	magna	0
Soricidae	Cryptotis	mayensis	0
Soricidae	Cryptotis	medellinia	0
Soricidae	Cryptotis	mera	0
Soricidae	Cryptotis	meridensis	0
Soricidae	Cryptotis	merriami	0
Soricidae	Cryptotis	mexicana	0
Soricidae	Cryptotis	montivaga	0
Soricidae	Cryptotis	nelsoni	0
Soricidae	Cryptotis	nigrescens	0
Soricidae	Cryptotis	obscura	0
Soricidae	Cryptotis	orophila	0
Soricidae	Cryptotis	parva	5
Soricidae	Cryptotis	peregrina	0
Soricidae	Cryptotis	peruviensis	0
Soricidae	Cryptotis	phillipsii	0
Soricidae	Cryptotis	squamipes	0
Soricidae	Cryptotis	tamensis	0
Soricidae	Cryptotis	thomasi	0
Soricidae	Cryptotis	tropicalis	0
Soricidae	Chimarrogale	hantu	0
Soricidae	Chimarrogale	himalayica	0
Soricidae	Chimarrogale	phaeura	0

Soricidae	Chimarrogale	platycephalus	0
Soricidae	Chimarrogale	styani	0
Soricidae	Chimarrogale	sumatrana	0
Soricidae	Chodsigoa	caovansunga	0
Soricidae	Chodsigoa	hypsibia	0
Soricidae	Chodsigoa	lamula	0
Soricidae	Chodsigoa	parca	3
Soricidae	Chodsigoa	parva	0
Soricidae	Chodsigoa	salenskii	0
Soricidae	Chodsigoa	smithii	0
Soricidae	Chodsigoa	sodalis	0
Soricidae	Episoriculus	caudatus	3
Soricidae	Episoriculus	fumidus	0
Soricidae	Episoriculus	leucops	2
Soricidae	Episoriculus	macrurus	0
Soricidae	Nectogale	elegans	0
Soricidae	Neomys	anomalus	0
Soricidae	Neomys	fodiens	0
Soricidae	Neomys	teres	0
Soricidae	Nesiotites	hidalgo	0
Soricidae	Nesiotites	similis	0
Soricidae	Soriculus	nigrescens	2
Soricidae	Megasorex	gigas	0
Soricidae	Notiosorex	cockrumi	0
Soricidae	Notiosorex	crawfordi	0
Soricidae	Notiosorex	evotis	0
Soricidae	Notiosorex	villai	0
Soricidae	Sorex	alaskanus	0
Soricidae	Sorex	alpinus	0
Soricidae	Sorex	antinorii	0
Soricidae	Sorex	araneus	0
Soricidae	Sorex	arcticus	2
Soricidae	Sorex	arizonae	0
Soricidae	Sorex	arunchi	0
Soricidae	Sorex	asper	0
Soricidae	Sorex	averini	0
Soricidae	Sorex	bairdi	2
Soricidae	Sorex	bedfordiae	0
Soricidae	Sorex	bendirii	3
Soricidae	Sorex	buchariensis	0
Soricidae	Sorex	caecutiens	0
Soricidae	Sorex	camtschatica	0

Soricidae	Sorex	cansulus	0
Soricidae	Sorex	cinereus	8
Soricidae	Sorex	coronatus	0
Soricidae	Sorex	cylindricauda	0
Soricidae	Sorex	daphaenodon	3
Soricidae	Sorex	dispar	2
Soricidae	Sorex	emarginatus	0
Soricidae	Sorex	excelsus	0
Soricidae	Sorex	fumeus	2
Soricidae	Sorex	gaspensis	0
Soricidae	Sorex	gracillimus	5
Soricidae	Sorex	granarius	0
Soricidae	Sorex	haydeni	0
Soricidae	Sorex	hosonoi	0
Soricidae	Sorex	hoyi	6
Soricidae	Sorex	isodon	0
Soricidae	Sorex	jacksoni	0
Soricidae	Sorex	kozlovi	0
Soricidae	Sorex	leucogaster	0
Soricidae	Sorex	longirostris	3
Soricidae	Sorex	lyelli	0
Soricidae	Sorex	macrodon	0
Soricidae	Sorex	maritimensis	0
Soricidae	Sorex	merriami	0
Soricidae	Sorex	milleri	0
Soricidae	Sorex	minutissimus	0
Soricidae	Sorex	minutus	0
Soricidae	Sorex	mirabilis	0
Soricidae	Sorex	monticolus	14
Soricidae	Sorex	nanus	0
Soricidae	Sorex	neomexicanus	0
Soricidae	Sorex	oreopolus	0
Soricidae	Sorex	orizabae	0
Soricidae	Sorex	ornatus	8
Soricidae	Sorex	pacificus	2
Soricidae	Sorex	palustris	9
Soricidae	Sorex	planiceps	0
Soricidae	Sorex	portenkoi	0
Soricidae	Sorex	preblei	0
Soricidae	Sorex	pribilofensis	0
Soricidae	Sorex	raddei	0
Soricidae	Sorex	roboratus	0

Soricidae	Sorex	samniticus	0
Soricidae	Sorex	satunini	0
Soricidae	Sorex	saussurei	2
Soricidae	Sorex	sclateri	0
Soricidae	Sorex	shinto	3
Soricidae	Sorex	sinalis	0
Soricidae	Sorex	sonomae	2
Soricidae	Sorex	stizodon	0
Soricidae	Sorex	tenellus	0
Soricidae	Sorex	thibetanus	0
Soricidae	Sorex	trowbridgii	5
Soricidae	Sorex	tundrensis	0
Soricidae	Sorex	ugyunak	0
Soricidae	Sorex	unguiculatus	0
Soricidae	Sorex	vagrans	3
Soricidae	Sorex	ventralis	0
Soricidae	Sorex	veraecrucis	3
Soricidae	Sorex	veraepacis	3
Soricidae	Sorex	volnuchini	2
Soricidae	Sorex	yukonicus	0
Talpidae	Condylura	cristata	2
Talpidae	Parascalops	breweri	0
Talpidae	Scalopus	aquaticus	16
Talpidae	Scapanulus	oweni	0
Talpidae	Scapanus	latimanus	12
Talpidae	Scapanus	orarius	2
Talpidae	Scapanus	townsendii	2
Talpidae	Desmana	moschata	0
Talpidae	Galemys	pyrenaicus	2
Talpidae	Neurotrichus	gibbsii	3
Talpidae	Scaptonyx	fusicaudus	0
Talpidae	Euroscaptor	grandis	0
Talpidae	Euroscaptor	klossi	0
Talpidae	Euroscaptor	longirostris	0
Talpidae	Euroscaptor	micrura	0
Talpidae	Euroscaptor	mizura	2
Talpidae	Euroscaptor	parvidens	0
Talpidae	Mogera	imaizumii	0
Talpidae	Mogera	insularis	3
Talpidae	Mogera	tokudae	2
Talpidae	Mogera	uchidai	0
Talpidae	Mogera	wogura	2

Talpidae	Parascaptor	leucura	0
Talpidae	Scaptochirus	moschatus	0
Talpidae	Talpa	altaica	0
Talpidae	Talpa	caeca	4
Talpidae	Talpa	caucasica	3
Talpidae	Talpa	europaea	3
Talpidae	Talpa	davidiana	0
Talpidae	Talpa	levantis	4
Talpidae	Talpa	occidentalis	0
Talpidae	Talpa	romana	6
Talpidae	Talpa	stankovici	2
Talpidae	Dymecodon	pilirostris	0
Talpidae	Urotrichus	talpoides	5
Talpidae	Uropsilus	andersoni	0
Talpidae	Uropsilus	gracilis	0
Talpidae	Uropsilus	investigator	0
Talpidae	Uropsilus	soricipes	0
Pteropodidae	Acerodon	celebensis	0
Pteropodidae	Acerodon	humilis	0
Pteropodidae	Acerodon	jubatus	3
Pteropodidae	Acerodon	leucotis	2
Pteropodidae	Acerodon	mackloti	5
Pteropodidae	Aethalops	aequalis	0
Pteropodidae	Aethalops	alecto	3
Pteropodidae	Alionycteris	paucidentata	0
Pteropodidae	Aproteles	bulmerae	0
Pteropodidae	Balionycteris	maculata	2
Pteropodidae	Casinycteris	argynnis	0
Pteropodidae	Chironax	melanocephalus	2
Pteropodidae	Cynopterus	brachyotis	8
Pteropodidae	Cynopterus	horsfieldii	4
Pteropodidae	Cynopterus	luzoniensis	0
Pteropodidae	Cynopterus	minutus	0
Pteropodidae	Cynopterus	nusatenggara	3
Pteropodidae	Cynopterus	sphinx	6
Pteropodidae	Cynopterus	titthaecheilus	3
Pteropodidae	Dobsonia	anderseni	0
Pteropodidae	Dobsonia	beauforti	0
Pteropodidae	Dobsonia	chapmani	0
Pteropodidae	Dobsonia	crenulata	0
Pteropodidae	Dobsonia	emersa	0
Pteropodidae	Dobsonia	exoleta	0

Pteropodidae	Dobsonia	inermis	2
Pteropodidae	Dobsonia	magna	0
Pteropodidae	Dobsonia	minor	0
Pteropodidae	Dobsonia	moluccensis	0
Pteropodidae	Dobsonia	pannietensis	2
Pteropodidae	Dobsonia	peronii	2
Pteropodidae	Dobsonia	praedatrix	0
Pteropodidae	Dobsonia	viridis	0
Pteropodidae	Dyacopterus	brooksi	0
Pteropodidae	Dyacopterus	spadiceus	0
Pteropodidae	Eidolon	dupreanum	0
Pteropodidae	Eidolon	helvum	3
Pteropodidae	Eonycteris	major	0
Pteropodidae	Eonycteris	robusta	0
Pteropodidae	Eonycteris	spelaea	4
Pteropodidae	Epomophorus	angolensis	0
Pteropodidae	Epomophorus	crypturus	0
Pteropodidae	Epomophorus	gambianus	2
Pteropodidae	Epomophorus	grandis	0
Pteropodidae	Epomophorus	labiatus	0
Pteropodidae	Epomophorus	minimus	0
Pteropodidae	Epomophorus	minor	0
Pteropodidae	Epomophorus	wahlbergi	0
Pteropodidae	Epomops	buettikoferi	0
Pteropodidae	Epomops	dobsonii	0
Pteropodidae	Epomops	franqueti	0
Pteropodidae	Haplonycteris	fischeri	0
Pteropodidae	Harpyionycteris	celebensis	0
Pteropodidae	Harpyionycteris	whiteheadi	2
Pteropodidae	Hypsignathus	monstrosus	0
Pteropodidae	Latidens	salimalii	0
Pteropodidae	Lissonycteris	angolensis	5
Pteropodidae	Macroglossus	minimus	4
Pteropodidae	Macroglossus	sobrinus	2
Pteropodidae	Megaerops	ecaudatus	0
Pteropodidae	Megaerops	kusnotoi	0
Pteropodidae	Megaerops	niphanae	0
Pteropodidae	Megaerops	wetmorei	2
Pteropodidae	Megaloglossus	woermanni	0
Pteropodidae	Melonycteris	fardoulisi	4
Pteropodidae	Melonycteris	melanops	0
Pteropodidae	Melonycteris	woodfordi	2

Pteropodidae	Micropteropus	intermedius	0
Pteropodidae	Micropteropus	pusillus	0
Pteropodidae	Myonycteris	brachycephala	0
Pteropodidae	Myonycteris	relicta	0
Pteropodidae	Myonycteris	torquata	0
Pteropodidae	Nanonycteris	veldkampii	0
Pteropodidae	Neopteryx	frosti	0
Pteropodidae	Notopteris	macdonaldi	0
Pteropodidae	Notopteris	neocaledonica	0
Pteropodidae	Nyctimene	aello	0
Pteropodidae	Nyctimene	albiventer	2
Pteropodidae	Nyctimene	cephalotes	2
Pteropodidae	Nyctimene	certans	0
Pteropodidae	Nyctimene	cyclotis	0
Pteropodidae	Nyctimene	draconilla	0
Pteropodidae	Nyctimene	keasti	3
Pteropodidae	Nyctimene	major	4
Pteropodidae	Nyctimene	malaitensis	0
Pteropodidae	Nyctimene	masalai	0
Pteropodidae	Nyctimene	minutus	2
Pteropodidae	Nyctimene	rabori	0
Pteropodidae	Nyctimene	robinsoni	0
Pteropodidae	Nyctimene	sanctacrucis	0
Pteropodidae	Nyctimene	vizcaccia	2
Pteropodidae	Otopteropus	cartilagonodus	0
Pteropodidae	Paranyctimene	raptor	0
Pteropodidae	Paranyctimene	tenax	2
Pteropodidae	Penthetor	lucasi	0
Pteropodidae	Plerotes	anchietae	0
Pteropodidae	Ptenochirus	jagori	0
Pteropodidae	Ptenochirus	minor	0
Pteropodidae	Pteralopex	acrodonta	0
Pteropodidae	Pteralopex	anceps	0
Pteropodidae	Pteralopex	atrata	0
Pteropodidae	Pteralopex	pulchra	0
Pteropodidae	Pteralopex	taki	0
Pteropodidae	Pteropus	admiralitatum	4
Pteropodidae	Pteropus	aldabrensis	0
Pteropodidae	Pteropus	alecto	4
Pteropodidae	Pteropus	anetianus	7
Pteropodidae	Pteropus	aruensis	0
Pteropodidae	Pteropus	banakrisi	0

Pteropodidae	Pteropus	brunneus	0
Pteropodidae	Pteropus	caniceps	2
Pteropodidae	Pteropus	capistratus	2
Pteropodidae	Pteropus	chrysoproctus	0
Pteropodidae	Pteropus	cognatus	0
Pteropodidae	Pteropus	conspicillatus	2
Pteropodidae	Pteropus	dasymallus	5
Pteropodidae	Pteropus	faunulus	0
Pteropodidae	Pteropus	fundatus	0
Pteropodidae	Pteropus	giganteus	4
Pteropodidae	Pteropus	gilliardorum	0
Pteropodidae	Pteropus	griseus	3
Pteropodidae	Pteropus	howensis	0
Pteropodidae	Pteropus	hypomelanus	16
Pteropodidae	Pteropus	insularis	2
Pteropodidae	Pteropus	intermedius	0
Pteropodidae	Pteropus	keyensis	0
Pteropodidae	Pteropus	leucopterus	0
Pteropodidae	Pteropus	livingstonii	0
Pteropodidae	Pteropus	lombocensis	3
Pteropodidae	Pteropus	loochoensis	0
Pteropodidae	Pteropus	lylei	0
Pteropodidae	Pteropus	macrotis	2
Pteropodidae	Pteropus	mahaganus	0
Pteropodidae	Pteropus	mariannus	3
Pteropodidae	Pteropus	melanopogon	0
Pteropodidae	Pteropus	melanotus	5
Pteropodidae	Pteropus	molossinus	0
Pteropodidae	Pteropus	neohibernicus	2
Pteropodidae	Pteropus	niger	0
Pteropodidae	Pteropus	nitendiensis	0
Pteropodidae	Pteropus	ocularis	0
Pteropodidae	Pteropus	ornatus	2
Pteropodidae	Pteropus	pelewensis	0
Pteropodidae	Pteropus	personatus	0
Pteropodidae	Pteropus	pilosus	0
Pteropodidae	Pteropus	pohlei	0
Pteropodidae	Pteropus	poliocephalus	0
Pteropodidae	Pteropus	pselaphon	0
Pteropodidae	Pteropus	pumilus	0
Pteropodidae	Pteropus	rayneri	5
Pteropodidae	Pteropus	rennelli	0

Pteropodidae	Pteropus	rodricensis	0
Pteropodidae	Pteropus	rufus	0
Pteropodidae	Pteropus	samoensis	2
Pteropodidae	Pteropus	scapulatus	0
Pteropodidae	Pteropus	seychellensis	2
Pteropodidae	Pteropus	speciosus	0
Pteropodidae	Pteropus	subniger	0
Pteropodidae	Pteropus	temminckii	2
Pteropodidae	Pteropus	tokudae	0
Pteropodidae	Pteropus	tonganus	3
Pteropodidae	Pteropus	tuberculatus	0
Pteropodidae	Pteropus	ualanus	0
Pteropodidae	Pteropus	vampyrus	6
Pteropodidae	Pteropus	vetulus	0
Pteropodidae	Pteropus	voeltzkowi	0
Pteropodidae	Pteropus	woodfordi	0
Pteropodidae	Pteropus	yapensis	0
Pteropodidae	Rousettus	aegyptiacus	6
Pteropodidae	Rousettus	amplexicaudatus	5
Pteropodidae	Rousettus	bidens	0
Pteropodidae	Rousettus	celebensis	0
Pteropodidae	Rousettus	lanosus	0
Pteropodidae	Rousettus	leschenaultii	3
Pteropodidae	Rousettus	linduensis	0
Pteropodidae	Rousettus	madagascariensis	0
Pteropodidae	Rousettus	obliviosus	0
Pteropodidae	Rousettus	spinalatus	0
Pteropodidae	Scotonycteris	ophiodon	0
Pteropodidae	Scotonycteris	zenkeri	3
Pteropodidae	Sphaerias	blanfordi	0
Pteropodidae	Styloctenium	wallacei	0
Pteropodidae	Syconycteris	australis	7
Pteropodidae	Syconycteris	carolinae	0
Pteropodidae	Syconycteris	hobbit	0
Pteropodidae	Thoopterus	nigrescens	0
Rhinolophidae	Rhinolophus	acuminatus	5
Rhinolophidae	Rhinolophus	adami	0
Rhinolophidae	Rhinolophus	affinis	9
Rhinolophidae	Rhinolophus	alcyone	0
Rhinolophidae	Rhinolophus	arcuatus	7
Rhinolophidae	Rhinolophus	beddomei	2
Rhinolophidae	Rhinolophus	blasii	4

Rhinolophidae	Rhinolophus	bocharicus	0
Rhinolophidae	Rhinolophus	borneensis	4
Rhinolophidae	Rhinolophus	canuti	2
Rhinolophidae	Rhinolophus	capensis	0
Rhinolophidae	Rhinolophus	celebensis	2
Rhinolophidae	Rhinolophus	clivosus	7
Rhinolophidae	Rhinolophus	coelophyllus	0
Rhinolophidae	Rhinolophus	cognatus	2
Rhinolophidae	Rhinolophus	convexus	0
Rhinolophidae	Rhinolophus	cornutus	5
Rhinolophidae	Rhinolophus	creaghi	2
Rhinolophidae	Rhinolophus	darlingi	2
Rhinolophidae	Rhinolophus	deckenii	0
Rhinolophidae	Rhinolophus	denti	2
Rhinolophidae	Rhinolophus	eloquens	2
Rhinolophidae	Rhinolophus	euryale	2
Rhinolophidae	Rhinolophus	euryotis	6
Rhinolophidae	Rhinolophus	ferrumequinum	7
Rhinolophidae	Rhinolophus	formosae	0
Rhinolophidae	Rhinolophus	fumigatus	6
Rhinolophidae	Rhinolophus	guineensis	0
Rhinolophidae	Rhinolophus	hildebrandtii	0
Rhinolophidae	Rhinolophus	hilli	0
Rhinolophidae	Rhinolophus	hillorum	0
Rhinolophidae	Rhinolophus	hipposideros	6
Rhinolophidae	Rhinolophus	imaizumii	0
Rhinolophidae	Rhinolophus	inops	0
Rhinolophidae	Rhinolophus	keyensis	4
Rhinolophidae	Rhinolophus	landeri	3
Rhinolophidae	Rhinolophus	lepidus	5
Rhinolophidae	Rhinolophus	luctus	6
Rhinolophidae	Rhinolophus	maclaudi	0
Rhinolophidae	Rhinolophus	macrotis	6
Rhinolophidae	Rhinolophus	madurensis	0
Rhinolophidae	Rhinolophus	maendeleo	0
Rhinolophidae	Rhinolophus	malayanus	0
Rhinolophidae	Rhinolophus	marshalli	0
Rhinolophidae	Rhinolophus	megaphyllus	5
Rhinolophidae	Rhinolophus	mehelyi	2
Rhinolophidae	Rhinolophus	mitratus	0
Rhinolophidae	Rhinolophus	monoceros	0
Rhinolophidae	Rhinolophus	montanus	0

Rhinolophidae	Rhinolophus	nereis	0
Rhinolophidae	Rhinolophus	osgoodi	0
Rhinolophidae	Rhinolophus	paradoxolophus	0
Rhinolophidae	Rhinolophus	pearsonii	2
Rhinolophidae	Rhinolophus	philippinensis	6
Rhinolophidae	Rhinolophus	pusillus	9
Rhinolophidae	Rhinolophus	rex	0
Rhinolophidae	Rhinolophus	robinsoni	3
Rhinolophidae	Rhinolophus	rouxii	2
Rhinolophidae	Rhinolophus	rufus	0
Rhinolophidae	Rhinolophus	ruwenzorii	0
Rhinolophidae	Rhinolophus	sakejiensis	0
Rhinolophidae	Rhinolophus	sedulus	0
Rhinolophidae	Rhinolophus	shameli	0
Rhinolophidae	Rhinolophus	shortridgei	0
Rhinolophidae	Rhinolophus	siamensis	0
Rhinolophidae	Rhinolophus	silvestris	0
Rhinolophidae	Rhinolophus	simulator	2
Rhinolophidae	Rhinolophus	sinicus	2
Rhinolophidae	Rhinolophus	stheno	2
Rhinolophidae	Rhinolophus	subbadius	0
Rhinolophidae	Rhinolophus	subrufus	2
Rhinolophidae	Rhinolophus	swinnyi	0
Rhinolophidae	Rhinolophus	thomasi	2
Rhinolophidae	Rhinolophus	trifoliatus	4
Rhinolophidae	Rhinolophus	virgo	0
Rhinolophidae	Rhinolophus	yunanensis	0
Rhinolophidae	Rhinolophus	ziama	0
Hipposideridae	Anthops	ornatus	0
Hipposideridae	Asellia	patrizii	0
Hipposideridae	Asellia	tridens	4
Hipposideridae	Aselliscus	stoliczkanus	0
Hipposideridae	Aselliscus	tricuspidatus	4
Hipposideridae	Cloeotis	percivali	2
Hipposideridae	Coelops	frithii	5
Hipposideridae	Coelops	robinsoni	2
Hipposideridae	Hipposideros	abae	0
Hipposideridae	Hipposideros	armiger	4
Hipposideridae	Hipposideros	ater	7
Hipposideridae	Hipposideros	beatus	2
Hipposideridae	Hipposideros	bicolor	7
Hipposideridae	Hipposideros	breviceps	0

Hipposideridae	Hipposideros	caffer	4
Hipposideridae	Hipposideros	calcaratus	2
Hipposideridae	Hipposideros	camerunensis	0
Hipposideridae	Hipposideros	cervinus	4
Hipposideridae	Hipposideros	cineraceus	2
Hipposideridae	Hipposideros	commersoni	0
Hipposideridae	Hipposideros	coronatus	0
Hipposideridae	Hipposideros	corynophyllus	0
Hipposideridae	Hipposideros	coxi	0
Hipposideridae	Hipposideros	crumeniferus	0
Hipposideridae	Hipposideros	curtus	0
Hipposideridae	Hipposideros	cyclops	0
Hipposideridae	Hipposideros	demissus	0
Hipposideridae	Hipposideros	diadema	15
Hipposideridae	Hipposideros	dinops	0
Hipposideridae	Hipposideros	doriae	0
Hipposideridae	Hipposideros	durgadasi	0
Hipposideridae	Hipposideros	dyacorum	0
Hipposideridae	Hipposideros	edwardshilli	0
Hipposideridae	Hipposideros	fuliginosus	0
Hipposideridae	Hipposideros	fulvus	2
Hipposideridae	Hipposideros	galeritus	4
Hipposideridae	Hipposideros	gigas	0
Hipposideridae	Hipposideros	grandis	0
Hipposideridae	Hipposideros	halophyllus	0
Hipposideridae	Hipposideros	hypophyllus	0
Hipposideridae	Hipposideros	inexpectatus	0
Hipposideridae	Hipposideros	inornatus	0
Hipposideridae	Hipposideros	jonesi	0
Hipposideridae	Hipposideros	lamottei	0
Hipposideridae	Hipposideros	lankadiva	0
Hipposideridae	Hipposideros	larvatus	5
Hipposideridae	Hipposideros	lekaguli	0
Hipposideridae	Hipposideros	lylei	0
Hipposideridae	Hipposideros	macrobullatus	0
Hipposideridae	Hipposideros	madurae	2
Hipposideridae	Hipposideros	maggietaylorae	2
Hipposideridae	Hipposideros	marisae	0
Hipposideridae	Hipposideros	megalotis	0
Hipposideridae	Hipposideros	muscinus	0
Hipposideridae	Hipposideros	nequam	0
Hipposideridae	Hipposideros	obscurus	0

Hipposideridae	Hipposideros	orbiculus	0
Hipposideridae	Hipposideros	papua	0
Hipposideridae	Hipposideros	pelingensis	0
Hipposideridae	Hipposideros	pomona	3
Hipposideridae	Hipposideros	pratti	0
Hipposideridae	Hipposideros	pygmaeus	0
Hipposideridae	Hipposideros	ridleyi	0
Hipposideridae	Hipposideros	rotalis	0
Hipposideridae	Hipposideros	ruber	2
Hipposideridae	Hipposideros	scutinares	0
Hipposideridae	Hipposideros	semoni	0
Hipposideridae	Hipposideros	sorenseni	0
Hipposideridae	Hipposideros	speoris	0
Hipposideridae	Hipposideros	stenotis	0
Hipposideridae	Hipposideros	sumbae	3
Hipposideridae	Hipposideros	thomensis	0
Hipposideridae	Hipposideros	turpis	3
Hipposideridae	Hipposideros	vittatus	0
Hipposideridae	Hipposideros	wollastoni	3
Hipposideridae	Paracoelops	megalotis	0
Hipposideridae	Rhinonicteris	aurantia	0
Hipposideridae	Triaenops	auritus	0
Hipposideridae	Triaenops	furculus	0
Hipposideridae	Triaenops	persicus	3
Hipposideridae	Triaenops	rufus	0
Megadermatidae	Cardioderma	cor	0
Megadermatidae	Lavia	frons	3
Megadermatidae	Macroderma	gigas	0
Megadermatidae	Megaderma	lyra	2
Megadermatidae	Megaderma	spasma	17
Rhinopomatidae	Rhinopoma	hardwickii	4
Rhinopomatidae	Rhinopoma	macinnesi	0
Rhinopomatidae	Rhinopoma	microphyllum	4
Rhinopomatidae	Rhinopoma	muscatellum	2
Craseonycteridae	Craseonycteris	thonglongyai	0
Emballonuridae	Saccolaimus	flaviventris	0
Emballonuridae	Saccolaimus	mixtus	0
Emballonuridae	Saccolaimus	peli	0
Emballonuridae	Saccolaimus	saccolaimus	5
Emballonuridae	Taphozous	achates	2
Emballonuridae	Taphozous	australis	0
Emballonuridae	Taphozous	georgianus	0

Emballonuridae	Taphozous	hamiltoni	0
Emballonuridae	Taphozous	hildegardeae	0
Emballonuridae	Taphozous	hilli	0
Emballonuridae	Taphozous	kapalgensis	0
Emballonuridae	Taphozous	longimanus	4
Emballonuridae	Taphozous	mauritianus	0
Emballonuridae	Taphozous	melanopogon	5
Emballonuridae	Taphozous	nudiventris	5
Emballonuridae	Taphozous	perforatus	4
Emballonuridae	Taphozous	theobaldi	2
Emballonuridae	Taphozous	troughtoni	0
Emballonuridae	Balantiopteryx	infusca	0
Emballonuridae	Balantiopteryx	io	0
Emballonuridae	Balantiopteryx	plicata	2
Emballonuridae	Centronycteris	centralis	0
Emballonuridae	Centronycteris	maximiliani	0
Emballonuridae	Coleura	afra	0
Emballonuridae	Coleura	seychellensis	2
Emballonuridae	Cormura	brevirostris	0
Emballonuridae	Cyttarops	alecto	0
Emballonuridae	Diclidurus	albus	2
Emballonuridae	Diclidurus	ingens	0
Emballonuridae	Diclidurus	isabellus	0
Emballonuridae	Diclidurus	scutatus	0
Emballonuridae	Emballonura	alecto	4
Emballonuridae	Emballonura	atrata	0
Emballonuridae	Emballonura	beccarii	3
Emballonuridae	Emballonura	dianae	3
Emballonuridae	Emballonura	furax	0
Emballonuridae	Emballonura	monticola	0
Emballonuridae	Emballonura	raffrayana	3
Emballonuridae	Emballonura	semicaudata	4
Emballonuridae	Emballonura	serii	0
Emballonuridae	Mosia	nigrescens	3
Emballonuridae	Peropteryx	kappleri	2
Emballonuridae	Peropteryx	leucoptera	2
Emballonuridae	Peropteryx	macrotis	0
Emballonuridae	Peropteryx	trinitatis	2
Emballonuridae	Rhynchonycteris	naso	0
Emballonuridae	Saccopteryx	antioquensis	0
Emballonuridae	Saccopteryx	bilineata	0
Emballonuridae	Saccopteryx	canescens	2

Emballonuridae	Saccopteryx	gymnura	0
Emballonuridae	Saccopteryx	leptura	0
Nycteridae	Nycteris	arge	0
Nycteridae	Nycteris	aurita	0
Nycteridae	Nycteris	gambiensis	0
Nycteridae	Nycteris	grandis	0
Nycteridae	Nycteris	hispida	0
Nycteridae	Nycteris	intermedia	0
Nycteridae	Nycteris	javanica	2
Nycteridae	Nycteris	macrotis	4
Nycteridae	Nycteris	madagascariensis	0
Nycteridae	Nycteris	major	0
Nycteridae	Nycteris	nana	0
Nycteridae	Nycteris	parisii	2
Nycteridae	Nycteris	thebaica	8
Nycteridae	Nycteris	tragata	0
Nycteridae	Nycteris	vinsoni	0
Nycteridae	Nycteris	woodi	2
Myzopodidae	Myzopoda	aurita	0
Mystacinidae	Mystacina	robusta	0
Mystacinidae	Mystacina	tuberculata	0
Phyllostomidae	Desmodus	rotundus	0
Phyllostomidae	Diaemus	youngi	0
Phyllostomidae	Diphylla	ecaudata	0
Phyllostomidae	Brachyphylla	cavernarum	3
Phyllostomidae	Brachyphylla	nana	0
Phyllostomidae	Erophylla	bombifrons	2
Phyllostomidae	Erophylla	sezekorni	4
Phyllostomidae	Phyllonycteris	aphylla	0
Phyllostomidae	Phyllonycteris	major	0
Phyllostomidae	Phyllonycteris	poeyi	2
Phyllostomidae	Anoura	caudifer	0
Phyllostomidae	Anoura	cultrata	0
Phyllostomidae	Anoura	geoffroyi	3
Phyllostomidae	Anoura	latidens	0
Phyllostomidae	Anoura	luismanueli	0
Phyllostomidae	Choeroniscus	godmani	0
Phyllostomidae	Choeroniscus	minor	0
Phyllostomidae	Choeroniscus	periosus	2
Phyllostomidae	Choeronycteris	mexicana	0
Phyllostomidae	Glossophaga	commissarisi	3
Phyllostomidae	Glossophaga	leachii	0

Phyllostomidae	Glossophaga	longirostris	7
Phyllostomidae	Glossophaga	morenoi	3
Phyllostomidae	Glossophaga	soricina	5
Phyllostomidae	Hylonycteris	underwoodi	2
Phyllostomidae	Leptonycteris	curasoae	0
Phyllostomidae	Leptonycteris	nivalis	0
Phyllostomidae	Leptonycteris	yerbabuenae	0
Phyllostomidae	Lichonycteris	obscura	0
Phyllostomidae	Monophyllus	plethodon	3
Phyllostomidae	Monophyllus	redmani	3
Phyllostomidae	Musonycteris	harrisoni	0
Phyllostomidae	Scleronycteris	ega	0
Phyllostomidae	Lionycteris	spurrelli	0
Phyllostomidae	Lonchophylla	bokermanni	0
Phyllostomidae	Lonchophylla	dekeyseri	0
Phyllostomidae	Lonchophylla	handleyi	0
Phyllostomidae	Lonchophylla	hesperia	0
Phyllostomidae	Lonchophylla	mordax	2
Phyllostomidae	Lonchophylla	robusta	0
Phyllostomidae	Lonchophylla	thomasi	0
Phyllostomidae	Platalina	genovensium	0
Phyllostomidae	Chrotopterus	auritus	0
Phyllostomidae	Glyphonycteris	behnii	0
Phyllostomidae	Glyphonycteris	daviesi	0
Phyllostomidae	Glyphonycteris	sylvestris	0
Phyllostomidae	Lampronycteris	brachyotis	0
Phyllostomidae	Lonchorhina	aurita	2
Phyllostomidae	Lonchorhina	fernandezi	0
Phyllostomidae	Lonchorhina	inusitata	0
Phyllostomidae	Lonchorhina	marinkellei	0
Phyllostomidae	Lonchorhina	orinocensis	0
Phyllostomidae	Lophostoma	brasiliense	0
Phyllostomidae	Lophostoma	carrikeri	0
Phyllostomidae	Lophostoma	evotis	0
Phyllostomidae	Lophostoma	schulzi	0
Phyllostomidae	Lophostoma	silvicolum	4
Phyllostomidae	Macrophyllum	macrophyllum	0
Phyllostomidae	Macrotus	californicus	0
Phyllostomidae	Macrotus	waterhousii	6
Phyllostomidae	Micronycteris	brosseti	0
Phyllostomidae	Micronycteris	hirsuta	0
Phyllostomidae	Micronycteris	homezi	0

Phyllostomidae	Micronycteris	matses	0
Phyllostomidae	Micronycteris	megalotis	0
Phyllostomidae	Micronycteris	microtis	2
Phyllostomidae	Micronycteris	minuta	0
Phyllostomidae	Micronycteris	sanborni	0
Phyllostomidae	Micronycteris	schmidtorum	0
Phyllostomidae	Mimon	bennettii	0
Phyllostomidae	Mimon	cozumelae	0
Phyllostomidae	Mimon	crenulatum	4
Phyllostomidae	Mimon	koepckeae	0
Phyllostomidae	Neonycteris	pusilla	0
Phyllostomidae	Phylloderma	stenops	3
Phyllostomidae	Phyllostomus	discolor	2
Phyllostomidae	Phyllostomus	elongatus	0
Phyllostomidae	Phyllostomus	hastatus	2
Phyllostomidae	Phyllostomus	latifolius	0
Phyllostomidae	Tonatia	bidens	0
Phyllostomidae	Tonatia	saurophila	3
Phyllostomidae	Trachops	cirrhosus	3
Phyllostomidae	Trinycteris	nicefori	0
Phyllostomidae	Vampyrum	spectrum	0
Phyllostomidae	Carollia	brevicauda	0
Phyllostomidae	Carollia	castanea	0
Phyllostomidae	Carollia	colombiana	0
Phyllostomidae	Carollia	perspicillata	0
Phyllostomidae	Carollia	sowelli	0
Phyllostomidae	Carollia	subrufa	0
Phyllostomidae	Rhinophylla	alethina	0
Phyllostomidae	Rhinophylla	fischerae	0
Phyllostomidae	Rhinophylla	pumilio	0
Phyllostomidae	Sturnira	aratathomasi	0
Phyllostomidae	Sturnira	bidens	0
Phyllostomidae	Sturnira	bogotensis	0
Phyllostomidae	Sturnira	erythromos	0
Phyllostomidae	Sturnira	lilium	8
Phyllostomidae	Sturnira	ludovici	3
Phyllostomidae	Sturnira	luisi	0
Phyllostomidae	Sturnira	magna	0
Phyllostomidae	Sturnira	mistratensis	0
Phyllostomidae	Sturnira	mordax	0
Phyllostomidae	Sturnira	nana	0
Phyllostomidae	Sturnira	oporaphilum	0

Phyllostomidae	Sturnira	thomasi	0
Phyllostomidae	Sturnira	tildae	0
Phyllostomidae	Ametrida	centurio	0
Phyllostomidae	Ardops	nichollsi	5
Phyllostomidae	Ariteus	flavescens	0
Phyllostomidae	Artibeus	amplus	0
Phyllostomidae	Artibeus	anderseni	0
Phyllostomidae	Artibeus	aztecus	3
Phyllostomidae	Artibeus	cinereus	0
Phyllostomidae	Artibeus	concolor	0
Phyllostomidae	Artibeus	fimbriatus	0
Phyllostomidae	Artibeus	fraterculus	0
Phyllostomidae	Artibeus	glaucus	0
Phyllostomidae	Artibeus	gnomus	0
Phyllostomidae	Artibeus	hirsutus	0
Phyllostomidae	Artibeus	incomitatus	0
Phyllostomidae	Artibeus	inopinatus	0
Phyllostomidae	Artibeus	jamaicensis	13
Phyllostomidae	Artibeus	lituratus	3
Phyllostomidae	Artibeus	obscurus	0
Phyllostomidae	Artibeus	phaeotis	4
Phyllostomidae	Artibeus	toltecus	2
Phyllostomidae	Artibeus	watsoni	0
Phyllostomidae	Centurio	senex	2
Phyllostomidae	Chiroderma	doriae	0
Phyllostomidae	Chiroderma	improvisum	0
Phyllostomidae	Chiroderma	salvini	2
Phyllostomidae	Chiroderma	trinitatum	0
Phyllostomidae	Chiroderma	villosum	2
Phyllostomidae	Ectophylla	alba	0
Phyllostomidae	Enchisthenes	hartii	0
Phyllostomidae	Mesophylla	macconnelli	2
Phyllostomidae	Phyllops	falcatus	2
Phyllostomidae	Platyrrhinus	aurarius	0
Phyllostomidae	Platyrrhinus	brachycephalus	0
Phyllostomidae	Platyrrhinus	chocoensis	0
Phyllostomidae	Platyrrhinus	dorsalis	0
Phyllostomidae	Platyrrhinus	helleri	2
Phyllostomidae	Platyrrhinus	infuscus	0
Phyllostomidae	Platyrrhinus	lineatus	2
Phyllostomidae	Platyrrhinus	recifinus	0
Phyllostomidae	Platyrrhinus	umbratus	3

Phyllostomidae	Platyrrhinus	vittatus	0
Phyllostomidae	Pygoderma	bilabiatum	2
Phyllostomidae	Sphaeronycteris	toxophyllum	0
Phyllostomidae	Stenoderma	rufum	2
Phyllostomidae	Uroderma	bilobatum	3
Phyllostomidae	Uroderma	magnirostrum	0
Phyllostomidae	Vampyressa	bidens	0
Phyllostomidae	Vampyressa	brocki	0
Phyllostomidae	Vampyressa	melissa	0
Phyllostomidae	Vampyressa	nymphaea	0
Phyllostomidae	Vampyressa	pusilla	0
Phyllostomidae	Vampyressa	thyone	0
Phyllostomidae	Vampyrodes	caraccioli	2
Mormoopidae	Mormoops	blainvillei	0
Mormoopidae	Mormoops	magna	0
Mormoopidae	Mormoops	megalophylla	4
Mormoopidae	Pteronotus	davyi	3
Mormoopidae	Pteronotus	gymnonotus	0
Mormoopidae	Pteronotus	macleayii	2
Mormoopidae	Pteronotus	parnellii	9
Mormoopidae	Pteronotus	personatus	2
Mormoopidae	Pteronotus	pristinus	0
Mormoopidae	Pteronotus	quadridens	2
Noctilionidae	Noctilio	albiventris	3
Noctilionidae	Noctilio	leporinus	3
Furipteridae	Amorphochilus	schnablii	0
Furipteridae	Furipterus	horrens	0
Thyropteridae	Thyroptera	discifera	2
Thyropteridae	Thyroptera	lavali	0
Thyropteridae	Thyroptera	tricolor	3
Natalidae	Chilonatalus	micropus	3
Natalidae	Chilonatalus	tumidifrons	0
Natalidae	Natalus	jamaicensis	0
Natalidae	Natalus	major	0
Natalidae	Natalus	primus	0
Natalidae	Natalus	stramineus	6
Natalidae	Natalus	tumidirostris	3
Natalidae	Nyctiellus	lepidus	0
Molossidae	Tomopeas	ravus	0
Molossidae	Chaerephon	aloysiisabaudiae	0
Molossidae	Chaerephon	ansorgei	0
Molossidae	Chaerephon	bemmeleni	2

Molossidae	Chaerephon	bivittatus	0
Molossidae	Chaerephon	bregullae	0
Molossidae	Chaerephon	chapini	2
Molossidae	Chaerephon	gallagheri	0
Molossidae	Chaerephon	jobensis	2
Molossidae	Chaerephon	johorensis	0
Molossidae	Chaerephon	leucogaster	0
Molossidae	Chaerephon	major	0
Molossidae	Chaerephon	nigeriae	2
Molossidae	Chaerephon	plicatus	5
Molossidae	Chaerephon	pumilus	0
Molossidae	Chaerephon	russatus	0
Molossidae	Chaerephon	shortridgei	0
Molossidae	Chaerephon	solomonis	0
Molossidae	Chaerephon	tomensis	0
Molossidae	Cheiromeles	parvidens	0
Molossidae	Cheiromeles	torquatus	3
Molossidae	Cynomops	abrasus	4
Molossidae	Cynomops	greenhalli	0
Molossidae	Cynomops	mexicanus	0
Molossidae	Cynomops	paranus	0
Molossidae	Cynomops	planirostris	0
Molossidae	Eumops	auripendulus	2
Molossidae	Eumops	bonariensis	3
Molossidae	Eumops	dabbenei	0
Molossidae	Eumops	glaucinus	2
Molossidae	Eumops	hansae	0
Molossidae	Eumops	maurus	0
Molossidae	Eumops	patagonicus	2
Molossidae	Eumops	perotis	3
Molossidae	Eumops	trumbulli	0
Molossidae	Eumops	underwoodi	2
Molossidae	Molossops	aequatorianus	0
Molossidae	Molossops	mattogrossensis	0
Molossidae	Molossops	neglectus	0
Molossidae	Molossops	temminckii	3
Molossidae	Molossus	aztecus	0
Molossidae	Molossus	barnesi	0
Molossidae	Molossus	coibensis	0
Molossidae	Molossus	currentium	3
Molossidae	Molossus	molossus	7
Molossidae	Molossus	pretiosus	0

Molossidae	Molossus	rufus	0
Molossidae	Molossus	sinaloae	2
Molossidae	Mops	brachypterus	2
Molossidae	Mops	condylurus	4
Molossidae	Mops	congicus	0
Molossidae	Mops	demonstrator	0
Molossidae	Mops	leucostigma	0
Molossidae	Mops	midas	2
Molossidae	Mops	mops	0
Molossidae	Mops	nanulus	0
Molossidae	Mops	niangarae	0
Molossidae	Mops	niveiventer	0
Molossidae	Mops	petersoni	0
Molossidae	Mops	sarasinorum	2
Molossidae	Mops	spurrelli	0
Molossidae	Mops	thersites	0
Molossidae	Mops	trevori	0
Molossidae	Mormopterus	acetabulosus	0
Molossidae	Mormopterus	beccarii	2
Molossidae	Mormopterus	doriae	0
Molossidae	Mormopterus	jugularis	0
Molossidae	Mormopterus	kalinowskii	0
Molossidae	Mormopterus	loriae	3
Molossidae	Mormopterus	minutus	0
Molossidae	Mormopterus	norfolkensis	0
Molossidae	Mormopterus	phrudus	0
Molossidae	Mormopterus	planiceps	0
Molossidae	Myopterus	daubentonii	2
Molossidae	Myopterus	whitleyi	0
Molossidae	Nyctinomops	aurispinosus	0
Molossidae	Nyctinomops	femorosaccus	0
Molossidae	Nyctinomops	laticaudatus	5
Molossidae	Nyctinomops	macrotis	0
Molossidae	Otomops	formosus	0
Molossidae	Otomops	johnstonei	0
Molossidae	Otomops	madagascariensis	0
Molossidae	Otomops	martiensseni	2
Molossidae	Otomops	papuensis	0
Molossidae	Otomops	secundus	0
Molossidae	Otomops	wroughtoni	0
Molossidae	Platymops	setiger	2
Molossidae	Promops	centralis	3

Molossidae	Promops	nasutus	5
Molossidae	Sauromys	petrophilus	5
Molossidae	Tadarida	aegyptiaca	5
Molossidae	Tadarida	australis	0
Molossidae	Tadarida	brasiliensis	9
Molossidae	Tadarida	fulminans	2
Molossidae	Tadarida	insignis	0
Molossidae	Tadarida	kuboriensis	0
Molossidae	Tadarida	latouchei	0
Molossidae	Tadarida	lobata	0
Molossidae	Tadarida	teniotis	2
Molossidae	Tadarida	ventralis	2
Vespertilionidae	Arielulus	aureocollaris	0
Vespertilionidae	Arielulus	circumdatus	0
Vespertilionidae	Arielulus	cuprosus	0
Vespertilionidae	Arielulus	societatis	0
Vespertilionidae	Arielulus	torquatus	0
Vespertilionidae	Eptesicus	andinus	0
Vespertilionidae	Eptesicus	bobrinskoi	0
Vespertilionidae	Eptesicus	bottae	7
Vespertilionidae	Eptesicus	brasiliensis	4
Vespertilionidae	Eptesicus	chiriquinus	0
Vespertilionidae	Eptesicus	diminutus	2
Vespertilionidae	Eptesicus	dimissus	0
Vespertilionidae	Eptesicus	floweri	0
Vespertilionidae	Eptesicus	furinalis	4
Vespertilionidae	Eptesicus	fuscus	12
Vespertilionidae	Eptesicus	gobiensis	3
Vespertilionidae	Eptesicus	guadeloupensis	0
Vespertilionidae	Eptesicus	hottentotus	3
Vespertilionidae	Eptesicus	innoxius	0
Vespertilionidae	Eptesicus	japonensis	0
Vespertilionidae	Eptesicus	kobayashii	0
Vespertilionidae	Eptesicus	matroka	0
Vespertilionidae	Eptesicus	nasutus	4
Vespertilionidae	Eptesicus	nilssonii	2
Vespertilionidae	Eptesicus	pachyotis	0
Vespertilionidae	Eptesicus	platyops	0
Vespertilionidae	Eptesicus	serotinus	10
Vespertilionidae	Eptesicus	tatei	0
Vespertilionidae	Hesperoptenus	blanfordi	0
Vespertilionidae	Hesperoptenus	doriae	0

Vespertilionidae	Hesperoptenus	gaskelli	0
Vespertilionidae	Hesperoptenus	tickelli	0
Vespertilionidae	Hesperoptenus	tomesi	0
Vespertilionidae	Lasiurus	atratus	0
Vespertilionidae	Lasiurus	blossevillii	4
Vespertilionidae	Lasiurus	borealis	0
Vespertilionidae	Lasiurus	castaneus	0
Vespertilionidae	Lasiurus	cinereus	3
Vespertilionidae	Lasiurus	degelidus	0
Vespertilionidae	Lasiurus	ebenus	0
Vespertilionidae	Lasiurus	ega	5
Vespertilionidae	Lasiurus	egregius	0
Vespertilionidae	Lasiurus	insularis	0
Vespertilionidae	Lasiurus	intermedius	2
Vespertilionidae	Lasiurus	minor	0
Vespertilionidae	Lasiurus	pfeifferi	0
Vespertilionidae	Lasiurus	salinae	0
Vespertilionidae	Lasiurus	seminolus	0
Vespertilionidae	Lasiurus	varius	0
Vespertilionidae	Lasiurus	xanthinus	0
Vespertilionidae	Nycticeinops	schlieffeni	0
Vespertilionidae	Nycticeius	aenobarbus	0
Vespertilionidae	Nycticeius	cubanus	0
Vespertilionidae	Nycticeius	humeralis	3
Vespertilionidae	Rhogeessa	aeneus	0
Vespertilionidae	Rhogeessa	alleni	0
Vespertilionidae	Rhogeessa	genowaysi	0
Vespertilionidae	Rhogeessa	gracilis	0
Vespertilionidae	Rhogeessa	hussoni	0
Vespertilionidae	Rhogeessa	io	0
Vespertilionidae	Rhogeessa	minutilla	0
Vespertilionidae	Rhogeessa	mira	0
Vespertilionidae	Rhogeessa	parvula	0
Vespertilionidae	Rhogeessa	tumida	0
Vespertilionidae	Scoteanax	rueppellii	0
Vespertilionidae	Scotoecus	albigula	0
Vespertilionidae	Scotoecus	albofuscus	2
Vespertilionidae	Scotoecus	hindei	2
Vespertilionidae	Scotoecus	hirundo	0
Vespertilionidae	Scotoecus	pallidus	0
Vespertilionidae	Scotomanes	ornatus	3
Vespertilionidae	Scotophilus	borbonicus	0

Vespertilionidae	Scotophilus	celebensis	0
Vespertilionidae	Scotophilus	collinus	0
Vespertilionidae	Scotophilus	dinganii	4
Vespertilionidae	Scotophilus	heathii	3
Vespertilionidae	Scotophilus	kuhlii	7
Vespertilionidae	Scotophilus	leucogaster	2
Vespertilionidae	Scotophilus	nigrita	2
Vespertilionidae	Scotophilus	nucella	0
Vespertilionidae	Scotophilus	nux	0
Vespertilionidae	Scotophilus	robustus	0
Vespertilionidae	Scotophilus	viridis	2
Vespertilionidae	Scotorepens	balstoni	2
Vespertilionidae	Scotorepens	greyii	0
Vespertilionidae	Scotorepens	orion	0
Vespertilionidae	Scotorepens	sanborni	0
Vespertilionidae	Nyctophilus	arnhemensis	0
Vespertilionidae	Nyctophilus	bifax	2
Vespertilionidae	Nyctophilus	geoffroyi	3
Vespertilionidae	Nyctophilus	gouldi	0
Vespertilionidae	Nyctophilus	heran	0
Vespertilionidae	Nyctophilus	howensis	0
Vespertilionidae	Nyctophilus	microdon	0
Vespertilionidae	Nyctophilus	microtis	0
Vespertilionidae	Nyctophilus	nebulosus	0
Vespertilionidae	Nyctophilus	timoriensis	3
Vespertilionidae	Nyctophilus	walkeri	0
Vespertilionidae	Pharotis	imogene	0
Vespertilionidae	Glischropus	javanus	0
Vespertilionidae	Glischropus	tylopus	2
Vespertilionidae	Nyctalus	aviator	0
Vespertilionidae	Nyctalus	azoreum	0
Vespertilionidae	Nyctalus	furvus	0
Vespertilionidae	Nyctalus	lasiopterus	0
Vespertilionidae	Nyctalus	leisleri	2
Vespertilionidae	Nyctalus	montanus	0
Vespertilionidae	Nyctalus	noctula	4
Vespertilionidae	Nyctalus	plancyi	2
Vespertilionidae	Pipistrellus	abramus	0
Vespertilionidae	Pipistrellus	adamsi	0
Vespertilionidae	Pipistrellus	aero	0
Vespertilionidae	Pipistrellus	angulatus	2
Vespertilionidae	Pipistrellus	ceylonicus	7

Vespertilionidae	Pipistrellus	collinus	0
Vespertilionidae	Pipistrellus	coromandra	0
Vespertilionidae	Pipistrellus	deserti	0
Vespertilionidae	Pipistrellus	endoi	0
Vespertilionidae	Pipistrellus	hesperidus	3
Vespertilionidae	Pipistrellus	hesperus	2
Vespertilionidae	Pipistrellus	inexspectatus	0
Vespertilionidae	Pipistrellus	javanicus	5
Vespertilionidae	Pipistrellus	kuhlii	3
Vespertilionidae	Pipistrellus	maderensis	0
Vespertilionidae	Pipistrellus	minahassae	0
Vespertilionidae	Pipistrellus	nanulus	0
Vespertilionidae	Pipistrellus	nathusii	0
Vespertilionidae	Pipistrellus	papuanus	0
Vespertilionidae	Pipistrellus	paterculus	2
Vespertilionidae	Pipistrellus	permixtus	0
Vespertilionidae	Pipistrellus	pipistrellus	2
Vespertilionidae	Pipistrellus	pygmaeus	0
Vespertilionidae	Pipistrellus	rueppellii	6
Vespertilionidae	Pipistrellus	rusticus	2
Vespertilionidae	Pipistrellus	stenopterus	0
Vespertilionidae	Pipistrellus	sturdeei	0
Vespertilionidae	Pipistrellus	subflavus	4
Vespertilionidae	Pipistrellus	tenuis	8
Vespertilionidae	Pipistrellus	wattsi	0
Vespertilionidae	Pipistrellus	westralis	0
Vespertilionidae	Scotozous	dormeri	0
Vespertilionidae	Barbastella	barbastellus	2
Vespertilionidae	Barbastella	leucomelas	2
Vespertilionidae	Corynorhinus	mexicanus	0
Vespertilionidae	Corynorhinus	rafinesquii	2
Vespertilionidae	Corynorhinus	townsendii	5
Vespertilionidae	Euderma	maculatum	0
Vespertilionidae	Idionycteris	phyllotis	0
Vespertilionidae	Otonycteris	hemprichii	0
Vespertilionidae	Plecotus	alpinus	0
Vespertilionidae	Plecotus	auritus	5
Vespertilionidae	Plecotus	austriacus	6
Vespertilionidae	Plecotus	balensis	0
Vespertilionidae	Plecotus	kolombatovici	0
Vespertilionidae	Plecotus	sardus	0
Vespertilionidae	Plecotus	taivanus	0

Vespertilionidae	Plecotus	teneriffae	0
Vespertilionidae	Chalinolobus	dwyeri	0
Vespertilionidae	Chalinolobus	gouldii	0
Vespertilionidae	Chalinolobus	morio	0
Vespertilionidae	Chalinolobus	neocaledonicus	0
Vespertilionidae	Chalinolobus	nigrogriseus	2
Vespertilionidae	Chalinolobus	picatus	0
Vespertilionidae	Chalinolobus	tuberculatus	0
Vespertilionidae	Eudiscopus	denticulus	0
Vespertilionidae	Falsistrellus	affinis	0
Vespertilionidae	Falsistrellus	mackenziei	0
Vespertilionidae	Falsistrellus	mordax	0
Vespertilionidae	Falsistrellus	petersi	0
Vespertilionidae	Falsistrellus	tasmaniensis	0
Vespertilionidae	Glauconycteris	alboguttata	0
Vespertilionidae	Glauconycteris	argentata	0
Vespertilionidae	Glauconycteris	beatrix	0
Vespertilionidae	Glauconycteris	curryae	0
Vespertilionidae	Glauconycteris	egeria	0
Vespertilionidae	Glauconycteris	gleni	0
Vespertilionidae	Glauconycteris	humeralis	0
Vespertilionidae	Glauconycteris	kenyacola	0
Vespertilionidae	Glauconycteris	machadoi	0
Vespertilionidae	Glauconycteris	poensis	0
Vespertilionidae	Glauconycteris	superba	0
Vespertilionidae	Glauconycteris	variegata	2
Vespertilionidae	Histiotus	alienus	0
Vespertilionidae	Histiotus	humboldti	0
Vespertilionidae	Histiotus	laephotis	0
Vespertilionidae	Histiotus	macrotus	0
Vespertilionidae	Histiotus	magellanicus	0
Vespertilionidae	Histiotus	montanus	3
Vespertilionidae	Histiotus	velatus	0
Vespertilionidae	Hypsugo	alaschanicus	0
Vespertilionidae	Hypsugo	anchietae	0
Vespertilionidae	Hypsugo	anthonyi	0
Vespertilionidae	Hypsugo	arabicus	0
Vespertilionidae	Hypsugo	ariel	0
Vespertilionidae	Hypsugo	bodenheimeri	0
Vespertilionidae	Hypsugo	cadornae	0
Vespertilionidae	Hypsugo	crassulus	0
Vespertilionidae	Hypsugo	eisentrauti	0

Vespertilionidae	Hypsugo	imbricatus	0
Vespertilionidae	Hypsugo	joffrei	0
Vespertilionidae	Hypsugo	kitcheneri	0
Vespertilionidae	Hypsugo	lophurus	0
Vespertilionidae	Hypsugo	macrotis	0
Vespertilionidae	Hypsugo	musciculus	0
Vespertilionidae	Hypsugo	pulveratus	0
Vespertilionidae	Hypsugo	savii	4
Vespertilionidae	Hypsugo	vordermanni	0
Vespertilionidae	Ia	io	0
Vespertilionidae	Laephotis	angolensis	0
Vespertilionidae	Laephotis	botswanae	0
Vespertilionidae	Laephotis	namibensis	0
Vespertilionidae	Laephotis	wintoni	0
Vespertilionidae	Mimetillus	moloneyi	2
Vespertilionidae	Neoromicia	brunneus	0
Vespertilionidae	Neoromicia	capensis	7
Vespertilionidae	Neoromicia	flavescens	0
Vespertilionidae	Neoromicia	guineensis	2
Vespertilionidae	Neoromicia	helios	0
Vespertilionidae	Neoromicia	melckorum	0
Vespertilionidae	Neoromicia	nanus	6
Vespertilionidae	Neoromicia	rendalli	2
Vespertilionidae	Neoromicia	somalicus	4
Vespertilionidae	Neoromicia	tenuipinnis	2
Vespertilionidae	Neoromicia	zuluensis	0
Vespertilionidae	Philetor	brachypterus	0
Vespertilionidae	Tylonycteris	pachypus	5
Vespertilionidae	Tylonycteris	robustula	2
Vespertilionidae	Vespadelus	baverstocki	0
Vespertilionidae	Vespadelus	caurinus	0
Vespertilionidae	Vespadelus	darlingtoni	0
Vespertilionidae	Vespadelus	douglasorum	0
Vespertilionidae	Vespadelus	finlaysoni	0
Vespertilionidae	Vespadelus	pumilus	0
Vespertilionidae	Vespadelus	regulus	0
Vespertilionidae	Vespadelus	troughtoni	0
Vespertilionidae	Vespadelus	vulturnus	0
Vespertilionidae	Vespertilio	murinus	2
Vespertilionidae	Vespertilio	sinensis	5
Vespertilionidae	Antrozous	pallidus	7
Vespertilionidae	Bauerus	dubiaquercus	0

Vespertilionidae	Cistugo	lesueuri	0
Vespertilionidae	Cistugo	seabrae	0
Vespertilionidae	Lasionycteris	noctivagans	0
Vespertilionidae	Myotis	abei	0
Vespertilionidae	Myotis	adversus	6
Vespertilionidae	Myotis	aelleni	0
Vespertilionidae	Myotis	albescens	0
Vespertilionidae	Myotis	alcathoe	0
Vespertilionidae	Myotis	altarium	0
Vespertilionidae	Myotis	anjouanensis	0
Vespertilionidae	Myotis	annamiticus	0
Vespertilionidae	Myotis	annectans	0
Vespertilionidae	Myotis	atacamensis	0
Vespertilionidae	Myotis	ater	2
Vespertilionidae	Myotis	auriculus	2
Vespertilionidae	Myotis	australis	0
Vespertilionidae	Myotis	austroriparius	0
Vespertilionidae	Myotis	bechsteinii	0
Vespertilionidae	Myotis	blythii	4
Vespertilionidae	Myotis	bocagii	3
Vespertilionidae	Myotis	bombinus	2
Vespertilionidae	Myotis	brandtii	2
Vespertilionidae	Myotis	bucharensis	0
Vespertilionidae	Myotis	californicus	4
Vespertilionidae	Myotis	capaccinii	0
Vespertilionidae	Myotis	chiloensis	0
Vespertilionidae	Myotis	chinensis	0
Vespertilionidae	Myotis	ciliolabrum	0
Vespertilionidae	Myotis	cobanensis	0
Vespertilionidae	Myotis	csorbai	0
Vespertilionidae	Myotis	dasycneme	0
Vespertilionidae	Myotis	daubentonii	7
Vespertilionidae	Myotis	davidii	0
Vespertilionidae	Myotis	dominicensis	0
Vespertilionidae	Myotis	elegans	0
Vespertilionidae	Myotis	emarginatus	3
Vespertilionidae	Myotis	evotis	6
Vespertilionidae	Myotis	fimbriatus	0
Vespertilionidae	Myotis	findleyi	0
Vespertilionidae	Myotis	formosus	7
Vespertilionidae	Myotis	fortidens	2
Vespertilionidae	Myotis	frater	4

Vespertilionidae	Myotis	gomantongensis	0
Vespertilionidae	Myotis	goudoti	0
Vespertilionidae	Myotis	grisescens	0
Vespertilionidae	Myotis	hajastanicus	0
Vespertilionidae	Myotis	hasseltii	4
Vespertilionidae	Myotis	hermani	0
Vespertilionidae	Myotis	horsfieldii	5
Vespertilionidae	Myotis	hosonoi	0
Vespertilionidae	Myotis	ikonnikovi	0
Vespertilionidae	Myotis	insularum	0
Vespertilionidae	Myotis	keaysi	2
Vespertilionidae	Myotis	keenii	0
Vespertilionidae	Myotis	laniger	0
Vespertilionidae	Myotis	leibii	0
Vespertilionidae	Myotis	levis	2
Vespertilionidae	Myotis	longipes	0
Vespertilionidae	Myotis	lucifugus	5
Vespertilionidae	Myotis	macrodactylus	3
Vespertilionidae	Myotis	macropus	0
Vespertilionidae	Myotis	macrotarsus	2
Vespertilionidae	Myotis	martiniquensis	2
Vespertilionidae	Myotis	melanorhinus	0
Vespertilionidae	Myotis	moluccarum	3
Vespertilionidae	Myotis	montivagus	4
Vespertilionidae	Myotis	morrisi	0
Vespertilionidae	Myotis	muricola	8
Vespertilionidae	Myotis	myotis	2
Vespertilionidae	Myotis	mystacinus	3
Vespertilionidae	Myotis	nattereri	2
Vespertilionidae	Myotis	nesopolus	2
Vespertilionidae	Myotis	nigricans	4
Vespertilionidae	Myotis	nipalensis	3
Vespertilionidae	Myotis	occultus	0
Vespertilionidae	Myotis	oreias	0
Vespertilionidae	Myotis	oxygnathus	0
Vespertilionidae	Myotis	oxyotus	2
Vespertilionidae	Myotis	ozensis	0
Vespertilionidae	Myotis	peninsularis	0
Vespertilionidae	Myotis	pequinius	0
Vespertilionidae	Myotis	planiceps	0
Vespertilionidae	Myotis	pruinosus	0
Vespertilionidae	Myotis	punicus	0

Vespertilionidae	Myotis	ricketti	0
Vespertilionidae	Myotis	ridleyi	0
Vespertilionidae	Myotis	riparius	0
Vespertilionidae	Myotis	rosseti	0
Vespertilionidae	Myotis	ruber	0
Vespertilionidae	Myotis	schaubi	2
Vespertilionidae	Myotis	scotti	0
Vespertilionidae	Myotis	septentrionalis	0
Vespertilionidae	Myotis	sicarius	0
Vespertilionidae	Myotis	siligorensis	4
Vespertilionidae	Myotis	simus	0
Vespertilionidae	Myotis	sodalis	0
Vespertilionidae	Myotis	stalkeri	0
Vespertilionidae	Myotis	thysanodes	4
Vespertilionidae	Myotis	tricolor	0
Vespertilionidae	Myotis	velifer	5
Vespertilionidae	Myotis	vivesi	0
Vespertilionidae	Myotis	volans	4
Vespertilionidae	Myotis	welwitschii	0
Vespertilionidae	Myotis	yanbarensis	0
Vespertilionidae	Myotis	yesoensis	0
Vespertilionidae	Myotis	yumanensis	6
Vespertilionidae	Miniopterus	africanus	0
Vespertilionidae	Miniopterus	australis	3
Vespertilionidae	Miniopterus	fraterculus	0
Vespertilionidae	Miniopterus	fuscus	0
Vespertilionidae	Miniopterus	gleni	0
Vespertilionidae	Miniopterus	inflatus	2
Vespertilionidae	Miniopterus	macrocneme	0
Vespertilionidae	Miniopterus	magnater	2
Vespertilionidae	Miniopterus	majori	0
Vespertilionidae	Miniopterus	manavi	2
Vespertilionidae	Miniopterus	medius	0
Vespertilionidae	Miniopterus	minor	3
Vespertilionidae	Miniopterus	natalensis	2
Vespertilionidae	Miniopterus	paululus	3
Vespertilionidae	Miniopterus	pusillus	0
Vespertilionidae	Miniopterus	robustior	0
Vespertilionidae	Miniopterus	schreibersii	16
Vespertilionidae	Miniopterus	shortridgei	0
Vespertilionidae	Miniopterus	tristis	5
Vespertilionidae	Harpiocephalus	harpia	4

Vespertilionidae	Harpiocephalus	mordax	0
Vespertilionidae	Murina	aenea	0
Vespertilionidae	Murina	aurata	0
Vespertilionidae	Murina	cyclotis	3
Vespertilionidae	Murina	florium	3
Vespertilionidae	Murina	fusca	0
Vespertilionidae	Murina	grisea	0
Vespertilionidae	Murina	hilgendorfi	0
Vespertilionidae	Murina	huttoni	2
Vespertilionidae	Murina	leucogaster	2
Vespertilionidae	Murina	puta	0
Vespertilionidae	Murina	rozendaali	0
Vespertilionidae	Murina	ryukyuana	0
Vespertilionidae	Murina	silvatica	0
Vespertilionidae	Murina	suilla	2
Vespertilionidae	Murina	tenebrosa	0
Vespertilionidae	Murina	tubinaris	0
Vespertilionidae	Murina	ussuriensis	0
Vespertilionidae	Kerivoula	africana	0
Vespertilionidae	Kerivoula	agnella	0
Vespertilionidae	Kerivoula	argentata	3
Vespertilionidae	Kerivoula	cuprosa	0
Vespertilionidae	Kerivoula	eriophora	0
Vespertilionidae	Kerivoula	flora	0
Vespertilionidae	Kerivoula	hardwickii	0
Vespertilionidae	Kerivoula	intermedia	0
Vespertilionidae	Kerivoula	lanosa	4
Vespertilionidae	Kerivoula	lenis	0
Vespertilionidae	Kerivoula	minuta	0
Vespertilionidae	Kerivoula	muscina	0
Vespertilionidae	Kerivoula	myrella	0
Vespertilionidae	Kerivoula	papillosa	2
Vespertilionidae	Kerivoula	pellucida	0
Vespertilionidae	Kerivoula	phalaena	0
Vespertilionidae	Kerivoula	picta	2
Vespertilionidae	Kerivoula	smithii	0
Vespertilionidae	Kerivoula	whiteheadi	3
Vespertilionidae	Phoniscus	aerosa	0
Vespertilionidae	Phoniscus	atrox	0
Vespertilionidae	Phoniscus	jagorii	0
Vespertilionidae	Phoniscus	papuensis	0
Manidae	Manis	crassicaudata	0

Manidae	Manis	culionensis	0
Manidae	Manis	gigantea	0
Manidae	Manis	javanica	0
Manidae	Manis	pentadactyla	3
Manidae	Manis	temminckii	0
Manidae	Manis	tetradactyla	0
Manidae	Manis	tricuspis	2
Felidae	Acinonyx	jubatus	6
Felidae	Caracal	caracal	8
Felidae	Catopuma	badia	0
Felidae	Catopuma	temminckii	3
Felidae	Felis	bieti	0
Felidae	Felis	catus	0
Felidae	Felis	chaus	10
Felidae	Felis	manul	3
Felidae	Felis	margarita	6
Felidae	Felis	nigripes	2
Felidae	Felis	silvestris	22
Felidae	Leopardus	braccatus	2
Felidae	Leopardus	colocolo	2
Felidae	Leopardus	geoffroyi	5
Felidae	Leopardus	guigna	2
Felidae	Leopardus	jacobitus	0
Felidae	Leopardus	pajeros	5
Felidae	Leopardus	pardalis	10
Felidae	Leopardus	tigrinus	4
Felidae	Leopardus	wiedii	11
Felidae	Leptailurus	serval	18
Felidae	Lynx	canadensis	3
Felidae	Lynx	lynx	5
Felidae	Lynx	pardinus	0
Felidae	Lynx	rufus	12
Felidae	Pardofelis	marmorata	2
Felidae	Prionailurus	bengalensis	11
Felidae	Prionailurus	iriomotensis	0
Felidae	Prionailurus	planiceps	0
Felidae	Prionailurus	rubiginosus	2
Felidae	Prionailurus	viverrinus	0
Felidae	Profelis	aurata	2
Felidae	Puma	concolor	6
Felidae	Puma	yagouaroundi	8
Felidae	Neofelis	nebulosa	4

Felidae	Panthera	leo	11
Felidae	Panthera	onca	9
Felidae	Panthera	pardus	8
Felidae	Panthera	tigris	8
Felidae	Uncia	uncia	0
Viverridae	Arctictis	binturong	6
Viverridae	Arctogalidia	trivirgata	14
Viverridae	Macrogalidia	musschenbroekii	0
Viverridae	Paguma	larvata	16
Viverridae	Paradoxurus	hermaphroditus	30
Viverridae	Paradoxurus	jerdoni	2
Viverridae	Paradoxurus	zeylonensis	0
Viverridae	Chrotogale	owstoni	0
Viverridae	Cynogale	bennettii	2
Viverridae	Diplogale	hosei	0
Viverridae	Hemigalus	derbyanus	4
Viverridae	Prionodon	linsang	3
Viverridae	Prionodon	pardicolor	2
Viverridae	Civettictis	civetta	6
Viverridae	Genetta	abyssinica	0
Viverridae	Genetta	angolensis	0
Viverridae	Genetta	bourloni	0
Viverridae	Genetta	cristata	0
Viverridae	Genetta	genetta	5
Viverridae	Genetta	johnstoni	0
Viverridae	Genetta	maculata	0
Viverridae	Genetta	pardina	0
Viverridae	Genetta	piscivora	0
Viverridae	Genetta	poensis	0
Viverridae	Genetta	servalina	5
Viverridae	Genetta	thierryi	0
Viverridae	Genetta	tigrina	2
Viverridae	Genetta	victoriae	0
Viverridae	Poiana	leightoni	0
Viverridae	Poiana	richardsonii	2
Viverridae	Viverra	civettina	0
Viverridae	Viverra	megaspila	0
Viverridae	Viverra	tangalunga	2
Viverridae	Viverra	zibetha	5
Viverridae	Viverricula	indica	12
Eupleridae	Cryptoprocta	ferox	0
Eupleridae	Eupleres	goudotii	2

Eupleridae	Fossa	fossana	0
Eupleridae	Galidia	elegans	3
Eupleridae	Galidictis	fasciata	2
Eupleridae	Galidictis	grandidieri	0
Eupleridae	Mungotictis	decemlineata	2
Eupleridae	Salanoia	concolor	0
Nandiniidae	Nandinia	binotata	4
Herpestidae	Atilax	paludinosus	11
Herpestidae	Bdeogale	crassicauda	5
Herpestidae	Bdeogale	jacksoni	0
Herpestidae	Bdeogale	nigripes	0
Herpestidae	Crossarchus	alexandri	0
Herpestidae	Crossarchus	ansorgei	2
Herpestidae	Crossarchus	obscurus	0
Herpestidae	Crossarchus	platycephalus	0
Herpestidae	Cynictis	penicillata	12
Herpestidae	Dologale	dybowskii	0
Herpestidae	Galerella	flavescens	0
Herpestidae	Galerella	ochracea	4
Herpestidae	Galerella	pulverulenta	3
Herpestidae	Galerella	sanguinea	26
Herpestidae	Helogale	hirtula	5
Herpestidae	Helogale	parvula	7
Herpestidae	Herpestes	brachyurus	6
Herpestidae	Herpestes	edwardsi	5
Herpestidae	Herpestes	fuscus	5
Herpestidae	Herpestes	ichneumon	11
Herpestidae	Herpestes	javanicus	12
Herpestidae	Herpestes	naso	0
Herpestidae	Herpestes	semitorquatus	2
Herpestidae	Herpestes	smithii	3
Herpestidae	Herpestes	urva	4
Herpestidae	Herpestes	vitticollis	2
Herpestidae	Ichneumia	albicauda	7
Herpestidae	Liberiictis	kuhni	0
Herpestidae	Mungos	gambianus	0
Herpestidae	Mungos	mungo	16
Herpestidae	Paracynictis	selousi	4
Herpestidae	Rhynchogale	melleri	2
Herpestidae	Suricata	suricatta	3
Hyaenidae	Crocuta	crocuta	0
Hyaenidae	Hyaena	brunnea	0

Hyaenidae	Hyaena	hyaena	0
Hyaenidae	Proteles	cristata	0
Canidae	Atelocynus	microtis	2
Canidae	Canis	adustus	6
Canidae	Canis	aureus	13
Canidae	Canis	latrans	19
Canidae	Canis	lupus	37
Canidae	Canis	mesomelas	2
Canidae	Canis	simensis	2
Canidae	Cerdocyon	thous	6
Canidae	Chrysocyon	brachyurus	0
Canidae	Cuon	alpinus	3
Canidae	Dusicyon	australis	0
Canidae	Lycalopex	culpaeus	6
Canidae	Lycalopex	fulvipes	0
Canidae	Lycalopex	griseus	0
Canidae	Lycalopex	gymnocercus	5
Canidae	Lycalopex	sechurae	0
Canidae	Lycalopex	vetulus	0
Canidae	Lycaon	pictus	5
Canidae	Nyctereutes	procyonoides	5
Canidae	Otocyon	megalotis	2
Canidae	Speothos	venaticus	3
Canidae	Urocyon	cinereoargenteus	16
Canidae	Urocyon	littoralis	6
Canidae	Vulpes	bengalensis	0
Canidae	Vulpes	cana	0
Canidae	Vulpes	chama	0
Canidae	Vulpes	corsac	2
Canidae	Vulpes	ferrilata	0
Canidae	Vulpes	lagopus	4
Canidae	Vulpes	macrotis	0
Canidae	Vulpes	pallida	5
Canidae	Vulpes	rueppellii	5
Canidae	Vulpes	velox	0
Canidae	Vulpes	vulpes	45
Canidae	Vulpes	zerda	0
Ursidae	Ailuropoda	melanoleuca	0
Ursidae	Helarctos	malayanus	2
Ursidae	Melursus	ursinus	2
Ursidae	Tremarctos	ornatus	0
Ursidae	Ursus	americanus	16

Ursidae	Ursus	arctos	16
Ursidae	Ursus	maritimus	0
Ursidae	Ursus	thibetanus	7
Otariidae	Arctocephalus	australis	0
Otariidae	Arctocephalus	forsteri	0
Otariidae	Arctocephalus	galapagoensis	0
Otariidae	Arctocephalus	gazella	0
Otariidae	Arctocephalus	philippii	0
Otariidae	Arctocephalus	pusillus	2
Otariidae	Arctocephalus	townsendi	0
Otariidae	Arctocephalus	tropicalis	0
Otariidae	Callorhinus	ursinus	0
Otariidae	Eumetopias	jubatus	0
Otariidae	Neophoca	cinerea	0
Otariidae	Otaria	flavescens	0
Otariidae	Phocarctos	hookeri	0
Otariidae	Zalophus	californianus	0
Otariidae	Zalophus	japonicus	0
Otariidae	Zalophus	wollebaeki	0
Odobenidae	Odobenus	rosmarus	3
Phocidae	Cystophora	cristata	0
Phocidae	Erignathus	barbatus	2
Phocidae	Halichoerus	grypus	2
Phocidae	Histriophoca	fasciata	0
Phocidae	Hydrurga	leptonyx	0
Phocidae	Leptonychotes	weddellii	0
Phocidae	Lobodon	carcinophaga	0
Phocidae	Mirounga	angustirostris	0
Phocidae	Mirounga	leonina	0
Phocidae	Monachus	monachus	0
Phocidae	Monachus	schauinslandi	0
Phocidae	Monachus	tropicalis	0
Phocidae	Ommatophoca	rossii	0
Phocidae	Pagophilus	groenlandicus	0
Phocidae	Phoca	largha	0
Phocidae	Phoca	vitulina	5
Phocidae	Pusa	caspica	0
Phocidae	Pusa	hispida	5
Phocidae	Pusa	sibirica	0
Mustelidae	Aonyx	capensis	6
Mustelidae	Aonyx	cinerea	3
Mustelidae	Enhydra	lutris	3

Mustelidae	Hydrictis	maculicollis	0
Mustelidae	Lontra	canadensis	7
Mustelidae	Lontra	felina	0
Mustelidae	Lontra	longicaudis	3
Mustelidae	Lontra	provocax	0
Mustelidae	Lutra	lutra	11
Mustelidae	Lutra	nippon	0
Mustelidae	Lutra	sumatrana	0
Mustelidae	Lutrogale	perspicillata	2
Mustelidae	Pteronura	brasiliensis	2
Mustelidae	Arctonyx	collaris	6
Mustelidae	Eira	barbara	9
Mustelidae	Galictis	cuja	4
Mustelidae	Galictis	vittata	4
Mustelidae	Gulo	gulo	6
Mustelidae	Ictonyx	libyca	4
Mustelidae	Ictonyx	striatus	19
Mustelidae	Lyncodon	patagonicus	2
Mustelidae	Martes	americana	13
Mustelidae	Martes	flavigula	9
Mustelidae	Martes	foina	11
Mustelidae	Martes	gwatkinsii	0
Mustelidae	Martes	martes	8
Mustelidae	Martes	melampus	3
Mustelidae	Martes	pennanti	3
Mustelidae	Martes	zibellina	16
Mustelidae	Meles	anakuma	0
Mustelidae	Meles	leucurus	5
Mustelidae	Meles	meles	8
Mustelidae	Mellivora	capensis	12
Mustelidae	Melogale	everetti	0
Mustelidae	Melogale	moschata	7
Mustelidae	Melogale	orientalis	2
Mustelidae	Melogale	personata	5
Mustelidae	Mustela	africana	2
Mustelidae	Mustela	altaica	4
Mustelidae	Mustela	erminea	37
Mustelidae	Mustela	eversmanii	7
Mustelidae	Mustela	felipei	0
Mustelidae	Mustela	frenata	42
Mustelidae	Mustela	itatsi	0
Mustelidae	Mustela	kathiah	2

Mustelidae	Mustela	lutreola	7
Mustelidae	Mustela	lutreolina	0
Mustelidae	Mustela	nigripes	0
Mustelidae	Mustela	nivalis	18
Mustelidae	Mustela	nudipes	2
Mustelidae	Mustela	putorius	7
Mustelidae	Mustela	sibirica	11
Mustelidae	Mustela	strigidorsa	0
Mustelidae	Mustela	subpalmata	0
Mustelidae	Neovison	macrodon	0
Mustelidae	Neovison	vison	15
Mustelidae	Poecilogale	albinucha	5
Mustelidae	Taxidea	taxus	5
Mustelidae	Vormela	peregusna	5
Mephitidae	Conepatus	chinga	7
Mephitidae	Conepatus	humboldtii	3
Mephitidae	Conepatus	leuconotus	3
Mephitidae	Conepatus	semistriatus	6
Mephitidae	Mephitis	macroura	4
Mephitidae	Mephitis	mephitis	13
Mephitidae	Mydaus	javanensis	3
Mephitidae	Mydaus	marchei	0
Mephitidae	Spilogale	angustifrons	5
Mephitidae	Spilogale	gracilis	7
Mephitidae	Spilogale	putorius	3
Mephitidae	Spilogale	pygmaea	3
Procyonidae	Bassaricyon	alleni	0
Procyonidae	Bassaricyon	beddardi	0
Procyonidae	Bassaricyon	gabbii	0
Procyonidae	Bassaricyon	lasius	0
Procyonidae	Bassaricyon	pauli	0
Procyonidae	Bassariscus	astutus	14
Procyonidae	Bassariscus	sumichrasti	5
Procyonidae	Nasua	narica	4
Procyonidae	Nasua	nasua	13
Procyonidae	Nasuella	olivacea	3
Procyonidae	Potos	flavus	7
Procyonidae	Procyon	cancrivorus	4
Procyonidae	Procyon	lotor	22
Procyonidae	Procyon	pygmaeus	0
Ailuridae	Ailurus	fulgens	2
Equidae	Equus	asinus	3

Equidae	Equus	burchellii	6
Equidae	Equus	caballus	3
Equidae	Equus	grevyi	0
Equidae	Equus	hemionus	7
Equidae	Equus	kiang	3
Equidae	Equus	quagga	0
Equidae	Equus	zebra	2
Tapiridae	Tapirus	bairdii	0
Tapiridae	Tapirus	indicus	2
Tapiridae	Tapirus	pinchaque	0
Tapiridae	Tapirus	terrestris	4
Rhinocerotidae	Ceratotherium	simum	2
Rhinocerotidae	Dicerorhinus	sumatrensis	3
Rhinocerotidae	Diceros	bicornis	6
Rhinocerotidae	Rhinoceros	sondaicus	3
Rhinocerotidae	Rhinoceros	unicornis	0
Suidae	Babyrousa	babyrussa	0
Suidae	Babyrousa	bolabatuensis	0
Suidae	Babyrousa	celebensis	0
Suidae	Babyrousa	togeanensis	0
Suidae	Hylochoerus	meinertzhageni	3
Suidae	Phacochoerus	aethiopicus	2
Suidae	Phacochoerus	africanus	4
Suidae	Potamochoerus	larvatus	6
Suidae	Potamochoerus	porcus	0
Suidae	Sus	ahoenobarbus	0
Suidae	Sus	barbatus	2
Suidae	Sus	bucculentus	0
Suidae	Sus	cebifrons	2
Suidae	Sus	celebensis	3
Suidae	Sus	oliveri	0
Suidae	Sus	philippensis	2
Suidae	Sus	salvanius	0
Suidae	Sus	scrofa	16
Suidae	Sus	verrucosus	2
Tayassuidae	Catagonus	wagneri	0
Tayassuidae	Pecari	tajacu	14
Tayassuidae	Tayassu	pecari	5
Hippopotamidae	Hexaprotodon	liberiensis	2
Hippopotamidae	Hippopotamus	amphibius	3
Camelidae	Camelus	bactrianus	2
Camelidae	Camelus	dromedarius	0

Camelidae	Lama	glama	3
Camelidae	Vicugna	vicugna	0
Tragulidae	Hyemoschus	aquaticus	0
Tragulidae	Moschiola	meminna	0
Tragulidae	Tragulus	javanicus	0
Tragulidae	Tragulus	kanchil	30
Tragulidae	Tragulus	napu	20
Tragulidae	Tragulus	nigricans	0
Tragulidae	Tragulus	versicolor	0
Tragulidae	Tragulus	williamsoni	0
Moschidae	Moschus	anhuiensis	0
Moschidae	Moschus	berezovskii	4
Moschidae	Moschus	chrysogaster	2
Moschidae	Moschus	cupreus	0
Moschidae	Moschus	fuscus	0
Moschidae	Moschus	leucogaster	0
Moschidae	Moschus	moschiferus	5
Cervidae	Alces	alces	2
Cervidae	Alces	americanus	2
Cervidae	Blastocerus	dichotomus	0
Cervidae	Capreolus	capreolus	4
Cervidae	Capreolus	pygargus	4
Cervidae	Hippocamelus	antisensis	0
Cervidae	Hippocamelus	bisulcus	0
Cervidae	Mazama	americana	12
Cervidae	Mazama	bororo	0
Cervidae	Mazama	bricenii	0
Cervidae	Mazama	chunyi	0
Cervidae	Mazama	gouazoubira	11
Cervidae	Mazama	nana	0
Cervidae	Mazama	pandora	0
Cervidae	Mazama	rufina	0
Cervidae	Mazama	temama	3
Cervidae	Odocoileus	hemionus	10
Cervidae	Odocoileus	virginianus	38
Cervidae	Ozotoceros	bezoarticus	5
Cervidae	Pudu	mephistophiles	0
Cervidae	Pudu	puda	0
Cervidae	Rangifer	tarandus	14
Cervidae	Axis	axis	0
Cervidae	Axis	calamianensis	0
Cervidae	Axis	kuhlii	0

Cervidae	Axis	porcinus	2
Cervidae	Cervus	elaphus	18
Cervidae	Cervus	nippon	16
Cervidae	Dama	dama	2
Cervidae	Elaphodus	cephalophus	4
Cervidae	Elaphurus	davidianus	0
Cervidae	Muntiacus	atherodes	0
Cervidae	Muntiacus	crinifrons	0
Cervidae	Muntiacus	feae	0
Cervidae	Muntiacus	gongshanensis	0
Cervidae	Muntiacus	muntjak	11
Cervidae	Muntiacus	puhoatensis	0
Cervidae	Muntiacus	putaoensis	0
Cervidae	Muntiacus	reevesi	3
Cervidae	Muntiacus	rooseveltorum	0
Cervidae	Muntiacus	truongsonensis	0
Cervidae	Muntiacus	vuquangensis	0
Cervidae	Przewalskium	albirostris	0
Cervidae	Rucervus	duvaucelii	3
Cervidae	Rucervus	eldii	3
Cervidae	Rucervus	schomburgki	0
Cervidae	Rusa	alfredi	0
Cervidae	Rusa	marianna	4
Cervidae	Rusa	timorensis	7
Cervidae	Rusa	unicolor	7
Cervidae	Hydropotes	inermis	2
Antilocapridae	Antilocapra	americana	5
Giraffidae	Giraffa	camelopardalis	6
Giraffidae	Okapia	johnstoni	0
Bovidae	Aepyceros	melampus	6
Bovidae	Alcelaphus	buselaphus	6
Bovidae	Alcelaphus	caama	0
Bovidae	Alcelaphus	lichtensteinii	0
Bovidae	Beatragus	hunteri	0
Bovidae	Connochaetes	gnou	0
Bovidae	Connochaetes	taurinus	5
Bovidae	Damaliscus	korrigum	3
Bovidae	Damaliscus	lunatus	0
Bovidae	Damaliscus	pygargus	2
Bovidae	Damaliscus	superstes	0
Bovidae	Ammodorcas	clarkei	0
Bovidae	Antidorcas	marsupialis	3

Bovidae	Antilope	cervicapra	2
Bovidae	Dorcatragus	megalotis	0
Bovidae	Eudorcas	rufifrons	5
Bovidae	Eudorcas	rufina	0
Bovidae	Eudorcas	thomsonii	2
Bovidae	Gazella	arabica	2
Bovidae	Gazella	bennettii	6
Bovidae	Gazella	cuvieri	0
Bovidae	Gazella	dorcas	6
Bovidae	Gazella	erlangeri	0
Bovidae	Gazella	gazella	6
Bovidae	Gazella	leptoceros	2
Bovidae	Gazella	saudiya	0
Bovidae	Gazella	spekei	0
Bovidae	Gazella	subgutturosa	4
Bovidae	Litocranius	walleri	2
Bovidae	Madoqua	guentheri	2
Bovidae	Madoqua	kirkii	4
Bovidae	Madoqua	piacentinii	0
Bovidae	Madoqua	saltiana	5
Bovidae	Nanger	dama	3
Bovidae	Nanger	granti	5
Bovidae	Nanger	soemmerringii	3
Bovidae	Neotragus	batesi	0
Bovidae	Neotragus	moschatus	4
Bovidae	Neotragus	pygmaeus	0
Bovidae	Oreotragus	oreotragus	5
Bovidae	Ourebia	ourebi	8
Bovidae	Procapra	gutturosa	0
Bovidae	Procapra	picticaudata	0
Bovidae	Procapra	przewalskii	2
Bovidae	Raphicerus	campestris	4
Bovidae	Raphicerus	melanotis	0
Bovidae	Raphicerus	sharpei	0
Bovidae	Saiga	borealis	2
Bovidae	Saiga	tatarica	0
Bovidae	Bison	bison	0
Bovidae	Bison	bonasus	3
Bovidae	Bos	frontalis	4
Bovidae	Bos	grunniens	2
Bovidae	Bos	javanicus	2
Bovidae	Bos	sauveli	0

Bovidae	Bos	taurus	3
Bovidae	Boselaphus	tragocamelus	0
Bovidae	Bubalus	bubalis	6
Bovidae	Bubalus	depressicornis	0
Bovidae	Bubalus	mindorensis	0
Bovidae	Bubalus	quarlesi	0
Bovidae	Pseudoryx	nghetinhensis	0
Bovidae	Syncerus	caffer	5
Bovidae	Taurotragus	derbianus	2
Bovidae	Taurotragus	oryx	3
Bovidae	Tetracerus	quadricornis	3
Bovidae	Tragelaphus	angasii	0
Bovidae	Tragelaphus	buxtoni	0
Bovidae	Tragelaphus	eurycerus	0
Bovidae	Tragelaphus	imberbis	0
Bovidae	Tragelaphus	scriptus	8
Bovidae	Tragelaphus	spekii	5
Bovidae	Tragelaphus	strepsiceros	5
Bovidae	Ammotragus	lervia	6
Bovidae	Budorcas	taxicolor	4
Bovidae	Capra	caucasica	3
Bovidae	Capra	falconeri	3
Bovidae	Capra	hircus	6
Bovidae	Capra	ibex	0
Bovidae	Capra	nubiana	0
Bovidae	Capra	pyrenaica	0
Bovidae	Capra	sibirica	0
Bovidae	Capra	walie	0
Bovidae	Capricornis	crispus	0
Bovidae	Capricornis	milneedwardsii	2
Bovidae	Capricornis	rubidus	0
Bovidae	Capricornis	sumatraensis	0
Bovidae	Capricornis	swinhoei	0
Bovidae	Capricornis	thar	0
Bovidae	Hemitragus	hylocrius	0
Bovidae	Hemitragus	jayakari	0
Bovidae	Hemitragus	jemlahicus	0
Bovidae	Naemorhedus	baileyi	0
Bovidae	Naemorhedus	caudatus	0
Bovidae	Naemorhedus	goral	2
Bovidae	Naemorhedus	griseus	2
Bovidae	Oreamnos	americanus	0

Bovidae	Ovibos	moschatus	0
Bovidae	Ovis	ammon	9
Bovidae	Ovis	aries	9
Bovidae	Ovis	canadensis	6
Bovidae	Ovis	dalli	2
Bovidae	Ovis	nivicola	4
Bovidae	Pantholops	hodgsonii	0
Bovidae	Pseudois	nayaur	0
Bovidae	Pseudois	schaeferi	0
Bovidae	Rupicapra	pyrenaica	2
Bovidae	Rupicapra	rupicapra	5
Bovidae	Cephalophus	adersi	0
Bovidae	Cephalophus	brookei	0
Bovidae	Cephalophus	callipygus	0
Bovidae	Cephalophus	dorsalis	2
Bovidae	Cephalophus	jentinki	0
Bovidae	Cephalophus	leucogaster	2
Bovidae	Cephalophus	natalensis	2
Bovidae	Cephalophus	niger	0
Bovidae	Cephalophus	nigrifrons	6
Bovidae	Cephalophus	ogilbyi	2
Bovidae	Cephalophus	rufilatus	0
Bovidae	Cephalophus	silvicultor	4
Bovidae	Cephalophus	spadix	0
Bovidae	Cephalophus	weynsi	3
Bovidae	Cephalophus	zebra	0
Bovidae	Philantomba	maxwellii	2
Bovidae	Philantomba	monticola	12
Bovidae	Sylvicapra	grimmia	13
Bovidae	Addax	nasomaculatus	0
Bovidae	Hippotragus	equinus	6
Bovidae	Hippotragus	leucophaeus	0
Bovidae	Hippotragus	niger	4
Bovidae	Oryx	beisa	2
Bovidae	Oryx	dammah	0
Bovidae	Oryx	gazella	0
Bovidae	Oryx	leucoryx	0
Bovidae	Kobus	ellipsiprymnus	13
Bovidae	Kobus	kob	8
Bovidae	Kobus	leche	4
Bovidae	Kobus	megaceros	0
Bovidae	Kobus	vardonii	2

Bovidae	Pelea	capreolus	0
Bovidae	Redunca	arundinum	0
Bovidae	Redunca	fulvorufula	3
Bovidae	Redunca	redunca	7
Balaenidae	Balaena	mysticetus	0
Balaenidae	Eubalaena	australis	0
Balaenidae	Eubalaena	glacialis	0
Balaenidae	Eubalaena	japonica	0
Balaenopteridae	Balaenoptera	acutorostrata	0
Balaenopteridae	Balaenoptera	bonaerensis	0
Balaenopteridae	Balaenoptera	borealis	2
Balaenopteridae	Balaenoptera	edeni	0
Balaenopteridae	Balaenoptera	musculus	4
Balaenopteridae	Balaenoptera	physalus	2
Balaenopteridae	Megaptera	novaeangliae	0
Eschrichtiidae	Eschrichtius	robustus	0
Neobalaenidae	Caperea	marginata	0
Delphinidae	Cephalorhynchus	commersonii	0
Delphinidae	Cephalorhynchus	eutropia	0
Delphinidae	Cephalorhynchus	heavisidii	0
Delphinidae	Cephalorhynchus	hectori	2
Delphinidae	Delphinus	capensis	0
Delphinidae	Delphinus	delphis	2
Delphinidae	Feresa	attenuata	0
Delphinidae	Globicephala	macrorhynchus	0
Delphinidae	Globicephala	melas	2
Delphinidae	Grampus	griseus	0
Delphinidae	Lagenodelphis	hosei	0
Delphinidae	Lagenorhynchus	acutus	0
Delphinidae	Lagenorhynchus	albirostris	0
Delphinidae	Lagenorhynchus	australis	0
Delphinidae	Lagenorhynchus	cruciger	0
Delphinidae	Lagenorhynchus	obliquidens	0
Delphinidae	Lagenorhynchus	obscurus	2
Delphinidae	Lissodelphis	borealis	0
Delphinidae	Lissodelphis	peronii	0
Delphinidae	Orcaella	brevirostris	0
Delphinidae	Orcinus	orca	0
Delphinidae	Peponocephala	electra	0
Delphinidae	Pseudorca	crassidens	0
Delphinidae	Sotalia	fluviatilis	0
Delphinidae	Sousa	chinensis	0

Delphinidae	Sousa	teuszii	0
Delphinidae	Stenella	attenuata	2
Delphinidae	Stenella	clymene	0
Delphinidae	Stenella	coeruleoalba	0
Delphinidae	Stenella	frontalis	0
Delphinidae	Stenella	longirostris	3
Delphinidae	Steno	bredanensis	0
Delphinidae	Tursiops	aduncus	0
Delphinidae	Tursiops	truncatus	3
Monodontidae	Delphinapterus	leucas	0
Monodontidae	Monodon	monoceros	0
Phocoenidae	Neophocaena	phocaenoides	3
Phocoenidae	Phocoena	dioptrica	0
Phocoenidae	Phocoena	phocoena	3
Phocoenidae	Phocoena	sinus	0
Phocoenidae	Phocoena	spinipinnis	0
Phocoenidae	Phocoenoides	dalli	2
Physeteridae	Kogia	breviceps	0
Physeteridae	Kogia	sima	0
Physeteridae	Physeter	catodon	0
Platanistidae	Platanista	gangetica	0
Platanistidae	Platanista	minor	0
Iniidae	Inia	geoffrensis	3
Iniidae	Lipotes	vexillifer	0
Iniidae	Pontoporia	blainvillei	0
Ziphiidae	Berardius	arnuxii	0
Ziphiidae	Berardius	bairdii	0
Ziphiidae	Hyperoodon	ampullatus	0
Ziphiidae	Hyperoodon	planifrons	0
Ziphiidae	Indopacetus	pacificus	0
Ziphiidae	Mesoplodon	bidens	0
Ziphiidae	Mesoplodon	bowdoini	0
Ziphiidae	Mesoplodon	carlhubbsi	0
Ziphiidae	Mesoplodon	densirostris	0
Ziphiidae	Mesoplodon	europaeus	0
Ziphiidae	Mesoplodon	ginkgodens	0
Ziphiidae	Mesoplodon	grayi	0
Ziphiidae	Mesoplodon	hectori	0
Ziphiidae	Mesoplodon	layardii	0
Ziphiidae	Mesoplodon	mirus	0
Ziphiidae	Mesoplodon	perrini	0
Ziphiidae	Mesoplodon	peruvianus	0

Ziphiidae	Mesoplodon	stejnegeri	0
Ziphiidae	Mesoplodon	traversii	0
Ziphiidae	Tasmacetus	shepherdi	0
Ziphiidae	Ziphius	cavirostris	0

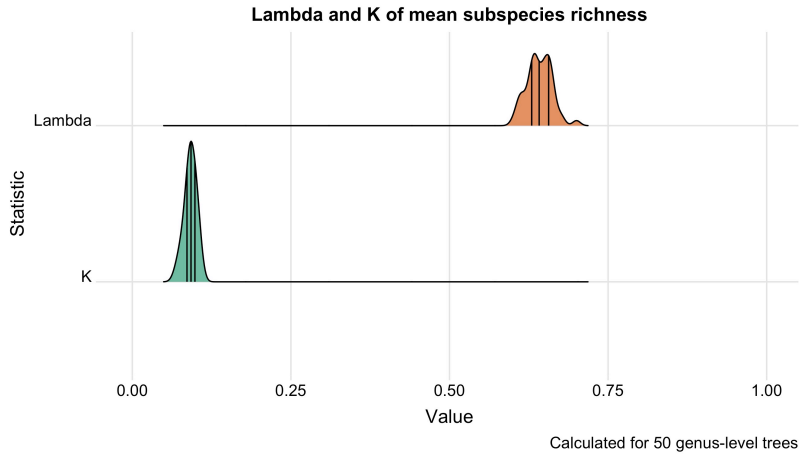
17 Appendix 2: Supplementary analyses and figures for Chapter 4

Note: These are the supplementary materials for van Holstein and Foley (2020).

17.1 Supplementary Figures

Figure 17-1: Phylogenetic signal in average subspecies richness

a) Distribution of values of lambda and K for average subspecies richness calculated on 50 genus-level trees



b) Distribution of values of lambda and k for experimental trait value distributions for 50 randomly generated trees

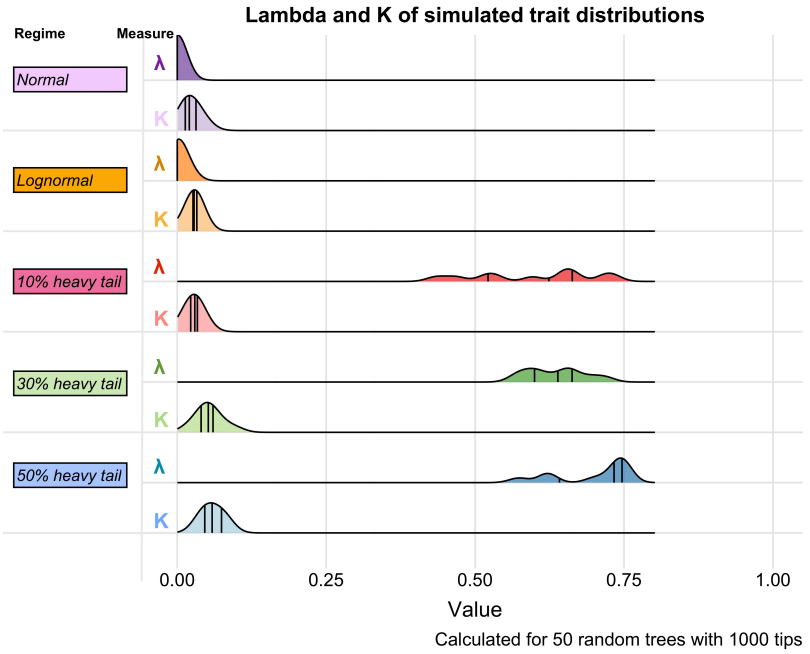


Figure 17-2: Distribution of p-values for a) interaction terms in phylogenetic regressions, b) models with interaction terms in phylogenetic ANOVAs

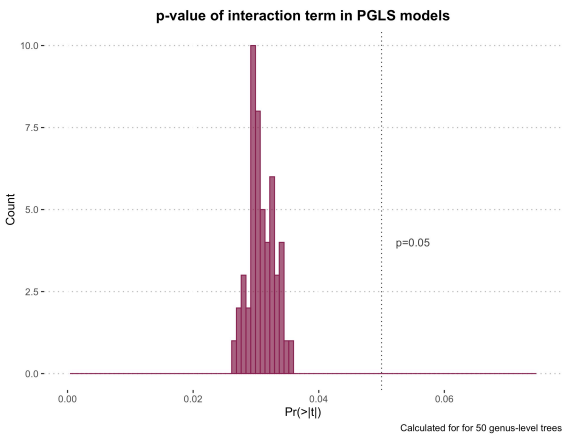
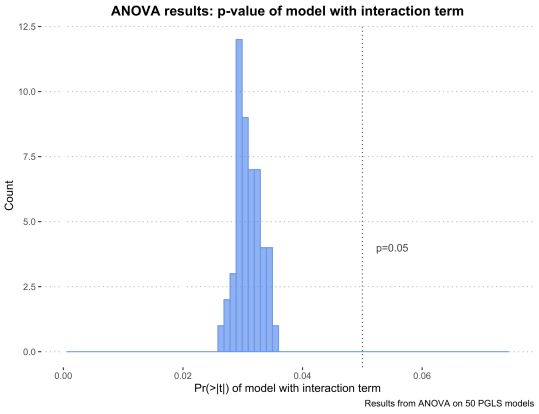
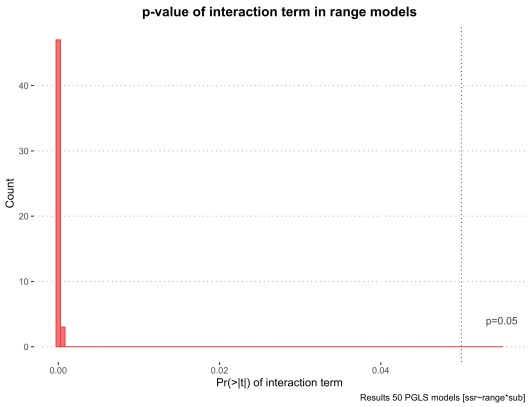
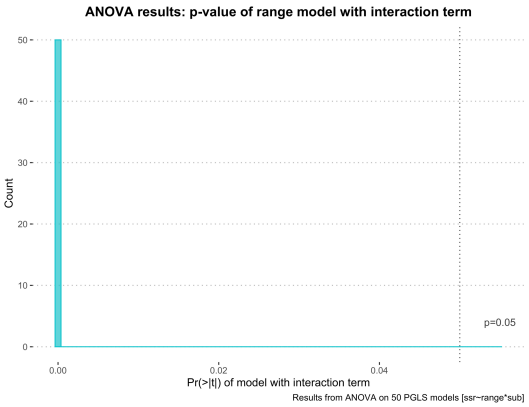
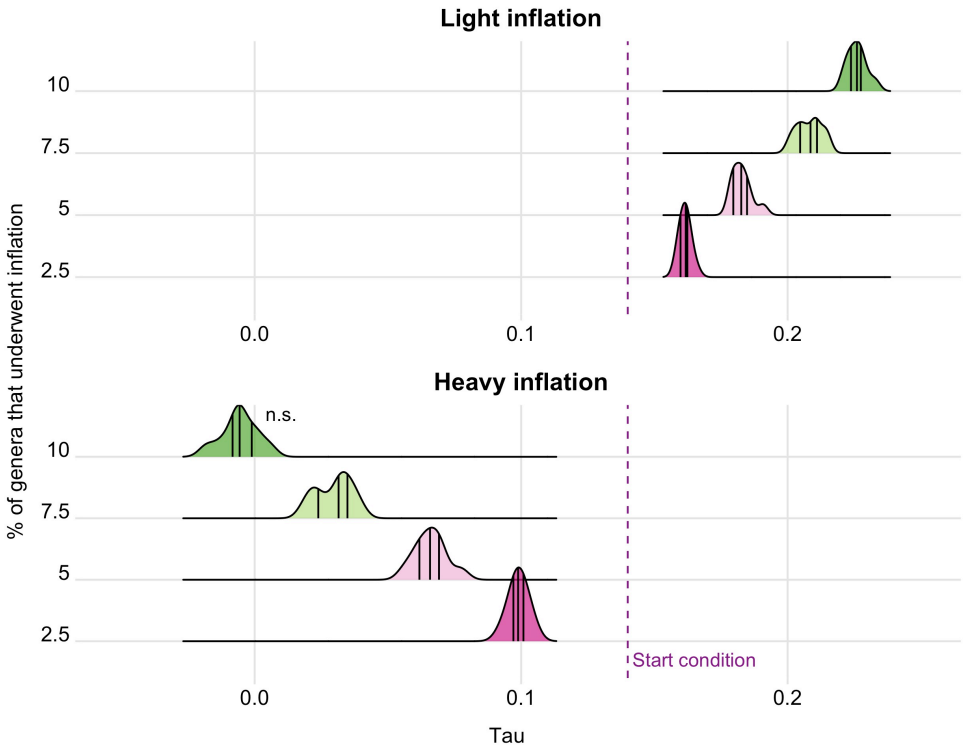
Subspecies richness and species richness	a) 	b) 
Subspecies richness and range size	a) 	b) 

Figure 17-3: The effect of taxonomic inflation on the correlation between species and subspecies richness.

Under "light" inflation (in which only one species per genus undergoes inflation), the correlation between species and subspecies richness increases with the proportion of genera that undergo inflation; this pattern is reversed under the regime of "heavy" inflation (in which all species in a genus undergo inflation). The start condition, of Tau=0.15, is indicated in purple. All correlations were significant ($p<0.05$) except for the scenario in which 10% of the dataset underwent "heavy" inflation.



17.2 Supplementary Materials and Methods

17.2.1 PGLS models

Revell (2010) recommends applying suitable branch length transformations, if necessary simultaneously optimized, in regression models. The phylogenetic regressions we report in the manuscript were run with lambda and kappa optimized (i.e. lambda="ML" and kappa="ML"), because AIC scores of these models were the second lowest (872.8) of all possible branch length transformation combinations (see Table 16-1). Models in which all three branch length transformations were optimized performed best (AIC=872.2), but the difference in AIC score between these models and those with only lambda and kappa optimized is less than 2, and a preference for the more complex model with all three transformations optimized is therefore not justified.

Table 17-1: AIC values of models with indicated branch length transformations

BL transformation	Median AIC score across 50 trees
None	1253.1
Lambda	874.9
Kappa	1150.2
Delta	1196.4
Lambda, Kappa	**872.8**
Lambda, Delta	873.9
Kappa, Delta	1072.5
Lambda, Kappa, Delta	**872.2**

17.2.2 Behaviour of Blomberg's K and Pagel's lambda depending on data distribution

I simulated 50 random pure-birth trees with 1000 tips each using the pbtree function in phytools, then generated a right-skewed dataset by randomly sampling from a lognormal distribution with a mean of 1.9 (since the mean of our dataset is 1.9 subspecies). Under this experimental condition, all values of lambda and K were both low (<0.1), so a simple positive skew in the data does not explain the observed asymmetry.

The distribution of actual observed subspecies richness, however, is heavy tailed, so I explored the potential impact of this by simulating datasets comprising 90, 70, and 50% values sampled from the lognormal distribution, and 10, 30, and 50% values (respectively) sampled from a uniform distribution with a lower bound of 5 and an upper bound of 15. The results of these regimes are shown in Figure 1b. Even when only 10% of the dataset contains random values from 5-15 (i.e., it is weakly heavy-tailed), the distribution of lambda shifts considerably rightward from its position under a pure lognormal (i.e. no heavy tail) regime, while K remains stationary.

As a control, I ran the experiment again with data drawn randomly from a normal distribution (i.e. the distribution of data was not right-skewed and had no heavy tail). This normal distribution had a mean of 1.9 and a standard deviation of 1. Since the data cannot be negative, I removed all values below 0 and replaced them by re-sampling from the normal distribution. The marked asymmetry in the distributions of values for lambda and K disappears under this regime (see Figure 1b). In this way we can explain the asymmetry in our estimates of lambda and K purely as a result of the distribution of our trait without invoking explanations based on evolutionary process, which has been shown to be

problematic given the complex relationship between process and phylogenetic signal (Revell, Harmon, & Collar, 2008).

17.2.3 Testing the effect of taxonomic inflation

1. Created a random dataset of 5000 observations of species richness (for which the median was 4) and subspecies richness (for which the median was 2), which had a Kendall correlation of 0.14 (similar to "all mammals")
2. **Light inflation regime (one subspecies in a genus gets inflated to species status):**
    a. Subsetted 2.5, 5, 7.5, 10% of simulated dataset, then "inflated" them:
        i. Species richness (n) increased by 1 $(n+1)$
        ii. Subspecies richness decreased accordingly $(n^2/n+1)$
3. **Heavy inflation regime (all subspecies in a genus get inflated to species status):**
    a. Subsetted 2.5, 5, 7.5, 10% of simulated dataset, then "inflated" them:
        i. All species were split, so new species richness = n^2
        ii. Because all species were completely split, all subspecies are now 1
4. Calculated new Kendall's tau

17.2.4 References

Revell, Liam J. 2010. "Phylogenetic Signal and Linear Regression on Species Data." *Methods in Ecology and Evolution* 1 (4): 319–29. https://doi.org/10.1111/j.2041-210x.2010.00044.x.

Revell, Liam J, Luke J Harmon, and David C Collar. 2008. "Phylogenetic Signal, Evolutionary Process, and Rate." *Systematic Biology* 57 (4): 591–601. https://doi.org/10.1080/10635150802302427.

18 Appendix 3: Composite tree

18.1 List of sources on which the tree is based

Dembo, Mana, Davorka Radovčić, Heather M Garvin, Myra F Laird, Lauren Schroeder, Jill E Scott, Juliet Brophy, et al. 2016. "The Evolutionary Relationships and Age of Homo Naledi: An Assessment Using Dated Bayesian Phylogenetic Methods." Journal of Human Evolution 97 (August): 17–26. https://doi.org/10.1016/j.jhevol.2016.04.008.

Leakey, Meave G, Fred Spoor, Frank H Brown, Patrick N Gathogo, Christopher Kiarie, Louise N Leakey, and Ian McDougall. 2001. "New Hominin Genus from Eastern Africa Shows Diverse Middle Pliocene Lineages." Nature 410 (6827): 433–40. http://dx.doi.org/10.1038/35068500.

Mendez, Fernando L., G. David Poznik, Sergi Castellano, and Carlos D. Bustamante. 2016. "The Divergence of Neandertal and Modern Human y Chromosomes." American Journal of Human Genetics. https://doi.org/10.1016/j.ajhg.2016.02.023.

Meyer, Matthias, Juan-Luis Arsuaga, Cesare de Filippo, Sarah Nagel, Ayinuer Aximu-Petri, Birgit Nickel, Ignacio Martínez, et al. 2016. "Nuclear DNA Sequences from the Middle Pleistocene Sima de Los Huesos Hominins." Nature 531 (7595): 504–7. https://doi.org/10.1038/nature17405.

Mounier, Aurélien, and Marta Mirazón Lahr. 2016. "Virtual Ancestor Reconstruction: Revealing the Ancestor of Modern Humans and Neandertals." Journal of Human Evolution 91 (February): 57–72. https://doi.org/10.1016/j.jhevol.2015.11.002.

Smith, Heather F., and Frederick E. Grine. 2008. "Cladistic Analysis of Early Homo Crania from Swartkrans and Sterkfontein, South Africa." Journal of Human Evolution. https://doi.org/10.1016/j.jhevol.2007.10.012.

Strait, D. S. 1999. "Cladistics and Early Hominid Phylogeny." Science. https://doi.org/10.1126/science.285.5431.1209c.

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Strait, David S., Frederick E. Grine, and Marc A. Moniz. 1997. "A Reappraisal of Early Hominid Phylogeny." Journal of Human Evolution. https://doi.org/10.1006/jhev.1996.0097.

Stringer, Chris. 2016. "The Origin and Evolution of Homo Sapiens." Philosophical Transactions of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rstb.2015.0237.

19 Appendix 4: Output of climate models

Table 1: Variability Selection Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Amplitude_100	-0.410^{***}		
	$(-0.693, -0.128)$		
Amplitude_200		-0.226	
		$(-0.560, 0.107)$	
Amplitude_500			-0.366^{**}
			$(-0.689, -0.043)$
Constant	1.053^{*}	0.987^{*}	1.106^{*}
	$(-0.039, 2.145)$	$(-0.186, 2.161)$	$(-0.033, 2.246)$
Observations	42	42	42
Akaike Inf. Crit.	-16.377	-10.915	-13.840
Bayesian Inf. Crit.	-11.310	-5.848	-8.773
Cox Snell pseudo-R2.	0.168451	0.0422535	0.109592
Likelihood.ratio.test (p)	0.0053785	0.17812	0.027245
Log likelihood	0.0053785	0.17812	0.027245
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 2: Variability Selection Hypothesis at genus level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Amplitude_100	-0.530^{**}		
	$(-0.982, -0.079)$		
Amplitude_200		-0.825^{***}	
		$(-1.388, -0.261)$	
Amplitude_500			-0.492^{*}
			$(-0.985, 0.002)$
GenusAus	-0.213	-0.987^{**}	-0.278
	$(-0.900, 0.474)$	$(-1.793, -0.181)$	$(-1.130, 0.574)$
GenusPar	-0.320	-1.188^{***}	-0.612
	$(-1.005, 0.365)$	$(-2.012, -0.363)$	$(-1.481, 0.257)$
Amplitude_100:GenusAus	-0.070		
	$(-0.699, 0.559)$		
Amplitude_100:GenusPar	0.509		
	$(-0.192, 1.210)$		
Amplitude_200:GenusAus		0.703^{*}	
		$(-0.016, 1.421)$	
Amplitude_200:GenusPar		1.181^{***}	
		$(0.328, 2.035)$	
Amplitude_500:GenusAus			0.058
			$(-0.646, 0.763)$
Amplitude_500:GenusPar			0.716
			$(-0.190, 1.621)$
Constant	1.336^{**}	1.935^{***}	1.422^{**}
	$(0.134, 2.537)$	$(0.644, 3.226)$	$(0.122, 2.723)$
Observations	42	42	42
Akaike Inf. Crit.	-10.526	-9.019	-6.955
Bayesian Inf. Crit.	0.559	2.065	4.129
Cox Snell pseudo-R2	0.313694	0.271193	0.225401
Likelihood.ratio.test (p)	0.0074076	0.020837	0.057065
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 3: Turnover Pulse Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Change_mean_100	−0.170		
	(−0.753, 0.413)		
Change_mean_200		0.374	
		(−0.353, 1.101)	
Change_mean_500			−0.382
			(−0.896, 0.131)
Constant	0.896	0.909	0.939
	(−0.292, 2.083)	(−0.269, 2.086)	(−0.224, 2.102)
Observations	42	42	42
Akaike Inf. Crit.	−10.595	−11.733	−12.134
Bayesian Inf. Crit.	−5.528	−6.667	−7.068
Cox Snell pseudo-R2	0.00810817	0.0248286	0.0505561
Likelihood.ratio.test (p)	0.55872	0.30414	0.13991
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 4: Turnover Pulse Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Change_mean_100	0.593**		
	(0.059, 1.126)		
Change_mean_200		1.664**	
		(0.227, 3.101)	
Change_mean_500			0.162
			(−0.695, 1.019)
GenusAus	0.004	0.113	0.136
	(−0.240, 0.248)	(−0.269, 0.494)	(−0.241, 0.513)
GenusPar	0.161	0.155	0.199
	(−0.228, 0.551)	(−0.302, 0.612)	(−0.258, 0.656)
Change_mean_100:GenusAus	−2.739***		
	(−3.765, −1.714)		
Change_mean_100:GenusPar	−0.958		
	(−3.176, 1.260)		
Change_mean_200:GenusAus		−2.182**	
		(−3.855, −0.510)	
Change_mean_200:GenusPar		−0.013	
		(−1.981, 1.956)	
Change_mean_500:GenusAus			−1.282**
			(−2.396, −0.168)
Change_mean_500:GenusPar			0.596
			(−0.718, 1.910)
Constant	0.829*	0.777	0.876
	(−0.113, 1.771)	(−0.336, 1.891)	(−0.226, 1.978)
Observations	42	42	42
Akaike Inf. Crit.	−25.769	−15.866	−13.478
Bayesian Inf. Crit.	−14.685	−4.781	−2.394
Cox Snell pseudo R2	0.478935	0.310904	0.304110
Likelihood.ratio.test (p)	4.8122e-05	0.0079516	0.0094325
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 5: Turnover Pulse Hypothesis at clade level - absolute change

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Abs_change_mean_100	0.004		
	(−0.839, 0.847)		
Abs_change_mean_200		−0.521	
		(−1.641, 0.600)	
Abs_change_mean_500			−0.361
			(−0.958, 0.236)
Constant	0.901	0.911	0.937
	(−0.292, 2.094)	(−0.269, 2.091)	(−0.236, 2.110)
Observations	42	42	42
Akaike Inf. Crit.	−10.999	−12.410	−11.725
Bayesian Inf. Crit.	−5.932	−7.343	−6.658
Cox Snell pseudo R2	2.35696e-06	0.0203044	0.0339452
Likelihood.ratio.test (p)	0.99206	0.3533	0.22845
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 6: Turnover Pulse Hypothesis at genus level - absolute change

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Abs_change_mean_100	−0.190		
	(−1.057, 0.676)		
Abs_change_mean_200		0.968	
		(−1.275, 3.211)	
Abs_change_mean_500			1.515*
			(−0.080, 3.110)
GenusAus	−0.279	0.273	0.373*
	(−0.678, 0.120)	(−0.235, 0.781)	(−0.066, 0.812)
GenusPar	−0.517**	0.288	0.413
	(−1.030, −0.003)	(−0.273, 0.849)	(−0.088, 0.914)
Abs_change_100:GenusAus	0.300		
	(−2.678, 3.277)		
Abs_change_100:GenusPar	4.025**		
	(0.141, 7.908)		
Abs_change_200:GenusAus		−2.941**	
		(−5.549, −0.334)	
Abs_change_200:GenusPar		0.983	
		(−2.011, 3.976)	
Abs_change_500:GenusAus			−2.631***
			(−4.377, −0.885)
Abs_change_500:GenusPar			−0.706
			(−2.574, 1.162)
Constant	1.177*	0.666	0.639
	(−0.019, 2.373)	(−0.483, 1.816)	(−0.449, 1.727)
Observations	42	42	42
Akaike Inf. Crit.	−12.069	−18.860	−17.624
Bayesian Inf. Crit.	−0.985	−7.775	−6.540
Cox Snell pseudo R2	0.169987	0.318803	0.354994
Likelihood.ratio.test (p)	0.16614	0.0064989	0.0024669
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 7: Variability Selection Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Amplitude_100	-0.353^{**}		
	$(-0.632, -0.073)$		
Amplitude_200		-0.214	
		$(-0.532, 0.105)$	
Amplitude_500			-0.345^{**}
			$(-0.648, -0.043)$
Constant	1.031^{**}	0.983^{*}	1.095^{**}
	$(0.015, 2.048)$	$(-0.091, 2.056)$	$(0.057, 2.133)$
Observations	39	39	39
Akaike Inf. Crit.	-20.490	-16.687	-19.670
Bayesian Inf. Crit.	-15.657	-11.854	-14.838
Cox Snell pseudo R2	0.14	0.04	0.12
Likelihood.ratio.test (p)	0.014	0.18	0.02
Log likelihood	14.04	0.18	0.02
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 8: Variability Selection Hypothesis at genus level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Amplitude_100	−0.088		
	(−0.505, 0.328)		
Amplitude_200		−0.552**	
		(−1.059, −0.045)	
Amplitude_500			−0.330*
			(−0.706, 0.045)
GenusAus	0.581**	−0.264	0.382
	(0.035, 1.126)	(−0.946, 0.418)	(−0.264, 1.028)
GenusPar	−0.008	−0.780**	−0.457
	(−0.563, 0.548)	(−1.459, −0.101)	(−1.092, 0.179)
Amplitude_100:GenusAus	−0.529*		
	(−1.074, 0.016)		
Amplitude_100:GenusPar	0.150		
	(−0.469, 0.769)		
Amplitude_200:GenusAus		0.350	
		(−0.303, 1.002)	
Amplitude_200:GenusPar		0.652*	
		(−0.097, 1.401)	
Amplitude_500:GenusAus			−0.294
			(−0.859, 0.272)
Amplitude_500:GenusPar			0.490
			(−0.175, 1.154)
Constant	0.549	1.242**	0.870*
	(−0.409, 1.506)	(0.161, 2.323)	(−0.106, 1.845)
Observations	39	39	39
Akaike Inf. Crit.	−24.609	−20.405	−25.288
Bayesian Inf. Crit.	−14.133	−9.930	−14.812
Cox Snell pseudo R2	0.49	0.41	0.49
Likelihood.ratio.test (p)	0.00	0.00	0.00
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 9: Turnover Pulse Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Change_mean_100	−0.327		
	(−0.856, 0.201)		
Change_mean_200		0.065	
		(−0.626, 0.756)	
Change_mean_500			−0.629***
			(−1.076, −0.182)
Constant	0.891	0.902	0.963*
	(−0.180, 1.961)	(−0.188, 1.993)	(−0.031, 1.958)
Observations	39	39	39
Akaike Inf. Crit.	−17.446	−16.533	−22.742
Bayesian Inf. Crit.	−12.613	−11.701	−17.909
Cox Snell pseudo R2	0.038	0.00	0.17
Likelihood.ratio.test (p)	0.21	0.85	0.006
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 10: Turnover Pulse Hypothesis at genus level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Change_mean_100	0.420*		
	(−0.010, 0.850)		
Change_mean_200		0.994	
		(−0.282, 2.269)	
Change_mean_500			−0.528*
			(−1.080, 0.024)
GenusAus	0.324***	0.354**	0.171
	(0.122, 0.525)	(0.014, 0.695)	(−0.112, 0.454)
GenusPar	−0.013	−0.041	−0.300*
	(−0.334, 0.307)	(−0.432, 0.351)	(−0.630, 0.029)
Change_mean_100:GenusAus	−2.324***		
	(−3.269, −1.380)		
Change_mean_100:GenusPar	0.930		
	(−1.637, 3.498)		
Change_mean_200:GenusAus		−1.123	
		(−2.665, 0.420)	
Change_mean_200:GenusPar		−0.277	
		(−2.044, 1.491)	
Change_mean_500:GenusAus			−0.543
			(−1.358, 0.271)
Change_mean_500:GenusPar			1.275**
			(0.295, 2.255)
Constant	0.517	0.544	0.837**
	(−0.238, 1.272)	(−0.428, 1.516)	(0.027, 1.646)
Observations	39	39	39
Akaike Inf. Crit.	−38.951	−23.460	−32.797
Bayesian Inf. Crit.	−28.476	−12.984	−22.322
Cox Snell pseudo R2	0.60	0.38	0.56
Likelihood.ratio.test (p)	0.00	0.00	0.00
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 11: Turnover Pulse Hypothesis at clade level - absolute change

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Abs_change_mean_100	−0.174		
	(−0.954, 0.606)		
Abs_change_mean_200		−1.019*	
		(−2.039, 0.001)	
Abs_change_mean_500			−0.422
			(−1.015, 0.172)
Constant	0.906	0.921*	0.751***
	(−0.182, 1.995)	(−0.118, 1.960)	(0.646, 0.855)
Observations	39	39	39
Akaike Inf. Crit.	−16.937	−21.022	−10.376
Bayesian Inf. Crit.	−12.104	−16.189	−5.544
Cox Snell pseudo R2	0.00	0.09	0.05
Likelihood.ratio.test (p)	0.65	0.05	0.15
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 12: Turnover Pulse Hypothesis at Genus level - absolute change

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Abs_change_mean_100	−0.332		
	(−1.037, 0.373)		
Abs_change_mean_200		−0.091	
		(−2.031, 1.849)	
Abs_change_mean_500			−0.784*
			(−1.640, 0.072)
GenusAus	0.041	0.315	0.092
	(−0.254, 0.336)	(−0.133, 0.764)	(−0.263, 0.447)
GenusPar	−0.332*	−0.162	−0.389*
	(−0.715, 0.051)	(−0.653, 0.329)	(−0.781, 0.003)
Abs_change_mean_100:GenusAus	1.716		
	(−0.839, 4.272)		
Abs_change_mean_100:GenusPar	1.712		
	(−1.577, 5.000)		
Abs_change_mean_200:GenusAus		−1.517	
		(−3.862, 0.829)	
Abs_change_mean_200:GenusPar		1.494	
		(−1.140, 4.128)	
Abs_change_mean_500:GenusAus			−0.301
			(−1.369, 0.767)
Abs_change_mean_500:GenusPar			1.528**
			(0.342, 2.715)
Constant	0.819*	0.617	0.917**
	(−0.138, 1.775)	(−0.345, 1.579)	(0.071, 1.763)
Observations	39	39	39
Akaike Inf. Crit.	−25.471	−30.241	−32.814
Bayesian Inf. Crit.	−14.996	−19.765	−22.339
Cox Snell pseudo R2	0.37	0.45	0.55
Likelihood.ratio.test (p)	0.00	0.00	0.00
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 13: Variability Selection Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Amplitude_100	0.151		
	(−0.042, 0.345)		
Amplitude_200		0.133*	
		(−0.017, 0.283)	
Amplitude_500			0.141**
			(0.001, 0.282)
Constant	0.669***	0.666***	0.639***
	(0.478, 0.860)	(0.491, 0.840)	(0.459, 0.819)
Observations	33	33	33
Akaike Inf. Crit.	−9.010	−9.129	−9.826
Bayesian Inf. Crit.	−4.708	−4.827	−5.524
Cox Snell pseudo R2	0.07	0.09	0.11
Likelihood.ratio.test (p)	0.12	0.08	0.048
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 14: Variability Selection Hypothesis at genus level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Amplitude_100	−0.038 (−0.610, 0.534)		
Amplitude_200		−0.041 (−0.317, 0.236)	
Amplitude_500			−0.032 (−0.238, 0.175)
GenusAus	−0.302 (−0.994, 0.389)	−0.311 (−0.770, 0.148)	−0.365* (−0.787, 0.057)
GenusPar	−0.035 (−0.860, 0.790)	0.060 (−0.602, 0.722)	0.285 (−0.627, 1.197)
Amplitude_100:GenusAus	0.223 (−0.407, 0.853)		
Amplitude_100:GenusPar	−0.284 (−1.042, 0.474)		
Amplitude_200:GenusAus		0.198 (−0.198, 0.594)	
Amplitude_200:GenusPar		−0.367 (−0.943, 0.208)	
Amplitude_500:GenusAus			0.236 (−0.118, 0.590)
Amplitude_500:GenusPar			−0.542 (−1.332, 0.249)
Constant	0.967*** (0.303, 1.631)	0.981*** (0.582, 1.380)	0.973*** (0.645, 1.300)
Observations	33	33	33
Akaike Inf. Crit.	−10.711	−9.697	−10.370
Bayesian Inf. Crit.	−1.640	−0.626	−1.299
Cox Snell pseudo R2	0.483	0.487	0.494
Likelihood.ratio.test (p)	0.00	0.00	0.00
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 15: Turnover Pulse Hypothesis at clade level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Change_mean_100	−0.146		
	(−0.799, 0.507)		
Change_mean_200		−0.151	
		(−0.740, 0.437)	
Change_mean_500			0.075
			(−0.410, 0.559)
Constant	0.814***	0.819***	0.801***
	(0.750, 0.879)	(0.749, 0.889)	(0.712, 0.889)
Observations	33	33	33
Akaike Inf. Crit.	−9.309	−9.166	−8.609
Bayesian Inf. Crit.	−5.007	−4.864	−4.307
Cox Snell pseudo R2	0.00	0.00	0.00
Likelihood.ratio.test (p)	0.65	0.60	0.75
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 16: Turnover Pulse Hypothesis at genus level

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Change_mean_100	−0.004 (−0.582, 0.573)		
Change_mean_200		0.120 (−0.573, 0.814)	
Change_mean_500			0.126 (−0.412, 0.665)
GenusAus	−0.210*** (−0.329, −0.090)	−0.182*** (−0.311, −0.053)	−0.260*** (−0.408, −0.111)
GenusPar	−0.380*** (−0.630, −0.129)	−0.295*** (−0.494, −0.095)	−0.392*** (−0.634, −0.149)
Change_mean_100:GenusAus	1.538** (0.183, 2.894)		
Change_mean_100:GenusPar	1.132 (−2.029, 4.293)		
Change_mean_200:GenusAus		0.503 (−0.594, 1.600)	
Change_mean_200:GenusPar		−0.160 (−1.729, 1.410)	
Change_mean_500:GenusAus			0.665 (−0.140, 1.470)
Change_mean_500:GenusPar			0.439 (−0.841, 1.718)
Constant	0.923*** (0.853, 0.994)	0.922*** (0.846, 0.998)	0.914*** (0.835, 0.994)
Observations	33	33	33
Akaike Inf. Crit.	−20.294	−14.189	−17.901
Bayesian Inf. Crit.	−11.223	−5.119	−8.830
Cox Snell pseudo R2	0.53	0.46	0.55
Likelihood.ratio.test (p)	0.00	0.00	0.00
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 17: Turnover Pulse Hypothesis at clade level - absolute change

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Abs_change_mean_100	0.507		
	(−0.565, 1.579)		
Abs_change_mean_200		0.622	
		(−0.439, 1.684)	
Abs_change_mean_500			0.318
			(−0.298, 0.933)
Constant	0.769***	0.745***	0.762***
	(0.663, 0.876)	(0.619, 0.872)	(0.649, 0.874)
Observations	33	33	33
Akaike Inf. Crit.	−10.978	−11.418	−10.034
Bayesian Inf. Crit.	−6.676	−7.116	−5.732
Cox Snell pseudo R2	0.03	0.04	0.032
Likelihood.ratio.test (p)	0.34	0.24	0.30
Note:			*p<0.1; **p<0.05; ***p<0.01

Table 18: Turnover Pulse Hypothesis at Genus level - absolute change

	Dependent variable:		
	DR		
	(1)	(2)	(3)
Abs_change_mean_100	0.100		
	(−0.849, 1.049)		
Abs_change_mean_200		0.501	
		(−1.144, 2.146)	
Abs_change_mean_500			0.179
			(−0.724, 1.082)
GenusAus	−0.207	−0.197*	−0.250***
	(−0.523, 0.109)	(−0.422, 0.028)	(−0.435, −0.064)
GenusPar	−0.371**	−0.329**	−0.378***
	(−0.659, −0.082)	(−0.643, −0.015)	(−0.644, −0.113)
Abs_change_mean_100:GenusAus	0.971		
	(−2.882, 4.824)		
Abs_change_mean_100:GenusPar	1.028		
	(−2.515, 4.571)		
Abs_change_mean_200:GenusAus		0.616	
		(−1.361, 2.592)	
Abs_change_mean_200:GenusPar		0.157	
		(−2.403, 2.716)	
Abs_change_mean_500:GenusAus			0.622
			(−0.471, 1.715)
Abs_change_mean_500:GenusPar			0.386
			(−1.088, 1.860)
Constant	0.914***	0.873***	0.901***
	(0.798, 1.030)	(0.693, 1.053)	(0.767, 1.034)
Observations	33	33	33
Akaike Inf. Crit.	−18.064	−19.642	−18.765
Bayesian Inf. Crit.	−8.993	−10.571	−9.695
Cox Snell pseudo R2	0.43	0.50	0.54
Likelihood.ratio.test (p)	0.00	0.00	0.00
Note:			*p<0.1; **p<0.05; ***p<0.01