Land use, food production, and the future of tropical forest species in Ghana

Benjamin Timothy Phalan

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Author's Declaration

This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and acknowledgements. The text does not exceed 300 pages, and no part has been submitted for another degree or diploma.

Benjamin Timothy Phalan

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Summary

Agriculture is arguably the greatest threat to tropical forest species. Conservation scientists disagree over the relative importance of two opposing strategies for minimising this threat: enhancing on-farm biodiversity, through wildlife-friendly farming practices, or sparing land for nature by using high-yielding farming methods on the smallest possible area to reduce the need to convert natural habitats. Previous theoretical work shows that understanding the relationship between population density and yield for individual species is crucial for determining whether one of these strategies, or a mixed strategy, will maximise their populations for a given food production target.

In this thesis, I aim to identify what land-use strategy will permit increases in food production with least impact on species in the forest zone of Ghana. Farm-fallow mosaic landscapes with shifting cultivation and native canopy trees produced only around 15% as much food energy per hectare as the highest-yielding oil palm plantations. In farm mosaics where perennial tree crops dominate, food production and profits were higher, but did not reach those of oil palm plantations. I surveyed birds and trees in forest, farm mosaic, and oil palm plantation, and combined these data with information on yields to assess the likely consequences of plausible future scenarios of land-use change. My results provide evidence of a strong trade-off between wildlife value and agricultural yield. Species richness was high in low-yielding farming systems, but there was considerable turnover between these systems and forests, with widespread generalists replacing narrowly endemic forest-dependent species. Species most dependent on forest as a natural habitat, those with smaller global ranges and those of conservation concern showed least tolerance of habitat modification. For virtually all species, including even widespread generalists, future land-

use strategies based on land sparing are likely to support higher populations of most species and minimise their risk of extinction compared to land-use strategies based on wildlife-friendly farming.

If food production is to increase in line with Ghana's population growth, a combination of efforts to improve forest protection and to increase yields on current farmed land is likely to achieve this at least cost to forest species. Efforts to better protect forests, which require further restrictions on human use, might be most effective if they can be closely linked to support for farmers to improve their yields. In the long term however, this strategy will only delay and not avert biodiversity loss, unless global society can limit its consumption.

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Abbreviations and glossary

AIC	Akaike's Information Criterion, a measure of model fit
AICc	AIC with a second order correction for small sample size
BOPP	Benso Oil Palm Plantation, Western Region, Ghana
BP	Years before present, where the "present" is conventionally 1950
CAP	Common Agricultural Policy of the European Union
CO_2	Carbon dioxide
CPO	Crude palm oil
CV	Coefficient of variation
dbh	Diameter at breast height (1.3 m), a standard measurement of tree diameter
EIA	Energy Information Administration, a section of the US Department of Energy
EOO	Extent of occurrence, a measure of the global range size of a species: "the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy" (IUCN 2001)
EU	European Union
FAO	Food and Agriculture Organization of the United Nations
ffb	Fresh fruit bunches of oil palm fruit (see Figure 4.22)
GAM	Generalized additive model
GDP	Gross Domestic Product, a measure of the total value of goods and services produced in a country in a given year
GH¢	Ghana cedi, the unit of currency of Ghana
GIS	Geographic Information System
GJ	Gigajoule: one billion joules (1 GJ = 10^9 J)
GMT	Greenwich Mean Time
GOPDC	Ghana Oil Palm Development Company, Eastern Region, Ghana
GPS	Global Positioning System
GSBA	Globally Significant Biodiversity Area (see: http://www.fcghana.com/programmes/nrmp/bio.html)
GWS	Ghana Wildlife Society, the BirdLife International partner in Ghana
ha	Hectare (100 × 100 m)
HIV/AIDS	Human Immunodeficiency Virus/Acquired Immunodeficiency Syndrome
IEA	International Energy Agency
ILUC	Indirect land-use change

IPCC	Intergovernmental Panel on Climate Change
IPM	Integrated Pest Management
IUCN	International Union for Conservation of Nature
J	Joule, the SI unit of energy (1 kJ = 0.239 kcal)
kcal	Kilocalorie, a pre-SI unit for energy (1 kcal = 4.184 kJ)
km	Kilometre
m	Metre
MCDS	Multiple Covariates Distance Sampling engine in program Distance
MJ	Megajoule (1 MJ = 10^6 J)
My	Million years
N	Nitrogen
NPLD	Non-pioneer light demander, a guild of trees capable of germinating in shade, but which require light to develop beyond the sapling stage
NTFP	Non-timber forest product
OER	Oil extraction ratio, the ratio of extracted oil to ffb mass
PES	Payments for ecosystem services
PJ	Petajoule (1 PJ = 10^{15} J)
PKO	Palm kernel oil
PVA	Population viability analysis
SAR	Species-area relationship, a power function, $S = cA^z$, which relates the number of species (S) to the area (A) of an island or patch of habitat; *c* and *z* are constants (Rosenzweig 1995).
TJ	Terajoule (1 TJ = 10^{12} J)
TOPP	Twifo-Praso Oil Palm Plantation, Central Region, Ghana
UBRE	Un-biased risk estimator, used for model selection with GAMs
UK	United Kingdom
UNPD	United Nations Population Division
UN-REDD	United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries
US	United States (of America)
USDA	United States Department of Agriculture

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Chapter 1

Introduction

Mosaic of farms, fallows and secondary forest near Benso, Western Region ‘it is not clear which are greater – the successes of modern high-intensity agriculture, or its shortcomings’

David Tilman (1998, p. 211)

1 Introduction

1.1 Rationale: biodiversity under pressure

1.1.1 Human impacts

Perhaps the greatest challenge facing humanity this century is to find ways of meeting the increasing demands of our civilisation without excessive damage to the biosphere on which we depend. The pressure of human demands on biodiversity and natural resources is at unprecedented levels, and continues to increase. Our impacts on biodiversity, as with other environmental impacts, are a product of human population size and per capita impact, as expressed conceptually by Ehrlich and Holdren in 1971:

$$I = P \cdot F$$

where *I* is total impact, *P* is human population size, and *F* is a function which describes per capita impact[1].

Human population growth has slowed at a global scale, but mid-range forecasts predict that it will continue until at least mid-century. Global population is expected to rise from its present level of 6.8 billion to at least 9 billion, before stabilising at 8-10 billion after 2050 (Lutz et al. 2001, Population Reference Bureau 2008; but see Turchin 2009). Population growth will be highest in least-developed countries, despite high mortality from HIV/AIDS, malaria and other diseases, as fertility rates are expected to remain high. The population of Africa is predicted to more than double between 2005 and 2050, reaching more than two billion.

Per capita impacts on biodiversity are determined largely by patterns of resource consumption and waste production. Overconsumption by affluent people exacerbates the impact of a large human population. Even without further population growth, if everyone in

[1] This relationship is more commonly written $I = P \cdot A \cdot T$ where *A* represents affluence and *T* represents technology. Affluence and technology are just two of the determinants of per capita impact. Others include behavioural choices and spatial patterns of resource consumption.

the world were to consume resources and produce waste at the same rate as people in Western Europe and North America, we would overshoot the planet's biocapacity by three to five times (Kitzes et al. 2008). Wealthier consumers use more energy and resources than the poor, for example by consuming a greater proportion of meat (Myers & Kent 2003). Even without considering the needs of other species, we are already exceeding the planet's ability to regenerate goods and services by more than 20% because of a combination of overpopulation and overconsumption (Kitzes et al. 2008).

Technology has the potential to exacerbate or ameliorate human impacts. Unfortunately, as technologies are typically developed reactively to overcome existing constraints, the net effect of technological progress has been to permit greater global population growth and increased per-capita impact. I discuss the potentially perverse effects of more efficient technologies in Chapter 8. Technological progress has largely been a good thing for human material well-being: the average person alive today is healthier and can expect to live longer than people in past centuries (Veenhoven 2005). However, this progress has come at great cost to the other species with which we share the planet (section 1.2).

1.1.2 Human demands for food and land

The primary way in which humans compete with other species is by using land to grow crops for food. All land used for agriculture was formerly natural habitat, such as forest or grassland, that was at some point converted to farmland. Between 30 and 40% of the planet's ice-free land is used for agriculture, and as much as three-quarters of it has been modified in some way by human activities (Vitousek et al. 1997, Foley et al. 2005, Ellis & Ramankutty 2008, Ramankutty et al. 2008). Humans compete with other species on that land by replacing natural vegetation with crop plants and pasture, and by using one-quarter to one-third of global net primary production each year (Imhoff et al. 2004, Haberl et al. 2007). Competition is increased by the fact that, at large scales, agriculture and the dense human populations it supports tend to be concentrated in areas of highest biological value (Balmford et al. 2001, Scharlemann et al. 2004).

Around one-third of the global cereal harvest goes to feed, not people directly, but livestock (Steinfeld et al. 2006). Livestock also consume at least 17% of the annual global catch of wild fish (J. Jacquet, pers. comm.). Livestock production accounts for 18% of global greenhouse gas emissions and 65-70% of all agricultural land, and is an inefficient way to transform sunlight into food energy (Steinfeld et al. 2006, Ramankutty et al. 2008). Reliance by more affluent and increasingly obese people on meat-rich diets is thus an important contributing factor to human demands for land and competition with other species.

The recent rapid expansion of biofuels markets adds further to human demands for land. At present, biofuels supply around 1% of global transportation fuels, and take up around 1% of all cropland (IEA 2006). Biofuel production is expected to have more than doubled from 2006 to 2010, and to double again from 2010 to 2020, encouraged by EU and US subsidies (EIA 2009). Despite this dramatic growth, even by 2030 biofuels will supply only 3-10% of global transport fuels, for which they will require between 34 and 59 million hectares of land (IEA 2006, EIA 2009). More land-efficient next-generation (ligno-cellulosic and algal) biofuels will not solve this problem: they too will require large areas of land if they are to contribute to fossil fuel reduction, and thus will compete with natural habitats, either directly, by replacing them, or indirectly, by displacing other crops (Williams et al. 2009).

While demand for land is increasing, vast areas have been so degraded by human activities that they are no longer productive. It has been estimated that around 1.5 million hectares of arable land are made so heavily salinized by inappropriate irrigation each year that they are no longer suitable for crop production (Foley et al. 2005). The productive capacity of as much as 40% of global croplands is threatened by some degree of soil erosion, nutrient depletion or loss of soil organic matter. These problems are especially acute in parts of sub-Saharan Africa (Lal 2009). Agricultural lands are also lost each year to urbanization and other infrastructure development. As cities tend to be built on fertile low-lying land, and cover between 70 and 350 million hectares globally (depending on how they are defined), losses to urbanization could be an important and relatively irreversible sink for productive cropland (Salvatore et al. 2005).

The future impacts of climate change cannot be predicted with any great accuracy, but are likely to include wide-ranging effects on patterns of land use and pressures on land. Some evidence suggests that climatic changes over the past 50 years, such as increased temperatures and declines in rainfall, are an important part of the reason for Africa's low agricultural productivity (Barrios et al. 2008). Those trends are likely to continue, and the yield-enhancing effect of rising CO_2 concentrations is unlikely to be enough to prevent yield declines from reduced soil moisture and changing rainfall patterns (Long et al. 2006). Current patterns of crop production and even of settlement will change: these shifts may or may not be sufficient to maintain agricultural yields (Stige et al. 2006, Seo et al. 2008).

Despite the various pressures to convert forests and other natural habitats to croplands, there are also now increasing incentives to maintain or even restore some of these lands with their original land cover. This is partly because as natural habitats shrink, the ecosystem services they provide become scarce and are increasingly valued, and partly because of improved understanding of the value of those services. Maintaining global carbon stocks stored in natural forests, wetlands and grasslands is recognised as an important part of strategies to avoid dangerous climate change, and as a result, there are new economic incentives to reduce, rather than increase, land conversion (Laurance 2008, Venter et al. 2009). There are other schemes, on a smaller scale, that seek to conserve forests and other natural land covers for other ecosystem services such as watershed protection and flood control (Ferraro & Kiss 2002). And of course forests have long been valued for their provision of other services, as diverse as timber, recreation, bushmeat and intrinsic value (Millennium Ecosystem Assessment 2005). There is also increasing interest in quantifying ecosystem services in fragmented and modified landscapes, and rewarding landowners for maintaining those services (Zander et al. 2007, Ricketts et al. 2008).

1.2 Biodiversity in decline

There is considerable evidence that human activities are having a large negative effect on global biodiversity. The current rate of extinction is at least 48 times the background rate from the fossil record for well-studied vertebrate taxa, and could be more than two orders of magnitude greater even than that (Baillie et al. 2004, Pimm et al. 2006). No other human impact on the biosphere is as irreversible.

Another way of measuring declines in biodiversity is by changes in global threat status within well-known taxa. Of those species for which sufficient information has been collated to asses their status, 25% of mammals, 12% of birds, 33% of amphibians, 42% of turtles and tortoises, 16% of freshwater crabs, 33% of reef-building corals and 31% of gymnosperms are listed assessed as being at an elevated risk of extinction (Baillie et al. 2004, Stuart et al. 2004, Carpenter et al. 2008, Schipper et al. 2008, Cumberlidge et al. 2009)[2]. The rate at which species are becoming more or less threatened has been quantified for birds and amphibians using a Red List Index: overall, both taxa have shown a steady deterioration since the 1980s, although there is evidence that loss of biodiversity would have been even greater without conservation interventions (Butchart et al. 2005, Butchart et al. 2006).

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[2] Most of these estimates are probably underestimates because some species which are "Data Deficient" are likely to be threatened. Estimates for taxa not listed here could be overestimates because only a small fraction of species have been assessed.

Further evidence of decline comes from the Living Planet Index, which is based on trends in populations of 1,686 vertebrate species since 1970 (Loh et al. 2008). It shows an overall decline in those populations of 28% since 1970. Considering only species of tropical forest (the biome to which this thesis relates), there has been an average decline in populations of 62%. Declines have also occurred in the Afro-tropics (19%), the tropics generally (51%), terrestrial ecosystems (33%), birds (20%) and mammals (19%). Tropical forests have not declined by 60% since 1970 on a global scale, but undoubtedly some populations of tropical forest species have declined by 100%, while others have remained stable or increased. Without understanding biases in the selection of study populations, it is not possible to say with certainty how representative the Living Planet Index is, but the consistency across biomes, geographic regions and taxa suggests that the direction, if not the precise magnitude, of the trends is accurate (Loh et al. 2005).

Less direct evidence of decline comes from the observation that natural habitats have diminished in extent. Since the dawn of agriculture, an estimated 25-50% of the world's tropical forest has been converted to other land covers (Lewis 2006). Disentangling the diverse causes of threat to wild species is complex, but it is clear that agriculture is one of the most, if not the most, important (Geist & Lambin 2002, Baillie et al. 2004). While there is a diversity of other, often interconnected, threats, the greatest threat to well-known terrestrial taxa is habitat loss and degradation, mostly driven by agricultural expansion and intensification.

Why does biodiversity loss matter? Many justifications are given for conserving biodiversity, ranging from the utilitarian to the aesthetic (Millennium Ecosystem Assessment 2005). Certainly, the ecosystem services provided by non-human species are essential for human existence. This thesis takes as an implicit starting point that biodiversity is worth conserving, the more so because extinction is irreversible. The approach taken here is a pragmatic one: given that human needs must be met, how can we achieve that with least damage to biodiversity? The question could in theory be turned on its head, although I do not attempt to do so here: if we are to avoid causing any extinctions, how much of the planet's land and biomass can we safely consume?

1.3 Possible solutions

There are many options for reducing the impact of farming on wild nature, but two general themes can be distinguished:

- measures to reduce impacts on wild species on farmland
- measures to reduce conversion of natural habitats to farmland

In the first category are included interventions such as retaining canopy trees, reducing grazing pressure, organic farming, and creating specific habitat features to benefit wildlife. These approaches can be labelled "wildlife-friendly farming", and are strongly advocated by European and North American conservationists (see Chapter 2). Landscapes with wildlife-friendly farming typically support greater species richness and abundance than conventional farmland, and also support more of the species of unconverted habitats. Despite these advantages, wildlife-friendly farming systems have weaknesses. Wildlife-friendly interventions typically incur a yield penalty: higher yields can be obtained without them. As a result, more land is required for any level of food production than with conventional farming. Also, wildlife-friendly farms fail to provide suitable habitat for many of the species of unconverted habitats.

Recognising these problems, an alternative approach, "land sparing", has been suggested (Green et al. 2005). Land sparing involves two sorts of actions: increasing yields on existing farmland to meet production targets, and ensuring that the resulting decrease in land requirements for farming is translated into reduced conversion of natural habitats.

Agricultural development programs typically focus on the first sort of interventions: increasing yields, while the most important tool of conservationists – the creation of protected areas – is of the second sort. Land sparing can also be criticised: it typically involves loss of biodiversity from the farmed landscape, and high-yield farming often has a range of negative effects including greenhouse gas emissions and water pollution (see Chapter 2). Land sparing and wildlife-friendly farming need not necessarily be in opposition, but they typically are. This is because there is frequently a trade-off, in that measures to enhance the biodiversity value of farmed land tend to reduce yields. When that is true, wildlife-friendly farming will require more land for any given quantity of agricultural production.

1.4 Objectives of this thesis

The purpose of this thesis is investigate the extent to which there is a trade-off between wildlife value and yield in farmed landscapes of southwest Ghana, and to assess whether wildlife-friendly farming, land sparing, or some combination of the two is likely to be the best strategy for maintaining the populations of wild species in those landscapes. In order to address those questions, I had several subsidiary aims:

1. To document variation in yields across a gradient of agricultural intensification,
2. To document variation in the densities of individual species across the same gradient and in baseline habitat, in two taxa: birds and trees,
3. To describe the form of density-yield functions for those species,
4. To investigate correlates of different types of response to increasing yield,
5. To synthesise this information to inform conservation strategies.

My a priori expectation, based on preliminary results, was that land sparing would be the better option for most species originally native to the study area. Therefore, whenever there was unavoidable ambiguity, I erred towards overestimating the yields and profits of low-yield farming systems, underestimating those of high-yield systems, and overestimating the biodiversity value of low-yield farmland, all of which made for a more stringent test of land sparing.

1.5 Outline of chapters

In Chapter 2, I review the conceptual background to the wildlife-friendly farming vs. land sparing debate, including the use of density-yield functions to assess individual species' responses to increasing yield. In Chapter 3, I summarise why I selected Ghana as a study site, and I describe the history of forests in Ghana and the agricultural crops and practices now in use. In Chapter 4, I assess the agricultural yields of farming systems in southwest Ghana, including low-yielding, wildlife-friendly farmland, and high-yield, wildlife-poor oil palm *Elaeis guineensis* plantations. In Chapter 5, I present results from bird surveys, and analyse whether the sensitivity of species to habitat disturbance from agriculture is related to traits that predispose them to a higher risk of extinction. In Chapter 6, I present similar analyses for trees, and discuss whether the richness of tree assemblages in wildlife-friendly landscapes is likely to be maintained over time. In Chapter 7, I combine information on yields with that on species' densities to model the potential impacts of four plausible future scenarios of land-use change in Ghana on their populations and risk of extinction. I conclude in Chapter 8 with a discussion of ways in which the models could be made more realistic in future, and of the necessary elements for land sparing to be effective in practice.

Chapter 2

Conceptual background

Four-year old oil palms at Benso Oil Palm Plantation ‘today's dominant conservation strategies cannot [work]. They divide the land into shares, so much for nature and so much for people. This inevitably leads to conflict. And since people are doing the dividing, you can be pretty sure which side will win.’

Michael Rosenzweig (2003, p. 9)

‘Some… claim that modern, intensive farming is risking the world’s biodiversity. However, they apparently think it’s more important to save man-made biodiversity, such as antique farmers’ varieties, than to save the rich web of unique species characteristic of a wild forest. We can save the farmers’ old varieties through gene banks and small-scale gene farms, without locking up half of the planet’s arable land as a low-yield gene museum.’

Norman Borlaug (Wall Street Journal, May 13, 2002)

2 Conceptual background

2.1 Biodiversity and agriculture

2.1.1 On-farm impacts of agriculture

High-yielding farms typically have low biodiversity value. Although there is not an inevitable or linear negative relationship between yield and biodiversity value (hence this thesis), the fact that intensively-managed, high-yielding farms tend to support few wild species is acknowledged even by the most vigorous proponents of wildlife-friendly farming (Perfecto & Vandermeer 2008). The first way in which humans reduce biodiversity in agricultural landscapes is by removing it directly to make room for domesticated species: removal and alteration of natural habitats is arguably the single greatest externality of farming. The amount of useful produce obtained from most plants used in agriculture is strongly proportional to the leaf area the crop maintains, integrated over its lifetime, and hence the amount of solar radiation intercepted for photosynthesis (Norman et al. 1995). So there is a near inevitability that many wild plants need to be displaced as competitors and, with them, their dependent animals, fungi, and other biodiversity. What remains are tolerated beneficial or neutral wild species, as well as species regarded by farmers as weeds and pests. Many species, such as trees, are physically destroyed, particularly when fire or heavy machinery is used in land clearing (Lawton et al. 1998, Cochrane 2003). Other organisms are displaced and individuals move elsewhere, although their populations are reduced by the loss of habitat. Some species persist in the modified landscape, and others, not previously present, are able to invade from surrounding areas (Brühl & Eltz in press).

After conversion, the replacement of structurally diverse farming systems with simplified ones leads to further biodiversity loss. Structurally diverse farming systems include some agroforestry systems and forest gardens, landscapes with small field sizes and well-vegetated field boundaries, and long-fallow systems with a mosaic of crop fields and regenerating secondary vegetation (Schroth et al. 2004). Some structurally diverse farming systems are only partially so by design. Limited access to technology may impose the retention of semi-natural habitats. For example, draining a wetland remnant within a farmed landscape to make it into arable land may not be practical because of lack of pumps or machinery to build ditches. So the wetland is retained, and perhaps used as a source of water for livestock, but would be converted if the means were more readily available. To maximise yields, cultivators typically replace native species of trees and shrubs with a small number of high-yielding, often non-native crop species. The use of agrochemicals typically has negative effects on the populations of non-target wild species in farmed landscapes, as well as reducing populations of pests (Gemmill-Herren et al. 2007). Conversion of natural habitats to agricultural lands alters environmental variables such as microclimate and soil properties, which can affect the ability of some species to survive or recolonise (Turner & Foster 2006). The disturbance created by land-use change can help invasive species to establish, that exclude or compete with native species (Walker 2006). Human presence can also have an adverse effect on populations of wild species, for example through hunting, harvesting and pest control (Porembski & Biedinger 2000, Fa et al. 2003, Chapman et al. 2004).

2.1.2 Off-farm effects of on-farm decisions

In addition to affecting on-farm biodiversity, decisions to farm in different ways also affect off-farm areas, through their impacts on the magnitude of edge effects, isolation of fragmented habitat, dispersal between fragments, and pollution. I discuss these important issues at greater length in Chapter 8. On-farm decisions about production methods also affect other areas indirectly, through markets. Pressure to increase agricultural production finds its outlet through a complex set of paths ending in the conversion of natural habitats, or in yield increases on farmland (Geist & Lambin 2002). For practical purposes, that pressure can be summarised as food demand: if there is greater global demand for food, then agricultural production globally needs to increase. I refer to the amount of food (or other agricultural products) demanded in a particular context as the “production target” throughout this thesis (see also section 2.4). For instance, the total amount of food that needs to be produced to feed the current global population is the current global production target. A major off-farm effect of on-farm decisions is that they affect how much of the production target needs to be produced from elsewhere. If farmers (or governments) in a large area (“province”) create the conditions so that they can farm at high yields, supply from that province will increase, prices will fall and less of the production target will need to be produced elsewhere. The scale over which these off-farm effects operate can be local, but it is typically international or global. I defer discussion to Chapter 8 of whether the introduction of yield-enhancing technologies alone is overall likely to improve or damage the prospects for intact habitats.

The effect of on-farm decisions on land-use change elsewhere is termed “indirect land-use change” (ILUC), and has become a controversial topic of discussion in land-use policy circles, particularly in the context of estimating greenhouse gas emissions from land-use change (Laurance et al. 2007, Gnansounou et al. 2008, Fargione et al. 2008, Panichelli et al. 2008, Searchinger et al. 2008, Kim et al. 2009). It is clear that such indirect effects exist, but measuring them or attributing unambiguous responsibility is difficult (Laurance et al. 2007). ILUC is closely tied to the concept of leakage (Ewers & Rodrigues 2008) and of rebound effects (Polimeni et al. 2008): if local efforts to make farms more wildlife-friendly reduce yields, then yields will have to be increased or land converted elsewhere to meet demand. Likewise, there is a leakage effect of habitat protection within a land-sparing strategy: a consequence of sparing forest is that yields have to be increased on farmland.

2.2 Wildlife-friendly farming and land sparing

2.2.1 Wildlife-friendly farming

I use the term "wildlife-friendly farming" to refer to farming practices that, deliberately or not, result in increased on-farm populations of at least some wild species relative to other systems. Figure 2.1a provides an illustration of a landscape incorporating wildlife-friendly practices such as retention of wooded patches. Typically, but not always, adoption of such systems incurs a yield penalty (Green et al. 2005). There is strong evidence that such yield penalties are prevalent. In the EU, for example, farmers are paid more than $2.5 billion per year to adopt environmentally sensitive practices (Balmford et al. 2005).

a b

Figure 2.1. Examples of (a) a landscape based on wildlife-friendly farming, and (b) a landscape based on land sparing. Image (a) shows a farm mosaic, with small field sizes, a diversity of crops, fallow land and remnant or planted patches of trees. Image (b) shows part of an oil palm plantation and an area of natural forest. Each image covers an area of roughly 4 km^2.

In many circumstances, the existence of a yield penalty is an inevitable consequence of the features of a farming system that make it favourable for biodiversity. Many farmed landscapes support large numbers of wildlife species because they contain fragments of natural or semi-natural habitats such as forest, grassland and wetland. These fragments often remain because they are on land that would be impractical or unprofitable to convert, or because farmers have not yet had the time, equipment or capital to convert them. If the conversion of such fragments would both increase the profitability or food energy output of the farm and diminish the populations of certain wild species, then it is clear that the farming system that includes the retention of such fragments is both wildlife-friendly and incurs a yield penalty. Such cases are not restricted to those where the wildlife exists mainly in natural habitat fragments. In many instances, wild species depend upon cropland and pasture, but can only do so because the management of the farmed land has features that allow them to find food and shelter. There are several intrinsic reasons why methods used to increase the yield and profitability of farming can make the persistence of wild species less likely, including the following:

(1) Physical competition

Wild plant species tend to compete for light and nutrients with domesticated crop plants, but often provide no usable products. They also support associated species including animals, fungi and epiphytes. Hence, reducing populations of wild plants on farmed land is likely both to increase yield and profitability whilst at the same time reducing populations of other species (e.g., Haro-Carrión et al. 2009).

(2) Life-history constraints

Annual yield and profitability of farming tends to be higher if more than one harvest can be taken from the same land within a year and if fallow periods (when land is taken out of production) can be reduced or avoided. Wild species have time constraints on their life-history processes. They require a minimum time in which to germinate and set seed, or to rear young in a fixed area, nest or burrow. Hence, the shortening of crop cycles by using faster-growing varieties, fertilisers, or mechanisation of land preparation and harvesting can lead to the shortening of periods in which wild species can perform these essential functions. Examples include the elimination of bird species that nest in crops or grassland when harvesting is mechanised (e.g., Green et al. 1997).

(3) Biocides

Pests, diseases and parasites of domesticated plants and animals tend to reduce yields and profitability. Eliminating or controlling pests will clearly have a negative effect on target species, and it can have effects on non-target species also. Pest control agents are often biocides or other biologically active substances that disrupt physiological processes, and so are more likely to have a negative than a positive effect on non-target species. Furthermore, domesticated crops and livestock are predominantly at low trophic levels (primary producers and herbivores) whereas wild species are more widely distributed across trophic levels. Hence, wild species can often be expected to be adversely affected by accumulation of persistent toxins, or disruption of food web connections, that are beneficial or neutral to domesticated species. The unanticipated effects of organochlorine pesticides on birds of prey are an example (e.g., Newton et al. 1993).

There are cases where maintaining some degree of ecological integrity is beneficial to humans and wild species alike. These include the benefits of associated biodiversity in providing pest control and pollination services, maintaining and restoring soil fertility, enhancing the well-being of land users, providing shade to livestock, protecting soil from erosion and storing carbon. While these synergies are to be welcomed and encouraged, the benefits provided by wild species can often be substituted or provided more cheaply by artificial inputs or non-native species. Managing a landscape for ecosystem services does not ensure that wild species will be able to persist in it (Scherr & McNeely 2007).

Alternative agriculture, organic farming, agroforestry and traditional farming systems are sometimes assumed to be wildlife-friendly, but none of those designations offers any guarantee that they support increased populations of wildlife. So, while these often meet the definition of wildlife-friendly farming systems, they do not invariably do so. To take an extreme example, an agroforestry system based on alien invasive species of trees and/or cover crops might be more damaging than beneficial to on-farm wildlife, even if it might be beneficial from the perspective of reducing soil erosion. To illustrate the range of existing wildlife-friendly farming systems, I summarise farming practices or interventions that have been claimed to provide benefits for farmland wildlife in Table 2.1, including a few which, while they might have agronomic advantages, are probably in fact detrimental to wildlife. Many of these interventions have well-documented and substantial benefits to native species, compared to other conventional farming methods. Diverse, structurally-complex agroforestry systems such as shaded coffee *Coffea* spp. and cocoa *Theobroma cacao*, have been the focus of dozens of empirical studies, which have confirmed for a range of taxa that they support greater species richness and more forest species than simplified, unshaded systems (reviews: Perfecto et al. 1996, Schroth & Harvey 2007, Bhagwat et al. 2008, Scales & Marsden 2008, Holbech 2009), although Ricketts et al. (2001) found that the species richness and abundance of moths in Costa Rica were better explained by how close coffee farms were to forest fragments than by the presence or absence of shade trees.

Table 2.1. Farm interventions that have been claimed to provide benefits for wildlife, with an assessment of whether they tend to benefit many (++), few (+), or no (.) native species, or to have mainly negative effects on native species (–). Examples of each sort of system are provided, alongside their limitations as a conservation tool, their collateral benefits and their collateral costs. (Based on reviews by Benton et al. 2003, Kleijn & Sutherland 2003, Gyasi et al. 2004, Schroth et al. 2004, Bengtsson et al. 2005, Pretty et al. 2006, Scherr & McNeely 2007, Bhagwat et al. 2008, Scales & Marsden 2008).

Intervention	Wildlife benefits	Limitations as a conservation tool	Collateral benefits	Collateral costs	Examples
Retain native canopy trees	++	Limited tree recruitment	Carbon storage, pest control	Can compete with crops	Shaded crops, swiddens
Plant native trees	++	Typically few species planted	Carbon storage	Can compete with crops	Shade trees in agroforests
Retain native vegetation	++	Edge effects, isolation	Pollination, pest control	Limits area for crops	Forest, grassland fragments
Retain small waterbodies	++	Depends on size, matrix quality	Pest control, water source	Limits area for crops	Ponds, streams, ditches
Introduce set-asides	++	Impermanent	Pollination services	Reduces potential yield	Uncut field margins
Introduce linear features	++	Edge effects	Barrier to livestock, wind	Can obstruct machinery	Hedgerows, live fences
Retain long fallow periods	++	Impermanent	Soil fertility	Limits area for crops	Bush fallow, grass fallow
Reduce grazing	++	Loss of native herbivores	Erosion control	Can reduce potential yield	Marginal grasslands
Avoid/reduce pesticide use	++	Little effect on habitat structure	Can enhance pest control	Can reduce pest control!	Organic farming, IPM
Avoid/reduce fertiliser use	++	Little effect on habitat structure	Reduced pollution	Can reduce potential yield	Organic farming
Retain isolated trees	+	Isolation	Shade for livestock	Can obstruct machinery	Remnant trees in pasture
Extend/reduce frequency of harvesting	+	Benefits few species	Reduced costs	Can reduce potential yield	Late mowing of meadows
Avoid/reduce tillage	+	Benefits few species	Erosion, carbon storage	Pest control costs	Maintenance of stubbles
Avoid/reduce use of fire	+	Clearance is still damaging	Erosion control	Pest control costs	*Proka* system in Ghana
Control water levels	+	Subject to crop requirements	Soil fertility	Can reduce potential yield	Flooded wet meadows
Create artificial nest sites	+	Benefits few species	Pest control	Direct costs	Nest boxes, skylark plots
Introduce mixed cropping	.	Few wild species	Pest control	Can increase labour costs	Homegardens, relay cropping
Introduce crop rotations	.	Few wild species	Soil fertility	Depends on profitability	Cereals rotated with legumes
Introduce perennial crops	.	Few wild species	Erosion control	Large initial investment	Oil palm, cocoa, etc.
Plant non-native trees	–	Can be invasive	Carbon storage	Can compete with crops	Shade trees in agroforests
Plant cover crops	–	Can be invasive	Soil fertility	Can compete with crops	Fast-growing legumes

2.2.2 Land sparing

Throughout this thesis, I use the term “land sparing” to refer to a land-use strategy that combines the protection of natural habitats on unfarmed land, with high-yielding methods on farmed land, so that the production target for agricultural produce within a province or other large area is met by increasing yields with minimal expansion of farmland. A landscape based on land sparing could look like that in Figure 2.1b. The greater the gap between the potential yields of high-yield farmland and those of feasible wildlife-friendly farming systems in the province, the more scope there is for natural habitats to be spared from conversion by increasing yields meeting production targets on existing farmed land. Typically, but not always, high-yield farming systems fail to support, on the farmland itself, many of the species originally native to the province, or support them only at very low population densities.

2.2.3 Other possibilities

Various intermediate strategies, between wildlife-friendly farming and land sparing, are possible, and critics of what they see as “black-and-white” thinking (Wiens 2007) often propose that a mixed strategy will be the best conservation strategy (Scherr & McNeely 2007, Fischer et al. 2008, Scherr & McNeely 2008). An example is agroforestry buffer zones between areas of forest and high-yield agriculture (Cullen et al. 2004, Koh et al. 2009). It might also be possible to reconcile high-yielding land uses with high population densities of at least some wild species: “reconciliation ecology” (Rosenzweig 2003). However, this seems unlikely to be possible for entire natural communities because of the inherent conflicts between farming and wildlife described in section 2.2.1. Proponents of wildlife-friendly farming systems argue that it can be high-yielding (Bhagwat & Willis 2008, Perfecto & Vandermeer 2008). While some forms of alternative or organic agriculture can certainly be high-yielding (Penning de Vries 2005, Pretty et al. 2006, Badgley et al. 2007), there is virtually no evidence to show that those systems can simultaneously support many wild species, nor that they are as high-yielding as all alternatives (Phalan et al. 2007, Phalan et al. 2009, Struebig et al. in press).

2.3 Density-yield functions

Two key questions therefore, which this thesis aims to answer in the context of southwest Ghana, are (1) how large is the difference in yield between wildlife-friendly farming systems and others that are less favourable for wild species (the yield penalty)? and (2) to what extent can wildlife-friendly farming systems provide suitable habitat for native species, compared to systems based on land sparing? If wildlife-friendly farming systems can support good populations of most native species, and if the yield penalty is small, then it is likely to be the best conservation strategy for a given production target (Perfecto & Vandermeer 2008). If, on the other hand, wildlife-friendly farming fails to support large populations of most species, and if the yield penalty is large, land sparing would be a better strategy. If the situation lies between those extremes, an intermediate strategy could be best.

A formal model for evaluating the trade-off between biodiversity conservation and food production and thereby identifying which strategy meets production needs at lowest cost to wild species was developed by Green et al. (2005). The model focuses on the relationship between the population density of a species in a place, and its agricultural yield: the density-yield function. Given any production target, the shape of this function can be used to identify the land-use strategy that will maximise the population of that species in the province, whether wildlife-friendly farming, land sparing, or something in between. Species' responses to increasing yield can be categorised as follows into five types based on the shape of their density-yield functions.

2.3.1 Supersensitive

Some species are intolerant of any modification of their habitat to allow agricultural production and only occur in virtually intact natural habitat. The population density of a Supersensitive species is reduced to zero at any yield > 0, producing an L-shaped density-yield function (Figure 2.2a). The number of Supersensitive species, defined as species unique to virtually unmodified habitat, ranges from less than 10% to more than 50% of all species present, for a range of vertebrate, invertebrate and plant taxa in tropical countries (Daily et al. 2001, Hughes et al. 2002, Green et al. 2005, Barlow et al. 2007a).

2.3.2 Sensitive

Sensitive species are those whose populations fall off rapidly with increasing yield: they have convex density-yield functions (Figure 2.2b). Some Supersensitive species as identified by empirical data collection would probably be revealed with greater sampling effort to be Sensitive species. Equally, greater sampling effort would likely also reveal more Supersensitive species than were initially detected, because many of them are rare and are therefore not detected in limited surveys of unmodified habitats. In any case, Supersensitive species are essentially just an extreme version of Sensitive species. Sensitive species make up the category for which farmed habitat is most likely to be an undetected demographic sink. That is, although they are recorded on farmed land, especially that near to unfarmed habitat, their population growth rates would be negative on farmed land if it were not for immigration from unfarmed land (see also section 2.6.3). For any given production target, the overall populations of both Supersensitive and Sensitive species will be highest in a farmed landscape based on land sparing (Green et al. 2005).

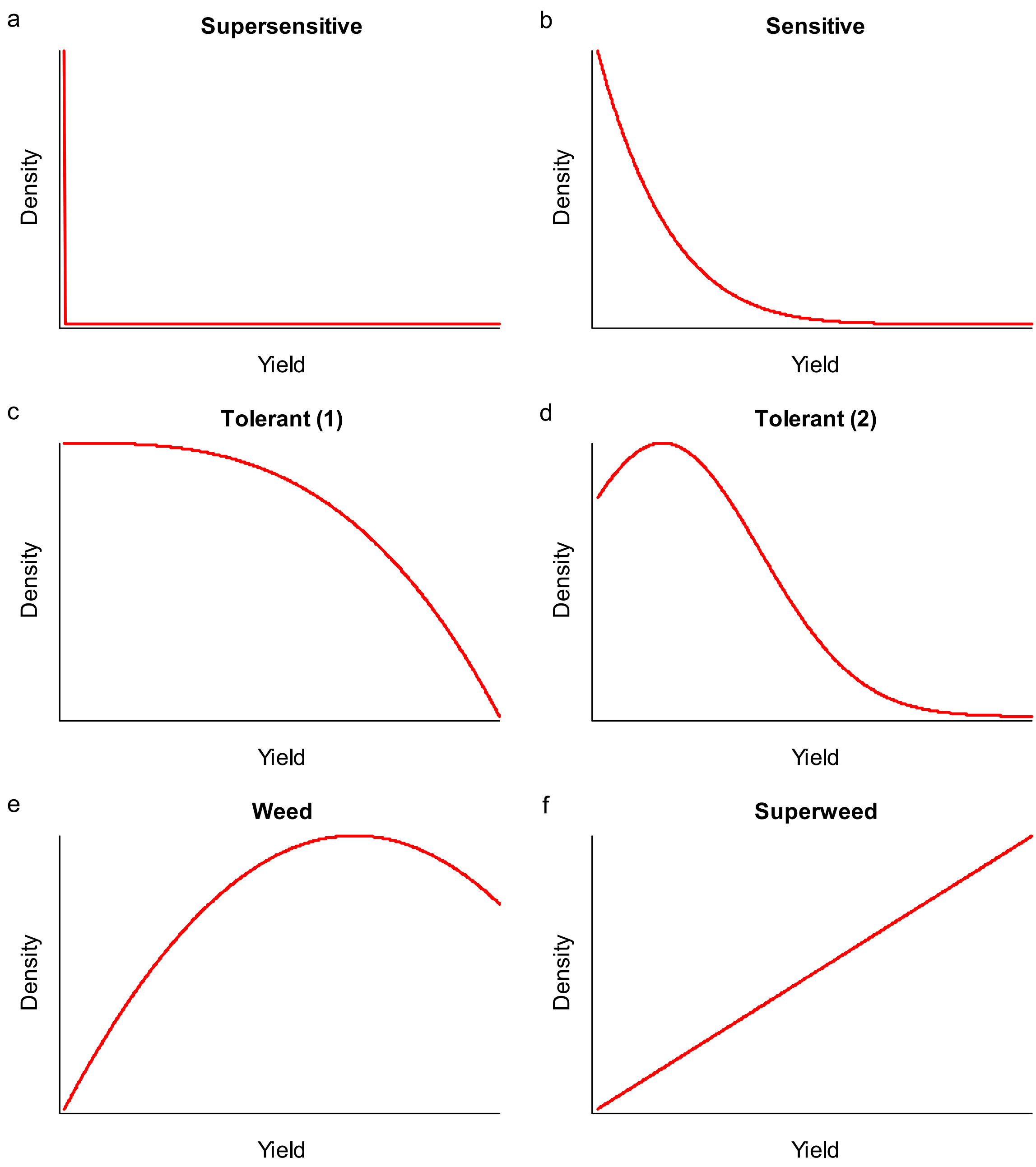

Figure 2.2. Idealised examples of density-yield functions, for (a) Supersensitive species, (b) Sensitive species, (c,d) Tolerant species, (e) Weeds and (f) Superweeds.

2.3.3 Tolerant

Tolerant species are those which can tolerate at least some forms of low-yield farming by maintaining relatively high (or even higher) population densities on farmed land compared to those in unfarmed land, but which nevertheless then declines as yield increases further. They have density yield functions which are either entirely (Figure 1.2c) or partly (Figure 1.2d) concave. Tolerant species will, for a given production target, generally have highest overall populations in a province where farming is based on wildlife-friendly farming practices at the lowest permissible yield. However, if they have peaked or only partly concave functions, their highest overall population can be at an intermediate or even maximum yield (depending on the production target, see Green et al. 2005 supplementary material, and section 2.4). I include all species with density-yield functions which are concave at any point as Tolerant, a conservative assumption if we expect most species to be Sensitive or Supersensitive[3].

2.3.4 Weeds

Weeds are species with their lowest population density at zero yield (Figure 2.2e). However, their highest population density is not found at the highest possible yield. These include species of the original habitat that have adapted successfully to agricultural habitats, but perhaps more typically, they include habitat generalists that naturally occur only at low densities at zero yield because the natural habitat there (e.g., forest) is not their main habitat. They also include species not originally present in the province, which do well in agricultural land-use types that resemble other biomes. Regardless of land-use strategy, these species will always have equivalent or larger overall populations in a province that is being farmed compared to one which is not.

2.3.5 Superweeds

Superweeds are a special type of weeds. They also have their lowest population density at zero yield, but they reach their highest population density at maximum yield (Figure 2.2f). These species will always increase as the production target increases, regardless of land-use strategy. They include the most adaptable and ever-present commensals of agricultural systems.

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[3] Strictly, I define species as Tolerant only if the concave part of the curve exceeds the perfect equalising trade-off, i.e., a straight line drawn from the density at zero yield to the density at maximum yield.

2.4 The production target

The production target is the total amount of food (or other agricultural commodity) that needs to be produced from a province. It would rarely be considered an explicit target in policy by political decision-makers: more often, it is a quantity determined indirectly, by market demand, and implemented through the decisions and actions of farmers and their customers. Market demand is in turn directly influenced by human population size and per capita consumption (section 2.1.2). For any given production target and any individual species, the yield level, and therefore land-use strategy (wildlife-friendly farming, land sparing, or intermediate) at which that species' overall population size in a province will be maximised can be determined from its density-yield function.

The trade-off approach developed by Green et al. (2005) is based on a simple, two-compartment model of a province, in which one compartment is farmed at a uniform yield and has a uniform density of a species, and the other is unfarmed (say, forest). A given production target can be met either by farming a small area at high yield and sparing a larger unfarmed area than would otherwise be the case (land sparing), or farming a large area at low yield. The latter strategy involves wildlife-friendly farming as regards Sensitive and many Tolerant species, in that their densities on farmed land are higher at low yield than at high yield. However, their total populations on farmed and unfarmed land combined will not necessarily be highest with low-yielding farming. If the production target is scaled such that a production target of one is equivalent to farming the entire province at maximum yield, then the overall population size of a species at a given yield can be found on a graph of density versus yield by locating the point at which the chord from the intercept of the density-yield curve to the point on the curve for the specified yield intersects a vertical line drawn at the production target value. When the production target is scaled in this way, yield levels lower than the production target are not permissible because the target would then not be met even if the whole province was farmed. The yield at which the species' population is maximized is therefore the yield that gives the highest intersection of the chord with the vertical line representing the production target (Figure 2.3). This method is ingenious because the overall population size of the species (relative to its value if the whole province consisted of intact habitat) is given by the *y* value of that chord at that intersection. As can be seen from Figure 2.3, the land-use strategy that will maximise the population of a species can depend on the production target, because in a two-compartment model the parts of the density-yield function with yields lower than the production target are not permissible.

In practice, real provinces have more than two compartments, and most landscapes are made up of a patchwork of different land uses, some of them being farmed at different yields. Empirical data on species' densities and yields for each land use type could be used in a model to estimate overall population sizes of species in such landscapes for a given yield. The overall population size is equal to the sum of the population sizes in each land-use compartment, where the compartment population size is the density of that species in that compartment multiplied by the area of the compartment. That is the approach I take in Chapter 7 when simulating future population sizes of species in my study area in Ghana.

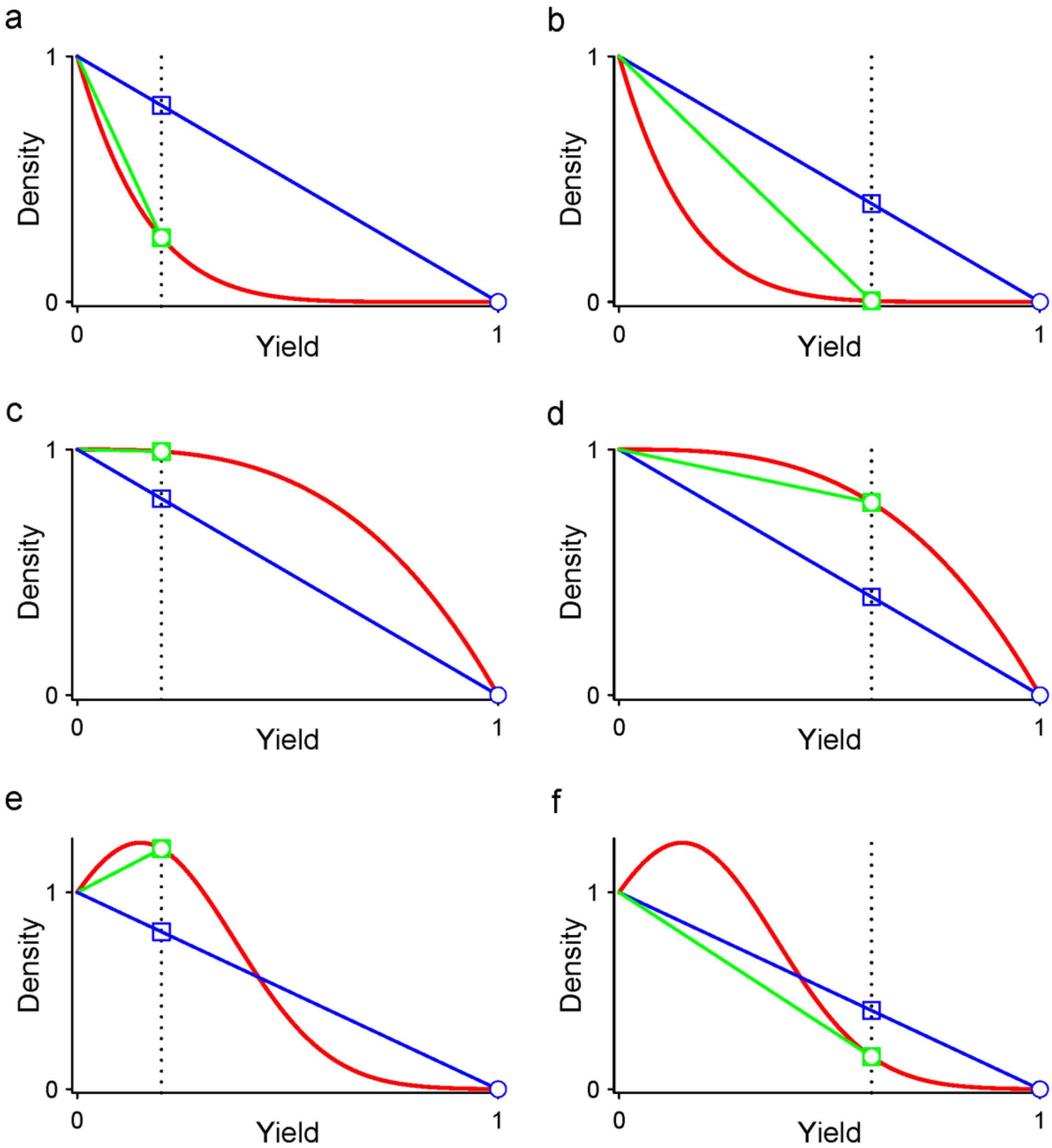

Figure 2.3. Idealised examples of density-yield functions (red lines), with the dotted line indicating a low production target (a,c,e), or a higher production target (b,d,f). In each case, the overall population size of the species in a landscape farmed at lowest yield is given by the *y* value at the green square, and the overall population in a landscape farmed at maximum yield is given by the *y* value at the blue square, relative to the population size if the entire province was unfarmed. For a Sensitive species, the overall population will be highest with land sparing at maximum yield whether the production target is (a) low or (b) high. For a Tolerant species, the overall population will be highest with wildlife-friendly farming at the minimum permissible yield whether the production target is (c) low or (d) high. However, for a Tolerant species with a more complex density-yield function, the overall population will be highest with wildlife-friendly farming at the lowest permissible yield if the production target is (e) low, but will be highest with land sparing at the maximum yield if the production target is (f) high. See text and Green et al. (2005 and supplementary information) for more detailed explanation.

2.5 Biodiversity surrogates

It is rarely practical to measure the population densities of all species of all taxa present in even a very small area, let alone across entire landscapes, although attempts have been made (Langreth 1994). The approach typically taken, when the aim is to assess the influence of disturbances such as land-use change or agricultural intensification, is to use cross-taxon surrogates, or "cross-taxon disturbance response indicators" (Gardner in prep.). These are taxa which can be used as surrogates of responses by less well-known taxa, as well as being of interest in their own right. Different taxa show considerable divergences in response to disturbance when measured using simple abundance or species richness metrics (Lawton et al. 1998, Schulze et al. 2004). However, when assessed by community similarity metrics, there is considerable congruence between the responses of large, well-studied taxa, including birds, trees, butterflies and dung beetles, to disturbance (Su et al. 2004, Barlow et al. 2007a). Similarly, while spatial congruence in patterns of species richness was low for a range of plant and animal taxa in Uganda, sets of priority forests selected using one taxon as a surrogate for others were quite efficient at capturing species richness in other taxa (Howard et al. 1998). No one taxon is a perfect surrogate for wider patterns of biodiversity, and few generalisations can be made from assessments based on very small numbers of species (e.g., Makowski et al. 2007, Tichit et al. 2007) so it is preferable to use a set of complementary indicator taxa rather than relying on one taxon or a small number of species. Birds appear to be good surrogates for large-scale patterns in other taxa (Rodrigues & Brooks 2007), and trees, as the main resource for herbivorous insects in forest habitats, can be expected to be good surrogates for the beetles and other insects which make up the majority of described species (see Chapter 6).

2.6 Measuring density-yield functions

There have been few attempts to measure density-yield functions empirically, and virtually all of them have been flawed in some respect. In this section I consider the minimum information required to measure density-yield functions adequately.

2.6.1 Sampling design

Studies of the wildlife value of modified landscapes frequently suffer from a number of design flaws and limitations, including the following: (1) The minimum requirements for robust generalisation, of selection of representative study sites and replication, are rarely met (Dunn 2004). (2) Although researchers strive to find reference habitats against which the effects of disturbance can be measured, these baseline habitats have themselves typically been modified, often heavily, resulting in under-estimation of disturbance impacts (Willis et al. 2004, Willis & Birks 2006, Gardner et al. 2009). (3) Sampling soon after habitat conversion has taken place, and long before "relaxation" will overestimate the number of species that can persist in modified landscapes. It can take decades to centuries before species committed to extinction by landscape modification die out completely (Brooks et al. 1999, Hanski 2000). (4) Enormous effort is required to adequately sample most taxa in tropical forest habitats, and sampling methods for many taxa are not able to fully sample the fauna or flora at all levels, from soil and leaf litter to the canopy, which can be 60 m above the ground (Malcolm and Ray 2000, Henry et al. 2004). Comprehensive sampling is easier in modified habitats, where the vegetation tends to be less dense, and the canopy, if there is one, tends to be more accessible, with the result that the biodiversity value of modified habitats can be overestimated relative to that of forests unless differential detectability of plants and animals in these different habitats is allowed for (Gardner et al. 2007a). (5) Even with some of the problems already noted, accumulation curves for species richness in forest are often steeper than for non-forest habitats, especially when scale is adequately addressed, indicating that considerably more sampling effort is needed to provide robust estimates of total species richness (Missa et al. 2009).

Studies also need to be conducted at scales which are both biologically relevant to the focal species, and which are relevant to decision-making. In many cases, this will require well-spaced sample sites of tens or hundreds of ha, and study areas of tens or hundreds of km^2 (e.g., Barlow et al. 2007b, Gardner et al. 2007b). Sampling is frequently limited to small-scale and closely-spaced study sites, which are vulnerable to edge effects and spillover effects from adjacent habitats. The term “edge effects” is typically used to refer to the effects on species’ populations in relatively intact habitats, of changed physical conditions and ecological interactions near edges with modified habitats: for example, the increased risk of wind and fire damage to trees in forests adjacent to pastureland (Laurance & Bierregaard 1997, Laurance 2000). I use the term “spillover effect” to refer to the sampling artefact caused by sampling in a modified habitat close to a more intact habitat: many of the species recorded are likely to be strays or visitors from the intact habitat, and might be unable to persist without it (Ricketts et al. 2001, Anand et al. 2008, Norris 2008, Sridhar 2009). Spillover effects are likely to be prevalent in many studies, as modified habitats are often sampled, for convenience, close to baseline habitats, and are likely to provide an overly optimistic assessment of the value of those modified habitats in the future. Similarly, if control sites are located in accessible parts of natural habitats near edges, they might provide an underestimate of the wildlife value of natural habitats. Spillover effects can result from source-sink dynamics, in which reproductive output is low, and species’ presence is only maintained by immigration from more suitable habitats (Brawn & Robinson 1996). There are three ways of addressing the problems of edge and spillover effects: (1) collect a measure of the importance of habitats to each species, e.g., by measuring their population densities, rather than simple presence/absence, (2) minimise the effects by sampling far enough from edges or source habitats for immigration and edge effects to be inconsequential, and (3) account for spillover and edge effects by measuring them (e.g., Ewers & Didham 2008). Ideally, researchers should combine (1) and (3), but in this study I combine (1) and (2).

2.6.2 Quantitative measurements of yield

The element most commonly lacking from studies of the wildlife value of modified landscapes is some quantitative measure of crop yield, economic value or opportunity cost (for an exception, see Makowski et al. 2007). This is essential for placing the results of biodiversity surveys into a decision-making context. For example, studies of neglected and abandoned plantations of tropical crops show that they can support high species richness and threatened forest species (Roth et al. 1994, Holbech 2009). However, if those land uses are unproductive and unprofitable, there is little justification for maintaining or expanding them. Their wildlife value would likely increase if they were allowed to revert to forest, while their agricultural productivity would increase with increased management. In order to generate density-yield functions and therefore have the means to evaluate the trade-off between increasing yields or expanding wildlife-friendly farming, a measure of yield is required.

When this aspect has been considered at all by ecologists, proxies for yield such as management intensity indices, percentage canopy cover or nitrogen inputs have typically been used (Steffan-Dewenter et al. 2007, Firbank et al. 2008). Maximising nitrogen inputs might be an appropriate objective for a fertiliser company, and measuring species' responses to increasing nitrogen is scientifically interesting, but to answer the question of how to minimise the trade-off between food production and biodiversity conservation, direct information on food production is required. Proxy measures are useful in understanding how biodiversity value changes across agricultural gradients, but unless they are directly proportional to yield, they are not useful for designing conservation strategies.

"Yield" refers to the output of agricultural produce per unit area of land. For studies at a landscape scale, it should be expressed in terms of total output per unit area and time (Kates et al. 1993). In other words, it should include production from all crops grown, and take into account unproductive fallow periods and uncultivated parts of the landscape, over an appropriately large area. In order to combine information from different crops, units such as kilograms of fruit need to be converted into standard currencies. The two most suitable currencies are food energy and monetary currencies. Food energy has the advantage that it is not affected by market fluctuations, and that it is directly relevant to human nutritional requirements (FAO 2004). However, it is not appropriate for some kinds of crops, such as fibre crops.

For combining food and non-food products, monetary currencies are more appropriate, although the value of specific products can fluctuate considerably depending on market prices. Monetary currencies have the added advantage of allowing the analysis to take account of input costs: high-yield farming sometimes relies on costly inputs of fertiliser or machinery, for example. Estimates of net monetary values will vary depending on decisions such as whether and how to include the cost of smallholders' labour (Batagoda et al. 2000). Monetary yield metrics can be considered as metrics of opportunity cost, which is the value of something you have to forego in order to do something else (Naidoo & Iwamura 2007). To conserve species' populations in wildlife-friendly farmland, farmers typically have to forego some part of their potential yield, while to conserve species using land sparing, farmers have to forego the production they could have had from the "spared" land.

In this thesis, I examine both food energy and monetary currencies for yield. The flows of goods and services in rural tropical landscapes also include non-agricultural components such as timber, bushmeat and other non-timber forest products (NTFPs), and ecosystem services such as water flow regulation and carbon storage (Campbell & Luckert

2002). I was not able to assess the value of these goods and services directly, but I discuss their significance in Chapter 4 and again in Chapter 8.

2.6.3 Quantitative metrics of biodiversity value

As will be explored further in Chapter 5, common aggregate measures of biodiversity value such as species richness, diversity indices and combined abundance do not provide sufficient information to be useful in assessing trade-offs between different land-use or management strategies, although they have been widely employed for this purpose (e.g., Perfecto et al. 2005, Dorrough et al. 2007, Steffan-Dewenter et al. 2007, Attwood et al. 2009, Firbank et al. 2008). There is a bewildering variety of ways to present species data from land-use comparisons (Basset et al. 2008), but some are more useful than others. Metrics of biodiversity value should, at a minimum, provide some measure of the value of a habitat to the species using it, and also provide some information on species identity.

A simple measure of the value of a land use to a species is that species' abundance or population density. At a landscape scale, measuring species' population densities in different land-use types provides a measure of the value of those land uses to those species, and implicitly takes into account the most acute local impacts of agrochemical use. However, at a fine temporal or spatial scale, density can be a misleading indicator, for four reasons: (1) source-sink dynamics, as discussed in section 2.6.1, (2) studies conducted in one season can miss the fact that certain habitats are critically important for a species during another season, (3) population density can be an indicator of past rather than present habitat quality, if individuals are slow to redistribute themselves, or immobile, as with trees, (4) low-quality habitats can contain high densities of immature or low-quality individuals which are unable to access high-quality habitat defended by territorial high-quality individuals (Van Horne 1983, Vickery 1992). The first of these problems can be addressed by sampling far enough from source habitats that immigration is inconsequential. The second can be addressed by sampling in different seasons. The third is reduced by sampling in areas where habitat modification occurred some time ago, rather than recently, and by considering species' life histories. The fourth is minimised by sampling at large rather than fine scales, and by using sampling techniques designed to detect mature reproductive individuals rather than immatures. Other, more complex metrics than density are also possible, such as breeding success (Mukherjee et al. 2002), or the reproductive value of individuals occupying an area (Searcy & Shaffer 2008), but the weaknesses of population density as a metric are outweighed by the advantage that it can be collected without great cost for a large number of species.

Biodiversity metrics which ignore species identity, such as richness and diversity, are inadequate for studies of trade-offs because maximising local richness or diversity is rarely an appropriate conservation objective. It is more important to maximise the contribution of a landscape to global richness and diversity, especially by minimising species' risk of global extinction, because global extinction is irreversible. Species' identities are important for this because not all species are at an equal risk of extinction under current or future conditions. Local species richness can rise while conservation value falls: for example, in a study by Bobo et al. (2006a), species richness of understorey plants was high in plots with annual crops, but almost no species were shared with closed-canopy forest, and crop species and non-native plants were included. Species' identities are taken into account in community similarity metrics, to the extent that these metrics incorporate information on whether each species occurs in the baseline natural habitat, but not to the extent of considering other attributes of species, such as the extent to which they are threatened with extinction, or are restricted to a small global range. These latter attributes are important from a conservation perspective, because they determine the extent to which local impacts will affect species' global populations, and therefore their risk of global extinction (Fermon et al. 2000, Dunn & Romdal 2005, Cleary & Mooers 2006). To better understand the conservation implications of habitat disturbance, it is necessary to distinguish species of current and potential conservation concern by identifying those with threatened status, small ranges, and those ecologically restricted to intact habitat (Hawthorne 1996). Decision-makers require species-specific information to be aggregated in some way, and summarising patterns of density-yield functions or estimated extinction probabilities (see Chapter 7) for groups of interest, such as restricted-range species, serves that purpose.

2.7 Conclusion

Evidence suggests that a trade-off between yield and biodiversity value is prevalent in agricultural landscapes, although that relationship is unlikely to be linear. With increasing recognition that on-farm decisions have off-farm impacts, it is apparent that wildlife-friendly farming interventions that reduce yield can have overall negative impacts on wild species by adding to pressure for production to increase elsewhere. Quantitative information is required, both on species' population densities in different land uses, including baseline "intact" habitat, and on the yield of those land uses, on which to base decisions about the extent to which increasing food production should come from expanding farmland area or raising yields. Impacts of farming vary enormously among species, so it is important to collect information on individual species rather than using aggregate measures such as species richness. Density-yield functions for individual species can be used to determine whether, at a given production target, their populations will be maximised with a wildlife-friendly farming strategy or a land-sparing strategy. Because each different strategy is likely to affect different species in different ways, it is especially important to determine the requirements of those species of highest current and potential future conservation concern.

Chapter 3

Study area: the forest zone of Ghana

Subri River Forest Reserve, Western Region

‘Nnua nyinaa bewu agya abɛ.’

“All trees will wither but the palm tree.”

Akan proverb

3 Study Area: the forest zone of Ghana

3.1 Reasons for selecting Ghana

I chose Ghana as the country for this study because it fulfilled almost all of a set of prior criteria. I considered only developing countries in the tropics, ideally with tropical forest, because of their irreplaceable biodiversity value and high degree of threat from agriculture (Scharlemann et al. 2004, Green et al. 2005). I narrowed the list of potential study regions to the following: the Atlantic Forests, Cerrado and Rondônia in Brazil, the Yucatán Peninsula in Mexico, Sumatra and Kalimantan in Indonesia, Sabah in Malaysia, West New Britain in Papua New Guinea, southwest Madagascar, northern India, Cameroon, Uganda, the Kenya Highlands, Côte D'Ivoire, Nigeria and Ghana, and searched for an area which met as many of the following criteria as possible (listed in roughly descending order of importance):

(1) Essential: meets the assumptions of the model.

(a) wide variation in agricultural yield (area large enough for this),

(b) some original habitat,

(c) habitat loss and yield independent of clear confounding variables such as altitude, climate, soils and geology (area small enough for this),

(d) preferably, has been farmed for at least several decades, so biodiversity has had time to adjust to changing land use.

(2) Practical: is a feasible area to work in.

(a) sufficient infrastructure to allow access to field sites,

(b) presence of existing research groups or organisations to provide local knowledge,

(c) language is one I already have some knowledge of or can learn easily,

(d) good field guides/reference collections/experts exist for indicator groups,

(e) area is politically fairly stable and free of civil war or guerrilla conflict.

(3) Preferable: is an area important for biodiversity conservation.

(a) a hotspot of species richness or endemism,

(b) there is a clear or immediate threat, or rapid habitat loss,

(c) plans or policies are likely to have a large impact on the area in the near future.

Southwest Ghana met all of these criteria, although it did not meet one additional criterion, having an established research station. It is markedly flat: most land across an area of approximately 25,000 km^2, comprising parts of the Western, Central, Eastern and Ashanti regions, lies below 200 m altitude. Hence, the inherent suitability of land across that area, both for agriculture and for forest species, is relatively constant. Elsewhere, forest often persists only on steep slopes and poor soils, where species' densities might be unrepresentative of fertile flat land. Several large fragments of forest remain (up to 588 km^2), and there is a range of agriculture, from low-yielding, wildlife-friendly smallholder mixed farm mosaic, to high-yielding, wildlife-poor industrial oil palm plantations. There are also groves of wild oil palms intermixed with other trees. Ghana has a long history of farming (Richards 1996), is politically stable, English-speaking, and has a history of research, with three well-established universities in or near the forest zone. I was interested in studying an oil palm dominated system, as this is a very important crop globally, little was known of its biodiversity impacts (Donald 2004), and expansion, driven by rising food and biofuel demand, is rapid (Fitzherbert et al. 2008). In addition, Ghana's forests, as part of the Upper Guinea forests, are of global conservation importance and have been greatly reduced by deforestation (Allport 1991, Martin 1991, Fairhead & Leach 1998, Brooks et al. 2006).

3.2 Forests in Ghana: past and present

3.2.1 Forest cover: paleoecology

The forests of tropical Africa have fluctuated considerably in extent in response to past climatic changes, especially over the last 800,000 years (Maley 1996). An understanding of how forest species might have been influenced by those changes is useful in anticipating their likely responses to future changes to forest cover. Forests were fragmented by savanna, and then expanded again, in cycles lasting around 100,000 years, as a result of changes in global climate (Maley 2001). Forests in Upper Guinea were reduced to their minimum during an arid phase from around 20,000 to 15,000 BP, when temperature was estimated to be 3-4°C lower than the present-day mean, and they were confined to refugia covering only a small area (~25%) of the present-day forest zone (Figure 3.1). For at least three-quarters of the past 800,000 years, African rainforests were less extensive and more fragmented than they would be in the absence of human influence today (Maley 2001). However, while present-day climatic conditions are close to providing conditions for maximum forest extension (Maley 1996), deforestation by people has resulted in patterns of forest cover in Upper Guinea which are at least as restricted and fragmented as they have been in the past, or more so (Figure 3.2). Forest cover has remained more intact in Lower Guinea and the Congo, but even there forests are increasingly threatened by logging and conversion (Laporte et al. 2007, Laurance et al. in press).

Based on findings of stone tools in Guinea and Sierra Leone, human presence in the Upper Guinea forests could date back to before 5,000 BP, but perhaps not much earlier. There is evidence of people further east in Nigeria from around 11,000 years BP (Richards 1996). It seems likely that humans moved into the Upper Guinea forests both from the east and west: yam farmers from the lower Niger, and rice farmers from the Upper Niger and Senegambia. Those early farmers probably relied as much on gathering wild foods, perhaps including the fruits of oil palms, as on the cultivation of crops such as yams and rice. Later, agricultural intensification and high population densities probably created conditions conducive to the spread of malaria, and the high modern rates of sickle-cell gene frequency in the Akan people of Ghana could be evidence for a long history of agriculture and human presence (Richards 1996). Using the same line of reasoning, the forests of southeast Liberia might be those that have most recently been colonised by agriculturalists.

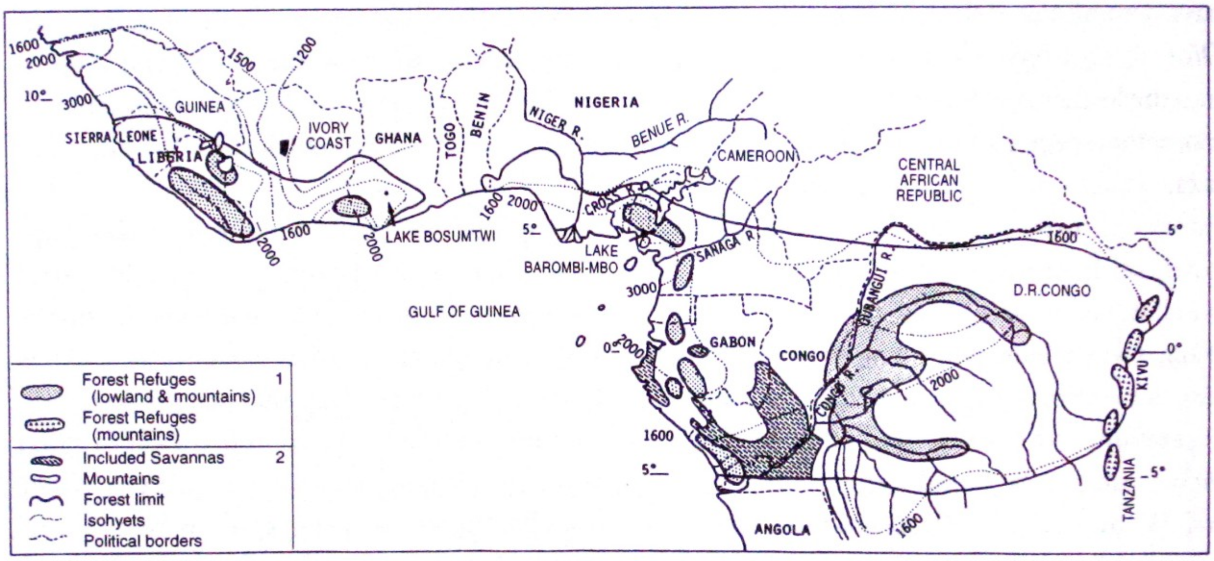

Figure 3.1. Schematic map of forest refugia in the Guineo-Congolian region of Africa during the last maximum arid phase around 18,000 BP, reproduced from Maley (2001). The key refers to (1) forest refuges in 18,000 BP, and (2) forest and savanna zones in the present.

Until the spread of iron tools and widespread cultivation of domesticated crops, human populations likely remained at relatively low densities and had little impact on forest extent (White 2001). Human activities do not invariably impede forest regeneration, and even in areas with regular fires, forests have been documented to recolonise savanna in Côte d'Ivoire, Cameroon, Central African Republic, Congo and eastern Ghana (Maley 2001, F. Dowsett-Lemaire, pers. comm.). This process seems to be assisted by the removal of vegetation cover by farmers and their livestock, which reduces the fuel available to wildfires, but is only possible at low human population densities, and with long-term abandonment of agricultural fallows. In central Africa, large-scale incursions of savanna into forest most likely permitted colonisation of those areas by humans (e.g., the Bantu expansion around 4,000 BP) rather than being caused by them (Vincens et al. 1999, White 2001, Marret et al. 2006).

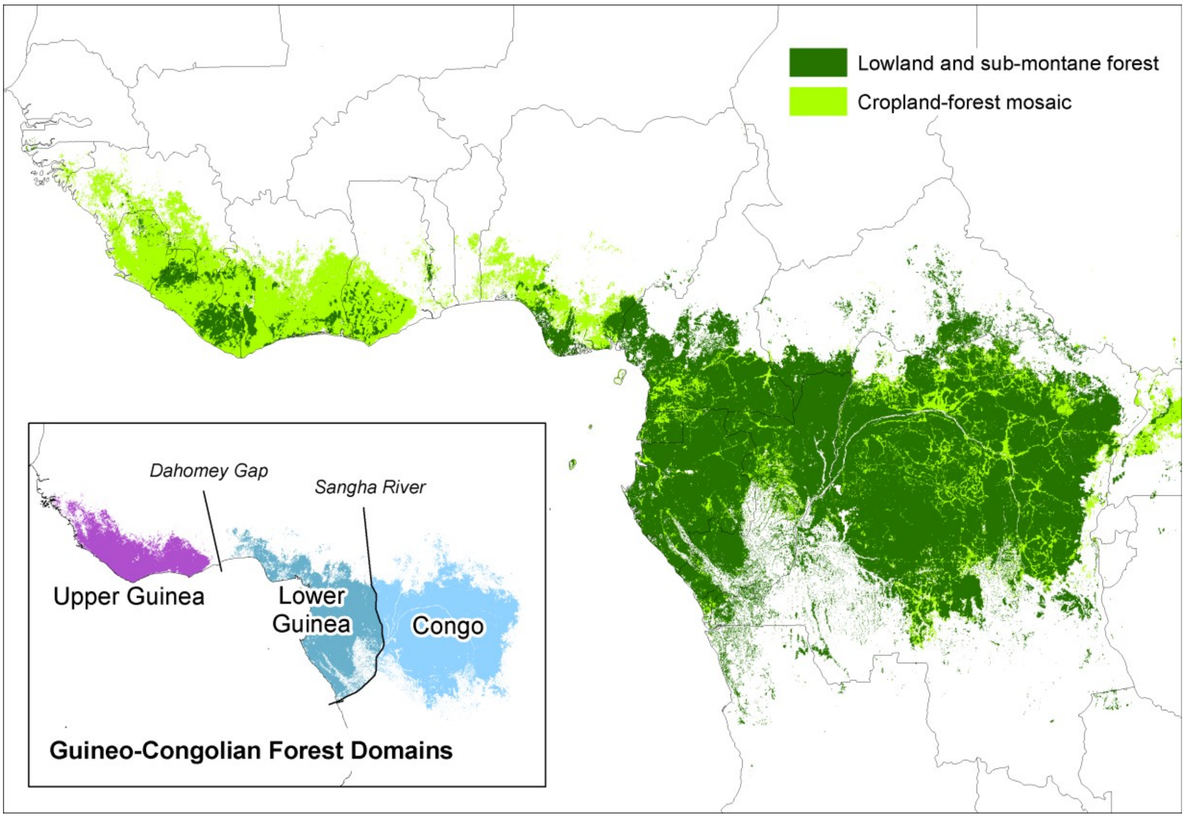

Figure 3.2. Intact forest cover (dark green) and modified forest landscapes (bright green) in the Upper Guinea, Lower Guinea and Congo domains of the Guineo-Congolian forest biome in 2000 (EC JRC 2003). These domains (inset) are the same as used in Chapters 5 and 6 to summarise the degree of endemism of birds and trees.

Vast deposits of oil palm nuts in forest streambeds along the borders between Central African Republic, Congo and Cameroon have been carbon-dated to between 2,300 and 1,000 BP (White & Edwards 2000). Oil palm pollen also appears with increasing frequency in many West African sediment cores during the last 2,000 years, and has been interpreted as an indication of cultivation by humans (Sowunmi 1999). An alternative explanation, however, is that oil palms expanded naturally when climatic changes favoured savanna expansion and forest retreat around 2,500 years BP (Maley & Chepstow-Lusty 2001). In southwest Nigeria, there are palm nut deposits which can be less equivocally linked to human presence, if not cultivation, as they contain shards of pottery over an extensive area (White & Oates 1999). These date to around 700 BP, since which time mature forests have regenerated.

3.2.2 Forest cover: recent history

From the 11^{th} to 18^{th} centuries, successive waves of Akan, Guan, Moshie, Ga, Ewe and other tribes swept into Ghana (La Anyane 1963). These newcomers started to settle along the coast and in parts of the forest zone, as well as displacing the previous occupants of the northern savannas. Perhaps the first commodity to be traded internationally – with the Moors – was the "grains of paradise" spice from the plant *Aframomum melegueta*. In the 15^{th} century, the Portuguese occupied much of the coast, and began trading in slaves as well as introducing new crops, including modern day staples such as maize, cassava and groundnuts. The population of southern Ghana was by this time relatively high, and forest cover might have reached a low point around the early seventeenth century. Portuguese traders were followed by the Danes, the Dutch and the English, and conflict between these groups of Europeans was only eased in the nineteenth century with the abolition of slavery. Rivalry continued between African tribes over access to European export markets. As a result of the slave trading and warfare, especially in the 17^{th} and 18^{th} centuries, human population densities almost certainly declined, allowing some regeneration of secondary forests (Fairhead & Leach 1998). By the end of the 19^{th} century, evidence suggests that between 5 and 5.5 million ha of the original 7 million ha forest zone was forested.

The most recent phase of deforestation in Ghana was initiated towards the end of the 19^{th} century, as export markets developed. Prior to 1895, international trade in monkey skins[4] was more important than that in cocoa, an indication of the abundance of forest mammals at that time (La Anyane 1963). However, exports to Europe of timber, cocoa and palm oil increased rapidly from the end of the 19th century, and Ghana was the world's largest producer of cocoa by the time the first World War started in 1914 (Hart 1982, Martin 1991). Cocoa booms are fuelled by the "forest rent", the agronomic benefits of planting on recently deforested land (Ruf & Siswoputranto 1995), and Ghana's cocoa boom had a massive effect on Ghana's forests. Population growth and agricultural expansion have continued to the present day, and of the original 7 million ha of forest in southwest Ghana (excluding the dry semi-deciduous fire zone), even the most optimistic commentators consider that there is only 2 million ha remaining (Fairhead & Leach 1998).

3.2.3 Implications of past forest change for conservation efforts

Understanding of past changes in forest cover has profound implications for modern conservation efforts. Identifying the locations of past forest refugia is important, because they still support higher concentrations of endemic species than elsewhere, including perhaps the most sensitive species, making them a priority for protection (Hamilton 1981). Van Rompaey (2002) suggests that instead of trying to distinguish primary from secondary forests, a more useful distinction in West Africa can be drawn between wetter, endemic-rich and disturbance-sensitive evergreen forests and drier, more resilient semi-deciduous forests, with few rare species or endemics. Past changes in forest extent, from climatic fluctuations as well as human activities, may already have generated an "extinction filter", wiping out an undocumented number of species (Balmford 1996). The corollary of this is that those species which have persisted to the present day in West Africa have survived thousands years of forest disturbance, and might be relatively resilient to future changes (Holmgren & Poorter 2007). However, the negative impacts of edge effects, fragment

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[4] Hundreds of thousands of skins, presumably mainly of *Colobus vellerosus*, now globally Vulnerable, were exported annually to supply demand in Europe and America for elegant ladies' muffs (Davey 1895).

isolation and a hostile matrix are likely to occur much more rapidly and to be more severe with anthropogenic deforestation than with climatic shifts which occurred over thousands of years. Additional pressures, such as logging, hunting and gold-mining, mean that the fragmentation of Ghana's forests by agricultural conversion has already driven some species that survived past forest fluctuations close to or over the brink of regional extinction (Oates et al. 2000).

3.2.4 Current status of forests

The main forest zones in Ghana have been distinguished on the basis of similarities between their tree species composition, which is determined largely by patterns of rainfall (Hall & Swaine 1976). The study sites selected for this thesis all fall within the moist evergreen and moist semi-deciduous forest zones (Figure 3.3), although parts of Cape Three Points, Subri River and Bonsa River forest reserves also show some affinities with the wet evergreen zone (Hawthorne & Abu-Juam 1995). As is clear from a comparison of Figure 3.3 with Figure 3.4, very little forest exists outside the forest reserves and wildlife protected areas managed by the state Forestry Commission. The forest reserves cover a total area of 1.77 million ha, around 20% of the forest zone, using a more expansive definition than that of Fairhead & Leach (1998). Recent estimates of deforestation in Ghana are that it is losing 2% of its forest annually (FAO 2006). Because of the FAO's expansive definition of forest, which includes wooded land with a canopy cover of more than 10%, this includes savanna woodland, and the deforestation rate could be lower in the forest zone, considering that there is virtually no unreserved forest left. A more plausible, probably conservative, estimate of deforestation in Upper Guinea as a whole is 1% per year (K Norris & J. Gockowski unpublished).

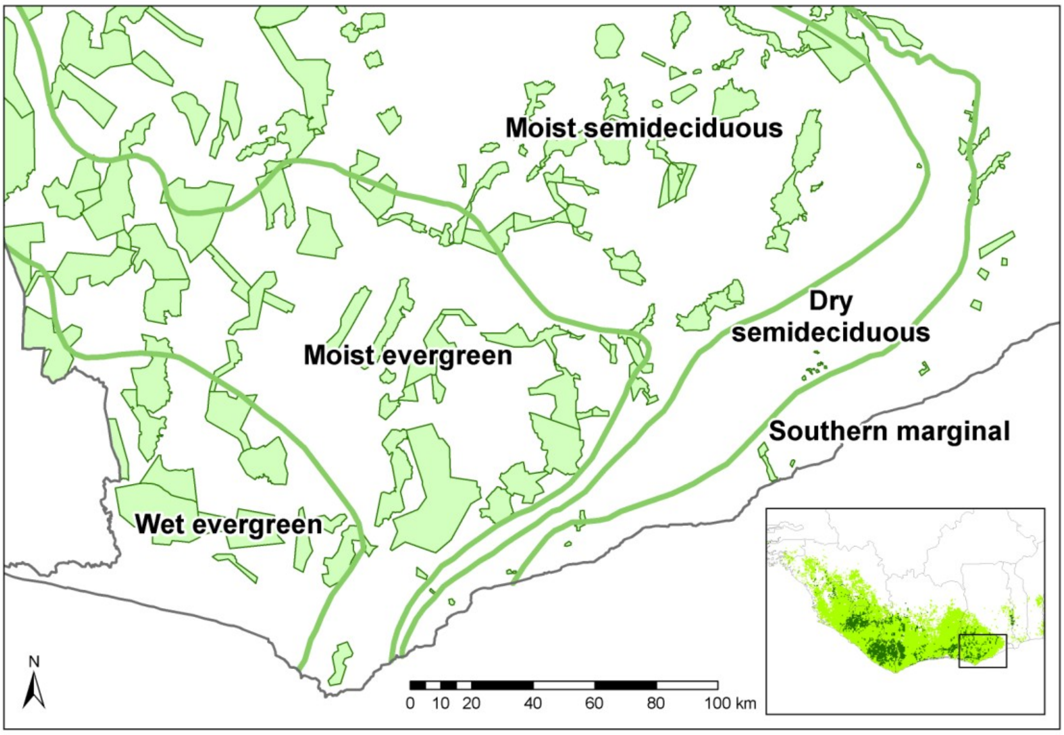

Figure 3.3. Forest reserves and forest zones in Ghana. Inset relates this map to that in Figure 3.2.

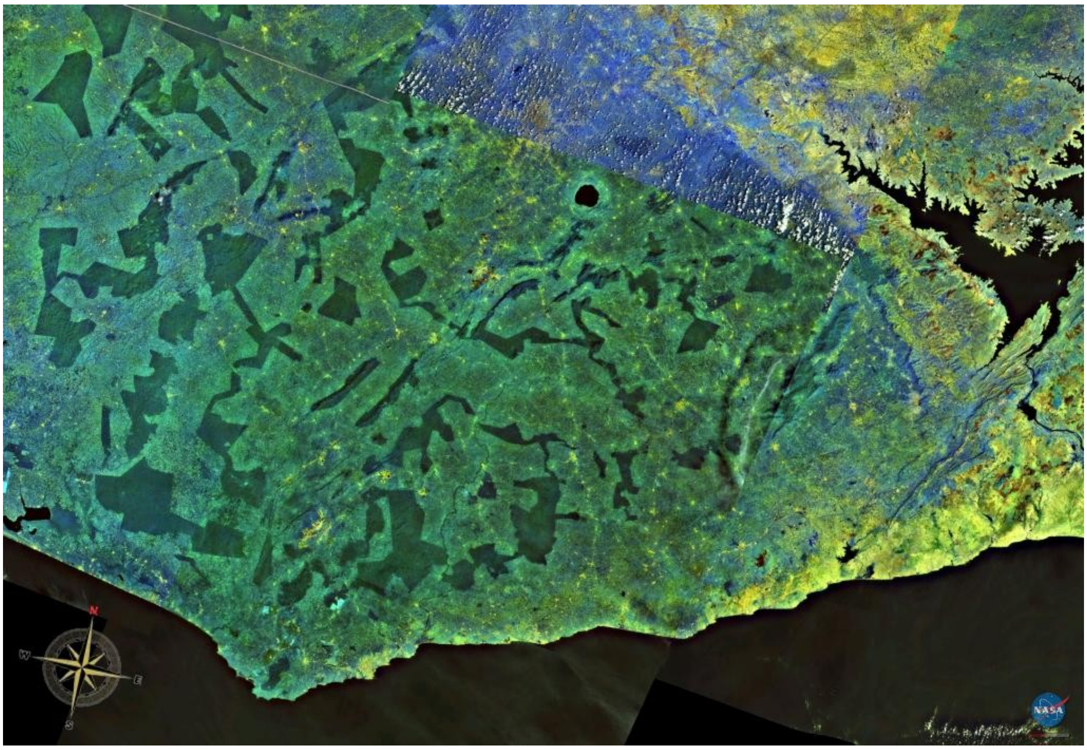

Figure 3.4. Recent satellite image of southwest Ghana (undated) showing that virtually no forest remains except that inside forest reserves and wildlife protected areas (image from NASA World Wind, 2006).

Although Ghana has managed to protect a greater proportion of its natural forests than many developed countries, most are production reserves, and have been degraded to varying degrees by fire, legal and illegal logging, virtually unregulated hunting, small-scale and large-scale mining, and legal and illegal encroachment for farming. Less than 16% of their area is in “ok” to “excellent” condition, and most is degraded to some extent, with more than 28% assessed as being in “very bad” condition or with no forest cover at all (Hawthorne & Abu-Juam 1995). A range of interventions has prevented this degradation becoming even worse. These have included indigenous strategies such as community protection of small sacred areas and customary taboos forbidding the hunting of certain animals, and government regulations such as restrictions on logging and no-logging zones covering entire forest reserves or parts of them, including Globally Significant Biodiversity Areas (Hawthorne 2001, Ntiamoa-Baidu 2001). There are five wildlife protected areas in the southwest of Ghana: Ankasa Resource Reserve/Nini-Suhien National Park, Bia National Park/Bia Resource Reserve, Bomfobiri Wildlife Sanctuary, Kakum National Park/Assin Attandanso Resource Reserve, and Owabi Wildlife Sanctuary. These are in theory protected from all damaging activities, but in practice while Ankasa and Nini-Suhien have been relatively well-protected, Bia Resource Reserve in particular has been severely damaged by logging, and both Bia reserves are subject to heavy hunting pressure.

3.3 Agriculture in Ghana

3.3.1 Major crops

The major crops grown in the forest zone of Ghana are cocoa, oil palm, rubber *Hevea brasiliensis*, cassava *Manihot esculenta*, maize *Zea mays*, plantain *Musa* spp., cocoyam (taro) *Colocasia* spp. and *Citrus* spp. Other crops include cola *Cola nitida*, yams *Dioscorea* spp., rice *Oryza glaberrima*, black pepper *Piper nigrum*, chilli pepper *Capsicum* spp., okra *Abelmoschus esculentus*, garden eggs *Solanum aethiopicum*, pineapples *Ananas comosus*, papaya *Carica papaya*, tomatoes *Solanum lycopersicum* and coffee. Because of trypanosomiasis, there are few livestock other than some goats, sheep and chickens in villages. Raising of pigs, grasscutters *Thryonomys swinderianus* and snails *Achatina* spp., and fish-farming, are done on a small scale.

As noted in section 3.2.2, Ghana was at one time the world's largest producer of cocoa, and its exports of cocoa made up around 40% of total world output at the time of the country's independence in 1957 (Hart 1982). However, the risks of relying too heavily on a single commodity crop were made painfully clear when international cocoa prices crashed in the mid-1960s (Government of Ghana 2005). The cocoa revenues that had financed infrastructure, education and other development initiatives suddenly dried up. The Ghanaian economy has never fully recovered from that crash, but cocoa remains today the country's most important cash crop, and one of its most important sources of foreign exchange earnings, alongside timber and gold (Vigneri 2008). Ghana supplies around 17% of world total production of cocoa (FAOSTAT 2009).

Unlike cocoa, oil palm is a native West African species and has been used by people for food for hundreds if not thousands of years (Maley & Chepstow-Lusty 2001). Although it originated in West Africa, global production is dominated by two countries in southeast Asia, Indonesia and Malaysia. Nigeria is the world's third largest producer, and has almost as much area under oil palms as Malaysia, but its yields are only 13% of those in Malaysia (FAOSTAT 2009). Ghana produces about 1% of the world total. According to information from the President's Special Initiative (PSI) on oil palm, Ghana produces far less palm oil – 100,000 tons – than it consumes: 240,000 tons (PSI 2005). However, these figures are contradicted by the FAO estimates of oil palm fruit production of around 2 million tonnes of oil palm fruits annually from 2004 to 2007. Even if oil was extracted relatively inefficiently from these fruits with an oil extraction ratio of 0.12 (commercial extraction ratios in Ghana are 0.16-0.21) this would be adequate to meet domestic demand. Regardless of the level of domestic demand, palm oil is in high demand on global vegetable oil markets so there is considerable scope for Ghana to increase production. Global production of palm oil exceeded that of soy oil in 2004, and now more of it is produced globally than of any other vegetable oil (FAOSTAT 2009).

The diets of both urban and rural Ghanaians are based heavily on domestic staples including cassava, maize, plantain, cocoyam and yams; imported rice is also a major component, particularly in urban centres. Production of cassava and plantain increased by more than 4% annually in West Africa's forest zone between 1988 and 2007: most of this increase came from an increase in planted area, although yields also increased by 0.6-0.8% over that time (Norris et al. submitted). Production of cocoyam also increased by more than 5% annually between 1998 and 2007 in the same region, exclusively by increases in planted area. Similar patterns were found for oil palm and cocoa: most recent increases in production have been from expansion of crop area, rather than from increases in yield (Norris et al. submitted).

3.3.2 Farming methods

The geology underlying southwest Ghana is very old: mainly igneous and metamorphic rocks dating from the Pre-Cambrian (Juo & Wilding 1996). Unlike wetter parts of the Guineo-Congolian forest biome, which have strongly weathered Ultisols and Oxisols, soils in the forest zone of Ghana are mainly fertile Alfisols. These soils are relatively suitable for agriculture, but they are very prone to erosion and compaction (Norman et al. 1995). It is perhaps unsurprising then, that most crops grown in southwest Ghana are either (1) grown in fallow cycles where fields are retired from cultivation for several years or even decades after cultivation, or (2) perennial tree crops.

In the forest zone, each farmer grows crops on one or more plots of land, each called a farm, and each of which is typically cultivated with a different crop or mixture of crops. Land clearance is done manually, with machetes, axes or chainsaws and usually with the use of fire, although there are also traditional no-burn methods (Gyasi et al. 2004). Farmers typically clear a new area (often < 1 ha) for food crops each year, while allowing previously cultivated land to rest in fallows, but fallow periods have become shorter as a result of increasing population densities. Land clearance and burning are carried out towards the end of the major dry season, around March. Farmers practice relay cropping, which is form of intercropping where not all the crops are planted at the same time (Norman et al. 1995). They typically plant maize first, and if cassava is not planted, two crops of maize can be harvested in the first year. More commonly, cassava is planted shortly after the maize, and harvested after around one year. Cocoyam is sometimes planted in place of cassava. Plantain takes about one year to reach maturity and can be harvested in the two subsequent years. Chilli pepper, vegetables and various species of yams are frequently intercropped with the main staples. Food crop farms are cultivated for 2-3 years before being allowed to revert to fallow bush. In most of southwest Ghana, this means that they are rapidly overgrown with *Chromolaena odorata*, an invasive non-native shrub.

Cash crop farms are established in a similar way, and farmers typically intercrop maize, cassava and other food crops with the young cocoa or oil palm seedlings for the first two to three years. In the case of cocoa, standing trees are mostly retained, at least for the first few years, though they are sometimes thinned out by ring-barking in older cocoa farms. Many cocoa farmers in recent years have adopted a hybrid cocoa variety that yields after 2-3 years and does not require any shade cover when mature, so the extent of shade cover in cocoa farms in southwest Ghana is very variable.

Oil palm, unlike cocoa, is grown on large commercial estates as well as by individual small farmers. There are four large oil palm estates in Ghana. In addition, further estates are under development in Western Region near Bogoso (Golden Star Oil Palm Plantation), in Central Region at Buaben (as a large outgrower scheme), and in the Volta Region with funding from the company Sithe Global. A mining company in Western

Region has adopted oil palm and *Jatropha curcas* as crops for rehabilitating mine sites after closure. Although the large oil palm estates are the most visible element of the industry in Ghana, most of the country's production comes from small farmers. Some farmers own plots of land which they manage with support from the "nucleus" plantations. In Ghana, the term "smallholder" is usually restricted to this sort of farmer. A greater number of farmers are "outgrowers", that is, they cultivate oil palm independently, but sell their palm fruits to the commercial mills. Farmers also sell oil palm fruits to local buyers, and in this case women process it into palm oil in small-scale village processing facilities, for local or at least in-country consumption.

3.3.3 Wildlife-friendly farming practices

Several of the farming systems and practices in southwest Ghana can be considered wildlife-friendly. Structurally diverse cocoa agroforests are recognised as supporting relatively high species richness of taxa such as birds and butterflies relative to unshaded systems, although they tend to support fewer species with small global ranges than forests do (Waltert et al. 2005, Bobo et al. 2006b, Bisseleua and Vidal 2008, Bisseleua et al. 2009, Holbech 2009). In Ghana, cocoa farms span a range of shade regimes, from "rustic" systems with a tall, diverse tree canopy usually composed mainly of original forest trees, to unshaded monospecific farms of cocoa, with no shade trees (Perfecto et al. 2005). Food crop farms and fallows also frequently contain remnant forest trees or wild oil palms, and isolated mangoes, avocadoes or other non-native fruit trees. To the extent that they involve the integration of trees, farms that include these elements can also be considered agroforestry systems (Bhagwat et al. 2008). Small hills, swampy areas and sacred sites are sometimes left uncleared, and can support native vegetation. Certain trees are sometimes protected by taboos (Gyasi et al. 2004). Wild oil palm trees are very low-yielding, and are tolerated in the farmed landscape not for their fruits, although these are occasionally harvested, but because they can be tapped to produce palm wine.

Fallow land is rapidly colonised by fast-growing plant species, including pioneer trees such as *Musanga cecropioides* and *Anthocleista* spp. Especially if it is near old-growth forest, it reverts over time to species-rich secondary forest, supporting an increasing number of forest-dependent species (Dunn 2004, Dent & Wright in press). Landscapes with a high proportion of fallow land, and with long-fallow shifting cultivation are therefore wildlife-friendly, although clearly, landscape-scale yields are likely to be inversely related to the area of land that is left uncultivated at any one time. Because of increasing population densities, the average length of fallow periods has decreased, and farmers are increasingly returning fallow land to cultivation before it has made the transition from *Chromolaena* to secondary forest, or converting the land to perennial crops (Boserup 1965, Norman et al. 1995).

Small-scale farmers in Ghana would traditionally not have had access to agrochemicals such as pesticides and fertilisers, but these are now widely used by farmers where they can afford them. Glyphosate-based herbicides are widely available, and are used to control weeds by small farmers as well as on large plantations. A range of insecticides is used, especially on cocoa and vegetables, and to treat stored grain. Pesticide use is relatively low in even the large oil palm plantations. However, fertiliser use in plantations is high, and includes muriate of potash and sulphate of ammonia as well as smaller quantities of nitrogen-phosphorous-potassium (NPK), kieserite and boron. From the perspective of agrochemical use, the most wildlife-friendly farming systems in southwest Ghana are probably those based on relay cropping of various crops without any chemical inputs, and surprisingly, high-yielding oil plantations which have been organically certified (including one of the plantations included in this study).

Wildlife-friendly landscapes, in addition to supporting higher populations of many species than landscapes with simplified cropping systems, provide a range of culturally important benefits to people. These include fruits, medicines and other non-timber "forest" products (NTFPs) from native as well as non-native species (Falconer 1992). Bush foods collected in farms and fallows include wild game, fish, crustaceans, beetle grubs, fruits, mushrooms and honey. Other products include wood for construction and food preparation implements, firewood and charcoal, palm fronds for baskets, screens and brooms, rattan for basket-weaving, leaves for wrapping food, “chewing sticks”, medicines, and the sap of oil palms and raphia palms. This last is either consumed as “palm wine”, a sweet drink, or fermented to produce *akpeteshie*, a local gin. Some of the most important NTFPs, such as larger game, and pestles and mortars for pounding *fufu*, are also or mainly provided by forests, and this is probably an important reason for why state-managed forest reserves have not come under more pressure to be converted to farmland. Many other products are provided by farms and especially fallow land, but there are few quantitative assessments of their economic importance in relation to land use.

3.3.4 Land tenure

No discussion of agriculture in Ghana would be complete without mention of the vexed issue of land tenure. Over past centuries, land ownership was determined by force, with occupying tribes taking control of the land by strength of arms. European colonisation initially did not involve much occupation of land: the Portuguese took control of ports along the coast in order to monopolise trade, but did not move far inland (La Anyane 1963). It was not until the English wars against the Ashanti in the late nineteenth century that Europeans seized control of lands further inland. Unlike the situation in eastern and southern Africa, there was no large-scale influx of European settlers, so colonial rule affected the upper levels of power without radically altering land ownership and use at a village level. Day-to-day administration of land tenure in Ghana is still largely based on the Ashanti system, although it has been modified over time and is now supplemented by the workings of a government Lands Commission.

The Ashanti land tenure system, which was more or less formalised under English colonial rule, is a hierarchical one. The ultimate, or allodial, land title is held by the paramount chief, or *Omanhene* (Vercruijsse 1988). The land is held and managed on behalf of the *omanhene* either by sub-chiefs or by extended family groups. These extended family groups are called *mbusua* (singular *ebusua*), and are united by a common female ancestor. The land controlled by an ebusua, or "family land", is administered by the lineage head, the *Ebusua Panyin*, typically a male elder who also sits on the village council. Both the *Omanhene* and other chiefs have ceremonial stools, which traditionally were seen as a repository of the spirits of the ancestors, and are also symbols of authority. Land controlled by them is hence sometimes known as "stool land".

Uncultivated land can be claimed for farming, with the permission of the *Ebusua Panyin*. While it is possible for farmers to make a gift of land to non-ebusua members, and even to sell land outright, most family land is only given out to members of the relevant *ebusua*. Although farms are frequently owned by men, inheritance of land in southern Ghana is typically matrilineal. Land is inherited by a man's brothers and by his sisters' sons, rather than by his own children. Although it resembles a feudal system in some respects, the Ashanti tenure system actually gives considerable autonomy to the farmer, whilst at the same time maintaining the interests of the wider community. Even in colonial and pre-colonial times, few taxes were apparently levied; the principal demand of the *Omanhene* of landholders was military. Men would be called on to fight against enemy tribes or colonial Europeans. Today, that tradition is effectively obsolete, although the authority of the *Omanhene* still has substantial cultural significance. Farmers have independence in how they manage their farms, and security of tenure as long as they continue to cultivate the land (and even for up to ten years or so of temporary abandonment in a fallow cycle).

This does not mean that the benefits of farming are equally distributed. A further level of hierarchy brings us to tenants, caretakers and hired labourers. These are really only relevant to perennial cash crops. Mixed food cropping is typically carried out by the landholder him- or herself. Tenant farmers typically farm plots of land under an agreement by which the landlord takes half of the harvest: the *abunu* system. Depending on the agreement, tenants are sometimes permitted to grow food crops for their own consumption in the first 2-3 years of perennial crop establishment. Caretakers are hired to look after a farm, often a cocoa farm, once it has been established, and receive one-third of the harvest in return: the *abusa* system. The majority of farmers rely on seasonal hired labour to some extent, especially for weeding and harvesting (La Anyane 1988). Reciprocal labour is common in cocoa farming during the main harvesting season. The cocoa farmer provides food to his neighbours, and assists them with their cocoa harvests in return for help splitting the cocoa pods.

The strength of control over land tenure by a diverse hierarchy of chiefs, *mbusua* and individuals makes the acquisition of large continuous tracts of land, for example by agro-industrial companies, difficult. This has meant that agricultural landscapes in southwest Ghana have remained largely a mosaic of small farms, with a relatively small number of large plantations of oil palm and rubber.

3.4 Site selection

I defined my study “province” by selecting four replicate landscape blocks, each comprised of three main land-use types, around the four large-scale oil palm plantations in Ghana. I defined the province as the total area of the seven administrative districts which contained the four blocks. Within each block, I selected an area of plantation, an area of farm mosaic (farms and uncultivated land) and an area of forest, using a simplified version of a land cover map from the Forestry Commission. The area of plantation in each case comprised the entire area of the plantation in question. I selected forest reserves as described below, and the area between each paired plantation and forest reserve constituted my selected farm mosaic area. The administrative districts making up the province are shown in Figure 3.5, the land cover map is shown in Figure 3.6, and the blocks are shown in Figure 3.7.

Using GIS, I identified all forest reserves within 20 km of each plantation (plantation outlines traced from Landsat imagery), and used a simple scoring system to assess the similarity of each reserve to its nearest plantation using soil type, annual precipitation, annual potential evapotranspiration, ecological zone and forest condition (Hawthorne & Abu-Juam 1995). I excluded forest reserves smaller than 20 km^2. I selected the highest-scoring forest reserve in each landscape for inclusion in the study. Subri River is a very large forest reserve, and precipitation varies considerably across it, so I selected only the subset of it in the same rainfall bands as the Twifo-Praso plantation, and excluded a large area degraded by plantations of non-native *Gmelina arborea* and *Cedrela odorata* trees. Bonsa River extends far to the north of Benso, so for logistical reasons I included only the part of it that was within a 20 km radius of the Benso Oil Palm Plantation. I then defined the area of farm mosaic between each plantation and its neighbouring forest reserve as part of the study landscape. I clipped out areas where the soil type differed from those in the nearest plantation to give the final study areas as shown in Figure 3.7.

To minimise the effects of sampling near edges (see Chapter 2), I excluded areas in all three land-use types within 500 m of the edge with another land use. A distance of 500 m was chosen as most edge effects occur over shorter distances (Laurance et al. 1997). To help maintain the independence of the study regions and for logistical reasons I excluded that part of the selected portion of Subri River Forest Reserve which fell within 20 km of the plantation in the neighbouring landscape. The GIS data provided by the Forestry Commission, including land cover maps and forest reserve outlines, were not always accurate. I retraced forest reserve and plantation boundaries where they clearly differed from those visible on Landsat imagery. In block I, I excluded from the farm mosaic areas of large-scale rubber plantations, and an area of “wetland” shown on the Forestry Commission land cover map, which was probably misclassified rubber plantation.

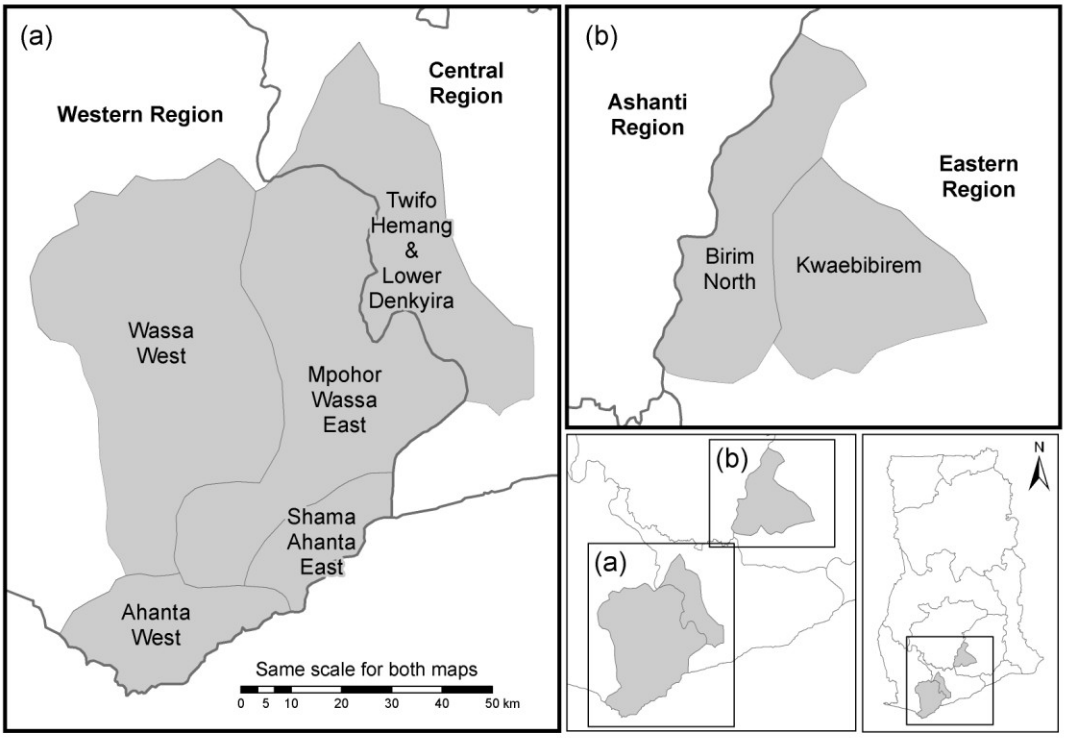

Figure 3.5. The seven administrative districts that constitute the study province.

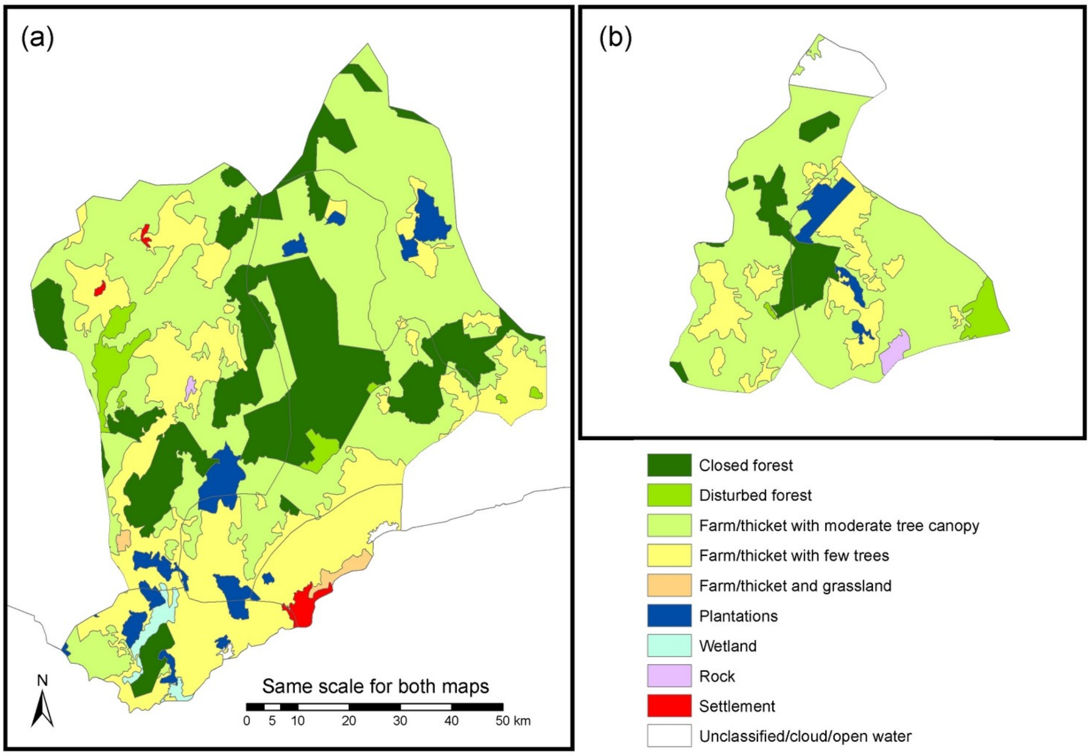

Figure 3.6. Land use within the study province, simplified from Forestry Commission land cover map as described in Appendix 3.

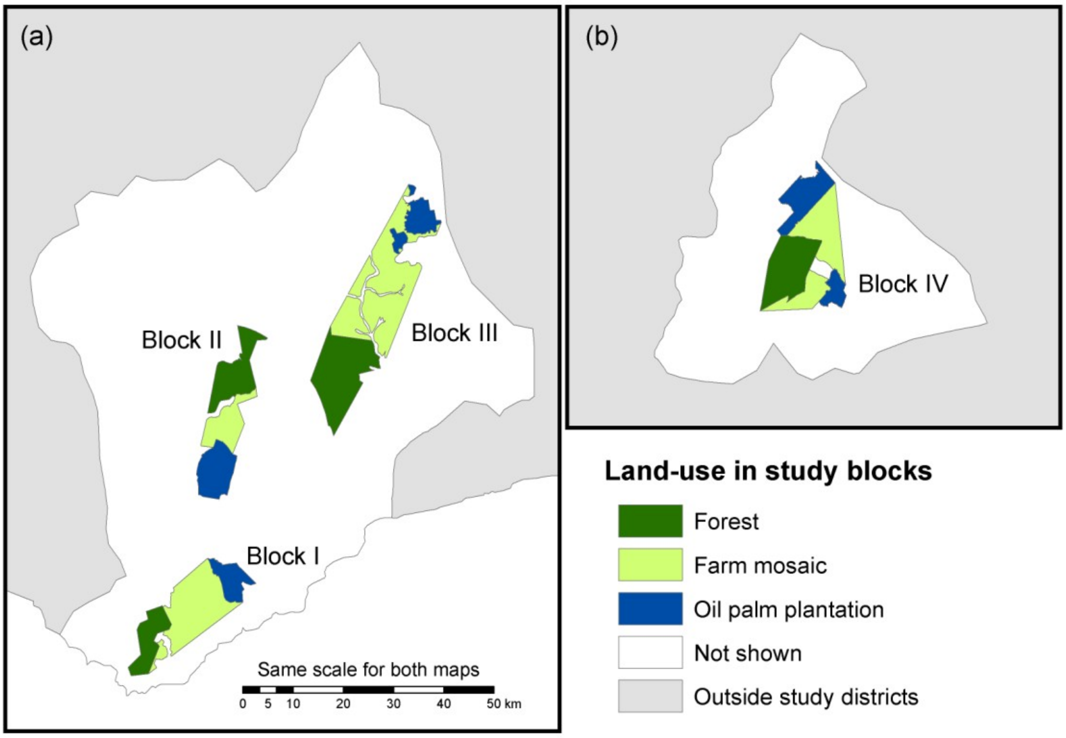

Figure 3.7. Four replicate blocks (labelled), each comprised of forest, farm mosaic and oil palm plantation, in the study province in southwest Ghana (see Figure 3.5 for administrative districts).

I selected two random study 1 km^2 squares in each of the three land-use types in each of the four blocks. I did this by projecting a 1 × 1 km grid over all of the landscapes, and numbering each square on the grid that fell fully within one of the land uses (forest, farm mosaic or plantation) within each landscape. I then selected two squares randomly from each land use within each landscape (Figure 3.8). I replaced one of the random farm mosaic squares with another randomly selected square, because it lay almost entirely over a small town (Agona Nkwanta, in block I). In order to capture wider variation in yield, I selected a third non-random farm mosaic square with anticipated high or low yields in each landscape, but because of time constraints, full data were only collected for that in landscape IV (square #24). The non-random square in landscape III (square #17) was used to replace one of the random squares (square #16) at short notice when I was refused permission by some local farmers to continue data collection there.

3.5 Overview of data collection

Within each of the 26 squares, I positioned 36 points using a GIS, regularly spaced 160 m apart on a square grid. The number of points and the spacing was a compromise between having sufficient samples to adequately represent each square, and positioning the points far enough apart to maintain their independence. I used the 36 points in each square for sampling field types (for determining yields), birds and trees (Table 3.1). In each farm mosaic square, I mapped field types at each of the 36 points (see Chapter 4). The two “plantation” squares in block I proved to contain a mosaic of oil palm plantation, small farms and uncultivated land, and so I also mapped field types in these squares as for farm mosaic squares. Having identified the farmer at each mapped point, I conducted interviews with a random selection of these farmers in the randomly-selected farm mosaic squares, selecting up to six (if available) for each crop in each square (see Chapter 4). I was only able to complete field type mapping in square #16, and not interviews or other data collection, before being refused permission to continue my research there, so I replaced it with square #17. Farmers in squares #9 and #10 were mostly from the same village (Benso) so for interviews I did not consider those two squares as independent.

I conducted 24 point counts for birds in each square, sampling 12 points in the dry season and 12 points in the wet season where possible (randomly selected without replacement on each visit). No point was counted twice (see Chapter 5). Before I could complete all of the “dry season” counts in Bonsa River forest (block II), the dry season came to an abrupt end, and heavy rain and flooding prevented me from reaching four of the points. I replaced these four points with new points located along a straight line parallel to the edge of the study square and 160 m from the nearest original row of points.

I sampled the same 24 points for trees in farm mosaic and plantation squares, although points in the three high-yielding oil palm plantations needed only cursory checking to verify that they did not contain any trees ≥ 10 cm diameter at breast height (dbh) other than oil palms (see Chapter 6). In forest, I sampled trees in plots centred at 12 of the points where birds had been counted. Each tree plot was 25 × 25 m.

In addition to the above, I conducted interviews with 37 local people about their use of NTFPs and bushmeat, but the results were not sufficiently quantitative to be included here. I also collected data on vegetation characteristics at each point sampled for birds, and I collected bees from 570 trap-days of pan-trap sampling, but those data are not considered further in this thesis. The reliability of the bee data was undermined by difficulties in adequately sampling the forest canopy.

Some illustrations of land use in the study area are given in Figure 3.9.

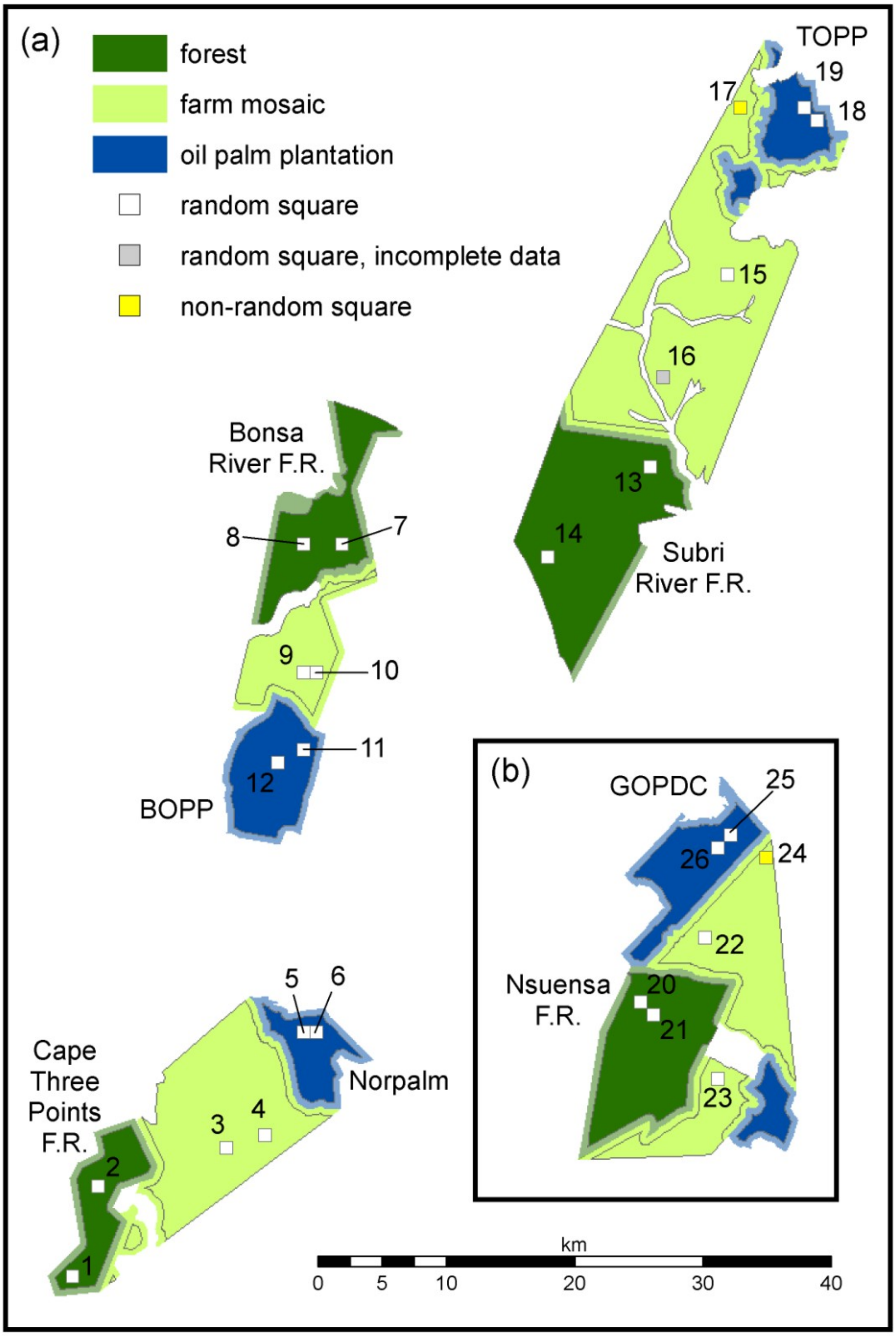

Figure 3.8. Location of study squares within each of the four blocks. For block numbers, see Figure 3.7.

Table 3.1. Sample sizes collected in each square, of points at which I mapped field types, number of interviews about farm costs, profits and yields, number of bird point counts, and number of tree sample plots. Squares #9 and #10 were treated as one sample for interviews.

Block	Land use	Square ID	Field type mapping	Interviews	Bird counts	Tree plots
I	forest	#1	-	-	24	12
	forest	#2	-	-	24	12
	farm mosaic	#3	36	12	24	24
	farm mosaic	#4	36	9	24	24
	plantation/farm	#5	36	-	24	24
	plantation/farm	#6	36	-	24	24
II	forest	#7	-	-	24	12
	forest	#8	-	-	24	12
	farm mosaic	#9	36	17	24	24
	farm mosaic	#10	36		24	24
	plantation	#11	-	-	24	24
	plantation	#12	-	-	24	24
III	forest	#13	-	-	24	12
	forest	#14	-	-	24	12
	farm mosaic	#15	36	11	24	24
	farm mosaic	#16	36	-	-	-
	farm mosaic	#17	36	12	24	24
	plantation	#18	-	-	24	24
	plantation	#19	-	-	24	24
IV	forest	#20	-	-	24	12
	forest	#21	-	-	24	12
	farm mosaic	#22	36	12	24	24
	farm mosaic	#23	36	13	24	24
	farm mosaic	#24	36	-	24	24
	plantation	#25	-	-	24	24
	plantation	#26	-	-	24	24
Totals			**432**	**86**	**600**	**504**

a. Closed-canopy forest: my camp in Cape Three Points Forest Reserve, Western Region.

b. Logged forest in Nsuensa/Aiyaola/Bediako Forest Reserve, Eastern Region.

c. Food crop field in farm mosaic near Benso, Western Region, with cocoyam and plantain in foreground, cassava in middle ground, and remnant native forest on hilltop in background.

d. Bushy food crop field in farm mosaic near Nyamendae, Western Region, with akyeampong *(Chromolaena odorata) in foreground, and uncultivated land with trees, including Musanga cecropioides and Anthocleista sp., in background.*

e. Immature oil palm plantation, about 3 years old, at Twifo-Praso Oil Palm Plantation, Central Region, with Pueraria phaseoloides, a leguminous cover crop

f. Mature oil palm plantation, about 25 years old, at Benso Oil Palm Plantation, Western Region.

Figure 3.9. Landscapes and habitats in the study area.

Chapter 4

Yields and profits of farming

Woman packing cassava and plantain for transport to market, near Benso, Western Region

‘I ask you to help me in clearing the forest,

Then I ask you to help me in felling the trees on the farm;

Then I ask you to help me in making mounds for the yam seeds;

But for harvesting the yams, I do not need your help.’

Akan funeral song

4 Yields and profits of farming

4.1 Introduction

The aim of this chapter is to quantify the yield and profit from the range of different agricultural land use found in the study area. The purpose of this is to compare the suitability of different farming systems for wild species with their yield and profit levels, so that the consequences for biodiversity and yield of farming in different ways can be assessed. I focus on agricultural yields and profits, but I also discuss briefly the importance of non-timber forest products (NTFPs), particularly bushmeat.

4.2 Methods

4.2.1 Mapping of field types

I mapped field types in all of the farm mosaic squares, and in the plantation/farm squares in block I. Obtaining the permission and co-operation of local communities was an important precursor to visiting the farm mosaic squares. In most cases, I started by visiting the district agricultural office, and from there made contact with the extension officer for the area in which the farm square was. I then visited the community with the officer, to meet the chief and if appropriate the chief farmer (and in some cases, to donate a customary bottle of schnapps). We arranged a subsequent visit when I returned to hold a meeting with the farmers to explain my research and allow them to ask questions before I started data collection.

I visited each farm square with a local farmer, and mapped field types at each of 36 points regularly spaced 160 m apart on a square grid. This took 2-3 days for each square. At each point I recorded the field types present within a radius of 30 m, and their coverage of that area. I also noted the name of the farmer of the field in which the point fell, informed by the local contact. (I use the terminology "field" here for clarity, but farmers themselves do not use that word, and describe each of their fields as a "farm"). I estimated (to the nearest 10%) the percentage of the 30 m circle occupied by each of the following crops:

- Oil palm
- Cocoa
- Orange
- Mixed food crops (food crop fields with immature tree crops were recorded as such and later defined as that tree crop, even if dominated by food crops; only food crop fields without tree crops were classified as "food crop" fields)
- Other crops (e.g., coconut, rubber, sugarcane)
- Cleared (land recently slashed or burnt for agriculture, but not yet planted)
- Uncultivated (e.g., fallow, secondary forest, *Raphia* swamps)
- Uncultivable (e.g., roads, buildings, waterbodies)

For each of those subdivisions of the 30 m radius, I recorded the following information separately:

- Maturity (for tree crops: oil palm, cocoa and orange were considered "mature" at 4-5 years when the canopy starts to close and the trees are producing a good crop)
- "Weed" height: low (<1 m), medium (1-2 m) or high (>2 m)
- Other information (e.g., level of shade over cocoa, varieties, cover crops, precise crop age where known, type of uncultivated land) which I do not analyse further

4.2.2 Farmer interviews

I took the lists of fields (with associated farmers) generated from the mapping exercise and categorised them by crop as follows: oil palm, cocoa, orange, food crops and immature tree crops. I randomly selected a sample of up to six fields (if available) for each crop in each square, starting with the crop with fewest fields, and interviewed the farmer of each field. I initially spent time talking to farmers and visiting their farms to learn about the various crops being grown and the management practices used (Figure 4.22). Prior to starting the interviews, I encouraged some farmers to keep daily records in a notebook of their labour, input costs and yields. This approach was trialled in the village of Subriso, north of Benso (i.e., not in one of my study squares) but it proved ineffective. Literacy levels were low, and even those farmers who were literate stopped maintaining records whenever I spent more than a few days away from the village. I also tried mapping some Subriso farmers' fields in detail using handheld GPS, but I stopped this when it became clear that it provoked suspicion among farmers, who were worried that my secret purpose was to appropriate their land for gold mining (cf. Amanor 1994, p. x). Mining company vehicles were a common sight around several of the study squares. Although neither the notebooks nor the mapping produced any usable data, they were useful in giving me an insight into farming practices.

Following discussions with farmers and extension officers, and pilot interviews with a draft format, I designed a structured interview protocol for agricultural costs, yields and revenues, including costs of basic processing (such as shucking maize and fermenting and drying cocoa beans) and transport to the point of sale. The interviews asked for detailed information about a particular, specified field (that identified during mapping), over a one-year recall period. I also asked all farmers about the costs involved in clearing, preparing and planting a new field, again tied to the same specific field where possible. Because such information is frequently difficult to recall, most of the questions were disaggregated in detail into component parts: hence, to find out the cost of weeding during the previous year, I asked farmers how many times they had weeded that field in the past year, and either how many people and how many days it took, if the labour was unpaid, or how much they had to pay for the hired labour per round. Based on what farmers told me, and incidentally using the same conversions as Upton (1973, cited by Lass 1985) I considered a day's work done by a woman as two-thirds, and that done by a child as one-third that of a man's. (This is not because women work less hard than men, but, because of their other responsibilities, women in Ghana typically spend less time on farm work than men.) There was some latitude within the questionnaire format for requesting information over shorter recall periods where those were likely to more reliable: for example, while farmers could often recall precise cocoa yields for an entire year, many could only recall a recent fraction of oil palm yields, as oil palm is harvested much more frequently, and throughout the year. I typically interviewed farmers in small groups with interested onlookers present, as this provided conditions for inaccurate responses to be challenged by others. In some cases, I also went to the houses or farms of individual farmers to interview them.

I standardised data on costs and yields derived from interviews to per-hectare values, converting from the local area units as described in section 4.2.3, and entered them into an Access database. For food crops where units such as bags, headloads and bunches were not standardised, I converted farmers' reports of revenues into yields in tonnes based on rural wholesale prices for the relevant region in the relevant month (Ministry of Food and Agriculture 2007). I used simple lifecycle models to estimate the average annual costs, yields and revenues of each crop. These models divided the lifecycle of each crop into two stages: immature and mature. There were also specific costs associated with the first year (land preparation and planting costs) and in the case of oil palm, a revenue in the final year, when palms are felled and sold to palm wine tappers. The costs in each stage were multiplied by the length of that stage and divided by the typical lifecycle of the crop to generate an estimate of mean annual gross cost. This was done assuming a three-year lifecycle for mixed food crops, a 20-year cycle for oil palm, a 30-year cycle for orange and a 50-year cycle for cocoa. Mean annual gross revenue and mean annual yield were calculated using the same approach.

In calculating costs, I costed family labour at the minimum contract wage (GH¢1.60 per day) as an estimate of the opportunity cost of labour. I also included the value of subsidised inputs, such as pesticides provided without charge by the government to cocoa farmers. I excluded the costs of rents or leases. Food crops are almost invariably intercropped with tree crops, to provide some food and/or income before the trees begin to produce fruit. I combined information on the costs and yields of intercropping in the first few years of tree crop farming, based on interviews of farmers who reported foodcrop costs, yields and revenues from immature tree crop fields, taking care not to double count costs such as land preparation and weeding. To produce means with standard errors and 95% confidence limits, I used bootstrapping to sum components with different sample sizes. In each instance, I took 9999 resamples of the original data, with replacement, using the program R, version 2.7.2.

4.2.3 Area units

Determining the size of local area units was crucial for accurate calculation of per-hectare costs, yields and profits. Farmers measure the area of their fields in "ropes", "poles" and "acres", but the definitions and sizes of these units varied from one village to another. In addition, the terms "pole" and "acre" were often used interchangeably. Because of this, I asked detailed questions about the area units used by each farmer, and checked these myself where possible.

The different area units used in villages from the study area are summarised in Table 4.1. Some of the variation in definitions is illustrated in Figure 4.1. Farmers first measure a piece of rope using a man's outstretched arms (arm span) as the basic unit. A rope is typically 12 arm spans in length, and is used to measure the sides of square fields on the ground. A square field with each side the length of the rope is referred to as a "rope". I encountered different definitions of area units, even within the same study square, although they appeared to be consistent within individual villages. For example, in square #15, the mainly Christian farmers of Tafrejoa used a pole of 24 × 24 arm spans, while a Muslim farmer in the same square from the adjacent village of Baakondzidzi used a pole of 30 × 30 arm spans, equivalent to a Tafrejoan acre. Confusingly, farmers typically referred to arm spans as "metres". When I observed and measured the calibration of an actual piece of rope in Nyamendae, I found that 12 "metres" (arm spans) in fact measured 22.88 m. This was used as the basis for translating local area units into hectares (Table 4.2).

Table 4.1. Area units used in different villages, based on arm spans (12 arm spans ≈ 22.88 m), such that, for example, the area of a "rope" in square #3 is calculated as 22.88 × 22.88 m = 523 m^2, or 0.0523 ha.

Block	Square	Village	"quarter"	"rope"	"pole"	"acre"
I	3, 4	Himakrom*, Mpanyinasa, Anyinase, Fretsi	-	12 × 12	36 × 36	-
II	9, 10	Benso, Ningo	-	-	40 × 40	40 × 40
III	15	Tafrejoa	-	-	24 × 24	30 × 30
	15	Baakondzidzi	-	-	30 × 30	-
	16	Nyamendae	-	-	24 × 24	-
	17	Eduabeng, Ntafriwaso	-	-	30 × 30	-
IV	22	Anweam	-	12 × 12	-	36 × 36
	23	Okumaning	-	24 × 24	36 × 36	36 × 36
	23	Afiafiso	12 × 12	24 × 24	-	36 × 36
	24	Asuom	-	-	-	24 × 24

* In Himakrom, the "old pole" was 48 × 48 arm spans, but farmers now use 36 × 36.

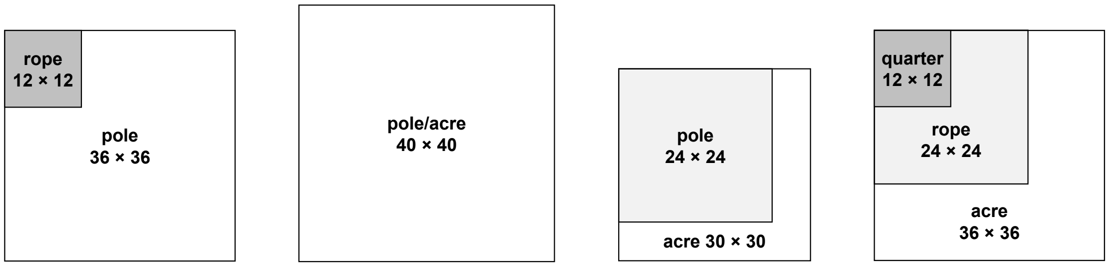

Figure 4.1. Illustrative scale examples of variation in the definition of local area units in different villages, with dimensions defined in arm spans (12 arm spans ≈ 22.88 m). Villages (blocks) from left to right: Himakrom (block I), Benso (block II), Tafrejoa (block III), Afiafiso (block IV).

Table 4.2. Size of local area units in hectares, rounded to four decimal places (unrounded units were used in calculations). For comparison, an international acre is 0.4047 ha.

Area unit (spans)	Local names	Area (hectares)
12 × 12	quarter/rope	0.0523
24 × 24	rope/pole/acre	0.2094
30 × 30	pole/acre	0.3272
36 × 36	pole/acre	0.4711
40 × 40	pole/acre	0.5817

I was able to ground-truth some area measurements on an opportunistic basis. I measured two recently-cleared fields in block I, using a rangefinder to measure each side and the diagonals. The first field was one rope (local measurement) and so would be expected to be 523 m^2 (Table 4.2). I estimated its area from my measurements as 495 m^2. The second field was two ropes and would be expected to be 1,047 m^2. I estimated its area from my measurements as 1,001 m^2. These measurements were within the measurement error of the rangefinder used to take them (± 1 m).

4.2.4 Construction of long-term price index

To reduce the effect on my estimates of short-term fluctuations in food prices, I calculated ten-year mean wholesale prices per unit weight of each commodity over the period 1998-2007. I constructed a price index by taking January prices in each year, adjusting them for inflation to 2007 values, and expressing them relative to the January 2007 price. National prices were used to construct the index, and the ten-year mean of the index for each crop was multiplied by the 2007 revenue received per hectare for that crop, to estimate the average revenue, given the same level of yield, over the ten-year period. Food prices were obtained from the Ministry of Agriculture, and inflation rates were obtained from the World Economic Outlook Database of the International Monetary Fund. The currency of Ghana, the cedi, was redenominated in July 2007, within the period in which I conducted interviews (October 2006 to August 2007), so I also converted all currency values to the new denomination (¢10,000 in old cedis = GH¢1 new Ghana cedi).

4.2.5 Farm yields

I estimated mean annual yields using simple lifecycle models based on information received from the farmers. Yield was calculated in tons per hectare, using a formulae of the following form for each food crop separately, where *m* is the number of years in which the crop is mature (harvested), Y_m is the reported yield of that crop in a year of harvesting, and *a* is the total number of years in the cycle:

$$Y = \frac{mY_m}{a}$$

For tree crops, I used a similar approach, with the difference that for one of the tree crops, oil palm, small yields were harvested from some immature fields. I therefore used a formula of the following form, where *i* is the number of immature years in the cycle and Y_i is the reported yield of the crop in an immature year (usually 0):

$$Y = \frac{iY_i + mY_m}{i + m}$$

4.2.6 Monthly logs

As an additional way of collecting yield information, I enlisted the help of agricultural extension officers to make monthly visits to as many of the oil palm farmers interviewed as possible, and to record the yields and revenues of each specified field in each month over a period of one year, using a simple, pre-printed form.

4.2.7 Plantation yields

Three of the oil palm plantations (in blocks II-IV) provided me with data on yields from past years. Using these data, which were broken down by age, I fitted polynomial models to establish an idealised yield curve. To estimate yields for the plantation in block I, for which I did not have access to comprehensive yield information, I assumed that the yield at each age was smaller than that in the nearest plantation by the same ratio as for maximum yields from mature palms. According to a manager who moved from that plantation to work at the plantation in block I, the expected maximum yields were 14 t/ha and 10 t/ha, respectively.

4.2.8 Food crop costs and revenues

Costs were estimated in several stages. At the field level, I combined preparation and maintenance costs as described in Table 4.3. Where square-level estimates are described, I treated adjacent squares #9 and #10 as a single square rather than independent squares, as the farmers in those squares were mostly from one village (Benso). Most of these costs were specific to the focal field. An exception is that most tools are used across a farmer's various fields, so their cost is not specific to the field. The cost of tools was calculated differently, by asking farmers their total expenditure on tools during the past year, and estimating a per-hectare value by dividing total expenditure by the total area of all of their fields combined.

These field-level costs were further aggregated for each field to produce an estimate of C_{field}, the annual cost of maintaining a food crop field, using the following formula, where a is the total number of years of the cycle (usually three):

$$C_{field} = \frac{C_p + aC_a}{a}$$

Table 4.3. Principles of estimation of costs of general inputs (other than planting and harvesting) for each food crop field, irrespective of the crop. All costs were standardised to per-hectare values for one year.

Variable	Description	Components
C_p	Preparation cost	Value of family labour for preparation
		Cost of hired labour for preparation
		Cost of fuel for chainsaw
		Other costs
C_a	Annual cost	Value of family labour for weeding, spraying, tool-making and other activities
		Cost of hired labour for weeding and spraying
		Cost of tools and herbicides

Within each field, two, three or four different crops were grown together. Their costs were calculated separately as they were planted and harvested on different cycles. Costs for specific individual food crops are shown in Table 4.4.

Table 4.4. Costs for specific individual food crops.

Variable	Description	Components
C_{p_s}	Preparation cost	Value of family labour for planting
		Cost of hired labour for planting
		Cost of seeds or seedlings
C_{m_s}	Mature cost	Value of family labour for harvesting and carrying
		Value of family labour for processing (maize only)

These values were combined for all the crops in a field to generate the annual cost of tending food crops, $C_{specific}$, during one cycle, using a formula of the following form, where there are n different crops, p_s is the number of years in which a specific crop s is planted, m_s is the number of years in which it is mature (harvested) and a is the total number of years in the cycle:

$$C_{specific} = \sum_{s=1}^{n} \frac{p_s C_{p_s} + m_s C_{m_s}}{a}$$

It was possible for p to be greater than one, and a was not necessarily the same as $p + m$. For example, it is possible to plant and harvest cassava twice on the same field within a three-year cycle ($p = 2$, $m = 2$, $a = 3$).

Because my data for some elements of C_{field} and $C_{specific}$ were non-independent for different fields within a study square (e.g., farmers were aware of other farmers' answers and claimed some costs were "the same") I took the mean of these variables for each square, and weighted it by the number of fields for which interview data were available within that square. I resampled the square-level means using these weights, such that a mean based on four fields was twice as likely to be resampled as a mean based on two fields. I then summed each pair of C_{field} and $C_{specific}$ estimates to produce 9999 estimates. These estimates were used to produce a bootstrapped mean and standard error of the mean annual cost of growing food crops:

$$C = C_{field} + C_{specific}$$

I calculated the mean annual gross revenue R_{gross} from food crops in a similar fashion for each field using crop-specific values of m, where R_s is the revenue from crop s during one year of harvesting:

$$R_{gross} = \sum_{s=1}^{n} \frac{m_s R_s}{a}$$

Again, I used the mean value for each square, and resampled these means using weights proportional to the number of fields sampled in each square. The net revenue (profit), R_{net}, was estimated by subtracting the bootstrapped estimates of cost from the bootstrapped estimates of gross revenue:

$$R_{net} = R_{gross} - C$$

4.2.9 Tree crop costs and revenues

I estimated the costs and revenues of tree crop cultivation using a similar approach to that used for food crops. At the field level, I summed various costs as described in Table 4.5.

For some of the crops, these costs were further subdivided because of missing data. For example, if 15 farmers provided information on the labour costs of preparation, but only 12 provided information on non-labour preparation costs, I calculated and bootstrapped these two sets of costs separately, before summing pairs of bootstrap estimates to generate 9999 estimates of C_p. I calculated costs and revenues separately for each tree crop. Rent payments, either as money or as part of the harvest, are often an important part of the cost of farming, but I excluded them as I was interested in the value of agricultural production, not who exactly captures that value. From that perspective, the extent to which landlords capture revenues through rents is irrelevant, though of course it is an important consideration in questions of social equity.

Table 4.5. Principles of estimation of costs for each tree crop field. All costs were standardised to per-hectare values for one year.

Variable	Description	Components
C_p	Preparation cost	Value of family labour for preparation and planting
		Cost of hired labour for preparation and planting
		Cost of hiring chainsaw (and cost of fuel)
		Cost of seeds/seedlings
C_i	Immature cost	Value of family labour for weeding, spraying, fertilising, harvesting, carrying, processing and other activities
		Cost of hired labour for weeding, spraying, fertilising, harvesting, carrying, processing and other activities
		Cost of tools, fertilisers, agrochemicals
		Other costs (e.g., equipment hire)
C_m	Mature cost	Categories as for C_i

As with food crops, most costs were specific to the focal field, but tools are used across a farmer's various fields, so their cost is not specific to the field. The cost of tools was calculated differently, by asking farmers their total expenditure on tools during the past year, and estimating a per-hectare value by dividing total expenditure by the total area of all of their fields combined. For crop-specific tools and equipment (e.g., the mats used for drying cocoa beans), I calculated their annual per-hectare cost by dividing their cost by the number of hectares of that crop managed by the farmer, and by their expected useful life in years.

I combined the resampled estimates of C_p, C_i and C_m (or where necessary, subdivisions of these variables) to calculate the mean annual costs C associated with a specific tree crop using a formula of the form, where i and m are the number of years of immaturity and maturity in the crop's cycle:

$$C = \frac{C_p + iC_i + mC_m}{i + m}$$

I used values of i of 4, 4 and 5, and of m of 16, 46 and 25 for oil palm, cocoa and orange respectively (based on discussion with farmers). I calculated the mean annual gross revenue R_{gross} from tree crops in a similar fashion for each field, where R_i is the revenue during each immature year, R_m is the revenue during each year of maturity, and R_f is the revenue from the final year (R_f only applies to oil palm):

$$R_{gross} = \frac{iR_i + mR_m + R_f}{i + m}$$

Again, I used the mean values from each square, and resampled these means using weights proportional to the number of fields sampled in each square. The net revenue (profit), R_{net}, was estimated by subtracting the bootstrapped estimates of cost from the bootstrapped estimates of gross revenue:

$$R_{net} = R_{gross} - C$$

4.2.10 Correction of labour inputs

The reported labour demands for weeding cocoa and oil palm fields in farm mosaic squares were more than double those reported from the oil palm plantations. Despite this, small-scale farms had more, taller weeds than did the plantations, and only small-scale farms had tall weeds > 2 m. Increased labour demands in orange and food crop fields could be plausible because those crops do not shade out weeds as effectively as cocoa and oil palm, but it seems highly unlikely that oil palm farmers devoted much more labour to weeding yet obtained much poorer results compared to plantations. Both small farmers and plantation staff relied on a similar mix of manual weeding and herbicides to control weeds. Mature cocoa farms are, if anything, even more heavily shaded and weed-free than oil palm farms, and should therefore not require more labour than oil palm farms. It seems likely that farmers consistently overestimated the labour requirements for weeding mature cocoa and oil palm, and I therefore reduced the reported labour requirements for weeding these crops to correspond to that reported by the plantation managers. This meant reducing the labour demands of weeding and spraying per hectare per year in mature fields from GH¢138 (oil palm) and GH¢82 (cocoa) to GH¢50. The effect of this was to increase the estimated net profit of small-scale cocoa and oil palm farming.

4.2.11 Plantation costs and revenues

I visited parts of plantations at different stages (cleared, immature, mature) and observed the different operations which take place (preparation, planting, weeding, pruning, harvesting, replanting), to become familiar with how plantations are managed. I discussed costs with senior management staff at each plantation, and constructed a set of spreadsheets to capture cost data for each activity at each age. I populated these spreadsheets with data provided by the plantation managers to produce an idealised model of plantation costs per hectare over a 25 year cycle, based on 2007 costs.

I used the expected yields from the polynomial models to estimate the costs of harvesting for each of the plantations, and then subtracted the costs at each age from the value of the palm fruits produced at that age. This gave the net profit of the plantation at each age. Palm fruit value was calculated at factory gate prices, unlike fruit value from small-scale farms which was calculated using farm gate prices. This was because the plantations' cost estimates include the cost of transporting fruit to the mill, while farmers' estimates do not. I then averaged the age-specific net profits to produce an overall average annual net profit. I did this (rather than simply use 2007 profits for each plantation) because the costs and yields in any one year depend on the proportion of the plantation being replanted, and the age distribution within the plantation. My estimates can be interpreted as average profits and yields of a set of idealised plantations with the same profits and yields as those I examined, but with exactly equal proportions of all 25 age-classes of oil palm.

The costs of setting up ancillary infrastructure such as office buildings, and other administrative costs, are accounted for as overheads at 15%, based on discussions with plantation managers. As I was interested in comparing plantations with small farms, I evaluated only the costs of producing oil palm fruit, and did not collect detailed information on the costs of processing the fruit into palm oil and palm kernel oil.

4.2.12 Food energy

The estimates of mean net annual yield for each crop, in tonnes per hectare, were converted into estimates of food energy using the USDA National Nutrient Database for Standard Reference (USDA 2008). The proportion of harvested mass discarded (peels, cobs, etc.) was subtracted, and the remaining mass was multiplied by the energy values shown in Table 4 and converted to an estimate of food energy in GJ/ha.

Palm fruit yields on the four plantations were converted into oil yields using recent information on the ratio of fruit processed to oil produced by each of the four plantations. In the case of oil palm fruit produced by small-scale farmers, the mean oil extraction ratio from the four plantations was used to estimate the oil yield. These oil yields were translated into food energy as for other crops, using the conversion factors in Table 4.6.

Table 4.6. Proportion of harvested mass of different crops discarded and food energy per unit mass of edible product. Source: USDA (2008), except for cocoa beans, from Duke (1983).

Food item	Refuse %	Food energy GJ/t
bananas	36	3.71
cassava	14*	6.67
chilli peppers (dried)	0	13.31
cocoa beans	0	19.09
cocoyam (=taro)	14	4.69
maize	0	15.27
oranges	27	1.97
palm kernel oil	0	36.99
palm oil	0	36.99
plantains	35	5.10
yam	14	4.94

* “Refuse %” for cassava was given by USDA (2008) as 0%, but I corrected it to 14%, because cassava is prepared in a similar way to yam and cocoyam.

4.3 Results

4.3.1 Mapping of field types

I mapped 36 points in each of ten farm mosaic squares, covering 10% of the area of each 1 × 1 km square. I conducted mapping between late October and early December 2006. An example of the level of detail mapped is shown in Figure 4.2. Oil palm was the dominant field type overall, making up 40% of the land mapped, and up to 85% in one square (Table 4.7). Cocoa was the second most important crop, covering 16% of the area overall. Orange covered 6% in total, and mixed food crops (without any tree crop) also covered 6%. Other crops covered only 2%, mostly coconut, but with a few plots of rubber, sugarcane, and cola. Overall, 71% of land was under active cultivation or cleared for cultivation, and 29% was uncultivable or not currently cultivated. Much of the uncultivated land consisted of fallow land that had been abandoned for 1-10 years, but it also included mature secondary forest patches and forest remnants, *Raphia* swamps, and areas formerly used for small-scale mining (*galamsay*). There was considerable variation between squares: uncultivated land covered as little as 6% of one square and as much as 70% of another.

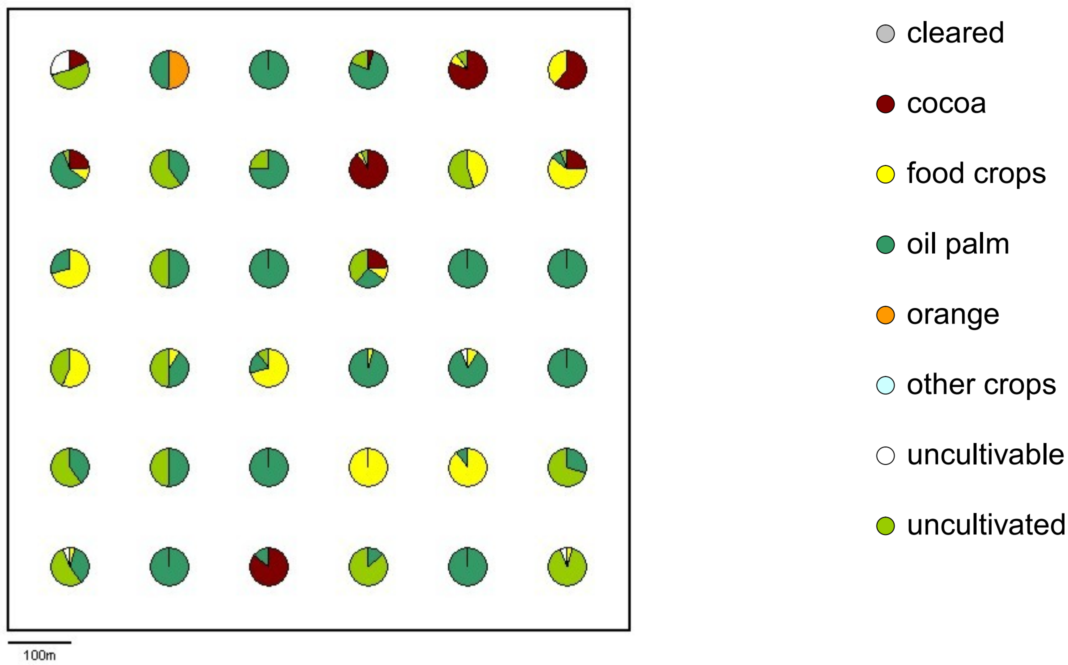

Figure 4.2. Example of field type mapping in a farm mosaic study square (#17), showing proportion of each field type mapped within a radius of 30 m around each of 36 points.

Table 4.7. Field types in study squares in southwest Ghana, from crop mapping.

Block	Square	Average area of each field type (%)							
		orange	cocoa	food crops	oil palm	other crops	cleared	uncult-ivable	uncult-ivated
Farm mosaic squares									
I	#3	1	0	2	80	4	1	1	12
	#4	0	0	5	72	7	1	0	15
II	#9	0	11	2	9	7	1	0	70
	#10	0	27	2	15	0	2	1	52
III	#15	0	47	12	16	0	0	3	22
	#16	0	43	3	1	0	0	1	50
	#17	1	12	17	46	0	0	1	23
IV	#22	31	3	16	44	0	0	0	6
	#23	28	13	3	35	0	4	0	17
	#24	1	6	1	85	0	0	0	8
Farm mosaic mean		**6**	**16**	**6**	**40**	**2**	**1**	**1**	**28**
Plantation/farm squares									
I	#5	0	0	6	80	0	0	3	11
	#6	0	0	9	49	3	0	3	37

4.3.2 Summary of interview sampling effort

I collected detailed information for 86 fields (also 37 bushmeat/NTFP recalls, not discussed further here). Sample sizes for individual crops were relatively small: 31 (mature oil palm), 14 (mature cocoa), 8 (mature orange), 26 (food crops grown with immature tree crops) and 7 (food crops grown without any tree crop), and I was unable to collect full information on all parts of the lifecycle for each field. For example, farmers were able to recall preparation costs for most of the fields, but obviously farmers with fields of immature tree crops could not provide any information on the costs and revenues of mature tree crops for those fields.

4.3.3 Price index

When adjusted for inflation, the prices of most agricultural produce in Ghana have fluctuated at close to their current levels over the past 27 years, although most have increased somewhat since the mid-1990s (Figure 4.3, Figure 4.4). The most striking exceptions to this are palm oil, which has decreased in price especially since the 1980s, and oranges, which have increased dramatically in price, especially since around 2000.

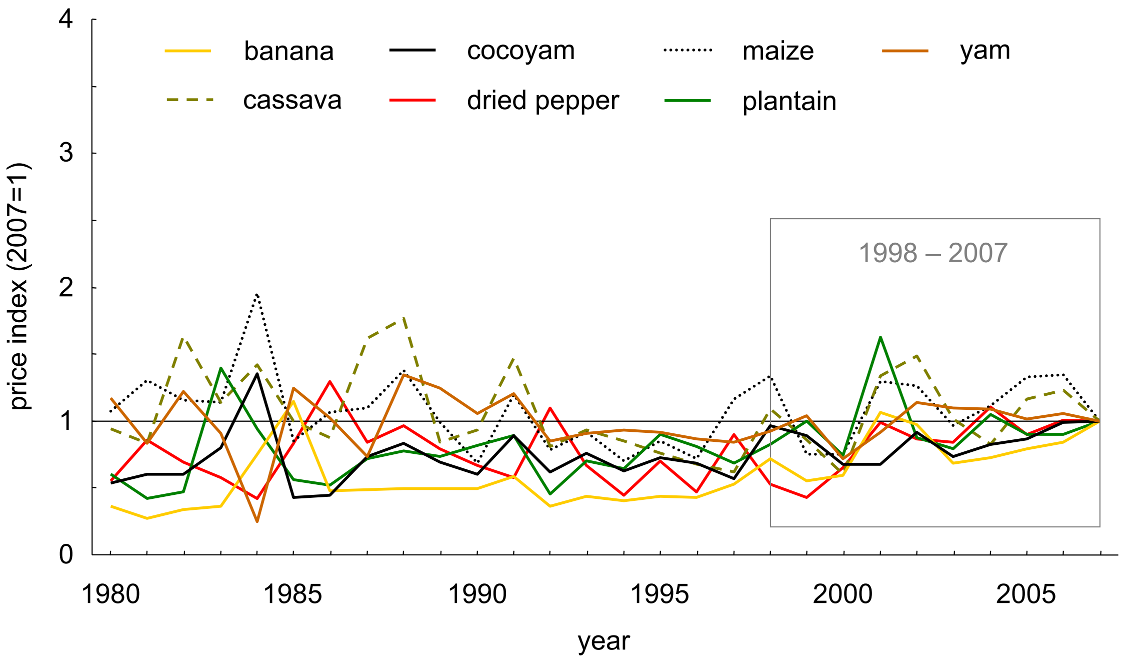

Figure 4.3. Inflation-adjusted wholesale prices of food crops in Ghana, 1980 to 2007 (January prices). Prices are standardised so that the January 2007 price for each commodity equals 1. The grey box denotes the ten-year period used for long term price calculations, 1998-2007. Source: Statistics, Research and Information Directorate, Ministry of Food & Agriculture, Accra, Ghana.

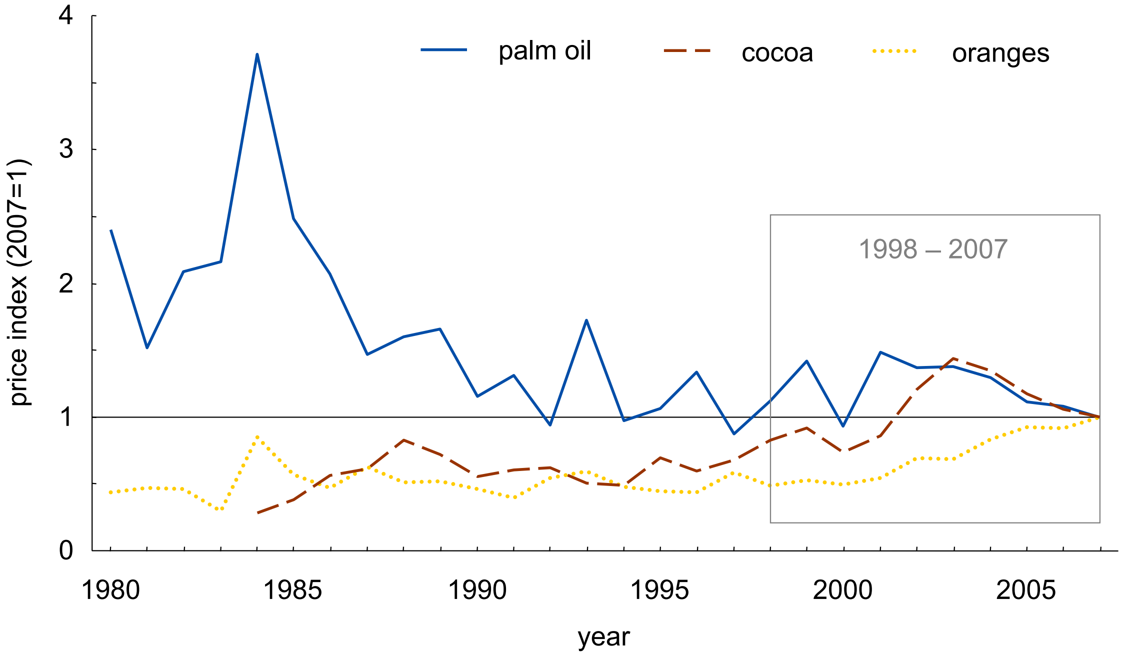

Figure 4.4. Inflation-adjusted wholesale prices of tree crops in Ghana, 1980 to 2007 (January prices). Prices are standardised so that the January 2007 price for each commodity equals 1. The grey box denotes the ten-year period used for long term price calculations, 1998-2007. Source: palm oil and orange prices from the Statistics, Research and Information Directorate, Ministry of Food & Agriculture, Accra, Ghana; Cocoa prices collated from Aryeetey et al. (2000), Boafo-Arthur (2007), ICCO (2008) and Cocobod (M. Vigneri, in litt.).

4.3.4 Farm yields

I calculated yields separately for each crop. Mean yields of tree crops during the mature part of their lifecycle were 6.43 t/ha (orange) and 0.58 t/ha (cocoa) fresh weight. The mean reported yield of mature oil palm fields was 8.56 t/ha, but see section 4.3.5 for an explanation of why a higher value was used. In the case of food crops, two main crop combinations were recorded: cassava-plantain fields (plus either cocoyam or banana) with a three-year cycle, and maize-cassava fields, with a two-year cycle. Mean annual yields from the lifecycle analysis are shown in Table 4.8. Note that yields are averaged across all fields of a certain type: for example, maize yields in fields with maize were 1,005 kg/ha, but only two of the six fields with adequate yield data had maize, so the mean yield averaged across the six fields was 335 kg/ha. Because the sampling design was based on selection of points, weighting by field area was not necessary.

Table 4.8. Mean annual yields (kg/ha) of crops in four types of fields in southwest Ghana, including food crops which are intercropped with tree crops during the first two to three years of their lifecycle. Cells are left blank where no report of a crop was made from that type of field.

Crop	**Field type**			
	cocoa	oil palm	orange	food crops
cocoa	538			
oil palm		7,950		
orange			5,370	
banana				53
cassava	75	187	125	4,467
cocoyam	6	16	11	349
maize	7	17	11	335
pepper	<1	<1	<1	
plantain	24	60	40	708
yam	<1	1	1	

4.3.5 Palm oil yield in relation to month

Of the 23 mature oil palm fields for which I had interview data, I was able to obtain monthly records for 21 of them, from January to December 2007, although there were missing values for some fields in some months. Farmers provided two pieces of information for each harvest in each month: the quantity harvested and the value of the harvest. Different farmers used different units for quantity, including bunches, baskets, tonnes, head pans and kilograms. In order to convert these varied units into metric tonnes, I used only the quantities reported in the most frequent unit measurement from each field, standardised the price per unit for each field to 1 in June 2007, and estimated the price per tonne in each month, based on a reported cost of GH¢50 in June 2007. (June 2007 was the only month for which I had both full information from every field, and a reported price per tonne). I then converted the reported mean monthly revenues from each square into tonnes using those monthly estimates of price per tonne.

Oil palm yields showed a distinct annual pattern, being highest in the months from February to June, and lowest in the second half of the year (Figure 4.5). Oil palm yields from mature fields, as calculated from the monthly logs (9.82 t/ha), were higher than those estimated from the interviews (8.56 t/ha). Both the bootstrapped means and variances were significantly different (F test, $F = 0.2012$, $p < 0.001$; Welch two-sample t-test: $t = 84.56$, $p < 0.001$). The yields calculated from monthly logs seem more likely to be accurate because of the shorter recall period, and are also conservative in that they err towards over-estimating farm mosaic yields, so they were used in subsequent calculations. I did not collect monthly data from immature oil palm fields, but the immature stage of the cycle has relatively little impact on lifecycle yield compared to the mature stage, so annual recalls for this are adequate.

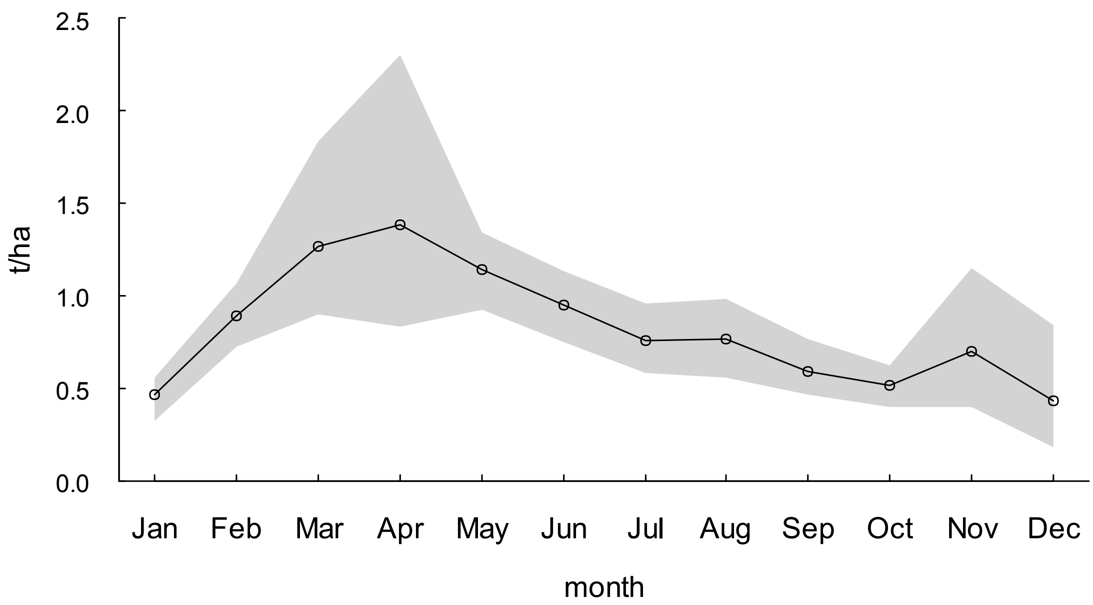

Figure 4.5. Mean monthly oil palm yields reported from 21 mature fields in farm mosaic in 2007 (mean ± bootstrapped 95% confidence limits based on monthly square-level means).

4.3.6 Plantation yields

Managers from three of the oil palm plantations (in blocks II-IV) provided me with data on yields from past years. Yield curves for each of the three plantations for which data were available were similar (Figure 4.9 - Figure 4.11). These are conservative (i.e., likely to underestimate the yields achievable in plantations in 2007 and later), as I included all past yield data and did not correct for increases in potential yields over time because of new varieties and improved cultural practices.

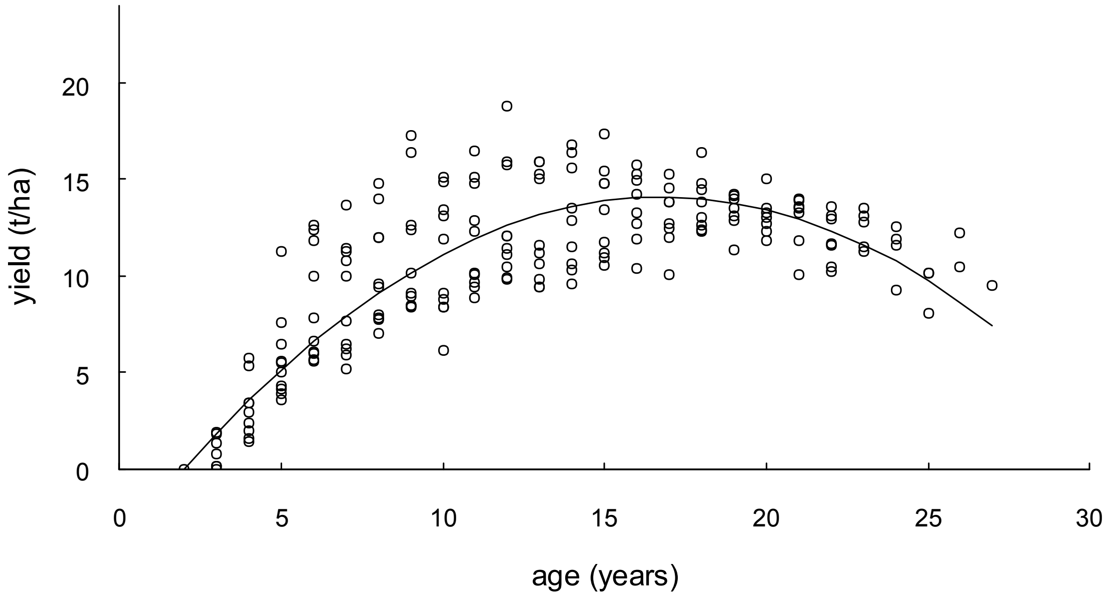

Figure 4.9. Oil palm fruit yields in tonnes/ha/year at plantation in block II, based on harvesting data from 1985 to 2005 (formula, where x = age − 2: $y = 1.904367x - 0.064338x^2$). Points represent the parts of the plantation, typically 100-500 ha, of a certain age in each year. The mean annual yield, averaged over 25 years (ages 0 to 24), is 9.51 t/ha.

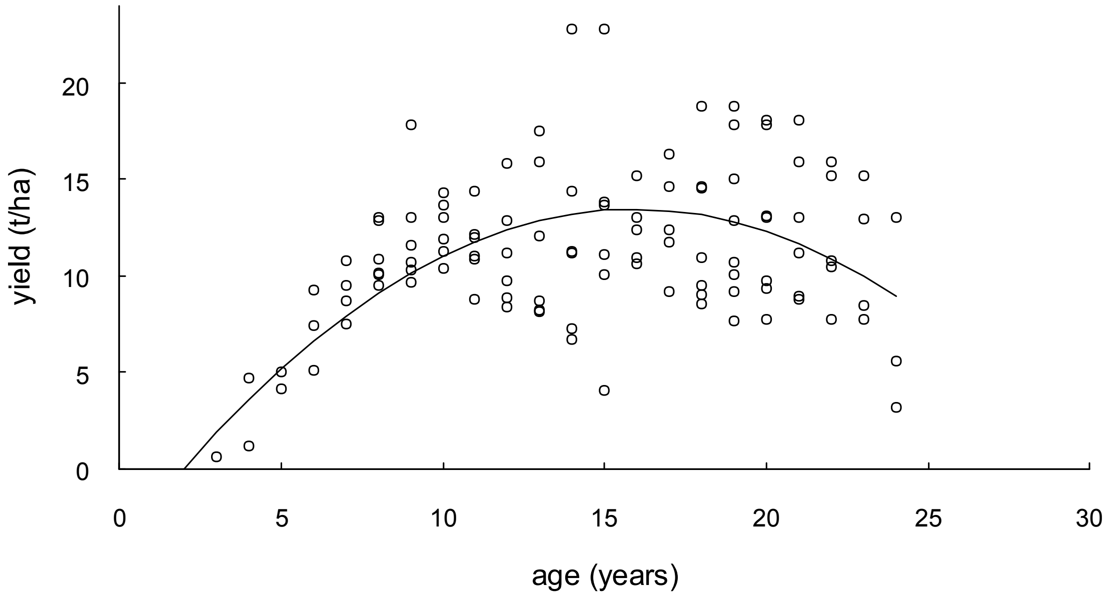

Figure 4.10. Oil palm fruit yields in tonnes/ha/year at plantation in block III, based on harvesting data from 1990 to 2005. (formula, where x = age − 2: $y = 1.935643x - 0.069562x^2$). The mean annual yield, averaged over 25 years (ages 0 to 24), is 9.03 t/ha.

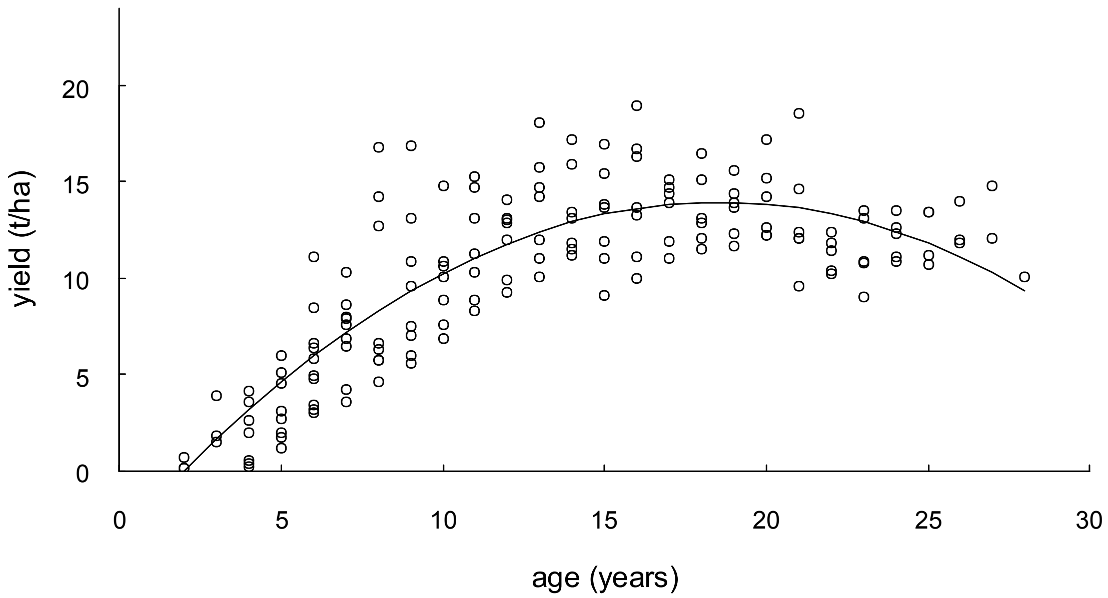

Figure 4.11. Oil palm fruit yields in tonnes/ha/year at plantation in block IV, based on harvesting data from 1984 to 2006. (formula, where x = age − 2: $y = 1.690219x - 0.051162x^2$). The mean annual yield, averaged over 25 years (ages 0 to 24), is 9.34 t/ha.

4.3.7 Food crop costs and revenues

The mean annual cost of mixed food crop production (± SE), where food crops were grown without tree crops, was GH¢424.62 ± 88.1 per hectare. The mean annual gross revenue was GH¢888.41 ± 153.8, and thus the net profit was GH¢463.79 ± 178.1 per hectare. These estimates cannot be compared directly with those from the tree crops, as they do not take into account the years that land must be left fallow after food crop farming. If, for example, the cultivation frequency is 33% (i.e., a field is cropped for three years, then left fallow for six years) the average net profit over the nine years would be GH¢155 per hectare. Rather than attempting to determine the length of fallow periods, this aspect was implicitly included by mapping the uncultivated proportion of each square. Much, though not all, of this uncultivated portion in most squares consisted of “resting” fallow land.

4.3.8 Tree crop costs and revenues

An example of the pattern of costs and revenues during an average tree crop lifecycle is shown in Figure 4.12, for oil palm. Those for cocoa and orange fields are similar, but without the windfall revenue from palm wine tappers in the final year. The mean annual costs and gross revenues from tree crops, including those of food crops intercropped in the first two to three years, are shown in Figure 4.13. The estimates of mean annual net profits of each crop (± SE), including intercrops, were GH¢128.08 ± 110.73 (cocoa), GH¢227.10 ± 52.05 (oil palm) and GH¢256.71 ± 73.77 (orange).

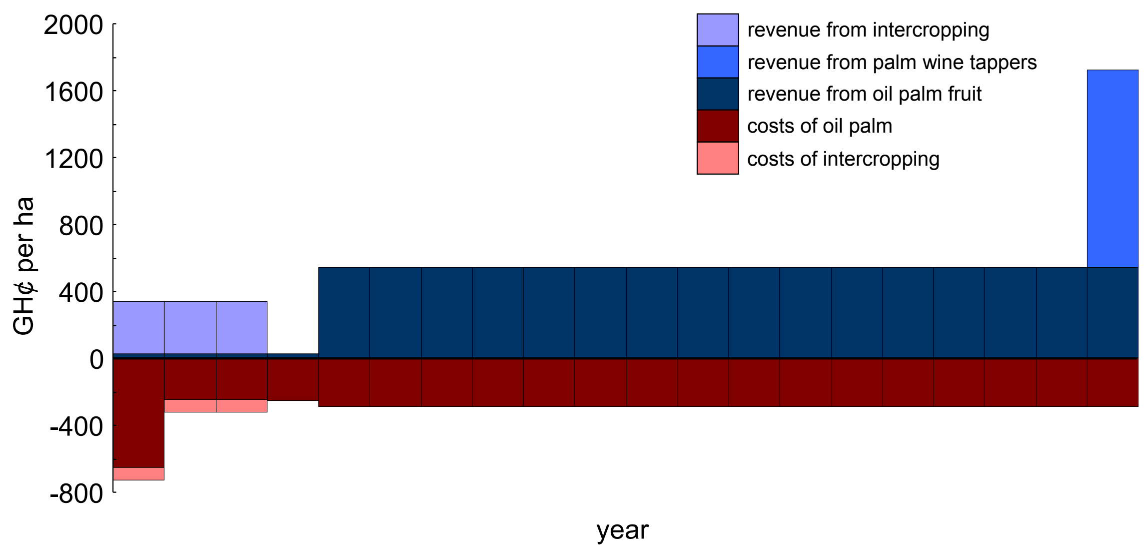

Figure 4.12. Simplified crop lifecycle for an average oil palm field, showing costs (red) and revenues (blue) in each of 20 years. Intercropping in the early years adds little additional cost but provides some revenue before the oil palms start to bear fruit.

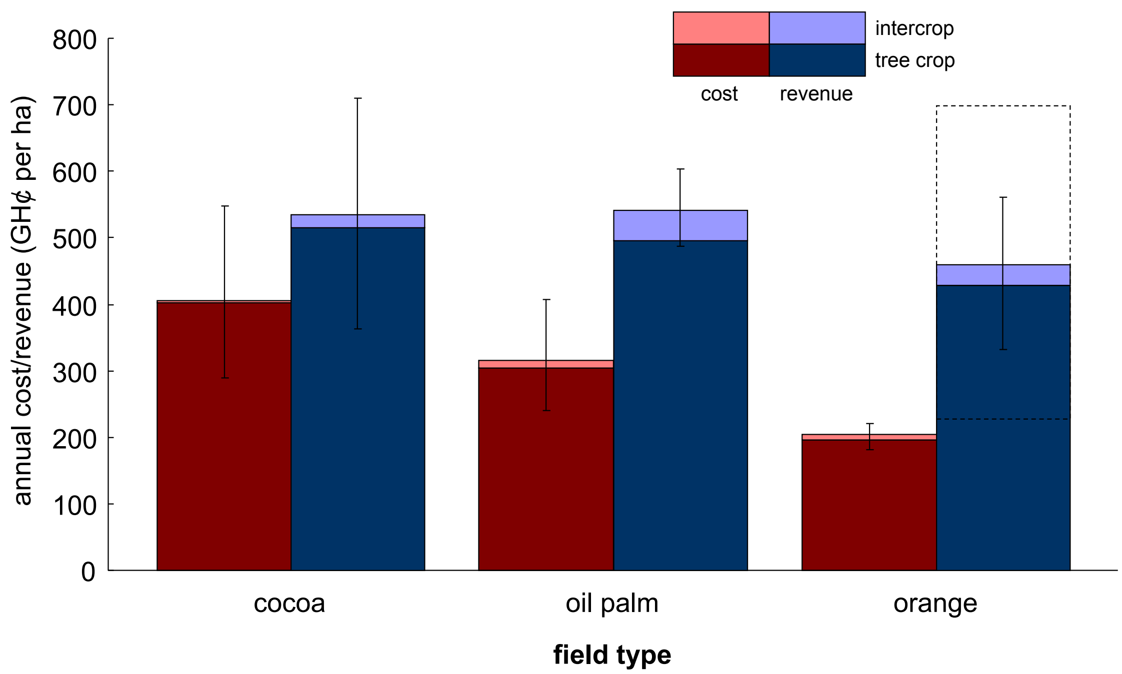

Figure 4.13. Mean annual costs (red) and gross revenues (blue) of three tree crop field types (± 95% confidence limits) over one lifecycle, including costs and revenues from intercropping in the first two to three years. Lifecycle length is 50 years for cocoa, 20 years for oil palm, and 30 years for orange. Revenues are based on long term (ten-year) mean prices as described in the text. The dashed lines show the gross revenue from orange fields when the long term price is based on either the maximum or minimum reported 2007 price.

4.3.9 Plantation costs and revenues

The initial costs of land preparation rely on heavy machinery and are high. They would be approximately doubled if I included land acquisition, which I did not. After the first year, costs are dominated initially by fertiliser, and later by the labour needed for harvesting. Harvesting oil palm fruit is labour-intensive, and is carried out in short rotations, each part of the plantation being harvested every two weeks.

There was considerable variation in the reported costs of plantation management, and thus in the reported net revenues (Table 4.14, Figure 4.15 - Figure 4.17). Profits were relatively low at the plantation in block I, as expected because of poor management practices in the past and thus low yields. More surprisingly, profits were also particularly low at the plantation in block III, largely because of high reported costs. This difference probably reflects differences in the accuracy of reported costs as much as it indicates “true” differences between plantations.

Table 4.14. Mean annual costs and revenues, and net profits, of oil palm plantations in the four study blocks in southern Ghana.

GH¢ per hectare	Block I	Block II	Block III	Block IV
gross cost	254.71	391.73	481.58	425.51
gross revenue	539.53	738.14	703.38	741.62
net profit	284.82	346.41	221.80	316.10

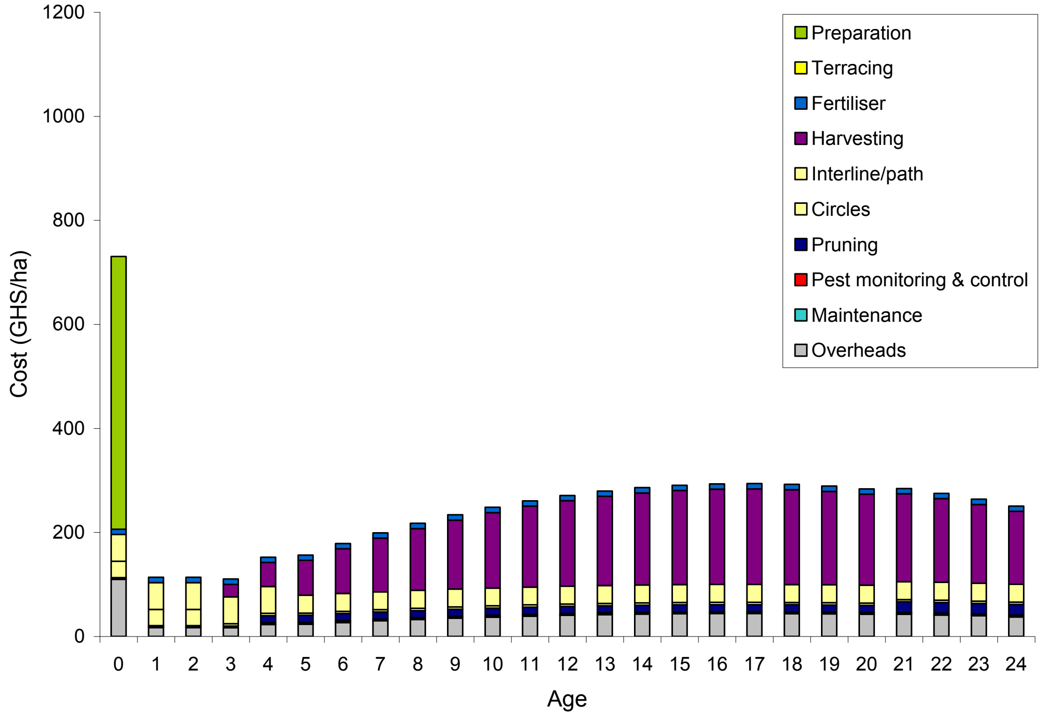

Figure 4.15. Plantation costs over a 25-year cycle, plantation in block I. Data for preparation cost were incomplete, so the value from the nearest plantation was substituted.

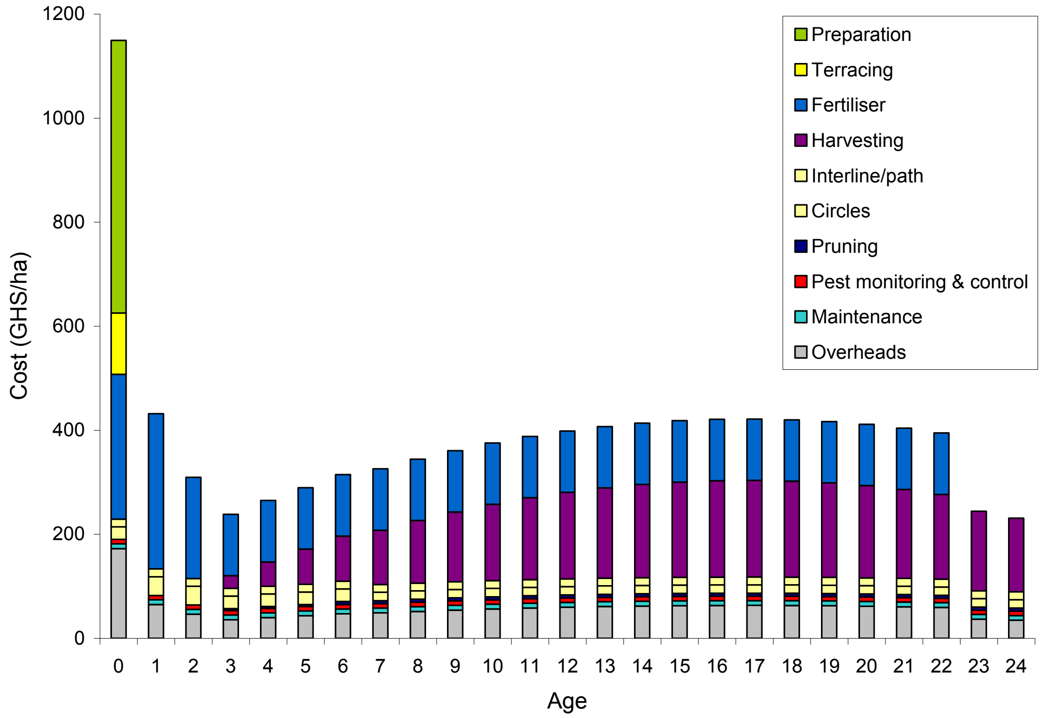

Figure 4.16. Plantation costs over a 25-year cycle at plantation in block II, assuming 97 m of terracing per ha (one quarter the rate of terracing as in recently planted areas, but representative of the plantation overall).

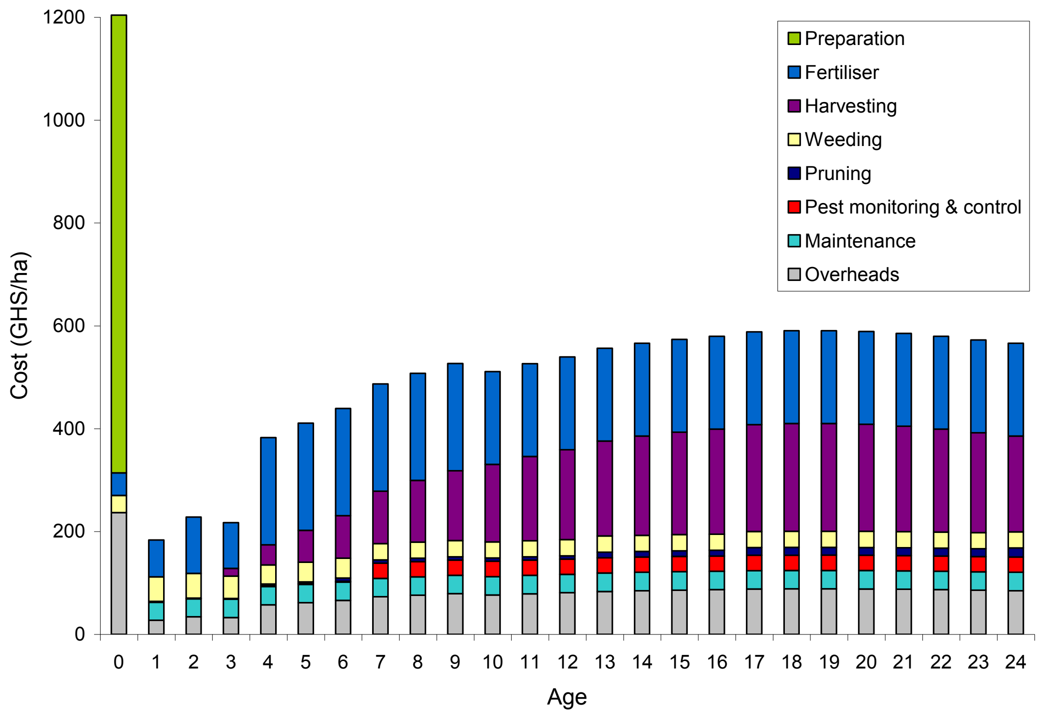

Figure 4.17. Plantation costs over a 25-year cycle, plantation in block III.

4.3.10 Food energy

Oil palm fields produced the largest quantity of food energy per hectare of the farm mosaic field types assessed during this study: 56 GJ/ha (Table 4.18). Food crop fields produced 35 GJ/ha, while orange and cocoa fields produced only 9 and 11 GJ/ha, respectively. Palm oil extraction ratios at the mills connected to the four plantations ranged from 16% to 21% (Table 4.19). Both palm oil and palm kernel oil have the same energy composition: 36.99 GJ per tonne (Table 4.6).

4.3.11 Square-level profits and food energy

The net profits and food energy for each land use were multiplied by the area of that land use in each square from the mapping (section 4.3.1) and summed to generate estimates of square-level profits (Figure 4.20) and food energy (Figure 4.21).

Table 4.18. Mean annual yields measured in terms of food energy (MJ/ha) of crops in four field types in southwest Ghana. Yields are averaged across a single crop cycle, of length 50, 20, 30 and 2-3 years for cocoa, oil palm, orange and food crops respectively. Actual food energy output is lower than shown for food crop fields if the necessary fallow period is included.

Crop	Field type			
	cocoa	oil palm	orange	food crops
cocoa	10,256			
oil palm		54,169		
orange			7,766	
banana				127
cassava	429	1,073	715	25,622
cocoyam	27	67	45	1,481
maize	101	254	169	5,114
pepper	1	2	2	
plantain	79	198	132	2,345
yam	1	4	2	
Total	**10,895**	**55,766**	**8,831**	**34,689**

Table 4.19. Oil extraction ratios from oil palm fruit, for crude palm oil (CPO) and palm kernel oil (PKO) from four oil palm plantations in Ghana.

Plantation (block)	Yield t/ha	CPO proportion	CPO t/ha	PKO proportion	PKO t/ha
I	6.79	0.16	1.11	0.02	0.10
II	9.51	0.19	1.76	0.02	0.15
III	9.03	0.18	1.65	0.02	0.14
IV	9.34	0.21	2.00	0.02	0.14

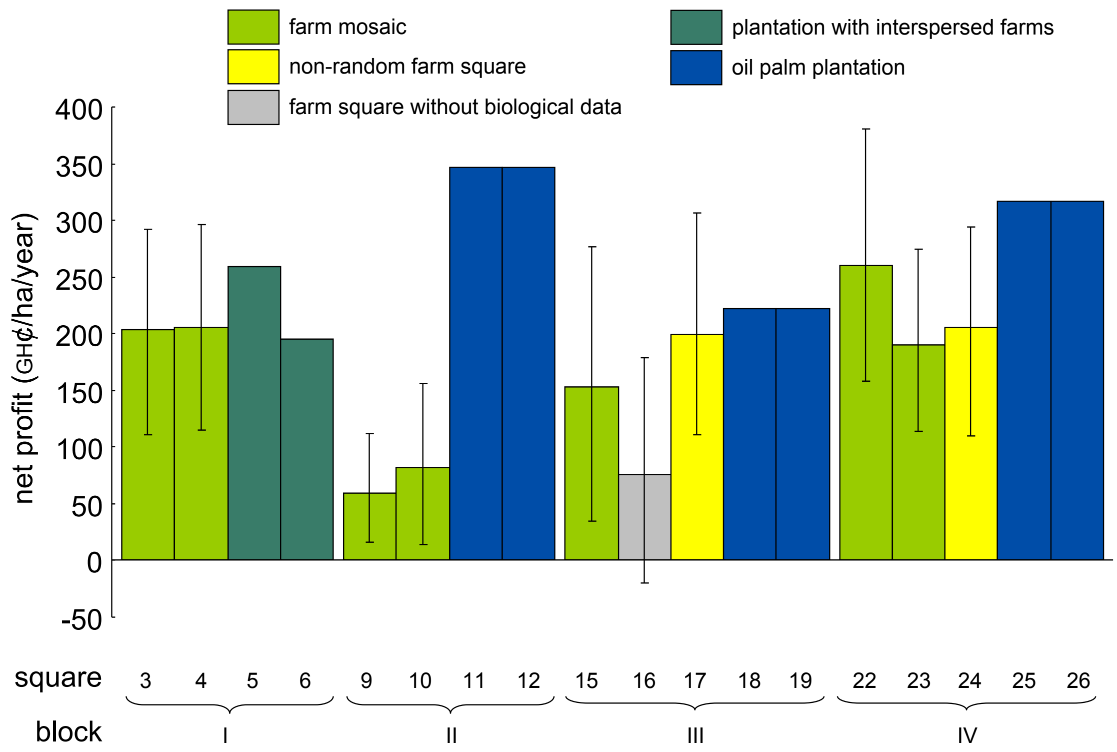

Figure 4.20. Mean annual agricultural profit per hectare (± 95% confidence limits) for each of 18 farm mosaic and plantation squares. No confidence limits were estimated for the plantation squares as only one estimate of yield was available for each.

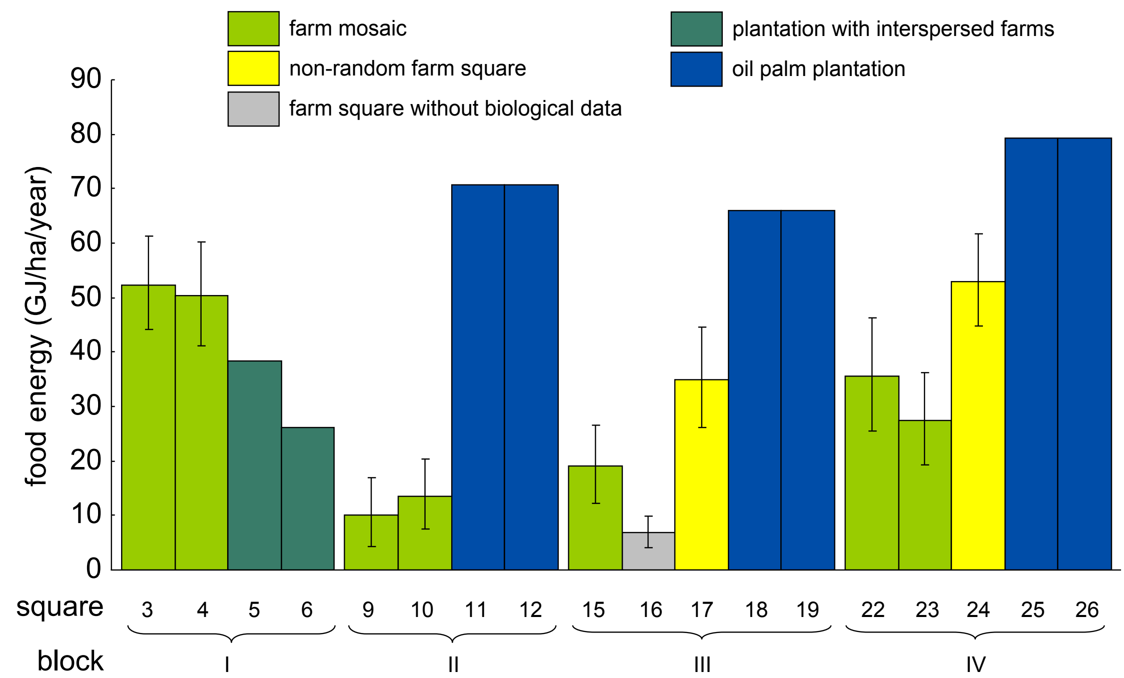

Figure 4.21. Mean annual food energy per hectare (± 95% confidence limits) for each of 18 farm mosaic and plantation squares. No confidence limits were estimated for the plantation squares as only one estimate of yield was available for each.

4.4 Discussion

4.4.1 How do oil palm yields and profits vary between small farms and plantations?

Estimated mean annual lifecycle yields of oil palm fields in the farm mosaic (7.95 t/ha) were only 16% lower than the yields from the highest-yielding plantation (9.51 t/ha). For reasons outlined in section 4.4.1, this comparison probably underestimates the size of the gap, but it does suggest that reasonably high oil palm yields are obtainable from at least some small-scale farms, perhaps especially when *tenera* variety palms are planted in optimal soils and some fertiliser is used. Some oil palm fields in the farm mosaic were much lower-yielding than this. My estimates are considerably higher than those of the FAO for Ghana. The FAO's ten-year mean in Ghana (1998-2007) was 8.0 t/ha, which refers to harvested area, and thus should be compared with my estimates of yields from mature fields (8.56 t/ha from interview data, 9.82 t/ha from monthly recalls). Oil palm yields in Ghana are far lower than those from some other countries: e.g., 17.4 t/ha in the world's leading producer, Indonesia, and 21.3 t/ha in Cameroon (ten-year means based on harvested area, FAOSTAT 2009). This can be explained by the prolonged dry season (November to March) and prevalence of cloud in addition to the fact that most production in Ghana is by small-scale farmers with limited access to fertilisers and other inputs.

There appear to be two main reasons that small-scale farm profits were lower than those of plantations: lower yields, and higher transport costs, because small-scale farming is more widely dispersed. Farm gate prices for oil palm fruit were on average 27% lower than mill gate prices, reflecting the high cost of transporting palm fruits to the mill. Concentration of production in large nucleus plantations is more profitable because it substantially minimises the distance over which bulky fresh fruit bunches (ffb) must be transported. Production cost was generally higher on plantations (GH¢38-53 per tonne ffb) than on small farms (mean GH¢38 per tonne ffb), but the increased yields on plantations were sufficient to ensure that the overall profitability per hectare of plantations was typically higher. In addition, the actual profits accruing to individual farmers are lower than those calculated, because of their need to pay rents, as explained in section 4.4.4.

Finally, I have not considered the varying efficiencies of different processing methods for palm oil from small farms. The oil extraction ratio (OER) in the most efficient mill was 21%, while it was 16% in the least efficient. That makes a considerable difference to the final quantity of oil obtainable from a tonne of palm fruits, and helps to explain the low output from squares #5 and #6. It is difficult to get accurate estimates of the OER of small-scale local processing: it has been estimated at 17%, but is probably typically lower (van den Berg, unpublished, p.36). I used the mean OER of the four mills (19%) for all farm mosaic production, which is likely to overestimate oil output, as part of farm mosaic production in all areas goes to small-scale local processors (Figure 4.22c).

4.4.2 How do my estimates of yields compare with those from other studies?

My estimates of farm mosaic yields for oil palm and cocoa were somewhat high by comparison with other estimates from Ghana, while my estimate for oranges appeared to be somewhat low. Yields from relay-cropped food crops are difficult to compare because of differences in the mixtures of crops grown, but my estimates are broadly consistent with other estimates.

The FAO estimates of cocoa yield in Ghana are clearly not based on much data: they were exactly 400 kg/ha from 2005 to 2007 (FAOSTAT 2009). Dormon et al. (2007) cite an official estimate of 360 kg/ha, and Boni et al. (2004) considered that good yields in the Sefwi Wiawso district in Western Region were 5-6 bags/ha (320-384 kg/ha), with 55% of the farmers reporting yields lower than that. Estimates from surveys by Vigneri (2007) and Teal et al. (2006) are even lower: 232-278 kg/ha in 2001-2004, with the smallest farms producing typically around twice the yield of the largest farms. These yields are an order of magnitude lower than those achieved on experimental farms under ideal conditions, for example 2,471 kg/ha by the Cocoa Research Institute (1973, quoted in Teal and Vigneri

2004). In this context, the yields I recorded in this study are somewhat high, but plausible: 584 kg/ha from mature cocoa, or 538 kg/ha on average over a 50-year lifecycle. Average cocoa yields in Ghana are low by comparison with other countries, a fact blamed on inadequate control of pests and diseases, low soil fertility and limited fertiliser use (Appiah et al. 2000, Boni et al. 2004, Dormon et al. 2007).

My estimate of orange yield from mature fields (6.43 t/ha) was smaller than the FAO estimate (7.5 t/ha during 1998-2007), but again plausible. Confidence in the FAO estimates is limited, as they were exactly 7.1428 t/ha from 2000 to 2003, and exactly 8.0 t/ha in three of the four years 2004 to 2007. The leading global producer of oranges is Brazil, with ten-year mean (1998-2007) yields of 22.1 t/ha (FAOSTAT 2009). Other major producers, such as the United States and Mexico, also have much higher yields than Ghana's. These major producers typically grow oranges in large-scale plantations with heavy use of fertilisers, lime and pesticides (Clay 2004). Ghana's lower yields are not unexpected, given that most production is relatively small scale, and with limited agrochemical application.

Comparisons with published yield estimates for food crops are not straightforward. Official yield estimates are frequently based on small experimental plots of a single crop, managed under ideal conditions (Dorosh 1989). However, in reality most food crops in rural Africa are grown mixed with other crops, and planting densities vary greatly. Losses from pests and diseases can be high (Figure 4.22d). Some root crops, notably cassava, can be left in the ground for a year or more without deteriorating, and might be harvested gradually over a long period, or not harvested at all, which complicates assessments of annual output. Yields as I have presented them (Table 4.8) are averaged across fields, including fields without that particular food crop, and are averaged across years, including years in which a particular crop was not harvested. Estimating yields for each crop based only on the fields and years in which they were harvested, my estimates of yields were 7.34

t/ha (cassava), 1.59 t/ha (plantain), 1.05 t/ha (cocoyam), 1.01 t/ha (maize) and 481 kg/ha (banana). Those yields are all considerably lower than the FAO's crop-specific yield estimates for Ghana (1998-2007, FAOSTAT 2009). This is not surprising, because these are yields from fields with multiple rather than single crops. It is more appropriate to convert yields to a common currency to compare multiple crop systems. Converting the FAO's estimates of these crops' mean yields to food energy using the same conversions as used in section 4.2.12 gives estimates of 70.56 GJ/ha (cassava), 22.91-28.18 (plantain, cocoyam and maize) and 10.33 GJ/ha (banana). These are broadly consistent with my estimate of 34.69 GJ/ha from mixed food crop fields. The suggestion here that monocropping of cassava could be more productive than relay cropping is not borne out by intercropping experiments, in which food energy yields of up to 146 GJ/ha were obtained from a combination of cassava and sweet potato, one-third more than from cassava alone (Moreno and Hart 1979, cited by Norman et al. 1995, p. 289). Given that at least 50% of cassava grown in Africa is intercropped, and the difficulties of defining yield for intercrops, the ten-year FAO estimate of 12.3 t/ha for cassava in Ghana (FAOSTAT 2009) is almost certainly unrealistic for typical small farm conditions.

The estimated revenues from small farming in this study are reasonably consistent with other information. A study of the profitability of different crops near two protected forests in southern Ghana found gross revenues per hectare that, when converted to 2007 currency, ranged from GH¢152-596 near Ankasa and GH¢540-1,520 near Bia (Sakyi-Dawson 1999). This is comparable to my estimates of gross revenue (GH¢429-888). Another study of rural farmers in southwest Ghana estimated household income from farming as equivalent to GH¢1,069 in 2007 (Appiah-Kubi 1999). Given a household size of 6, this translates to GH¢178 per person. I did not estimate household or personal income from farming, but given population densities of around one person per hectare, my estimates appear to be not dissimilar, though mostly somewhat higher. Naidoo and Iwamura (2007) map gross agricultural revenues in southwest Ghana as being frequently above US$356 per hectare, equivalent to GH¢340. My estimates of gross agricultural revenue (excluding bushmeat) at square level varied from GH¢170 in the least productive farm mosaic square to GH¢742 in the most productive plantation squares. More intensive verification work would be needed to confirm the accuracy of my estimates, but they seem to be broadly consistent with those from other studies.

4.4.3 How important are NTFPs, including bushmeat?

As noted in section 3.3.3, non-timber forest products play a significant cultural role in rural livelihoods, but most assessments of their importance have been focused on household use, and have not assessed the contribution of different land-use types to their availability. From interviews and discussions with local people, it was clear that they used a great many species of species of plants and animals from forests, farm mosaic and even from large-scale plantations. In terms of its perceived contribution to food security, bushmeat is probably the most significant of the NTFPs. Previous estimates of bushmeat offtake from forest-farm mosaic landscapes range from 2 kg/ha/year of meat from forests in the Congo Basin (Fa et al. 2002), to 2-6 kg/ha/year of undressed meat in largely forested landscapes of Cameroon and Nigeria (Fa et al. 2006), and an estimated sustainable harvest of 10 kg/ha/year from a forest-farmland mosaic with 59% uncultivated land in southwest Ghana (Holbech 2001). Taking the highest of these estimates, and assuming, as Holbech does, that 75% of carcass weight is edible meat, this translates to at most 0.04 GJ/ha/year of food energy (using food composition information for raw antelope meat, USDA 2008). This is equivalent to only 0.5% of the food energy yield from crops in the lowest-yielding farm mosaic square. In terms of protein, bushmeat is more significant, but again taking the highest value from Holbech (2001), it adds less than 10% to the protein yield from crops of even the square with lowest protein yield, and less than 4% to the protein yield from crops in the square with highest protein yield (unpublished data). This is despite the fact that most of the crops grown are starchy and oil crops, and not high in protein. It would appear then, that food security based on bushmeat is not a strong argument for maintaining wildlife-friendly landscapes in southwest Ghana.

What about the economic value of bushmeat? Here, it could be more important, but it was difficult to make direct comparisons with my data on crop profits because it is difficult to estimate the costs of bushmeat hunting. These include the costs of guns, cartridges, lanterns and snares, the opportunity cost of time spent hunting, and the risk of returning empty-handed. Ignoring those costs, the gross value of bushmeat as estimated by Holbech (2001) and adjusted to 2007 prices was GH¢26.3/ha (unpublished data). This is equivalent to almost 16% of the gross revenue from crops in the square with lowest revenue, or 44% of the net profit in the square with lowest profit. For some members of rural communities, it is clear that bushmeat can be an important source of income, perhaps especially in the more wildlife-friendly squares where much of the land is uncultivated at any one time. However, it seems unlikely that this would greatly increase the economic value of farm mosaic relative to forest, because forests are also an important location for bushmeat hunting. Even assuming that no bushmeat at all is obtained from the highest-yielding farm mosaic squares (which is not true even of plantations), the increased food energy, protein, gross revenue and net profit generated from crops in those squares was more than enough to compensate overall for the loss of bushmeat. More comprehensive studies of bushmeat production from different, well-defined land uses would be useful to better understand the implications of agricultural development on bushmeat supply, but my approximations suggest that farmers in Ghana are acting rationally by increasing crop output even if it compromises bushmeat availability in farm mosaic.

4.4.4 To what extent are my estimates biased?

Within the bounds of the confidence limits, I believe my estimates are reasonably accurate, but if there are biases they are likely to be towards underestimating the costs and overestimating the yields and profits of small-scale farming. I valued the labour of farmers and their families at the minimum wage: it might be worth more, closer to the wages that farmers pay for hired labour, which would reduce estimates of net profit. I also reduced the estimates of labour for weeding and spraying because I had evidence that they were too high (as described in section 4.2.10). Basing profit estimates on long term prices increased my estimates of gross revenue for oil palm and cocoa, and reduced them for oranges. Without these changes to labour costs and prices, many oil palm and cocoa fields were apparently operating at a net loss, something that might very well happen in particular years depending on fluctuations in climate and market prices, but seems unlikely to be true in the long term. In addition, part of the calculated profits would typically be payable to the landowner as rents, so the actual profits made by individual farmers are lower than the value produced by the land. The financial status of small farmers is thus considerably less secure than a naïve interpretation of my results would suggest.

In contrast, any bias in my estimates of plantation yields and profits is more likely to lean towards underestimation. My use of historical yield records to estimate lifecycle crop production underestimates current yields, because of the planting of better varieties and improved management practices. In estimating profits, I used the mill gate price of palm fruits as a shadow price for the value of palm fruits produced within each nucleus plantation. This is somewhat artificial, because the production of palm fruits is embedded within the larger economic enterprise of each company, which manages mill and plantation together as a single unit. It would be entirely rational even for a company to make an internal loss on its plantation activities, provided that the losses were more than compensated by the value added during processing. Companies only set their mill gate prices higher than breakeven prices because they must compete with other buyers of palm fruits.

4.4.5 What are other causes of variation in yield and profit estimates?

There is a range of other caveats which apply to the estimates, some of which are responsible for the wide confidence limits (e.g., in Figure 4.20). This lack of precision is probably a result of considerable real variation in environment and management between fields, as well as of measurement error (see e.g., Tittonell et al. 2008). Within each crop, there are different varieties with variation in growing seasons, yields, and management needs. For example, *santum* cassava can be harvested after six months (*santum* is a name for sweet potato), whereas *gudiga* cassava takes a year to mature, but can be left in the ground for up to a year without spoiling. Farmers, even in the same village, disagreed about the relative value of different crops. In square #22, for example, one farmer said "an orange farm is better than an oil palm one as you can harvest once and then you have money in bulk. Financially, orange is more reliable than oil palm." Another farmer from the same square, interviewed on the same day said, "the price for orange is not good. When the [fruit juice] factory at Asamankese is finished it will be better … the money from oil palm is better at the moment – you can get 3 million cedis from an acre [GH¢637/ha]. With orange you only get 1.5 million per acre [GH¢318/ha]" (cf. Figure 4.13). Yield varies with the age and variety of the crop, soil condition and the extent to which fertilisers have been used, and a combination of such factors could easily combine to produce a situation where the profits from an oil palm field exceed profits from an orange field for one farmer, while the reverse is true for another. I had insufficient sample sizes to quantify the effect of different crop management practices, but this information is less important when the aim is to quantify yields at the landscape scale, given the mix of management practices in use.

Further noise is introduced by the use of non-standardised definitions, and small sample sizes. For example, palm oil yields were variously expressed in terms of fresh fruit bunches (which vary in size and quality), tonnes, hundredweight, baskets, head pans, buckets and mini bags of loose fruit, and "thirteens" of palm oil. Prices are typically not fixed, and are subject to negotiation. Prices of produce vary depending on season (orange prices are low in January but high in April), year (see Figure 4.3) and location (rural prices are usually lower than urban prices, because of transport costs). Different markets are available for some products. For example, oil palm farmers can sell their fruit at a fixed price to middlemen who will transport them to the large mills, or they can sell them to local mills at prices that fluctuate more widely depending on supply, or they can sell to market women from nearby towns, or they can process the fruits locally into palm oil and sell that. There is also a further complication in that farmers do not sell some of their produce, but consume it within their family. Valuing non-marketed produce at market prices is unavoidable, but probably inflates its value relative to the prices obtainable were it marketed (Hart 1982, p. 129). Farmers in my study typically sold a large proportion of their oil palm fruit to middlemen and some to local mills or market women. Conversion of reported oil palm yields from prices into tonnes is thus subject to some error because prices are not fixed, but this approach seemed to give generally reasonable results. Because I distributed sampling effort between four blocks, I was unable to sample each block as thoroughly as if I had sampled only one. In addition, it sometimes took a long time to find the randomly selected farmers in each square, and interview sample sizes were smaller than planned. It is unlikely that small sample sizes would result in much systematic bias, but they do reduce precision.

The possibility of inaccurate reporting by interviewees is inevitably a concern in a study of this type (Freeman 1987, Boni et al. 2004). I worked to build trust by making several visits to each village before starting interviews, learning some rudimentary *Twi*, chatting with farmers and explaining my work, and by conducting interviews through reliable local translators, such as agricultural officers who were known to and trusted by the villagers. I tailored recall periods for different questions depending on what I believed would be easiest for farmers to remember, and to avoid the problem that people often remember past events as being more recent than they actually were (Bernard et al. 1984). For example, there are well-defined seasons for harvesting cocoa and oranges, and farmers were generally able to recall precisely the previous year's yield, measured in standard sacks or boxes, respectively. Oil palm is different, being harvested every two to three weeks throughout the year, and with a range of often non-standard units, so here I relied on recall of the yield from recent harvests, harvesting frequency through the year, and recall of harvest size in each month. As seen in section 4.3.5, monthly recalls were probably more accurate. Time allocation to labour was assessed in relation to particular activities and their frequency (e.g., the number of weeding rounds in a year, and the number of man-days required to complete one round). To minimise the risk of farmers confusing definitions (e.g., reporting partial days as full man-days), deliberately providing false information (e.g., reporting high costs in hope I would offer some financial support), or confusing real and aspirational activities (e.g., reporting aspirational levels of weeding when real levels were lower) I became as familiar as possible with the practicalities of peasant farming in Ghana, challenged suspect responses, and conducted interviews in the presence of knowledgeable local contacts.

In calculating the costs, yields and revenues of farming, I used idealised models of their lifecycles. Tree crops were assumed to have a fixed-length lifecycle, when in fact the lifecycles of crops in different fields vary. The high pay-off from selling oil palm trees to palm wine tappers sometimes tempts farmers to fell their palms when they are younger than the 20-25 years over which they could maximise their profits from oil palm fruit. This is a common strategy when farmers face cashflow constraints and when oil palm fruit prices are low, although the price they receive is lower for younger palms. Similarly, it is not uncommon for cocoa farms to be abandoned when prices are low, an eventuality that does not fit neatly into a lifecycle model (Franzen & Borgerhoff Mulder 2007). However, changing the length of crop lifecycles has a relatively small impact on net profits.

Increasing the length by 25% increases net profits by only around 5% for each of the tree crops, while reducing the length of the lifecycle by 25% reduces net profits by 8-9%.

I used non-parametric bootstrapping to estimate means and 95% confidence limits for estimates of costs, yields and revenues. Because observations within each square were not independent, I used square-level means in the bootstrapping, weighted by the number of fields with information from that square. The result of this was that the maximum possible number of observations for any variable was seven (remembering that no interviews were conducted in square #16, and interview data from squares #9 and #10 were combined). The actual number of observations was often less than seven. Orange fields, for example, were found almost exclusively in two squares in block IV, so I had only two square-level estimates for each of the costs, yields and revenues of orange farming. That was the most extreme case, but illustrates the point that 95% confidence limits based on such small bootstrapped sample sizes are likely to lack precision.

4.5 Conclusion

Based on mapping of the extent of cultivated and uncultivated land, and interviews with farmers and plantation managers, I estimated that farm mosaic squares produce as little as 9% or as much as 67% as much food energy yield per hectare, at a landscape scale, as the highest-yielding oil palm plantation. Farm mosaic squares produced as little as 17% or as much as 75% as much net profit per hectare as the most profitable plantation. The lowest-yielding and least profitable farm mosaic squares were those with the greatest proportion of uncultivated land (fallow, swamp and remnant or secondary forest) and thus likely to be the most wildlife-friendly. All farm mosaic landscapes contained some wildlife-friendly features, including mature native trees and structurally diverse cocoa agroforests. Bushmeat, while it is of great cultural significance and an important source of income for some people, probably plays only a minor role in providing food energy or protein compared to crops.

a. Mature, semi-shaded cocoa farm in Western Region, with a cocoa variety known locally as "old agric".

b. Food crop farm dominated by plantain, Central Region.

c. Women in Central Region separating palm kernels from fibre, as part of local palm oil processing.

*d. Weevils (*Sitophilus *sp.) on maize: one of several insect pests the small-scale farmer has to contend with.*

e. Farmer Eric Mensah harvesting cassava tubers for household consumption, Western Region.

f. Trucks waiting to unload oil palm fruits for processing at Twifo-Praso Oil Palm Plantation, Central Region.

g. Oranges rotting in a field in Eastern Region, because the farmer failed to find a buyer in time.

Figure 4.22. Some illustrations of crops in southwest Ghana.

Chapter 5

Bird diversity and abundance

*Olive-bellied Sunbird (*Nectarinia chloropygia*) in farm mosaic, Central Region* ‘it is not easy to judge the diversity of bird species in a specific area of rainforest’

Claude Martin (1991, p. 103)

5 Species' responses to yield: birds

5.1 Introduction

5.1.1 Birds as surrogates

In addition to the intrinsic, aesthetic and other values of birds in their own right, they are among the most frequently used surrogates for wider biodiversity (Rodrigues & Brooks 2007). They include species which are extremely sensitive to environmental change as well as others which are among the most adaptable commensals of humans. Bird taxonomy is relatively stable, most bird species can be readily identified in the field, and many aspects of their biology are known. They are thus also good indicators of environmental change, although like any indicator they have limitations (Butchart et al. 2005). More than 12% of all bird species are globally threatened: fewer than in any other taxon that has been fully assessed, and perhaps indicating that birds are particularly resilient to global change (Vié et al. 2009). The single greatest source of threat to birds, and many other taxa, is agricultural development (BirdLife International 2008). Birds are especially threatened by agriculture in the developing world, in tropical forests and in areas with concentrations of restricted-range endemics (Scharlemann et al. 2004, Green et al. 2005, BirdLife International 2008).

The extent to which birds and other species can survive in agricultural landscapes is still poorly understood, particularly in the tropics (Gardner et al. 2009). Numerous field-based studies have addressed the issue, but they have often been poorly designed and lacked a solid theoretical underpinning (Fischer & Lindenmayer 2007, Gardner et al. 2007a). As discussed in Chapter 2, to understand the consequences of agricultural change it is necessary to understand its impacts on the populations of different species. Simple metrics based on incidence and aggregate richness and diversity are too crude, because they fail to provide information even on large changes in species composition and in species' populations (Maas et al. 2009). Conversion of forests and other near-intact natural habitats is typically beneficial to some species but detrimental to others, and deciding on appropriate conservation action will be difficult until we better understand which species will be "winners" and which "losers" as a result of human activities, and what the net effect on whole species assemblages is likely to be (McKinney & Lockwood 1999).

5.1.2 Birds and agriculture in West Africa

Previous studies of birds and land use in the West African forest zone have examined the value of forest fragments, logged forests, secondary forests, fallows, timber tree plantations, rustic cocoa farms, abandoned coconut plantations, cocoa/coffee/plantain agroforestry and annual crops (Karr 1976, Blankespoor 1991, Lawton et al. 1998, Beier et al. 2002, Holbech 2005, Waltert et al. 2005, Manu et al. 2007, Holbech 2009; reviewed in Norris et al. submitted). Overall, bird species richness, and the number of species shared with nearby forest controls, were lowest in agricultural systems with few trees. In fallows, agroforestry systems and annual crop farms, forest-dependent species such as ant-followers and insectivores were less abundant, while generalists and non-forest species such as sunbirds and granivores were more abundant than in forest (Blankespoor 1991, Waltert et al. 2005). Holbech (2009) found a high proportion of forest bird species in overgrown coconut, timber and cocoa plantations located in or near forests in southwest Ghana. A more isolated plantation had lower diversity and was less similar to forest, suggesting that while forest birds were visiting plantations, they were still reliant on adjacent forest habitat. The fact that these plantations had not been maintained for several years suggests that they were neither high-yielding nor profitable.

5.1.3 Bird census methods

Although excellent field guides and sound recordings exist for virtually all species in West Africa, accurate censusing of tropical forest birds is difficult. Methods range from simple presence/absence surveys, allowing comparisons of species composition and richness between sites; to methods giving measures of relative abundance, such as timed species-counts and mist-netting; to assessments of density, using either point counts or line transects (Remsen & Good 1996, Bibby et al. 1998). Labour-intensive methods, such as territory or spot-mapping, are usually used in studies of one or a few species and/or confined to a small area, but have also been used to describe entire bird communities (Brosset & Erard 1986, Terborgh et al. 1990). There is typically a trade-off between achieving sampling coverage over a wide area, and collecting more detailed and complete information from each sample.

A problem that is sometimes neglected is that differences in detectability can have a large effect on comparisons of bird populations and community composition between different land-use systems. For many species detectability tends to be lower in forest than in more open converted habitats, so the reduction in bird richness and numbers in open, modified habitats relative to dense, tall forest is underestimated. Distance sampling, in which probability of detection is modelled as a function of distance from the observer, offers a partial solution (Buckland et al. 2001, Buckland et al. 2008). It cannot correct for deficiencies in the ability of observers to detect and identify birds – often an issue in species-rich tropical forests where many detections are based on sound – but it can help to reduce bias associated with differences in detectability between different species and different habitats. Methods have been developed to allow the fitting of detection functions to pooled data for multiple species, which can enable ornithologists to estimate densities even for species with few data (Alldredge et al. 2007). Sampling of tropical assemblages is almost invariably incomplete, but species richness estimators, which are based on the frequency of rare species in samples, can be useful in estimating the numbers of undetected species and the proportion of species common to different study sites (Chao 2005).

5.1.4 Aims of this chapter

The aims of this chapter were to:

1. Describe the bird communities of forest, farm mosaic and oil palm plantations in southwest Ghana,
2. Estimate the densities of individual bird species in near-intact habitat and across a gradient of agricultural production (with "yield" measured alternatively as food energy or net profit),
3. Describe the form of density-yield functions for those species and classify them into broad groups according to their responses,
4. Investigate whether species with traits predisposing them to higher extinction risk were also those with the most sensitive responses to increasing yield.

I selected species-level traits that correlate with elevated extinction risk: dependence on forest habitat, degree of endemism, global range size and global threat status (Davies et al 2004, Payne & Finnegan 2007, Cardillo et al. 2008, Harris & Pimm 2008). These traits are all correlated with each other, so cannot be interpreted as independent. Other traits, such as large body size, low population density, poor dispersal ability and low rate of reproduction, also tend to predispose species to a higher risk of extinction (Johnson 2002, Brook et al. 2006, Brook et al. 2008), but I did not investigate those here. My a priori expectations were that species which were most strongly associated with forest habitat, narrowly endemic, with small global range sizes and those already most threatened would be most negatively affected by increasing yield (e.g., Brook et al. 2003, Jetz et al. 2007, Devictor et al. 2008).

5.2 Methods

5.2.1 Survey methods

I used a distance sampling point transect method to survey birds in forest, farm mosaic and plantation land-use types, between 26 January and 19 November 2007. I censused a total of 600 different points: 24 points in each of 25 squares (Chapter 3). I visited each square at least twice, censusing 12 points on each visit, so that sampling spanned both dry and wet seasons (Table 5.1). Seasonal rainfall in Ghana varies from year to year and from region to region, and it was not always possible to time visits to be unambiguously “dry season” or “wet season”. Southwest Ghana has two peaks of rainfall, in May-June and in September-November. I considered these months as “wet season”, and the rest of the year as “dry season”. April is arguably wet season, but it was still mainly dry when I visited block IV (the driest block) in that month. Some of the intended “dry season” counts in Bonsa River forest (block II) were actually carried out in November, towards the end of the wet season (Table 5.1).

Table 5.1. Timing of point counts through the year in each block and land use. Number of point counts is given in parentheses after each set of dates. See text for further discussion.

Block	Land use	“Dry season”	“Wet season”
I	Forest	15-23 Mar (24)	7 Oct (12), 15-16 Oct (12)
	Farm mosaic	6-10 Mar (24)	29 Sep - 2 Oct (24)
	Plantation/farm	28 Feb - 2 Mar (24)	30 Sep - 1 Oct (24)
II	Forest	31 Aug - 3 Sep (12)	5-10 May (24), 17-19 Nov (12)
	Farm mosaic	21-28 Aug (24)	11-12 May (24)
	Plantation	13-15 Aug (24)	13-14 May (24)
III	Forest	18-23 Feb (24)	21-25 Sep (24)
	Farm mosaic	30 Jan - 4 Feb (24)	11-13 Sep (24)
	Plantation	26 Jan - 2 Feb (24)	9-12 Sep (24)
IV	Forest	18-25 Apr (24)	26 Oct - 6 Nov (24)
	Farm mosaic	3-9 Apr (24 + 12)	22-24 Oct (24 + 12)
	Plantation	29 Mar - 1 Apr (24)	20-21 Oct (24)

On each visit, points were randomly selected without replacement from a pre-defined set of 36 points regularly spaced 160 m apart on a square grid (in farm mosaic squares, these were the same points at which I mapped field types, section 4.2.1). They were thus essentially a random sample of places in each square, so mean densities at points could be used to estimate square-level density. In forest and farm mosaic, where access to points was often difficult because of thick vegetation, I located and marked each point at least one day in advance, cutting an access route (with help from local guides) where necessary, and, where thick canopy prevented GPS navigation to the point itself, measuring its distance on a compass bearing from the nearest reliable GPS point. Points were located without regard to their suitability as vantage points, although I did clear sufficient vegetation at each point to allow me stand and turn unimpeded.

I counted birds at each point for 10 minutes, with no settling-in period. I started almost all counts (97%) between 06:00 and 10:30 local time (=GMT). I recorded any birds flushed while approaching or leaving the point at their original position. I recorded birds in compact clusters (e.g., flocks of estrildids or pairs of bulbuls) as one detection, with a cluster size (number in the group). I measured or estimated the direct distance from the point to the centre of each cluster (or to each individual bird), as well as the angle of elevation, from which I was able to calculate the horizontal distance. I checked distance estimates regularly using a Bushnell laser rangefinder. I also recorded the minute in which I detected each cluster/bird, and whether they were seen or heard, or both, but I do not analyse these data further here. For most of the "wet season" counts, I recorded bird sounds during the count using an Edirol R-09 digital recorder, and later checked some uncertain identifications with F. Dowsett-Lemaire, one of the foremost experts on the vocalisations of African birds (e.g., see Dowsett-Lemaire 2002).

I used additional techniques to record other species present in each 1km^2 square and more widely in each land-use type in the study region, by visiting different habitats within each square (especially ponds and rivers), by observing mixed-species flocks, by watching at ant swarms and at flowering or fruiting trees, and by listening for nocturnal species in the evening and at night. However, I could not standardise effort between land-use types and these observations were too incomplete to include in a formal analysis.

5.2.2 Data processing

I discarded all detections with a horizontal distance of > 80 m, all observations of birds that flew over or through the count area and detections of birds that entered the count area during the count. I also removed all observations of swallows and swifts prior to analysis, as my methods were unsuitable for censusing these largely aerial species, especially from under a forest canopy. I removed any observations that were not identified to species, except as explained in the following paragraph.

In a few cases, a large proportion of the observations of two closely related species could not be separated in the field, so these were pooled for analysis. These species were the firefinches (Bar-breasted and Blue-billed), the *Gymnobucco* barbets (Bristle-nosed and Naked-faced), two coucals (Blue-headed and Senegal) and the orioles (Black-winged and Western Black-headed). Scientific names of all species are given in Appendix 1. These eight species were treated as four “species” in the analyses throughout. However, whenever I had the opportunity to specifically identify a bird belonging to one member of these species-pairs, I did so, including casual observations. Using the resulting ratio of one species to the other for each species-pair, I was later able to derive overall density estimates for each of the eight species in each of the three main land-use types.

5.2.3 Species richness

I estimated total species richness in each square, setting points as samples, using the incidence-based Chao2 estimator in EstimateS, version 8.2 (Colwell 2009). I estimated the total species richness of the three land-use types in each block using the abundance-based Chao1 estimator, with squares as samples. I used the bias-corrected formula for Chao1 and

Chao2, except where the CV for incidence distribution was greater than 0.5, in which cases I recomputed them using the classic formula of Colwell (2009). I also estimated the number of species shared between different land-use types within each block, using Chao's coverage-based estimator of shared species. I further produced sample-based species accumulation curves for each land-use type, setting squares as samples (Colwell 2009). For calculating each estimator, I used 50 runs, including all samples in each run in randomized order. I treated each unknown cluster size (e.g., where birds were heard but not seen) as a "1" in EstimateS.

5.2.4 Individual species' densities

I estimated the density of each species using Distance, version 6.0 (Thomas et al. 2009, www.ruwpa.st-and.ac.uk/distance). I entered data into Distance with squares set as samples, and point counts within each square set as replicates. The cluster size for each species was taken as the mean of the observed cluster sizes for that species. For species with at least 40 records in one land-use type, or at least 20 records in each of two or three land uses, I fitted a single-species detection function for those land uses with enough observations, with land-use type as a covariate. There were 22 species with sufficient data to fit a single-species detection function. For these species in some habitats, and for all other species, I had insufficient observations to fit a species-specific detection function, so for these species I pooled species into groups for modelling of detection functions (cf. Alldredge et al. 2007). These "detectability groups" were based on three characteristics of each species: vegetation stratum, diet and activity. I classified species' preferred vegetation strata into five classes: high-mid (canopy and upperstorey species), low-mid (midstorey species), mid-open (species of bushes and trees in more open habitats), low-open (species usually at or near ground level in open habitats) and low-skulking (species that skulk in low vegetation, making them difficult to see). I grouped species according to diet into carnivores, frugivores, granivores, insectivores, nectarivores and omnivores. I divided species into those that rarely sit still (e.g., sunbirds) and those that often stay still for long periods (e.g., kingfishers). Based on these characteristics, I defined 16 "detectability groups", which incidentally included observations of those species analysed individually, where relevant. I considered using a measure of calling frequency to assist with classifying species into detectability groups, but for less common species, it was often difficult to distinguish whether they were rarely heard because they called infrequently, or simply because they were scarce.

I considered three models for each of the 22 species and 16 groups thus defined: a separate detection function for each land-use type, provided there were at least 40 observations in each; a detection function for the species or group with land use as a covariate (using the multiple covariate distance sampling (MCDS) engine of Distance), provided there were at least 20 observations in each; or a single detection function for the species or group, with no covariates. In each case, I tested the following key functions and adjustments for detection functions: half-normal and hazard-rate with cosine adjustment, half-normal with hermite polynomial adjustment, and hazard-rate with simple polynomial adjustment (Buckland et al. 1993). I examined models for goodness of fit using the Kolmogorov-Smirnov probability test and Cramer-von-Mises uniform and cosine probability tests, and for plausibility. Of the plausible models offering a good fit, I selected the model with the lowest AICc. This led in some cases to selecting models which did not include any differences between habitats: therefore, the differences in densities between habitats within those groups were exactly proportional to the differences between the encounter rates within 80 m. In other cases, different detection functions were selected for data from one group in different habitats.

5.2.5 Density-yield curves

I fitted generalized additive models (GAMs) to density data for each species plotted against two measures of yield: food energy and net profit (from Chapter 4). I did not fit models for species found only in forest (Supersensitive species, see Chapter 2). Instead I assumed an extreme L-shaped relationship between density and yield for those species, with a density of zero at all non-zero values of yield. I fitted GAMs using the package `mgcv` in R, using a quasipoisson error structure with log link (Wood 2006). Use of the quasipoisson rather than poisson errors results in the same curve being fitted, but inflates the standard error to account for overdispersion. Bird densities were not integer values, so I could not model density directly as the dependent variable. However, I was able to fit models in which the number of observations of a species in a square (i.e. the count of clusters, including single birds) was the dependent variable. To do this, I incorporated into the model an offset term equal to `log(cluster count divided by density)`. This accounted for the effective average area sampled from a typical point (as estimated in Distance) and the mean cluster size. I calculated an offset term for each species and land-use type separately.

A decision that affects GAM fits is the choice of the dimension of the basis used to represent smooth terms, k. Larger values of k allow a greater number of degrees of freedom for each model term. From preliminary examination of models for a number of species, it was clear that using the default basis dimension (k = 10) tended to produce models that had greater variation in slope (wiggliness) than was justified by the relatively few data points. A dimension of k = 5 generated smoother results, and was used for all species except as noted below. A gamma value of 1.4 was used in all models, to reduce the risk of overfitting, as recommended by Wood (2006, p. 224).

I fitted two models to data for each species-yield combination: one that included block as a factor, and one in which block was ignored. Some fitted models were not plausible, because some of the fitted values were much higher than any of the observed values. This typically occurred when most of the observed values were zero, with a small number of nonzero values. For the 126 species which occurred in at least one non-forest square, the distribution of the ratio of the maximum fitted value to the maximum observed value, using densities versus food energy, was as in Table 4.1. I considered GAMs as plausible if the maximum fitted density was no more than twice the maximum observed density.

Table 5.2. Ratios of the maximum fitted density to maximum observed density, for GAMs fitted initially to individual species' densities plotted against food energy yield.

Ratio	Number of species
0 – 1	98
1 – 2	3
2 – 4	1
4 – 10	4
10 – 100	2
> 100	18

If both models were plausible, they were compared using an F-test at a significance level of $p = 0.05$ (with Bonferroni correction for 126 comparisons, at each currency for yield). If only the model without block was plausible, it was selected. If only the model with block was plausible, but it was not supported by the F-test, or if neither model was plausible, I refitted the model without block to the average density and yield for each habitat-block combination, reducing the number of data points from 25 to 12. These data points were more widely spaced and therefore caused fewer problems with model fitting. If this fitted model was still not plausible, I reduced k to 4 or 3 until I found a plausible model. If I still failed to find a plausible model by these methods, I simply noted the yield of the square in which the species was recorded at its highest density. In a small number of cases where I suspected (judging by eye) that models were under- or over-fitted, I varied k upwards or downwards respectively, to see if there was a visually better-fitting model. If the UBRE score (a criterion related to AIC) was lower for the new model, it was accepted. In most cases, simplification was not supported by the UBRE scores. For example, I suspected that bimodal curves (e.g., Woodland Kingfisher) might be overfitted, but while reducing k to 4 typically coerced these to unimodal fits, it also increased the UBRE score, so the bimodal model was retained. I classified density-yield curves into the five response categories defined in section 2.3: Supersensitive, Sensitive, Tolerant, Weeds and Superweeds.

5.2.6 Correlates of density-yield response category

I investigated whether variation in the categorised degree of dependence on forest of each species was related to the yield level at which they reached their maximum density, and whether variation in (1) their degree of dependence on forest habitat, (2) their global threat status, (3) their degree of endemism, and (4) their global range size as measured by EOO, were related to the responses of species to increasing yield (Supersensitive, etc.). I obtained information on the habitat requirements of each bird species encountered in the study from the World Bird Database held by BirdLife International (S. Butchart, pers. comm.). Using the information held in this database, I defined the natural habitat of each species using four categories of decreasing dependence on forest as natural habitat:

1. *Forest dependent*. Species listed as being found only in forest, and not in shrubland, savanna, desert, grassland, extensive wetlands or rocky areas (51 species).

2. *Forest major*. Species with forest as their only "major" habitat, but also found in shrubland, savanna, desert, grassland, extensive wetlands or rocky areas (48 species).

3. *Forest generalist*. Other species that occur in forest, but for which it is not a major habitat. Six species with forest as major habitat, but with another major habitat among shrubland, savanna, desert, grassland, extensive wetlands and rocky areas, were also included in this category (59 species).

4. *Non-forest*. Species not listed as occurring in forest (9 species).

I defined "forest" as including all tropical/subtropical forest types, excluding temperate and boreal forests. I considered only habitats used by species when in West Africa (therefore excluding habitats used by Palearctic migrants in the breeding season). I defined "extensive wetlands" as including bogs, marshes, swamps, fens, peatlands and shrub-dominated wetlands, but excluding lakes, springs, oases, rivers, streams, creeks and small marshes/pools, as this second set of habitats are typically contained within other more extensive land-use types. I also ignored artificial habitats, as I wanted the habitat classes to reflect firstly whether species occur naturally in forest, and secondly the importance of forest as opposed to other natural habitats for each species. A species listed as occurring in forest, along rivers, and in artificial habitats (e.g., rural gardens), but not listed in any other habitats, was therefore defined as a forest dependent using my criteria.

I obtained the global threat status of each species from the World Bird Database and from IUCN (2009). I obtained lists of restricted range and biome-restricted birds from Ntiamoa-Baidu et al. (2001). Using these, I categorised each species as endemic to Upper Guinea (four species), endemic to the Guineo-Congolian biome (87 species), or widespread (76 species) (cf. Figure 3.2, see also Dowsett-Lemaire & Dowsett 2001). I obtained the EOO of most species from the World Bird Database. I supplemented or replaced these EOOs with estimates from maps in Orme et al. (2005; I. Owens, pers. comm.) for 12 species without EOO estimates, for two species for which the BirdLife EOOs were clearly inaccurate (Black-necked Weaver and Olive Sunbird) and for a further 17 species all with an identical provisional estimate. To assess the significance of relationships between continuous and ordinal variables, I used the Spearman rank correlation test. I tested the significance of the relationship between response category and other ordinal variables with the asymptotic linear-by-linear association test in R (`lbl_test` in the `coin` package; Hothorn et al. 2008). I grouped Superweeds with Weeds for chi-square tests, and where necessary, I collapsed other factor levels, to meet the criterion that no more than 20% of the expected values should be <5 (Dytham 2003).

5.3 Results

5.3.1 Species richness

After preparing the data for analysis as described above, I was left with a total of 4,317 point count observations of at least 4,889 individual birds, of 167 species. The highest species richness (both observed and estimated) was in the forest squares of block IV, closely followed by the lowest-yielding farm mosaic square in block II (Figure 5.1). I recorded 105 species in forests, 119 species in farm mosaic, and 36 species in plantation, excluding farm/plantation. (Including the two mixed plantation/farm squares, I recorded 54 species in plantation.) The most abundant species in each land use overall were: in forest, Icterine Greenbul, Yellow-whiskered Greenbul and Collared Sunbird; in farm mosaic, Orange-cheeked Waxbill, Little Greenbul and Olive-bellied Sunbird; and in plantation (excluding plantation/farm), Grey-backed Camaroptera, Black-necked Weaver and Tawny-flanked Prinia (Appendix 1). Species richness estimators and species accumulation curves suggested that sampling effort was sufficient to find the majority of species for which my survey technique was suitable, but also that some species went undetected in all land-use types (Figure 5.2).

Overall, the numbers of observed species shared between land-use types were 63 (forest and farm mosaic), 12 (forest and plantation, excluding plantation/farm), 21 (forest and plantation, including plantation/farm), 31 (farm mosaic and plantation, excluding plantation/farm) and 46 (farm mosaic and plantation, including plantation/farm). I estimated the number of species and shared species between land uses within each block, to better assess the degree of overlap in species composition (Figure 5.3). In block I, plantation/farm shared an estimated 34% of the species found in forest, more than farm mosaic (21%). In blocks II-IV, farm mosaic shared an estimated 42-59% (mean 48%) of the species in forest within the same blocks. I estimated that the plantations in blocks II-IV shared only 9-11% (mean 10%) of the bird species found in forests in those blocks.

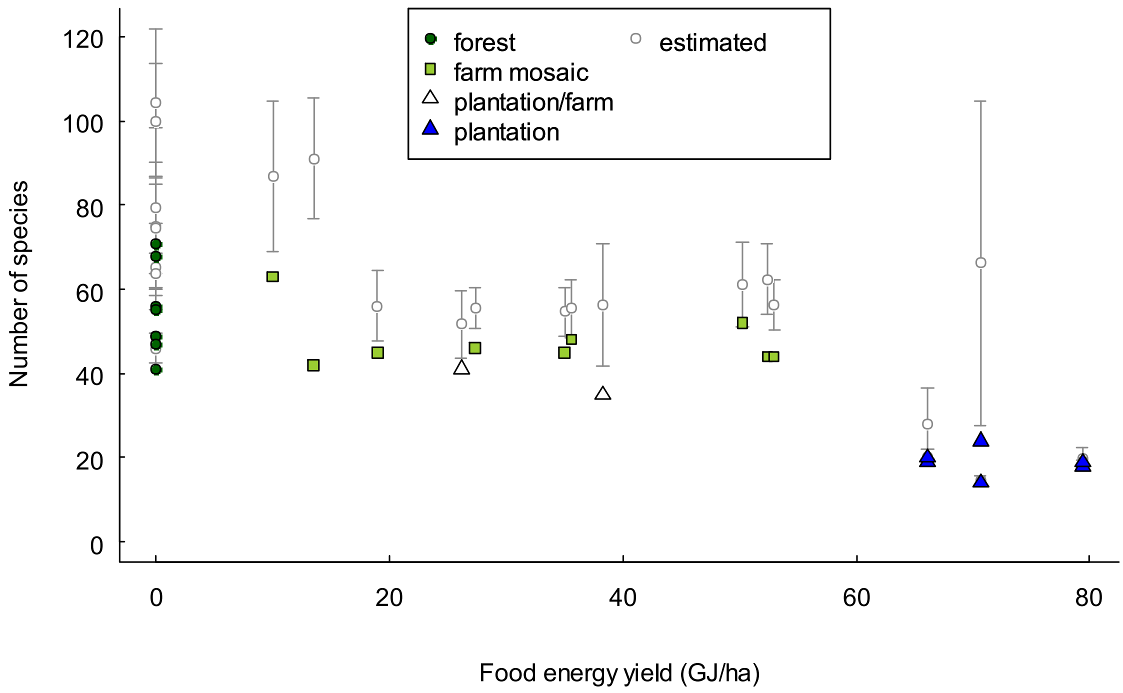

Figure 5.1. Observed and estimated bird species richness in each 1 km^2 square, in relation to land use (symbols) and food energy yield (x axis). Estimated species richness (mean ± SD) was computed using the Chao2 estimator, with point counts (n = 24 in each square) as sampling units (Colwell 2009).

I recorded at least 45 further species in the squares which were not detected during point counts (Appendix 1). Of these, 22 were of species for which my methods were evidently inefficient and probably differentially so in different habitats: swallows, raptors, swifts, nocturnal species and aquatic species. The other species comprised seven forest-dependent species (all seen only in forest), nine forest major species, three forest generalists and four non-forest species. I observed other species within the study blocks but outside the study squares.

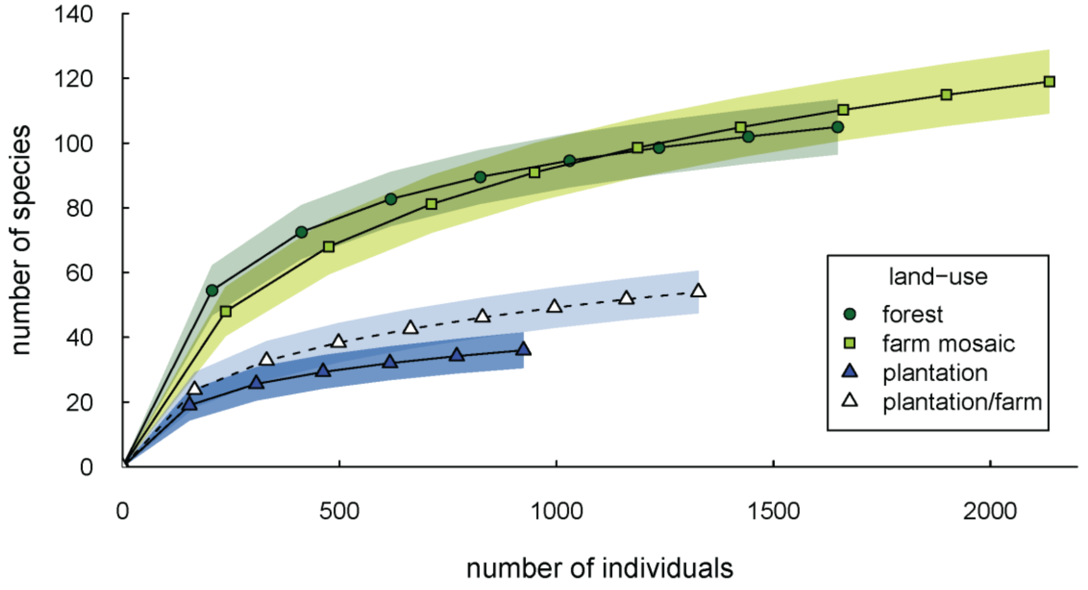

Figure 5.2. Sample-based species accumulation curves with 95% confidence intervals for forest (circles), farm mosaic (squares) and plantation (triangles), plotted against cumulative number of individuals. Alternative curves are shown for plantations with two plantation/farm mosaic squares excluded (blue) and included (white). The increment between each pair of symbols on a curve represents the number of species and individuals added, on average, by the sampling of points within an additional 1 km^2 square.

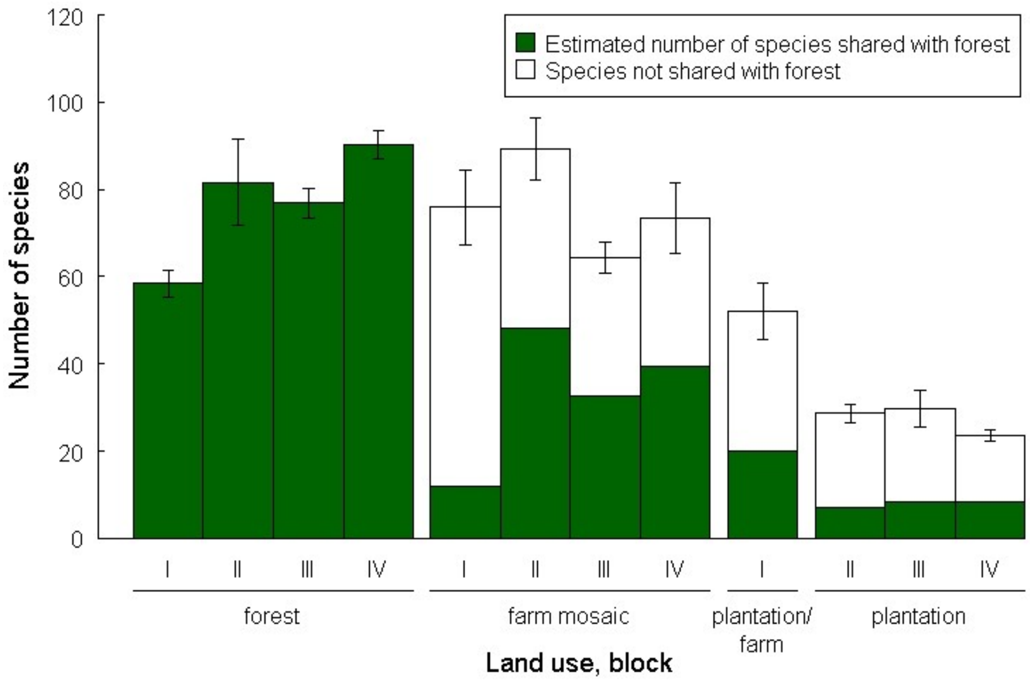

Figure 5.3. Estimated species richness of birds in each land-use type in each block (total height of bars ± SD), and estimated number of species shared between that land use and forest in the same block (green), computed using the Chao1 abundance-based estimator, with squares set as samples, and Chao's coverage-based estimator of shared species (Colwell 2009). Square #24 excluded.

5.3.2 Density-yield curves

I was able to fit GAMs to the data for all but three species when plotted against food energy, and all but six species when plotted against net profit. For those species for which I could not fit a model, because of sparse or unusually distributed data, I was still able to classify their response (all were Weeds). The 41 species recorded only on forest counts were all defined as Supersensitive species. In relation to food energy yield, 45 species were defined as Sensitive, 37 species were tolerant, 36 species were Weeds and eight species were Superweeds (Figure 5.4). In relation to net profit, the same 41 species were defined as Supersensitive, 31 species were defined as Sensitive, 39 species were Tolerant, 46 species were Weeds and ten species were Superweeds. The type of response varied in some species depending on the yield currency used. This was because it shifted the order and spacing of values on the x axis (Figure 5.5).

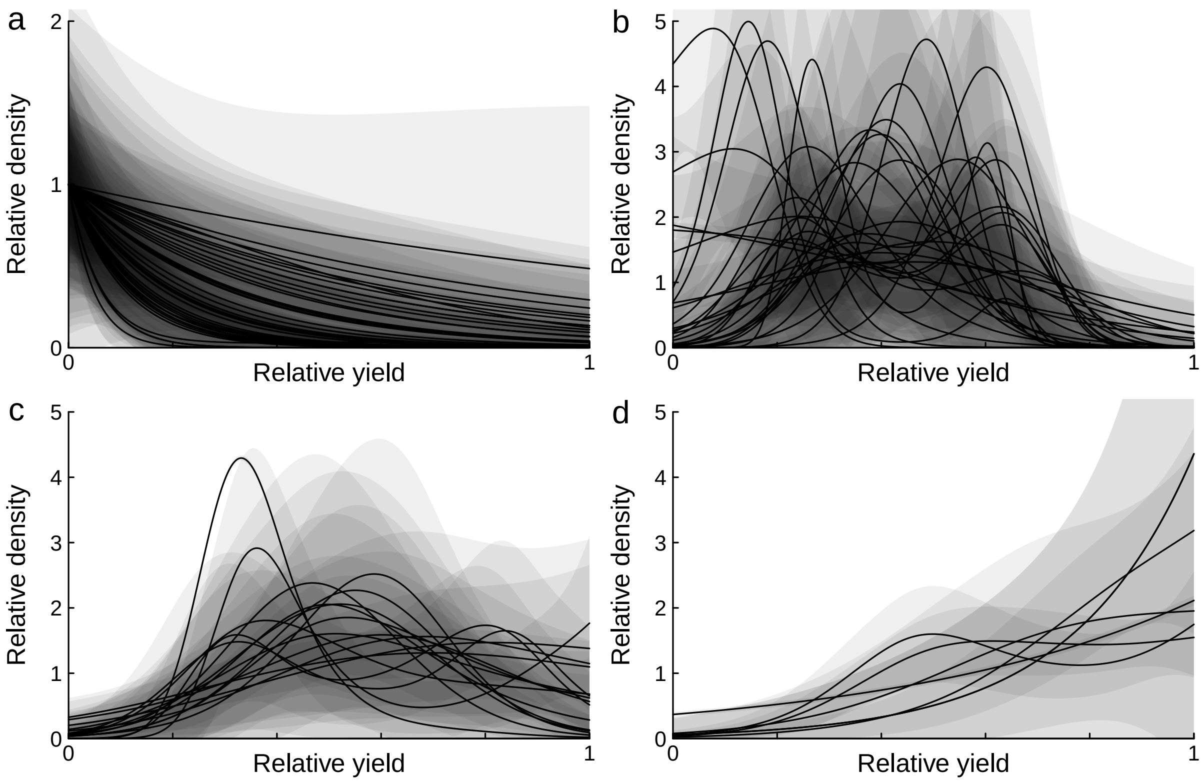

Figure 5.4. Density-yield relationships for bird species in southwest Ghana, with yield measured as food energy produced per hectare per year. Shown are responses by (a) Sensitive species, (b) Tolerant species, (c) Weeds and (d) Superweeds. Each curve represents the GAM for one species, with 95% confidence intervals shown by shading. Densities are expressed relative to maximum density in (a), or relative to mean density across the curve in (b,c,d). The small number of curves extending outside the plotted scales were removed to make the plots easier to interpret. Plots in relation to net profit were qualitatively very similar.

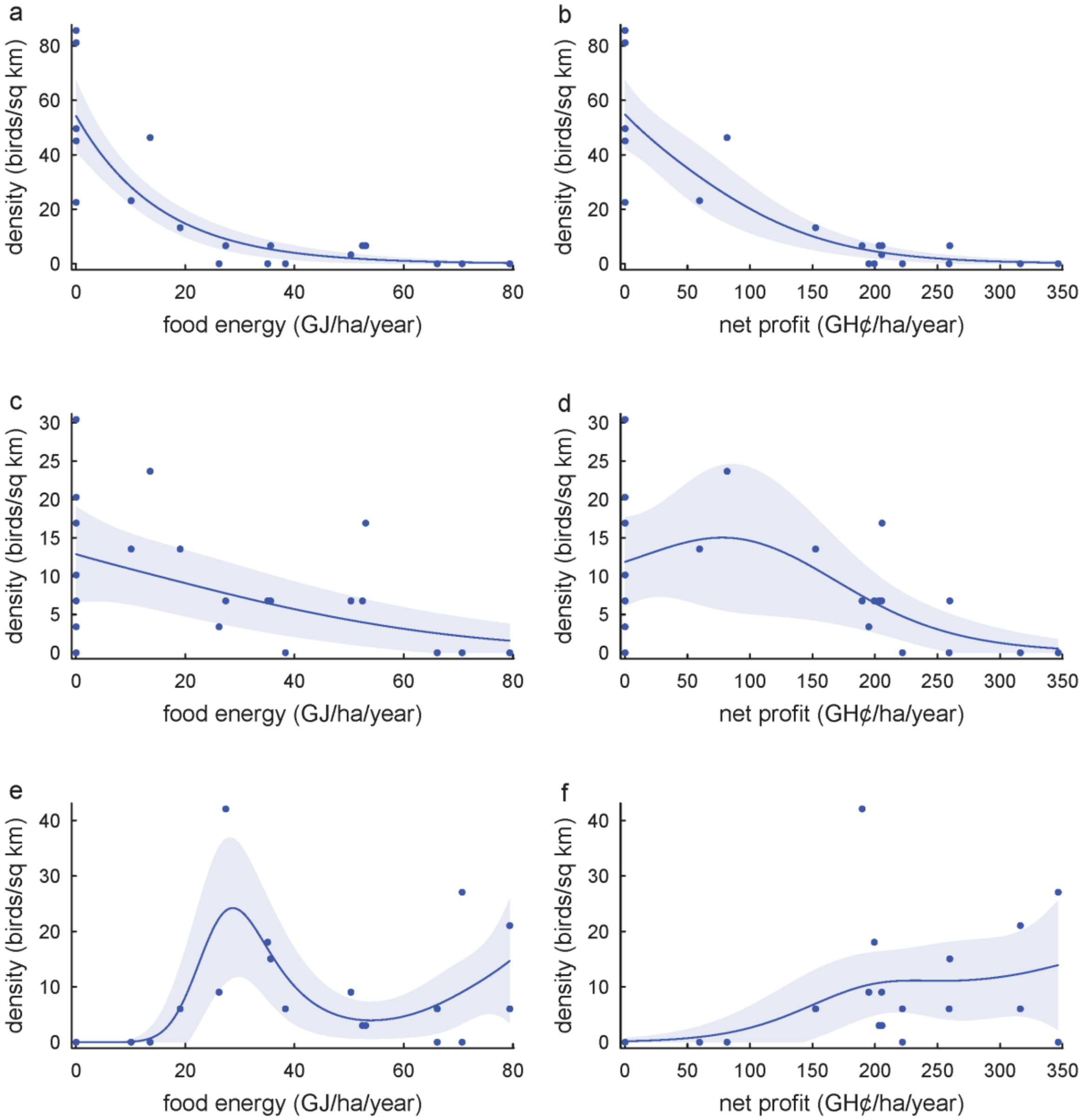

Figure 5.5. Density-yield curves for three bird species, to illustrate the effect of using different currencies for yield. Green Hylia was classed as Sensitive in relation to both food energy (a) and net profit (b). Speckled Tinkerbird was classed as Sensitive in relation to food energy (c), but Tolerant in relation to net profit (d). Red-faced Cisticola was classed as a Weed in relation to food energy (e), but a Superweed in relation to net profit (f). Each circle represents a density estimate for a 1 km^2 square; lines represent GAMs ± 95% confidence limits.

5.3.3 Correlates of response: forest dependence

Around half (46-52%) of the 167 bird species reached their maximum density at zero yield, for both yield currencies. The species reaching maximum density at higher yields were significantly less likely to be species highly dependent on forest habitat (Figure 5.6). This relationship was very highly significant for both currencies of yield (Spearman rank correlation, dependence on forest as ordinal variable, against yield at maximum density: $r_s = 0.57$, $p < 0.001$ (food energy); $r_s = 0.59$, $p < 0.001$ (net profit), n = 167 species).

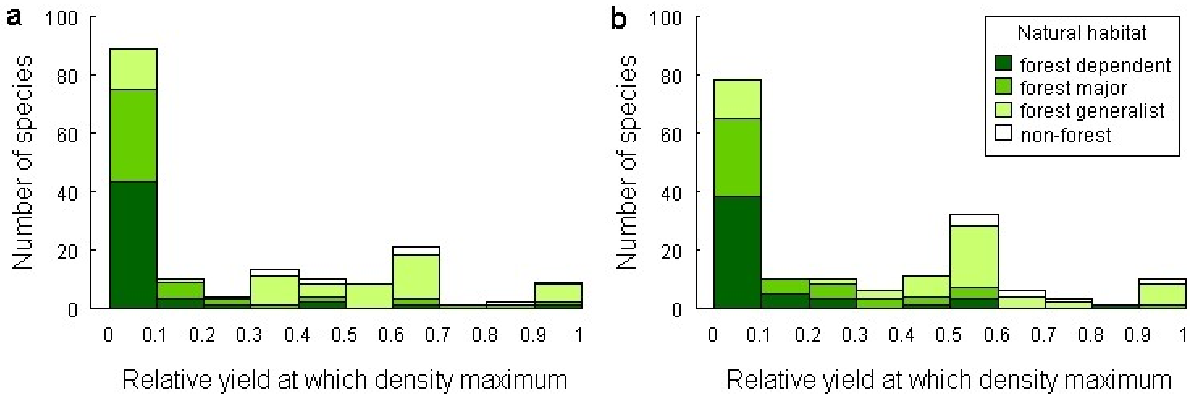

Figure 5.6. Frequency distribution of relative yields at which bird species reach maximum density, for (a) food energy, and (b) net profit. Coloured sections of bars indicate degree of dependence on forest as a natural habitat.

There was also an association between degree of dependence on forest, and density-yield response category (Figure 5.7). The majority of Supersensitive and Sensitive species were forest dependents or forest majors, and the majority of Weeds and Superweeds were forest generalists or non-forest species. Tolerant species were more or less equally divided between forest dependents, forest majors and forest generalists. There was a very highly significant association between degree of forest dependence and response category, for both yield currencies (linear-by-linear association tests, Superweeds combined with Weeds: $\chi^2 = 58.38$ (food energy); $\chi^2 = 54.95$ (net profit); df = 1, $p < 0.001$, n = 167 for both tests).

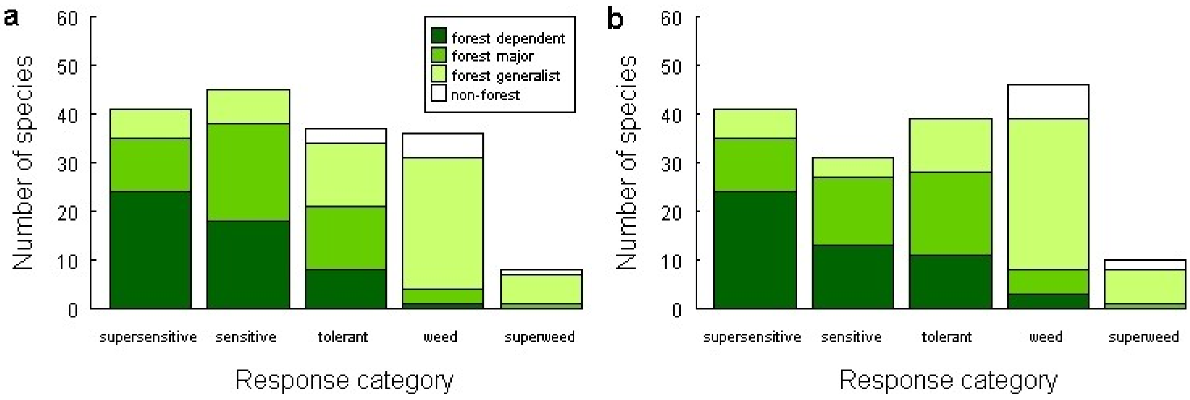

Figure 5.7. Number of bird species falling into different response categories to yield, for (a) food energy, and (b) net profit. Coloured sections of bars indicate degree of dependence on forest as a natural habitat.

5.3.4 Correlates of response: global threat

In all, I recorded nine (or possibly ten) globally threatened, Near Threatened or Data Deficient species, all in forests, but I detected only four of these on point counts (Table 5.3). Based on point count data, all four of these species were classed as Supersensitive. However, I observed two of the species in Table 5.3 outside forest: Grey Parrot (in oil palm plantations and flying over farm mosaic) and Copper-tailed Starling (once in farm mosaic more than 1 km from the nearest forest reserve). Based on other evidence, Grey Parrot might qualify as Tolerant to some degree of agricultural disturbance, but exploitation for the pet trade is a major additional threat: as much as 21% of the global population is removed from the wild each year (Dändliker 1992, BirdLife International 2009). All of the other species in Table 5.3 are probably Sensitive or Supersensitive, although three of them have been recorded visiting abandoned, overgrown plantations in close proximity to intact forest (Holbech 2009).

Table 5.3. Globally threatened, Near Threatened and Data Deficient birds recorded during counts ●, recorded at other times ○, heard only (○), or possibly seen (?) in forest in each study block I-IV. Source: IUCN (2009). Threat categories: VU = Vulnerable, NT = Near Threatened, DD = Data Deficient.

Species	Status	I	II	III	IV
Green-tailed Bristlebill	VU	●	●	●	○
Yellow-bearded Greenbul	VU	●	●	○	
Grey Parrot	NT	○	○	○	○
Brown-cheeked Hornbill	NT	(○)		○	○
Yellow-casqued Hornbill	NT	(○)			
Lagden's Bush-shrike	NT				(?)
Rufous-winged Illadopsis	NT			○	
Copper-tailed Starling	NT		●	●	●
Red-fronted Antpecker	NT		○	○	
Tessmann's Flycatcher	DD				●

5.3.5 Correlates of response: endemism and range size

With respect to their degree of global endemism, all Upper Guinea endemics and most Guineo-Congolian biome-restricted species (62-73%) were Sensitive or Supersensitive, while most species also found outside the biome (74-79%) were Tolerant, Weeds or Superweeds (Figure 5.8). Tolerant species were more or less equally divided between Guineo-Congolian and widespread species. For chi-square analysis, I combined Upper Guinea endemics with the rest of the Guineo-Congolian species, and I combined Superweeds with Weeds. There was a very highly significant association between endemism and response, for both yield currencies (linear-by-linear association tests : χ^2 = 45.03 (food energy); χ^2 = 43.18 (net profit); df = 1, $p < 0.001$, n = 167 for both tests).

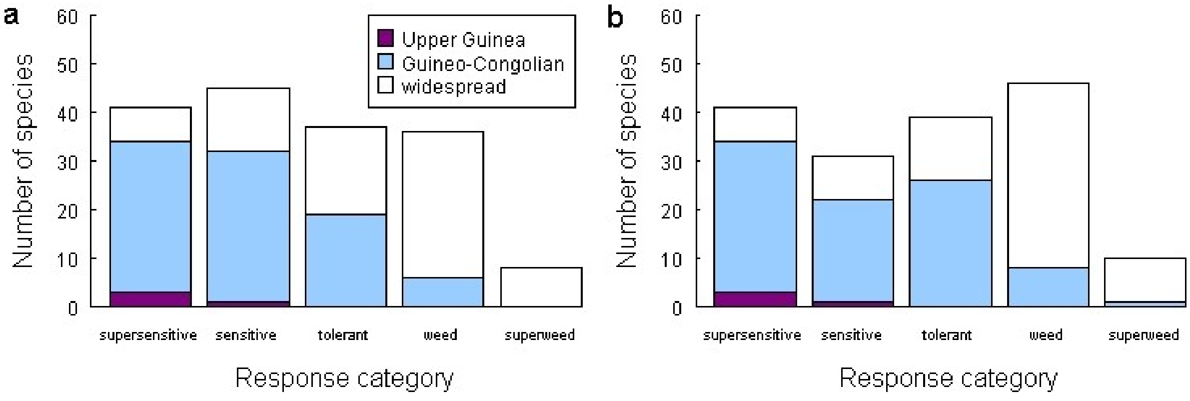

Figure 5.8. Number of bird species falling into different response categories to yield, for (a) food energy, and (b) net profit. Colours indicate degree of global endemism.

Birds most negatively affected by increasing yield tended to have small global ranges (Figure 5.9). This relationship was highly significant whether densities were plotted against food energy yield or against net profit (Spearman rank correlation between EOO and ordinal response category in both cases: $r_s = 0.51$, $p < 0.001$, $n = 167$ species).

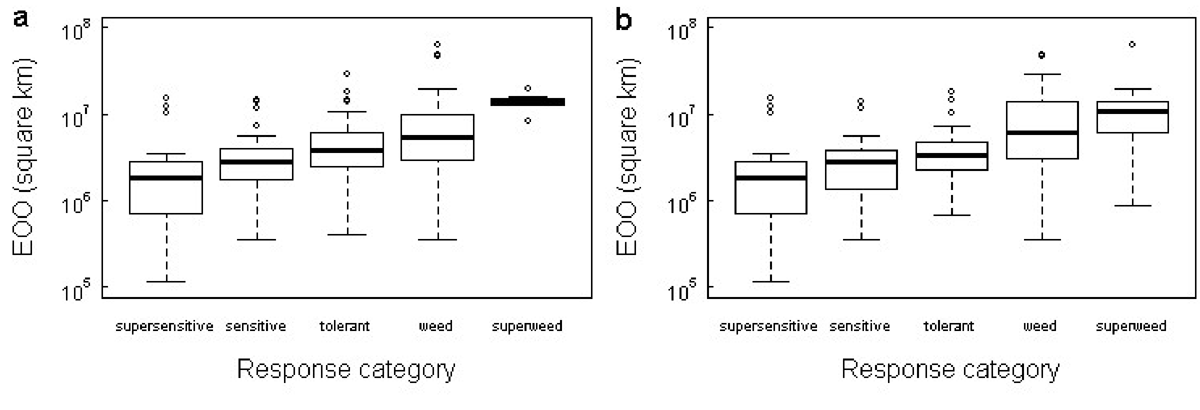

Figure 5.9. Global range sizes of bird species (Extents of Occurrence, EOO) with different types of response to increasing yield, for (a) food energy yield, and (b) net profit. Note log scale on y axes. Boxplots show median (thick line), interquartile range (boxes), data no more than 1.5 times interquartile range (whiskers) and outliers (circles).

5.4 Discussion

5.4.1 Winners and losers from agricultural change

My finding that farm mosaic habitats supported high bird species richness, including many forest species, was consistent with other studies, which have used this observation to argue for the promotion of wildlife-friendly farming (Daily et al. 2001, Hughes et al. 2002, Bhagwat et al. 2008, Philpott et al. 2008). My observations were also consistent with other recent work demonstrating that oil palm plantations support few forest species: an estimated 10% of forest birds, compared to a mean of 15% of species observed directly across a range of taxa (Fitzherbert et al. 2008). The relatively high diversity of low-yielding farming systems can be explained by a number of factors: they typically retain habitat features, such as forest remnants and shade trees; they introduce new habitat features, such as clearings and field boundaries; they often maintain a complex structure, with multiple vegetation strata; and they can provide resources which are relatively scarce in mature forests, such as grass seeds and nectar (Waltert et al. 2005). Oil palm plantations are biologically impoverished for the same reasons: all forest vegetation is typically cleared; they are uniform and highly simplified versions of forest habitats; and while some resources (e.g., palm fruits and rodents) become more abundant and benefit a few species, these are far outweighed by the many resources lost that were important to a greater number of species (Aratrakorn et al. 2006, Danielsen et al. 2008, Fitzherbert et al. 2008).

My results were also consistent with observations that while species richness often remains high in diverse agroforestry systems and similar “countryside” habitats, there is considerable turnover, and the densities of many of the forest species that do occur in farmed areas are greatly reduced (Waltert et al. 2005, Barlow et al. 2007a, Maas et al. 2009). I found that species which naturally occur only in forest tended to be less resilient to agricultural change than species with a wider range of natural habitats. Narrow endemics and species with small global EOOs were more negatively affected by increasing yields than widespread species, and all of the globally red-listed species which I encountered were wholly or mainly dependent on forest. One of those species, the Grey Parrot, often roosts in oil palm plantations, but cannot breed in them because they lack old trees with holes (Dändliker 1992).

My results indicate then, that closer examination of individual species' responses to increasing yield reveals a very different picture to that suggested by patterns of species richness. While some species (Weeds and Superweeds) benefited from agricultural conversion, these were mainly widespread habitat generalists. The majority of forest-dependent, narrowly endemic, biome-restricted, threatened and near threatened species would have higher populations under a land-sparing than a wildlife-friendly farming strategy, for any given production target. Some forest-dependent and biome-restricted birds were relatively tolerant of low-yield farming. However, the "losers" from agricultural change in southwest Ghana, even in what are often seen as relatively benign, wildlife-friendly land uses, were the species of highest current conservation importance, and those most likely to be of concern in the future.

5.4.2 Caveats

As can be seen from Figure 5.2, I did not detect every bird species present in the study area. This is almost invariably the case in tropical species inventories, even with considerable sampling effort (e.g., Barlow et al. 2007a). Missing species were of four kinds. First, there were scarce or inconspicuous species which were present and which I would have recorded with further survey effort, but which by chance I did not detect on point counts (section 5.3.1). Second, there were species which were present and for which my survey methods were suitable, but which I was unable to record because I was not familiar with the calls. Third, there were species which would be present at some times, but which were not present when I conducted my surveys. Fourth, there were species for which my survey methods were ineffective. The first set of species were those whose numbers were estimated using Chao1 and Chao2 estimators (Figure 5.1). Setting aside a single anomalous value for expected species richness in plantation, the mean percentage difference between observed and expected species richness was greater in forest squares than in farm mosaic or plantation. Regarding the second set of species, the fact that the rate of species accumulation in forest increased most quickly initially, then slowed more than in farm mosaic (Figure 5.2), along with the fact that most detections were aural and the thick vegetation and high canopy often prevented visual contact with birds, suggests that these were most numerous in forest. In particular I did not record a number of species from point counts which were undoubtedly present, including Blue-throated Roller, Buff-spotted Woodpecker, Olivaceous Flycatcher, Johanna's Sunbird and Forest Penduline Tit (F. Dowsett-Lemaire, pers. comm.), although I did see all but the last of these species at other times in forest. The third set of species could include irruptive species and migrants. Because I sampled during all seasons of the year, I am unlikely to have systematically missed more seasonal migrants in one land-use type than another. The fourth category includes aerial species such as swifts and swallows, waterbirds and raptors (e.g., Congo Serpent Eagle), and nocturnal species such as owls and nightjars. In summary, missing species are disproportionately likely to have been forest species than birds from other land-use types, and therefore my conclusions about the high proportion of species that would benefit from maintenance of a large area of forest are likely conservative.

Distance sampling did not fully correct for differences in detectability between habitats. The effective detection radius in forest was often estimated to be larger than that in farm mosaic. A priori, one would expect the opposite: that detectability would decrease more rapidly with distance in forest. The probable explanation for this is that point counts in forest were more often in violation of the distance sampling assumption that the probability of detection of a bird at distance zero was 1.0 (Buckland et al. 2001). The height of the forest canopy was frequently of a similar magnitude to the effective detection radius, implying that birds restricted to the upper canopy were unlikely to be adequately recorded. Also, unless birds vocalised it would often have been possible to miss skulking species, even within a few metres. There were too few visual observations of most species in forest to account for this in the fitting of detection functions, for example by including mode of detection as a factor covariate. I recorded some species only outside forest which would be expected to occur as abundantly in forest, e.g., African Goshawk and Green Sunbird. However, I also recorded some species only in forest which can occur in small numbers in farm mosaic, e.g., Golden Greenbul and Little Green Sunbird. On balance, I am likely to have missed and underestimated the densities of more species in forest than in other land-use types, again making my conclusions about the high proportion of species that would benefit from the maintenance of a large area of forest conservative.

I did not explicitly account for the effects of covariates such as time of year, distance to other land uses, or fine-scale habitat variables. Some birds vary considerably in detectability depending on time of year: during the dry season, doves, turacos, most cuckoos, coucals, barbets, most warblers, sunbirds and flycatchers are vocal, while illadopsises, alethes and some bulbuls fall silent for at least part of it (Dowsett-Lemaire & Dowsett 2009a). Because my surveys covered all seasons, I was unlikely to miss any species simply because it was seasonally silent, but I might well have underestimated the densities of such species. To minimise the influence of adjacent land uses, I avoided sampling near edges, and all points in farm mosaic and plantation were ≥1 km from the nearest forest, but even the presence of forest within several km of sampling points could have an influence on the birds recorded (Anand et al. 2008). Species such as parrots and some hornbills regularly forage several kilometres away from forest, even if they depend on it for breeding (pers. obs.). Hence, some of the species recorded in farm mosaic and plantation would almost certainly have been absent if substantial areas of forest had not been present in the region. This too makes my conclusions about the high proportion of supersensitive and sensitive species conservative.

Variables such as the intensity of logging in forests, and the extent to which undergrowth is allowed to develop in farms, have a considerable influence on bird faunas (Holbech 2005, Holbech 2009). I implicitly accounted for many of these fine-scale differences in vegetation structure and management intensity, because they tend to correlate with yield at a landscape scale. By using yield as a currency, and by choosing to focus at the landscape scale, I was measuring the value to birds of the systems that farmers currently find feasible, and the value of systems to the farmers in currencies which are most relevant to decision-making. I felt it was more useful to focus on large-scale issues that have a major effect on birds, rather than on the detail of fine-scale management actions (Chan & Daily 2008). By sampling the landscape randomly, I aimed to avoid the pitfall of extrapolating from misleading "best-case" examples of wildlife-friendly farming, for example where agroforestry systems adjacent to forest receive frequent visits from forest birds (Ranganathan et al. 2008).

5.5 Conclusion

My results provide evidence that the bird species of most current and potential future conservation concern in southwest Ghana are likely to have larger regional populations with land sparing than with the dominant local systems of wildlife-friendly farming, for a given production target. Species richness in farm mosaic habitats was often close to that in forest, but behind this pattern there was considerable turnover. Examination of individual species' responses to increasing yield revealed that the majority of forest-dependent, biome-restricted and red-listed birds, and those with small global ranges, declined with increasing yield, even at low yields. These species' populations are only likely to be maintained if most remaining forest cover is protected. There was a considerable number of species with densities that increased with increasing yield. However, these tended to be widespread habitat generalists of low conservation concern. Hence, there were winners and losers from forest conversion, and the losers tended to be the species which are of most conservation concern now, and those most likely to be of concern in the future because of their dependence on forest and small global ranges. Oil palm plantations, although they supported few bird species, and even fewer forest birds, have the potential, counter-intuitively, to help conservation efforts, but only if their high yields are used to reduce pressure to clear forests.

Chapter 6

Tree diversity and abundance

*Trunk of a young Onyina (*Ceiba pentandra*) tree*

‘Large trees were planted at new settlements, and when they fell,

their fall was thought to presage the dissolution of society.’

Elizabeth Allo Isichei (1997, p. 347)

When an *Asantehene* died, it was said,

“Odupon atutu.”

“A great tree has fallen.”

6 Species' responses to yield: trees

6.1 Introduction

6.1.1 Trees are important

Directly or indirectly, trees provide many of the resources as well as the physical structure on which most other forest plants and animals depend. Spatial patterns in tree species richness and abundance are likely to broadly correlate with patterns of other forest species, from mycorrhizal fungi to epiphytic orchids, fig wasps, herbivorous beetles and tree-roosting bats (e.g., Schulze et al. 2004, Schmit et al. 2005, Faria et al. 2006, Harvey et al. 2006, Sobek et al. 2009, but see Howard et al. 1998). Erwin's famous estimate that there could be 30 million species of arthropods is based directly on the number of tree species in tropical forests (Erwin 1982). Whatever the reliability of that estimate, it is clear that trees, in addition to their own immense intrinsic, cultural and other values, are essential for the survival of many other species. Trees also provide a range of important services to people: timber, non-timber forest products, regulation of water flow and water quality and, currently the most topical, carbon storage (Lewis et al. 2009). Although the global conservation status of more than 8,000 trees has been assessed, coverage is far from complete, and the fact that the majority of taxa that have been assessed are listed as threatened cannot be taken to be representative of all trees (Newton & Oldfield 2008). Nevertheless, there is little reason to think that trees are any less threatened globally than are other tropical forest taxa (Hubbell et al. 2008).

6.1.2 Agroforestry and tree conservation

Agroforestry is the deliberate integration of trees into farming systems, including preserving existing trees and planting new ones (Schroth et al. 2004). A common theme in the literature on tropical forest zone agro-ecosystems is the need for greater emphasis on the promotion of diverse agroforestry systems, as a way of conserving trees and other species (Leakey 1998, Perfecto et al. 2005, Ashley et al. 2006, Méndez et al. 2007, Oke & Odebiyi 2007, Soto-Pinto et al. 2007, Bhagwat et al. 2008, Bisseleua et al. 2009). In support of this idea, tree species diversity can be very high in agroforestry systems such as shaded coffee farms in Mexico and the "cabrucas" of Brazil, and can include rare and threatened species (Moguel & Toledo 1999, Cassano et al. 2009). Beyond this, maintaining native trees in "matrix" habitats can improve the ability of some other species to disperse between isolated forest remnants (Kupfer et al. 2006, Vandermeer & Perfecto 2007, Asensio et al. in press, Franklin & Lindenmayer in press). Trees in agricultural landscapes can enable species of other forest taxa to persist after habitat conversion, and can assist with seed dispersal of other plants by acting as foci for frugivorous birds and bats (Dunn 2004, Herrera & García 2009). If agroforestry systems are high-yielding and profitable (features which probably correlate broadly negatively with their biodiversity value), they can reduce pressure for forest clearance (Schroth et al. 2004).

However, there are also good reasons why further promotion of agroforestry systems might not be the most appropriate conservation action for tropical trees, especially when seen through the lens of trade-offs between land sparing and wildlife-friendly farming (Chapter 2). Evidence suggests that over time, farmers of agroforestry systems tend to favour a smaller number of fast-growing, often exotic "useful" shade trees, whilst killing and preventing the regeneration of unfavoured species (Gyasi et al. 2004, Sonwa et al. 2007, Anand et al. 2008, Ambinakudige & Sathish 2009, Cassano et al. 2009). The regeneration of slow-growing, shade-tolerant native species, even if they are represented in farmland by remnant individuals, is unlikely unless farmland is abandoned. While isolated mature trees might serve as refuges for other species and as foci for possible future regeneration (Dunn 2000, Herrera & García 2009, Nadkarni & Haber 2009), extensive farmland abandonment – as was common in previous centuries of traditional shifting agriculture – is unlikely unless human pressure is reduced. There is little doubt that human pressure will continue to increase in the West African forest zone for the foreseeable future, and so tree species diversity in agricultural land is likely to diminish further. Many shade-tolerant tree species are unlikely to persist in farmland and will probably not survive in the long term unless large areas of forest are protected from disturbance (Hill & Curran 2003, Laurance et al. 2006, Metzger 2009). Observations that the matrix around forest fragments has significant effects on tree mortality and recruitment need not imply that matrix management is the most appropriate solution: minimising the exposure of forests to matrix-mediated edge effects could be as or more effective (Laurance et al. 2002, Nascimento et al. 2006).

West African trees have been relatively well-studied within forest reserves, but information about their ability to survive in agricultural land uses is scanty. Persistence of forest tree species in agricultural landscapes is likely to depend on a number of factors, including the active retention, planting or destruction of trees by farmers, ability of trees to regenerate in brighter, drier more open habitats, and the persistence of associated species such as seed dispersers. There is some evidence that many of the endemic plants of the Upper Guinea forests are well adapted to disturbance, with relatively wide distributions within the area and with more light-demanding than shade-demanding species (Holmgren & Poorter 2007). This suggests that Upper Guinea tree species might be relatively resilient to habitat modification, because they have survived through severe disturbances in the past, probably including farming, elephant damage, fire and drought (van Gemerden et al. 2003, Hawthorne 1996). It could be that West Africa has already experienced an extinction filter (Balmford 1996) and has lost its most disturbance-sensitive species. Even if this is the case, it has not lost all of them. The endemic plant species with the smallest ranges in West Africa tend to be shade-demanding and restricted to moist forests, suggesting that these species are still at considerable risk of extinction from further deforestation (Holmgren & Poorter 2007).

6.1.3 Aims of this chapter

The aims of this chapter are to:

1. Describe tree species richness in forest, farm mosaic and oil palm plantations in southwest Ghana, and the extent to which species are shared between different land uses,
2. Estimate the densities of individual tree species across a gradient of agricultural production (with "yield" measured alternatively as food energy or net profit) and in near-intact habitat,
3. Describe the form of density-yield functions for those species and classify them into broad groups according to their responses,
4. Investigate whether species of most current and potential conservation concern are also those with the most sensitive responses to increasing yield

As with birds, I selected species-level traits that correlated with conservation concern: degree of shade-dependence, degree of endemism and conservation priority. My a priori expectations were that species which were most shade-dependent, narrowly endemic and of highest current conservation priority would be those most negatively affected by agriculture (Bongers et al. 2009, Pardini et al. 2009).

6.2 Methods

6.2.1 Survey methods

I enumerated trees in 504 sample plots spread across 25 squares, between August and December 2007. Of these plots, 144 were in the three high-yielding oil palm plantations and needed only cursory checking to verify that they did not contain any trees ≥ 10 cm diameter at breast height (dbh) other than oil palms. Sample plots were 25 × 25 m, which I measured by extending a 12.5 m tape in each cardinal compass direction from each GPS point, and using compass bearings to locate the corners. The points were a subset of those where I mapped crops and surveyed birds (see Chapters 2, 4 and 5): 12 plots in each forest square (half of the bird points), and 24 points in each farm mosaic or plantation square (all of the bird points). The increased sampling effort in agricultural land uses was to improve the precision of my density estimates, as trees were present at much lower density in those land uses than in forest. The difference in sampling effort makes my results conservative: I am likely to have underestimated the number of rare species restricted to forest compared with that in farm mosaic. Trees were identified and measured mainly by Kweku Dua, a tree spotter from the Forestry Commission, using standard local names which were translated to scientific names following Hawthorne (1990). Scientific names of all species are given in Appendix 2. A few plots were enumerated by Patrick Ekpe and Amponsah from the Herbarium at the University of Ghana, Legon. I located and measured each plot, recorded the data, collected voucher specimens where there was any doubt about the identification, and identified some specimens in the field using standard references (Hawthorne 1990, Hawthorne & Gyakari 2006). Most of the specimens were later confirmed or identified with reference to herbarium material by Patrick Ekpe, with a few being referred to William Hawthorne at the University of Oxford.

We measured and identified every tree with a dbh of 10 cm or more, ignoring non-native species, palms and lianas. Identifications were based primarily on bark and slash characters and overall form, secondarily on leaves, and very rarely on flowers or fruits. Non-native species were excluded because they were largely planted crops of a few species (e.g., cocoa, orange) and of little biodiversity value. There were only two native palm species: oil palm and *Raphia hookeri*. Old leaf bases remain attached to the trunks of palms and impede accurate measurement, and because oil palms were naturally the most abundant species in plantations, measuring all palms would have vastly increased the level of effort required, yet provided little useful information. Lianas were ignored because they were not consistently recorded from the outset, and they could not be readily identified. We took dbh measurements using standard protocols, measuring above buttresses where present, recording if trees were damaged above or below the point of measurement, and estimating the dbh for trees with very tall buttresses (3% of trees recorded). We measured all stems of trees with multiple stems ≥ 10 cm dbh, recording that they belonged to one individual. Trees at the edge of the plot were included only if the midpoint of the trunk at ground level fell within the plot. In a few cases where this was difficult to judge, I flipped a coin.

In a few cases, trees could not be consistently separated to species level, and so several "species" analysed were in fact difficult genera. This applied to *Anthocleista* spp. (*A. nobilis*, *vogelii*), *Berlinia* spp. (mainly *B. confusa*), *Erythrina* spp. (*E. vogelii* and perhaps other species), *Picralima*/*Hunteria* spp. (probably mainly *H. eburnea*), *Tabernaemontana* spp., *Vitex* spp. (*V. ferruginea* and perhaps other species) and *Zanthoxylum* spp. (*Z. gilletii* and perhaps other species). These genera were treated as seven "species" in the analyses throughout. It was also necessary, after entering all records, to correct some synonyms (e.g., *Isomacrolobium vignei* = *Anthonotha vignei*). Eight individual trees could not be identified and were excluded from further analysis.

6.2.2 Data analysis

I estimated total species richness in each square and land-use type, and the number of species shared with forest, as described for birds in section 5.2.3, using EstimateS, version 8.2 (Colwell 2009). I used two alternative measures of tree density: the number of stems per unit area (stem density), and the summed basal area of each species per unit area (basal area density). Basal area density is a useful measure because it gives greater weight to larger trees, which are likely to play a more important ecological role than small trees by supporting other species, producing larger quantities of flower and fruit, etc. Basal area was calculated for each stem using the standard formula for the area of a circle: $\pi \times (\text{dbh}/2)^2$. I fitted GAMs to stem density data plotted against two measures of yield, using an offset term, as for birds (see section 5.2.5). For basal area density, it was not possible to use an offset, because the relationship between the stem count and basal area depended on the size of each tree and hence was different for each plot. To fit GAMs to the basal area density data, I used a Gamma error structure with log link, and added 0.01 of the value of the maximum density to each density value so that there were no zeroes (Wood 2006). I set other values (default $k = 5$, gamma = 1.4) as for the quasipoisson models. I classified density-yield curves into the five response categories defined in section 2.3, as for birds: Supersensitive, Sensitive, Tolerant, Weeds and Superweeds.

6.2.3 Correlates of density-yield response category

I tested whether the yield level at which species reached their maximum density was related to variation in their categorised dependence on intact forest (major guild), and whether species' response categories (Supersensitive, etc.) were related to variation in (1) their dependence on intact forest, (2) their degree of endemism, and (3) their conservation status in Ghana as assessed using the star system (Hawthorne & Abu-Juam 1995, Hawthorne 2001). I collated information on the ecological attributes and conservation status of each species, with assistance from S. Jayson, using standard references (Hawthorne 1995, Hawthorne 1996, Poorter et al. 2004). Tropical forest trees can be divided into "guilds", based mainly on the extent to which they require light or shade during germination and establishment. Trees were classified into five guilds: shade-bearer (99 species), non-pioneer light-demander (NPLD, 51 species), pioneer (48 species), swamp (17 species) and climber/strangler (four species). Excluding the minor swamp and climber/strangler guilds, the three major guilds were treated as an ordinal variable, with shade-bearer > NPLD > pioneer in terms of dependence on intact forest habitat. Each species was classified according to its degree of endemism into four categories: Upper Guinea (36 species), Guinea-wide (=Upper and Lower Guinea, 64 species), Guineo-Congolian (74 species) and widespread (43 species) (see Figure 3.2). For 32 of those species, for which endemism information was not provided by standard references, I used the locations of specimen records from the Global Biodiversity Information Facility (http://www.gbif.org/) and countries of occurrence from USDA (2009).

All native forest tree species in Ghana have been assigned a "star rating", which is a measure of their conservation priority (Hawthorne 1996). The star categories are based mainly on species' rarity globally and in Ghana, with some additional consideration of ecology and taxonomy (Table 6.1). Species of highest priority are those categorised as Black, Gold or Blue stars (45 species in my samples). "Reddish" stars (Scarlet, Red and Pink) are not nationally or globally rare but are threatened by exploitation for timber or other purposes (41 species in my samples). Species with no particular rarity value are designated as Green star species (133 species in my samples). For each correlate, I treated each of the seven genera with unseparated species mentioned in section 6.2.1 as if it were a single species. So, all records of *Berlinia* spp., for example, were treated as being of a Guinea-wide, green star species on the basis of their commonest representative, *B. confusa*, even though they might also have included *B. occidentalis*, an Upper Guinea endemic and gold star species. I used the star rating system as a measure of conservation concern rather than the IUCN Red List, because global red list assessments for West African trees are still very incomplete. Only 33 of my species have been added to the IUCN red list (IUCN 2009), and most of these assessments are based on version 2.3 of the Categories and Criteria, which has now been superseded (Newton & Oldfield 2008). Of those 33 species, 28 are classified by the IUCN as Vulnerable or Endangered, and five are in the now obsolete set of Lower Risk categories: all are classified as Red star or higher by Hawthorne. To assess the significance of the relationship between major guild and yield at which species reach maximum density, I used the Spearman rank correlation test (Sokal and Rohlf 1995). I tested the significance of the relationship between correlates and response type with the asymptotic linear-by-linear chi-square association test in R (`lbl_test` in the `coin` package; Hothorn et al. 2008). Because of the small number of Weeds and Superweeds, I combined them with Tolerant species for chi-square analysis. There were no Tolerant Upper Guinea species, so I combined Upper Guinea and Guinea-wide species for chi-square analysis. To avoid low expected cell frequencies, I also combined Black and Gold stars, and all "reddish" stars.

Table 6.1. "Star" categories of conservation priority for species in Ghana, including a measure of how these categories correspond to the mean known range size of such species in Africa, abbreviated from Hawthorne (1996) who gives a full explanation of how species were assigned to categories.

Star	Degree squares in Africa	Description
Black	1.6 ± 0.5	Urgent attention to conservation needed. Rare internationally, and at least uncommon in Ghana.
Gold	7.8 ± 3.8	Fairly rare internationally and/or locally. Ghana has some inescapable responsibility for maintaining these species.
Blue	24.5 ± 12.6	Widespread internationally but rare in Ghana, or *vice versa*.
Scarlet	39.6 ± 16	Common, but under serious pressure from exploitation.
Red		Common, but under pressure from exploitation.
Pink		Common and moderately exploited. Also non-exploited species of high potential value.
Green	69.2 ± 49.8	No particular conservation concern.

6.3 Results

6.3.1 Species richness

I recorded a total of 3,308 stems overall, belonging to 3,192 identified native trees of 219 species. These comprised 202 species recorded in forest, 93 in farm mosaic, and 16 in the two plantation/farm squares. There were no trees ≥ 10 cm dbh in any of the plots in the three high-yielding plantations, other than oil palms. The most abundant species in each land use overall were: in forest, *Berlinia* spp., *Carapa procera*, *Dialium aubrevillei* and

Gilbertiodendron limba; in farm mosaic, *Macaranga barteri*, *Musanga cecropioides*, *Macaranga hurifolia* and *Anthocleista* spp.; and in plantation/farm, *Ficus exasperata* (Appendix 3). Although I surveyed only half as many plots per 1 km^2 square in forest as in the agricultural land uses, I recorded far more stems, and far more species, in forest plots. Estimates of species richness suggested that there was a considerable additional number of species to be found in each square and land use, with up to 200 species estimated in one forest square, and a similar number in one of the low-yielding farm mosaic squares (Figure 6.1, Figure 6.2).

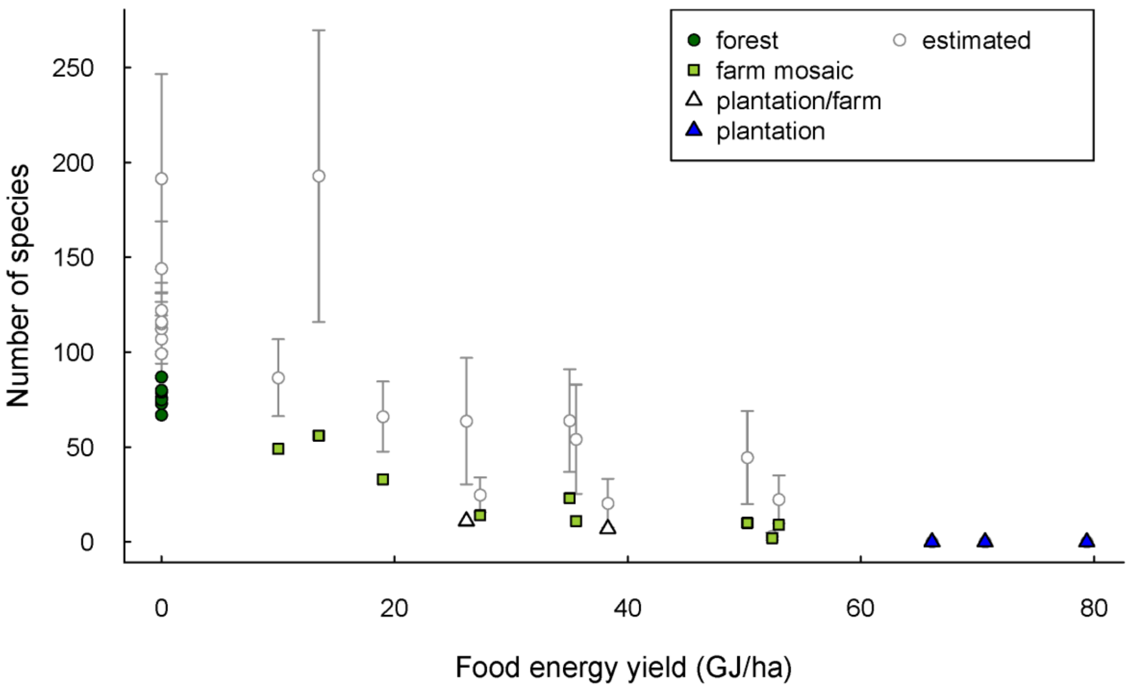

Figure 6.1. Observed and estimated tree species richness in each 1 km^2 square, in relation to land use (symbols) and food energy yield (x axis). Estimated species richness (mean ± SD) was computed using the Chao2 estimator, with plots (n = 12 in each forest square, 24 in other squares) as sampling units (Colwell 2009).

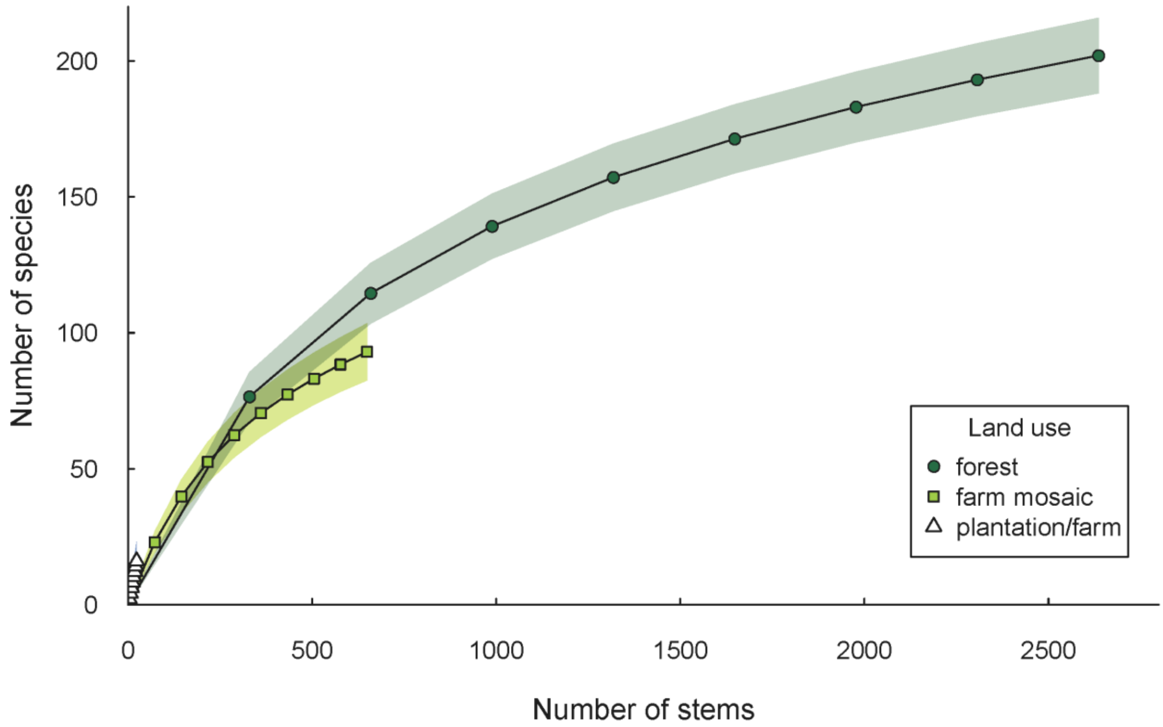

Figure 6.2. Sample-based species accumulation curves for forest (circles), farm mosaic (squares) and plantation/farm (triangles), plotted against cumulative number of individual stems. The increment between each pair of symbols on a curve represents the number of species and individual stems added, on average, by the sampling of plots within an additional 1 km^2 square. Shading shows 95% confidence intervals. The number of plots (and hence area) sampled per 1 km^2 square in each of farm mosaic and plantation/farm was double that in forest.

Overall, the numbers of observed species shared between land-use types were 77 (forest and farm mosaic), 12 (forest and plantation/farm) and 13 (farm mosaic and plantation/farm). I estimated the number of species and shared species between land uses within each block, to better assess the degree of overlap in species composition (Figure 6.3). Agricultural habitats always had lower estimated tree species richness than forests, and shared most (an estimated 60-75%) of their species with forest in the same block. The farm mosaic with the highest species richness, in block II, supported only an estimated 47% of the species found in forest in that block. It contained small remnant patches of forest (~1 ha) on small hilltops and steep slopes. That with the lowest species richness, in block I, supported only an estimated 2% of the species in forest, and an estimated 13 species altogether.

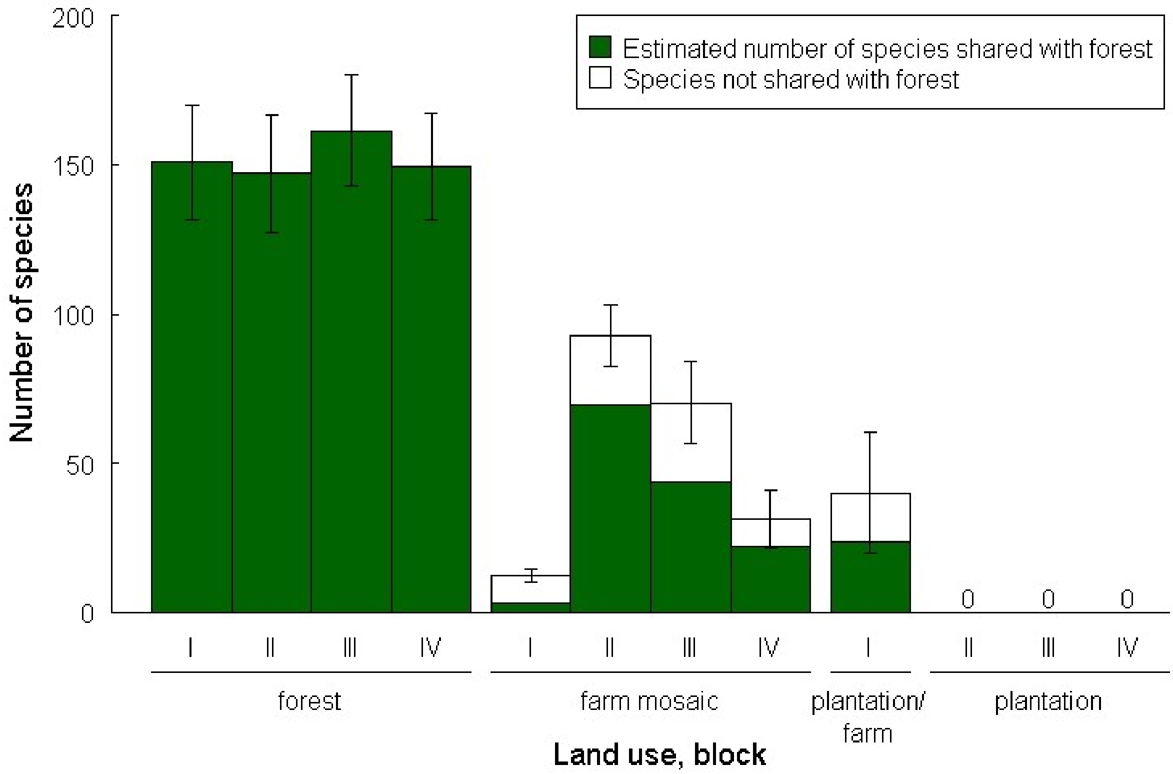

Figure 6.3. Estimated species richness of trees in each land-use type in each block (bars ± SD), and estimated number of species shared between that land use and forest in the same block (green), computed using the Chao1 abundance-based estimator, with squares set as samples, and Chao's coverage-based estimator of shared species (Colwell 2009). Square #24 was excluded.

6.3.2 Density-yield curves

I was able to fit GAMs to the data for almost all species, except for: two species (stem density vs. food energy or vs. net profit), one species (basal area density vs. food energy) or no species (basal area density vs. net profit). For those species for which I could not fit a model, because of sparse or unusually distributed data, I was still able to classify their response (all were Weeds). The 123 species recorded only in forest were classed as Supersensitive species. Among the remaining species, there was some variation between yield currencies and density currencies in the breakdown of response categories, but the patterns were broadly similar for each set of density-yield functions. Of these 96 species, 61 were Sensitive, 30 were Tolerant and five were Weeds (stem density vs. food energy, Figure 6.4, Figure 6.5); 54 were Sensitive, 36 were Tolerant and six were Weeds (stem density vs. net profit); 70 were Sensitive, 21 were Tolerant and five were Weeds (basal area density vs. food energy); and 67 were Sensitive, 23 were Tolerant, three were Weeds and three were Superweeds (basal area density vs. net profit). Of the seven species which were classified as Weeds or Superweeds at least once, one was represented in the samples by 16 stems, one by 3 stems, and the remainder only by one stem (Figure 6.5).

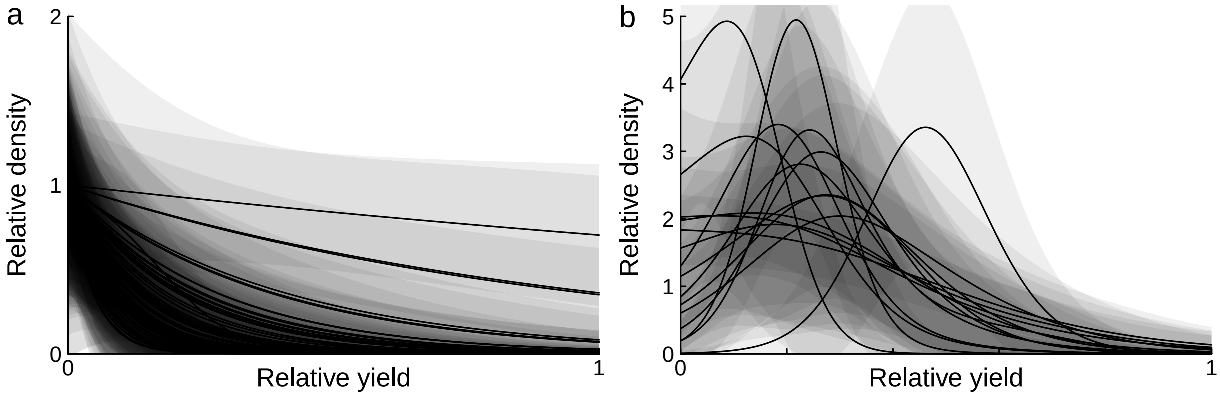

Figure 6.4. Density-yield relationships for tree species in southwest Ghana, with yield measured as food energy produced per hectare per year, and density measured as stem density. Shown are responses by (a) Sensitive species and (b) Tolerant species. Each curve represents the GAM for one species, with 95% confidence intervals shown by shading. Densities are expressed relative to maximum density in (a), or relative to mean density across the curve in (b). Curves with relative density values exceeding five were removed to make the plots easier to interpret. Plots based on basal area density vs. food energy, stem density vs. net profit, and basal area density vs. net profit, were all qualitatively very similar.

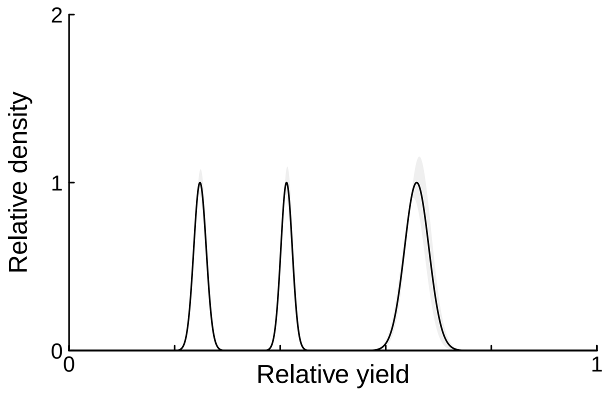

Figure 6.5. Very few tree species were classified as Weeds or Superweeds. This figure shows density-yield functions for *Alchornea cordifolia*, *Cathormion altissimum* and *Trema orientalis* (stem density vs. food energy). Because each of these species was represented in my samples by only a single individual (as were two other species for which I could not fit a model but also categorised as Weeds), the density-yield curves would likely be different shapes with further sampling effort. All five species also occur in forest (Hawthorne 1995). Densities are expressed relative to maximum density. Plots for Weeds based on basal area density vs. food energy, stem density vs. net profit, and basal area density vs. net profit, were similar.

6.3.3 Correlates of density-yield response category

The dependence of trees on forest was even more marked than for birds. The few tree species that reached maximum density in agricultural landscapes tended to belong to the pioneer guild, while the species that reached maximum density in forest tended to be shade-bearers (Figure 6.6). This relationship was highly significant for all four combinations of yield currency and density measure (Spearman rank correlations, with major guild as an ordinal variable and yield at which maximum density reached in original continuous scale: $r_s = 0.39$ (stem density vs. food energy); $r_s = 0.47$ (stem density vs. net profit); $r_s = 0.41$ (basal area density vs. food energy); $r_s = 0.37$ (basal area density vs. net profit); $p < 0.001$, $n = 198$ for all tests).

There was also a highly significant association between major guild and response category (Figure 6.7). Again, treating both major guild and response category as ordinal variables, species with the most sensitive responses to yield were significantly more likely to be shade-bearers, and Weeds were more likely to be pioneers, for all four combinations of yield currency and density measure (linear-by-linear association tests, with Superweeds, Weeds and Tolerant species combined: $\chi^2 = 43.81$ (stem density vs. food energy); $\chi^2 = 47.71$ (stem density vs. net profit); $\chi^2 = 46.77$ (basal area density vs. food energy); $\chi^2 = 42.95$ (basal area density vs. net profit); df = 1, $p < 0.001$, $n = 198$ for all tests).

Tree species endemic to smaller areas were significantly more likely to be sensitive to increasing yield (Figure 6.8). All Upper Guinea endemics were categorised as Supersensitive or Sensitive. Chi-square tests confirmed that there was a highly significant relationship between endemism and response for all four combinations of yield currency and density measure, treating both degree of endemism and response as ordinal variables (linear-by-linear association tests, with Superweeds, Weeds and Tolerant species combined, and Upper Guinea and Guinea-wide species combined: $\chi^2 = 50.05$ (stem density vs. food energy); $\chi^2 = 53.12$ (stem density vs. net profit); $\chi^2 = 47.94$ (basal area density vs. food energy); $\chi^2 = 46.88$ (basal area density vs. net profit); df = 1, $p < 0.001$, n = 219 for all tests).

Trees of highest conservation concern (as assessed by the star rating system) were those most negatively affected by increasing yield (Figure 6.9). All of the species of most conservation concern (Black, Gold and Blue), except one Gold star species, were Sensitive or Supersensitive. This relationship was highly significant for all four combinations of yield currency and density measure, treating both star and response as ordinal variables (linear-by-linear association tests with Superweeds, Weeds and Tolerant species combined, Black and Gold stars combined, and all "reddish" stars combined: $\chi^2 = 24.61$ (stem density vs. food energy); $\chi^2 = 22.10$ (stem density vs. net profit); $\chi^2 = 24.29$ (basal area density vs. food energy); $\chi^2 = 23.08$ (basal area density vs. net profit); df = 1, $p < 0.001$, n = 219 for all tests).

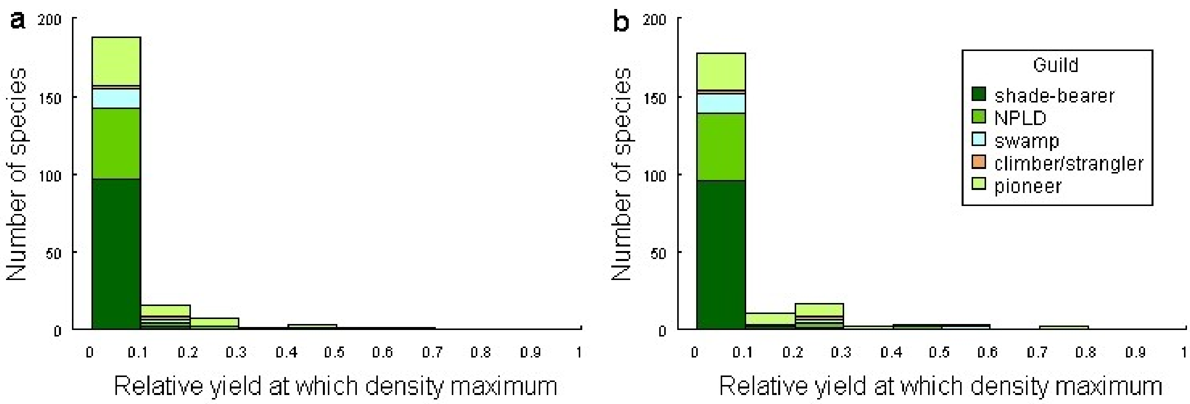

Figure 6.6. Frequency distribution of relative yields at which tree species reached maximum stem density, for (a) food energy, and (b) net profit. Coloured sections of bars indicate guild, with shade-bearers the most reliant on shaded forest habitat for germination and establishment, and pioneers the most tolerant of open unshaded habitats. Plots for basal area density were very similar.

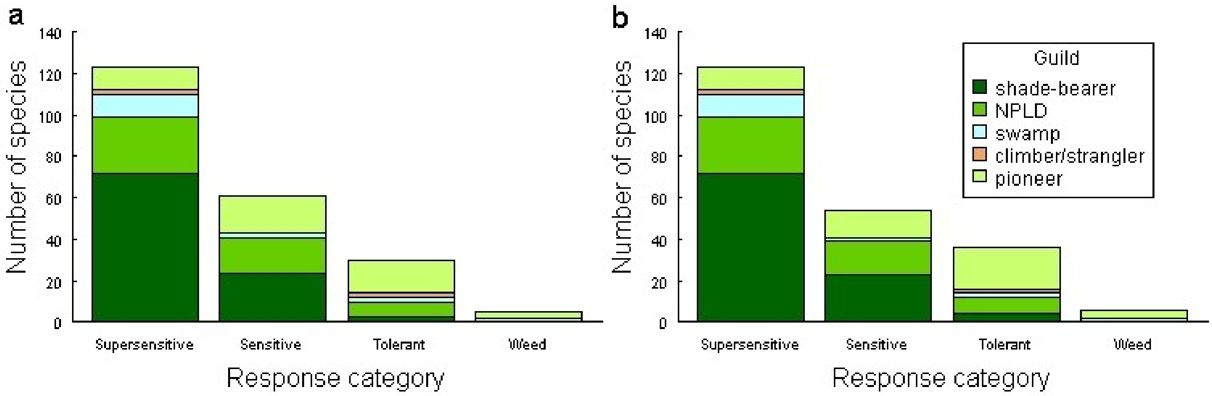

Figure 6.7. Number of tree species falling into different response categories to yield (bars), in relation to guild (colours), for (a) food energy, and (b) net profit. No species were categorised as Superweeds. Responses here are based on stem density data; distributions of responses for basal area density data were very similar, except that three species were categorised as Superweeds in relation to net profit.

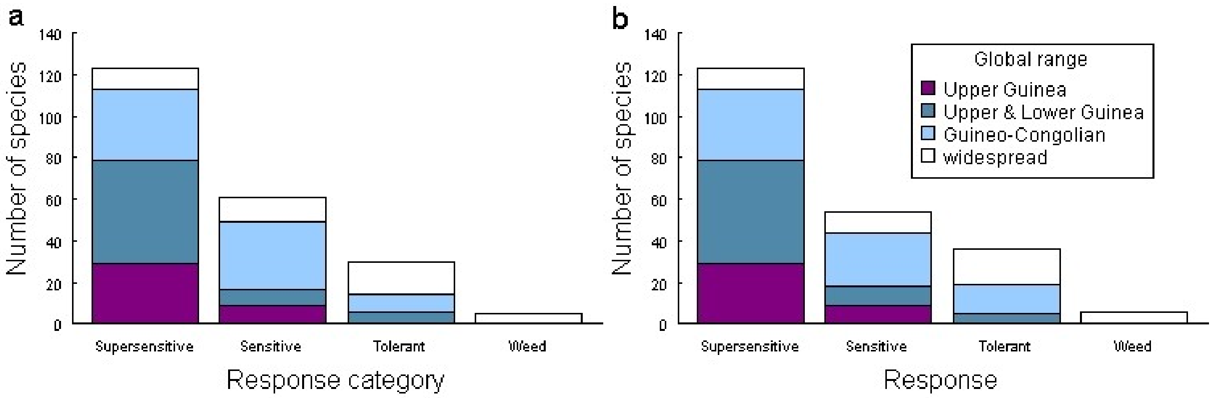

Figure 6.8. Number of tree species falling into different response categories to yield (bars), in relation to degree of endemism (colours), for (a) food energy, and (b) net profit. Responses here are based on stem density data; distributions of responses for basal area density data were very similar, except that there were three species with a Superweed response to net profit.

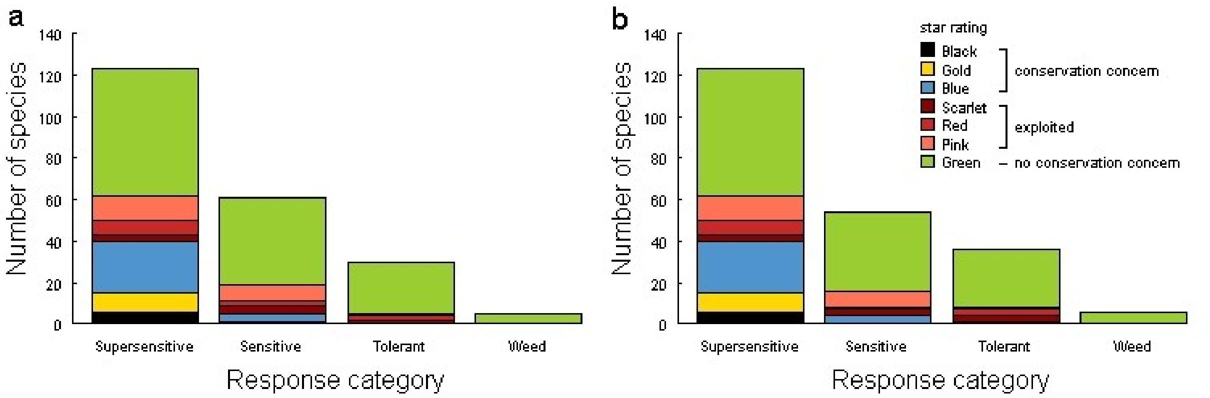

Figure 6.9. Number of tree species falling into different response categories to yield (bars), in relation to star rating (colours), for (a) food energy, and (b) net profit. Responses here are based on stem density data; distributions of responses for basal area density data were very similar, except that there were three species with a Superweed response to net profit.

6.4 Discussion

6.4.1 Value of agricultural habitats for trees

My results for trees were even more clear cut than those for birds (Chapter 5): trees as a group were far less tolerant of agricultural conversion than birds. There are a number of reasons why this might be the case. Trees compete directly with crops for nutrients, water and light, at least to some extent, so they tend to be actively managed by farmers. In all of the farm mosaic landscapes I worked in, farmers tolerated and even protected some species of "useful" trees – those which provided non-timber forest products such as medicines, or which were kept in reserve for their timber. However, even in the most rustic cocoa farms, it was not unusual to see less desirable trees being killed by ring-barking (pers. obs.). Trees typically take a long time to disperse and grow to maturity, and hence to recolonise a disturbed landscape. Unlike birds, I found few tree species that actually benefitted from the replacement of forests with wildlife-friendly farmland: the exceptions were mostly widespread pioneer species of no conservation concern. Shade-bearer species almost all responded badly to increasing yield: they might be able to regenerate in forest remnants or shaded cocoa farms in wildlife-friendly farmland, but the former are vulnerable to isolation and edge effects and the risk of future conversion, and in the latter only saplings of "useful" species are likely to be allowed to regenerate.

Despite suggestions that Upper Guinea endemics might be relatively resilient to habitat disturbance, all 38 Upper Guinea endemics recorded were Supersensitive or Sensitive to increasing yield, that is they were absent or present only at low density in even the lowest-yielding farmed landscapes. This is strong evidence that agricultural land use, even of relatively low intensity, constitutes more disturbance than these species can tolerate. Endemic species are of particular interest because what happens to them in West Africa will determine what happens to them globally, whereas only part of the global population of other species occurs in the Upper Guinea forests. Virtually all of the species of conservation concern that I recorded were either restricted to forest or were classed as sensitive to increasing yield. The main exception to this were the "reddish" star species: trees that are relatively widespread across Africa, but which are threatened by overexploitation. Interestingly, only one Pink star species ("common and moderately exploited", or "non-exploited species of high potential value") was classed as Tolerant of increasing yield. All other Pink star species were Sensitive or Supersensitive, and all other "reddish" star species in the Tolerant class were considered to be already under pressure from exploitation. This could suggest that while forests are serving as a refuge for species of economic value, agroforestry systems outside forests are failing to protect valuable species from overexploitation. There might be a case to be made for targeted conservation of the most diverse and complex shaded systems, but my results suggest that these are less typical in southwest Ghana than the exuberantly vegetated landscapes might suggest, and that efforts to protect and restore forests would benefit many more species.

6.4.2 Implications for ecological interactions

As species of trees dwindle and disappear regionally and globally, co extinctions of dependent species such as specialist pollinators and herbivores are likely (Koh et al. 2004). Trees in turn are affected by changes in the populations of pollinators, seed dispersers and seed and seedling predators in modified landscapes (Cordeiro & Howe 2003, Ickes et al. 2005, Mortensen et al. 2008, Babweteera & Brown 2009). Forest elephants *Loxodonta cyclotis* play an important role in dispersing large tree seeds, although a comprehensive review suggests that few if any tree species in Ghana are exclusively dependent on them for regeneration (Hawthorne & Parren 2000). In addition, human disturbances such as logging and agricultural conversion have probably largely replaced the role of elephants in creating habitat for pioneer tree species and light-loving herbaceous plants. However, if most large mammals and birds are hunted out of Ghana's forests, a process that is already well underway, tree regeneration will very likely be affected. The Miss Waldron's Red Colobus

Procolobus badius waldroni is already almost certainly extinct in Ghana and perhaps globally (Oates et al. 2000, McGraw 2005). Other mammals and even birds, such as the larger hornbills, are under serious pressure from hunting, a threat from which they have little protection except in the few forest zone wildlife protected areas and tiny sacred groves.

6.4.3 Caveats

As can be seen from Figure 6.2, my inventories of tree species in the study area were incomplete. Considerable further sampling effort would be required to find every species. In fact, it is quite likely that undescribed species exist in Ghana. *Synsepalum ntimii*, which I recorded in Cape Three Points forest reserve (block I), was only described in recent years, and the taxonomy of one of the *Xylopia* spp. (aff. *pynaertii*), also from Cape Three Points, has yet to be resolved. Sampling trees less than 10 cm dbh would have increased the number of species recorded in each plot, but it is difficult and time-consuming to identify seedlings and saplings, especially of rarer species. By sampling more intensively in farm mosaic and plantation land uses, I introduced a slight bias in favour of finding more rare species restricted to those land uses, although the fact that so many species were shared with forest suggests that most rare species in farm mosaic are very likely shared with forest too. Because there are so many fewer trees in farm mosaic than in forest, and because the richest farm mosaic (rustic shade cocoa) is derived from forest and supports few seedlings and saplings relative to forest, incomplete sampling is likely to have reduced my estimates of species richness more in forest than elsewhere, making my estimations of the number of species that would benefit more from land sparing than from wildlife-friendly farming conservative. The fact that many of the tree species found in farm mosaic are unlikely to be able or permitted to regenerate there, in particular, means that I have probably overestimated the value of farm mosaic for trees, relative to the importance of forest, when long-term persistence is considered.

I did not focus my sampling on “best-case” examples of wildlife-friendly farming, for example by selecting only the most heavily shaded cocoa farms with a high density of native trees. I could therefore be criticised for not focusing on the most promising wildlife-friendly farming systems at a fine scale. However, my interest was at larger scales, and in what was essentially a random sample of parts of the landscape of southwest Ghana. I likewise did not attempt to direct my sampling within forest reserves towards localities that had been less damaged by logging, and my randomly sited forest plots, which sometimes included skid trails or parts of logging roads, are a conservative baseline from which to compare more highly modified land uses. Of course, random selection did not remove all bias: I still had only two 1 km^2 squares in each land-use type in each block, and these might, by chance, have given an unrepresentative picture. Of particular concern was that I was refused permission to survey trees in the random square with the greatest coverage of shaded cocoa farms (square #16). It was replaced at short notice with a non-random square that had fewer cocoa farms (square #17). Despite these shortcomings, I am confident that my results are representative of the farming systems prevalent in the study region.

6.5 Conclusion

My results provided evidence that most tree species in southwest Ghana, including those most dependent on forest, those with the most restricted ranges and those of most conservation concern, would have higher populations at a given level of agricultural production in a landscape based on land sparing than one based on wildlife-friendly farming. Not only did forests hold many more species of trees than farm mosaic, they also supported considerably greater populations of most species that were found outside forest, including most shade-bearers, all Upper Guinea endemics and virtually all species of high conservation priority (Black, Gold and Blue star species). The majority of species that would benefit from wildlife-friendly farming were more widespread, pioneer species of no conservation concern (Green star species). Although no trees ≥ 10 cm dbh were found in sample plots in the three high-yield plantations other than oil palms, this and other species-poor but high-yielding farming systems could allow Ghana to increase its agricultural production with less impact on native trees than by expanding the area of wildlife-friendly agroforestry systems into the remaining forests.

Chapter 7

Possible futures

Boundary between Neung South Forest Reserve (left) and Benso Oil Palm Plantation (right)

‘...it is instructive to attempt to imagine what this planet is likely to look like in another century... something deeply distasteful and oppressive suggests itself — a world of monocultures and plantations stretching beyond horizons, of tiny depauperate nature reserves... of cities besieged by their own size and incompetence, of cultures and societies shaped by trivia and compulsion… We can also attempt to imagine how we would like the planet to be, now and ever after: diverse and rich in species and spaces, patchworked with sprawling, still mysterious nature reserves and generously landscaped farmland, dotted with self-sustaining cities, and inhabited by a rich mix of peoples and traditions...’

Nigel Collar (2003, p. 268)

7 Possible futures

7.1 Introduction

7.1.1 Agriculture in Ghana's economy

Agriculture is the largest sector of Ghana's economy and provides employment to more than 60% of its population (Government of Ghana 2005). It is therefore unsurprising that plans for the modernisation of agriculture are a key element of the Government's policies on economic growth and poverty reduction. Government documents are enthusiastic about the prospects of introducing irrigation, promoting non-traditional export crops such as papaya, mangoes, pineapples and cashew nuts, and developing modern fish farms to provide protein for domestic markets. There are Presidential Special Initiatives (PSIs) to promote the development of oil palm and cassava production and processing, and recent growth in the contribution of the agricultural sector to Ghana's GDP has been between 4% and 7.5% per year (Government of Ghana 2005). If an annual growth rate of 4% is maintained, the total value of the sector will double within 18 years. However, Africa has a long history of ambitious, large-scale, agricultural development projects that ultimately failed because they were inappropriately tailored to local conditions or undermined by fickle international markets (Adams 1992). Hence, although government policies have the intention of making agriculture the engine of economic growth, sufficient to promote future industrialisation, it is also possible that, in a few decades' time, most farmers will still be growing crops more or less as they are doing today.

The aim of this chapter is to explore the consequences of what those different futures could mean for biodiversity, given trends in population growth and per capita demand for food. The intention is not to make specific predictions about the future: there are too many uncertainties, which increase rapidly the further one looks ahead. Climate change, for example, is likely to have large impacts on agricultural output and on species' distributions (Thomas et al. 2004, Burke et al. 2009). Rather, the intention was to examine, under a range of plausible assumptions, the potential effects of agricultural change, under different land-use strategies, on birds and trees in part of southwest Ghana, using those groups as surrogates for wider biodiversity, and using that geographical region as a microcosm to illustrate the choices facing tropical forest nations more generally.

7.1.2 Aims of this chapter

In more detail, the aims of this chapter are to:

1. Identify a plausible "production target" for Ghana in 2047, based on trends in population growth, food demand and international trade,
2. Identify a set of plausible scenarios of future land-use change for the study province in southwest Ghana, based on the production target and consistent with recent trends in land-use change and agricultural yields,
3. Combine these patterns of future land use with the density-yield curves of bird and tree species to estimate their population sizes for each scenario, and use those to assess the risk that species would, by 2047, be committed to extinction within the study province.

I chose to take 2007 as the start year for the scenarios because the bulk of my field data were collected in 2007. When considering changes in species' status, I also use a pre-agricultural baseline: extrapolating species' populations in fragmented forests in 2007 backwards to estimate what their populations might have been in the absence of agriculture. My assumption is that virtually all of the study province would have been forested in the absence of agriculture. This would be debatable at the fringes of the forest zone (Fairhead & Leach 1998), but for southwest Ghana it appears plausible (Maley 1996). I chose to develop scenarios over a 40-year period, to 2047, because that was a long enough period for significant changes to occur, but short enough that those changes will occur within my lifetime, and within the lifetimes of many of those making the decisions that will determine which scenario comes closest to the truth. Also, global population growth is projected to level off by around that year.

7.2 Setting the context

7.2.1 Identifying the future production target

I considered two of the main drivers of agricultural development: population growth and increases in per capita consumption of food. I evaluated the prospects for these two drivers in Ghana and globally. For population, I used linear interpolation between five-yearly medium term projections to 2050 by the United Nations (UN 2009). Between 2007 and 2047, the population of Ghana is projected to increase from 22.9 million to 43.7 million, an increase of 91%. Over the same period, the global population is projected to increase from 6.7 billion to 9.1 billion people, an increase of 36%.

Mean annual per capita food energy consumption in Ghana (food energy consumed per person, not including crops fed to meat-producing animals) declined in the 1970s, but has been increasing steeply and fairly steadily since the mid-1980s (Figure 7.1). In 2003, it was estimated as 11.21 MJ/capita/day (FAOSTAT 2009). This was close to the mean of all developing countries in 2003, of 11.16 MJ/capita/day, and above the average daily recommended energy intake for the Ghanaian population, estimated for 2005, of 8.92 MJ/capita/day (FAO 2004). However, it was considerably lower than the mean for all developed countries in that year, of 13.94 MJ/capita/day (FAOSTAT 2009). Food energy consumption has been increasing less quickly in the developing world overall than it has in Ghana, so I used the recent rate of increase in consumption in the developing world as a conservative estimate of future change in Ghana. I made this estimate additionally conservative by basing my projection only on estimates from 1984 onwards: visual inspection of the data suggested that the rate of increase was faster before than after 1984.

Using a linear regression model based on the period 1984-2003 gave a good fit ($r^2 = 0.95$, $F_{1,18} = 362.9$, $p < 0.001$) and projected a consumption rate for the developing world in 2047 of close to that of the developed world in 2003 (Figure 7.1). I did not assume any increase in per capita consumption in the developed world. Combining these projections of population size and per capita consumption, total food consumption in Ghana was projected to more than double between 2007 and 2047: an increase of 128.7%. Combining the population and food consumption projections for the developing and the developed world, global food energy consumption was projected to increase by 56.6%.

I next considered the extent to which food produced in Ghana is exported, as this will determine the extent to which future production targets will be driven by foreign rather than domestic markets. I calculated the total production, for Ghana as a whole, of all of the major edible crops in the province, converting them to food energy as in Chapter 4. I then calculated the total exports of those crops, including processed products made from oil palm fruits and oranges, again converting these to food energy units. Ghana exported just 10.1% of its production of the specified crops in 2007 (Table 7.1). Based on this, I estimated that Ghana would have to increase its food energy production by 121.4% by 2047, if it were to keep pace with increases in total consumption domestically (89.9% of its market) and globally (10.1% of its market). I assumed that production in the province would have to increase at the same rate as overall production in Ghana. The production target was expressed in terms of food energy, because unlike net profit, food energy demand will not be greatly affected by changes in prices and input costs between 2007 and 2047. It translates to an annual percentage increase of 2.01%.

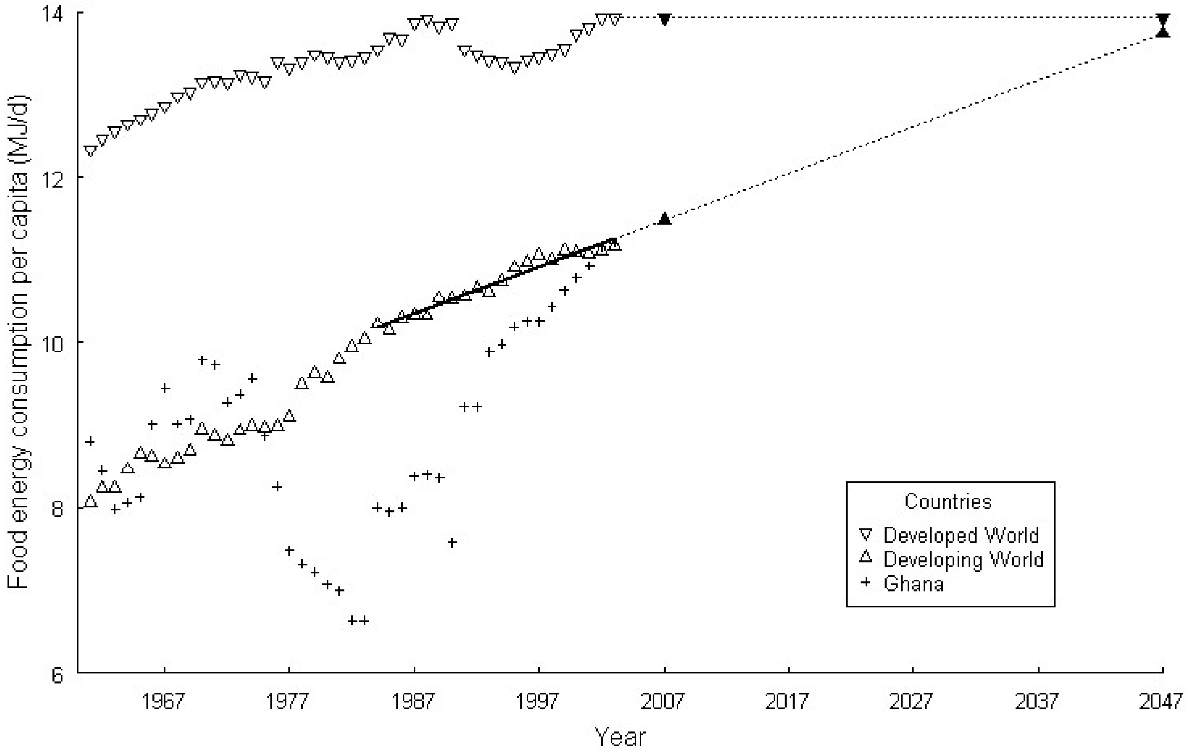

Figure 7.1. Per capita food consumption in the developed world, the developing world and Ghana from 1961 to 2003 (open symbols), with projections for 2007 and 2047 (filled symbols). Food consumption for the developing world was extrapolated to 2047 (lower dotted line) by linear regression from the period 1984 to 2003 (solid line), while that in the developed world was assumed to remain at the same level in 2007 and 2047 as in 2003. Source: FAOSTAT (2009).

Table 7.1. Food production and exports of selected edible crops from Ghana in 2007, in tonnes and in food energy expressed in TJ (1 TJ = 1 × 10^{12} J). Source: FAOSTAT (2009).

Food item	Production	Exports	Production	Exports
	tonnes	tonnes	TJ	TJ
Cocoa beans	615,000	506,358	11,740	9,666
Oil palm fruit	1,900,000	-	14,191	-
Palm kernel oil	-	384	-	14
Palm kernels	-	712	-	13
Palm oil	-	92,000	-	3,403
Oranges	480,000	3,473	690	5
Orange juice	-	1,568	-	3
Cassava	9,650,000	-	55,354	-
Plantain	2,930,000	175	9,713	1
Bananas	57,500	12,755	137	30
Maize	1,100,000	173	16,797	3
Cocoyam (taro)	1,662,000	0	6,704	-
Yams	3,550,000	0	15,082	-
Total food energy			**130,408**	**13,138**
Exports as % of Production				**10.1%**

7.2.2 Constraints on agricultural development

In imagining possible futures for agricultural development in Ghana, there are some constraints on what is possible. I considered two important constraints: the rate at which yields can increase and the suitability of land for agriculture. The mean annual rate of increase in food energy yield (energy per unit area of cropland per year) from 1979 to 1999, of the 23 most energetically important crops considered by Ewers et al. (2009), was 1.27% in developed countries and 2.10% in developing countries (R. Ewers, unpublished data). India, over that period, achieved an annual rate of 2.94%. In Ghana, the mean rate of increase was 1.16% per annum. Although information on yields in Africa and other developing regions is hampered by a lack of rigorous data collection, there is some recent evidence from Africa to suggest that yields are typically far below their potential, and can be doubled or more, at least locally, within a few years (Pretty et al. 2006, Badgley et al. 2007, Sanchez 2009, Sanchez et al. 2009). Even if spread over 20 years, a doubling of yield is equivalent to an annual increase of more than 3.5%. I did not consider annual rates of yield growth higher than this, and I also assumed that yields would never exceed the 2007 yields of the highest-yielding plantation, in any scenario.

The scenarios assumed that all currently farmed and all forested land within the study province was suitable for high-yield agriculture. Based on information from the Soils Research Institute in Ghana, 90% of the land within the province was “suitable” for oil palm cultivation to some degree (“moderately suitable” to “very suitable”), with a further 6% being “marginally suitable” and only 4% unsuitable (Figure 7.2). Even land unsuitable for oil palm is likely to be suitable for other crops. Two of the plantations I studied are mainly or partly located on land that is only “moderately suitable”. I therefore considered it a reasonable approximation to assume that all currently farmed or forested land is biophysically suitable for conversion to agriculture.

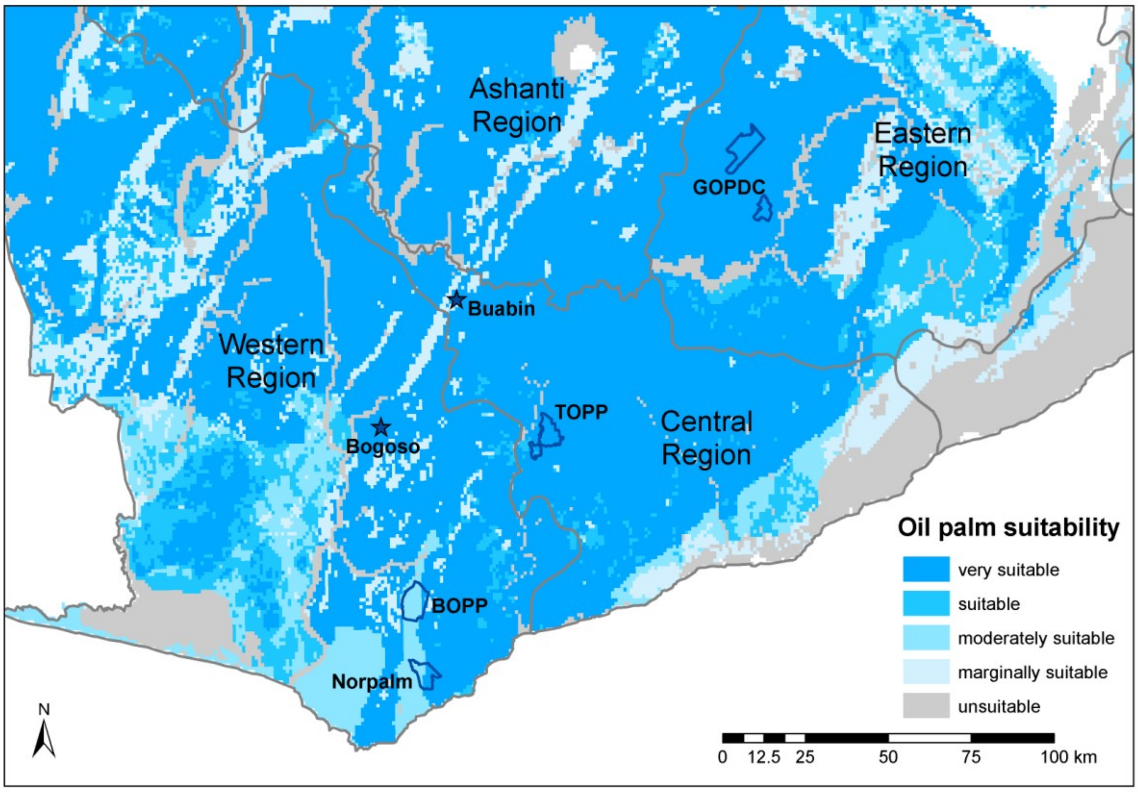

Figure 7.2. Biophysical suitability of land in southwest Ghana for oil palm cultivation, based on soils and climate. The four plantations studied in this thesis are outlined in dark blue. Two of them are located partly on land which was only "moderately suitable". Two further plantations in the early stages of development are marked with stars. Map produced from a suitability layer supplied by the Soils Research Institute, Accra.

7.2.3 Land use in 2007

I defined the study province as comprising the seven districts within which my sample sites fell, as illustrated in Figure 3.5. I estimated current land use in the province using a GIS land cover map from the Forestry Commission (Table 7.2, Figure 3.6). I did not have access to information about how or when this map was created, but it corresponded well to land use as I observed it on the ground in 2007. I did not include uncultivable land uses (urban areas, mines, open water, and a small area of "wetland", probably misclassified) in the scenarios: combined, these made up <2% of the area of the province. I estimated total food energy production in 2007 by multiplying the area of each agricultural land use by the mean yield of all of the randomly selected farm mosaic squares representative of it (Chapter 4): 12.3 GJ/ha for farm mosaic with moderate tree cover (squares #9, #10, #15 and #16), 41.4

GJ/ha for farm mosaic with few trees (squares #3, #4, #22 and #23) and 67.2 GJ/ha for plantations (squares #5, #11, #12, #18, #19, #25 and #26). I did not use information from square #6 because it was not entirely within plantation as mapped by the Forestry Commission, nor squares #17 and #24 because they had not been randomly selected.

Table 7.2. Land use within the study province. In the third column, "Unknown" land use is assigned to the known land uses in proportion to their known area. For further details and definitions see Appendix 1.

	Classified (km^2)	Including Unknown (km^2)	As % of cultivable
Farm mosaic (with trees)	4,498	4,561	50%
Farm mosaic (few trees)	2,236	2,267	25%
Forest	1,907	1,934	21%
Plantation	350	355	4%
Uncultivable	142	144	-
Unknown	129	-	-
Total cultivable	**-**	**9,117**	**100%**
Total classified	**9,132**	**-**	**-**
Total	**9,261**	**9,261**	**-**

7.3 Land-use scenarios

7.3.1 Patterns of land-use change

I modelled four scenarios, starting from the current situation in the study region in 2007, and using a four-compartment land-use model, with each compartment representing the area of one of the four cultivable land-use types (including forest) in section 7.2.3. In all four scenarios, yields and areas of the land uses were selected so that the food energy production target in 2047 was met exactly. The pattern of land use in 2007, and in 2047 for each of the four scenarios, is shown in Figure 7.3. In all of the scenarios, plantation yields were increased by 2047 to the level of the highest-yielding plantation in 2007: 79.4 GJ/ha (squares #25 and #26). Yields in the two types of farm mosaic were kept constant, and the average yield from the combined area of the two types was increased by reducing the proportion of farm mosaic with trees, and replacing it with farm mosaic with few trees. Production could also be increased by increasing the area of farm mosaic by converting forest to farm mosaic, or by converting forest or farm mosaic to plantation.

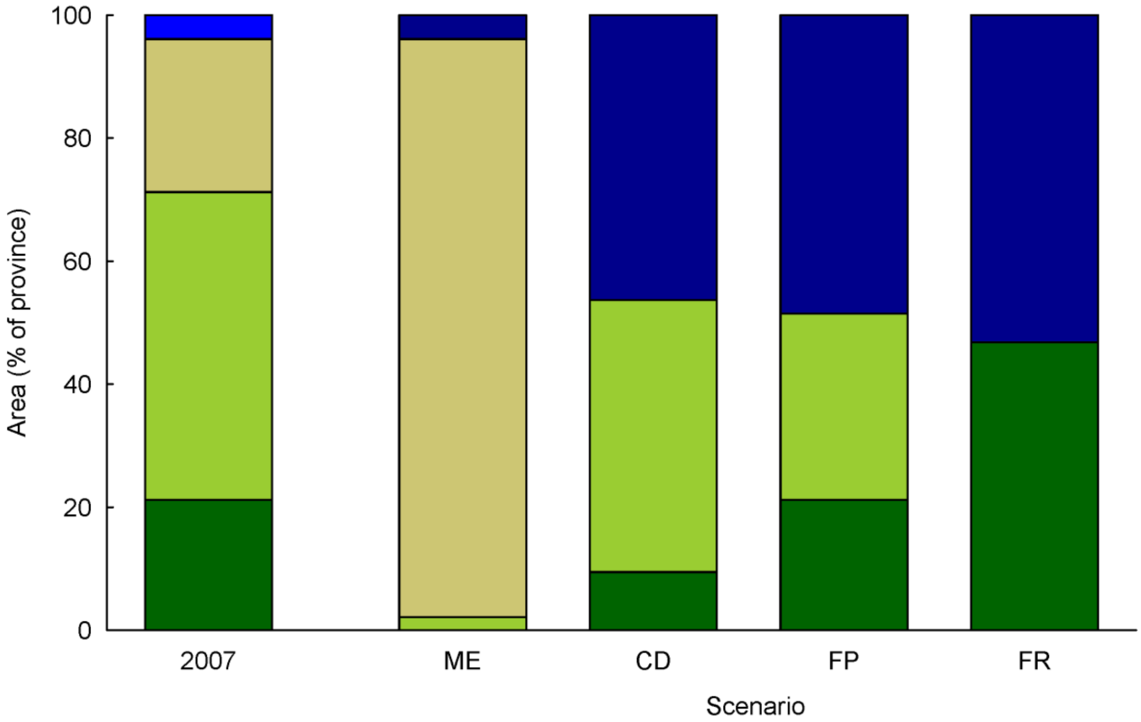

Figure 7.3. Patterns of land use in the province in 2007, and in each of four scenarios in 2047: ME (Mosaic Expansion), CD (Continued Deforestation), FP (Forest Protection) and FR (Forest Recovery). Colours indicate land use: blue (plantation with mean 2007 yields), dark blue (plantation with maximum yields), pale olive (farm mosaic with few trees), light green (farm mosaic with moderate tree cover), dark green (forest).

7.3.2 Mosaic Expansion Scenario (ME)

In this scenario, the objective is to maintain the area of farm mosaic without allowing plantations to expand. In order to achieve this and meet the 2047 production target, it is necessary to convert all forest and much of the wooded farm mosaic to higher-yielding unwooded farm mosaic (Figure 7.3: ME). When yield is measured as overall food energy production divided by total agricultural area, the mean annual rate of yield increase is

1.40%. Although this is the lowest rate of yield increase of the four scenarios, it is greater than the recent rate of yield increase in Ghana of 1.16%. Even with all forest area being converted to agricultural land, it would not have been possible to meet the production target assuming that recent rate of yield increase. This is a wildlife-friendly farming strategy, as increases in production come primarily from the expansion of farm mosaic, to the maximum extent possible.

7.3.3 Continued Deforestation Scenario (CD)

Deforestation continues at the recent rate of 2% per year (FAO 2006), so that by 2047 a little less than half (45%) of the forest still present in 2007 remains (Figure 7.3: CD). This scenario is "business-as-usual" in terms of deforestation, but to prevent even more rapid deforestation while achieving the production target, overall yields on agricultural land have to increase, by on average 1.65% per year. In order to maintain some low-yielding, wildlife-friendly farmland, the area of plantations expands, such that by 2047, they cover almost half of the province. This is a mixed strategy, between land sparing and wildlife-friendly farming, as the expansion of high-yielding plantations allows some wildlife-friendly farm mosaic with high tree density and forest to be substantial parts of the 2047 land cover

7.3.4 Forest Protection Scenario (FP)

The priority is to ensure that all existing forest is protected from encroachment. The required annual increase in production is met by increasing yields in agricultural land: an annual average increase of 2.01%. This is achieved by converting farm mosaic to high-yielding plantations (Figure 7.3: FP). This is a land-use strategy based on land sparing, because the area of forest is kept constant and production is increased by increasing yields on agricultural land. It also has a wildlife-friendly farming component, in that high yields from plantations permit much of the farm mosaic with trees to remain in 2047.

7.3.5 Forest Recovery Scenario (FR)

All agricultural land is converted to high-yielding plantations by 2047, freeing up land for natural reforestation (Figure 7.3: FR). Because the area of agricultural land is smaller each year, the annual rate of increase in yields is highest in this scenario: 3.01% when averaged across all agricultural land. I assume that all spared land is reforested, and that by 2047 the reforested area has comparable densities of forest birds and trees compared to existing forest. Because of this, and because of political and social realities, this is the least plausible of the scenarios, but it is an informative thought experiment for reasons discussed later, in section 7.5.2, and is even more strongly based on the concept of land sparing than Forest Protection.

7.3.6 Assessments of extinction risk

For each of the bird and tree species for which I had fitted a model in Chapters 5 and 6, I calculated their risk of extinction in the province (extirpation) in 2007 and in 2047, under each scenario. I based the extinction risk estimate on population sizes derived from the density-yield functions that related the numbers of birds or stems per unit area to food energy yield. Extinction risk is an estimate of the probability that a species is committed to eventual extinction within the region because of environmental and demographic stochastic processes if its modelled population size remains the same. Actual regional extinctions might take a short or a long time (the relaxation time, Brooks et al. 1999). Although the province is smaller than the world range of most or all of the species considered, I use the more familiar term “extinction” rather than “extirpation”, which is a more accurate term for local extinction. The calculated risk is equivalent to the global risk of being committed to extinction for species which undergo the same changes in relative population size in all parts of their global range outside the study province as they do within it. As I am using southwest Ghana as a case study to represent agricultural development and land-use change in tropical forest countries more generally, it is appropriate to think in terms of global extinction as well as regional extirpation.

Although orders of magnitude more frequent now than in the past, global extinctions of species are rare events which are difficult to observe and verify: species' lifetimes are of the order of 1-10 million years in the absence of human intervention (Whitmore & Sayer 1992, Pimm et al. 2006). Consequently, understanding of the causes of extinction is based mainly on observations of local extinctions (extirpations) and on the processes leading to population decline. The most frequently-used method to estimate the potential impacts of land-use change on extinction risk is the species-area relationship, or SAR (Pimm & Askins 1995, Pimm et al. 1995, Brooks et al. 1997, Brooks et al. 1999, Thomas et al. 2004, Pimm et al. 2006). The SAR relates the number of species found in a region, or a fragment of habitat, to the area of that region. As the area of the region or habitat decreases, the number of species persisting in it is predicted to decline increasingly rapidly with decreasing area (Rosenzweig 1995).

In my calculations I assume that effects usually attributed to habitat extent in SAR analyses have their effects because of changes in population size. For each species, I first estimated its pre-agricultural baseline population, P_1. I estimated this as the population that could have inhabited the area of the Upper Guinea forest when it was at its minimum extent between 15,000 and 20,000 years ago, as all of the species now present in Upper Guinea must have survived through that 5,000-year ancient bottleneck in forest cover (see section 3.2.1). A precise estimate is not possible from a schematic paleoecological map: I used an estimate from Figure 3.1 that 25% of forest existed during the bottleneck. I estimated P_1 for each species by multiplying its mean density at zero yield (in forest) by the total area of cultivable land in the province (9,117 km^2), multiplied by 25%. I then calculated the population size of each species in 2007, and in 2047 for each scenario, by taking its estimated density at each projected yield in each land use (land uses as in Figure 7.3), and multiplying by the area of that land use projected for that year (P_i). I calculated the extinction risk for each species in each of 2007 and 2047, using the following formula:

$$\text{risk} = 1 - (P_i/P_1)^z$$

where P_1 was the pre-agricultural population size, and P_i was the later population size, in 2007 or 2047. This is Method 1 of Thomas et al. (2004). Estimates of extinction risk for species endemic to an area typically use a value of $z = 0.25$ for the exponent, but because the species in my study are not endemic to the province, I used a more conservative value of $z = 0.15$. This takes into account the likelihood that species' populations could be "rescued" from extinction by recolonisation from adjacent areas, and is the midpoint of the range of values described by Rosenzweig (1995) for the SAR in different parts of mainlands (0.12-0.18). Any species with $P_i \geq P_1$, including those considered unlikely to have had pre-agricultural populations in the province, was assigned an extinction risk of zero. I did this based on the assumption that all species are likely to have persisted for a very long period (≥ 1 My) at or above their estimated pre-agricultural population size and should therefore have a very low extinction risk if their modern populations were higher than in pre-agricultural times. These species also include those characteristic of other biomes, such as savanna and grassland, that are likely to decrease in extent outside the province less than forest. Hence, these species are also expected to persist because their populations will be supplemented through immigration and recolonisations. A risk value of one would indicate a certain probability of extinction in the province, which would only occur if all of the habitat used by a species had disappeared. I summarised extinction risk for birds and trees in each of 2007 and 2047 for each of the groups defined in Chapters 5 and 6, i.e., natural habitat and degree of endemism (birds), and guild, degree of endemism and conservation concern (trees).

7.4 Outcomes for species

7.4.1 Changes in population size: birds

Projected changes in population size varied among the natural habitat groupings of bird species defined in Chapter 5. The estimated population sizes of forest-dependent birds (as defined in that chapter) were tied closely to the estimated area of forest left in the study province in 2047 (Figure 7.4). Twenty-four out of 51 forest-dependent species disappeared completely in the Mosaic Expansion scenario, in which no forest remained. The populations of the majority of forest-dependent birds was roughly halved when forest was reduced to 45% in the Continuing Deforestation scenario, while populations of many species stayed at close to their 2007 levels in Forest Protection, in which forest cover was unchanged. The populations of many forest-dependent species increased in the Forest Recovery scenario, although one species (Crested Malimbe) declined to zero.

The patterns were similar for forest major species (Figure 7.4, mid-green bars). In Mosaic Expansion, 11 out of 47 forest major birds were extirpated from the province, while the populations of six species increased relative to 2007. Populations of most of these species were slightly above half of their 2007 level in Continuing Deforestation, and slightly below their 2007 level in Forest Protection. Three forest major species disappeared in the Forest Recovery scenario, while others increased relative to 2007.

Changes in population size were more variable for forest generalists (Figure 7.4, pale green bars). Some species increased in all scenarios, and this was especially true of Mosaic Expansion. Mosaic Expansion did however, also see the complete loss of six out of the 46 forest generalists. Continuing Deforestation and Forest Protection each lost one forest generalist species, and Forest Recovery lost three. Populations of the eight non-forest species (Figure 7.4, white bars) increased most consistently in Mosaic Expansion, but none of those species disappeared entirely from any of the scenarios.

7.4.2 Extinction risk: birds

Birds suffered the greatest increase in extinction risk in the scenarios based most strongly on wildlife-friendly farming: Continued Deforestation, and especially Mosaic Expansion. This was true for all groupings of birds by natural habitat, except for non-forest species which had a zero extinction risk in all scenarios (Table 7.3, Figure 7.5). The increase in extinction risk was greatest for forest-dependent species (57% in Mosaic Expansion), but even for forest generalists, extinction risk was higher in Mosaic Expansion than in scenarios based most strongly on land sparing (Forest Protection and Forest Recovery).

Similarly, extinction risk was highest in Mosaic Expansion for all groupings of birds by degree of endemism, even widespread species (Table 7.4, Figure 7.6). The increase in extinction risk was greatest for Upper Guinea endemics (88% in Mosaic Expansion), but even for widespread species, extinction risk was higher in Mosaic Expansion than in the scenarios based most strongly on land sparing. Overall, extinction risk for birds was zero in Forest Recovery, as this scenario featured a higher percentage forest cover than that estimated for the ancient bottleneck. Extinction risk in Forest Protection was similar to that in 2007, and extinction risk in Continued Deforestation was slightly elevated in 2047 in comparison with 2007.

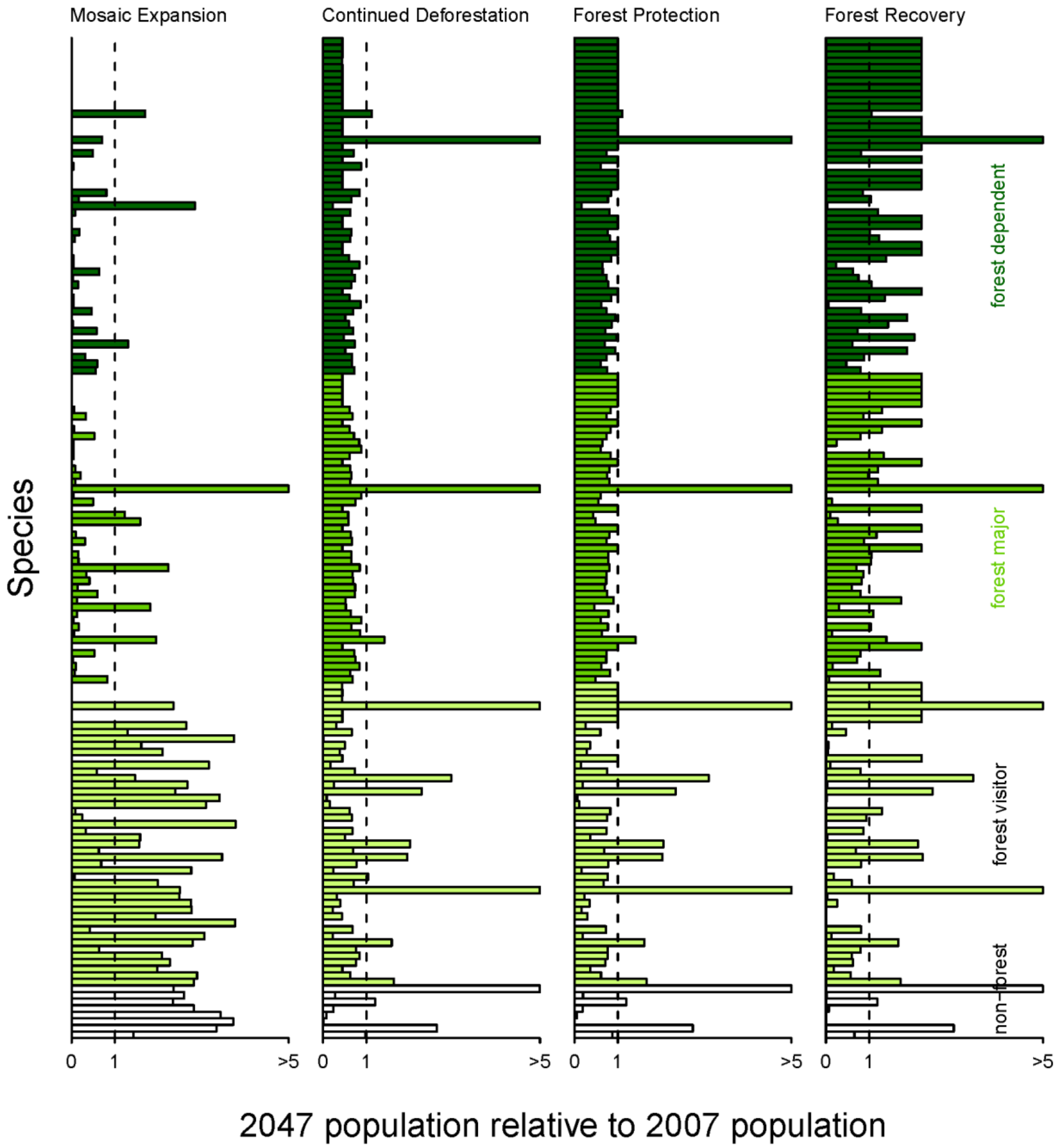

Figure 7.4. Estimated province-wide populations in 2047 of 152 bird species relative to their estimated populations in 2007 based upon a simple land-use model, under four scenarios. Each bar denotes one species. The horizontal extent of each bar indicates the ratio of that species' population in 2047 to that in 2007, with 1 (dashed line) indicating no change. Colours indicate natural habitat of each species, as labelled. Of the 167 species recorded on counts, 15 are excluded (all Weeds): three for which it was not possible to fit a model, and 12 which did not occur in any of the simple yield compartments used in the scenarios.

Table 7.3. Mean extinction risk, expressed as a percentage, for birds according to their natural habitat (degree of dependence on forest). A value of 100% means that all species in a category are committed to extinction; a value of 0% means no species is committed to extinction. Scenario names are abbreviated as in Figure 7.3.

Natural habitat	2007	ME	CD	FP	FR
Forest dependent	1%	57%	7%	1%	0%
Forest major	1%	35%	4%	1%	0%
Forest generalist	0%	16%	2%	0%	0%
Non-forest	0%	0%	0%	0%	0%
All species	**1%**	**35%**	**4%**	**1%**	**0%**

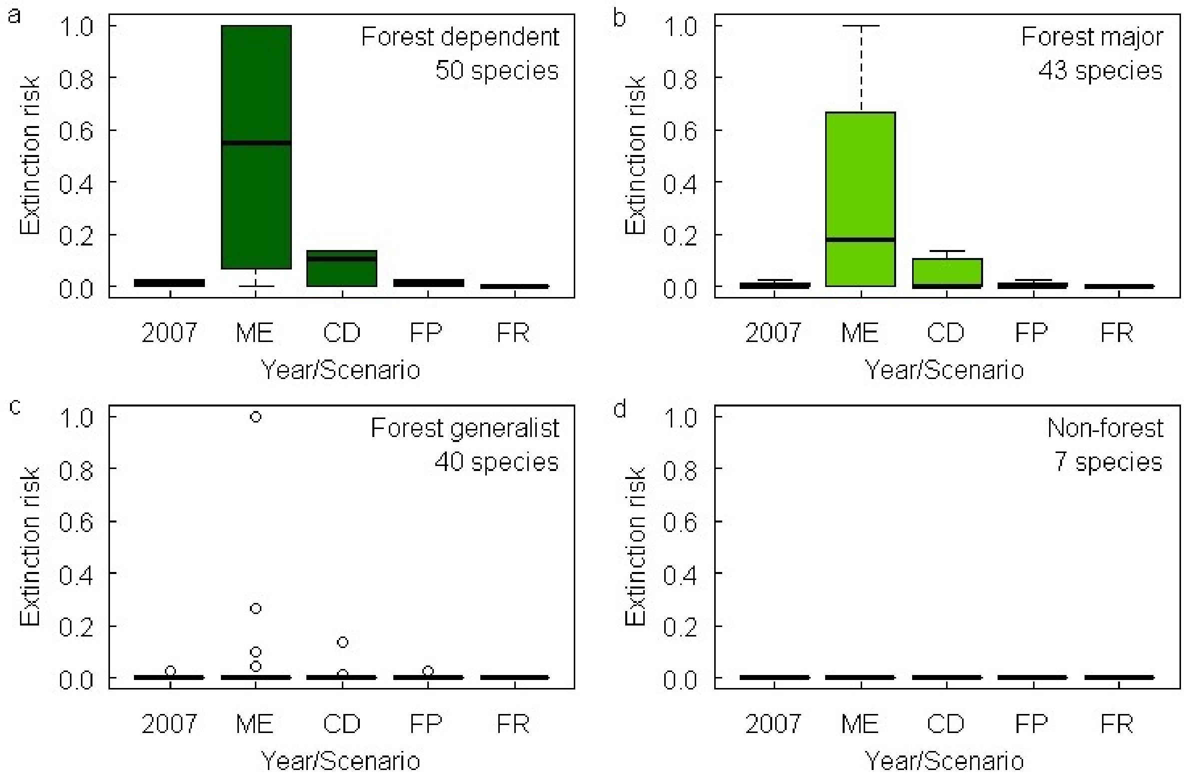

Figure 7.5. Extinction risk in 2007, and in 2047 for four scenarios, of 140 species of birds: (a) forest dependent, (b) forest major, (c) forest generalist, and (d) non-forest species. Extinction risk in the absence of agriculture was assumed to be zero. Boxplots show median (thick line), interquartile range (boxes), data no more than 1.5 times interquartile range (whiskers) and outliers (circles). Scenario names are abbreviated as in Figure 7.3.

Table 7.4. Mean extinction risk, expressed as a percentage, for birds according to their global range (degree of endemism). A value of 100% means that all species in a category are committed to extinction; a value of 0% means no species is committed to extinction. Scenario names are abbreviated as in Figure 7.3.

Global range	2007	ME	CD	FP	FR
Upper Guinea	2%	88%	13%	2%	0%
Guineo-Congolian	1%	45%	6%	1%	0%
Widespread	0%	16%	2%	0%	0%
All species	**1%**	**35%**	**4%**	**1%**	**0%**

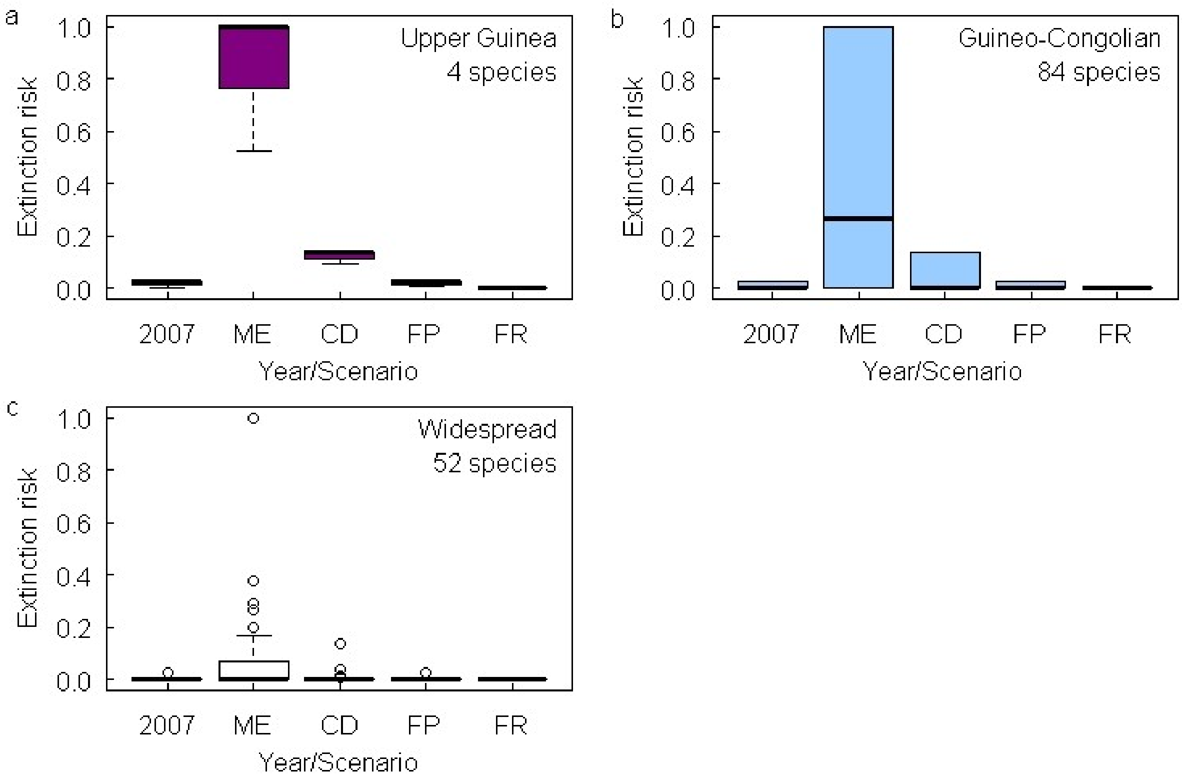

Figure 7.6. Extinction risk in 2007, and in 2047 for four scenarios, of 140 species of birds estimated as present in the province in the absence of agriculture, for (a) Upper Guinea, (b) Guineo-Congolian, and (c) widespread species. Extinction risk in the absence of agriculture was assumed to be zero. Boxplots show median (thick line), interquartile range (boxes), data no more than 1.5 times interquartile range (whiskers) and outliers (circles). Scenario names are abbreviated as in Figure 7.3.

7.4.3 Changes in population size: trees

Far more strongly than for birds, the estimated population sizes of most tree species in all scenarios depended mainly on how much forest there was left (Figure 7.7). Populations of most species were greatest in Forest Recovery. Mosaic Expansion was disastrous for the species of high conservation concern – the Black, Gold and Blue star species. Only five of those species survived until 2047 in Mosaic Expansion, and even those were reduced to tiny populations. All of the species of high conservation concern survived in the other three scenarios, with Forest Recovery having the largest population sizes for all species and Continued Deforestation having the smallest. Some of the exploited "reddish" star (Scarlet, Red and Pink) trees declined, in all scenarios. In Mosaic Expansion, 22 "reddish" star species had disappeared completely by 2047, while none disappeared in Continuing Deforestation or Forest Protection, and two were lost in Forest Recovery. Sixty-one out of 128 Green star species disappeared by 2047 in Mosaic Expansion, none disappeared completely in Continuing Deforestation or Forest Protection, and five were lost in Forest Recovery.

7.4.4 Extinction risk: trees

Patterns of extinction risk of tree species in 2047 in the different scenarios were broadly similar for different guilds (Table 7.5, Figure 7.8). For all guilds, extinction risk was highest in Mosaic Expansion, next highest in Continuing Deforestation, similar to that in 2007 for Forest Protection, and lowest in Forest Recovery. Apart from the four species of climbers and stranglers, mean extinction risk was highest for shade-bearers (84% in Mosaic Expansion). Of the other guilds, pioneers had the lowest extinction risk in most scenarios.

When considering trees by their degree of endemism, there was again a similar pattern: in 2047, species in all categories were at highest extinction risk in Mosaic Expansion, and at lowest risk in Forest Recovery (Table 7.6, Figure 7.9). Upper Guinea and Guinea-wide (Upper & Lower Guinea) species had a higher extinction risk in all scenarios

(87-88% in Mosaic Expansion) than Guineo-Congolian and more widespread species. Comparing extinction risk in 2047 between different star categories, again it was highest in Mosaic Expansion and lowest in Forest Recovery, for all star categories, even Green (Table 7.7, Figure 7.10).

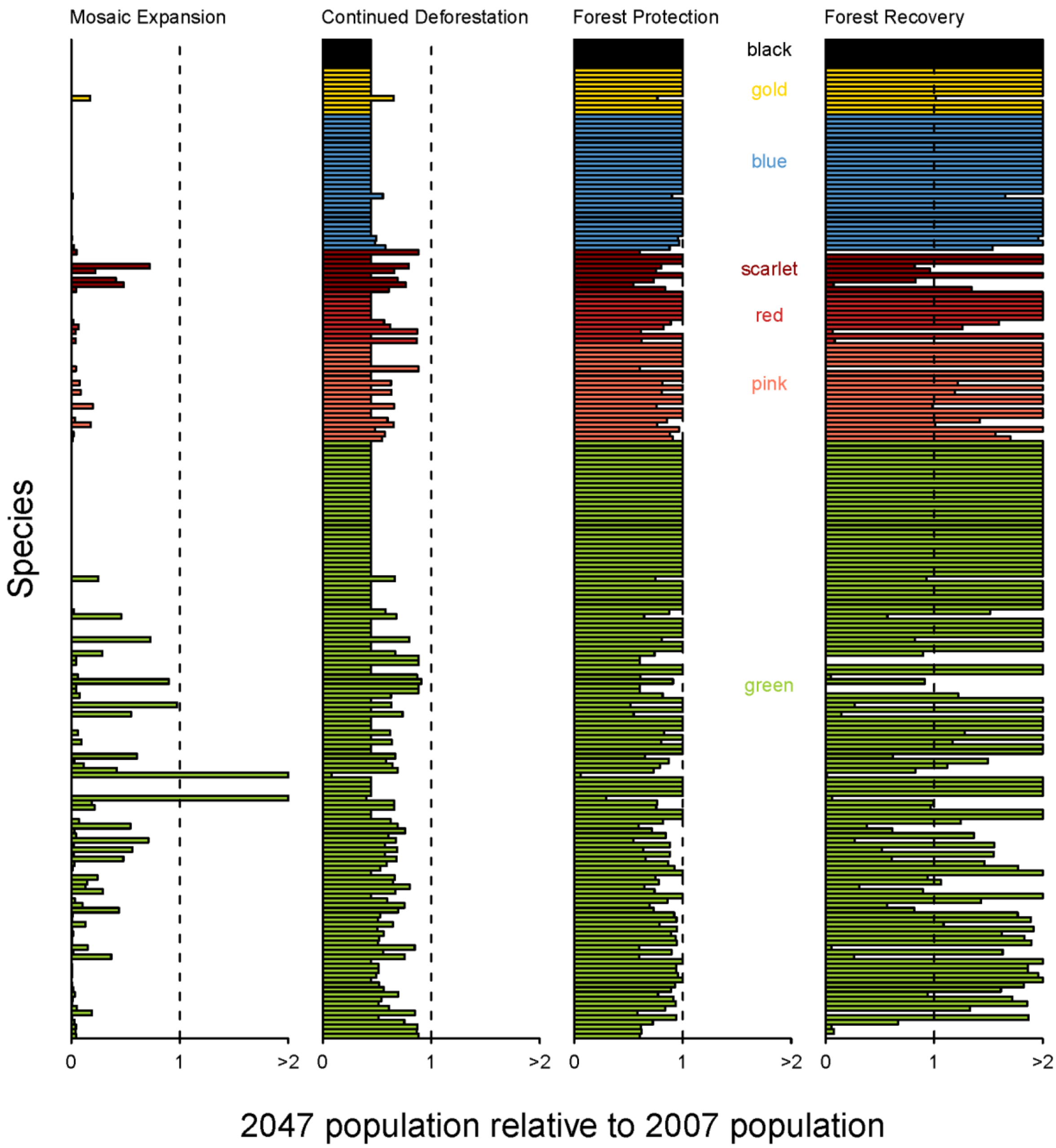

Figure 7.7. Estimated province-wide populations in 2047 of 214 tree species relative to their estimated populations in 2007 based upon a simple land-use model, under four scenarios. Each bar denotes one species. The horizontal extent of each bar indicates the ratio of that species' population in 2047 to that in 2007, with 1 (dashed line) indicating no change. Colours indicate star rating of each species, in descending order of conservation priority, from Black (highest priority) to Green (no conservation concern). Of the 219 species recorded in sample plots, five are excluded (all Weeds): two for which it was not possible to fit a model, and three which did not occur in any of the simple yield compartments used in the scenarios (see Figure 6.5).

Table 7.5. Mean extinction risk, expressed as a percentage, for trees according to their guild. A value of 100% means that all species in a category are committed to extinction; a value of 0% means no species is committed to extinction.

Guild	**2007**	**ME**	**CD**	**FP**	**FR**
Shade-bearer	2%	84%	12%	2%	0%
NPLD	1%	68%	9%	1%	0%
Swamp	2%	79%	11%	2%	0%
Climber/strangler	2%	100%	14%	2%	0%
Pioneer	1%	31%	4%	1%	0%
All species	**1%**	**69%**	**9%**	**2%**	**0%**

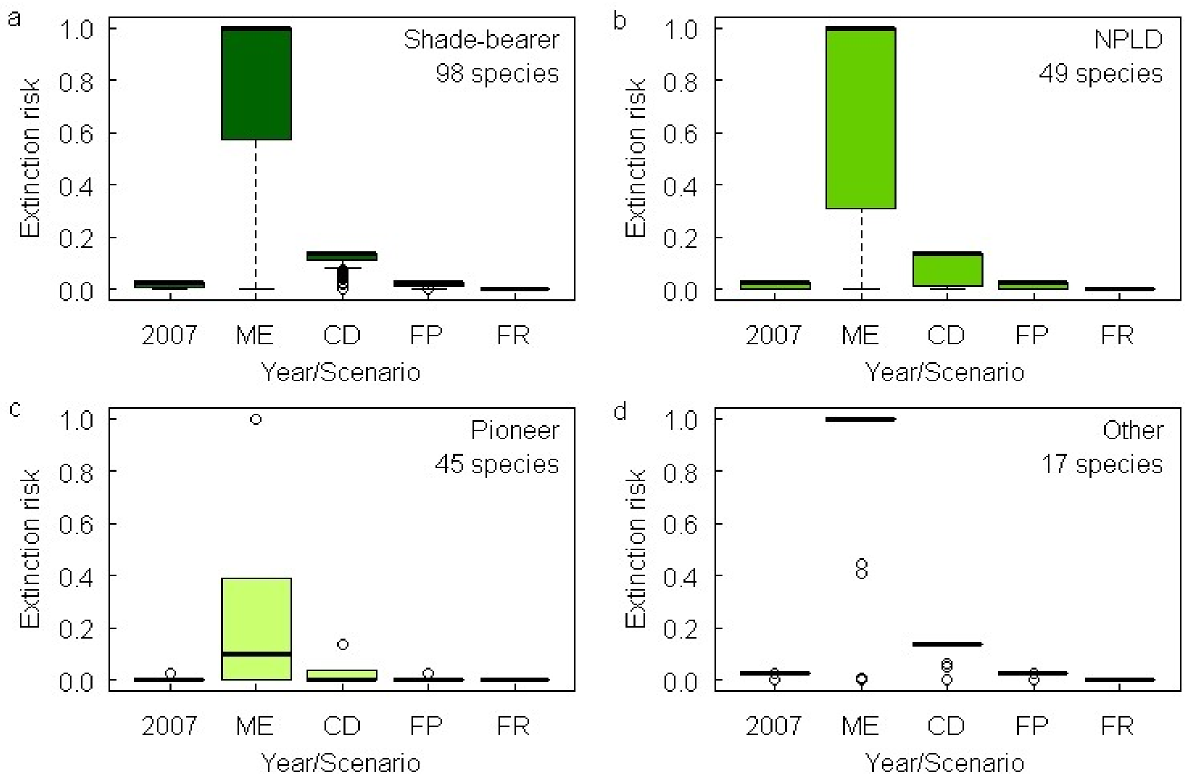

Figure 7.8. Extinction risk in 2007, and in 2047 for four scenarios, of 209 species of trees estimated as present in the province in the absence of agriculture, for members of (a) shade-bearing, (b) NPLD, (c) pioneer, and (d) other guilds (swamp, climbers and stranglers). Extinction risk in the absence of agriculture was assumed to be zero. Boxplots show median (thick line), interquartile range (boxes), data no more than 1.5 times interquartile range (whiskers) and outliers (circles). Scenario names are abbreviated as in Figure 7.3.

Table 7.6. Mean extinction risk, expressed as a percentage, for trees according to their global range (degree of endemism). A value of 100% means that all species in a category are committed to extinction; a value of 0% means no species is committed to extinction. Scenario names are abbreviated as in Figure 7.3.

Global range	**2007**	**ME**	**CD**	**FP**	**FR**
Upper Guinea	2%	87%	12%	2%	0%
Upper & Lower Guinea	2%	88%	12%	2%	0%
Guineo-Congolian	1%	62%	8%	1%	0%
Widespread	1%	33%	4%	1%	0%
All species	**1%**	**69%**	**9%**	**2%**	**0%**

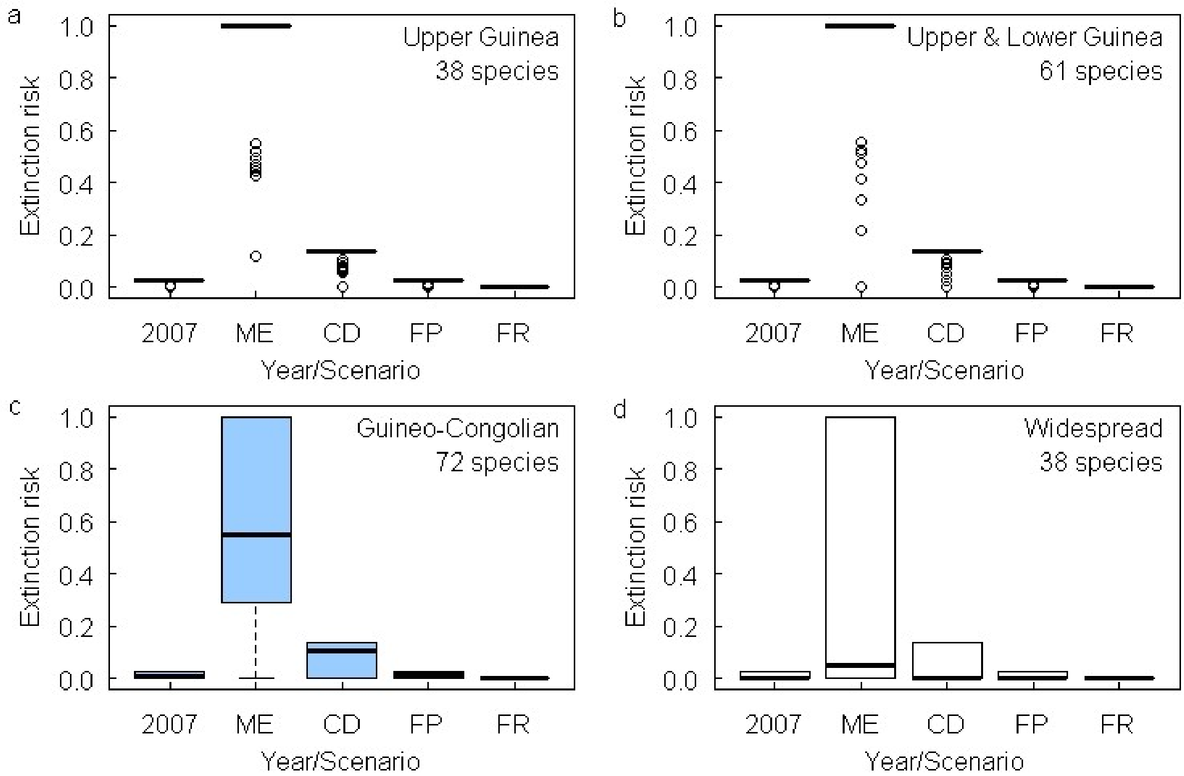

Figure 7.9. Extinction risk in 2007, and in 2047 for four scenarios, of 209 species of trees estimated as present in the province in the absence of agriculture, for (a) Upper Guinea, (b) Upper & Lower Guinea, (c) Guineo-Congolian, and (d) widespread species. Extinction risk in the absence of agriculture was assumed to be zero. Boxplots show median (thick line), interquartile range (boxes), data no more than 1.5 times interquartile range (whiskers) and outliers (circles). Scenario names are abbreviated as in Figure 7.3.

Table 7.7. Mean extinction risk, expressed as a percentage, for trees according to their star rating (conservation priority, where Black is highest priority and Green is of no conservation concern). A value of 100% means that all species in a category are committed to extinction; a value of 0% means no species is committed to extinction. Scenario names are abbreviated as in Figure 7.3.

Star rating	2007	ME	CD	FP	FR
Black	2%	100%	14%	2%	0%
Gold	2%	92%	12%	2%	0%
Blue	2%	93%	13%	2%	0%
Scarlet	1%	43%	5%	1%	0%
Red	2%	70%	9%	2%	0%
Pink	2%	73%	10%	2%	0%
Green	1%	60%	8%	1%	0%
All species	**1%**	**69%**	**9%**	**2%**	**0%**

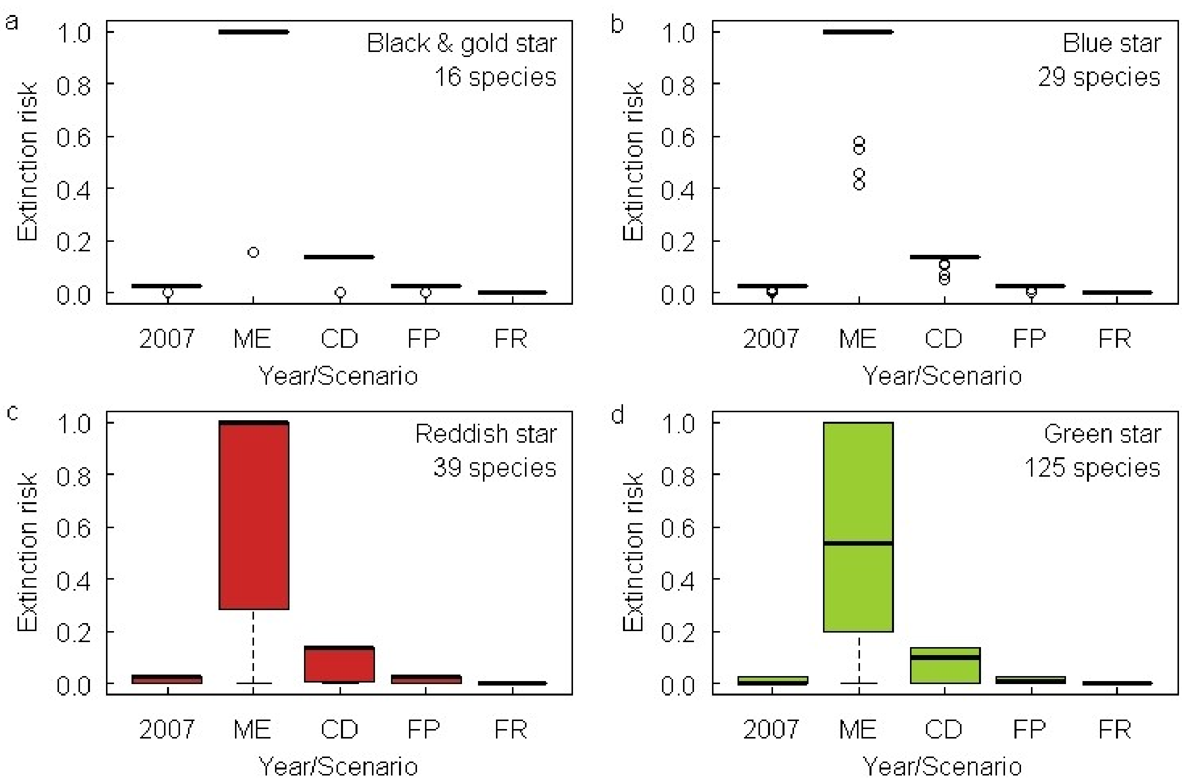

Figure 7.10. Extinction risk in 2007, and in 2047 for four scenarios, of 209 species of trees estimated as present in the province in the absence of agriculture, for (a) Black and Gold star, (b) Blue star, (c) "reddish" star (Scarlet, Red, Pink) and (d) Green star species. Extinction risk in the absence of agriculture was assumed to be zero. Boxplots show median (thick line), interquartile range (boxes), data no more than 1.5 times interquartile range (whiskers) and outliers (circles). Scenario names are abbreviated as in Figure 7.3.

7.5 Discussion

7.5.1 Is such a high production target plausible?

Will Ghana really need to produce 121% more food in 2047 than it did in 2007? This is a difficult question to answer, but there seems little likelihood of population growth slowing more rapidly than it is already projected to, and it is also unreasonable to expect that Ghanaians will be content to settle for a poorer diet than that currently enjoyed by the 1.2 billion people in the "developed" world. My projections that global food supply will have to increase by 57% by 2047 were perhaps even conservative, when compared to projections that the major global cereal producers would have to double their production between the 1990s and 2030 (Alexandratos 1999). The production target was based partly on data from the FAO, which are widely acknowledged as being often unreliable (Ewers et al. 2009). However, these data are the only globally comprehensive information on crop production and food consumption available, and in any case, the scenarios were not intended to make precise predictions, but to illustrate the differences between plausible futures. FAO and UNPD definitions of "developed" and "developing" countries differ slightly (Balmford et al. 2005). However, because the scenarios were mainly based on projected demand within Ghana rather than globally, this had virtually no effect (~0.1%) on the production target.

As people get wealthier, they tend to eat more meat (Myers & Kent 2003, Fa et al. in press). My calculations assume that crops will be eaten directly by people, but if they are instead used to feed livestock, which are then eaten by people, an even greater quantity of crops will be required, because the conversion from crops to meat is inefficient (Rosegrant et al. 1999, Wirsenius 2003, Marlow et al. 2009). Further pressure to produce more agricultural commodities is coming from rapidly growing markets for biofuels (Corley 2009), and newly emerging markets for other non-food crop-based products such as biopolymers (Beilen & Poirier 2008). Already, forest reserves in the drier north of Ghana have been converted to *Jatropha* plantations for biofuel (Dowsett-Lemaire & Dowsett

2009b). Given these additional pressures, it seems likely that the production target estimated here is not only plausible, but probably conservative.

A second question is: will all of the additional food production have to take place in Ghana? Its national production target could be reduced considerably if Ghana were to increase its reliance on imports. There are several reasons why this is unlikely to occur or, if it occurred, would not benefit biodiversity more widely. First, crop yields in “developing” countries, especially in Africa, are typically far below their potential (Tittonell et al. 2008); there is less scope to increase yields in the developed world, where optimal levels of nutrient application have been met, and frequently exceeded. So, as well as providing most of the new markets for agricultural products over the coming decades, developing countries will also likely to have to provide much of the increase in supply, placing pressure on the places most rich in biodiversity (Scharlemann et al. 2004). Second, there is a question of social justice. Ghana, like other countries in which agriculture makes up a major part of the economy, will be hoping to generate its fair share of the wealth from growing global markets for agricultural products. Becoming more reliant on subsidised imports from developed countries would not help it to develop a viable domestic economy. Ghana might not in any case be able to afford to rely more on imports without expanding farmland to produce more export crops, because export crops are a major source of foreign revenue (Government of Ghana 2005). Finally, there is no guarantee that the imports would not come from agricultural expansion into areas important for biodiversity (e.g., Butler & Laurance 2009). For example, reducing pressure on Ghana’s forests by wholesale conversion in the Congo would not be a desirable solution from the perspective of biodiversity conservation.

However, one could argue that high value crops, such as exotic fruits and vegetables, and raw materials for pharmaceuticals, food additives and cosmetics could produce more income from less land and could therefore be a more promising option than staple food crop expansion for a country such as Ghana to increase its revenue from agriculture without increasing its need for land. Crops such as these do have economic merit at least, and some are already being grown successfully in Ghana (e.g., pineapples, chilli peppers). However, these crops do not help to supply demand for staple foods or provide food security for the nation, and while they might provide incomes for some farmers, staple food crops still need to be grown somewhere. Also, the market value of what are now high value crops is liable to fluctuate, as Ghana discovered to its cost in the case of cocoa in the 1960s. Demand, and therefore markets, for staple crops is more reliable. As already discussed, if Ghana chooses to rely on imports of staple food crops, the net effect is leakage: yields will have to be increased in other countries, or forest cleared, so that production targets (food demand) continue to be met. High value crops then, at best only shift the problem elsewhere. This might be useful if focused in areas of exceptionally high biodiversity, but there is also the risk that promoting a high value crop in such a situation might backfire and increase conversion, as discussed further in Chapter 8.

7.5.2 Wildlife-friendly farming vs. land sparing

The results of this chapter indicate that, for a given production target, a land-use strategy based strongly on wildlife-friendly farming (Mosaic Expansion) has very little to commend it from the perspective of bird or tree conservation. An intermediate strategy (Continuing Deforestation) is considerably better, but for virtually all species, the scenarios based on land sparing (Forest Protection and Forest Recovery), are best. This was true whether assessed using direct changes in species' populations or increases in their extinction risk. One interesting and unanticipated observation from these scenarios is that in order to maintain a large area of wildlife-friendly farmland, it is necessary to "spare" it by increasing yields elsewhere: wildlife-friendly farming delivered through the means of land sparing!

The Forest Recovery scenario is probably not a plausible model for Ghana's forests in the immediate future. It does, however, provide some indication of what other tropical forest countries, e.g., Liberia and Congo Basin nations, still have to lose. It also illustrates the biodiversity gains that might be made by reforestation in Ghana in the future if high-yield farming reduces the need for agricultural land, although the populations of forest species would take much longer to recover than I have assumed for convenient comparison here (Dunn 2004). If edge effects and spillover effects are important in Ghana's fragmented forests, as is likely, the advantages of Forest Recovery and the disadvantages of Mosaic Expansion would likely be even greater than those modelled.

Because I chose a very conservative baseline for estimating ancient population size (25% of what populations would be if the entire province was forest), all of the scenarios might provide overly optimistic projections for 2047. The Forest Recovery scenario implies that more than half of the province would be farmed at high yield, with oil palm or other crops. This is not an appealing prospect, but far less appealing is the prospect of the final fragmentation and erosion of the last of Ghana's forests in Mosaic Expansion. The distinction between Nigel Collar's two opposing visions of the future, in the quote opening this chapter, probably has as much to do with different production targets as it has to do with different land-use strategies. Nevertheless, land-use strategy is clearly important: mean extinction risk was zero in 2047 in Forest Recovery, and only 1-2% in Forest Protection, while it was 35% overall for birds and 69% for trees in Mosaic Expansion. These numbers give an indication of the number of species likely to be committed to extinction unless forest loss is later reversed. So, while a lower production target would result in fewer negative impacts on bird and tree populations in any strategy, the choice of strategy does make a big difference.

7.5.3 Why estimate extinction risk?

Estimates of extinction risk are inevitably subject to considerable uncertainty. Nevertheless, they are useful, because they provide an estimate of the probability of long-term persistence of a species – the inverse of extinction risk – which has a curvilinear relationship with population size, decreasing increasingly rapidly with declining population size (Butchart et al. 2004). While the contributions of individual species to some ecosystem functions and services might scale linearly with population size (e.g., timber from a tree species), their contributions to others are probably dependent most crucially simply on whether a viable population of the species is present or not (e.g., redundancy, such that one species can maintain an ecosystem function if another species declines; Elmqvist et al. 2003). Metrics of extinction risk can be interpreted as measures of the disproportionate loss of unique genetic information and of ecosystem function that occurs when species decline to very low population levels or when they go extinct. Unlike simple measures of population changes, extinction risk metrics do not suffer from the undesirable property that the positive effect of an increase in one species is equivalent to the negative effect of a decline by the same proportion in another.

I used the empirical species-area relationship (SAR) to convert population changes to estimates of extinction risk. Population viability analysis (PVA) would be a preferable approach, but requires detailed demographic information about each species (Fieberg & Ellner 2000), which is not available for diverse tropical communities. An approach similar to that used by the IUCN Red List could also have been used (Mace et al. 2008). However, Red List extinction risk categories based on population decline cannot be directly translated into quantitative estimates of extinction risk, are not referenced to a historical baseline, and are designed to assess extinction risk to global rather than regional populations (Butchart et al. 2004, Brooke 2009). The species-area relationship was not developed as a way of estimating individual species' extinction probabilities, and there are as yet few empirical tests of its suitability for that purpose. It is actually assumed to represent the outcome of a dynamic equilibrium between processes that add species to an inventory (colonisation and speciation) and processes that delete them (extirpation and extinction). It has been used successfully to predict the impacts of deforestation in defined regions on the number of bird extinctions (Pimm & Askins 1995) and the number of bird species threatened with extinction (Brooks & Balmford 1996, Brooks et al. 1997, Brooks et al. 1999). However, the fact that the SAR can predict community-wide patterns of extinction does not necessarily imply that it is appropriate for predicting the extinction probability of individual species (Buckley & Roughgarden 2004). An even more conservative approach to estimating extinction risk from land-use change would be to assume that a species is at risk only if it loses all suitable habitat, but this would clearly be overly conservative (Hubbell et al. 2008).

Despite those caveats, there are at least three reasons to believe that my estimates of extinction probability could be conservative. (1) I used a low value of z, the SAR exponent. This was in recognition that mainland forests are not as isolated from other forests as, say, oceanic islands are from each other, and declining species could be “rescued” from extirpation by dispersal (Brooks et al. 1997). (2) I used a conservative baseline value for the ancient population sizes of each species, in recognition that they have persisted through thousands of years of natural forest fragmentation. (3) My projections do not include the impacts of threatening processes other than land-use change on species, such as the impacts of invasive species or over-exploitation. These are likely to have disproportionately large effects on forest species as forests dwindle and become fragmented (Laurance et al. 2002). Hence, forest extent reduction might have larger effects than expected from the SAR because many empirically-observed SAR patterns were established before the effects of humans were large. Climate change is likely to have a profound impact on West African forests over timescales of decades and centuries (Stager 2001). During past climatic fluctuations, species were able to shift their ranges, impeded only by natural barriers such as coastlines and mountain ranges. The fragmentation and physical disruption of natural habitats by human agriculture is likely to reduce the chances of species making such range shifts in the future. Habitat fragmentation has further edge effects, although edge:area ratios and the average degree of isolation of forests in Ghana could either increase or decrease with further deforestation, depending on whether small isolated fragments are converted, or whether the remaining larger blocks of forest are subdivided (Fahrig 2003).

7.5.4 Other caveats and uncertainties

Any attempt to develop scenarios for so distant a date as 2047 is vulnerable to criticisms. Some of these are generic criticisms of the trade-off model, such as the exclusion of some negative externalities, omission of other ecosystem services such as bushmeat and carbon storage, simplification to a land-use compartment model (forest, farm mosaic, plantation), and exclusion of spatial effects such as edge effects and dispersal. I discuss those at more length in the final chapter of this thesis. Others are specific criticisms of the assumptions used in the scenarios, which I discuss below.

A number of uncertainties could affect my projections of future supply and demand. Farmers might switch to growing different crops, which might be better or worse at supporting native species. Agricultural technologies such as improved varieties, better integrated pest management and appropriate use of fertiliser might enhance crop productivity with minimal impact on biodiversity (Pretty et al. 2006). There might be constraints on the uptake of some technologies, for example as phosphate fertilisers and fossil fuels become scarcer and more expensive (Youngquist 1999, Cordell et al. 2009). Climate change is likely to have a large impact on spatial and seasonal rainfall patterns, potentially compromising food production in large parts of Africa (Barrios et al. 2008). Climate models suggest that there will be large changes in growing season temperature in Ghana by 2050, and that maize yields will fall in some parts of southwest Ghana, but increase in other parts, by 2055 (Jones & Thornton 2003, Burke et al. 2009). I did not have the data on which to base assumptions about the influence of changing crops, new agricultural practices or shifting climates, but none of these things is likely to alter my main conclusion that the most effective way of conserving native biodiversity in southwest Ghana is to protect natural habitat, even if that necessitates increasing yields on farmland so that production targets are met.

Another potential criticism is that Ghanaians would find the total conversion to agricultural land of their remaining forests politically and socially unacceptable. The boundaries of forest reserves in Ghana have been remarkably stable since they were first established in the first half of the twentieth century, despite large increases in population since that time, and loss of virtually all forest outside reserves (Hawthorne & Abu-Juam 1995). Forests play an important role in the economy and culture of Ghana, and their importance in providing timber, bushmeat and a home for traditional deities is widely appreciated. I do not presume that complete conversion by 2047 is very likely, but the Mosaic Expansion scenario is useful in highlighting that for this not to happen, yields will have to increase even faster than they have done in recent years, and/or the food that Ghana will require will have to come from somewhere else. A scenario of large-scale conversion of forests to agricultural land is unfortunately not entirely implausible. Forest reserves are increasingly being converted to tree plantations of fast-growing exotics such as *Gmelina arborea* and *Cedrela odorata* (essentially timber crops) and *taungya* systems (agroforestry systems where farmers grow food crops interspersed with timber trees). There is also ongoing legal and illegal encroachment in some reserves for farming of cocoa and other crops. In some of the more degraded parts of forest reserves, where timber trees have been depleted, fire is frequent, and alien invasive shrubs such as *Chromolaena odorata* are well established, "conversion … to plantations of exotics seems the only realistic, if final, solution to their degraded state" (Hawthorne 1996, p. 142). Ghana's forests will increasingly face that grim prospect, unless efforts are redoubled to protect them from fire, excessive logging, and agricultural encroachment.

7.6 Conclusion

Despite some caveats, the results of this chapter suggest very strongly that, given a plausible production target for 2047, a land-use strategy that minimises forest conversion will result in higher populations of most bird and tree species than a strategy that focuses on wildlife-friendly farming. This was true not only for endemics and habitat specialists, but for trees of all kinds, and for all birds except for a few non-forest species, and species not expected to have occurred in the province in the absence of agriculture. If the development of agriculture in Ghana is to keep pace with population growth and changing diets, it is likely to be best, from a conservation perspective, for the country to focus on yield-enhancing technologies and innovations, alongside effective forest protection, rather than attempting to conserve the biodiversity of traditional agroforestry systems. A lower production target would reduce the future impact of food production on wild species, but unless it resulted from lower than expected population growth or per capita consumption, it would simply shift the problem elsewhere.

Chapter 8

Discussion and conclusions

Immature oil palms at Benso Oil Palm Plantation, with forest in background

‘Economic pressures will always be in the direction of intensifying use… At what point does one say, “Stop! Enough!”? Sustainable use admits of no line in the sand.’

John Terborgh (1999, p. 139)

‘Juggernauts [such as the world economy] do not respect lines in the sand.’

Bill Adams (2004, quoted by Brockington et al. 2008, p. 17)

8 Discussion

In this final chapter, I summarise my main findings, describe how the modelling approach I use could be refined in the future, discuss the policy implications of the wildlife-friendly farming and land sparing concepts, and outline what I see as the four main requirements for successful land sparing in practice.

8.1 Summary of findings

The analyses reported in this thesis provide evidence that there is a trade-off between the biodiversity value and yields of farmed land in southwest Ghana. Structurally complex, traditional agroforestry landscapes, with abundant native canopy trees, small remnant forest patches and regenerating vegetation on fallow land produced only around 15% as much food energy per hectare as the highest-yielding plantation in the study. These complex landscapes supported higher species richness of birds and trees than farmed land that produced higher yields (whether measured using food energy or net profit). Species richness of birds was similar to that in forest, and included many species shared with forest. However, many of those were present at much lower densities than in forest, and would therefore have higher overall populations in a hypothetical province with high-yielding agriculture than with low-yielding agriculture, for a given production target.

There was considerable turnover of bird species along the gradient of yield from forest to high-yielding farmland, with habitat generalists and species characteristic of non-forest biomes, both usually with large geographical ranges, replacing forest-dependent birds with smaller global ranges. The species least able to persist even in the most structurally complex, low-yielding farmed landscapes tended to be those which were naturally specialised to forest habitat, had small global ranges, and were already of conservation concern. In the case of trees, there was less species turnover along the yield gradient, but fewer species in the farm mosaic, and even many of the common, widespread species were heavily dependent on forest.

Future scenarios in which food production targets are met mainly by increasing yields on farmland resulted in a smaller proportion of species committed to extinction and higher predicted populations of most species than scenarios based on the expansion of lower-yielding farmland into forest. Interestingly, large areas of the lowest-yielding wildlife-friendly farmland were only maintained in scenarios based on land sparing, a reminder that the maintenance of wildlife-friendly farming systems is likely to depend on yield increases elsewhere. Extinction risk for all groupings of birds and trees was highest in the future province with the lowest-yielding farming scenario, and lowest in those with high-yielding farming combined with habitat protection.

8.2 Towards a more realistic model of the trade-off

8.2.1 Pollution and other negative externalities

An important weakness of the simple model used here to forecast species' overall population sizes is that it ignores negative effects of agriculture on unfarmed habitats and other areas away from the farmed landscape Green et al. 2005). This is particularly relevant to some forms of high-yielding farming which rely heavily on synthetic fertilisers and pesticides (Vandermeer & Perfecto 2005, Matson & Vitousek 2006, Fischer et al. 2008, Perfecto & Vandermeer 2008; Pretty 2008). These can impose a range of negative effects externally. Fertiliser run-off from farmland contributes to the formation of "dead zones" in shallow coastal waters (Diaz & Rosenberg 2008). The fossil fuels and fertilisers used in many high-yield farming systems produce greenhouse gases including carbon dioxide and nitrous oxide, which contribute to climate change (Crutzen et al. 2008), and thereby cause negative effects on species' population densities in natural habitats (as well as on human well-being). Pesticides can cause direct mortality of organisms on, near and far from farmland (Daly et al. 2007, Rohr et al. 2008). It is important to realise that what is relevant to the adequacy of the trade-off model of Green et al. (2005) is the magnitude of the impacts of farming on population density of wild species away from the farmland itself. Negative impacts of farming practice, including fertilisers and pesticides, on species' population densities on farmland are already handled correctly by the model.

Not all high-yielding systems involve the use of agrochemicals, and low-yielding farming can also have high externalities when measured per unit of output (e.g., erosion of peatlands by subsidised and otherwise unprofitable sheep farming in the UK). There are ways of reducing the negative externalities of high-yield farming, using innovations such as integrated pest management, integrated nutrient management (e.g., with biochar, composting, N-fixing cover crops and microfertilisation), banning the most harmful pesticides, using pest-resistant crop varieties, no-till methods, replacing annual crops with perennials, artificial wetlands to capture nutrient runoff and more efficient use of water (Scherr & McNeely 2007, Lal 2008, Pretty 2008). There is considerable scope for increasing fertiliser use in sub-Saharan Africa without negative impacts on freshwater systems (Vanlauwe & Giller 2006). More fundamental changes, such as substituting labour for fossil fuel inputs, for example, will depend on economic and social contexts (Rosset 1997). Large-scale farming, while presenting an enormous threat to biodiversity, also offers important opportunities for conservationists to have an influence: changing the policies of a few corporations can result in improved management across vast areas of the tropics, while changing the practices of millions of peasant farmers is more difficult (Butler & Laurance 2008).

Quantifying the distant effects of pollutants in aquatic systems and unfarmed habitats is difficult but it is potentially possible, and could be used to produce modified versions of the projections of the size of species' overall populations and extinction risk in southwest Ghana to replace and supplement those I presented in Chapter 7. Such an analysis, whilst worthwhile, would probably not change my conclusions. Of the major crops, it is cocoa rather than oil palm which requires heavy pesticide use. The highest-yielding oil palm plantation in this study used integrated pest and soil fertility management, and has converted much of its area over a period of years to certified organic production (E. Wiafe, pers. comm.)

8.2.2 Edge effects

A special case of a negative external effect of farming on natural habitats is the occurrence of edge effects in areas adjacent to converted lands. Edge effects are most severe within a few hundred metres of the habitat edge, and decline with distance from it (Laurance et al. 1997, Ewers & Didham 2008). Low-yielding farming systems occupy a greater proportion of the province for any given production target, and therefore are likely to expose a greater proportion of natural habitat to edge effects such as increased incidence of fire, hunting and invasion by non-native species because of the higher average length of edge per unit area of natural habitat. However, while edge effects of low-yielding farming systems are likely to affect a greater length of edge than those of many high-yielding systems, the effects of the latter per unit length of edge may be more severe (Laurance et al. 2004).

There are several requirements for modelling edge effects, in the context of evaluating the biodiversity value of different land-use strategies. (1) Empirical measurements of the penetration distance and effects on population densities of different sorts of edges. (2) Spatially explicit land-use models. (3) Spatially-explicit projections of future land-use change. If those requirements are fulfilled, it would become possible to evaluate, in a spatially-explicit way, the impact on populations of wild species of different plausible landscape configurations. This could include the evaluation of “hard” vs. “soft” edges, including buffer zones of wildlife-friendly farmland between high-yield farmland and natural habitat. It would also rejuvenate the SLOSS (Single Large Or Several Small) debate with a new twist: the integration of information on opportunity cost, measured in terms of yield (Groeneveld 2005). Previous debate has focused on whether more species will be able to maintain their populations over time in fewer, large patches of habitat, or in a greater number of smaller patches, using area as an implicit measure of cost (Ovaskainen 2002). The protection of fewer, larger habitat patches will tend to reduce the extinction risk within fragments, and the influence of edge effects, but a network of many smaller fragments could represent more species, and minimise extinction risk for metapopulations. Matrix quality can have a considerable impact on adjacent habitats (Nascimento et al. 2006). However, that need not imply that the most effective conservation strategy is matrix management. By integrating information about how species' populations near edges are influenced to different degrees by matrix quality, one could investigate whether it might be more effective (for a given opportunity cost, measured as yield foregone) to minimise the exposure of habitat to edge effects by protecting large intact blocks of habitat, or to promote activities that make matrix habitats more benign.

8.2.3 Dispersal

Fragmented metapopulations will only be able to persist in the long term if dispersal is possible between fragments. An argument in favour of wildlife-friendly farming is that it could provide a benign matrix that allows organisms to disperse between habitat patches (Vandermeer & Perfecto 2007, Perfecto & Vandermeer 2008). It is the case that some low-yielding systems are much more benign for a range of species than some high-yielding systems, and can be more permeable to dispersing organisms (Ewers & Didham 2006). However, the permeability of a given matrix habitat configuration varies considerably among species, and interior specialists are less likely to be able to penetrate even apparently benign matrix habitats (Ries & Debinski 2001). Increasing the area of core habitat, or of large fragments as "stepping stones", could well benefit the populations and even dispersal probabilities of these most vulnerable species more than any modifications to the matrix

(Falcy & Estades 2007). Wildlife-friendly interventions to improve or maintain the quality of the matrix for dispersing individuals will come at a cost to the area of natural habitat if they reduce yields. Matrix quality is likely to be important for the dispersal of many species, but that should not obscure the fact that it is even more important for those species to have sufficient habitat to disperse to, and persist in.

The prospects for dispersal could affect estimates of extinction risk based simply on changes in land cover. There are likely to be species still present in Ghanaian forests which are committed to regional extinction because of the fragmentation and isolation of its forests. This is even more likely to apply to species currently present at low densities in the farmed landscape: the fact that they can disperse through it and are occasionally recorded there does not mean that they are capable of maintaining populations there (Sridhar 2009). Wildlife-friendly farming landscapes seem likely to be carrying a very high extinction debt, unless population density is high on farmland or farmland populations are constantly replenished from nearby natural habitats. Extinction debt is likely to be minimised in large relatively intact areas, and to be greatest in highly modified landscapes with tiny habitat patches (Fischer & Lindenmayer 2007). Whether land sparing is a better option than wildlife-friendly farming depends on whether the overall extinction risk to a species is reduced more by the protection of large intact habitat patches than it is increased by the deterioration of matrix quality. As with edge effects, future spatially explicit land-use models that incorporate dispersal dynamics and other aspects of metapopulation dynamics could provide estimates of the extent to which this will affect species' populations and their risks of extinction.

8.2.4 Other benefits and costs

In this thesis, I have for practical reasons focused on food energy and net profit, to the exclusion of the many other goods and services provided by tropical agro-ecosystems and forests (Batagoda et al. 2000). These include direct, local and regional benefits from timber, bushmeat, non-timber forest products (NTFPs), and also ecosystem services that provide benefits to people indirectly and more widely, such as carbon storage and water regulation (Fisher et al. 2009).

Clearly, it is of considerable interest to understand the extent to which plausible future landscapes will continue to provide these services and benefits. Based on present knowledge, it would be possible to estimate the magnitude of some of these services and benefits, given different land-use configurations (e.g., carbon storage, Wade et al. in prep.). Assessments of the value of different land uses could then be integrated with information about yields and species' densities to predict the future benefits likely to be provided by different plausible landscape configurations, as well as species' populations. Evaluating how best to reconcile trade-offs between the provision of various different benefits as well as minimising species' extinction risk would likely be more complicated and potentially susceptible to error when more benefits are considered (Tenerelli & Monteleone 2008). Currencies other than food energy and profit might need to be considered, such as energy use or water use. However, this is precisely the sort of complex information on multiple objectives required by decision-makers, so that they can understand the magnitude of any trade-offs and attempt to balance different objectives.

One objective that is increasingly of interest is ecosystem resilience (Fischer et al. 2008, Fischer et al. 2009). Contrary to assumptions that wildlife-friendly, low-yielding landscapes will be more resilient, my results suggest that for a given production target, a landscape based on land sparing would be more ecologically resilient. If land sparing allows more species and greater cover of natural vegetation to persist, with larger populations and a lower risk of extinction, then the ecosystem is likely to be less susceptible to marked changes due to loss of keystone and other influential species (Chapter 7). However, this resilience at a large scale might come at a cost to the resilience of crop production at finer scales. If land sparing is achieved by the use of a restricted range of crop species or varieties, for example, there might be an increased risk of catastrophic pest outbreaks and crop failure, and/or increased costs of pest control (Landis et al. 2008). Such risks might be decreased by using elements of "eco-agriculture" thinking (Scherr & McNeely 2007), but with the emphasis on maintaining high yields in the long term, rather than fooling ourselves that we can combine high yields and effective conservation of wild species on the same land.

In addition to using yield, profit and similar currencies as measures of opportunity cost, assessments of the trade-offs between different conservation strategies would be improved by the incorporation of (1) other costs, such as the direct management costs of maintaining wildlife-friendly farming interventions or protecting habitats, and (2) the chances of interventions succeeding (Balmford et al. 2003, Chan & Daily 2008). The latter could be based on past experience of similar interventions, and could include estimates of likely rebound effects (discussed in section 8.3.2). They would also be improved by considering spatial variation in the suitability of landscapes to provide various potential values, including spatial variation in their suitability for different species. Southwest Ghana conveniently has minimal variation in topography and agricultural suitability across a large area, but even there, there are likely to be some opportunities at a fine scale to conserve habitats at low opportunity cost (e.g., on steep-sided hills or poor soils).

8.3 Wildlife-friendly farming and land sparing in practice

8.3.1 Strategies are constrained to start from current land use

No landscape is a blank slate, and there is little advantage to designing "optimal" land-use configurations without taking into account current land use (Fischer et al. 2008). One reason for this is that proposed solutions need to be capable of implementation and to take into account social and political realities. Another is that species' populations do not respond immediately to land-use change. The full biotic recovery of an abandoned agricultural area by regeneration of native habitats can take centuries (Dunn 2004). Because it is harder to restore populations than to maintain them in the first place, conservation strategies should focus on how they can maintain the populations of as many species as possible, subject to the constraints of cost and limited resources. A critical question then is, at what point in the land-use cascade should conservationists attempt to have an influence (Terborgh & Van Schaik 1996)? Will conservation efforts be more effective if they focus on preventing conversion of low-yielding, wildlife-friendly farmland to high-yielding farmland, or on preventing conversion of forest to farmland? Given limited resources and leakage effects, an emphasis on one is likely to compromise the other (section 2.1.2). The results of this thesis suggest that conservation efforts in southwest Ghana will be more effective at maintaining species' populations if they focus on protecting or even expanding existing forests, even if a consequence is that existing low-yielding, wildlife-friendly farmland is increasingly converted to wildlife-poor but higher-yielding land uses so that production targets are met.

8.3.2 The problem of rebounds

In this thesis, I have focused mainly on the question of whether or not landscapes based on land sparing are a desirable objective from a conservation perspective in the context of southwest Ghana. Having confirmed that they appear to be so, a further, and quite distinct question is: will high-yielding farming spare natural habitats for conservation (Manning et al. 2006, Jackson et al. 2007, Vandermeer & Perfecto 2007, Harvey et al. 2008, Perfecto & Vandermeer 2008)? The answer to this deceptively simple question is complex. Evidence suggests that at local scales, innovations that increase the productivity of tropical agriculture can either increase or decrease the rate of conversion of natural habitats, while at larger scales (at the level of nation states), there is a weak tendency for increases in yields to be associated with reduced expansion of agricultural land and lower rates of loss of natural forests (Barbier & Burgess 1997, Angelsen & Kaimowitz 2001, Ewers et al. 2009). There are no reports of increases in crop yield resulting in perfect land sparing in practice, where perfection consists of a given proportional increase in yield resulting a decrease by the same proportion in per capita area of land converted from natural habitat to agriculture. Explanations for an increase in conversion or less than perfect land sparing with increasing yield include the following: (1) If high-yield farming is more profitable, conversion becomes more economically attractive, and might be feasible in places where previously the costs exceeded the potential benefits. (2) If innovations that increase yields also free up labour, by mechanisation for example, they might allow labour-constrained farmers to more rapidly expand their farms, as land-clearance is a labour-intensive activity for peasant farmers. (3) If high-yield farming increases demand, for example by permitting the population of an area to increase, then the rate of habitat conversion, at least locally, is unlikely to slow. (4) If high-yield farming is encouraged by subsidies, it might continue to expand even when prices would otherwise have fallen because of oversupply (Angelsen & Kaimowitz 1998, Angelsen & Kaimowitz 2001, Matson & Vitousek 2006, Ewers et al. 2009). These are all examples of the rebound effect: increases in land-use efficiency do not necessarily reduce the amount of land used, and can even “backfire” and increase it (Alcott 2005, Ewers & Rodrigues 2008, Polimeni et al. 2008). Another risk is that habitats “spared” by increasing yields will be used for other purposes than food production or wildlife conservation (Ewers et al. 2009).

However, there are cases where conversion has been slowed down with the introduction of yield-enhancing technologies, for reasons which are essentially the reverse of the above: (1) If new technologies are more appropriate for established farmland than for conversion frontiers, farmers might be attracted to consolidate production on the best existing land rather than expanding. An example might include cases where access to irrigation infrastructure is important. (2) If high-yield farming is labour-intensive, it might draw labourers away from frontiers of habitat conversion. (3) If demand for food and other agricultural products is relatively inelastic, as is the case with staples, and is not distorted by subsidies, high-yield farming reduces the area required to supply it (Angelsen & Kaimowitz 2001, Wunder 2004, Ewers et al. 2009). Because innovations that reduce labour demands and increase profits are more likely to be widely adopted by farmers than those which are labour and capital intensive, it seems likely that increased habitat conversion will be the most likely local consequence of innovations that increase yield. However, because even many peasant farmers are now part of the global economy, increases in production in one part of the world are likely to reduce prices and curtail the need for expansion in other parts of the world. What is clear is that relying on yield increases alone to spare natural habitats is not sufficient to ensure that land sparing occurs.

Rebound effects are an issue for both wildlife-friendly farming and land sparing. With both strategies, there is a likelihood that even successful local interventions will have negative impacts on species' populations elsewhere, through leakage of demand or from the various effects described above. These effects can also be manifested in other ways. If they help green a company's credentials, commitments to practise wildlife-friendly farming (or land sparing via biodiversity offsetting; Burgin 2008, Walker et al. 2009) could give it a "license" to convert habitats it might otherwise have been excluded from: a problem that complicates efforts to certify responsible palm oil production (Struebig et al. in press). Because resources for conservation are limited, pursuing relatively ineffective strategies will distract resources and attention from potentially more useful and deserving activities (Phalan et al. 2009).

Specific interventions will be needed to control rebound effects, e.g., policies that make increasing yields on existing land more economically attractive, and converting new land less so. Such interventions could include technologies that are labour or capital intensive, in places distant from frontiers of habitat conversion, which can draw people away from those frontiers, combined with disincentives to convert habitats, such as stronger enforcement of environmental laws (Van Schaik & Kramer 1997). Policies that prevent the degradation of agricultural land and which encourage restoration of degraded agricultural land are likely to be important in coming decades in reducing pressure to convert natural habitats (Fitzherbert et al. 2008, Gibbs et al. 2008). Another way to make conversion less economically attractive is to increase the price of land, which is what effective protected areas do by reducing the amount of land which is available for conversion. It is well established that farmer innovation is promoted by land scarcity (Boserup 1965). A land reservation strategy should focus first on the most important areas for biodiversity, because if acquiring reserves pushes up land prices, it will increase the cost of acquiring subsequent reserves (Armsworth et al. 2006).

8.3.3 Permanence

The benefits of many wildlife-friendly farming interventions offer little guarantee of being maintained in the long term (decades). As I discussed in Chapter 6, the diversity and populations of trees in diverse agroforestry systems will almost certainly decay over time, as the extinction debt is paid and species composition shifts from slow-growing shade-bearers to fast-growing pioneers and exotics. The issue of permanence also applies to interventions such as set-aside (Herkert 2009). The recent abolition of compulsory set-aside in the European Union as part of the Common Agriculture Policy (CAP) "health check" removed one of the most important wildlife-friendly initiatives in European farmland, albeit mainly for a small number of farmland birds (DEFRA 2009). A landscape pattern based on land sparing, whereby areas of natural habitat are clearly defined and designated for conservation, is less vulnerable to vagaries of markets and fashions, and offers a clearer and more permanent way of "drawing a line in the sand" (Terborgh 1999). In tropical forest countries, there are still large areas of natural forest and other habitats where this is possible. No form of nature conservation will succeed in the long term without appropriate regulation, whether that comes top-down from state governments or bottom-up from local communities. I discuss how the quality of governance should help to inform conservation strategies in section 8.4.4.

8.3.4 Social issues

In this thesis, I have focused mainly on questions of biology and economics, but if my findings are to have any practical relevance, consideration of social aspects is essential (Adams 2007). Establishment of large plantations or reforestation projects by displacing people from their land, or land to which they have customary rights, would clearly be undesirable from the perspective of social justice (Cernea 1997). Apart from the negative impacts on the well-being of the displaced people, the chances of a land-sparing strategy succeeding in the long term will be reduced if local people fail to receive tangible benefits from it (Brockington & Igoe 2006). The geographical separation of conservation and development activities is anathema to some commentators, who argue that benefits should be directed towards those bearing the opportunity costs of conservation, and that people should not be deprived of access to natural resources (Brockington et al. 2008). Others argue that without such geographical separation and restrictions on access, conservation is doomed to fail (Terborgh 1999). My evaluations of wildlife-friendly farming and land sparing are based on comparisons of different strategies with the same overall level of cost and benefit (in terms of yields and yields foregone), but it is clear that identifying the social institutions that would most effectively ensure equitable benefit-sharing from land sparing would be useful (Balmford & Whitten 2003).

Land sparing does not depend on displacing existing land users. Most farmers in sub-Saharan Africa are severely constrained by lack of credit, good planting materials and access to information about pest and nutrient management. There is considerable scope for increasing yields by supporting farmers directly to overcome these constraints, without threatening their autonomy (Sanchez et al. 2007, Sanchez 2009). For palm oil processing plants to be cost-effective, they require a nucleus plantation to ensure a cheap and steady supply of palm fruits, with minimal transport costs (Corley & Tinker 2003). The establishment of such plantations need not depend on land appropriation, although in some parts of the world, oil palm companies have been guilty of human rights abuses in the acquisition of land (Tauli-Corpuz & Tamang 2007). Increasing population densities mean that more and more people are attempting to earn a living from the same land, which can lead to tensions and to the exclusion of some (Amanor 1999, Amanor 2006). In Ghana, most palm oil production is from land under the control of the traditional authority structures within local communities, and managed by local farmers. These include smallholder projects, in which farmers, provided with credit, extension services and a ready market by nearby oil palm companies, are producing yields not far below those achieved in the highest-yielding plantations (I. Quarm, G. Vandersmissen, pers. comm.). Other things being equal, yields of some crops are higher on smaller farms with high labour inputs, so concentration of land into the hands of a few powerful landowners is not a requirement for land sparing (Barrett 1996, Vigneri 2007).

There are other issues than autonomy over land and distribution of benefits. For small farmers, avoiding crop failure and the consequent catastrophic loss of food security or income is often as important a consideration as maximising average profits (Barrett 1996). It cannot be assumed that these risks are lower in traditional systems that avoid integration with global markets. Despite growing a variety of different crops to reduce risk, peasant farmers are vulnerable to climatic fluctuations and pest outbreaks, which have less effect on farmers in developed economies. In a subsistence economy, there is a real risk of death and starvation if crops fail. By integrating into global markets, farmers can reduce those risks by having access to savings and credit to buffer the effects of crop failure. There are risks to farmers if they switch from subsistence cropping to a reliance on income from cash crops, but unless they participate in regional and global markets, there is little prospect of them escaping from poverty. Like farmers in developed countries, most are probably happy to spread their risks between those they face from local environmental fluctuations and those they might face from global market fluctuations (Hart 1982).

8.4 Elements required for successful land sparing

8.4.1 The need for limits

Based on the preceding sections, I consider that there are four elements required for successful land sparing. The first is the need for limits to production set by society. Without limits, the wildlife-friendly farming vs. land sparing debate is irrelevant: all suitable land will be converted to whatever form of agriculture offers highest returns. There are at least three compelling reasons to set such limits, at least at a global scale. (1) It is increasingly apparent that by converting natural habitats, and low-yield farming systems to high-yielding agriculture, we are compromising the ecosystem services and benefits that those lands provide to people, such as carbon storage, control of flooding and pollination (Millennium Ecosystem Assessment 2005). (2) By allowing human population and consumption to increase to the point where it requires all suitable land to be farmed at high yields, we expose ourselves to an increased risk of societal collapse, if, for example, climate change reduces the capacity of that land to provide food (Diamond 2005). The fact that global food production is increasingly dependent on “marginal” and “fragile” lands (Scherr & McNeely 2008) raises concerns about long-term sustainability. (3) Many people, including myself, feel that we have an ethical imperative to respect other life. Human use of land and other resources is already having a major impact on other species, and if it is not constrained, it will cause numerous further extinctions (Wilson 2002).

There has been an extensive debate, especially since the 1970s, about the limits of the earth’s capacity to support human population growth and economic growth (Meadows et al. 1972, Myers & Simon 1994, Gardner 2004). Regardless of the extent to which the future course of humanity is constrained by physical limits, setting our own limits before they are imposed on us is sensible. If we do face unpalatable constraints, as seems likely, setting limits before we reach them will help us to adapt. If we are still far from being limited by physical resources, then we can afford to set limits on the consumption of resources such as land without affecting the prospects for economic growth. Regardless of whether we are approaching limits, current patterns of economic growth and our increasing consumption of resources are undeniably propelling other species towards extinction (Czech 2008).

How can such limits be set? There are two main sets of possible strategies, focusing either on the demand side, or on the supply side. (1) On the demand side, efforts to reduce global population growth, and ultimately to stabilise or even reduce human population, are necessary. Population growth has been a necessary prerequisite to the development of a specialised, industrialised society, but paradoxically now poses a considerable threat to that society. Equally important is the need to minimise per capita consumption of agricultural products. Promoting diets low in meat, and curbing use of biofuels and other non-food crop products, would help. (2) On the supply side, caps and quotas can be imposed to set limits on consumption of resources (e.g., land and water) and emissions of pollutants (e.g., greenhouse gas emissions, water pollutants). Setting limits on greenhouse gas emissions offers perhaps the best prospect in the near future of constraining agricultural expansion into natural habitats which are important both for carbon storage and biodiversity. Reservation of protected areas, if enforced, effectively sets a cap on land use, with agricultural production constrained to come from land outside protected areas. Setting and enforcing caps in the context of wildlife-friendly farming, such as a minimum level of wildlife value that farmed landscapes should support, is more difficult. Incorporating the full economic costs of ecological degradation into markets (e.g., carbon markets, Venter et al. 2009) has the potential to help slow the rate of global ecological degradation, bearing in mind that the market is a good servant but a poor master.

8.4.2 Habitat protection

Land sparing is not land sparing unless natural (or semi-natural) habitats are spared, so the second element required for successful land sparing is habitat protection. Setting aside formal protected areas is just one way in which this can be achieved. Others include community-managed conservation areas, conservation concessions, managed logging concessions, and land protected by PES (payments for ecosystem services) or biodiversity offset schemes (Ferraro & Kiss 2002, Terborgh et al. 2002, Rice 2003, Meijaard & Sheil 2007, Brockington et al. 2008, Burgin 2008). The United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in developing countries (UN-REDD), while not developed as a biodiversity conservation tool, will, it is hoped, lead to improved protection of forests important for biodiversity, although it could also have negative impacts on low-carbon habitats of high biodiversity value (Laurance 2008, Miles & Kapos 2008). Wunder (2004) considers other specific policies that governments could use to reduce habitat conversion at forest frontiers, including heavy taxes on logging companies and removal of fuel subsidies.

8.4.3 Increasing agricultural yields

Protection of habitats does not on its own ensure that yields will increase on agricultural land so that production targets can be met and pressure to overcome protection is reduced. The third necessary element for successful land sparing is agricultural development to increase yields. It is important that this is done in such a way as to minimise the negative impacts of those yield increases, e.g., soil erosion, water pollution and greenhouse gas emissions. Some of the interventions mentioned in section 8.2.1 can in the right circumstances increase yields at the same time as reducing negative environmental impacts, e.g., integrated pest and nutrient management, resistant varieties, N-fixing cover crops, replacing annuals with perennials and more efficient use of water. Others are likely to have some negative impacts, but these can be controlled if extension services are up to the job of providing relevant advice, e.g., increasing fertiliser use, augmenting soils with biochar, appropriate pesticide use, and the reduction or elimination of fallow periods (Scherr & McNeely 2007). Farmer field schools, in which farmers share knowledge with each other, could be a more effective way of disseminating information in Ghana than the underpaid and often poorly educated extension officers employed for this purpose (Gyasi et al. 2004). Other options include increasing farmers' access to credit, markets and especially to information about effective management practices and market needs (Sanchez 2009, Sanchez et al. 2009). Reducing wastage during storage, processing and consumer use would also help limit the need for more production. In a Ghanaian context, some interventions (e.g., increasing fertiliser use) are not incompatible with wildlife-friendly farming techniques and could be implemented without greatly reducing the wildlife value of farmland. However, they should be viewed primarily as a means of maintaining soil fertility, enhancing crop yields and increasing long-term productivity. Where there is a conflict between increasing yields further and maintaining wildlife-friendly features of farmland, my results suggest that the former, backed up by the protection of natural habitats, could be more appropriate from a conservation perspective.

The World Bank and others have recommended that public spending on agricultural research and development should be 1-2% of agricultural GDP. However, in West Africa it is the lowest in Africa: 0.4% of agricultural GDP (Beintema and Stads 2004). Clearly, investment in agriculture will need to increase if countries like Ghana are to sustain sufficient yield increases to avoid large-scale forest conversion. Interventions to increase agricultural productivity will be most effective at "sparing" land for nature if they are made distant from frontiers of habitat conversion. Encouraging development near the boundaries of protected areas could backfire if it increases immigration and undermines protection – a pattern that has been observed in some Integrated Conservation and Development Projects (ICDPs; Oates 1999). From this perspective, interventions that seek to restore and enhance agricultural productivity on degraded lands could help countries like Ghana to meet their production targets and provide livelihood opportunities without compromising biodiversity conservation (Van Schaik & Kramer 1997). From the perspective of social justice, such interventions should provide farmers with opportunities so that they can freely choose to relocate (if relocation is desirable); forced resettlement would have negative effects on their well-being and could undermine support for conservation (Brockington et al. 2008). Interventions should also respect the customary rights of existing land users and landowners. In Ghana's forest zone, many of the people farming near forest edges are recent immigrants, so it is not unreasonable to expect that they and/or their children would be willing to pursue economic opportunities elsewhere if they were made available. The scope for creating such opportunities is illustrated by the relatively recent success of pineapple farming in the dry coastal strip west of Accra (Takane 2004). There are opportunities to develop other crops such as mango in a similar way; *Jatropha* is another possibility, but because biofuel demand is far more elastic than that for edible crops, *Jatropha* development will be less likely to decrease pressure on forests in Ghana. High value export crops could generate income for farmers from a relatively small area of land (Sanchez & Swaminathan 2005). They would be most effective at supporting land sparing if they were grown away from frontiers of habitat conversion, if there were mechanisms in place to ensure that cultivation of imported foodstuffs was not compromising important habitats in other countries, and if they could be directly linked to reducing pressure on natural habitats, for example by employing labourers from the frontier. As discussed in sections 7.5 and 8.3.2, these qualifiers are unlikely to be met.

8.4.4 Governance

The final element required for successful land sparing is competent governance. Without institutions to define limits, intervene to protect habitats, and provide support to farmers to increase their yields, hopes for land sparing are liable to be disappointed. The most appropriate institution to carry out these activities will be context-dependent: some argue that the most appropriate managers of forests and other habitats are the local people who depend on them, while others argue that conservation objectives will be sidelined by local priorities unless experts and governments are involved in management. It seems clear that inclusive, participatory management involving both local and wider interests is necessary (Adams & Hutton 2007). Precisely what options are available for limits to be set, habitats to be spared and yields to be increased will vary greatly depending on context: thinking outside the box will often be needed.

The outcomes for conservation of various interventions will to some extent be determined by the ability of institutions to formulate and implement sound policies and regulations. (1) If institutions are weak, the setting of limits and the co-ordination of habitat protection and agricultural development are less likely to succeed. In such a context, conservation actions focused on the protection of key habitats are probably most appropriate. (2) If institutions are effective at protecting important habitats from conversion, then investments in agricultural productivity could have positive outcomes for habitat protection. (3) Finally, if institutional capacity is sufficiently strong to determine limits, protect habitats and control rebound effects, interventions that additionally enhance the wildlife value of farmland without reducing yields could augment the conservation value of protected habitats. Unfortunately, institutions in most of the developing world are still at (1), while developed world and global institutions have only recently begun to grapple with the concept of setting limits, such as those currently being negotiated for greenhouse gas emissions, and are therefore probably only at (2).

8.5 Conclusion

The results of this thesis suggest that for a plausible future production target, land-use strategies that minimise forest conversion or promote forest expansion will result in higher future populations of most bird and tree species than a strategy based on wildlife-friendly farming. If the development of agriculture in Ghana is to keep pace with population growth and changing diets, it is likely to be best, from a conservation perspective, for farmers to focus on increasing yields on agricultural land, rather than trying to maintain it as a wildlife-friendly mosaic. The human population of Africa is projected to more than double in the next 50 years, and to switch to more meat-rich diets, so these results have wide implications. They give some cause for optimism: with sufficient investments in agricultural productivity, large-scale expansion into forests will not be necessary, and populations of all bird and tree species native to the Upper Guinea forests can be conserved. However, my analyses also provide evidence for a sobering message: if protected areas are too small to conserve biodiversity, then agricultural lands, despite their vast extent and despite opportunities for wildlife-friendly farming, are likely to be even worse. Efforts will need to be redoubled to find ways of maintaining natural habitats in Ghana and the rest of Africa in the face of the enormous increase in human resource consumption that coming decades will bring. In the long term, neither wildlife-friendly farming nor land sparing is a complete solution: they will only delay and not avert biodiversity loss unless global society is able to limit its consumption.

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Appendix 1

Bird densities in different land use types

Densities are given in number of individuals per km^2. Sample sizes are eight squares each in forest and farm mosaic, and six in oil palm plantations (additional squares in farm mosaic were excluded; Norpalm plantation, which was actually a mosaic of farms and plantation, was excluded). Note that four species-pairs species were recorded only to genus level on many occasions, so were grouped for Distance analysis (see Chapter 5). In this table, those species-pairs' densities are allocated to their component species based on the observed ratio of each pair of species in each of the three major land use types, and 95% confidence limits are not given for those species. Some species that would be expected to occur were probably systematically missed or under-recorded on counts, because of identification difficulties or other reasons as elaborated in Chapter 5.

I thank Françoise Dowsett-Lemaire for drawing my attention to the species most likely to have been missed or under-recorded. Species not recorded, or certainly under-recorded in forest, include African Goshawk, Violet-backed Hyliota *Hyliota violacea*, Forest Penduline Tit *Anthoscopus flavifrons*, Green Sunbird and Johanna's Sunbird *Nectarinia johannae*. Black-collared Lovebird *Agapornis swindernianus*, Purple-throated Cuckoo-shrike *Campephaga quiscalina*, Little Grey Flycatcher *Muscicapa epulata* and Shrike Flycatcher *Megabyas flammulatus* might be expected to occur in forest, but not abundantly. I encountered the first of those species in Subri River forest reserve, but not in any of the squares. Also, in forest I almost certainly recorded many Tiny Sunbirds erroneously as Olive-bellied Sunbirds, where the former species can be expected to be more abundant in that habitat. Species which would not be expected to occur in undisturbed forest (at least in closed evergreen forest) include African Piculet, Woodland Kingfisher, Yellow-browed Camaroptera, Kemp's Longbill, Green Crombec, Brown Illadopsis and Olive-bellied Sunbird.

In farm mosaic, Brown-crowned Tchagra *Tchagra australis* and Lead-coloured Flycatcher *Myioparus plumbeus* might have been expected to occur. Golden Greenbul, Violet-backed Hyliota, Tiny Sunbird and Little Green Sunbird, while predominantly forest species, might also be expected at low densities in low-yield farm mosaic. In southern Benin, F. Dowsett-Lemaire and R. Dowsett found Simple Greenbul to be common in overgrown oil palm plantations, but plantations in Ghana probably lacked high densities of this species because they are weeded regularly.

Six species are included in the table which have zero density estimates in all habitats. Four of these, Grey Kestrel, Laughing Dove, Spotted Honeyguide and Rufous-winged Illadopsis, were recorded on point counts but never within 80 metres, so were excluded from Distance analysis. These species are therefore also included in the list of additional species recorded “off-effort” at the end of this appendix.

A further two species, Yellow-rumped Tinkerbird and Orange Weaver, were recorded during point counts only in the Norpalm plantation in block I; observations from that plantation are not incorporated here as the “plantation” was in fact a mosaic of farms and oil palm plantation, and the aim of this table is to provide density estimates for well-defined habitat classes.

Scientific name	Common name	Density (individuals per square km)								
		Forest			Farm mosaic			Oil palm plantation		
		mean	95% confidence limits		mean	95% confidence limits		mean	95% confidence limits	
Francolinus bicalcaratus	Double-spurred Francolin	**0.0**	0.0	0.0	**1.7**	0.0	5.1	**0.0**	0.0	0.0
Francolinus ahantensis	Ahanta Francolin	**0.0**	0.0	0.0	**9.2**	0.0	18.6	**2.1**	0.0	6.5
Butorides striata	Green-backed Heron	**0.0**	0.0	0.0	**1.3**	0.0	3.8	**0.0**	0.0	0.0
Bubulcus ibis	Cattle Egret	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**6.8**	0.0	17.5
Falco ardosiaceus	Grey Kestrel	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Milvus migrans	Black Kite	**0.0**	0.0	0.0	**0.3**	0.0	0.8	**0.0**	0.0	0.0
Necrosyrtes monachus	Hooded Vulture	**0.0**	0.0	0.0	**0.5**	0.0	1.5	**0.0**	0.0	0.0
Polyboroides typus	African Harrier Hawk	**0.3**	0.0	0.8	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Accipiter tachiro	African Goshawk	**0.0**	0.0	0.0	**0.5**	0.0	1.5	**0.7**	0.0	2.2
Urotriorchis macrourus	Long-tailed Hawk	**0.5**	0.0	1.2	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Buteo auguralis	Red-necked Buzzard	**0.0**	0.0	0.0	**0.3**	0.0	0.8	**0.0**	0.0	0.0
Lophaetus occipitalis	Long-crested Eagle	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.3**	0.0	1.1
Sarothrura pulchra	White-spotted Flufftail	**8.0**	0.0	16.7	**29.9**	0.9	59.0	**0.0**	0.0	0.0
Columba iriditorques	Western Bronze-naped Pigeon	**0.6**	0.0	1.4	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Streptopelia semitorquata	Red-eyed Dove	**1.5**	0.0	4.4	**5.9**	1.8	9.9	**13.9**	0.0	28.9
Stigmatopelia senegalensis	Laughing Dove	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Turtur afer	Blue-spotted Wood Dove	**0.0**	0.0	0.0	**22.6**	13.1	32.2	**0.4**	0.0	1.3
Turtur tympanistria	Tambourine Dove	**13.9**	7.9	20.0	**9.6**	2.3	16.9	**4.5**	0.6	8.4
Turtur brehmeri	Blue-headed Wood Dove	**10.0**	3.4	16.6	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Treron calvus	African Green Pigeon	**14.8**	8.7	20.8	**4.3**	0.5	8.2	**0.0**	0.0	0.0
Poicephalus gulielmi	Red-fronted Parrot	**0.6**	0.0	1.7	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Tauraco macrorhynchus	Yellow-billed Turaco	**35.6**	15.6	55.5	**1.1**	0.0	3.4	**0.0**	0.0	0.0
Crinifer piscator	Western Grey Plantain-eater	**0.0**	0.0	0.0	**0.6**	0.0	1.7	**0.0**	0.0	0.0
Cuculus solitarius	Red-chested Cuckoo	**1.2**	0.0	2.7	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Cuculus clamosus	Black Cuckoo	**4.8**	1.2	8.4	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Cercococcyx olivinus	Olive Long-tailed Cuckoo	**3.6**	0.7	6.6	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Chrysococcyx klaas	Klaas's Cuckoo	**2.0**	0.0	4.5	**2.0**	0.5	3.5	**0.0**	0.0	0.0
Chrysococcyx cupreus	African Emerald Cuckoo	**11.2**	5.2	17.2	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Chrysococcyx caprius	Didric Cuckoo	**0.0**	0.0	0.0	**1.5**	0.1	2.9	**0.0**	0.0	0.0
Ceuthmochares aereus	Yellowbill	**19.1**	7.6	30.6	**4.2**	0.2	8.2	**0.0**	0.0	0.0
Centropus leucogaster	Black-throated Coucal	**1.1**	0.0	2.5	**1.1**	0.0	3.3	**0.0**	0.0	0.0
Centropus monachus	Blue-headed Coucal	**0.0**	-	-	**16.7**	-	-	**12.4**	-	-
Centropus senegalensis	Senegal Coucal	**0.0**	-	-	**5.1**	-	-	**0.9**	-	-
Bubo poensis	Fraser's Eagle Owl	**0.4**	0.0	1.2	**0.0**	0.0	0.0	**0.5**	0.0	1.6
Caprimulgus climacurus	Long-tailed Nightjar	**0.0**	0.0	0.0	**1.3**	0.0	3.8	**0.0**	0.0	0.0
Apaloderma narina	Narina's Trogon	**0.5**	0.0	1.5	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Eurystomus glaucurus	Broad-billed Roller	**0.0**	0.0	0.0	**1.0**	0.0	2.3	**0.0**	0.0	0.0
Halcyon badia	Chocolate-backed Kingfisher	**2.4**	0.0	4.9	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Halcyon senegalensis	Woodland Kingfisher	**0.6**	0.0	1.7	**6.4**	2.2	10.6	**0.0**	0.0	0.0
Halcyon malimbica	Blue-breasted Kingfisher	**2.0**	0.5	3.5	**1.5**	0.0	3.5	**0.0**	0.0	0.0
Ceyx pictus	African Pygmy Kingfisher	**0.0**	0.0	0.0	**15.7**	6.7	24.8	**1.5**	0.0	4.7
Merops gularis	Black Bee-eater	**0.0**	0.0	0.0	**7.6**	0.0	17.9	**0.0**	0.0	0.0
Merops pusillus	Little Bee-eater	**0.0**	0.0	0.0	**2.0**	0.0	4.7	**2.7**	0.0	8.6
Merops albicollis	White-throated Bee-eater	**0.0**	0.0	0.0	**10.5**	2.7	18.3	**0.0**	0.0	0.0
Tockus fasciatus	African Pied Hornbill	**4.8**	0.9	8.6	**12.3**	7.5	17.1	**5.2**	0.0	11.6
Tropicranus albocristatus	White-crested Hornbill	**0.7**	0.0	2.2	**2.8**	0.0	6.4	**0.0**	0.0	0.0
Bycanistes fistulator	Piping Hornbill	**2.6**	0.0	6.1	**2.6**	0.0	7.6	**0.0**	0.0	0.0
Gymnobucco calvus	Naked-faced Barbet	**6.0**	-	-	**5.0**	-	-	**0.0**	-	-
Gymnobucco peli	Bristle-nosed Barbet	**11.9**	-	-	**3.4**	-	-	**0.0**	-	-
Pogoniulus scolopaceus	Speckled Tinkerbird	**11.0**	3.5	18.5	**10.6**	6.3	14.8	**0.0**	0.0	0.0
Pogoniulus atroflavus	Red-rumped Tinkerbird	**1.8**	0.6	3.1	**0.9**	0.0	2.2	**0.0**	0.0	0.0
Pogoniulus subsulphureus	Yellow-throated Tinkerbird	**17.2**	9.3	25.1	**4.0**	0.4	7.6	**0.0**	0.0	0.0
Pogoniulus bilineatus	Yellow-rumped Tinkerbird	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Buccanodon duchaillui	Yellow-spotted Barbet	**11.5**	4.9	18.1	**1.7**	0.0	4.1	**0.0**	0.0	0.0
Tricholaema hirsuta	Hairy-breasted Barbet	**3.7**	1.3	6.1	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Lybius vieilloti	Vieillot's Barbet	**0.0**	0.0	0.0	**2.1**	0.0	4.1	**0.0**	0.0	0.0
Trachyphonus purpuratus	Yellow-billed Barbet	**3.1**	0.7	5.5	**0.6**	0.0	1.4	**0.0**	0.0	0.0
Prodotiscus insignis	Cassin's Honeybird	**1.2**	0.0	3.6	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Indicator maculatus	Spotted Honeyguide	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Sasia africana	African Piculet	**0.7**	0.0	2.2	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Thripias pyrrhogaster	Fire-bellied Woodpecker	**3.0**	0.0	6.2	**0.5**	0.0	1.5	**0.0**	0.0	0.0
Smithornis rufolateralis	Rufous-sided Broadbill	**3.0**	0.0	6.1	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Bias musicus	Black-and-white Flycatcher	**0.0**	0.0	0.0	**3.0**	0.5	5.4	**0.0**	0.0	0.0
Platysteira cyanea	Brown-throated Wattle-eye	**0.0**	0.0	0.0	**2.8**	0.0	8.2	**0.0**	0.0	0.0
Platysteira castanea	Chestnut Wattle-eye	**21.6**	12.5	30.7	**7.4**	0.0	18.4	**0.0**	0.0	0.0
Prionops caniceps	Red-billed Helmet-shrike	**1.3**	0.0	4.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Tchagra senegalus	Black-crowned Tchagra	**0.0**	0.0	0.0	**12.5**	0.0	31.6	**0.0**	0.0	0.0
Dryoscopus gambensis	Northern Puffback	**0.0**	0.0	0.0	**5.6**	0.0	13.8	**0.0**	0.0	0.0
Dryoscopus sabini	Sabine's Puffback	**8.1**	3.2	12.9	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Laniarius leucorhynchus	Sooty Boubou	**0.0**	0.0	0.0	**3.9**	0.0	9.2	**0.0**	0.0	0.0
Coracina azurea	Blue Cuckoo-shrike	**5.4**	0.5	10.3	**0.8**	0.0	2.4	**0.0**	0.0	0.0
Lanius collaris	Common Fiscal	**0.0**	0.0	0.0	**5.9**	0.0	11.9	**0.0**	0.0	0.0
Oriolus brachyrhynchus	Western Black-headed Oriole	**28.2**	-	-	**0.0**	-	-	**0.0**	-	-
Oriolus nigripennis	Black-winged Oriole	**15.8**	-	-	**1.8**	-	-	**0.0**	-	-
Dicrurus atripennis	Shining Drongo	**8.1**	1.2	15.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Dicrurus adsimilis	Velvet-mantled Drongo	**10.9**	2.6	19.2	**2.0**	0.0	4.5	**0.0**	0.0	0.0
Trochocercus nitens	Blue-headed Crested Flycatcher	**9.6**	0.0	19.3	**1.4**	0.0	4.1	**0.0**	0.0	0.0
Terpsiphone rufiventer	Red-bellied Paradise-flycatcher	**63.0**	39.4	86.6	**36.1**	27.2	45.0	**8.8**	3.1	14.5
Erythrocercus mccallii	Chestnut-capped Flycatcher	**1.0**	0.0	2.9	**3.7**	0.0	11.0	**0.0**	0.0	0.0
Corvus albus	Pied Crow	**0.0**	0.0	0.0	**1.8**	0.0	4.1	**34.4**	18.4	50.4
Pholidornis rushiae	Tit-hylia	**1.0**	0.0	2.9	**1.0**	0.0	2.9	**0.0**	0.0	0.0
Cisticola erythrops	Red-faced Cisticola	**0.0**	0.0	0.0	**11.6**	2.0	21.3	**10.0**	0.1	20.0
Cisticola cantans	Singing Cisticola	**0.0**	0.0	0.0	**3.4**	0.0	7.8	**0.0**	0.0	0.0
Cisticola lateralis	Whistling Cisticola	**0.0**	0.0	0.0	**17.2**	9.4	24.9	**18.5**	0.0	45.4

Scientific name	**Common name**	**Density (individuals per square km)**								
		Forest			**Farm mosaic**			**Oil palm plantation**		
		mean	95% confidence limits		**mean**	95% confidence limits		**mean**	95% confidence limits	
Prinia subflava	Tawny-flanked Prinia	**0.0**	0.0	0.0	**39.7**	5.5	73.9	**72.9**	55.1	90.6
Apalis nigriceps	Black-capped Apalis	**2.0**	0.0	4.1	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Apalis sharpii	Sharpe's Apalis	**20.7**	15.8	25.6	**0.5**	0.0	1.5	**0.0**	0.0	0.0
Camaroptera brachyura	Grey-backed Camaroptera	**0.0**	0.0	0.0	**184.7**	121.6	247.8	**153.0**	59.2	246.8
Camaroptera superciliaris	Yellow-browed Camaroptera	**16.8**	0.0	33.6	**12.5**	2.3	22.8	**0.0**	0.0	0.0
Camaroptera chloronota	Olive-green Camaroptera	**0.0**	0.0	0.0	**15.5**	0.0	32.6	**0.0**	0.0	0.0
Pycnonotus barbatus	Common Bulbul	**0.0**	0.0	0.0	**126.4**	76.7	176.0	**51.0**	37.4	64.5
Andropadus virens	Little Greenbul	**10.1**	3.2	17.1	**258.6**	189.8	327.4	**13.1**	1.3	24.9
Andropadus gracilis	Little Grey Greenbul	**6.7**	1.2	12.3	**1.6**	0.0	4.8	**0.0**	0.0	0.0
Andropadus ansorgei	Ansorge's Greenbul	**5.4**	0.5	10.3	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Andropadus curvirostris	Cameroon Sombre Greenbul	**4.4**	1.5	7.3	**4.2**	0.2	8.2	**0.0**	0.0	0.0
Andropadus gracilirostris	Slender-billed Greenbul	**40.3**	23.1	57.6	**8.0**	0.0	20.6	**0.0**	0.0	0.0
Andropadus latirostris	Yellow-whiskered Greenbul	**134.6**	87.5	181.8	**19.9**	0.0	42.5	**0.0**	0.0	0.0
Calyptocichla serina	Golden Greenbul	**0.5**	0.0	1.5	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Baeopogon indicator	Honeyguide Greenbul	**9.4**	4.6	14.2	**1.6**	0.0	4.8	**0.0**	0.0	0.0
Ixonotus guttatus	Spotted Greenbul	**5.4**	0.0	12.3	**3.2**	0.0	9.5	**0.0**	0.0	0.0
Chlorocichla simplex	Simple Greenbul	**0.0**	0.0	0.0	**59.7**	42.4	77.0	**0.0**	0.0	0.0
Thescelocichla leucopleura	Swamp Palm Bulbul	**19.7**	3.5	35.8	**41.5**	0.0	93.3	**0.0**	0.0	0.0
Phyllastrephus albigularis	White-throated Greenbul	**0.6**	0.0	1.6	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Phyllastrephus icterinus	Icterine Greenbul	**150.3**	73.3	227.3	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Bleda syndactylus	Red-tailed Bristlebill	**4.5**	1.6	7.3	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Bleda eximius	Green-tailed Bristlebill	**2.2**	0.0	4.6	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Bleda canicapillus	Grey-headed Bristlebill	**12.8**	5.0	20.6	**2.3**	0.0	5.1	**0.0**	0.0	0.0
Criniger barbatus	Western Bearded Greenbul	**25.6**	11.4	39.8	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Criniger calurus	Red-tailed Greenbul	**15.5**	10.6	20.3	**9.7**	0.0	21.0	**0.0**	0.0	0.0
Criniger olivaceus	Yellow-bearded Greenbul	**1.7**	0.0	4.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Nicator chloris	Western Nicator	**10.8**	3.3	18.2	**4.0**	1.7	6.3	**0.0**	0.0	0.0
Hippolais polyglotta	Melodious Warbler	**0.0**	0.0	0.0	**0.5**	0.0	1.5	**0.0**	0.0	0.0
Macrosphenus kempi	Kemp's Longbill	**9.0**	0.1	18.0	**5.2**	1.3	9.0	**0.0**	0.0	0.0
Macrosphenus concolor	Grey Longbill	**35.9**	22.7	49.2	**0.5**	0.0	1.5	**0.0**	0.0	0.0
Hylia prasina	Green Hylia	**53.5**	39.3	67.7	**13.2**	2.8	23.7	**0.0**	0.0	0.0
Eremomela badiceps	Rufous-crowned Eremomela	**1.0**	0.0	2.9	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Sylvietta virens	Green Crombec	**3.7**	0.0	7.8	**19.8**	12.9	26.7	**6.8**	0.0	14.2
Illadopsis cleaveri	Blackcap Illadopsis	**11.6**	5.6	17.6	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Illadopsis rufescens	Rufous-winged Illadopsis	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Illadopsis rufipennis	Pale-breasted Illadopsis	**17.2**	6.8	27.7	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Illadopsis fulvescens	Brown Illadopsis	**6.9**	0.1	13.7	**1.7**	0.0	5.1	**0.0**	0.0	0.0
Zosterops senegalensis	Yellow White-eye	**0.0**	0.0	0.0	**5.0**	0.0	12.3	**0.0**	0.0	0.0
Lamprotornis cupreocauda	Copper-tailed Starling	**3.4**	0.2	6.7	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Lamprotornis splendidus	Splendid Starling	**11.2**	0.0	24.2	**14.5**	7.0	21.9	**0.0**	0.0	0.0
Onychognathus fulgidus	Forest Chestnut-winged Starling	**1.1**	0.0	3.4	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Neocossyphus poensis	White-tailed Ant-thrush	**1.5**	0.0	4.4	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Stizorhina fraseri	Finsch's Flycatcher-thrush	**24.5**	13.1	35.9	**3.7**	0.0	11.0	**0.0**	0.0	0.0
Turdus pelios	African Thrush	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**2.3**	0.0	7.4
Alethe diademata	Fire-crested Alethe	**6.9**	3.1	10.7	**1.7**	0.0	3.9	**0.0**	0.0	0.0
Stiphrornis erythrothorax	Forest Robin	**12.1**	3.2	20.9	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Fraseria ocreata	Fraser's Forest Flycatcher	**0.5**	0.0	1.5	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Fraseria cinerascens	White-browed Forest Flycatcher	**1.3**	0.0	3.8	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Muscicapa striata	Spotted Flycatcher	**0.0**	0.0	0.0	**2.5**	0.0	7.5	**0.0**	0.0	0.0
Muscicapa comitata	Dusky-blue Flycatcher	**0.0**	0.0	0.0	**12.4**	3.2	21.6	**18.9**	2.6	35.3
Muscicapa tessmanni	Tessmann's Flycatcher	**0.6**	0.0	1.8	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Myioparus griseigularis	Grey-throated Flycatcher	**2.6**	0.0	7.6	**1.3**	0.0	3.8	**0.0**	0.0	0.0
Anthreptes fraseri	Fraser's Sunbird	**15.9**	6.3	25.5	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Anthreptes rectirostris	Green Sunbird	**0.0**	0.0	0.0	**1.8**	0.0	5.5	**0.0**	0.0	0.0
Anthreptes collaris	Collared Sunbird	**78.7**	21.8	135.6	**66.4**	44.6	88.2	**16.6**	0.7	32.4
Nectarinia seimundi	Little Green Sunbird	**1.4**	0.0	4.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Nectarinia olivacea	Olive Sunbird	**70.6**	53.2	88.1	**38.4**	23.7	53.0	**0.0**	0.0	0.0
Nectarinia verticalis	Green-headed Sunbird	**0.0**	0.0	0.0	**1.8**	0.0	5.5	**0.0**	0.0	0.0
Nectarinia cyanolaema	Blue-throated Brown Sunbird	**75.1**	32.9	117.2	**21.5**	0.0	44.6	**0.0**	0.0	0.0
Nectarinia adelberti	Buff-throated Sunbird	**12.6**	0.0	25.8	**19.4**	3.5	35.2	**0.0**	0.0	0.0
Nectarinia chloropygia	Olive-bellied Sunbird	**14.5**	0.0	30.0	**215.4**	169.3	261.4	**16.0**	7.4	24.6
Nectarinia minulla	Tiny Sunbird	**3.6**	0.0	10.7	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Nectarinia cuprea	Copper Sunbird	**0.0**	0.0	0.0	**21.1**	0.0	47.4	**0.0**	0.0	0.0
Nectarinia coccinigaster	Splendid Sunbird	**0.0**	0.0	0.0	**16.4**	0.0	38.3	**0.0**	0.0	0.0
Nectarinia superba	Superb Sunbird	**11.5**	0.0	28.6	**14.7**	0.0	37.8	**0.0**	0.0	0.0
Passer griseus	Northern Grey-headed Sparrow	**0.0**	0.0	0.0	**3.2**	0.0	9.3	**0.0**	0.0	0.0
Ploceus nigricollis	Black-necked Weaver	**0.0**	0.0	0.0	**185.7**	78.6	292.7	**103.3**	65.8	140.7
Ploceus aurantius	Orange Weaver	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Ploceus cucullatus	Village Weaver	**0.0**	0.0	0.0	**75.0**	39.9	110.1	**4.7**	0.0	11.0
Ploceus nigerrimus	Vieillot's Black Weaver	**0.0**	0.0	0.0	**93.7**	3.3	184.1	**10.6**	0.4	20.7
Ploceus tricolor	Yellow-mantled Weaver	**1.5**	0.0	4.4	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Ploceus albinucha	Maxwell's Black Weaver	**2.9**	0.0	7.3	**0.0**	0.0	0.0	**0.0**	0.0	0.0
Malimbus scutatus	Red-vented Malimbe	**3.8**	0.0	8.6	**17.9**	0.0	36.1	**5.7**	0.0	17.9
Malimbus nitens	Blue-billed Malimbe	**5.9**	3.4	8.4	**1.9**	0.0	5.5	**0.0**	0.0	0.0
Malimbus malimbicus	Crested Malimbe	**0.0**	0.0	0.0	**0.5**	0.0	1.5	**0.0**	0.0	0.0
Malimbus rubricollis	Red-headed Malimbe	**5.5**	1.0	9.9	**0.9**	0.0	2.7	**0.0**	0.0	0.0
Euplectes hordeaceus	Black-winged Bishop	**0.0**	0.0	0.0	**152.6**	0.0	356.3	**2.7**	0.0	6.4
Euplectes macroura	Yellow-mantled Widowbird	**0.0**	0.0	0.0	**7.9**	0.0	18.0	**0.0**	0.0	0.0
Nigrita fusconotus	White-breasted Nigrita	**3.4**	0.0	6.8	**0.8**	0.0	2.4	**0.0**	0.0	0.0
Nigrita bicolor	Chestnut-breasted Nigrita	**2.9**	0.0	6.0	**20.9**	5.8	36.0	**35.4**	0.0	78.1
Nigrita canicapillus	Grey-crowned Nigrita	**17.1**	6.4	27.8	**10.9**	5.5	16.3	**1.3**	0.0	3.1
Pyrenestes ostrinus	Black-bellied Seedcracker	**0.0**	0.0	0.0	**2.6**	0.0	5.9	**0.0**	0.0	0.0
Spermophaga haematina	Western Bluebill	**0.0**	0.0	0.0	**2.3**	0.0	5.2	**0.0**	0.0	0.0
Lagonosticta rubricata	Blue-billed Firefinch	**0.0**	0.0	0.0	**3.2**	0.0	9.3	**0.0**	0.0	0.0

Scientific name	Common name	Density (individuals per square km)								
		Forest			**Farm mosaic**			**Oil palm plantation**		
		mean	95% confidence limits		**mean**	95% confidence limits		**mean**	95% confidence limits	
Estrilda melpoda	Orange-cheeked Waxbill	**0.0**	0.0	0.0	**268.2**	132.4	403.9	**56.4**	21.6	91.3
Lonchura cucullata	Bronze Mannikin	**0.0**	0.0	0.0	**37.9**	0.0	93.9	**0.0**	0.0	0.0
Lonchura bicolor	Black-and-white Mannikin	**0.0**	0.0	0.0	**107.3**	37.2	177.3	**12.8**	0.5	25.1
Vidua macroura	Pin-tailed Whydah	**0.0**	0.0	0.0	**0.0**	0.0	0.0	**0.8**	0.0	2.4
Motacilla flava	Yellow Wagtail	**0.0**	0.0	0.0	**1.8**	0.0	4.0	**0.0**	0.0	0.0
Anthus leucophrys	Plain-backed Pipit	**0.0**	0.0	0.0	**0.9**	0.0	2.6	**1.2**	0.0	3.7

Additional species recorded "off-effort" within or flying over the study squares included the following 45 species:

Long-tailed Cormorant *Phalacrocorax africanus*

Palm-nut Vulture *Gypohierax angolensis*

Western Marsh-harrier *Circus aeruginosus*

Congo Serpent-eagle *Dryotriorchis spectabilis*

Black-shouldered Kite *Elanus caeruleus*

Grey Kestrel *Falco ardosiaceus*

African Hobby *Falco cuvierii*

Latham's Forest Francolin *Francolinus lathami*

Nkulengu Rail *Himantornis haematopus*

Levaillant's Cuckoo *Clamator levaillantii*

Laughing Dove *Stigmatopelia senegalensis*

Grey Parrot *Psittacus erithacus*

Red-chested Owlet *Glaucidium tephronotum*

African Wood Owl *Strix woodfordii*

Common Swift *Apus apus*

Little Swift *Apus affinis*

African Palm Swift *Cypsiurus parvus*

Sabine's Spinetail *Rhaphidura sabini*

White-bellied Kingfisher *Alcedo leucogaster*

Rosy Bee-eater *Merops malimbicus*

Blue-throated Roller *Eurystomus gularis*

White-headed Wood-hoopoe *Phoeniculus bollei*

Black-casqued Hornbill *Ceratogymna atrata*

Brown-cheeked Hornbill *Bycanistes cylindricus*

Red-billed Dwarf Hornbill *Tockus camurus*

Black Dwarf Hornbill *Tockus hartlaubi*

Spotted Honeyguide *Indicator maculatus*

Willcocks's Honeyguide *Indicator willcocksi*

Brown-eared Woodpecker *Campethera caroli*

Buff-spotted Woodpecker *Campethera nivosa*

Lesser Striped Swallow *Hirundo abyssinica*

Ethiopian Swallow *Hirundo aethiopica*

Preusss Cliff Swallow *Hirundo preussi*

Rufous-chested Swallow *Hirundo semirufa*

Square-tailed Saw-wing *Psalidoprocne nitens*

Fanti Saw-wing *Psalidoprocne obscura*

African Pied Wagtail *Motacilla aguimp*

Brown-chested Alethe *Alethe poliocephala*

Whinchat *Saxicola rubetra*

Olivaceous Warbler *Hippolais pallida*

Olivaceous Flycatcher *Muscicapa olivascens*

Grey-throated Flycatcher *Myioparus griseigularis*

Rufous-winged Illadopsis *Illadopsis rufescens*

Red-fronted Antpecker *Parmoptila rubrifrons*

Magpie Mannikin *Lonchura fringilloides*

Appendix 2

Number of trees (stems) of each species recorded in each square

The total area sampled in each square (sum of plot areas) was 7,500 m^2 in each forest square, and 15,000 m^2 in each plantation and farm mosaic square.

$\geq$ 10 cm dbh

Land use	Forest								Farm mosaic									Plantation/ farm	
block	**A**		**B**		**C**		**D**		**A**		**B**		**C**		**D**			**A**	
square	**1**	**2**	**7**	**8**	**13**	**14**	**20**	**21**	**3**	**4**	**9**	**10**	**15**	**17**	**22**	**23**	**24**	**5**	**6**
Afrostyrax lepidophyllus	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
Aidia genipiflora	2	0	0	0	0	0	8	1	0	0	0	0	0	0	0	0	0	0	0
Albizia adianthifolia	1	0	0	0	0	0	1	2	0	0	2	6	1	0	0	1	0	1	0
Albizia ferruginea	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0
Albizia zygia	0	0	0	0	0	0	2	5	0	2	3	13	2	2	0	7	0	0	1
Alchornea cordifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Allanblackia parviflora	0	0	9	7	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Alstonia boonei	0	0	0	0	1	0	6	5	0	0	6	2	3	0	1	0	0	0	0
Amanoa strobilacea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphimas pterocarpoides	0	0	1	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Anisophyllea meniaudii	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Anopyxis klaineana	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthocleista spp.	0	0	0	0	0	0	0	0	1	6	8	13	9	0	0	0	0	0	0
Anthonotha fragrans	3	0	0	0	0	2	0	1	0	0	0	2	0	0	0	0	0	0	0
Anthonotha macrophylla	1	0	0	0	4	1	0	7	0	0	0	0	0	0	0	0	0	0	1
Anthonotha vignei	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antiaris toxicaria	1	0	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	1
Antidesma laciniatum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antrocaryon micraster	0	0	0	0	0	0	1	0	0	0	1	3	0	0	0	0	0	0	0
Aporrhiza urophylla	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacocalyx jasminiflora	1	4	0	1	0	0	13	15	0	0	1	1	0	0	0	0	0	0	0
Baphia nitida	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Baphia pubescens	1	1	1	1	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0
Beilschmiedia mannii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berlinia spp.	45	22	5	3	6	14	9	7	0	0	5	1	0	0	0	0	0	0	0
Blighia sapida	3	4	6	8	5	2	4	4	0	0	1	1	0	0	0	0	0	0	0
Blighia welwitschii	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0
Bombax buonopozense	0	0	0	0	0	0	0	4	0	0	0	2	0	1	1	2	1	0	0
Bridelia atroviridis	0	0	0	2	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1
Buchholzia coriacea	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Bussea occidentalis	0	0	0	0	0	1	6	2	0	0	0	0	0	0	0	0	0	0	0
Calpocalyx brevibracteatus	3	9	3	7	7	4	17	20	0	0	0	4	0	0	0	0	0	0	0
Canarium schweinfurthii	1	0	0	3	0	1	2	0	0	0	1	0	1	0	0	0	0	0	0
Carapa procera	2	43	12	18	0	0	3	7	0	0	7	3	2	1	0	3	0	0	0
Cassipourea hiotou	0	4	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0
Cathormion altissimum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ceiba pentandra	1	0	0	0	1	1	0	0	0	0	7	1	1	1	0	2	2	0	0
Celtis adolfi-friderici	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
Celtis mildbraedii	0	0	0	0	17	0	17	21	0	0	0	0	1	0	0	0	0	0	0
Celtis zenkeri	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
Chrysophyllum pruniforme	1	4	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Chrysophyllum subnudum	10	1	0	10	0	1	0	3	0	0	1	0	0	0	1	0	0	0	0
Cleidion gabonicum	14	6	0	0	8	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cleistopholis patens	1	0	0	0	3	1	2	2	0	1	3	2	2	0	0	0	0	0	0
Coelocaryon oxycarpum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelocaryon sphaerocarpum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cola caricifolia	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cola chlamydantha	0	13	5	5	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Cola gigantea	0	0	14	2	15	2	7	10	0	0	0	0	1	0	0	0	0	0	0
Cola lateritia	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cola nitida	3	6	2	5	22	4	0	1	0	0	0	1	1	0	0	1	0	0	0
Cola verticillata	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copaifera salikounda	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corynanthe pachyceras	1	3	0	3	0	1	3	1	0	0	0	0	0	0	0	0	0	0	0
Coula edulis	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Craterispermum caudatum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cylicodiscus gabunensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cynometra ananta	0	11	26	0	0	13	0	0	0	0	3	1	0	0	0	0	0	0	0
Cynometra megalophylla	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dacryodes klaineana	2	4	4	25	12	14	2	2	0	0	3	1	0	0	0	0	0	0	0
Daniellia ogea	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Daniellia thurifera	1	16	1	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0
Deinbollia grandifolia	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Desplatsia chrysochlamys	1	0	0	2	1	0	1	0	0	0	3	0	0	0	0	0	0	0	0
Dialium aubrevillei	24	11	0	25	4	18	1	0	0	0	2	2	0	0	0	0	0	0	0
Didelotia idae	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diospyros canaliculata	0	0	0	0	0	0	10	7	0	0	0	0	0	0	0	0	0	0	0
Diospyros gabunensis	21	8	6	0	15	15	0	0	0	0	0	1	0	0	0	0	0	0	0
Diospyros kamerunensis	4	8	10	8	21	3	3	3	0	0	1	1	0	0	0	0	0	0	0

Land use	Forest								Farm mosaic									Plantation/ farm	
block	**A**		**B**		**C**		**D**		**A**		**B**		**C**		**D**			**A**	
square	**1**	**2**	**7**	**8**	**13**	**14**	**20**	**21**	**3**	**4**	**9**	**10**	**15**	**17**	**22**	**23**	**24**	**5**	**6**
Diospyros sanza-minika	3	6	3	15	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0
Diospyros vignei	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Diospyros viridicans	0	0	0	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Discoglypremna caloneura	0	0	0	0	2	2	10	5	0	0	0	1	1	0	0	0	0	0	0
Distemonanthus benthamianus	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0
Drypetes aubrevillei	0	0	0	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Drypetes aylmeri	5	8	8	22	3	14	0	0	0	0	2	0	0	0	0	0	0	0	0
Drypetes pellegrinii	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Drypetes principum	16	21	7	0	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Ehretia trachyphylla	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enantia polycarpa	0	0	2	2	5	2	1	2	0	0	0	0	0	0	0	0	0	0	0
Englerophytum oubanguiense	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entandrophragma angolense	1	0	0	0	0	0	7	1	0	0	1	0	0	0	0	0	0	0	0
Entandrophragma cylindricum	0	0	0	0	4	1	0	2	0	0	0	0	0	0	0	0	0	0	0
Eriocoelum racemosum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erythrina spp.	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Erythrophleum ivorense	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ficus exasperata	0	0	0	0	0	0	1	1	0	0	0	6	2	1	0	0	0	4	1
Ficus lutea	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ficus lyrata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ficus recurvata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ficus sur	0	0	0	0	0	0	2	4	0	1	5	4	1	1	0	0	0	2	0
Ficus trichopoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ficus vogeliana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Funtumia africana	1	1	2	4	37	8	0	7	0	0	18	15	1	0	0	0	0	0	1
Funtumia elastica	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Garcinia gnetoides	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Gilbertiodendron bilineatum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gilbertiodendron limba	0	39	8	25	0	7	0	0	0	0	1	0	0	0	2	0	0	0	0
Gilbertiodendron preussii	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gilbertiodendron splendidum	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Greenwayodendron oliveri	0	2	2	3	4	7	5	2	0	0	0	0	0	0	0	0	0	0	0
Guarea cedrata	1	0	0	0	5	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Guarea thompsonii	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Guibourtia ehie	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hallea ledermannii	0	0	2	3	0	1	0	0	0	0	29	1	3	0	0	0	0	0	0
Hannoa klaineana	0	3	3	9	7	1	7	8	0	0	4	6	5	0	0	0	0	0	0
Harungana madagascariensis	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	1	0	1	0
Heritiera utilis	4	4	9	16	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Hexalobus crispiflorus	0	1	6	5	5	2	1	0	0	0	0	0	0	3	0	0	0	0	0
Homalium letestui	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Homalium stipulaceum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenostegia afzelii	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Isolona campanulata	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Khaya ivorensis	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Klainedoxa gabonensis	0	0	1	1	1	4	0	1	0	0	0	0	0	0	0	0	0	0	0
Lannea welwitschii	0	0	0	0	1	0	3	1	0	0	0	0	0	1	1	0	2	0	0
Leptaulus daphnoides	5	0	3	3	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0
Leptonychia pubescens	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Lonchocarpus sericeus	0	0	0	0	0	0	0	1	0	5	0	0	1	0	0	0	0	0	1
Lophira alata	1	0	2	5	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0
Macaranga barteri	0	0	0	0	0	5	1	3	0	0	31	22	1	6	0	0	0	0	0
Macaranga heterophylla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macaranga hurifolia	0	0	0	1	0	0	0	0	0	0	35	15	0	0	0	0	0	0	0
Maesobotrya barteri	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0
Mammea africana	1	2	0	13	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Manilkara obovata	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maranthes chrysophylla	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maranthes glabra	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mareya micrantha	0	2	0	0	1	0	4	2	0	0	0	1	0	0	0	0	0	0	0
Margaritaria discoidea	3	0	0	0	0	1	0	0	0	0	2	1	0	2	0	4	0	0	1
Massularia acuminata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Memecylon lateriflorum	1	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microdesmis puberula	2	3	2	2	31	0	2	0	0	0	0	3	0	0	0	0	0	0	0
Milicia excelsa	1	0	2	0	0	0	0	1	0	0	0	1	2	0	0	0	1	0	0
Milicia regia	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Monodora myristica	2	2	0	1	10	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Morinda lucida	0	0	0	0	0	0	0	0	0	2	0	0	0	0	9	2	1	0	2
Morus mesozygia	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0
Musanga cecropioides	0	0	0	1	1	1	6	0	0	0	30	22	5	0	0	0	0	0	0

Land use	Forest								Farm mosaic									Plantation/ farm	
block	A		B		C		D		A		B		C		D			A	
square	1	2	7	8	13	14	20	21	3	4	9	10	15	17	22	23	24	5	6
Myrianthus arboreus	1	0	2	0	3	0	6	3	0	0	0	2	0	0	1	1	0	0	0
Myrianthus libericus	6	1	10	1	12	1	1	0	0	0	1	1	1	0	0	0	0	0	0
Napoleonaea vogelii	2	1	0	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Nauclea diderrichii	1	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
Nauclea pobeguinii	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Neolemonniera clitandrifolia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nesogordonia papaverifera	0	0	0	0	3	0	5	5	0	0	0	0	0	0	0	0	0	0	0
Newbouldia laevis	0	0	0	0	3	0	3	0	0	0	0	0	2	0	0	0	0	0	0
Newtonia duparquetiana	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Omphalocarpum ahia	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ongokea gore	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ouratea calophylla	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxyanthus speciosus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panda oleosa	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parinari excelsa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parkia bicolor	2	1	1	2	1	0	2	6	0	0	2	0	0	0	0	0	0	0	0
Pausinystalia lane-poolei	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pentadesma butyracea	0	2	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petersianthus macrocarpus	4	0	1	0	2	2	1	0	0	0	1	1	1	0	0	0	0	0	0
Phyllocosmus africanus	3	1	0	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0
Picralima/Hunteria spp.	1	3	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piptadeniastrum africanum	0	1	3	2	7	1	2	5	0	0	2	2	0	0	0	0	0	0	0
Pouteria altissima	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pouteria aningeri	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Protomegabaria stapfiana	8	3	33	8	2	2	0	0	0	0	4	1	0	1	0	0	0	0	0
Pseudospondias microcarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Psydrax subcordata	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Pterygota macrocarpa	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pycnanthus angolensis	5	2	1	1	2	2	2	1	0	0	0	4	1	0	2	1	0	0	0
Rauvolfia vomitoria	0	0	0	0	0	0	1	0	0	0	0	1	2	1	0	1	1	0	0
Rhodognaphalon brevicuspe	5	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Ricinodendron heudelotii	0	0	1	0	2	0	9	2	0	3	1	1	1	0	0	0	0	0	0
Rinorea oblongifolia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rothmannia hispida	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rothmannia whitfieldii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scaphopetalum amoenum	0	6	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schefflera barteri	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scottellia klaineana	5	7	6	9	3	5	2	1	0	0	1	0	0	0	0	0	0	0	0
Scytopetalum tieghemii	8	3	7	10	7	2	0	1	0	0	0	0	0	0	0	0	0	0	0
Shirakiopsis aubrevillei	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Soyauxia grandifolia	0	0	0	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Soyauxia velutina	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spathandra blakeoides	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spathodea campanulata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Sterculia oblonga	2	1	0	0	3	0	3	3	0	0	0	0	0	0	0	0	0	0	0
Sterculia rhinopetala	4	0	0	0	16	0	6	3	0	0	0	0	0	0	0	0	0	0	0
Sterculia tragacantha	0	0	0	0	0	0	0	1	0	0	8	3	3	2	0	0	1	0	0
Strephonema pseudocola	1	2	4	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0
Strombosia glaucescens	24	11	7	10	4	9	4	1	0	0	0	0	0	0	0	0	0	0	0
Symphonia globulifera	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Synsepalum afzelii	0	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Synsepalum brevipes	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synsepalum ntimii	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tabernaemontana spp.	5	0	0	0	7	0	0	0	0	0	2	7	0	6	0	0	0	2	0
Terminalia ivorensis	0	0	0	0	0	0	0	0	0	0	4	0	3	1	1	2	1	0	0
Terminalia superba	1	0	1	0	1	2	3	2	0	0	2	0	1	1	1	0	0	0	0
Tetrorchidium didymostemon	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tieghemella heckelii	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Treculia africana	1	0	1	0	3	2	0	2	0	0	0	0	0	2	0	0	0	0	0
Trema orientalis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tricalysia discolor	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tricalysia macrophylla	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichilia monadelpha	0	1	6	3	5	2	6	9	0	0	0	1	0	0	0	0	0	0	0
Trichilia prieuriana	8	0	1	1	1	0	14	11	0	0	0	1	0	0	0	0	0	0	0
Trichilia tessmannii	0	0	1	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0
Trichoscypha arborea	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Trilepisium madagascariense	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Triplochiton scleroxylon	0	0	0	0	2	0	13	3	0	0	0	0	0	1	0	0	0	0	0
Turraeanthus africanus	0	0	0	0	0	0	6	6	0	0	0	0	0	0	0	0	0	0	0
Uapaca guineensis	0	0	20	11	0	13	0	1	0	0	2	0	0	0	0	0	0	0	0

Land use	Forest								Farm mosaic									Plantation/ farm	
block	**A**		**B**		**C**		**D**		**A**		**B**		**C**		**D**			**A**	
square	**1**	**2**	**7**	**8**	**13**	**14**	**20**	**21**	**3**	**4**	**9**	**10**	**15**	**17**	**22**	**23**	**24**	**5**	**6**
unidentified	1	0	2	2	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Uvariodendron angustifolium	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vitex spp.	3	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	0	0
Warneckea cinnamonoides	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Warneckea guineense	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
Xylia evansii	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xylopia quintasii	1	1	0	1	3	5	0	3	0	0	0	0	0	0	0	0	0	0	0
Xylopia sp. cf. pynaertii	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xylopia staudtii	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xylopia villosa	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Zanthoxylum spp.	0	0	1	0	3	1	8	4	0	0	0	0	0	0	0	0	0	0	0

Appendix 3

Landcover classification from Forestry Commission GIS landcover map, and how it relates to my land-use classes and districts.
All areas are in square kilometres.

FC landcover classes		**My land-use classes**		**District**							**Total**
Value	***Landcov***	**Chapter 3**	**Chapter 7**	**Ahanta West**	**Birim North**	**Kwae Bibirem**	**Mpohor Wassa**	**Shama Ahanta**	**Twifo Heman**	**Wassa West**	
1	Moderately closed tree (>15 trees/ha) canopy with herb and bush cover	Farm/thicket with moderate tree canopy	Farm mosaic (with trees)	85	762	683	959	0	840	1,168	**4,498**
2	Moderately dense herb/bush with scattered trees (<15 trees/ha)	Farm/thicket with few trees	Farm mosaic (few trees)	350	163	208	353	299	197	629	**2,200**
12	Mosaic of thickets & grass with/without scattered trees	Farm/thicket and grassland	Farm mosaic (few trees)					26		9	**35**
3	Closed forest (>60 %)	Closed forest	Forest	55	122	91	664		195	578	**1,704**
6	Open forest (<60 %)	Disturbed forest	Forest		3	62	34		6	98	**203**
10	Planted cover	Plantations	Plantation	60	1	79	63	6	58	84	**350**
8	Settlement	Settlement	Uncultivable	4				31		8	**42**
11	Rock	Rock	Uncultivable			26				6	**31**
14	Wetland	Wetland	Uncultivable	53						2	**55**
17	Lagoon	Unclassified/ cloud/open water	Uncultivable	4				10			**13**
4	Unclassified/cloud	Unclassified/ cloud/open water	Unknown		129						**129**
Total classified cultivable area				550	1,051	1,123	2,073	332	1,297	2,565	**8,990**
Total classified uncultivable area				61	0	26	0	40	0	15	**142**
Classified cultivable area as % of classified area											**98%**
Total cultivable area, including 98% of Unknown				550	1,178	1,123	2,073	332	1,297	2,565	**9,117**
Total area				611	1,180	1,149	2,073	372	1,297	2,580	**9,261**