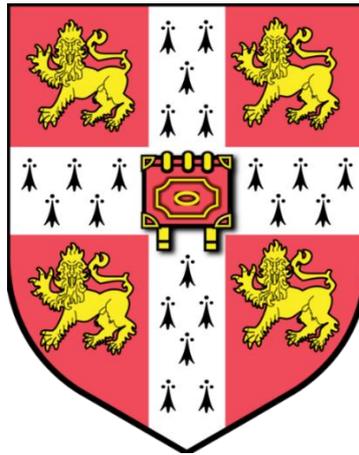


**Understanding the impacts of land-use change and  
management decisions within oil palm on  
insect assemblages in Peninsular Malaysia and Borneo**



Martina Faika Harianja  
Downing College

Insect Ecology Group  
Department of Zoology, University of Cambridge

**July 2023**

**This thesis is submitted for the degree of Doctor of Philosophy**



## **Declaration**

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

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

It does not exceed the prescribed word limit for the Biology Degree Committee.

## **Thesis summary**

### **Understanding the impacts of land-use change and management decisions within oil palm on insect assemblages in Peninsular Malaysia and Borneo**

Matina Faika Harianja

Being one of the world's biodiversity hotspots, Southeast Asia's rainforest is home to an extremely high density of species. However, the region has lost a high proportion of its rainforest as a result of logging and conversion to agriculture since the early 1970s, causing declines in species diversity across wide-ranging taxa. Studies have found that this loss has been driven by changes in microclimatic conditions, resources (for feeding, breeding, protection against predators, and refuge during extreme weather events), and connectivity. Invertebrates, in particular, have been found to decline in richness, abundance, and biomass with land-use change (although logging seems to have much less of an impact than converting forest to agriculture), causing concerns over the various functions they support in the ecosystem, including nutrient recycling, pollination, and biological control.

Despite an increasing number of studies, the effects of habitat change and alternative management options on many invertebrate taxa remain unknown, making studies assessing them a priority for informing targeted and successful conservation efforts. In this thesis, I investigated the impacts of rainforest logging and conversion to oil palm on semi-aquatic bugs (Gerromorpha, Hemiptera), representing aquatic communities, as well as management decisions by oil palm smallholders within existing plantations on butterflies (Rhopalocera, Lepidoptera), representing terrestrial

communities. Studies took place in Sabah, Malaysian Borneo for semi-aquatic bugs (**Chapters 2 – 4**) and Selangor, Peninsular Malaysia for butterflies (**Chapters 5 & 6**). In Selangor, I also studied the effects of environmental conditions at a smaller scale, particularly how habitat structure and complexity within smallholder plantations affected the resource-use behaviour of butterflies.

In **Chapter 2**, I developed length-biomass equations which can be used to predict the biomass of semi-aquatic bugs from their body lengths. Biomass can be a good indicator of ecosystem function but obtaining these data can be costly and difficult. I found that power regression equations gave the most accurate estimations of biomass across life stages, particularly when taking into account the body forms of semi-aquatic bugs. In **Chapter 3**, I investigated the impacts of forest conversion for logging and oil palm on semi-aquatic bug communities. Despite being sensitive to anthropogenic disturbance and ecologically important (they are predators of invertebrates and prey for some invertebrates and vertebrates), semi-aquatic bugs are little studied in the region. The abundance and species richness were lower following forest conversion, whilst total biomass was not affected, potentially indicating the robustness of prey availability for predators of semi-aquatic bugs. In **Chapter 4**, I assessed the effects of within-stream physical structure and maintaining forested margins around oil palm streams on semi-aquatic bugs. I found that, at the small-scale (along 10-meter transect), there was a significantly higher abundance of semi-aquatic bugs in oil palm streams with forested margins than those without, as well as significantly different community composition. However, species richness and total biomass remained unaffected.

In **Chapter 5**, I investigated the effects of smallholder management decisions, in terms of replanting and crop choices after replanting (monoculture vs polyculture), on

butterfly assemblages. I found that smallholders managed their plantations in widely different ways, resulting in differing habitat structure and complexity across plantations, but that broad management decisions (immature monoculture, immature polyculture, and mature monoculture plantations) did not significantly impact the density or species richness of butterflies. Despite this, finer scale differences, such as more understory vegetation, including nectar sources for adult butterflies, as well as polyculture farming, increased the density of butterflies. In **Chapter 6**, I studied the impacts of habitat structure and complexity, associated with management decisions, on the resource-use behaviour of butterflies. Although data were limited, I found that the novel methods developed for this chapter are promising and can provide detailed information at a small scale, which could be applied in other habitat types.

In conclusion, this thesis found that semi-aquatic bugs are sensitive to rainforest logging and conversion to oil palm. I also demonstrated that conservation management around streams (by maintaining forested margins) and within plantations (by maintaining understory vegetation including hostplants and nectar sources, as well as polyculture farming) can increase the abundance of semi-aquatic bugs and butterflies, respectively. I also demonstrated that agricultural habitats do not support forest-dependent species, at least within the two taxa studied here. Therefore, in addition to the evident negative impacts on many other taxa that existing studies have found, this confirms that preventing further forest conversion remains a priority for biodiversity conservation. Nevertheless, conservation management options I have identified open up opportunities to better support persisting species within altered habitats, particularly oil palm systems, potentially increasing biodiversity and associated ecosystem processes across the wider landscape.

## **Statement of contribution and information about funding source and research permit**

I (Martina F. Harianja) wrote Chapters 1 and 7 (General introduction and discussion) with inputs from my primary PhD supervisor (Prof. Edgar C. Turner). Data chapters (Chapters 2 – 6) are works resulting from collaborations. For all these data chapters, I led the studies, with Chapters 2 – 4 being based on samples collected as part of a previous project (the SAFE [Stability of Altered Forest Ecosystems] Project, Ewers et al., 2011), which were used here due to the impacts of COVID-19. Chapter 5 and 6 are based on entirely novel data that I collected, as part of the ESSTA (Ecological and Social studies in Smallholder Tropical Agriculture) Project, after COVID-19 restrictions had finished.

Chapter 2 has been published in *Entomologia Experimentalis et Applicata* ([Harianja et al., 2023a](#)), Chapters 3, 4, and 5 are under review by peer-review academic journals (*Freshwater Biology*, *Frontiers in Forests and Global Change*, and *Journal of Applied Ecology*, respectively), and Chapter 6 is in preparation for a resubmission.

Details for each data chapter are below:

### **Chapters 2 – 4:**

Conceptualisation of the studies were by Sarah H. Luke and Edgar C. Turner. The methodology for the collection of environmental data and semi-aquatic bugs was prepared by Sarah H. Luke, Holly Barclay, David C. Aldridge, William A. Foster, Edgar C. Turner, and Vun K. Chey. Environmental data and semi-aquatic bugs were collected by Sarah H. Luke and Holly Barclay. The methodology for biomass estimation was prepared by Martina F. Harianja, Edgar C. Turner, and Sarah H. Luke. Sorting, counting,

and identification of semi-aquatic bugs were conducted by Martina F. Harianja, with some documented references from Sarah H. Luke. Measurements of body lengths of semi-aquatic bug samples and biomass weighing were conducted by Martina F. Harianja. Data on environmental parameters and semi-aquatic bugs were curated by Sarah H. Luke and Martina F. Harianja, respectively. Data analyses and preparations of figures were conducted by Martina F. Harianja, with advice from Edgar C. Turner and Sarah H. Luke. Maps of the study sites were generated by Sarah H. Luke. Initial drafts for Chapters 2 – 4 were all written by Martina F. Harianja and were finalised with inputs from Edgar C. Turner, Sarah H. Luke, Holly Barclay, David C. Aldridge, William A. Foster, and Vun K. Chey. Two anonymous reviewers provided comments and suggestions for each chapter, which have helped improved the overall contents (six reviewers for Chapters 2 – 4 in total).

The Southeast Asia Rainforest Research Partnership, Danum and Maliau Basin Management Committees, the Stability in Altered Forest Ecosystems (SAFE) Project and Benta Wawasan provided permission for Sarah H. Luke and Holly Barclay to work in the different areas and gave logistical support in the field. Min Sheng Khoo, Johnny Larenus, Alice Milton, and the SAFE Project research assistants helped with data collections from the study sites. Jakob Damgaard, Lars Vilhelmsen, Henrik Enghoff helped Sarah H. Luke with identification of semi-aquatic bug samples in Copenhagen. Mick Webb, based in the London Natural History Museum, helped Martina F. Harianja to connect with Herbert Zettel and obtained access to semi-aquatic bug collections in the London Natural History Museum. Herbert Zettel provided help to Martina F. Harianja in identifying semi-aquatic bugs. Rahia Mashood, Jacek Zalewski, Daniel White, and Russell Stebbings helped with the technical matters for weighing the semi-aquatic bug

samples. Matthew Hayes contributed to the photographs of semi-aquatic bugs in the “Methods and materials” section of Chapter 2. Yoav Zemel and Lennie Wells, based in the University of Cambridge's Statistical Laboratory, helped Martina F. Harianja with biomass estimation using power regressions (Chapter 2) as well as coding for the reproducibility of Canonical Correspondence Analysis (CCA) outputs (Chapter 3 and 4) in R, respectively.

## **Chapter 5 & 6:**

Studies were conceptualised by Martina F. Harianja and Edgar C. Turner. Development of methods for the butterfly survey and environmental data were prepared by Martina F. Harianja, Edgar C. Turner, Jake Stone, and Sarah H. Luke. The establishment of smallholder network was conducted by Jake Stone, Martina F. Harianja, Wan Zaki Wan Mamat, Muhammad A. Hadi, and Badrul Azhar. All butterfly surveys for both chapters were conducted by Martina F. Harianja, Wan Zaki Wan Mamat, and Muhammad A. Hadi, with Jake Stone helping at the beginning of data collection for Chapter 6. Environmental data for Chapter 5 were collected by Jake Stone, Wan Zaki Wan Mamat, and Muhammad A. Hadi, whilst for Chapter 6 data were collected by Martina F. Harianja, Wan Zaki Wan Mamat, and Muhammad A. Hadi. Environmental data for Chapter 5 were curated by Jake Stone and Martina F. Harianja, whilst for Chapter 6 data curation was by Martina F. Harianja. Butterfly data was curated by Martina F. Harianja. Data analysis and preparation of figures and tables were conducted by Martina F. Harianja, with advice from Edgar C. Turner. Maps of the study sites were generated by Jake Stone. Initial drafts were written by Martina F. Harianja, and was finalised with

inputs from Edgar C. Turner, Jake Stone, Badrul Azhar, Wan Zaki Wan Mamat, Muhammad A. Hadi, and Sarah H. Luke. Four anonymous reviewers provided feedback for each chapter, which have helped improved the contents (eight reviewers for Chapters 5 and 6 in total).

Oil palm smallholders in Banting, Selangor, Malaysia provided permissions to Martina F. Harianja, Jake Stone, Wan Zaki Wan Mamat, and Muhammad A. Hadi to access their plantations. Syafiq Salehuddin and Valentine Reiss-Woolever assisted with establishment of the study plots. Muhammad Syafiq Yahya and Sharifah Nur Atikah provided guides which have helped with the identification of understory vegetation within the smallholding plantations. Matthew Lewis helped Martina F. Harianja with trialling the method used in Chapter 6.

## **Funding source information**

**1. Work for Chapters 2 – 4:** The Jardine Foundation and the Cambridge Trust provided funding for Martina F. Harianja, the Natural Environment Research Council (NERC) (studentship 1122589), Proforest, the Varley Gradwell Travelling Fellowship, the Tim Whitmore Fund, the Panton Trust, the Cambridge University Commonwealth Fund, and the Hanne and Torkel Weis-Fogh Fund provided funding for Sarah H. Luke, and the S.T. Lee Fund funded Holly Barclay.

**2. Work for data Chapter 5 & 6:** The Jardine Foundation, the Cambridge Trust, and Tim Whitmore Fund provided funding for Martina F. Harianja, the Biotechnology and Biological Sciences Research Council (BBSRC) provided funding for Jake Stone (USN: 304338625), and BBSRC (BB/T012366/1) funded plot establishments in smallholding oil palm plantations in Banting, Selangor, Peninsular Malaysia.

## **Research permit information**

**1. Work for Chapters 2 – 4:** The Sabah Biodiversity Council granted permission for Sarah H. Luke and Holly Barclay to conduct research in Sabah, Malaysia (access licence reference numbers, JKM/MBS.1000-2/2(03), JKM/MBS.1000-2/2(37), JKM/MBS.1000-2/2(68)).

**2. Work for Chapter 5 & 6:** The Economic Planning Unit (EPU) of Malaysia's Prime Minister's Department provided permission to conduct research in Banting, Selangor, Malaysia for Martina F. Harianja (Ref: EPU 40/200/19/3727/9) and Jake Stone (Ref: MEA 40/200/19/3705).

## **Data set and analytic codes availability statement**

All data sets and analytic codes used in this thesis are available at Zenodo repository:

Chapter 2: [Data set and analytic codes supporting “Length-biomass equations to allow rapid assessment of semi-aquatic bug biomass in tropical streams”](#) (Harianja et al., 2022),

Chapter 3: [Data set and analytic codes supporting "The effects of land-use change on semi-aquatic bugs \(Gerromorpha, Hemiptera\) in rainforest streams in Sabah, Malaysia"](#) (Harianja et al., 2023b),

Chapter 4: [Data set and analytic codes supporting "The impacts of within-stream physical structure and riparian buffer strips on semi-aquatic bugs in Southeast Asian oil palm"](#) (Harianja et al., 2023c),

Chapter 5: [Data set and analytic codes supporting "How do management decisions impact butterfly assemblages in smallholding oil palm plantations in Peninsular Malaysia?"](#) (Harianja et al., 2023d),

Chapter 6: [Data set and analytic codes supporting "Direct observation to assess the effects of habitat structure and complexity on resource-use behaviour of butterflies: a study case in smallholding oil palm plantations in Peninsular Malaysia"](#) (Harianja et al., 2023e).

## Acknowledgements

I thank my PhD supervisors, Prof Edgar Turner and Prof Sarah Luke, for their immense support throughout my studies. Ed and Sarah have been very helpful, and I am grateful for all the advice, encouragement, patience, and support they have provided and shown. Working on the semi-aquatic bug samples collected from Borneo and conducting fieldwork in Peninsular Malaysia have been very rewarding, and all these have been possible through opportunities that Ed and Sarah have opened for me.

I applied for a PhD mainly because of the encouragement from my late father, who was very motivated to see me pursue further studies. But after a couple of months of starting my studies, the COVID-19 pandemic happened, and my dad passed away in March 2021. It was devastating, but families (from my father's and mother's sides, including my aunt, who recently passed away) and friends helped us (my mum and my siblings) during that time. I am thankful to my PhD supervisors who provided their support, the Jardine Foundation that covered my flight to my home country and my quarantine soon after returning to the UK, and my friends who called and prayed for me (particularly Chakrita, Ben, Jenny, and Antony) as well as providing quick answers for all my quarantine-related questions (especially Zunda). Throughout my studies, I am grateful to my mum, sisters, brother, brother-in-law, and nieces for their prayers, endless support, and humour, and who are always available for calls.

I also thank my PhD advisors, Prof David Aldridge and Prof Lynn Dicks, for their detailed and constructive criticism on my project plans and reports throughout the years. I am also grateful to all the collaborators and contributors to my PhD research projects, who have provided advice and help (details are in the “**Statement of contribution**”

[page vii – xi]). I thank Dr Badrul Azhar (my supervisor during my fieldwork, and who is based in the UPM [Universiti Putra Malaysia]) for his support, friendliness, and generosity. I still remember the time he spent driving and taking my colleagues and me to the UPM Forest Plot. I thank the EPU (Economic Planning Unit) of Malaysia's Prime Minister's Department for the permission to conduct research in Banting, Selangor, Malaysia, and Mr Muhammad Jawad bin Tajuddin for his kind support throughout the process. I am lucky to have had brilliant colleagues and great company during my fieldwork: Zaki, Amir, and Jake (and I still laugh very hard over pictures and videos I took during the fieldwork). I am thankful for consent from the farmers in Banting to access their plantations and conduct research. I also thank Wak (Pak Tabingon) and his family for hosting my colleagues and me in Banting. My friends and people whom I met in Banting have enriched my fieldwork experience, especially: Syafiq and Sharifah (for helpful weed identification catalogue), Sui Peng and her sister Sui Kim (for taking Jake and me to hike Gunung Angsi and introducing us to the most delicious beverage in the world [coconut shake!]), Woei Ong (for friendliness and a beautiful Birdwing butterfly pin), and Dr Norhisham who showed Jake and me the UPM butterfly collections. I am also thankful for all the friendly faces in the Insect Ecology Group (who helped with coding and project related matters), especially Matt Hayes and Russell, who helped me several times with my work on semi-aquatic bug samples. I also thank Helen Waters, a past member of the group, who guided me in using R during my master's, so I can use the program better. I thank Dr James Herbert-Read and Dr Konstans Wells for their helpful feedback on this thesis.

I am grateful for the scholarship from the Jardine Foundation and the Cambridge Trust. I am also thankful for a recommendation letter written by late Dr RC Hidayat

Soesilohadi, who was very supportive with my PhD application. I thank Olga and Dion, who shared information and advice about the scholarship, and Ratih, who let me stay in her place before my scholarship interview and a meeting with my supervisors in Cambridge. I am thankful for my uncle, who is very kind and drove me to and from airports in Jakarta. I thank the Tim Whitmore Fund and the Jardine Foundation for funding my fieldwork and the Biotechnology and Biological Sciences Research Council (BBSRC) that have contributed to the fieldwork costs. I thank my college (Downing College), Arfah Nasution Memorial Fund, the Cambridge Philosophical Society, and the Jardine Foundation for funding my attendance at academic conferences during my studies. I thank Dr Antoni Ferraz de Oliveira, my first tutor at Downing, for his warm welcome at the start of my studies and his support for my funding application to present at the BES (British Ecological Society) conference in 2019. I thank all the course instructors in the university's training programs and advisors in the university's career service who have shared their knowledge and experience, which have enriched my studies and helped me prepared for the next steps.

I am grateful for the Cambridge Indonesia Association that has made me find friends during my time in Cambridge, especially: Chakrita (for prayer and introducing me to things and some people in Cambridge) and Ben (for prayer and chats on insects), Jenny and Antony (for prayer, warmth, and kindness, including support when my dad passed away), Dewi (for delicious cooking), Hanif and Pina (for humour and kindness, including for letting me stayed in their place in between my fieldwork), and Tante Renny and Om Douglas (for friendliness and generosity through delightful Indonesian dishes and invitations!). I am also glad to have been part of the St Mark's choir, where I can join a lovely group and its Sunday services, which I always find uplifting. I am grateful

for my time in Cambridge and cherish all the friendships and experiences (including those I did not mention here). I have learned a lot from everyone I have interacted with.

***“Great are the works of the Lord, studied by those who love them.” - Psalm 111: 2***

## Table of contents

Title page.....	i
Declaration.....	iii
Thesis summary.....	iv
Statement of contribution and information about funding source and research permit.....	vii
Data set and analytic codes availability statement.....	xii
Acknowledgements.....	xiii
<b>Chapter 1:</b> General introduction – threats to biodiversity and ecosystem functions in Southeast Asia, with an emphasis on insects and Peninsular Malaysia and Borneo.....	1
<b>Chapter 2:</b> Length–biomass equations to allow rapid assessment of semi-aquatic bug biomass in tropical streams.....	33
<b>Chapter 3:</b> The effects of land-use change on semi-aquatic bugs (Gerromorpha, Hemiptera) in rainforest streams in Sabah, Malaysia.....	85
<b>Chapter 4:</b> The impacts of within-stream physical structure and riparian buffer strips on semi-aquatic bugs in Southeast Asian oil palm.....	138
<b>Chapter 5:</b> How do management decisions impact butterfly assemblages in smallholding oil palm plantations in Peninsular Malaysia?.....	179
<b>Chapter 6:</b> Direct observation to assess the effects of habitat structure and complexity on resource-use behaviour of butterflies: a study case in smallholding oil palm plantations in Peninsular Malaysia.....	229
<b>Chapter 7:</b> General discussion.....	265
References.....	279

# **Chapter 1: General introduction – threats to biodiversity and ecosystem functions in Southeast Asia, with an emphasis on insects and Peninsular Malaysia and Borneo**

## **Abstract**

Southeast Asia is one of the most biodiverse regions on earth but has experienced among the highest rates of forest conversion. Modifications of natural systems by humans in the region have altered environmental conditions, the structure of ecological assemblages and ecosystem processes. A growing number of studies have assessed the impacts of anthropogenic disturbance on taxa, but much attention has focussed on charismatic vertebrates, such as elephants, orangutans, and tigers, with other taxa, such as insects (Hexapoda, Arthropoda), which carry out numerous ecological functions, often being understudied. In this chapter, I lay out a general overview of the state of biodiversity in Southeast Asia, including existing studies on insect diversity, as well as persisting threats to wildlife in the region, including insects. I also discuss the functions insects play in the environment and explain the importance of conservation of insects for the stability of ecosystem functioning, including provision of ecosystem services for humans. To complete this chapter, I provide taxonomic, life history, and ecological information on the two focal taxa investigated in this thesis: semi-aquatic bugs (Gerromorpha, Hemiptera) and butterflies (Rhopalocera, Lepidoptera). I finish with summaries of all data chapters (Chapter 2 – 6).

## **1.1 | Current state of biodiversity and ecosystem functioning in Southeast Asia**

### **1.1.1 What is the level of biodiversity in Southeast Asia?**

Southeast Asia is estimated to have had (prior to conversion) primary vegetation covering as large an area as 4,307,800 square kilometres, with 56,120 and 6,220 plant and vertebrate species found in the region, respectively (Myers et al., 2000 - this estimation included Yunnan province in China, eastern Bangladesh, and north-eastern India, which are considered parts of Indo-Burma). Among these species, 29,332 and 2,276 endemic plant and vertebrate species have been recorded (Myers et al., 2000). Information on the exact number of invertebrate species found in the region is lacking (Giam et al., 2010), but it is estimated to be much higher than the vertebrate species, with insects (Hexapoda, Arthropoda) making up around 95% of all species (Myers et al., 2000).

Sodhi et al. (2004) outlined several drivers for the extremely high level of biodiversity in Southeast Asia, of which the rise and fall of sea level throughout geological times is thought to be the most important factor (Sodhi et al., 2004). Geographical isolation during times of high sea level (Sodhi et al., 2004) are likely to have driven reproductive isolation and speciation, while falls in sea level may have reconnected populations and facilitated migration into the region from temperate Northern Asia (Sodhi et al., 2004). Finally, the warm climate and high level of

precipitation in the region is likely to have allowed organisms to grow and reproduce throughout the year, potentially resulting in high speciation rates (Sodhi et al., 2004).

### **1.1.2 Ecology of tropical rainforests**

Tropical rainforests in Malaysia are evergreen and characterised by humid microclimate and tall tree canopy (45 meters or more) (Alias, 1995; Edwards et al., 2014), with rains that fall throughout the year (Hewitt et al., 2010). There are no distinct differences in radiation, temperature, or precipitation within a year (Kumagai et al., 2005). The average annual air temperature and precipitation in the rainforests in Southeast Asia is 27-degree Celsius and 2,800mm, respectively (Daisuke et al., 2013). Southeast Asian lowland rainforests are dominated by broadleaf trees of the Dipterocarpaceae family (Brown & Whitmore, 1992; Hewitt et al., 2010; Whitmore, 1984), and contain epiphytes (Alias, 1995). Malaysia's rainforest is estimated to contain over 8,000 flowering plant species, 200 mammal species, 600 bird species, 110 snake species, and thousands of insect species (Alias, 1995).

Rainforests play numerous functions, ranging from provision of oxygen and food sources for both terrestrial and aquatic organisms (e.g., from inputs of leaf litters into waterways), carbon sequestration, control of surface runoff, and water conservation (Kumagai et al., 2005). For wildlife, rainforests provide more microhabitats than any other biomes, one key reason for the extremely high biodiversity they contain, and why disruption to or removal of rainforests causes declines in species diversity (Gardner et al., 2009; Spitzer et al., 1993). However, Southeast Asia lost about 14.5% of its forest cover between 2000 and 2010 (Hughes, 2017; Miettinen et al., 2011), compared to the

73% of forest cover across the total land area that was still present in the region in 1973 (Hughes, 2017).

## **1.2 | Effects of logging and oil palm in Southeast Asia**

### **1.2.1 Effects of logging**

Globally, intact forest landscapes (continuous forest with no evidence of human influence and a minimum size of 500 square kilometres) have declined by 1.5 million square kilometres since the 2000s (Kan, et al., 2023). The major drivers for this loss are logging, agriculture, mining, and construction of facilities for energy, and all these factors are influenced by international demands (mostly from timber markets [51%] and mining and energy needs [26%]) (Kan et al., 2023). In Southeast Asia, the rate of deforestation is the highest compared to other tropical regions (Giam et al., 2010), and logging (with Dipterocarps dominating markets of tropical timbers, Krishnapillay, 2004) has been one of the main drivers (Wilcove et al., 2013). Historically, the growth of industrial-level logging at the global scale started around the 1940s, i.e., post second world war, and was characterised as clear-cutting (Shearman et al., 2012). In Southeast Asia, industrial-level logging started around the 1970s (Gaveau et al., 2014), and the region is the main producer of tropical timbers globally (Asner et al., 2009). The main product from logging is timber for infrastructure and furniture, while the rest is used for production of paper (Pasternack et al., 2022). In Sabah (one of the states in Malaysian Borneo), 47% of the land area (around 36,049 km square) is categorised as Permanent Forest Estate (PFE), but 74% of this is used as production forest, while the rest is

protected (Hewitt et al., 2010). In the eastern part of Sabah, most of the cleared land has been planted with oil palm, with other areas are used for timber production (Hewitt et al., 2010).

Logging alters the vertical and horizontal structural complexity of forests, with closed canopy conditions being lost when trees are cut down for timber, (Riutta et al., 2018), causing the loss of microhabitats for canopy-dwelling taxa (Willott et al., 2000). The recovery of canopy cover to its initial state can take decades. Furthermore, the development of road access can cause destruction to the vegetation where the roads are developed, as well as compaction of topsoil and subsoil, reducing the amount of water stored below ground (Douglas, 2022). Such compaction also results in more surface runoff and hence erosion (Douglas, 2022). Furthermore, logging can change the vegetation composition of an area (Hamer et al., 2003), with some species benefitting from the higher light (such as climbers/ vines), but others declining (Edwards et al., 2014). One study conducted in Sabah, Malaysian Borneo found a differing assemblage composition of fruit-feeding butterflies between primary forest and forest that had been selectively logged 10-12 years before, but there was no significant difference in the diversity of butterflies (Hamer et al., 2003). In particular, the selectively logged forest was dominated by butterflies that preferred gaps, with reduction of butterflies that preferred shade (Hamer et al., 2003).

In addition to the above examples, there is mounting evidence that logging in the region has driven a decline in species diversity (Gibson et al., 2011; Meijaard et al., 2020; Wilcove et al., 2013) and altered community composition across terrestrial and aquatic taxa (Wilcove et al., 2013; Luke et al., 2014). Apart from of the loss of microhabitats and resources required by wildlife because of logging, the creation of

logging roads has made it easier for poaching to take place (Edwards et al., 2014). The high rate of rainforest loss in Southeast Asia represents a significant threat to biodiversity, particularly because of the high number of species and level of endemism in the region (Myers et al., 2000). For invertebrates (including insects), understanding this issue is urgent because, despite their many functions in the ecosystem, insects are understudied (Luke et al., 2023) and rarely legally protected (Strayer, 2006).

Besides affecting wildlife, anthropogenic disturbance on land and water often has impacts on humans as well. Many studies and cases have provided evidence for such cascading effects (e.g., Jha et al., 2013; Wu et al., 1999). For example, forest clearance around the great lake in Cambodia, resulted in lower fish catches (Dudgeon, 2000; Welcomme, 1979). However, despite all these impacts, logged forests can still be valuable for conservation and provide more and better microhabitats and resources for wildlife than agricultural landscapes or even primary forests (particularly that are isolated or surrounded by other land-uses, causing loss of connectivity) (Edwards et al., 2014). For example, some species can benefit from the canopy gaps created from timber harvesting (Edwards et al., 2014). Logged forests also can store more carbon (Riutta et al., 2018) and often have lower local air temperatures than agricultural landscapes (Edwards et al., 2014). Nevertheless, although some species appear to benefit from logging, other taxa can still be disadvantaged. Therefore, further studies assessing the impacts of logging on understudied taxa are needed.

## 1.2.2 Effects of rainforest conversion to oil palm

The leading agricultural drivers for rainforest conversion in Southeast Asia are rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) cultivation (Wilcove et al., 2013). Palm oil is the most consumed vegetable oil source worldwide (210Mt), used as cooking oil, feed for animals, ingredients for food and beverages, cosmetics, and biofuel (Meijaard et al., 2020). Additionally, oil palm is the most efficient source of vegetable oil (in terms of oil production per hectare), far higher than other oil-producing crops, such as soybean and rapeseed (Meijaard et al., 2020). In particular, the annual average oil palm yield is 4.2 tons ha<sup>-1</sup> year<sup>-1</sup>, whilst soybean and rapeseed produce 0.4- and 1.2-tons ha<sup>-1</sup> year<sup>-1</sup>, respectively (Comte et al., 2012). Globally, the highest production of palm oil occurs in Malaysia and Indonesia (accounting for 70% of total crop area globally, Gómez et al., 2023). Oil palm was first introduced to Southeast Asia in the 1950s from tropical Africa (Meijaard et al., 2020) and its global area coverage has tripled since the 1980s (Comte et al., 2012). The initial expansion of oil palm resulted in large-scale deforestation and caused the loss of biodiversity (Foster et al., 2011; Meijaard et al., 2020). For example, the expansion of oil palm is calculated to have contributed to 50% of rainforest loss in Malaysian Borneo between 1972 and 2015 (Meijaard et al., 2020).

Species declines can be driven by a change in habitat features or loss of microhabitats. For instance, in Sumatra, Indonesia, rainforest conversion to rubber or oil palm changes the community composition of canopy ants (Nazarreta et al., 2020) and reduces the species richness, abundance, and average biomass (mg/ m<sup>2</sup>) of parasitoid wasps (Azhar et al., 2022). Such a loss or decline in species can reduce prey availability

for larger organisms, as well as impacting functions that these species contribute to in the system, such as being predators and decomposers (ants) or predators and parasitoids of pests (wasps).

How plantations are managed have impacts on the environment, affecting biodiversity and ecological processes. Management of oil palm plantations include management during replanting, as well as soil, crop, and within-plantation management. Oil palm is a perennial crop that is replanted approximately every 25 years (Snaddon et al., 2013). Canopy cover and complexity of the crop develops as oil palm ages, helping to maintain relatively cooler microclimatic conditions, particularly in comparison to newly replanted or younger plantations (Luskin & Potts, 2011). Consequently, less extreme microclimatic conditions in older plantations can support a wider range of species, particularly those that depend on a relatively cool temperature and higher humidity. For instance, a study conducted in industrial oil palm plantations in Sumatra, Indonesia have shown that mature plantations can support more frog species than immature plantations (Kurz et al., 2016).

The application of fertilizers as well as herbicides and pesticides within oil palm plantations are known to be harmful for soil and aquatic biota (Darras et al., 2019; Izah et al., 2016), and cause health problems to people who spray the chemicals (Sulaiman et al., 2019). Furthermore, different management of within-plantation conditions by growers can have varying impacts on microclimatic conditions and local organisms. For instance, some growers leave understory vegetation in their plantations (Luke et al., 2020; Tohiran et al., 2019), while others regularly cut or spray them with herbicides (Allen et al., 2015), causing loss of microhabitats and resources for some species (e.g., Azhar et al., 2015; Luke et al., 2019a). Additionally, leaving the plantation floor clear of

understory plants can increase surface runoff, which results in the loss of material that is important for soil cycling, such as silicon (Greenshields et al., 2023).

Large-scale oil palm plantations tend to grow oil palm only (monoculture), while smallholders also grow oil palm as a polyculture (Shuhada et al., 2020). Polyculture is often practiced during the early years of oil palm cultivation to gain additional income before oil palm begins to produce fruit bunches, usually at three years of age. As the oil palm matures, smallholders generally switch to monoculture. Such variability in crop management can affect the population dynamics of species occupying the agricultural landscape. For instance, oil palm polyculture with fruit crops can support higher numbers of fruit-feeding butterfly species (Asmah et al., 2017) as well as butterflies that use other parts of the crop as their host plants, such as caterpillars of *Erionota thrax* (Hesperiidae) that feed on banana leaves (Okolle et al., 2006).

### **1.2.3 Ecology of and threats to lotic ecosystems in the region (streams and rivers)**

Of the global land surface, freshwater ecosystems cover only 2.3% (Reid et al., 2019), with insects in the order of Diptera being the major freshwater animal taxon worldwide (Covich et al., 1999). Tropical streams and rivers in Southeast Asia (including Malaysia) are usually permanent (filled with water all year long) and provide a habitat for numerous species (Dudgeon, 2000). For instance, the Kapuas River in Borneo is known to contain 290 species of fishes (Dudgeon, 2000). Additionally, there are many terrestrial species that are closely linked to riverine habitats in the region, including proboscis monkeys

(that occupy trees along riverbanks), tapirs, elephants, and rhinoceros (Dudgeon, 2000). However, the exact number of species of freshwater invertebrates in Southeast Asia is unknown (Dudgeon, 2000, Strayer, 2006). Some common freshwater invertebrates that can be found in the region include polychaetes, amphipods, isopods, bivalves, gastropods, decapods (crabs, shrimps, prawns), and a range of freshwater insects (e.g., chironomids, caddisflies, hemipterans, plecopterans, damselflies and dragonflies, and moths) (Dudgeon, 2000).

Within lotic systems, invertebrates play numerous functions, such as being food for other species or predators of other organisms, litter decomposers, and contribute to nutrient cycling (Covich et al., 1999; Spence & Andersen, 1994; Macadam & Stockan, 2015; Malmqvist, 2002). For instance, benthic invertebrates are known to decompose approximately 20 – 73% of leaf litter that enter headwater streams (Covich et al., 1999). Furthermore, due to their high sensitivity to environmental disturbance, such as metal pollution, some aquatic insects are good indicators of stream condition (e.g., those in the order of Ephemeroptera, Plecoptera, and Trichoptera, Batty et al., 2010), and are used as a tool to assess water quality (such as the Biological Monitoring Working Party scores, Maltby et al., 2010). Finally, freshwater insects also provide many other services for humans, including being inspiration for producing arts and literatures (Macadam & Stockan, 2015).

Environmental conditions of streams and rivers are affected by several factors, ranging from climate, geology, topography, to modifications by humans (Tang et al., 2020). In Southeast Asia, monsoon winds have important roles in the ecology of streams and rivers. They can control the amount of precipitation and water flowing in streams (“seasonal flow”), causing drought during the dry season in some areas (although the

dry season is generally not distinct in tropical wet climatic areas [Kishimoto-Yamada & Itioka, 2015]), but flooding during the wet season (Dudgeon, 2000). Such dynamics can change the species assemblage between seasons, although an aseasonal pattern in assemblage composition is more common in areas with a tropical wet climate (Kishimoto-Yamada & Itioka, 2015), where there are no significant differences in macroclimatic conditions throughout the year (Kumagai et al., 2005).

The condition of catchment and riparian areas (areas that surround a water body) can also have a large influence on freshwater biota (Dudgeon, 2000; Tang et al., 2020). This is because freshwater systems receive impacts and inputs from the catchment and riparian areas (“land-water continuum”), which then affect freshwater assemblages. For instance, studies have found that deforestation alters the dynamics of seasonal flow in tropical Asian streams by increasing surface runoff, which then causes sedimentation and increases the intensity of flash floods during the wet season (Dudgeon, 2000). Additionally, erosion and siltation increase water turbidity and reduce primary productivity (Dudgeon, 2000; Welcomme, 1979), as well as changing the physical characteristics of freshwater systems (such as a reduction in channel width and depth due to sedimentation, Luke et al., 2017a). Consequently, aquatic species that are highly dependent on the natural state of water characteristics or specific features within a stream can be lost or reduced in abundance (e.g., Kano et al., 2019; Konopik et al., 2015; Luke et al., 2017b; Mercer et al., 2014). For instance, forest loss can cause declines in fish species, due to siltation and loss of allochthonous inputs, such as woody debris and leaf litter (Lo et al., 2020). Considering all these factors, impacts of anthropogenic disturbances therefore can be more severe on freshwater than terrestrial ecosystems, with

the rate of loss of freshwater species being up to three times higher than their terrestrial counterparts (Birnie-Gauvin et al., 2023).

Cultivation of oil palm also impacts streams and rivers. Oil palm plantations have ditches for drainage and often have streams and rivers running through them. Runoff of nutrients and pollutants (such as herbicides, pesticides, and wastewater) into waterways can alter chemical and physical conditions of stream or river (Comte et al., 2012). Consequently, this can cause declines in species richness or abundance (e.g., Carvalho et al., 2018; Deere et al., 2022; Luke et al., 2017b), and altered assemblage or community composition of aquatic species (e.g., Chellaiah & Yule, 2018; Dias-Silva et al., 2020a). Furthermore, deforested riparian areas tend to cause more erosion, sedimentation (de Paiva et al., 2017), hotter water temperature (Rojas-Castillo et al., 2023), and result in lower allochthonous inputs for freshwater animals (Juen et al., 2016; Luke et al., 2017b; de Paiva et al., 2017; Rojas-Castillo et al., 2023). Considering all the above, understanding the specific impacts of oil palm management can help to improve efforts to increase the sustainability of palm oil production, as well as make it more effective by tailoring management options to the type of stakeholders (industry or smallholding).

Other threats to freshwater biota come from modifications of waterways by humans through abstraction, channelization, and dam constructions (Dudgeon, 2000). All these modifications can alter or reduce the flow regime of waterways, and impact freshwater species (Poff, 2009). For instance, construction of dams can alter the flood regime in rivers, which naturally occur during the wet season in monsoonal Asia (including Southeast Asia) (Dudgeon, 2000), limiting peak flow which river organisms are naturally adapted to (Dudgeon, 2000; Scott et al., 2019). Additionally, pollution, such as wastewater from agriculture, industries, and housing (Dudgeon, 2000) as well as

plastics (Azevedo-Santos et al., 2021), contaminate waterways and affect freshwater biota by changing or removing their microhabitats. Overharvesting (Dudgeon, 2000) and biomass burning of peat and rainforest (Chaturvedi & Mansi, 2022) are also threats to freshwater species in the region. Finally, climate change can exacerbate the existing impacts that are already caused by human actions (to Bühne et al., 2021; Dudgeon, 2000). For instance, increasing water temperature, which can result from both more-open conditions during forest disturbance as well as from the impacts of climate change, can affect the physiology and reproduction of fishes, potentially causing loss of sensitive species (Ficke et al., 2007).

### **1.3 | Conservation efforts in altered systems in Southeast Asia**

In addition to protecting intact forest areas, conservation efforts in Southeast Asia have been conducted within altered systems, such as logged forest and agricultural landscapes. To reduce the negative impacts of logging, approaches have been suggested, such as leaving old-growth fragments within logged forest areas as refuges for canopy-dwelling and temperature-sensitive taxa and preventing rapid conversion and loss of logged forest to other habitats (Edwards et al., 2014). Additionally, programs have been initiated to encourage and provide incentives for protection of forests, such as the REDD+ (Reduce Emissions from Deforestation and forest Degradation, and enhance carbon stocks), which include carbon credit schemes (Duchelle et al., 2018).

In the context of oil palm, The Roundtable on Sustainable Palm Oil (RSPO) was founded to improve the sustainability of palm oil production. The RSPO was founded in

2004 and provides advice (principles and criteria) for industries and smallholders on managing oil palm to promote the sustainability of its production, covering economic, environment, and social aspects (RSPO, 2018). Stakeholders (companies and smallholders) receive certification of their products once they fulfil the criteria set by the RSPO. For ecosystem health and biodiversity, several recommendations are included in Principle 7, ranging from integrated pest management (IPM), waste, soil, and water management, reduction of air pollution and greenhouse gas (GHG) emissions, prohibition of fire use, as well as advice related to practices for land clearing (RSPO, 2018). For water management, the principle and criteria are accompanied by the “RSPO Manual on BMPs (Best Management Practices) for the management and rehabilitation of riparian reserves”, which provides detailed advice and information on more-sustainable management of freshwater systems within plantations (Barclay et al., 2017).

Maintaining riparian buffer strips along streams/ rivers within plantations is included in the RSPO’s principle and criteria for water quality protection, bank stabilisation, flood protection, carbon storage and sequestration, and biodiversity conservation (Barclay et al., 2017). The size of riparian buffer strips within agricultural landscapes depends on the regulations within each country, but when absent, the RSPO recommends waterways to maintain or restore at least five meters of riparian buffer strips on each side of one to five-meter permanent water bodies, with larger buffers recommended for larger waterways (Barclay et al., 2017). However, the recommended minimum size of buffer strips for water quality protection and bank stability may not be sufficient to protect biodiversity (Barclay et al., 2017; Luke et al., 2019b), making assessments of the impacts of buffer strips on differing taxa an important conservation question to improve protection for wildlife.

## 1.4 | Knowledge gaps

Despite a growing number of studies assessing ecological impacts of anthropogenic disturbances on biodiversity, understanding of the responses to land-use change of several functionally important taxa, such as insects, is still lacking (Lo, et al., 2020). Furthermore, despite the potential conservation value of logged forests (Edwards et al., 2014; Struebig et al., 2013), there is still a gap in understanding of how differing taxa respond to logging. Addressing these gaps can improve strategies for biodiversity conservation. There are also gaps in understanding of the impacts of management within oil palm systems on biodiversity and ecosystem processes (Popkin et al., 2022).

Widely differing management practices within industrial and smallholding oil palm plantations can have substantial but different effects on local species. For example, the impacts of replanting on persisting taxa within oil palm plantations are relatively understudied (Popkin et al., 2022). Understanding of how environmental disturbance and management decisions affect different taxa is required urgently to make restoration projects successful. To achieve this goal, indicator taxa are often used to simplify monitoring of different management approaches. However, comprehensive evidence, based on a wider range of taxa, is needed for understanding patterns, because protection that is based on a single species may not always benefit other taxa (Borgelt et al., 2022). This is because different species may have differing requirements. Similarly, varying management practices can result in different impacts, thus understanding how they can benefit different taxa is useful to improve conservation efforts.

## **1.5 | Ongoing ecological projects for improving biodiversity conservation in Southeast Asia**

There are several ongoing large-scale projects in Southeast Asia, aiming to assess and understand the impacts of rainforest conversion on biodiversity and ecological processes, as well as how oil palm plantations can be managed to be more hospitable for wildlife and maintain ecosystem functioning. These include the SAFE (Stability of Altered Forest Ecosystems) Project in Sabah, Malaysian Borneo (Ewers et al., 2011; <https://safeproject.net/>), the BEFTA (Biodiversity and Ecosystem Functions in Tropical Agriculture) Programme in Riau, Sumatra, Indonesia (Luke et al., 2020; <http://oilpalmbiodiversity.com/>), and the ESSTA (Ecological and Social studies in Smallholder Tropical Agriculture) Project in Peninsular Malaysia.

The SAFE Project is based on a collaboration among researchers (the South East Asia Rainforest Research Partnership (SEARRP), <https://www.searrp.org/>), the local government (Sabah Foundation, <https://www.ysnet.org.my/>), and an oil palm industry (Benta Wawasan, <https://www.bentawawasan.com.my/corporate/company-profile/>). Similarly, the BEFTA Programme is a collaboration between academic researchers and an oil palm industry (Sinar Mas Agro Resources and Technology Research Institute (SMARTRI), <https://smartri.id/home/>). Finally, the ESSTA Project is a collaboration between academic researchers and oil palm smallholders in Peninsular Malaysia. These large-scale research collaborations are important, not only to allow the extensive collection of the comprehensive data needed to understand the impacts of land-use change and management practices within agricultural landscapes on the environment and biodiversity, but also to provide a means by which results can be shared and

disseminated. This thesis benefits from the SAFE and the ESSTA projects, with Chapters 2 – 4 using semi-aquatic bug samples collected from the SAFE Project sites, and Chapters 5 and 6 using butterfly samples from the ESSTA Project sites.

## **1.6 | Focal taxa in this thesis**

### **1.6.1 Gerromorpha, Hemiptera**

#### ***Taxonomy, distribution, and life history***

Gerromorpha is a suborder within Hemiptera, consisting of semi-aquatic bugs which generally live on the surface of water (Andersen, 1982). There are around 2000 species of semi-aquatic bugs worldwide, although the exact number of species may be higher (Chen et al., 2021). Members in the group use surface tension to walk, skate, or row on the water and their legs are modified in different ways for this function (Andersen, 1982; Andersen et al., 2002). The bodies of semi-aquatic bugs are covered by hairs (micro- and macrotrichiae) which functions to prevent the bugs from drowning and are rainproof (Finet et al., 2018). Most semi-aquatic bug species live in freshwater systems, with a few being associated with the marine ecosystem (e.g., those in the genera of *Halobates*, *Halovelia*, *Haloveloides*, and *Xenobates*) (Andersen et al., 2002; Cheng, 1973). In addition, a few species of semi-aquatic bugs are terrestrial (Crumière et al., 2016). Evolutionarily, semi-aquatic bugs are known to be a monophyletic group (Andersen, 1982; Damgaard, 2008; Zettel, 2014). The life cycle of semi-aquatic bugs is categorised as incomplete metamorphosis due to the absence of a pupal stage. Gerridae and Veliidae are the commonest families in the Gerromorpha (Andersen et al., 2002).

## *Ecology*

The life cycle starts with an egg, proceeds to the nymphal stage (four or five instars), and ends as adults (Andersen et al., 2002). The eggs are attached to substrates in or near the water (such as aquatic vegetation, leaf litter, and protruding rocks) (Cheng, 1973; Cheng et al., 2001), on floating vegetation (Cheng et al., 2001), in cavities or holes (such as tree holes, pitcher plants, and bromeliad plants (Kovac & Yang, 2000), in the soil-litter, or as a gelatinous mass (Andersen, 1982). The nymphs are similar to the adults, but they generally have softer bodies and less developed (paler) colour patterns (Andersen et al., 2002; Cheng et al., 2001). The length of time needed for eggs to hatch depends on the temperature in the environment (Cheng et al., 2001).

Semi-aquatic bugs are fluid-feeding predators and use their pair of fore legs to catch and hold prey (Cheng et al., 2001). They detect prey items visually or by sensing ripples on the water surface created by the prey (Cheng et al., 2001), using mechanoreceptors on their legs, which are also used to detect predators (Finet et al., 2018). They generally feed on other invertebrates (e.g., smaller arthropods, ostracods, or cladocerans [Andersen et al., 2002]), which are either aquatic or fall from terrestrial margins into the water bodies (Cheng et al., 2001). They are also reported to eat immature stages of mosquitoes as well as planthoppers, thus providing services for humans in the control of disease vectors and pests (Andersen et al., 2002; Nakasuji & Dyck, 1984). A range of invertebrates and vertebrates are predators of semi-aquatic bugs, such as spiders and fishes (Spence & Andersen, 1994; Zimmermann & Spence, 1989). As a defence from predators, semi-aquatic bugs can have cryptic colouration or form aggregations on the water surface (Cheng et al., 2001; Foster & Trehene, 1981).

Different species of semi-aquatic bugs have different preferences for microhabitats on the water, and this is associated with differing adaptations of their body parts (**Table S1.1**). Since environmental change can alter the microhabitat of waterways, it can also change the composition of semi-aquatic bugs. Indeed, studies conducted in South America have shown that forest conversion for agriculture shifted the composition of semi-aquatic bug communities (Dias-Silva et al., 2020a; Juen et al., 2016). Interestingly, microhabitat preference can also differ across life stages in several species (Lansbury & Zettel 1997). For instance, the nymphs of the Genus *Rhagovelia* prefer slower-flowing water, while the adults prefer faster currents (Lansbury & Zettel 1997). In contrast, both nymphs and adults of the Genus *Strongylovelia* prefer slow moving parts of a stream (Lansbury & Zettel 1997).

Another characteristic within populations of semi-aquatic bugs is that they can contain both winged and wingless adults. Generally, the number of wingless individuals is higher than winged (Cheng et al., 2001; Polhemus, 1994). However, an exception occurs in the Genus *Limnometra*, in which all adults are generally winged, and wingless individuals are rarely found (Polhemus, 1994). When present, the wings can be either long (which is functional for flight) or short (called brachypterous and too short for flight) (Cheng et al., 2001). Changes in the environment can also affect the proportion of winged and wingless adults. This could be because producing wings is considered costly and therefore winged individuals are more frequent in temporary habitats, such as temporary pools (since the ability to move to other water bodies becomes a priority, compared to those living in permanent streams and lakes [Andersen et al., 2002; Cunha et al., 2020]). Indeed, the presence of wings has been found to be associated with habitat permanence (e.g., ponds, streams) and quality (Cunha et al., 2020; Spence, 1983, 1988).

Most semi-aquatic bug species display sexual dimorphism (Cheng et al., 2001). Dimorphism can be in terms of size (males are usually smaller than females) or modified structures which exist only in one of the sexes (Cheng et al., 2001). Despite not always being clear, males and females can be differentiated by the differing structures of their genitalia, which are located on the eighth and ninth segments of their abdomens (Andersen, 1982). For instance, female and male individuals of the Genus *Ptilomera* can be distinguished easily by dorsolateral lobes at the last abdominal segment in females, but curved paramere (with setae) in males (Jehamalar et al., 2018). In addition, males of many species of *Metrocoris* have spines and teeth on their front legs, adapted to grasp females during mating (Cheng et al., 2001).

### ***Gaps in ecological studies on semi-aquatic bugs in Southeast Asia***

Semi-aquatic bugs are sensitive to heavy metal pollution (Nummelin et al., 2007) and have a relatively high dispersal ability (Cunha et al., 2020). Therefore, they represent a useful model to study environmental change within streams (Cunha & Juen, 2020; Cunha et al., 2020; Dias-Silva et al., 2020; Hall et al., 1985). The strong effects of stream environmental variables on this group have been shown in studies that found a lower diversity of semi-aquatic bugs in habitats that received anthropogenic disturbance (Cunha & Juen, 2017; Cunha et al., 2015; Dias-Silva et al., 2020). However, studies assessing the impacts of anthropogenic disturbance on this group are lacking in Southeast Asia, and we are aware of no studies that have specifically studied the effects of habitat change on this group in the region.

## **1.6.2 Rhopalocera, Lepidoptera**

### ***Taxonomy, distribution, and life history***

Butterflies (Rhopalocera) are included in the order Lepidoptera, along with moths, categorised by the presence of scales on their wings. There are approximately 15,000–21,000 butterfly species worldwide, with tropical regions housing the highest diversity of butterflies (Stork, 2018). There are 1051 and 944 butterfly species in Peninsular Malaysia (Corbet and Pendlebury, 2020) and Borneo (Otsuka, 2001), respectively. Butterflies undergo complete metamorphosis, including an egg, larval, pupal (chrysalis), and adult stage. The larvae and adult butterflies feed on different food sources, and this is related to differing feeding structures. In particular, the larvae have chewing mouth parts with large mandibles to chew the leaves of plants. On the other hand, the adults use their long proboscises to draw nectar from flowering plants. The larvae are often specialised and selective over what species of plants can act as their hosts.

### ***Ecology***

Butterflies primarily need nectar sources and host plants to support them (Corbet and Pendlebury, 2020). In areas where these two key requirements are present, they are often found in high abundance. In the food web, butterflies play several different functions. The larvae are herbivores and can be pests in monoculture plantations (Okolle et al., 2006). The adults are pollinators for many wild plants (Corbet and Pendlebury, 2020) and are prey items of other animals (Wourms & Wasserman, 1985).

Butterflies are ectotherms, largely relying on the temperature of the environment to control their body temperature (Bladon et al., 2020). In the morning, they can be seen sunning (basking) to prepare for flight but can also seek cooler microclimates to cool down. Considering their life history, many butterfly species can be lost with habitat change, due to the loss of their hostplants, specific nectar sources for specialist species, favourable microclimatic conditions, and refugia (Dumbrell & Hill, 2005). Therefore, these factors could explain why many butterfly species disappear when primary forests are converted for agriculture (Koh, 2007).

In addition to changes in habitat structure, the loss of sensitive butterfly species could be partly because of changes in microclimate (Bladon et al., 2020), with both tropical and temperate species showing wide variation in their tolerance towards high temperatures (Laird-Hopkins et al., 2023). Furthermore, some studies have found that climate change can exacerbate the effects of anthropogenic disturbance on butterfly assemblages, by having additional impacts on local temperatures (e.g., Habel et al., 2021; Molina-Martínez et al., 2016). Considering all these factors, to improve butterfly conservation within altered habitats, it is important to identify persisting species within agricultural landscapes, understand the biology and behaviour of the persisting butterflies, then to manage the areas in ways that butterflies can be supported, such as by providing food resources across their life stages, as well habitat heterogeneity to facilitate butterfly thermoregulation (Bladon et al., 2020).

## *Gaps in ecological studies on butterflies in Southeast Asia*

Studies have shown that habitat modification by land-use change alters assemblage composition of butterflies across landscape types and regions (e.g., Börschig et al., 2013; Habel et al., 2021; Koh, 2007; Molina-Martínez et al., 2016), but there are many unanswered ecological questions related to management effects within altered habitats. Given the importance of butterflies in the ecosystem (Koh, 2007), providing information on how plantations can be managed to support healthier butterfly populations is necessary in improving the sustainability of agricultural practices, including in oil palm.

## **1.7 | Conclusion and summary of chapters**

Overall, threats to biodiversity in Southeast Asia, including within Peninsular Malaysia and Borneo, are numerous and understanding how these impact organisms across taxa will inform management to restore habitats and maintain ecosystem functioning. This is particularly urgent for Southeast Asia, since the region houses a high proportion of global species but has been relatively little studied. In this thesis, I investigated the impacts of forest logging and conversion to oil palm, particularly focusing on semi-aquatic bugs (Gerromorpha, Hemiptera) and butterflies (Rhopalocera, Lepidoptera) in Malaysian Borneo and Peninsula Malaysia, respectively. The first until third data chapter (**Chapter 2 – 4**) cover studies on semi-aquatic bugs, which took place in Sabah, Malaysian Borneo across land uses (tropical rainforests, logged forests, and industrial oil palm plantations), while **Chapters 4 and 5** cover studies on butterfly assemblages in smallholding plantations in Selangor, Peninsular Malaysia. In the final part of my thesis,

I provide a general discussion covering all data chapters as a synthesis. Since the work in **Chapter 2 – 6** are the result of collaborations, I used “we” for all these chapters.

## **Chapter 2**

I investigated the best-fit body length-biomass equations to estimate the biomass of semi-aquatic bugs. I investigated several equations and found that power regressions that took the body form of semi-aquatic bugs into account are the most accurate to predict the biomass of the bugs across life stages. The equations produced can help monitoring of semi-aquatic bugs in tropical streams by supporting the inclusion of biomass in the assessment.

## **Chapter 3**

I assessed the effects of forest degradation for logging and oil palm on semi-aquatic bugs. I found that there was a decline in abundance and richness following forest conversion, although total biomass was not affected. This may indicate that the provision of prey items for the predators of semi-aquatic bugs remained stable, albeit with a reduction in abundance and richness of the bugs. At the demographic level, there were no significant differences in the proportion of juveniles or winged individuals, or the sex ratio of *Ptilomera* sp. (the most common morphospecies in the study areas and easily sexed), along the gradient of disturbance.

## **Chapter 4**

I investigated the effects of within-physical structure and maintaining forested stream margins (“riparian buffer strips”) within oil palm landscapes on semi-aquatic bugs. I found that, at the small-scale (along 10-m transect), streams with riparian buffer strips had a higher abundance (nearly twice as abundant) and richness (by two species) of semi-aquatic bugs than those without, but overall total biomass of the bugs and proportion of female *Ptilomera* sp. was not affected. Within-stream physical factors that were associated with a higher abundance of semi-aquatic bugs were: wider wetted width, more isolated pools, shallower slopes, and lower percentage of deadwood. There was a significantly differing community composition between streams with and without riparian buffer strips. Finally, there was a higher proportion of juveniles in streams with higher canopy openness, higher percentage of deadwood, lower percentage of pebbles, and narrower wetted widths.

## **Chapter 5**

I studied how management decisions taken by oil palm smallholders affected butterfly assemblages within plantations. I incorporated the impacts of replanting and crop management afterwards (replanting with monoculture vs polyculture). This study is the first that incorporates such overall aspects of management decisions by smallholders. I found that plantations with differing broad management decisions (mature monoculture, immature monoculture, and immature polyculture) did not have significantly different density and richness of butterflies. However, I identified several environmental factors that were associated with the density of butterflies within plantations. Maintaining

understory vegetation, particularly nectar sources and hostplants, and polyculture farming were associated with a higher density of butterflies. Edge effects (types of neighbouring habitats) are also an important factor determining the density of butterflies within plantations.

## **Chapter 6**

I investigated the impacts of habitat structure and complexity within smallholding plantations on the resource-use behaviours of two common species of butterflies in the study sites (*Leptosia nina* and *Ypthima* spp.). Results showed that the structure and complexity of habitats within plantations overlapped across management decisions and resulted in limited impacts on how the two butterfly species used resources. Although low numbers of observations made it difficult to draw firm conclusions from the results, it was clear that the methods used in this study are tractable and can produce detailed information at a fine scale in assessing resource-use behaviours of butterflies, which could be replicated in other studies.

## **Chapter 7**

In this final chapter, I present a synthesis based on findings from all the data chapters.

## Supplementary materials

**Table S1.1** Common genera or species of tropical semi-aquatic bugs (Gerromorpha, Hemiptera) in Southeast Asia and their preferred microhabitats. Information at the genera level is based on several species. If the information is just on one species, the species name is provided (see the foot notes). Therefore, unless specified, the listed habitats represent several species within a genus. When information is not available for a particular genus, it is put as “NA”.

Genera	Preference for microhabitat	Habitat				Specialised structures on legs	Movement behaviour on water surface	Distribution/ Occurrence	References
		Types of water bodies	If streams, slow or fast moving	If streams, acidic or non-acidic water	If streams, altitude of habitats				
<i>Cylindrostethus</i> (Gerridae)	Pools, quiet parts of streams	Forest streams	Slow moving but also in turbulent streams <sup>1</sup>	Non-acidic	Lowland but also rocky upland <sup>1</sup>	None	Strong kick then long glide	Tropical West Africa, Ceylon, India, Southeast Asia, and South America (the Amazon Basin)	Chen & Nieser, 1992; Cheng et al., 2001; Polhemus, 1994
<i>Limnogonus</i> (Gerridae)	Pools, still water <sup>2</sup>	Forest streams, waterfalls, seepage rocks, rock pools, lakes, reservoirs, ponds, marshes <sup>2</sup> ,	Slow moving	Non-acidic	Lowland	None	NA	Southeast Asia, China, India, Australia, Central and South America, Southern parts of Africa	Chen & Nieser, 1992; Cheng et al., 2001; GBIF

Genera	Preference for microhabitat	Habitat				Specialised structures on legs	Movement behaviour on water surface	Distribution/ Occurrence	References
		Types of water bodies	If streams, slow or fast moving	If streams, acidic or non-acidic water	If streams, altitude of habitats				
		swamps <sup>2</sup> , temporary pools, ditches at roadside <sup>2</sup> and in agricultural farms, and brackish water.							Secretariat, 2022a; Herring, 1951; Yang et al., 1999; Ye et al., 2017
<i>Limnometra</i> (Gerridae)	Stagnant waters <sup>3</sup>	Forest streams, peaty streams, mangrove swamps, shaded puddles <sup>3</sup> , mountainous streams, creeks, and waterfalls	Slow and fast moving	Acidic and non-acidic	Upland	None	Similar with <i>Cylindrostethus</i> but less efficient in gliding than <i>Cylindrostethus</i>	Tropical Asia, India, Northern parts of Australia	Chen & Nieser, 2002; Cheng et al., 2001; GBIF Secretariat, 2022b; Nieser & Chen, 1992; Polhemus, 1994
<i>Metrocoris</i> (Gerridae)	Still or smoothly flowing pools	Shaded streams, waterfalls, seepage	Slow and fast moving	Non-acidic	Upland and lowland	None	Stroke and glide across the water surface	Central, East, West, and Southeast Asia, Tropical Africa	Chen & Nieser, 2002, 1993a; GBIF

Genera	Preference for microhabitat	Habitat				Specialised structures on legs	Movement behaviour on water surface	Distribution/ Occurrence	References
		Types of water bodies	If streams, slow or fast moving	If streams, acidic or non-acidic water	If streams, altitude of habitats				
		rocks, mountainous streams, creeks							Secretariat, 2022c; Yang et al., 1999
<i>Microvelia</i> (Veliidae)	Near shore, stagnant waters, or pools	Forest and peaty streams as well as lakes, reservoirs, ponds, and temporary pools	Slow moving	Acidic and non-acidic	Lowland	None	NA	East, Central, South, and Southeast Asia, America, West Europe, Central and South Africa, Australia	Andersen et al., 2002; GBIF Secretariat, 2022d; Molano et al., 2016; Yang et al., 1997
<i>Ptilomera</i> (Gerridae)	Riffles, avoid stagnant waters <sup>4</sup>	Forest and peaty streams	Slow and fast moving	Acidic and non-acidic	Lowland	Middle tarsi and tibiae have brushes (ribbon-like hairs) for rowing <sup>4</sup>	Continuous rowing	South and Southeast Asia	GBIF Secretariat, 2022e; Kim et al., 2022; Polhemus, 1994; Yang et al., 1997, 1999

Genera	Preference for microhabitat	Habitat				Specialised structures on legs	Movement behaviour on water surface	Distribution/ Occurrence	References
		Types of water bodies	If streams, slow or fast moving	If streams, acidic or non-acidic water	If streams, altitude of habitats				
<i>Potamometropsis</i> (Gerridae)	Flowing parts of streams or pools	Permanent water bodies, including small montane streams with high current velocity	Fast flowing streams	NA	Upland	Swimming hairs on middle tibiae	Skating on smooth current <sup>5</sup>	Borneo, Sumatra, Sulawesi, The Philippines	GBIF Secretariat, 2022f; Polhemus & Zettel, 1997
<i>Rhagovelia</i> (Veliidae)	Mostly shaded running water, although few species can be found in open water. The presence of current is a must.	Forest and peaty streams, mountainous streams, creeks, and waterfalls	Fast, moderately slow, and slow moving	Acidic and non-acidic	Upland	Middle tarsi with swimming fans	Some skate against the water current while many others in this genus stroke and glide	Southeast Asia, New Guinea, Australia, New Caledonia, Japan, Arabia, North and South America, Africa	Andersen et al., 2002; Chen & Nieser, 2002; Polhemus & Polhemus, 1988; Yang et al., 1999
<i>Rheumatogonus</i> (Gerridae)	Fast running water	Forest and peaty streams, mountainous streams, creeks, and waterfalls	Slow, moderate, and fast moving	Acidic and non-acidic	Upland	Fringe of hairs on middle tibiae	Skate on water surface	Southeast Asia, India, Sri Lanka	Chen & Nieser, 2002; Cheng et al., 2001; GBIF Secretariat, 2022g; Mohd Ishadi

Genera	Preference for microhabitat	Habitat				Specialised structures on legs	Movement behaviour on water surface	Distribution/ Occurrence	References
		Types of water bodies	If streams, slow or fast moving	If streams, acidic or non-acidic water	If streams, altitude of habitats				
<i>Strongylovelia</i> (Veliidae)	Large side pools <sup>6</sup>	Shaded forest, peaty streams, estuaries with light salinity <sup>6</sup> , swamp forest	Slow moving	Acidic and non-acidic	NA	None	Move in straight lines and can jump if threatened	Borneo, Singapore, The Philippines (Palawan), China, Taiwan, India, Wallacea, and Papuan realms	et al., 2014; Yang et al., 1999 Andersen et al., 2002; Freitag & Zettel, 2012; GBIF Secretariat, 2022h; Lansbury, 1993; Lansbury & Zettel, 1997; Yang et al., 1997; Ye et al., 2015
<i>Tenagogonus</i> (Gerridae)	Quiet edge of streams	Forest and peaty streams <sup>7</sup> , swampy streams <sup>8</sup>	Slow moving <sup>7</sup>	Acidic <sup>7</sup>	NA	None	NA	Myanmar, Sumatra, the Philippines, New Guinea, Africa,	Chen & Nieser, 1992; Cheng et al., 2001; GBIF

Genera	Preference for microhabitat	Habitat				Specialised structures on legs	Movement behaviour on water surface	Distribution/ Occurrence	References
		Types of water bodies	If streams, slow or fast moving	If streams, acidic or non-acidic water	If streams, altitude of habitats				
								Northern part of Australia	Secretariat, 2022i; Yang et al., 1997
<i>Ventidius</i> (Gerridae)	Slow flowing water	Forest (well-shaded <sup>9</sup> ) and peaty streams, riverbanks or margins, lakes, reservoirs or ponds, mangrove swamps	Slow and fast moving	Acidic and non-acidic	Hilly and lowland	None	Stroke and glide across the water surface	Southeast Asia	Chen & Zettel, 1999; Cheng et al., 2001; Yang et al., 1997

<sup>1</sup>Turbulent streams for *Cylindrostethus scrutator* (Polhemus, 1994)

<sup>2</sup>Based on observations on *Limnogonus hesione* (Herring, 1951)

<sup>3</sup>Based on observations on *Limnometra femorata* (Zettel & Chen, 2000)

<sup>4</sup>Based on observations on *Ptilomera tigrina* (Kim et al., 2022)

<sup>5</sup>Based on observations on *Potamometropsis kundesana* (Polhemus & Zettel, 1997)

<sup>6</sup>Based on observations on *Strongylovelia palawanensis* (Freitag & Zettel, 2012)

<sup>7</sup>Based on observations on *Tenagogonus maai* (Cheng et al., 2001)

<sup>8</sup>Based on observations on *Tenagogonus insularis* (Yang et al., 1997)

<sup>9</sup>Based on observations on *Ventidius harrisoni* (Yang et al., 1997)

## **Chapter 2: Length–biomass equations to allow rapid assessment of semi-aquatic bug biomass in tropical streams**

**Martina F. Harianja<sup>1</sup>, Sarah H. Luke<sup>2,1</sup>, Holly Barclay<sup>3,1</sup>, Vun K. Chey<sup>4</sup>, David C. Aldridge<sup>1</sup>, William A. Foster<sup>1</sup> & Edgar C. Turner<sup>1</sup>**

<sup>1</sup>Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK,

<sup>2</sup>School of Biosciences, University of Nottingham, Sutton Bonington Campus, Nr Loughborough, LE12 5RD, UK,

<sup>3</sup>School of Science, Monash University Malaysia, Jalan Lagoon Selatan, 47500 Subang Jaya, Selangor Darul Ehsan, Malaysia, and

<sup>4</sup>Forest Research Centre (Sepilok), Sabah Forestry Department, PO Box 1407, 90715 Sandakan, Sabah, Malaysia

**Key words:** semi-aquatic bugs, length–biomass relationships, body forms, life stages, power regression, Sabah, Gerromorpha, Hemiptera, water quality, bioindicator, indicator species, habitat disturbance.

Published in *Entomologia Experimentalis et Applicata*, 171, 102–115. doi:

[10.1111/eea.13247](https://doi.org/10.1111/eea.13247)

## **Abstract**

Length–biomass equations are relatively easy and cost-effective for deriving insect biomass. However, the exact relationship can vary between taxa and geographical regions. Semi-aquatic bugs are abundant and are indicators of freshwater quality, but there are no studies investigating the effect of habitat disturbance on their biomass, although it is useful in assessing ecological processes. We identified the best-fit length–biomass models to predict the biomass of semi-aquatic bugs (Hemiptera, Gerromorpha) collected from streams in Sabah, Malaysia. We used 259 juvenile and adult semi-aquatic bugs to compare a range of plausible length–biomass functions, and to assess whether relationships differed across the following families and body forms: (1) *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae*, which are subfamilies within *Gerridae* consisting of small-to-large bugs that have long and slender bodies, (2) *Halobatinae*, a subfamily within *Gerridae*, consisting of small-to-medium bugs with wide heads and thoraxes as well as short abdomens, and (3) *Veliidae*, which are small bugs with stout bodies. Estimation used five fitting functions – linear regression, polynomial regression order 2, 3, and 4, and power regression – on the following groupings: three body forms combined; each body form with life stages (juvenile and adult) combined; and each body form with life stages separated. Power regressions were the best fit in predicting the biomass of semi-aquatic bugs across life stages and body forms, and the predictive power of models was higher when the biomass of different body forms was calculated separately (specifically for *Halobatinae* and *Veliidae*). Splitting by life stages did not always result in additional improvement. The equations from this study expand the scope of possible future ecological research on semi-aquatic bugs, particularly in Southeast Asia, by allowing more studies to consider biomass-related questions.

## **Introduction**

The status of a particular assemblage or community in a habitat is often initially described in terms of abundance and richness – that is, by counting individuals and taxa. However, functional traits, such as feeding group, trophic level, body size, and biomass, are needed to assess the role that different taxa play in ecosystem processes (Dobson et al., 2006; de Bello et al., 2010; Sackett et al., 2010; Slade et al., 2011; Thompson et al., 2012; Jabiol et al., 2013; Luke, et al., 2014; Rousk, 2016). For instance, understanding how land-use change affects the biomass of insects can indicate the importance of their roles in dung burial and seed dispersal (Slade et al., 2011) and can also provide information about the amount of food available for predators (Turner & Foster, 2009; Kunin, 2019; Wagner, 2020). Therefore, as a complement to diversity, biomass data can be used as a tool to assess the ecological status of insects, habitats, and the value of conservation strategies. Despite this, biomass data can be difficult to collect. For example, a sensitive balance can be expensive, and accurate measurements for small-sized insects can be an issue for studies in the field (Rogers et al., 1977; Sample et al., 1993). Additionally, the sample size of ecological studies can be large, necessitating a great investment in time to weigh each individual. Furthermore, handling, and drying samples can cause damage, which can reduce the ability to carry out other work on the samples subsequently, such as identification and preparation of voucher specimens (Gruner, 2003). Hence, estimating biomass from body length measurements is much easier and quicker, as well as avoiding damage to specimens. Several studies have obtained predicted biomass using well fitted length–biomass regressions, with a small error when compared with measured biomass of the same samples (Rogers et al., 1977; Sample et al., 1993; Giustini et al., 2008; Wardhaugh, 2013; Kinsella et al., 2020),

making such equations a feasible and useful alternative to drying and weighing all specimens for primary studies.

Differences in body form should be considered when carrying out biomass estimation (Schoener, 1980; Sample et al., 1993). Body form or shape is determined by the proportion of body length and width, and can differ across taxonomic groups, life stages, and geographical regions where samples were collected (Gowing & Recher, 1985). Different taxa can have different body forms, although insects often have a similar body form at the family level (Sample et al., 1993). In addition to the difference of body forms between taxa, the life stage of insects could be an important factor in determining the accuracy of biomass estimation (Rogers et al., 1977). This is because there is a stark difference in body form between juvenile and adult individuals of insect species with complete metamorphosis (Rogers et al., 1977). On the other hand, for insects that undergo incomplete metamorphosis, the same length–biomass equation used on both juvenile and adult individuals could produce reliable biomass estimates (Rogers et al., 1977), although studies confirming this across a range of taxa are lacking. Furthermore, body forms can also be affected by geographical regions, related to adaptations within a particular taxonomic level, such as within the same order, to different climates and habitat conditions (Schoener, 1980). Because of this, a length–biomass equation developed for a taxon in one region may not always be suitable to estimate the biomass of that taxon in another region (Schoener, 1980). For example, power equations –  $y = a(x)^b$ , with  $y =$  biomass,  $x =$  insect body length, and  $a$  and  $b$  are coefficients – to estimate the biomass of terrestrial hemipteran insects in tropical rainforest in Costa Rica and temperate deciduous-conifer forest in the USA had different coefficients  $a$  and  $b$  (Schoener, 1980). The difference could be because the samples used from the tropical

rainforest in Costa Rica consisted of hemipteran species that were longer and thinner (possibly because of a higher incidence of twig-mimicking insects) than those from the temperate deciduous-conifer forest in the USA (Schoener, 1980), affecting the resulting equations. Although this has not yet been specifically assessed, it is likely that a similar trend might also be seen at lower taxonomic levels. Therefore, for biomass estimates to be as reliable as possible, it is important to develop specific length–biomass equations for each insect family (Sample et al., 1993), body form (Schoener, 1980; Sample et al., 1993; Wardhaugh, 2013), life stage (Rogers et al., 1977), and also for different regions (Schoener, 1980; Gowing & Recher, 1985).

Gerromorpha is an infraorder of Hemiptera, which consists of semi-aquatic bugs that live on the surface of freshwater or marine ecosystems (Andersen, 1982), and can be found in all continents except Antarctica (Spence & Anderson, 1994). Semi-aquatic bugs are predator-scavengers that feed on invertebrates in the water and those falling from riparian vegetation (Spence & Anderson, 1994), and are prey for fishes (Foster & Treherne, 1981; Armisén et al., 2015) and other invertebrates such as back swimmers (Lang, 1980) and fishing spiders (Zimmermann & Spence, 1989). Semi-aquatic bugs undergo incomplete metamorphosis in which the development involves nymphal and adult stages (Andersen, 1982). Nymphs have a similar appearance to the adults but differ in body size and lack wings and reproductive organs (Andersen, 1982). There is sexual dimorphism within some species of semi-aquatic bugs, in which there are substantial differences in body size or body parts (Andersen, 1997). However, in other species, sexual dimorphism is much less marked, and sexes can be difficult to distinguish because, for example, the ovipositor or clasper is reduced (Andersen, 1982). Another characteristic of this group is the presence of wing polymorphism, meaning that there

are winged (long or short) and wingless adult individuals (Andersen, 1982). Furthermore, wing emergence is associated with habitat permanence (such as ponds or streams) and quality (Spence, 1983, 1989; Cunha et al., 2020). For instance, higher abundances of winged bugs have been found in primary forests than in oil palm in the Amazon (Cunha et al., 2020).

There have been several studies investigating the impacts of habitat change in freshwater ecosystems on semi-aquatic bugs (Ditrich et al., 2008; Dias-Silva et al., 2020a,b; da Silva Giehl et al., 2020), which have shown that they are vulnerable and sensitive to habitat alteration (Cunha et al., 2015, 2020; Vieira et al., 2015; Cunha & Juen, 2017, 2020; Guterres et al., 2020, 2021; Sundar et al., 2021). For example, studies have found lower beta-diversity of semi-aquatic bugs in altered habitats compared to forests, perhaps because water temperature was higher and water pH was more acidic in altered habitats (Dias-Silva et al., 2020b). In contrast, a recent study in Brazil found that species richness of semi-aquatic bugs was higher in altered than undisturbed savanna streams, particularly in habitats characterised by wet and open soils on flat areas (da Silva Giehl et al., 2020). One possible reason for this discrepancy was the higher number of prey items in these habitats (da Silva Giehl et al., 2020). Currently, impacts of habitat disturbance are particularly severe in many tropical regions, where large areas are undergoing rapid land-use change for expansion of agriculture, urbanisation, and industrialisation (Hosonuma et al., 2012). Considering their importance and vulnerability, semi-aquatic bugs have the potential to act as bioindicators (Nummelin et al., 2007; Saha & Gupta, 2019), informing biodiversity conservation. However, no studies have yet focused on changes in their biomass as a result of habitat disturbance. Because there has been no work to quantify length–biomass equations for tropical

members of this group, large-scale studies of habitat change effects on semi-aquatic bug biomass are difficult to conduct.

Among insect groups that have been processed for biomass estimation, equations obtained from terrestrial bugs across a variety of regions (Rogers et al., 1977; Schoener, 1980; Sample et al., 1993; Ganihar, 1997; Gruner, 2003), or from semi-aquatic bugs collected in a subtropical region (Smock, 1980), could potentially be applicable to tropical semi-aquatic bugs. However, even though these belong to the same order (Hemiptera), it is likely that semi-aquatic bugs have different body forms from their terrestrial counterparts, due to their adaptation to live on the water surface. In addition, tropical groups could vary compared to sub-tropical groups owing to the differing species found, which is associated with differences in climate and the types of stream ecosystems inhabited. Developing a reliable length–biomass equation for tropical Gerromorpha will allow greater exploration of the impacts of land-use change on this group and associated wider ecosystem functioning – something which diversity data alone cannot address.

In this study, we quantified the length–biomass relationship of semi-aquatic bugs from three groups (separated based on family and body form), collected across a land-use gradient in Sabah, Malaysian Borneo. We selected plausible fitting functions based on the likely relationship between length and volume and previous studies of length–biomass in terrestrial Hemiptera (Rogers et al., 1977; Schoener, 1980; Sample et al., 1993; Ganihar, 1997; Gruner, 2003) as well as aquatic and semi-aquatic insects collected in a subtropical region (Smock, 1980). Specifically, we assessed: (1) What is the best model to predict the biomass of semi-aquatic bugs (Gerromorpha) from their body lengths? (2) Does the relationship change between juvenile and adult bugs? (3) Does the

relationship change between different body forms of semi-aquatic bugs? And (4) Do our selected best models predict biomass better than models constructed using general Hemiptera or subtropical semi-aquatic bugs, both obtained from published literature? By using semi-aquatic bugs collected from pristine and disturbed habitats, we ensured that a wide range of species were included and that the equations constructed from this study will allow a robust universal length–biomass estimation of semi-aquatic bugs. By facilitating the study of semi-aquatic bug biomass without the need for sophisticated equipment, we hope this work will facilitate the use of semi-aquatic bugs as important indicators of environmental health in tropical ecosystems.

## **Materials and methods**

### **Collection sites**

Data collection in the field took place in 2011–2013 in Sabah, Malaysian Borneo. Semi-aquatic bugs were collected with other freshwater invertebrates from stream sites within four major land-use types that are common within the region: old growth forest (OG), logged forest (LF), oil palm with forested riparian buffer strips (OPB), and oil palm without forested riparian buffer strips (OP) (**Figure S2.1**). The mean ( $\pm$  SE) altitude of all stream sites was  $236 \pm 26$  m above sea level, and the mean slope of each catchment was  $18.24 \pm 0.81^\circ$  (Luke et al., 2017b). Study sites included streams within Danum Valley Conservation Area ( $117^\circ 48.75'E$ ,  $5^\circ 01'N$ ), Maliau Basin Conservation Area ( $116^\circ 54'E$ ,  $4^\circ 49'N$ ), and the SAFE (Stability of Altered Forest Ecosystems; Ewers et al., 2011) project sites in the Kalabakan Forest Reserve ( $116^\circ 57'–117^\circ 42'E$ ,  $4^\circ 38'–4^\circ 46'N$ ) (Luke et al., 2017b). In total, 12 streams were sampled, including three in OG,

four in LF, three in OPB, and two in OP. The collection sites were headwater streams that ranged in mean wetted width from 3.26 to 7.83 m, contained areas of riffle and pool habitats, and were dominated by rocky substrate. At streams that were surrounded by forested riparian buffer strips, and continuous logged or old-growth forest, the surrounding forest habitat varied in quality, with mean canopy openness values – measured using a spherical densiometer; see Lemmon (1956) for more details – ranging from 5.9 to 68.8%, and mean tree density values ranging from 0 to 38.36 m<sup>2</sup> ha<sup>-1</sup>. OP streams had oil palm planted to the edge of the streams – for more details see Luke et al. (2017b).

### **Insect collection**

Semi-aquatic bugs were sampled along a 200-m transect in each stream. Along each transect, we walked five 10-m sub-transects (but were nine sub-transects in Gaharu and six in each Maliau and Selangan Batu) to collect the bugs. All semi aquatic bugs within the sub-transect were caught using hand-held nets and stored in 70% ethanol.

### **Insect identification and processing**

All individuals were identified to family and classified to morphospecies level following Andersen (1982) with additional information from other key publications (Polhemus & Polhemus, 1988; Chen & Nieser 1992, 1993a,b; Nieser & Chen, 1992; Polhemus & Zettel, 1997; Chen & Zettel, 1998) and advice from taxonomic experts (see “**Statement of contribution**” [page viii] for details). Each individual was also identified into one of the three distinct groups based on family and body form, consisting of both juveniles and adults: (1) Cylindrostethinae, Gerrinae, and Ptilomerinae, three subfamilies within the

Gerridae family that consist of small to large bugs with slender bodies (in this study: adult lengths were 4–17 mm, widths 1–4 mm; juvenile lengths were 1–13 mm, widths 0.5–3 mm); (2) Halobatinae, a subfamily of the Gerridae that comprises bugs with wide heads and thoraxes and short abdomens (Andersen, 1982) (in this study: adult lengths were 3–5.5 mm, widths 2–3 mm; juvenile lengths were 1–3 mm, widths 0.25–2 mm); and (3) Veliidae which are small bugs with stout bodies (in this study: adult lengths were 1–3.5 mm, widths 0.5–1.5 mm; juvenile lengths were 0.5–3 mm, widths 0.25–1 mm) (**Table S2.1, Figure 2.1**). Juveniles in our samples are likely to include a range of instars, but we could not divide these specifically because the key identification guide by Andersen (1982) provided detailed descriptions for only the first few instars across families, and no other specific descriptions exist. We also did not divide adults into females and males due to feasibility issues. In particular, although a few species in this study could be easily separated by the presence of ovipositors or claspers, most others had reduced genital parts making this division difficult.

### **Biomass calculations**

For biomass calculations, we selected a subset of semi-aquatic bug samples using a stratified random sampling method across the following characteristics: the three groups split based on families and body forms – (1) Cylindrostethinae, Gerrinae, and Ptilomerinae; (2) Halobatinae; and (3) Veliidae –, adults / juveniles, and land use types. We also made sure that a spread of individuals from across all stream sites were chosen. We aimed to have a broad range of body lengths represented in each category. To achieve this, we selected 45 individuals within each body form group for each juvenile and adult life stage comprising short, medium, and long individuals (**Table S2.1, Figure**

**S2.2**). So, in total we aimed to have 45 juveniles and 45 adults for each body form group. If the body was observed to be damaged on any specimen, the specimen was not used and another specimen was selected at random in the same category, choosing the same sample location as far as possible (**Figure S2.3**). Following this protocol and owing to low numbers (when substitution with a good specimen was not possible), only 34 adult individuals from the Halobatinae group were sampled (but 45 juveniles were used, as planned). Therefore, in total there were 259 individuals selected for biomass calculations. There were fewer morphospecies in the Halobatinae group (three and five morphospecies for juveniles and adults, respectively), which resulted in less variation (**Table S2.1, Figure S2.2B**), when compared with Cylindrostethinae, Gerrinae, and Ptilomerinae (eight morphospecies for each juvenile and adult covering all subfamilies in the group; **Table S2.1, Figure S2.2A**) or Veliidae (three and 11 morphospecies for each juvenile and adult; **Table S2.1, Figure S2.2C**). To assess length, individuals were first taken from the ethanol, dabbed dry, and their length was measured from the tip of the head to the end of the last segment of the abdomen, using a millimetre block with gradations to the nearest 1 mm. After selection, each individual was kept in a separate tube with ethanol. The resulting selection contained a good spread of replicates across the lengths available (**Figure S2.2**).

To measure the biomass of the 259 selected specimens, individuals were taken out from the ethanol, dabbed dry, and their length was remeasured to the nearest 0.25 mm from the same measurement locations as before, using underlaid graphing paper. Insects were then dried in batches on a Thermo Scientific hot plate at a temperature of 50 °C. Specimens were weighed every 2 h until the largest specimen's biomass was constant. As the largest specimens would take the longest to dry, this ensured that all

specimens were dried to a constant weight. The average amount of time needed for the largest specimens to reach constant biomass was 4.5 h. All insects were then weighed when fully dry using a Sartorius balance (to a higher resolution;  $d = 0.002$  mg).

## Statistical analysis

All visualisations and analyses were done in R v.4.0.4 (R Core Team, 2021) with R Studio v.1.3.959 (R Studio Team, 2020). Analyses was carried out using basic R syntax and package *plotrix* (Lemon, 2006), whereas for visualisations, packages used were *tidyverse* (Wickham et al., 2019), *cowplot* (Wilke, 2020), *ggpubr* (Kassambara, 2020), and *gridExtra* (Auguie, 2017).

### *Comparisons of five fitting functions and curves across body form groups and life stages*

Five functions were fitted to the length–biomass data and compared: linear regression, polynomial regression order 2, 3, and 4, and power regression. Power regression followed Sample et al. (1993). The equations used in this study are as follows:

Linear regression:  $y = a + b(x)$ ,

Polynomial regression order 2:  $y = c + a(x) + b(x)^2$ ,

Polynomial regression order 3:  $y = d + c(x) + a(x)^2 + b(x)^3$ ,

Polynomial regression order 4:  $y = e + d(x) + c(x)^2 + a(x)^3 + b(x)^4$ ,

Power regression:  $y = a(x)^b$ ,

with  $y$  = predicted biomass,  $x$  = body length of an individual insect, and a–e are

coefficient parameters.

In this study, we aimed to construct universal length–biomass equations of semi-aquatic bugs which were collected from a gradient of land use. We therefore did not split our samples based on land-use types for any analysis. Fitting of functions was done on (1) combined body form groups (across life stages), (2) each body form group with life stages combined, and (3) each body form group with life stages separated. To obtain the values of coefficient  $b$  and the adjusted  $R^2$  for the power regressions, we log-transformed both length and biomass variables and ran the ‘lm’ function. We then used  $a = e^x$  to obtain the values of coefficient  $a$ , with  $x$  = the intercept value of the linear regression run with the ‘lm’ function. We compared the adjusted  $R^2$  values between the above three groupings of fitting functions to assess whether the biomass estimation was similar across body form groups and life stages.

#### *Comparison of measured and predicted biomass*

We assessed the biomass prediction of our best fitting length–biomass relationships on semi-aquatic bug samples (on each body form group as well as each life stage) by comparing them with the measured biomass in this study. We also made comparisons with the predictions derived from six published relationships. These included: five published length–biomass relationships for terrestrial Hemiptera collected from Costa Rica (Schoener, 1980), India (Ganihar, 1997), and USA (Rogers et al., 1977; Schoener, 1980; Sample et al., 1993; Gruner, 2003) and one relationship specific for semi-aquatic bugs collected from a subtropical region in North Carolina, USA (Smock, 1980) (Table 1). Family or species identities of the terrestrial Hemiptera used to develop the length–biomass relationships in Ganihar (1997), Gruner (2003), Rogers et al. (1977), Sample et

al. (1993), and Schoener (1980) were not recorded in the publications, so we used a general equation of all Hemiptera combined from each of these studies to give biomass predictions. Species of aquatic and semi-aquatic insects in Smock (1980) were mentioned, and so, as well as using the general equation of all Hemiptera in the study, we also used equations developed specifically for semi-aquatic bugs: *Gerris remigis* Say and *Metrobates hesperius* Uhler (Gerridae), and *Rhagovelia obesa* Uhler (Veliidae) (**Table 2.1**).

In some of the studies, power regression equations were linearised (Rogers et al., 1977; Smock, 1980; Sample et al., 1993; Ganihar, 1997). When a linearised regression equation was used to predict biomass in the studies [ $\ln(y) = \ln(a) + b \ln(x)$ , with  $y =$  biomass,  $x =$  body length, and  $a$  and  $b$  coefficient parameters], we transformed the coefficient ' $\ln(a)$ ' to ' $a$ ' [by  $e^{\ln(a)}$ ] so it could be used in a power regression (**Table 2.1**). We used Wilcoxon tests with Bonferroni correction for the comparisons between the means of measured and predicted biomass, with predicted biomass obtained from the best fit equations of combined body form groups (across life stages) and each group with life stages combined, as well as equations in the six other studies. Wilcoxon tests were chosen because biomass data were not normally distributed.

## **Results**

### **What is the best model to predict biomass of semi-aquatic bugs from their body lengths?**

Power regressions produced the highest adjusted  $R^2$  values across all body form groups and life stages, except for juvenile and combined Veliidae (i.e., juveniles and adults

grouped together), where polynomial regression had marginally higher adjusted  $R^2$  value (**Table 2.2, Figures S2.4-S2.13**). In addition, power regression fitted on combined body form groups (across life stages) gave higher adjusted  $R^2$  values in most cases (adjusted  $R^2 = 0.95$ ), except when compared with juvenile *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae*, which had a slightly higher value as a single group (adjusted  $R^2 = 0.97$ ) (**Table 2.2**).

Curves created using the power regression equations were similar between combined body form groups and each group with life stages combined, although group-specific curves were a better fit for *Halobatinae* and *Veliidae* (**Figure 2.2**). Even though adjusted  $R^2$  values of power regressions differed when combined and separated life stages were compared, the curves were similar for each group (**Figure 2.3**).

### **Does the relationship change between juvenile and adult bugs, and does the relationship change between body forms of semi-aquatic bugs?**

Comparisons between measured and predicted biomass of juvenile and adult semi-aquatic bugs – with predicted biomass obtained using power regression equations fitted on combined body form groups and each group with life stages combined – showed no significant difference in *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae* and adult *Veliidae* (**Table 2.3**). However, the measured and predicted biomass of *Halobatinae* (both life stages) and juvenile *Veliidae* differed significantly, when the predictions were made using the equation fitted on combined body groups (**Table 2.3**). There was no significant difference in each of the *Halobatinae* and *Veliidae* (across life stages) when biomass predictions used equations fitted on each group with life stages combined (**Table 2.3**).

## **Do our selected best models predict biomass better than models constructed using published general Hemiptera or subtropical semi-aquatic bugs?**

Fitting functions from Rogers et al. (1977), Sample et al. (1993), Schoener (1980) as well as Smock (1980) on general Hemiptera, *G. remigis*, and *M. hesperius* were able to provide reliable biomass estimates of both juvenile and adult Cyldrostethinae, Gerrinae, and Ptilomerinae (shown by no significant difference between measured biomass and predictions derived from published equations) (**Table 2.4**). None of the nine sources from the six studies could estimate the biomass of Halobatinae across all life stages (**Table 2.4**). In most cases, equations from the published studies could not provide reliable biomass estimates for both juvenile and adult Veliidae, with only equations from Gruner (2003) and Smock (1980) predicting biomass for the juveniles, and the equation from Rogers et al. (1977) for the adults (**Table 2.4**).

## **Discussion**

We found that power regression equations, particularly those constructed for specific body forms, produced good biomass estimates for semi-aquatic bugs across life stages (both juvenile and adult). Power regression has also been found to best predict insect biomass for a range of taxa, when compared with several different approaches (linear, logarithmic, and exponential) in other studies (Rogers et al., 1977; Smock, 1980; Ganihar, 1997). This finding is likely to be related to the scaling relationship between length and volume, as well as specific differences in how insects grow and assimilate new biomass. For example, mechanistic growth models produced for insects by Maino & Kearney (2015) – taken from 50 individual insects from six orders, i.e., Coleoptera,

Lepidoptera, Hemiptera, Hymenoptera, Orthoptera, Diptera, and Neuroptera – identified reduced investment in structural biomass over time in insects as they grow. Straus & Aviles (2017) found that allometric scaling between size and weight decreased as insects got larger, suggesting that larger insects have a lower tissue density, or more internal air spaces. Other factors may also influence the specific relationship between length and biomass as insects grow, including levels of food resources which, when low, can result in insects using reserves to compensate for an increase in size (Maino & Kearney, 2015).

The curve fitted on combined body form groups was more similar to that fitted on the *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae* than on *Veliidae* and *Halobatinae*, probably because there were more insects in the *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae* group, and so they dominated the body length and weight ranges of all samples combined. This might also explain why group-specific curves fitted better for *Halobatinae* and *Veliidae*, which differ markedly in their shape from *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae*. As a result, biomass estimation using power regression equations fitted on combined body form groups performed well only for the *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae* across both life stages, but not for *Halobatinae* and *Veliidae*. On the other hand, power regression equations fitted specifically for each group with life stages combined could well estimate the biomass of each group across life stages. Therefore, studies working exclusively on semi-aquatic bugs should use body-form specific biomass equations. An alternative could be to include width measurements in the analysis, allowing differences in shape related to biomass to be better explained. This has been suggested in studies comparing taxa from different families (Sample et al., 1993), but our findings indicate that such an approach could also be useful for within-family studies, as seen with bugs in the *Cylindrostethinae*,

Gerrinae, and Ptilomerinae that have a different body form to those in the Halobatinae, despite belonging to the same family (Gerridae).

When life stages were combined or separated for each group, all resulting curves for biomass estimates were similar, although with varying adjusted  $R^2$  values. This indicates that an equation specific for the body form is sufficient for predicting the biomass of that group across life stages. This finding was also reported by Rogers et al. (1977), indicating that combining juvenile and adult stages in biomass calculations may be a tractable option across groups, particularly for insects that undergo incomplete metamorphosis, in which the juveniles and the adults have similar body forms. Although we did not consider the differing instars for juveniles in this study or differences between sexes, we would argue that, as the combined biomass predictions we obtained were good for both juveniles and adults of a particular body form and there were no obvious morphological differences differentiating instars or sexes in most cases in this study, the equation is most likely giving good predictions across a range of instars and both sexes. However, further investigations could provide more clarity in this by testing equations specific to particular instars and for males and females separately.

The length–biomass equations obtained from six other sources [Rogers et al., 1977; Schoener, 1980; Sample et al., 1993; Smock (1980) on general Hemiptera, *G. remigis*, and *M. hesperius*] could produce a good biomass estimate for both juvenile and adult Cyndrostethinae, Gerrinae, and Ptilomerinae, whereas coefficients from three other sources [Smock (1980) on *R. obesa*; Ganihar, 1997; Gruner, 2003] resulted in inconsistent biomass predictions for both juvenile and adult life stages. However, no sources could provide a consistent and reliable biomass estimate for both juvenile and adult Halobatinae and Veliidae samples in this study. Therefore, although fitting

functions at the order or family level can be useful, attention should also be paid to any variation in body forms between samples belonging to the same family. If such variation exists, separating samples into different body form groups may be needed to obtain accurate biomass estimates.

In most cases, an equation obtained from one species can predict the biomass of other species belonging to the same body form group. For instance, equations obtained from *G. remigis* and *M. hesperius* (both Gerridae; Smock, 1980) provided good biomass estimates for juvenile as well as adult Cyldrostethinae, Gerrinae, and Ptilomerinae. However, it should be noted that, in another case, the equation obtained from *R. obesa* (Veliidae; Smock, 1980) could not provide a good estimate for either juveniles or adults within the Veliidae group. This might be owing to species-specific idiosyncrasies in shape.

Our results also indicate that body form is a more important factor for biomass estimation than geographical region. For example, biomass equations derived from *G. remigis* and *M. hesperius* (Smock, 1980) provided a good biomass estimate for both juvenile and adult Cyldrostethinae, Gerrinae, and Ptilomerinae in this study, even though collection site and climate (North Carolina, USA) were different from the specimens collected in this study (Sabah, Malaysia). Therefore, length–biomass equations constructed in this study are likely to be applicable to predict the biomass of semi-aquatic bugs across regions.

This paper lays the groundwork for studying the biomass of this group in a relatively easy, cheap, and accurate way. We anticipate that surveys of semi-aquatic bugs have the potential to provide a tractable and cost-effective means of monitoring

environmental change in tropical freshwater systems and hope that the relationships defined here will support further research in this area. To obtain the most accurate estimates for these studies, we recommend using length–biomass equations that are specific to different body forms for semi-aquatic bugs of all life stages.

## Tables and Figures

**Table 2.1** Studies that estimated insect biomass using equations, from which coefficients were used to predict biomass of semi-aquatic bug samples in this study. Taxa investigated were terrestrial bugs collected from a range of countries across several climatic regions (Rogers et al., 1977; Sample et al., 1993; Ganihar, 1997; Schoener, 1980; Gruner, 2003), as well as semi-aquatic bugs from a sub-tropical region (Smock, 1980). These studies used either linearised [ $\ln(y) = \ln(a) + b \ln(x)$ ] or power [ $y = a(x)^b$ ] regressions. When a linearised regression was used, the coefficient ‘ $\ln(a)$ ’ was transformed to coefficient ‘ $a$ ’ to be used in power regressions in this study.

Reference	Location of insect collection	Taxa investigated in the study	Taxon selected for biomass prediction in this study	Coefficient parameter ‘ $a$ ’ <sup>1</sup> or ‘ $\ln(a)$ ’ <sup>2</sup> and ‘ $b$ ’ in the study	Coefficient parameter ‘ $a$ ’ after being transformed from ‘ $\ln(a)$ ’	Equation used for this study <sup>3</sup>
Ganihar, 1997	Goa, India	Arthropods in 20 categories	Hemiptera (terrestrial bugs)	$\ln(a) = -3.8893 \pm 0.3387$ , $b = 2.7642 \pm 0.3113$	$a = 0.020$	$y = 0.020x^{2.764}$
Gruner, 2003	Hawaii, USA	Arthropods in 14 orders	Heteroptera (terrestrial bugs)	$a = 0.0411$ , $b = 1.9340$	Transformation not needed	$y = 0.041x^{1.934}$
Rogers et al., 1977	Washington, USA	Arthropods in nine groups	Hemiptera (terrestrial bugs)	$\ln(a) = -2.998 \pm 0.113$ , $b = 2.270 \pm 0.081$	$a = 0.049$	$y = 0.049x^{2.270}$
Sample et al., 1993	West Virginia, USA	Insects in 13 orders	Hemiptera (terrestrial bugs)	$\ln(a) = -4.784 \pm 0.313$ , $b = 3.075 \pm 0.147$	$a = 0.008$	$y = 0.008x^{3.075}$
Schoener, 1980	Costa Rica and Massachusetts, USA	Insects in eight orders	Hemiptera (terrestrial bugs) collected from the tropical rainforest in Costa Rica	$a = 0.027 \pm 0.419$ , $b = 2.28 \pm 0.76$	Transformation not needed	$y = 0.027x^{2.280}$
Smock, 1980	North Carolina, USA	Aquatic and semi-aquatic insects in eight orders	Hemiptera	$\ln(a) = -3.461 \pm 0.311$ , $b = 2.40 \pm 0.21$	$a = 0.031$	$y = 0.031x^{2.40}$
			<i>Gerris remigis</i>	$\ln(a) = -4.200 \pm 0.916$ , $b = 2.60 \pm 0.45$	$a = 0.014$	$y = 0.014x^{2.60}$
			<i>Metrobates hesperius</i>	$\ln(a) = -4.080 \pm 0.525$ , $b = 2.66 \pm 0.34$	$a = 0.016$	$y = 0.016x^{2.66}$
			<i>Rhagovelia obesa</i>	$\ln(a) = -4.791 \pm 1.018$ , $b = 2.78 \pm 0.40$	$a = 0.008$	$y = 0.008x^{2.78}$

<sup>1</sup>When the equation in the study was  $y = a(x)^b$ , <sup>2</sup>When the equation in the study was  $\ln(y) = \ln(a) + b \ln(x)$ , <sup>3</sup>With transformed coefficient parameter  $a$ , if needed.

**Table 2.2** Equations and adjusted R<sup>2</sup> values of five fitting functions (linear regression, polynomial regression order 2, 3, and 4, and power regression) on semi-aquatic bugs belonging to three body form groups: (1) Cylindrostethinae, Gerrinae, and Ptilomerinae, (2) Halobatinae, and (3) Veliidae. Regressions were done on combined body form groups as well as on each group with life stages combined and separated. The regression for each group was developed using measurements from 45 juveniles and 45 adults for each body form group, except for Halobatinae, which was based on 45 juveniles and 34 adults due to a limited number of adult specimens. The highest adjusted R<sup>2</sup> value in each category is highlighted in bold.

Body form group	Life stage	Fitting function	Equation	Adjusted R <sup>2</sup>
Gerromorpha	All taxa with all life stages combined	Linear regression	$y = -3.2 + 1.4x$	0.74
		Polynomial regression, order 2	$y = 0.83 - 0.52x + 0.13x^2$	0.85
		Polynomial regression, order 3	$y = -0.56 + 0.51x - 0.037x^2 + 0.0068x^3$	0.86
		Polynomial regression, order 4	$y = 0.51 - 0.6x + 0.27x^2 - 0.023x^3 + 0.00091x^4$	0.86
		Power regression	$y = 0.053x^{2.190}$	<b>0.95</b>
Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile and Adult combined	Linear regression	$y = -7.7 + 1.8x$	0.70
		Polynomial regression, order 2	$y = 2 - 0.87x + 0.15x^2$	0.79
		Polynomial regression, order 3	$y = -1.4 + 0.81x - 0.071x^2 + 0.0079x^3$	0.79
		Polynomial regression, order 4	$y = 4.3 - 3.5x + 0.87x^2 - 0.07x^3 + 0.0021x^4$	0.79
		Power regression	$y = 0.040x^{2.271}$	<b>0.94</b>
	Juvenile only	Linear regression	$y = -4.5 + 1.5x$	0.87
		Polynomial regression, order 2	$y = 1.1 - 0.64x + 0.15x^2$	0.94
		Polynomial regression, order 3	$y = -0.49 + 0.4x - 0.03x^2 + 0.0084x^3$	0.94
		Polynomial regression, order 4	$y = -2.5 + 2.2x - 0.52x^2 + 0.06x^3 - 0.0018x^4$	0.94
		Power regression	$y = 0.039x^{2.362}$	<b>0.97</b>
	Adult only	Linear regression	$y = -13 + 2.3x$	0.68
		Polynomial regression, order 2	$y = 14 - 3.4x + 0.26x^2$	0.75
		Polynomial regression, order 3	$y = -24 + 9.4x - 1.1x^2 + 0.042x^3$	0.77
		Polynomial regression, order 4	$y = 26 - 14x + 2.8x^2 - 0.22x^3 + 0.0064x^4$	0.77
		Power regression	$y = 0.030x^{2.349}$	<b>0.86</b>
Halobatinae	Juvenile and Adult	Linear regression	$y = -0.65 + 0.55x$	0.83

Body form group	Life stage	Fitting function	Equation	Adjusted R <sup>2</sup>	
	combined	Polynomial regression, order 2	$y = -0.18 + 0.15x + 0.068x^2$	0.86	
		Polynomial regression, order 3	$y = 0.077 - 0.18x + 0.19x^2 - 0.013x^3$	0.86	
		Polynomial regression, order 4	$y = 0.061 - 0.15x + 0.17x^2 - 0.0091x^3 - 0.00033x^4$	0.86	
		Power regression	$y = 0.072x^{2.218}$	<b>0.92</b>	
	Juvenile only	Linear regression	$y = -0.35 + 0.38x$	0.75	
		Polynomial regression, order 2	$y = -0.046 + 0.025x + 0.092x^2$	0.76	
		Polynomial regression, order 3	$y = 0.29 - 0.59x + 0.43x^2 - 0.057x^3$	0.76	
		Polynomial regression, order 4	$y = -0.23 + 0.65x - 0.62x^2 + 0.32x^3 + 0.048x^4$	0.75	
		Power regression	$y = 0.068x^{2.300}$	<b>0.85</b>	
	Adult only	Linear regression	$y = -1.2 + 0.7x$	0.67	
		Polynomial regression, order 2	$y = -0.4 + 0.3x + 0.048x^2$	0.66	
		Polynomial regression, order 3	$y = 5.4 - 4.2x + 1.2x^2 - 0.089x^3$	0.65	
		Polynomial regression, order 4	$y = 140 - 140x + 53x^2 - 8.4x^3 + 0.5x^4$	0.67	
		Power regression	$y = 0.141x^{1.704}$	<b>0.68</b>	
	Veliidae	Juvenile and Adult combined	Linear regression	$y = -0.23 + 0.25x$	0.81
			Polynomial regression, order 2	$y = 0.095 - 0.15x + 0.1x^2$	0.87
Polynomial regression, order 3			$y = -0.14 + 0.29x - 0.14x^2 + 0.041x^3$	<b>0.88</b>	
Polynomial regression, order 4			$y = 0.14 - 0.43x + 0.48x^2 - 0.18x^3 + 0.028x^4$	0.88	
Power regression			$y = 0.041x^{2.320}$	0.87	
Juvenile only		Linear regression	$y = -0.12 + 0.16x$	0.85	
		Polynomial regression, order 2	$y = -0.036 + 0.048x + 0.034x^2$	<b>0.86</b>	
		Polynomial regression, order 3	$y = 0.06 - 0.15x + 0.16x^2 - 0.023x^3$	0.86	
		Polynomial regression, order 4	$y = -0.09 + 0.3x - 0.31x^2 + 0.17x^3 - 0.029x^4$	0.86	
		Power regression	$y = 0.037x^{2.322}$	0.81	
Adult only		Linear regression	$y = -0.25 + 0.27x$	0.84	
		Polynomial regression, order 2	$y = 0.067 - 0.11x + 0.094x^2$	0.87	
		Polynomial regression, order 3	$y = -0.43 + 0.76x - 0.35x^2 + 0.069x^3$	0.87	
		Polynomial regression, order 4	$y = 1.6 - 3.7x + 3x^2 - 0.98x^3 + 0.12x^4$	0.88	
		Power regression	$y = 0.049x^{2.229}$	<b>0.94</b>	

**Table 2.3** Comparison of measured and predicted biomass of juvenile (J) and adult (A) semi-aquatic bugs from the three body form groups obtained in this study, using coefficients from power regression, fitted on combined body form groups ( $y = 0.053x^{2.190}$ ,  $N = 259$ ) and each group with life stages combined ( $y = 0.040x^{2.271}$  for Cyndrostethinae, Gerrinae, and Ptilomerinae, based on  $n = 45$  juveniles and 45 adults;  $y = 0.072x^{2.218}$  for Halobatinae, based on  $N = 45$  juveniles and  $N = 34$  adults; and  $y = 0.041x^{2.320}$  for Veliidae, based on  $N = 45$  juveniles and 45 adults). Bold  $p$ -value indicates that there is a significant difference between the measured and predicted biomass ( $p$ -value $<0.05$ ).

Body form group	Life stage	Mean ( $\pm$ SE) biomass (mg)		Fitting function	W	P <sup>1</sup>
		Measured	Predicted			
Cylindrostethinae, Gerrinae, and Ptilomerinae	J	6.042 $\pm$ 0.931	5.338 $\pm$ 0.752	$y = 0.053x^{2.190}$	965	0.70
	J	6.042 $\pm$ 0.931	4.863 $\pm$ 0.699	$y = 0.040x^{2.271}$	920	0.46
	A	10.365 $\pm$ 1.725	10.639 $\pm$ 1.295	$y = 0.053x^{2.190}$	1107	0.45
	A	10.365 $\pm$ 1.725	9.889 $\pm$ 1.238	$y = 0.040x^{2.271}$	1053	0.75
Halobatinae	J	0.349 $\pm$ 0.044	0.234 $\pm$ 0.026	$y = 0.053x^{2.190}$	763	<b>0.043</b>
	J	0.349 $\pm$ 0.044	0.324 $\pm$ 0.037	$y = 0.072x^{2.218}$	979	0.79
	A	1.424 $\pm$ 0.114	1.016 $\pm$ 0.085	$y = 0.053x^{2.190}$	299	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	1.435 $\pm$ 0.123	$y = 0.072x^{2.218}$	568	0.91
Veliidae	J	0.154 $\pm$ 0.015	0.194 $\pm$ 0.019	$y = 0.053x^{2.190}$	1263.5	<b>0.042</b>
	J	0.154 $\pm$ 0.015	0.165 $\pm$ 0.017	$y = 0.041x^{2.320}$	1033	0.87
	A	0.317 $\pm$ 0.037	0.319 $\pm$ 0.034	$y = 0.053x^{2.190}$	1102	0.47
	A	0.317 $\pm$ 0.037	0.280 $\pm$ 0.031	$y = 0.041x^{2.320}$	903	0.38

<sup>1</sup>Comparisons between measured and predicted biomass were based on Wilcoxon test with Bonferroni correction.

**Table 2.4** Comparison of measured and predicted biomass using coefficients from six studies: five on terrestrial Hemiptera (fitting function source 1–5) and one on semi-aquatic bugs from a sub-tropical region (fitting function source 6–9). The measured values for each body form group were based on 45 juveniles (J) and 45 adults (A), except for adult Halobatinae, which were based on 34 individuals. Bold *p*-value indicates that there is a significant difference between the measured and predicted biomass (*p*-value<0.05).

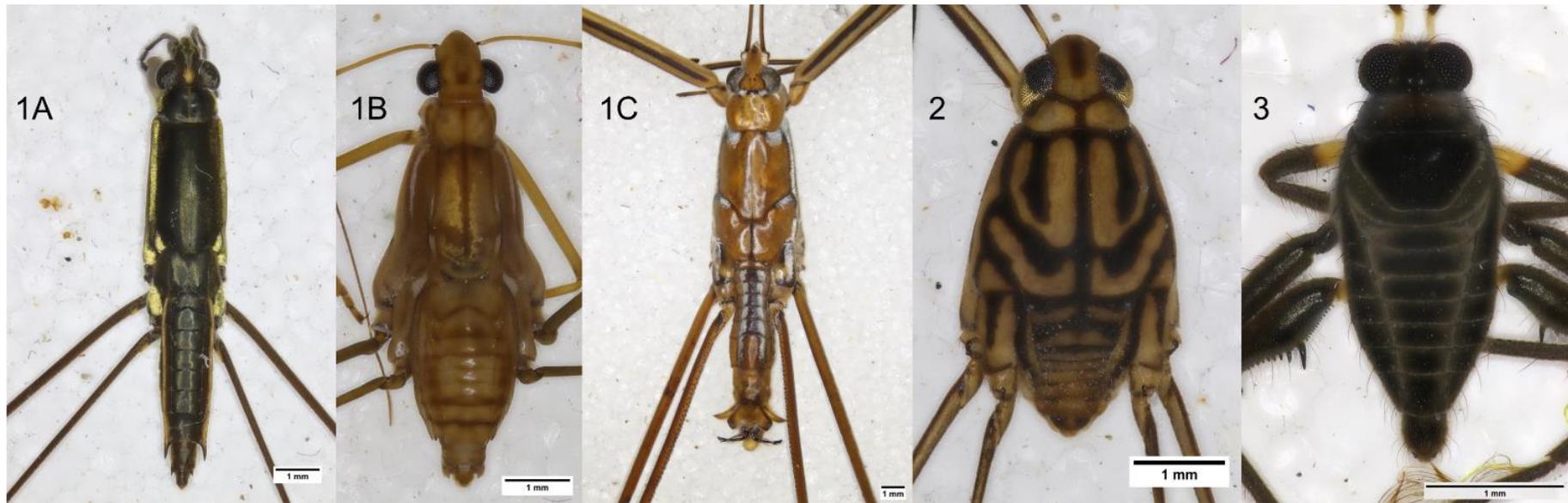
Body form group	Life stage	Mean ± biomass (mg)		Fitting function	Fitting function source <sup>1</sup>	W	P <sup>2</sup>
		Measured	Predicted				
Cylindrostethinae, Gerrinae, and Ptilomerinae	J	6.042 ± 0.931	7.741 ± 1.236	$y = 0.020x^{2.764}$	1	1078	0.60
	J	6.042 ± 0.931	2.289 ± 0.300	$y = 0.041x^{1.934}$	2	730	<b>0.022</b>
	J	6.042 ± 0.931	5.944 ± 0.855	$y = 0.049x^{2.270}$	3	1014	0.99
	J	6.042 ± 0.931	6.488 ± 1.091	$y = 0.008x^{3.075}$	4	968	0.72
	J	6.042 ± 0.931	3.352 ± 0.483	$y = 0.027x^{2.280}$	5	807	0.098
	J	6.042 ± 0.931	5.092 ± 0.755	$y = 0.031x^{2.40}$	6	917	0.44
	J	6.042 ± 0.931	3.678 ± 0.569	$y = 0.014x^{2.60}$	7	791	0.074
	J	6.042 ± 0.931	4.842 ± 0.758	$y = 0.016x^{2.66}$	8	869	0.25
	J	6.042 ± 0.931	3.216 ± 0.515	$y = 0.008x^{2.78}$	9	743	<b>0.029</b>
	A	10.365 ± 1.725	17.806 ± 2.571	$y = 0.020x^{2.764}$	1	1272	<b>0.036</b>
	A	10.365 ± 1.725	4.279 ± 0.471	$y = 0.041x^{1.934}$	2	670	<b>0.005</b>
	A	10.365 ± 1.725	12.083 ± 1.512	$y = 0.049x^{2.270}$	3	1171	0.20
	A	10.365 ± 1.725	16.146 ± 2.503	$y = 0.008x^{3.075}$	4	1153	0.26
	A	10.365 ± 1.725	6.832 ± 0.858	$y = 0.027x^{2.280}$	5	842	0.17
	A	10.365 ± 1.725	10.693 ± 1.396	$y = 0.031x^{2.40}$	6	1076	0.61
	A	10.365 ± 1.725	8.119 ± 1.123	$y = 0.014x^{2.60}$	7	862	0.23
	A	10.365 ± 1.725	10.851 ± 1.526	$y = 0.016x^{2.66}$	8	1028	0.90
	A	10.365 ± 1.725	7.427 ± 1.077	$y = 0.008x^{2.78}$	9	808	0.099
Halobatinae	J	0.349 ± 0.044	0.142 ± 0.019	$y = 0.020x^{2.764}$	1	525	<b>&lt;0.001</b>
	J	0.349 ± 0.044	0.147 ± 0.015	$y = 0.041x^{1.934}$	2	557	<b>&lt;0.001</b>
	J	0.349 ± 0.044	0.230 ± 0.027	$y = 0.049x^{2.270}$	3	762	<b>0.042</b>
	J	0.349 ± 0.044	0.074 ± 0.011	$y = 0.008x^{3.075}$	4	241	<b>&lt;0.001</b>

Body form group	Life stage	Mean $\pm$ biomass (mg)		Fitting function	Fitting function source <sup>1</sup>	W	P <sup>2</sup>
		Measured	Predicted				
	J	0.349 $\pm$ 0.044	0.128 $\pm$ 0.015	$y = 0.027x^{2.280}$	5	496.5	<b>&lt;0.001</b>
	J	0.349 $\pm$ 0.044	0.162 $\pm$ 0.020	$y = 0.031x^{2.40}$	6	610	<b>0.001</b>
	J	0.349 $\pm$ 0.044	0.086 $\pm$ 0.011	$y = 0.014x^{2.60}$	7	312	<b>&lt;0.001</b>
	J	0.349 $\pm$ 0.044	0.103 $\pm$ 0.014	$y = 0.016x^{2.66}$	8	418	<b>&lt;0.001</b>
	J	0.349 $\pm$ 0.044	0.057 $\pm$ 0.008	$y = 0.008x^{2.78}$	9	178.5	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.861 $\pm$ 0.094	$y = 0.020x^{2.764}$	1	226	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.550 $\pm$ 0.040	$y = 0.041x^{1.934}$	2	68	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	1.051 $\pm$ 0.092	$y = 0.049x^{2.270}$	3	330	<b>0.002</b>
	A	1.424 $\pm$ 0.114	0.537 $\pm$ 0.066	$y = 0.008x^{3.075}$	4	103	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.587 $\pm$ 0.051	$y = 0.027x^{2.280}$	5	93	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.798 $\pm$ 0.074	$y = 0.031x^{2.40}$	6	187	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.478 $\pm$ 0.048	$y = 0.014x^{2.60}$	7	68	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.594 $\pm$ 0.062	$y = 0.016x^{2.66}$	8	114	<b>&lt;0.001</b>
	A	1.424 $\pm$ 0.114	0.352 $\pm$ 0.038	$y = 0.008x^{2.78}$	9	20	<b>&lt;0.001</b>
Veliidae	J	0.154 $\pm$ 0.015	0.111 $\pm$ 0.013	$y = 0.020x^{2.764}$	1	711.5	<b>0.014</b>
	J	0.154 $\pm$ 0.015	0.126 $\pm$ 0.011	$y = 0.041x^{1.934}$	2	851	0.19
	J	0.154 $\pm$ 0.015	0.190 $\pm$ 0.019	$y = 0.049x^{2.270}$	3	1261.5	<b>0.044</b>
	J	0.154 $\pm$ 0.015	0.056 $\pm$ 0.007	$y = 0.008x^{3.075}$	4	440	<b>&lt;0.001</b>
	J	0.154 $\pm$ 0.015	0.105 $\pm$ 0.011	$y = 0.027x^{2.280}$	5	700	<b>0.011</b>
	J	0.154 $\pm$ 0.015	0.132 $\pm$ 0.014	$y = 0.031x^{2.40}$	6	837	0.16
	J	0.154 $\pm$ 0.015	0.069 $\pm$ 0.007	$y = 0.014x^{2.60}$	7	495.5	<b>&lt;0.001</b>
	J	0.154 $\pm$ 0.015	0.082 $\pm$ 0.009	$y = 0.016x^{2.66}$	8	585	<b>&lt;0.001</b>
	J	0.154 $\pm$ 0.015	0.045 $\pm$ 0.005	$y = 0.008x^{2.78}$	9	398.5	<b>&lt;0.001</b>
	A	0.317 $\pm$ 0.037	0.211 $\pm$ 0.026	$y = 0.020x^{2.764}$	1	722	<b>0.018</b>
	A	0.317 $\pm$ 0.037	0.194 $\pm$ 0.019	$y = 0.041x^{1.934}$	2	659	<b>0.004</b>
	A	0.317 $\pm$ 0.037	0.318 $\pm$ 0.035	$y = 0.049x^{2.270}$	3	1066	0.67
	A	0.317 $\pm$ 0.037	0.115 $\pm$ 0.015	$y = 0.008x^{3.075}$	4	467	<b>&lt;0.001</b>
	A	0.317 $\pm$ 0.037	0.177 $\pm$ 0.019	$y = 0.027x^{2.280}$	5	602.5	<b>&lt;0.001</b>

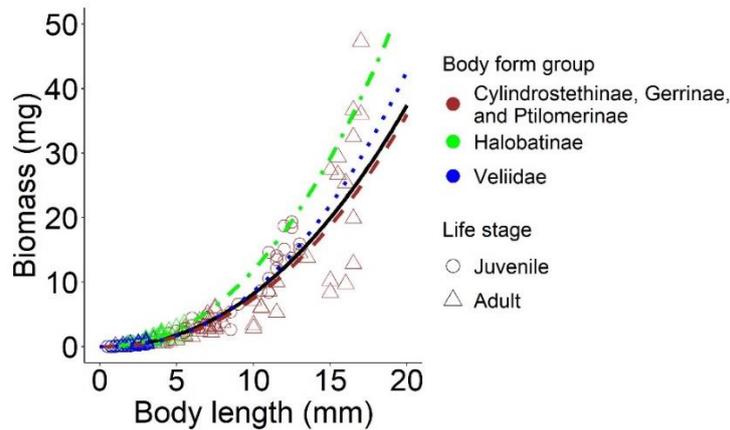
Body form group	Life stage	Mean ± biomass (mg)		Fitting function	Fitting function source <sup>1</sup>	W	P <sup>2</sup>
		Measured	Predicted				
	A	0.317 ± 0.037	0.228 ± 0.026	$y = 0.031x^{2.40}$	6	760	<b>0.041</b>
	A	0.317 ± 0.037	0.125 ± 0.015	$y = 0.014x^{2.60}$	7	500	<b>&lt;0.001</b>
	A	0.317 ± 0.037	0.152 ± 0.018	$y = 0.016x^{2.66}$	8	552	<b>&lt;0.001</b>
	A	0.317 ± 0.037	0.085 ± 0.010	$y = 0.008x^{2.78}$	9	436	<b>&lt;0.001</b>

<sup>1</sup>Fitting function from the following publication: (1) Ganihar, 1997; (2) Gruner, 2003; (3) Rogers et al., 1977; (4) Sample et al., 1993; (5) Schoener, 1980; (6) Smock, 1980 (on general Hemiptera); (7) Smock, 1980 (on *Gerris remigis*); (8) Smock, 1980 (on *Metrobates hesperius*); (9) Smock, 1980 (on *Rhagovelia obesa*).

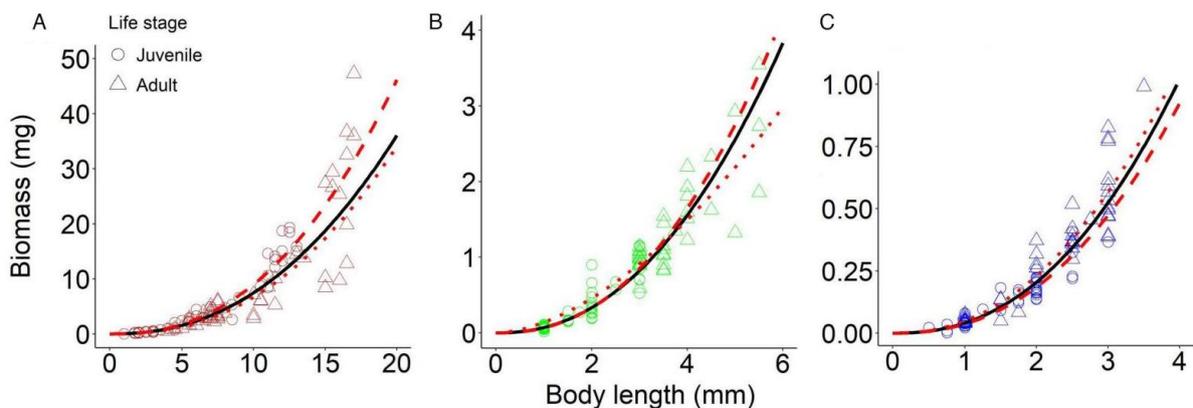
<sup>2</sup>Comparisons between measured and predicted biomass were based on Wilcoxon test with Bonferroni correction.



**Figure 2.1** Example photos to show the families and body forms of semi-aquatic bugs analysed in this study. (1A) Cylindrostethinae, (1B) Gerrinae, and (1C) Ptilomerinae – with small to large slender bodies; in this study adult length of this first group was 4–17 mm and width 1–4 mm, juvenile length was 1–13 mm and width 0.5–3 mm. (2) Halobatinae – with small to medium bodies with wide head and thorax as well as short abdomen; in this study adult length was 3–5.5 mm and width 2–3 mm, juvenile length was 1–3 mm and width 0.25–2 mm. (3) Veliidae – with small stout bodies; in this study adult length was 1–3.5 mm and width 0.5–1.5 mm, juvenile length was 0.5–3 mm and width 0.25–1 mm. Photos courtesy of Matthew Hayes.



**Figure 2.2** Four curves fitted on all juvenile and adult semi-aquatic bug samples, each with coefficients obtained from power regression fitted on: combined body form groups (black solid line;  $y = 0.053x^{2.190}$ ); Cylindrostethinae, Gerrinae, and Ptilomerinae (brown dashed line;  $y = 0.040x^{2.271}$ ); Halobatinae (green dashed-dotted line;  $y = 0.072x^{2.218}$ ); and Veliidae (blue dotted line;  $y = 0.041x^{2.320}$ ). All the curves, except the combined body form groups, were obtained from power regressions on each group with life stages combined.



**Figure 2.3** Three power regressions fitted on all juvenile and adult semi-aquatic bug samples of (A) Cylindrostethinae, Gerrinae, and Ptilomerinae, (B) Halobatinae, (C) and Veliidae. Curves for each body form group were created with coefficients obtained from power regression fitted on each group with life stages combined (black solid line;  $y = 0.040x^{2.271}$  for Cylindrostethinae, Gerrinae, and Ptilomerinae,  $y = 0.072x^{2.218}$  for Halobatinae, and  $y = 0.041x^{2.320}$  for Veliidae); juvenile individuals only (red dashed line;  $y = 0.039x^{2.362}$  for Cylindrostethinae, Gerrinae, and Ptilomerinae,  $y = 0.068x^{2.300}$  for Halobatinae, and  $y = 0.037x^{2.322}$  for Veliidae); and adult individuals only (red dotted line;  $y = 0.030x^{2.349}$  for Cylindrostethinae, Gerrinae, and Ptilomerinae,  $y = 0.141x^{1.704}$  for Halobatinae, and  $y = 0.049x^{2.229}$  for Veliidae).

## Supplementary materials

**Table S2.1** Details about the semi-aquatic bug specimens used in this study. Specimens were categorised into three body form groups (separated based on family and the form of their bodies): 1) Cydrirosthinae, Gerrinae, and Ptilomerinae; 2) Halobatinae; and 3) Veliidae, for biomass estimation. Each specimen was also separated based on their life stage (juvenile or adult). Each body form group had 45 juveniles and 45 adults, except Halobatinae which had 45 juveniles and 34 adults due to a limited number of suitable (available and undamaged) adult specimens (in the table below, these were indicated as ‘NA’). Within each group of 45 (or 34) individuals there was a mix of short, medium, and long individuals. In total, there were 259 individuals used in this study. Specimens were part of a larger data set of semi-aquatic bugs, which were collected from streams in a range of land-use types: old growth forest (OG), logged forest (LF), oil palm with riparian buffer strips (OPB), and oil palm without riparian buffer strips (OP). For this study, the semi-aquatic bugs were selected using stratified random sampling for biomass estimation, i.e., within body form, life stage, and size categories, individuals were chosen randomly from the full range of streams.

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
1	<i>Ptilomera</i> sp.	Ptilomerinae	Cydrirosthinae, Gerrinae, and Ptilomerinae	Juvenile	Short	3	1	OP	Binuang
2	<i>Ptilomera</i> sp.	Ptilomerinae	Cydrirosthinae, Gerrinae, and Ptilomerinae	Juvenile	Short	1	0.5	OP	Binuang
3	<i>Ptilomera</i> sp.	Ptilomerinae	Cydrirosthinae, Gerrinae, and Ptilomerinae	Juvenile	Short	3	1	OP	Selangan Batu
4	<i>Ptilomera</i> sp.	Ptilomerinae	Cydrirosthinae, Gerrinae, and Ptilomerinae	Juvenile	Short	3.5	1.5	OPB	Gaharu
5	<i>Ptilomera</i> sp.	Ptilomerinae	Cydrirosthinae, Gerrinae, and Ptilomerinae	Juvenile	Short	2	1	OPB	Gaharu
6	<i>Cydrirosthethus</i> sp.	Cydrirosthethinae	Cydrirosthethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	4.5	1.5	OPB	Keruing
7	Morphospecies48	Ptilomerinae	Cydrirosthethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	1.75	0.75	OPB	Merbau
8	<i>Potamometropsis</i> sp.	Ptilomerinae	Cydrirosthethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	2	1	LF	LF - 1
9	Morphospecies48	Ptilomerinae	Cydrirosthethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	1.75	0.75	LF	LF - 1
10	Morphospecies48	Ptilomerinae	Cydrirosthethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	2.5	1	LF	LF - 4

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
11	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	4.5	1.5	LF	LF - 2
12	Morphospecies42	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	3	1	LF	LF - 3
13	<i>Tenagobius</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	2.5	1	OG	Maliau
14	<i>Tenagobius</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	2	1	OG	Rhinopool
15	<i>Limnometra</i> sp.	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	4	1.5	OG	VJR
16	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	9	3	OP	Selangan Batu
17	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	5	2	OP	Selangan Batu
18	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	7.5	2	OPB	Gaharu
19	<i>Cylindrostethus</i> sp.	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	8.5	2	OPB	Keruing
20	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	8.5	3	OPB	Keruing
21	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	5.5	2	OPB	Merbau
22	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	6	2	LF	LF - 1
23	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	7	2.5	LF	LF - 4
24	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	8	3	LF	LF - 4
25	<i>Tenagobius</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	5.5	2	LF	LF - 2
26	<i>Tenagobius</i> sp.2	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	5.5	2	LF	LF - 3
27	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Short	4.5	1.5	OG	Maliau
28	Morphospecies42	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	6.5	2	OG	Maliau
29	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	6	2	OG	Rhinopool
30	<i>Tenagobius</i> sp.2	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Medium	6.5	2	OG	VJR
31	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	11	3	OP	Binuang
32	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	12.5	3	OP	Selangan Batu
33	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	13	3	OP	Selangan Batu
34	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	11	3	OPB	Gaharu
35	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	10.5	3	OPB	Keruing
36	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	11.5	3	OPB	Merbau
37	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	12.5	3	OPB	Merbau
38	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	12.5	3	LF	LF - 1

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
39	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	12	3	LF	LF - 4
40	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	11.5	3	LF	LF - 2
41	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	12	3	LF	LF - 2
42	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	11.5	3	LF	LF - 3
43	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	11	3	OG	Maliau
44	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	13	3	OG	Rhinopool
45	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Juvenile	Long	12	3	OG	VJR
46	<i>Rheumatogonus</i> sp.1	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	4.5	1	OP	Binuang
47	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	5	2	OP	Selangan Batu
48	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	5.5	NA	OPB	Gaharu
49	<i>Cylindrostethus</i> sp.	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	6	2	OPB	Keruing
50	<i>Rheumatogonus</i> sp.1	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	5.5	1.75	OPB	Keruing
51	<i>Cylindrostethus</i> sp.	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	6.5	2	OPB	Keruing
52	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7	2	LF	LF - 1
53	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7	2.5	LF	LF - 1
54	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7.5	2.5	LF	LF - 2
55	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7.25	2	LF	LF - 3
56	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7	3	LF	LF - 3
57	<i>Rheumatogonus</i> sp.5	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	5.5	1.5	OG	Maliau
58	<i>Rheumatogonus</i> sp.1	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	4	1	OG	Rhinopool
59	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	6.5	2.75	OG	Rhinopool
60	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7	3	OG	Rhinopool
61	<i>Cylindrostethus</i> sp.	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	10	2	OPB	Keruing
62	<i>Limnometra</i> sp.	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	11.5	3	LF	LF - 2
63	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7	3	LF	LF - 3
64	<i>Cylindrostethus scrutator</i>	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	10.5	2	OPB	Keruing
65	<i>Cylindrostethus scrutator</i>	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	10	2	OPB	Keruing
66	<i>Cylindrostethus scrutator</i>	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	10.5	2	OPB	Keruing

Replicate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
67	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	7.5	2	LF	LF - 1
68	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	7.5	2	LF	LF - 3
69	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	8	2	LF	LF - 1
70	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	7.5	2	LF	LF - 3
71	<i>Potamometropsis</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	7.5	3	OG	Maliau
72	<i>Limnometra</i> sp.	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	11.5	3	OG	Maliau
73	<i>Limnometra</i> sp.	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	11	3	OG	Rhinopool
74	<i>Limnometra</i> sp.	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Medium	10	3	OG	VJR
75	<i>Tenagogonus</i> sp.1	Gerrinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Short	7	3	OG	Rhinopool
76	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	15	4	OP	Binuang
77	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	15	3	OP	Selangan Batu
78	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	16	3.5	OPB	Gaharu
79	<i>Cylindrostethus scrutator</i>	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	13.5	2	OPB	Keruing
80	<i>Cylindrostethus scrutator</i>	Cylindrostethinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	13	2.5	OPB	Keruing
81	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	15.5	4	OPB	Merbau
82	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	16	3.5	LF	LF - 1
83	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	17	4	LF	LF - 1
84	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	16.5	4	LF	LF - 4
85	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	16.5	3.5	LF	LF - 2
86	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	16.5	3.5	LF	LF - 3
87	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	15	3	OG	Maliau
88	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	16.5	3	OG	Maliau
89	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	17	4	OG	Rhinopool
90	<i>Ptilomera</i> sp.	Ptilomerinae	Cylindrostethinae, Gerrinae, and Ptilomerinae	Adult	Long	15.5	4	OG	VJR
91	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	1	OPB	Gaharu
92	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	1	OG	Maliau
93	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	1	OP	Selangan Batu
94	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.75	OG	Maliau

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
95	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Rhinopool
96	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.5	OPB	Gaharu
97	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.5	OG	Maliau
98	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.25	OP	Selangan Batu
99	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.25	OG	Rhinopool
100	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.5	OG	Rhinopool
101	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.5	OG	Rhinopool
102	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.5	OG	Maliau
103	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	1.5	1	OG	Maliau
104	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	0.5	OG	Rhinopool
105	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Short	1	1	OG	Rhinopool
106	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	1.5	1	OP	Selangan Batu
107	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	1.5	1	OP	Selangan Batu
108	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OPB	Gaharu
109	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.5	OPB	Gaharu
110	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.25	OPB	Gaharu
111	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.25	OPB	Gaharu
112	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	1.5	1	LF	LF - 1
113	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	2.5	1.75	LF	LF - 1
114	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Maliau
115	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.5	OG	Rhinopool
116	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Rhinopool
117	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Maliau
118	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	1.75	1	OG	Rhinopool
119	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	1.5	1	OG	Maliau
120	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Rhinopool
121	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Maliau
122	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	2	OG	Maliau

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
123	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Rhinopool
124	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	2	OPB	Gaharu
125	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	2	OPB	Gaharu
126	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.5	OG	Rhinopool
127	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	1.5	LF	LF - 1
128	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	2	OG	Maliau
129	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.5	OP	Selangan Batu
130	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	2.5	1.5	OG	Rhinopool
131	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	2	2	OPB	Gaharu
132	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1	OG	Maliau
133	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	1.5	OG	Rhinopool
134	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Medium	2	1.5	OG	Rhinopool
135	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Juvenile	Long	3	1.5	OG	VJR
136	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2	OG	Rhinopool
137	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OP	Selangan Batu
138	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OPB	Gaharu
139	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OPB	Gaharu
140	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2	OPB	Gaharu
141	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Rhinopool
142	<i>Ventidius</i> sp.2	Halobatinae	Halobatinae	Adult	Short	3.5	2	OG	Maliau
143	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Maliau
144	<i>Ventidius</i> sp.2	Halobatinae	Halobatinae	Adult	Short	3.5	2	OG	Maliau
145	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2	OG	Rhinopool
146	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Rhinopool
147	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Maliau
148	<i>Ventidius</i> sp.2	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Rhinopool
149	<i>Ventidius</i> sp.2	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Rhinopool
150	<i>Ventidius</i> sp.2	Halobatinae	Halobatinae	Adult	Short	3	2	OG	Rhinopool

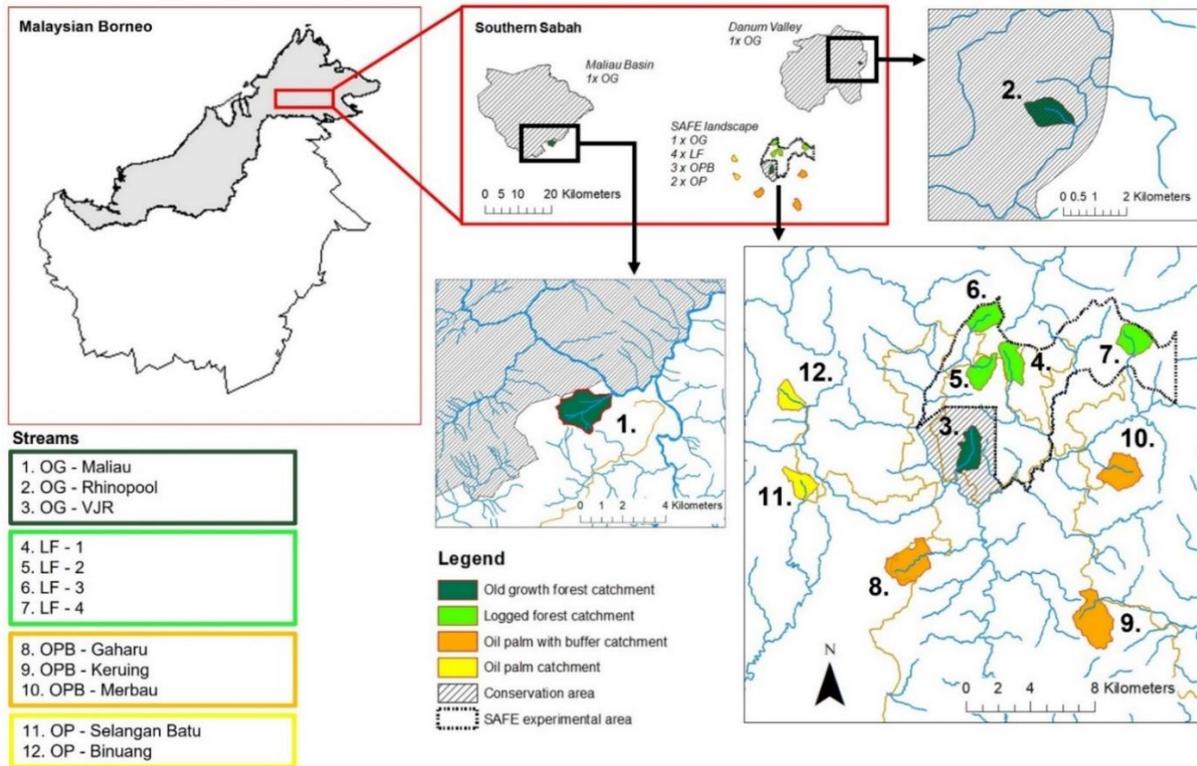
Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
151	<i>Ventidius</i> sp.2	Halobatinae	Halobatinae	Adult	Medium	3.75	2.5	OG	Rhinopool
152	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Long	5.5	2.5	OG	VJR
153	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2.5	OPB	Gaharu
154	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4.5	2.5	OPB	Gaharu
155	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2.5	OPB	Keruing
156	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3	2.5	OPB	Gaharu
157	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4	2.5	LF	LF - 1
158	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2	OG	Maliau
159	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Short	3.5	2	OG	Maliau
160	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4	2.75	OPB	Gaharu
161	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4	2.5	OG	Rhinopool
162	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4.5	2	OG	Maliau
163	<i>Ventidius</i> sp.3	Halobatinae	Halobatinae	Adult	Medium	4	2.5	OG	Rhinopool
164	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4	2.5	OG	Rhinopool
165	<i>Ventidius</i> sp.1	Halobatinae	Halobatinae	Adult	Medium	4	2.5	OG	Rhinopool
166	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
167	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
168	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
169	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Long	5.5	3	OPB	Keruing
170	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
171	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
172	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
173	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
174	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
175	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
176	<i>Metrocoris</i> sp.2	Halobatinae	Halobatinae	Adult	Long	5	2.5	LF	LF - 3
177	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Long	5	2	OG	Rhinopool
178	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
179	<i>Metrocoris</i> sp.1	Halobatinae	Halobatinae	Adult	Long	5.5	2	OG	Rhinopool
180	NA	Halobatinae	Halobatinae	Adult	Long	NA	NA	NA	NA
181	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1	0.5	OPB	Gaharu
182	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1	0.75	OPB	Merbau
183	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	0.75	0.5	OPB	Merbau
184	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1	0.5	OPB	Gaharu
185	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	0.5	0.25	OPB	Gaharu
186	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1	0.5	OPB	Merbau
187	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	0.75	0.5	LF	LF - 1
188	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Short	1	0.75	LF	LF - 2
189	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Short	1	0.75	LF	LF - 3
190	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Short	0.75	0.5	LF	LF - 2
191	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Short	1	1	LF	LF - 3
192	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Short	1.25	0.75	OG	Maliau
193	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1	0.5	OG	Maliau
194	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Juvenile	Short	1	0.5	OG	Rhinopool
195	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1	0.5	OG	VJR
196	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OP	Selangan Batu
197	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OP	Selangan Batu
198	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	2.5	1	OPB	Gaharu
199	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OPB	Keruing
200	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OPB	Merbau
201	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	1.5	0.75	OPB	Gaharu
202	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Medium	1.5	1	LF	LF - 1
203	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	LF	LF - 4
204	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Medium	1.75	1	LF	LF - 2
205	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	LF	LF - 3
206	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Juvenile	Medium	1.75	1	LF	LF - 3

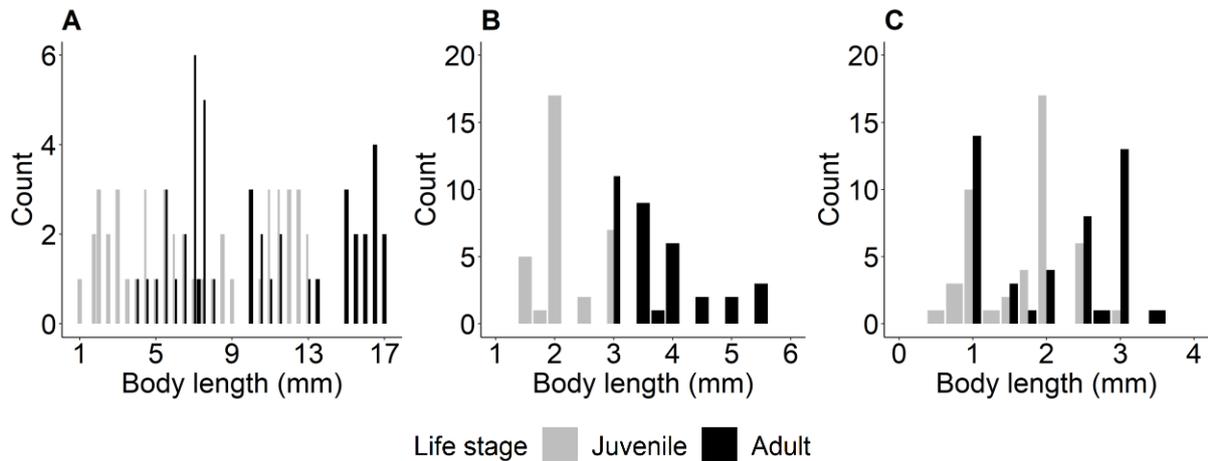
Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
207	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OG	Maliau
208	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	1.75	1	OG	Rhinopool
209	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	0.75	OG	Rhinopool
210	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OG	VJR
211	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OPB	Gaharu
212	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	2.5	1	LF	LF - 2
213	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	0.75	OPB	Gaharu
214	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	2.5	1	OPB	Gaharu
215	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OPB	Keruing
216	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OPB	Merbau
217	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	LF	LF - 1
218	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	2.5	1	LF	LF - 1
219	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	2.5	1	LF	LF - 4
220	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	LF	LF - 2
221	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	LF	LF - 3
222	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	3	1	OG	Maliau
223	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Short	1.75	0.75	OG	Rhinopool
224	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Medium	2	1	OG	VJR
225	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Juvenile	Long	2.5	1	OG	VJR
226	<i>Microvelia</i> sp.4	Microveliinae	Veliidae	Adult	Short	1	0.5	LF	LF - 2
227	<i>Microvelia</i> sp.4	Microveliinae	Veliidae	Adult	Short	1	0.5	OG	Rhinopool
228	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Short	1	0.75	OG	Rhinopool
229	<i>Microvelia</i> sp.4	Microveliinae	Veliidae	Adult	Short	1	0.5	OG	VJR
230	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Short	1	0.5	OG	Rhinopool
231	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Short	1	0.75	OG	Maliau
232	<i>Microvelia</i> sp.5	Microveliinae	Veliidae	Adult	Short	1	0.75	LF	LF - 1
233	<i>Microvelia</i> sp.5	Microveliinae	Veliidae	Adult	Short	1	0.5	LF	LF - 3
234	<i>Microvelia</i> sp.3	Microveliinae	Veliidae	Adult	Short	1	0.75	LF	LF - 1

Repl- cate	Morphospecies	Subfamily	Group	Life stage	Body length range	Body length	Body width	Land-use type	Stream
235	<i>Microvelia</i> sp.4	Microveliinae	Veliidae	Adult	Short	1	0.5	LF	LF - 2
236	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Short	1.5	0.75	OG	Maliau
237	<i>Microvelia</i> sp.4	Microveliinae	Veliidae	Adult	Short	1	1.5	OG	Maliau
238	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Short	1	0.75	OG	Maliau
239	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Short	1	0.75	OG	Rhinopool
240	Morphospecies40	Microveliinae	Veliidae	Adult	Short	1	1	OG	VJR
241	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OPB	Gaharu
242	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OPB	Keruing
243	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OPB	Merbau
244	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OPB	Gaharu
245	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OPB	Keruing
246	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OPB	Merbau
247	<i>Microvelia</i> sp.2	Microveliinae	Veliidae	Adult	Short	1.5	0.75	LF	LF - 1
248	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Adult	Medium	2	1	LF	LF - 2
249	<i>Microvelia</i> sp.2	Microveliinae	Veliidae	Adult	Medium	2	1	LF	LF - 2
250	<i>Microvelia</i> sp.1	Microveliinae	Veliidae	Adult	Medium	2	1	LF	LF - 3
251	<i>Microvelia</i> sp.2	Microveliinae	Veliidae	Adult	Medium	2	1	LF	LF - 3
252	<i>Rhagovelia</i> sp.5	Rhagoveliinae	Veliidae	Adult	Long	3	1	OG	Maliau
253	<i>Strongylovelia</i> sp.	Haloveliinae	Veliidae	Adult	Medium	1.75	0.75	OG	Rhinopool
254	<i>Rhagovelia</i> sp.6	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	OG	VJR
255	<i>Microvelia</i> sp.2	Microveliinae	Veliidae	Adult	Short	1.5	0.75	OG	VJR
256	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OPB	Keruing
257	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OP	Selangan Batu
258	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OPB	Gaharu
259	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OPB	Gaharu
260	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	2.75	1	OPB	Keruing
261	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OPB	Merbau
262	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	LF	LF - 1

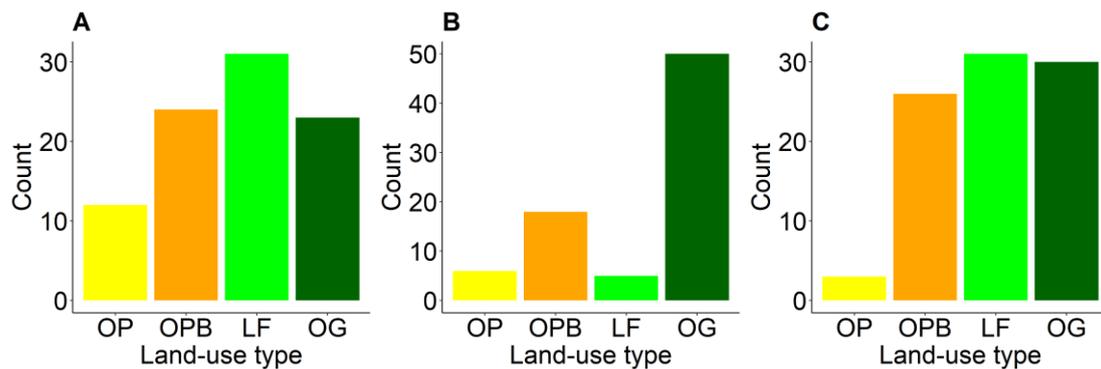
<b>Repli- cate</b>	<b>Morphospecies</b>	<b>Subfamily</b>	<b>Group</b>	<b>Life stage</b>	<b>Body length range</b>	<b>Body length</b>	<b>Body width</b>	<b>Land-use type</b>	<b>Stream</b>
263	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	LF	LF - 4
264	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3.5	1	LF	LF - 2
265	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Medium	2.5	1	LF	LF - 3
266	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	LF	LF - 3
267	<i>Rhagovelia</i> sp.4	Rhagoveliinae	Veliidae	Adult	Long	3	1	OG	Maliau
268	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OG	Rhinopool
269	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1	OG	Rhinopool
270	<i>Rhagovelia</i> sp.1	Rhagoveliinae	Veliidae	Adult	Long	3	1.25	OG	VJR



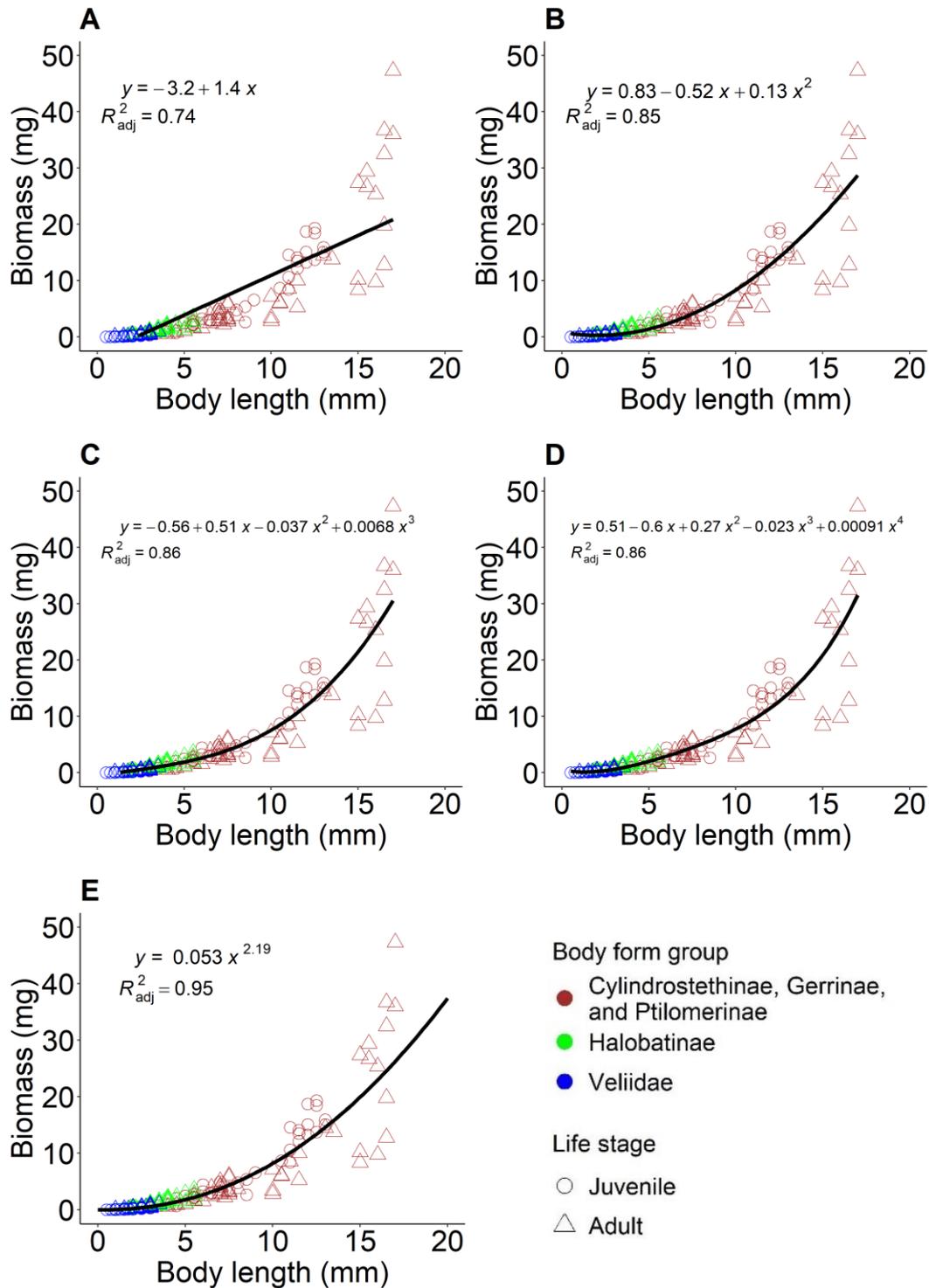
**Figure S2.1** Map showing locations where semi-aquatic bugs were collected from four types of land use (old growth forest/ OG; logged forest/ LF; oil palm with riparian buffer strips/ OPB; and oil palm without riparian buffer strips/ OP) in Sabah, Malaysian Borneo. The 12 sampled streams were spread across Danum Valley Conservation Area, Maliau Basin Conservation Area, and SAFE (Stability of Altered Forest Ecosystem) Project sites within southern Sabah, Malaysian Borneo (red box, and inset).



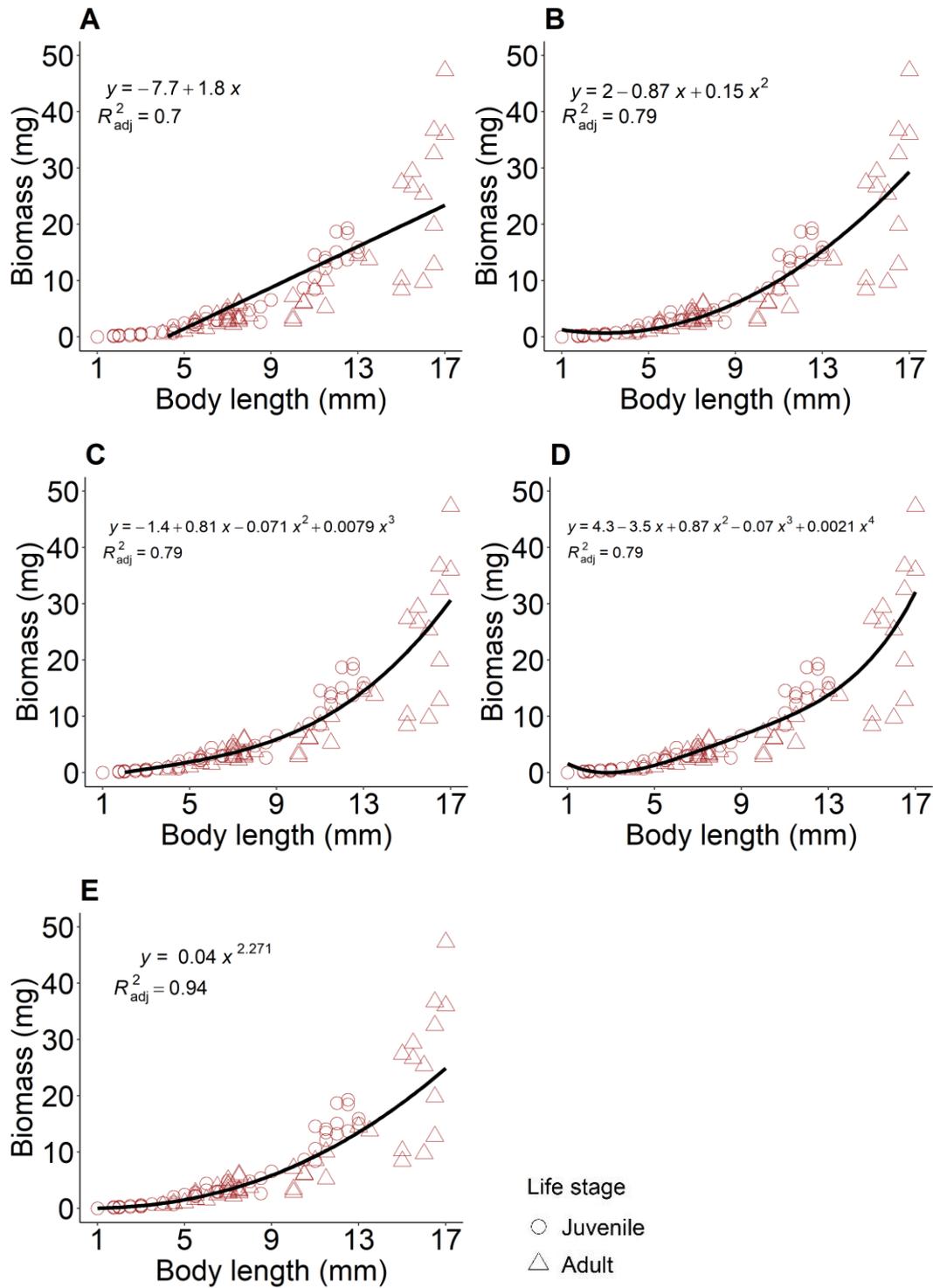
**Figure S2.2** Number of semi-aquatic bugs (Gerromorpha) used per body form group: Cylindrostethinae, Gerrinae, and Ptilomerinae (A); Halobatinae (B); and Veliidae (C) across the range of body lengths found in the samples. In this study, the adult lengths of Cylindrostethinae, Gerrinae and Ptilomerinae (A) were 4–17 mm, and the juvenile lengths were 1–13 mm. For Halobatinae (B), the adult lengths were 3–5.5 mm, and the juvenile lengths were 1–3 mm. For Veliidae (C), the adult lengths were 1–3.5 mm, and the juvenile lengths were 0.5–3 mm. A representative number of semi-aquatic bugs from across all land-use types were used, particularly when the specimens were available and undamaged. Otherwise, semi-aquatic bugs from other land-use types were used (OP = oil palm, OPB = oil palm with riparian buffer strips, LF = logged forest, OG = old-growth forest).



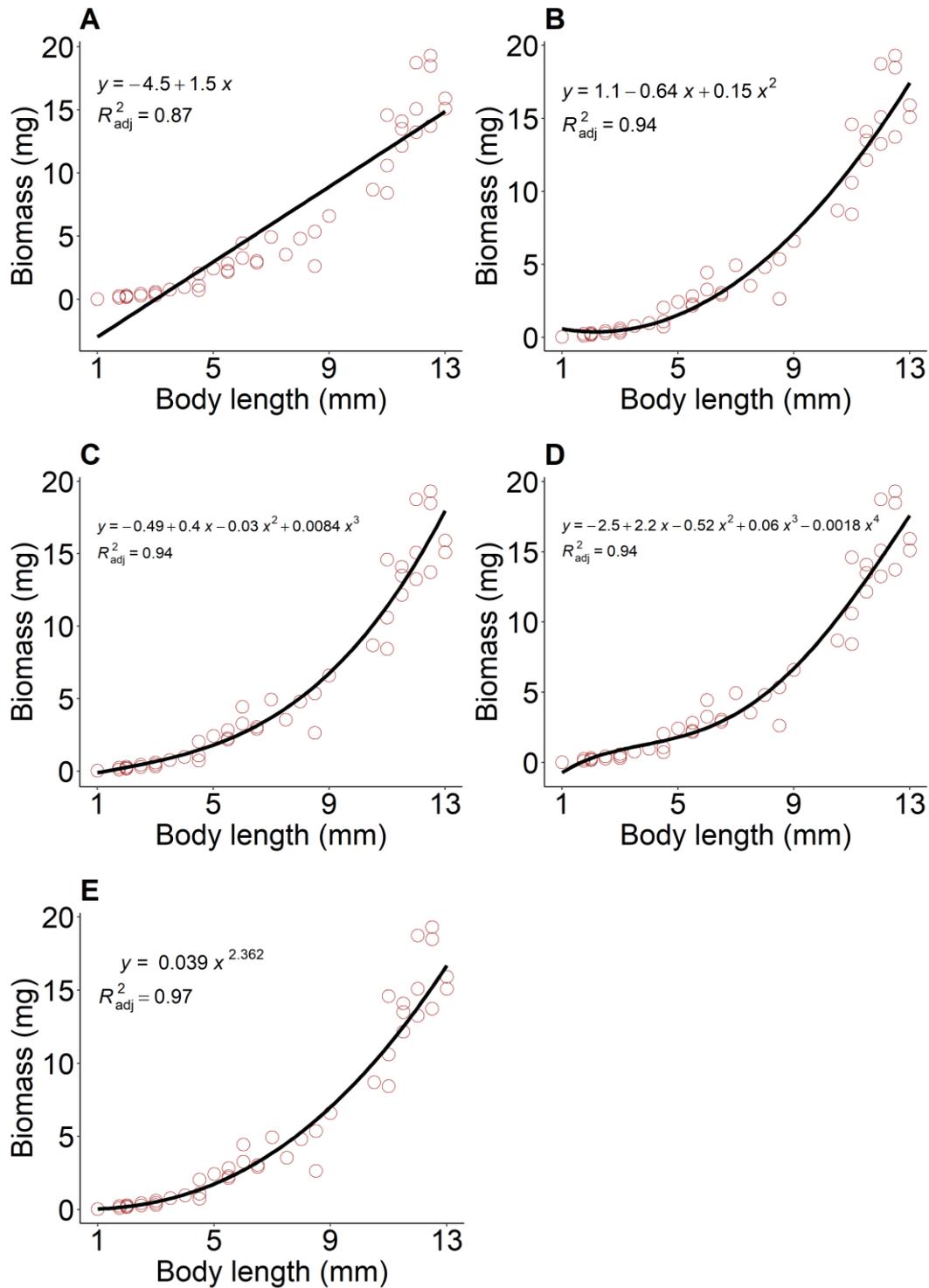
**Figure S2.3** Number of semi-aquatic bugs (Gerromorpha) used per body form group and land-use type: Cylindrostethinae, Gerrinae, and Ptilomerinae (A), Halobatinae (B), and Veliidae (C). When available and undamaged, we used a representative number of semi-aquatic bugs from across all land-use types. Otherwise, semi-aquatic bugs from other land-use types were used (OP = oil palm, OPB = oil palm with riparian buffer strips, LF = logged forest, OG = old-growth forest).



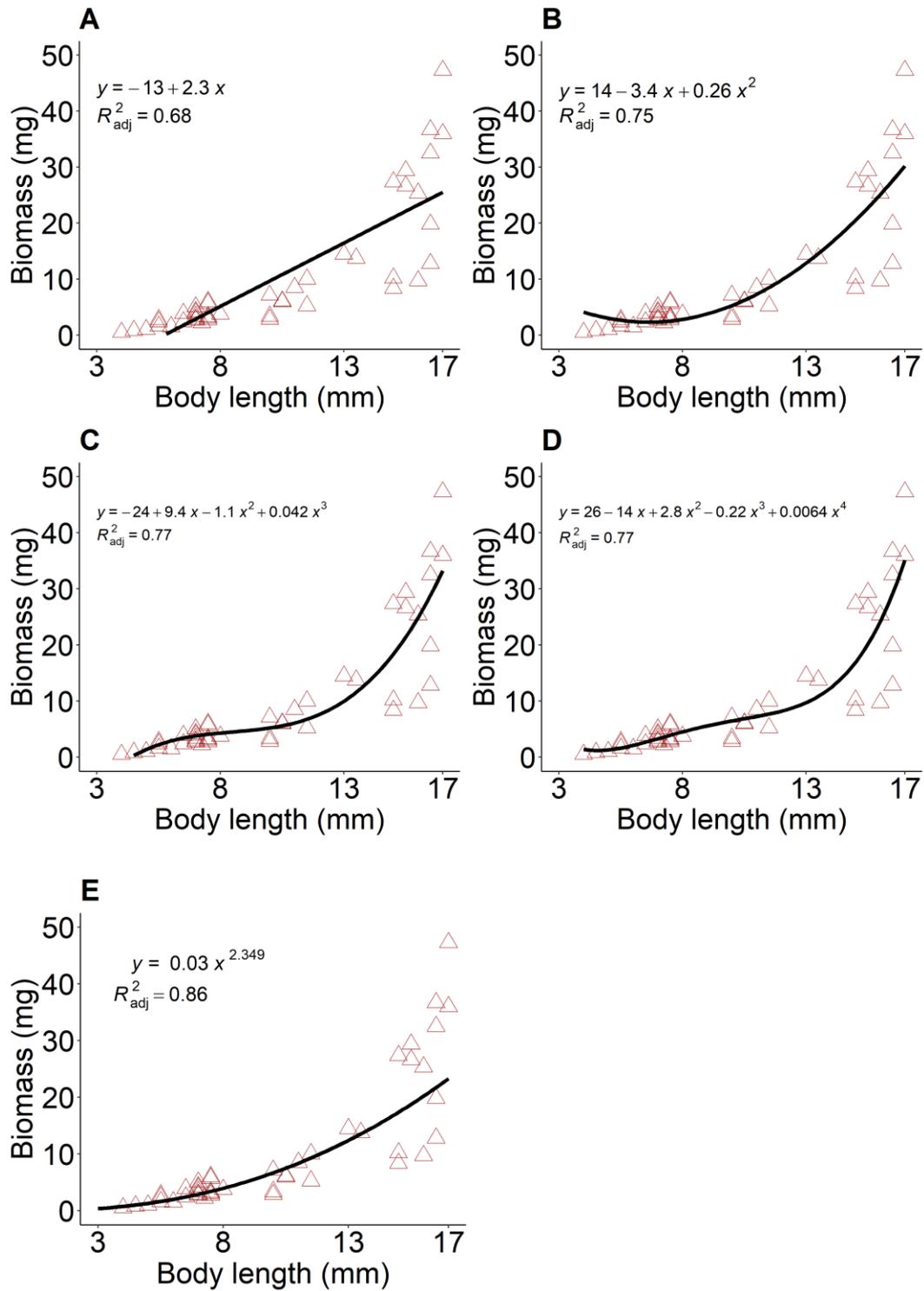
**Figure S2.4** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on all body form groups of semi-aquatic bugs (Gerromorpha) with both life stages (juvenile and adult) combined. The equation and the adjusted  $R^2$  value for each model is shown.



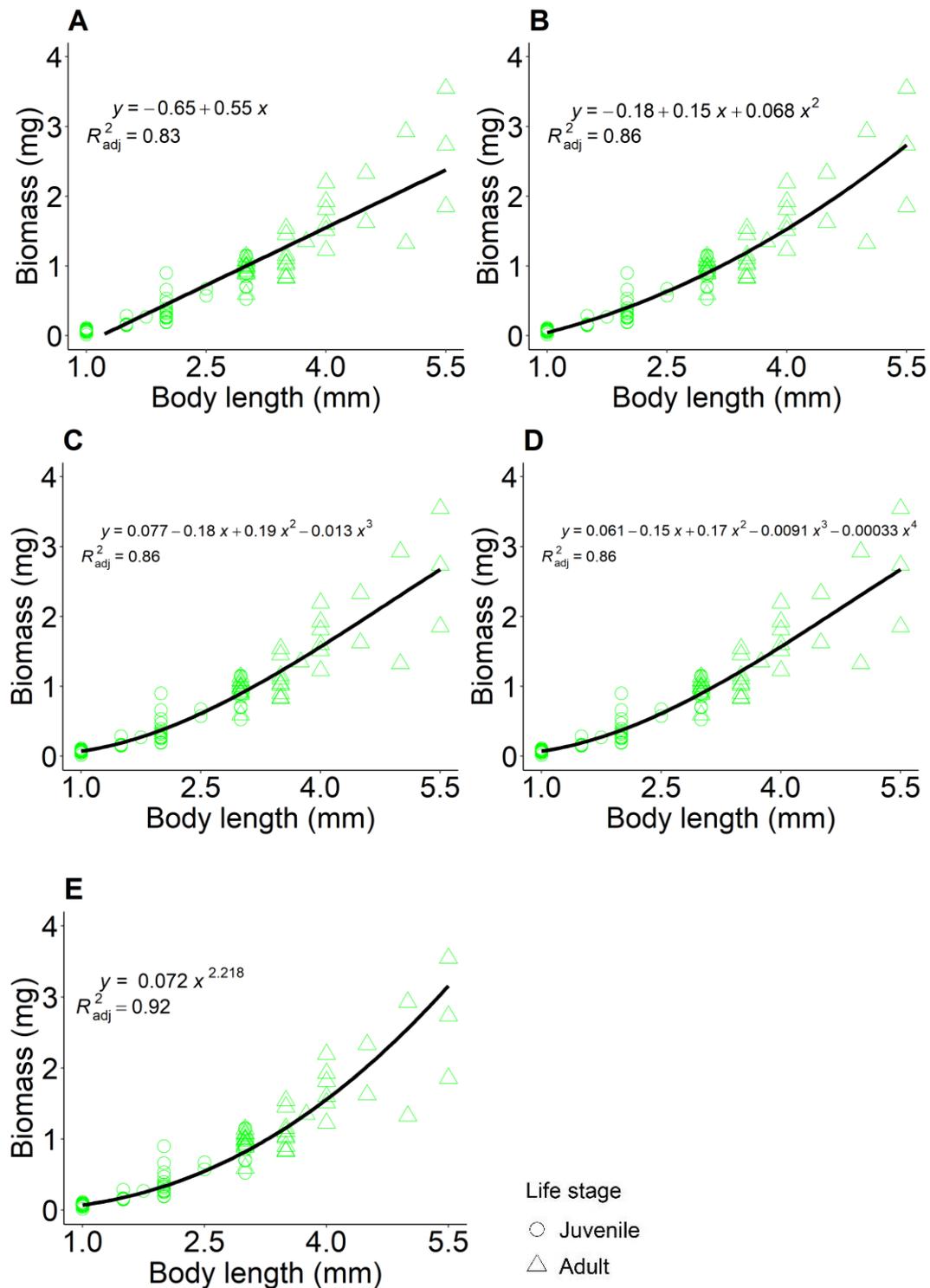
**Figure S2.5** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Cylindrostethinae, Gerrinae, and Ptilomerinae with juvenile and adult life stages combined. The equation and the adjusted  $R^2$  value for each model is shown.



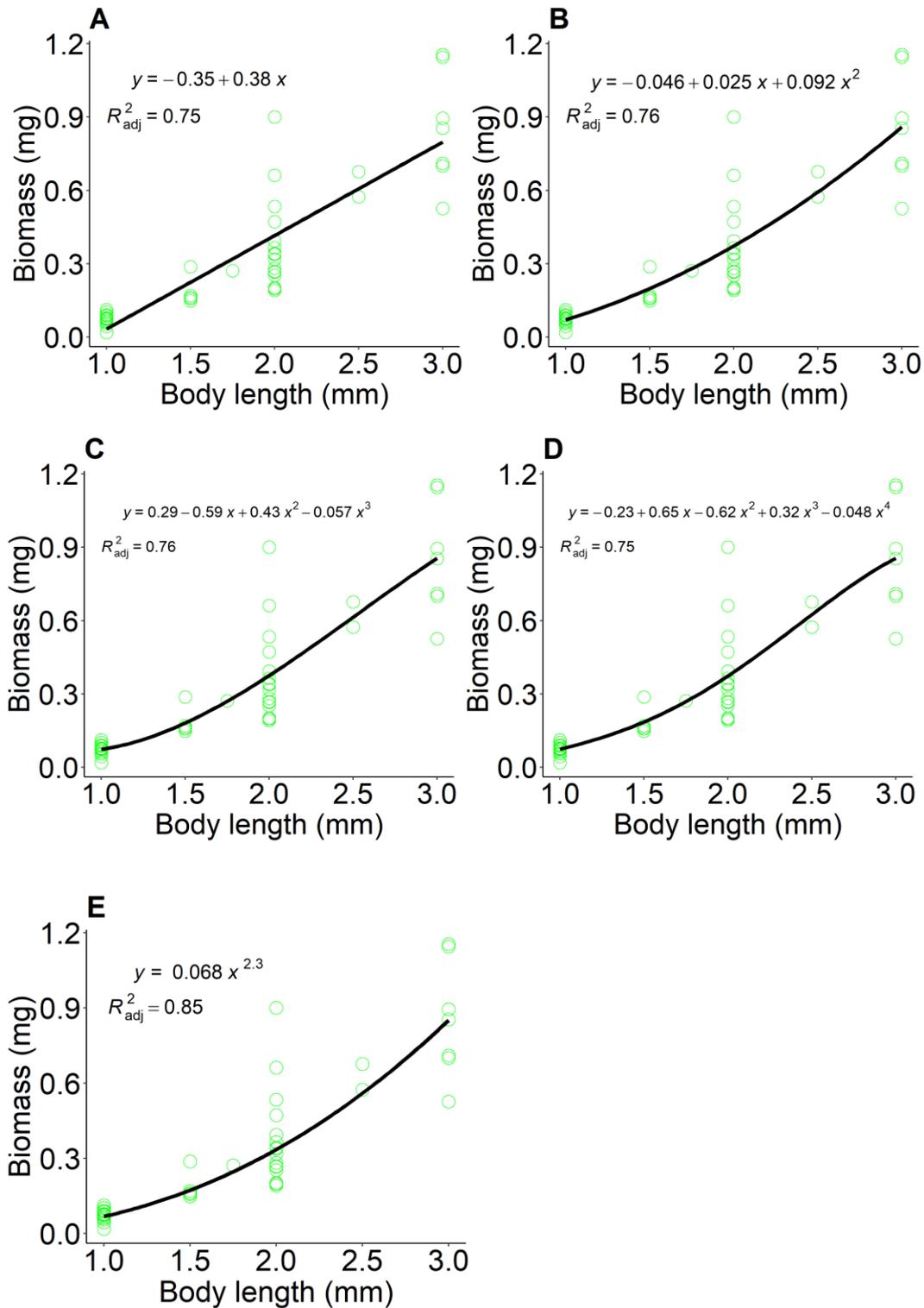
**Figure S2.6** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Cyliodrostethinae, Gerrinae, and Ptilomerinae with juvenile life stage only. The equation and the adjusted  $R^2$  value for each model is shown.



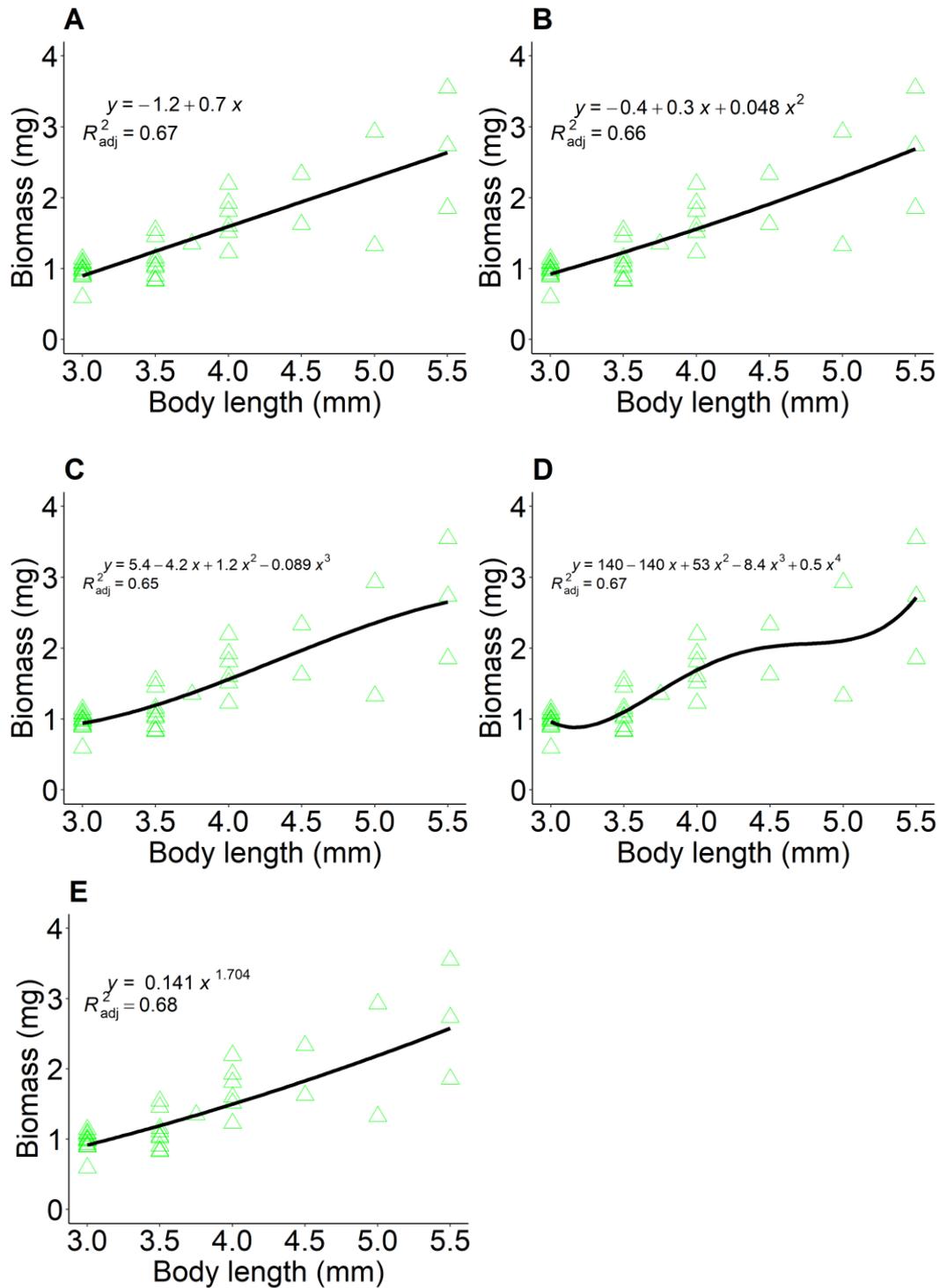
**Figure S2.7** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on *Cylindrostethinae*, *Gerrinae*, and *Ptilomerinae* with adult life stage only. The equation and the adjusted  $R^2$  value for each model is shown.



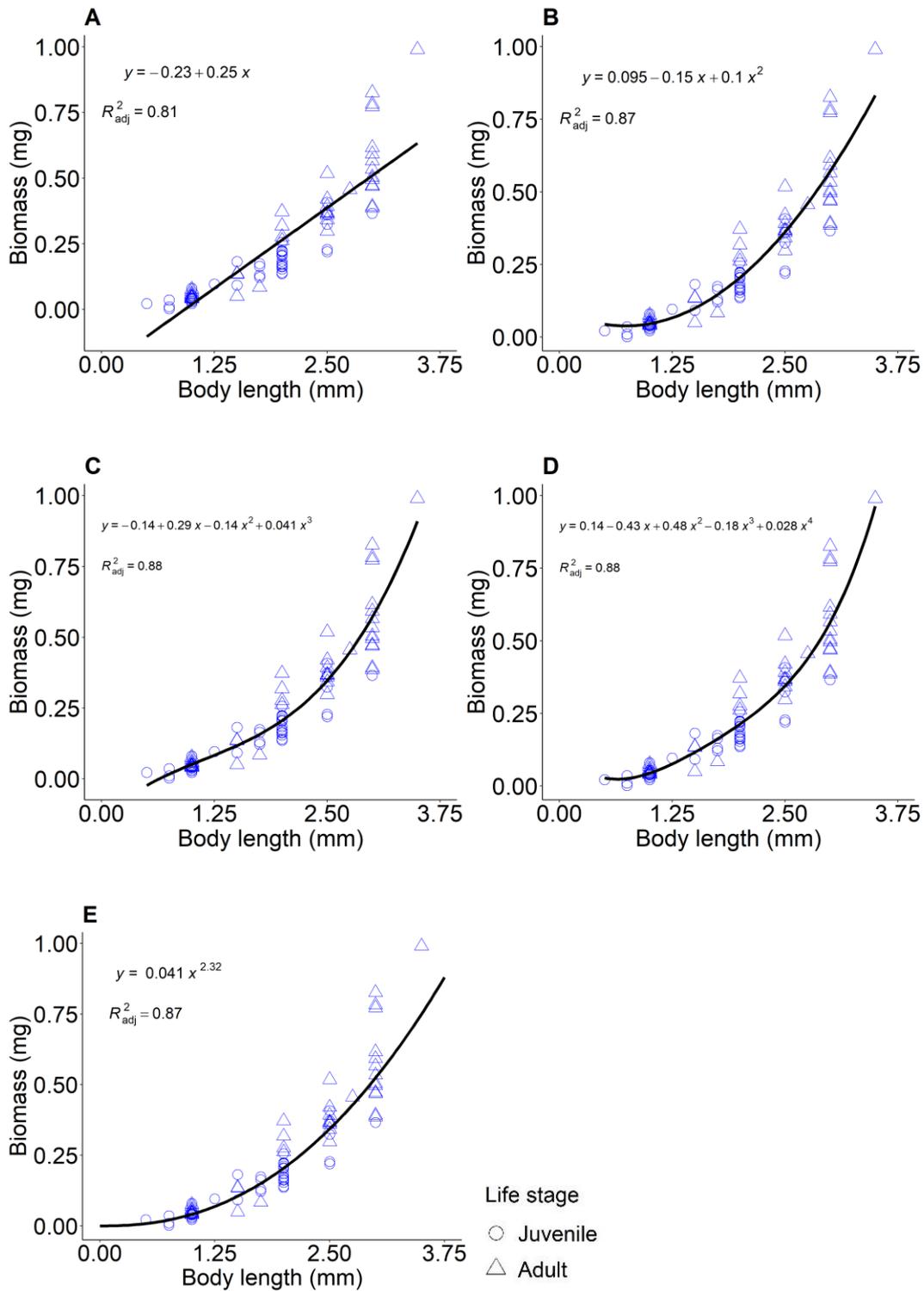
**Figure S2.8** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Halobatinae with juvenile and adult life stages combined. The equation and the adjusted  $R^2$  value for each model is shown.



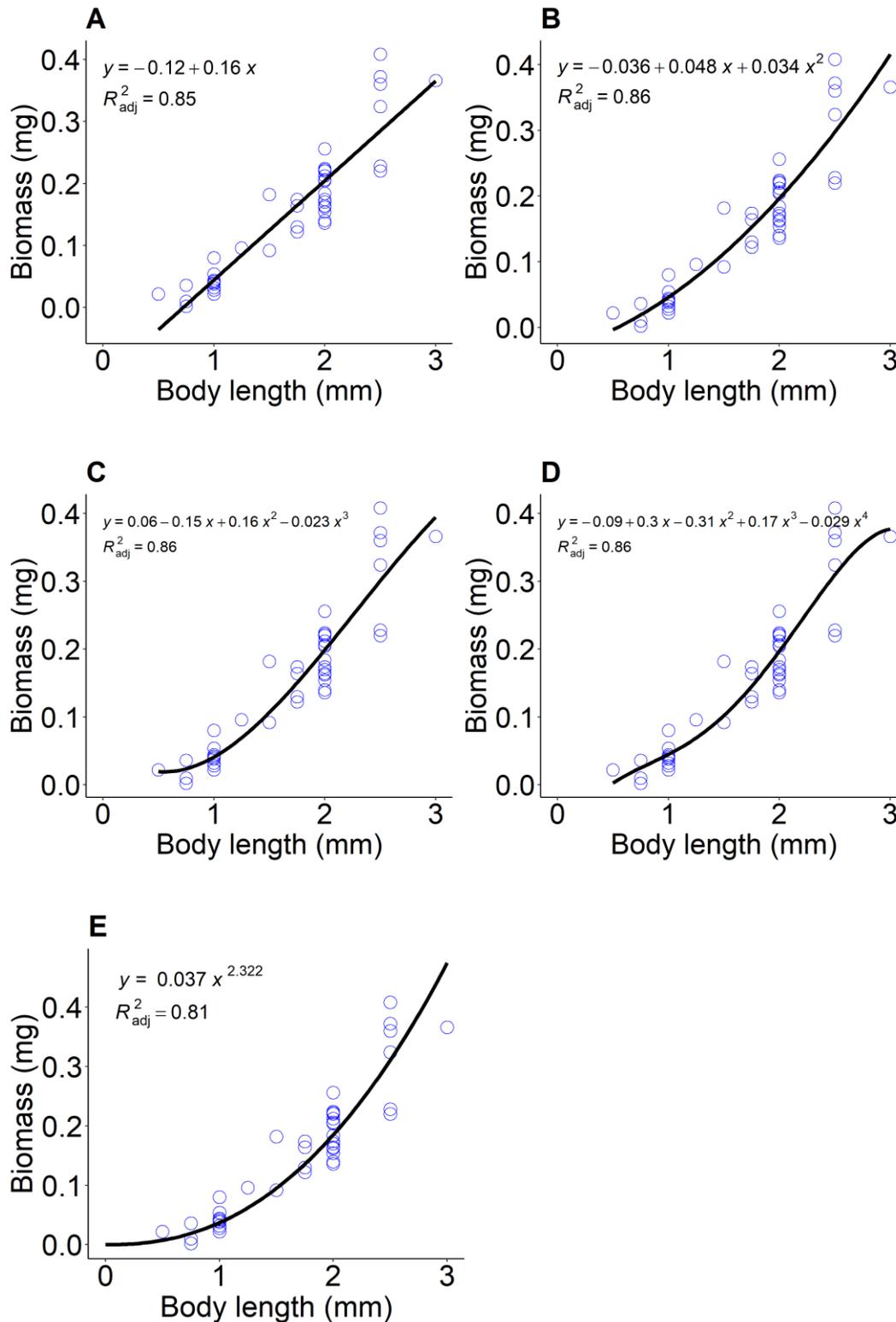
**Figure S2.9** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Halobatinae with juvenile life stage only. The equation and the adjusted  $R^2$  value for each model is shown.



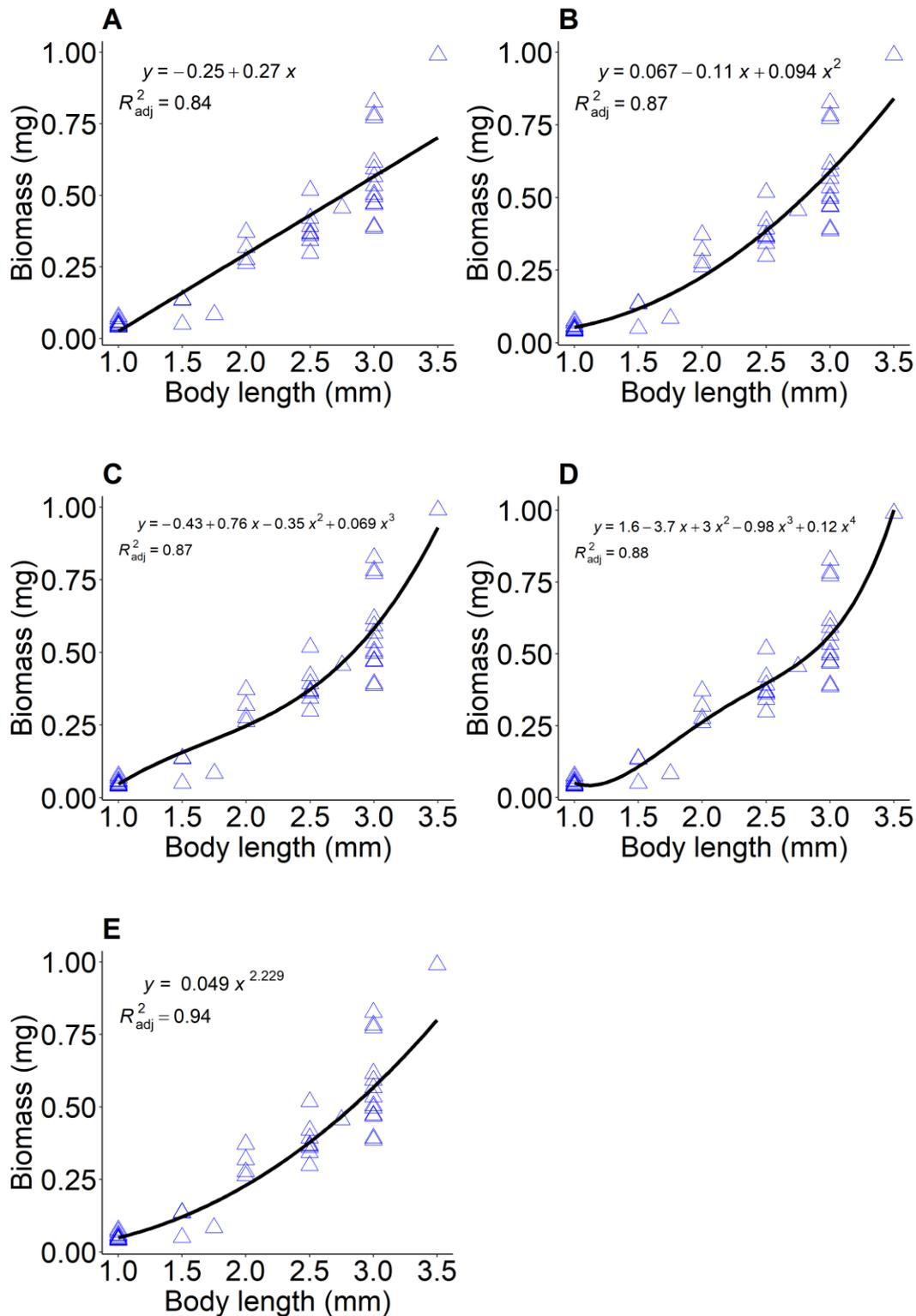
**Figure S2.10** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Halobatinae with adult life stage only. The equation and the adjusted  $R^2$  value for each model is shown.



**Figure S2.11** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Veliidae with juvenile and adult life stages combined. The equation and the adjusted  $R^2$  value for each model is shown.



**Figure S2.12** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Veliidae with juvenile life stage only. The equation and the adjusted  $R^2$  value for each model is shown.



**Figure S2.13** Linear regression (A), polynomial regression order 2 (B), polynomial regression order 3 (C), polynomial regression order 4 (D), and power regression (E) fitted on Veliidae with adult life stage only. The equation and the adjusted  $R^2$  value for each model is shown.

### **Chapter 3: The effects of land-use change on semi-aquatic bugs (Gerromorpha, Hemiptera) in rainforest streams in Sabah, Malaysia**

**Martina F. Harianja<sup>1</sup>, Edgar C. Turner<sup>1</sup>, Holly Barclay<sup>3,1</sup>, Vun K. Chey<sup>4</sup>, David C. Aldridge<sup>1</sup>, William A. Foster<sup>1</sup> & Sarah H. Luke<sup>2,1</sup>**

<sup>1</sup>Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK,

<sup>2</sup>School of Biosciences, University of Nottingham, Sutton Bonington Campus, Nr Loughborough, LE12 5RD, UK,

<sup>3</sup>School of Science, Monash University Malaysia, Jalan Lagoon Selatan, 47500 Subang Jaya, Selangor Darul Ehsan, Malaysia, and

<sup>4</sup>Forest Research Centre (Sepilok), Sabah Forestry Department, PO Box 1407, 90715 Sandakan, Sabah, Malaysia

**Key words:** Gerromorpha (Hemiptera), land-use, logging, oil palm, Malaysia, abundance, richness, total biomass, community composition.

Under review by *Freshwater Biology*.

## Abstract

Land-use change and agricultural expansion have caused marked biodiversity loss in Southeast Asia but impacts and management strategies on freshwater communities have been very little studied. Semi-aquatic bugs are abundant in streams, prey for many other animals, and sensitive to environmental change, making them an important group to study in this context. We investigated the effects of logging and forest conversion to oil palm on semi-aquatic bugs in Sabah, Malaysia, and the potential value of retaining riparian buffer strips in oil palm, by sampling across 12 rivers along an existing land-use gradient. We recorded catchment, riparian, and stream-scale environmental parameters and surveyed semi-aquatic bugs within streams in old-growth forest, logged forest, and oil palm with (OPB) and without buffer strips (OP). We recorded the abundance, richness, total biomass, and proportion of juveniles and winged adult individuals of all species, as well as the sex ratio of *Ptilomera* sp. (a common species throughout the land-use gradient), as possible indicators of disturbance effects. Abundance and richness, but not total biomass, of all semi-aquatic bugs were lower in areas with greater habitat disturbance. Average abundance in old-growth forest was more than twice, four, and six times higher than that in logged forest, OPB, and OP, respectively. Average richness in old-growth forest was higher than in logged forest by two species, but more than twice and three times higher than in OPB and OP, respectively. Riparian buffer strips in oil palm had little effect on the abundance and richness of semi-aquatic bugs. We found no significant differences in the proportion of juveniles, winged adult individuals, or the sex ratio of *Ptilomera* sp. along the disturbance gradient. We found differing community composition across the disturbance gradient. Our study highlights the importance of protecting forest from further conversion for conservation of semi-aquatic bugs.

## Introduction

Freshwater ecosystems cover only 2.3% of the earth's land surface, yet provide myriad functions for humans and wildlife, including habitats for approximately 9.5% of animal species globally (Reid et al., 2019). Streams are common freshwater features with numerous functions. For instance, characteristics of streams influence flooding, nutrient cycling and decomposition, and streams can provide resources for humans, such as fresh water, food materials, and cultural values (Carpenter et al., 2011). However, since the 1960s, streams have become among the most threatened habitats on earth, because of human action affecting their properties (Dudgeon et al., 2006; Reid et al., 2019).

Land-use and climate change, introduced species, overfishing, construction of dams and channelization, and pollution by contaminants and microplastics, are all major threats to stream ecosystems (Allan, 2004; Hester & Gooseff, 2010; Reid et al., 2019). At the catchment scale, conversion of forest for logging and agriculture has caused erosion, sedimentation, and has altered the nutrient cycle within streams through inputs of pollutants by surface, subsurface, and groundwater runoff (Hancock, 2002; Sidle et al., 2006; Syers, 1979). This in turn has reduced the diversity or abundance of many taxa, due to loss of habitat and supplies of food (e.g., leaf litter), as well as increase in water temperature, nutrient content, and other pollutants (Chopra et al., 2011; Lima et al., 2022; Luke, et al., 2017b; Md Rawi et al., 2013; Weijters et al., 2009).

More local effects of habitat change around stream margins and within streams themselves can also influence stream communities and conditions directly. For example, crop planting to the edge of streams can reduce bank stability and riparian habitat complexity, and applications of pesticides and fertilisers can increase chemical inputs to

streams (Corbacho et al., 2003; Tanaka et al., 2021; Wantzen & Mol, 2013). Loss of tree cover around streams can also reduce shading and result in warming of streams, which can alter the growth, survival, and reproduction of aquatic species (Sweeney, 1993). In contrast, practices such as maintaining forested margins along streams can buffer microclimatic conditions within streams, stabilise banks, and filter nutrients from the surrounding agricultural landscapes (Luke et al., 2019). Forested margins also provide resources for aquatic species through allochthonous inputs, such as dead leaves, wood, and terrestrial fauna which fall onto the water (Chellaiah & Yule, 2018; Tank et al., 2010). The loss of forested strips along stream margins in agricultural catchments has been associated with decreases in species richness and changes in the structure of macroinvertebrate communities (Arnaiz et al., 2011).

In Southeast Asia, logging and forest conversion for agriculture (e.g., oil palm) have expanded significantly since the 1980s (Gibbs et al., 2010; Pendrill et al., 2022). Despite the impacts on the terrestrial environment and the likely consequences within waterways, there have been relatively few studies assessing the effects of land-use change on freshwater ecosystems, particularly in Southeast Asia (Dudgeon et al., 2006; van Klink et al., 2021). Forest conversion to oil palm has caused declines in richness and abundance of numerous taxa (Meijaard et al., 2020), declines in arthropod biomass (e.g., Turner & Foster, 2009), and altered species composition (Savilaakso et al., 2014). Many forest species that are associated with freshwater systems are lost due to habitat conversion (Kano et al., 2019; Konopik et al., 2015; Luke et al., 2017b; Mercer et al., 2014). Considering the high levels of biodiversity in Southeast Asia (Myers et al., 2000) and the high number of freshwater species that are vulnerable to environmental change (Strayer & Dudgeon, 2010), more evidence on impacts of human-driven land

modifications is urgently needed in this region.

Within freshwater systems, some invertebrates play a keystone role by acting as primary producers, herbivores, predators, and detritivores (Covich et al., 1999; Wallace & Webster, 1996). Semi-aquatic bugs (Gerromorpha, Hemiptera) are intimately associated with freshwater habitats and are abundant in streams (Andersen, 1982). Generally, they exploit the water surface throughout their life cycle (Andersen, 1982), where they feed on and are eaten by various aquatic and terrestrial species (Foster & Treherne, 1981; Spence & Andersen, 1994; Zimmermann & Spence, 1989).

Such adaptations make this group vulnerable to change, both in the water and surrounding catchment and riparian environment. For example, changes in the surface tension could affect the movement of semi-aquatic bugs on the water surface, reducing their ability to catch prey and avoid predators (Hall, 1985). Deforestation may also reduce the litter supply used as a substrate for egg laying by some species in this group (Bush & Hu, 2005; Sweeney, 1993), and the number of prey items for the bugs (Ceneviva-Bastos & Casatti, 2014). Studies have found that semi-aquatic bugs are sensitive to habitat change. For instance, research in the Brazilian Amazon found a lower richness of semi-aquatic bugs in agricultural areas following forest conversion (Cunha et al., 2015; Cunha & Juen, 2017) and changes in their community structure in Brazilian savanna streams with deforested margins (Dias-Silva et al., 2020a).

Habitat change can also affect the physiology and breeding success of semi-aquatic bugs. For example, one study in Brazil found a higher abundance of winged individuals in forest streams than in oil palm, perhaps owing to reduced resources in oil palm (Cunha et al., 2020). Furthermore, since males and females can have different

requirements for nutrition (Teder & Kaasik, 2023), habitat change could also affect the sex ratio of the population. For instance, female insects can be more vulnerable to food stress than their male counterparts (Teder & Kaasik, 2023), hence if environmental disturbance causes a reduction or loss of food resources, the proportion of males and females in a population could alter. The proportion of adult to juvenile bugs could be affected as well, for example because of a reduction in reproductive success (perhaps related to lower numbers of adult females in a population as a result of environmental change), although we are not aware that this has yet been investigated, particularly in semi-aquatic bugs.

*Ptilomera*, a widespread genus in the Gerridae, is distributed from India to Southeast Asia (Polhemus & Polhemus, 2001). They can be recognized easily by their relatively large body size (up to ~2cm), in comparison to many species of semi-aquatic bugs (Polhemus & Polhemus, 2001). *Ptilomera* are often common and can be found in flowing freshwater bodies (Polhemus & Polhemus, 2001). They can be sexed easily by inspecting differing structures at the abdominal apex in males and females, with a curved paramere with setae being found in males, but dorsolateral lobes being present in the last abdominal segment in females (Jehamalar et al., 2018). Owing to their commonness and clear sexual dimorphism, *Ptilomera* represent a potentially useful group for measuring the impacts of habitat change on ratios of males to females.

To date, there has been no study assessing the effects of land-use change on semi-aquatic bugs in Southeast Asia. Currently, there is no information about the conservation status of any species in this group in Southeast Asia (IUCN, 2022), despite the high level of threat posed by land-use change in this region (Hughes, 2017). We investigate the impact of catchment and riparian forest quality and stream environmental conditions on:

(1) the abundance, total biomass, richness, and community composition of semi-aquatic bugs, and (2) the proportion of juvenile versus adult, winged versus wingless, and female versus male *Ptilomera* sp..

## **Materials and methods**

### **Study sites**

During 2011 – 2014 we surveyed streams in the Danum Valley Conservation Area (117°48.750E and 5°010N), Maliau Basin Conservation Area (116°540E, 4°490N) and the SAFE Project landscape (Stability of Altered Forest Ecosystems, area in the Kalabakan Forest Reserve, 116°570E to 117°420E, 4°380N to 4°460N, Ewers et al., 2011) in Sabah, Malaysian Borneo (**Figure 3.1**). The climate category in the region is tropical, and the average annual air temperature is 27-degree Celcius (Daisuke et al., 2013). Generally, there is little seasonality (Luke, et al., 2017a). The sites are characterised by high mean annual rainfall, i.e., 2882.9mm in Danum Valley and 2455mm in the SAFE Project sites (Luke, et al., 2017a).

We selected 12 streams to survey, which represented a gradient of land use change, choosing from an existing network of streams, established as part of the larger SAFE Project. Habitats comprised old growth forest, logged forest, as well as oil palm with and without riparian buffer strips. We surveyed three stream sites surrounded by old growth forest (OG): Danum Valley (Rhinopool), Maliau Basin (Maliau), and the Virgin Jungle Reserve (VJR) at the SAFE Project. There has never been any logging in the Rhinopool site, whilst the Maliau and VJR sites have been logged at non-commercial levels. Logging in Maliau occurred in around 2009, to provide timber for the field centre.

Although the VJR has not been logged legally, it shows evidence of illegal logging, which is likely to have occurred when the surrounding area was logged in around 1978, and again in the late 1990s to the early 2000s in three rounds (Struebig et al., 2013).

Selectively logged forest (LF) sites were located within the SAFE Project experimental area, whilst oil palm sites with and without riparian buffer strips (OPB, OP) were located close to the project area (**Figure 3.1**). Logged forest (LF) consisted of four stream sites, the catchments of which had all been commercially logged since the 1970s at differing intensities, removing a total of about 113 m<sup>3</sup> of timber per hectare (LF-1, 2, 3, and 4). In the 1990s and 2000s, several rounds of logging also occurred, and this removed another 66 m<sup>3</sup> of timber per hectare (Luke, et al., 2017a). During the study, there was no active management in the logged forest sites.

Oil palm sites with riparian buffers strips (OPB) were in Gaharu, Keruing, and Merbau oil palm estates, while oil palm without riparian buffer strips (OP) were in Binuang and Selangan Batu estates, and all were under similar management by Benta Wawasan, an oil palm company. OPB catchments mainly consisted of mature oil palm (planted between 1999 and 2009), but each had varying amounts of riparian vegetation and forest cover remaining along stream margins (Luke, et al., 2017a), while in OP oil palm was of a similar age and planted up to the stream margin. The average width of forested buffer strips in Gaharu, Keruing, and Merbau were 331m, 68m, and 26m respectively, and were continuous in all cases, with some plantation roads crossing the catchments (Luke, et al., 2017b). Oil palms in all estates were planted approximately nine metres apart, together with a cover crop established at the time of planting to reduce erosion (Luke, et al., 2017a).

Within each stream, data were collected approximately 2km downstream from the stream source, to ensure comparability in catchment area and relative position in the catchment across streams. At this point (termed as the “0m point”), the sites’ mean altitude and slopes were 236m, asl  $\pm$  SE 26m and  $18.24^\circ \pm$  SE  $0.81^\circ$  respectively, and the size of the upstream catchments were  $3.16\text{km}^2 \pm$  SE  $0.31\text{km}^2$  (Luke, et al., 2017b). The average channel and wetted widths recorded across streams in the study ranged from 5.977 to 15.891m and 3.262 to 7.853m, respectively, the average maximum depths ranged from 13.477 to 52.1 cm, and average flow speeds ranged from 0.098 to 0.969 m/s (see **Table S3.1** for data on individual streams).

## **Environmental data collection**

### *Catchment quality*

Catchment scale forest quality data were obtained from forest stand structure maps, produced by Pfeifer et al., (2016). The maps were created using RapidEye™ satellite images taken in 2012 and 2013 as well as ground measurements of forest quality from 193 plots in the SAFE Project sites in 2010 and 2011. These gave information about mean above ground living biomass (AGB [t/ha]), percentage forest cover (FCO), and leaf area index (LAI) across the study landscape (Luke, et al., 2017b; Pfeifer et al., 2016). We clipped forest stand structure maps to the scale of each stream catchment, which was approximately 2km upstream from the “0m point” (**Figure S3.1**), using an ASTER Digital Elevation Model (DEM) (a product of METI and NASA) and ArcMap Hydrology toolbox (Environmental Systems Research Institute (ESRI) 2014), and then computed the mean forest quality values for each catchment (Luke, et al., 2017b). For

more details about the measurement of catchment forest quality, see Luke, et al. (2017b) and Pfeifer et al. (2016).

### *Riparian quality*

We assessed the riparian forest quality of each stream site during June – December 2011 – 2013. We resurveyed all stream sites (except Rhinopool) in May – August 2014. Measurements at each site were taken at points at 50m intervals along a 500m transect going upstream from the “0m” starting point (**Figure S3.1**). At each point, measurements were taken approximately 10m up the left and right side of the banks, or at the nearest area of level ground beyond that. Data were collected along a 500m transect going upstream to quantify conditions upstream of the transect, as well as within the transect itself. This was because upstream effects were most likely to affect downstream communities. The 500m scale was chosen as a compromise to achieve this, while also being feasible on foot in the field.

We recorded canopy openness using a spherical densiometer (Lemmon, 1956), percentage vine cover by eye, forest quality using the SAFE Project scale which provides a rapid assessment of local vegetation composition and structure (Ewers et al., 2011), and density of trees using a relascope (Bitterlich, 1984). Canopy openness was measured by holding the densiometer at chest height facing upstream, away from stream, downstream, and towards stream. We then calculated the mean of the canopy openness for each point. Both percentage vine cover and forest quality were assessed visually within 10m of each measurement point. The SAFE Project forest quality scale ranged from 0 to 5, with 0 = oil palm; 1 = very poor - no trees, open canopy with ginger/ vines

or low scrub; 2 = poor - open with occasional small trees over ginger/ vine layer; 3 = okay - small trees fairly abundant/ canopy at least partially closed; 4 = good – a lot of trees, some large, canopy closed; 5 = very good - closed canopy with large trees, no evidence of logging. The measurement of tree density with a relascope was done by turning 180° from upstream, away from stream, and downstream and counting the number of trees seen above the division size. We used a half-circle turn to avoid gaps created by the stream. The 180° calculation was then doubled to give an estimate for 360°, after which it was doubled again to get an estimate of tree basal area (m<sup>2</sup> ha<sup>-1</sup>). Finally, we calculated the means of all variables to represent each stream.

### *Stream quality*

Within-stream environmental data measurements in each site were taken singly in non-flood conditions in either April – August 2012, November – December 2012, or April – June 2013, along a 200m transect from the “0m point” and going upstream (**Figure S3.1**). Data collected provided information about the structure, habitat complexity, as well as the physicochemical and biological characteristics of the streams. Several stream physical characteristics were measured at points at 10m intervals along the transect, including: flow speed by recording the time needed for a tennis ball to travel along a 2-m string (measured at the point of the fastest flow [rapids or riffles]) and repeated three times, and then mean calculated), canopy openness measured using a spherical densiometer in the middle of each stream at four directions (upstream, left, and right sides of the stream, and downstream, mean taken), and wetted width of the stream using a tape measure.

Characteristics of the whole river channel were also assessed by recording the percentage cover of rocks, pebbles, sand, dead-wood, rapids, riffles, connected pools, and isolated pools between pairs of successive 10m points, as well as slope using a clinometer. Dead wood were large wood blocks from very large branches, or portions of or the whole part of tree trunks, with >5% cover. Pools, riffles, and rapids were characterised according to water speed, with pools being still water without ripples, riffles being flowing water with a rippled surface, and rapids being fast-flowing white water. Finally, we collected data on the stream chemical characteristics, which were recorded at points at 50m intervals and included: water temperature, pH, and conductivity, measured using electronic probes (Hanna Combo pH and EC Meter, Hanna Instruments, Woonsocket, Rhode Island, USA). These chemical characteristics were collected once at each stream (except Rhinopool) between April and December 2012, and once in June 2013 only at Rhinopool. We then calculated the means of each variable for each stream for use in later analyses.

### **Semi-aquatic bug collection and processing**

Within each stream site, semi-aquatic bugs were collected once in July – September 2011, June – August 2012, or May – June 2013 using hand-held nets with mesh of 1mm or less (a method that has been used before successfully in similar surveys [e.g., Ditrich et al., 2008]), from five sub-transects along the 200m transects used for environmental measures (so starting at the “0m point” as well). Each sub-transect was 10m long, and was randomly placed within the 200m, but in a way that ensured upper (130-200m), middle (70-130m), and lower (0-70m) parts of the 200m transect were all represented (hereafter, the sub-transect is termed as “10m transect”, **Figure S3.1 & Table S3.2**). We

chose this method of sampling to ensure that combined samples were representative of each stream catchment (rather than of a specific sample area, the characteristics of which varied across the 500m transect), and this could be compared to environmental characteristics at the scale of the whole catchment. All the bugs found along each “10m transect” were collected and then stored in 70% ethanol. Adult bugs were identified to family and morphospecies level using identification books and relevant papers (Andersen, 1982; Chen & Nieser 1992, 1993a, 1993b; Chen & Zettel 1998; Nieser & Chen, 1992; Polhemus & Polhemus, 1988; Polhemus & Zettel, 1997), with advice from taxonomic experts (see “**Statement of contribution**” [page viii] for details).

The biomass of semi-aquatic bugs was calculated using body length measurements (measured to the nearest 1mm for each individual using graph paper) with power regression body length-biomass equations developed in another study by Harianja et al., 2023a (Chapter 2). Calculations were done by considering families and body forms of the bugs collected in this study:  $y = 0.040x^{2.271}$  for Cyndrostethinae, Gerrinae, and Ptilomerinae;  $y = 0.072x^{2.218}$  for Halobatinae; and  $y = 0.041x^{2.320}$  for Veliidae, with  $y$  being the biomass and  $x$  being the body length of individual bugs. Total biomass (sum of biomass) of semi-aquatic bugs from all 10m transects of each stream was then used for subsequent analyses.

To consider whether there were changes in the demographic structure of the bug community, we separated adult and juvenile individuals based on the number of tarsal segments and wing presence (i.e., if the tarsi had only one segment and/or no wings, the individual was a juvenile, if there were at least two segments and/or wings, it was an adult) [Andersen, 1982]). Finally, one species, *Ptilomera* sp., which showed clear dimorphism in genitalia between sexes, was separated into males and females. We did

not do this for other species since the dimorphism was less clear (e.g., reduced sexual appendages), making such a split unreliable.

### **Statistical analysis**

All analyses and visualisations were carried out in R version 4.0.4 (R Core Team, 2021) with R Studio version 2022.07.1+554 (R Studio Team, 2022). Analyses were done with basic R syntax and package “dplyr” (Wickham et al., 2021), “car” (Fox & Weisberg, 2019) to check the equality of variance using Levene’s test, and “plotrix” (Lemon, 2006) to calculate standard errors. For visualisations, packages used were “tidyverse” (Wickham et al., 2019), “cowplot” (Wilke, 2020), and “gridExtra” (Auguie, 2017). For specific analyses and visualisations, we used differing packages with details below.

#### *Catchment, riparian, and stream quality*

We ran three separate principal component analyses (PCA) to reduce the dimensionality and summarise the parameters representing environmental conditions across our sites (separate PCA for catchment, riparian, and stream scales), and to generate uncorrelated key axes of environmental variation (**Table S3.3-S3.5, Figure S3.2-S3.4**) (Jolliffe, 1986). Before running the PCA, we did not make any transformation to our data. For each PCA, we used a correlation matrix in which we normalised the environmental data due to differing units (Jolliffe, 1986), using the ‘scaling = TRUE’ function in R. For the stream quality PCA, we excluded one of the percentage cover categories (sand) from analyses, because its value was already implied by inclusion of all other percentage cover categories. As predictors for the subsequent analyses, we used PC axes that explained

the majority of variation among environmental parameters (choosing axes which explained >60% of the variation for each scale, which we used as our stopping criterion [see Jolliffe, 1986]) for each of catchment, riparian, and stream scales. We used available R syntax to run principal component analyses (PCA) and “factoextra” (Kassambara & Mundt, 2020) to produce PCA biplots.

To assess the extent of variation in environmental conditions at the catchment and riparian scales, and therefore whether parameters could be used as separate independent predictors in later analyses, we ran a correlation test between the catchment and riparian first principal component (PC) scores. We found that there was a moderate but not significant correlation between the catchment and the riparian scales ( $r = 0.562$ ,  $t = 2.151$ ,  $df = 10$ ,  $p = 0.056$ ), so we decided to do further analyses separately, as both scales included non-overlapping information.

*Impacts of land-use change on semi-aquatic bug abundance, total biomass, richness, and community composition*

Repeat samplings of bug communities across multiple years at Maliau and Selangan Batu showed no significant interannual differences in abundance, total biomass, or richness data (**Appendix S3.1, Table S3.6-S3.7**). Hence, collection period was not included in analyses. In streams with repeat measures, data from just one year (2012) was used for subsequent analyses. We used generalised linear models (GLM) to assess the effects of environmental conditions (separate models for catchment, riparian, and stream-scale PC scores, considering that environmental variables were measured at different scales) on the summed values per river of semi-aquatic bug abundance, total

biomass, and richness. Juveniles were excluded in the richness analysis, as it was not possible to assign them reliably to morphospecies, but they were included in the abundance and total biomass analyses. Site PC scores and semi-aquatic bug parameters (abundance, total biomass, and richness) were used as predictor and response variables respectively.

Models took the following structure: Abundance/ Total Biomass/ Richness ~ CatchmentPC1/ RiparianPC1/ StreamPC1 + StreamPC2. For these models, we multiplied the scores of StreamPC2 by -1, so we could produce visualizations with scores that follow the gradient of land-use, from the most to least disturbed. For abundance, a negative binomial model with log link was chosen because of overdispersion. For total biomass, we used a gaussian distribution with identity link. For richness, a Poisson model with log link was used. In all models, we checked the residuals for normality and homogeneity of variance using diagnostic plots created on fitted and residual values. Because there was an outlier in the abundance data (a replicate from Rhinopool that had very high abundance), we ran analyses both with and without the outlier to check the influence of this point on our conclusions. We used “lme4” (Bates et al., 2015) to run generalised linear models (GLM), and “MASS” (Venables & Ripley, 2002) to run negative binomial models. To check overdispersion for GLM models, we used “performance” (Lüdecke et al., 2021), while “see” (Lüdecke et al., (2021) and “Rcpp” (Eddelbuettel, 2013; Eddelbuettel & Balamuta, 2018; Eddelbuettel & Francois, 2011) were used to check model assumptions.

We ran a Canonical Correspondence Analysis (CCA) with 999 random permutation tests under reduced model to assess the effects of environmental conditions at each scale (CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2) on the

community composition of semi-aquatic bugs (using adult individuals only). We used “vegan” (Oksanen et al., 2020) to run constrained canonical analyses (CCA) and produce the CCA triplot.

*Impacts of land-use change on the proportion of juveniles/ adults, winged/ wingless individuals for all species, and female/ male Ptilomera sp.*

We assessed the effects of environmental conditions across land-use types on the proportion of juveniles and winged adults for all species and female *Ptilomera* sp.. We used GLMs with CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2 scores as predictors and the proportion data as response variables. Binomial families with logit link were chosen in all cases. In all models, we checked the residuals for normality and homogeneity of variance using diagnostic plots.

## **Results**

*Catchment, riparian, and stream quality*

PCAs showed that the first principal component (PC1) at both catchment and riparian scales explained most of the variation in the environmental variables (92% and 77.7% respectively). At the catchment scale, PC1 scores were positively correlated with high values of forest cover (PC1 loading 0.594), leaf area index (LAI) (PC1 loading 0.583), and aboveground biomass (AGB) (PCA loading 0.552) (**Table S3.3 & Figure S3.2**). At the riparian scale, PC1 scores were positively correlated with high values of forest quality (PCA loading 0.554), basal area (PCA loading 0.503), and vine cover (PCA

loading 0.392), as well as low canopy openness (PCA loading -0.534) (**Table S3.4 & Figure S3.3**). At the stream scale, PCA scores were more evenly spread between axes 1 and 2, with PC1 and PC2 scores explaining 45.7% and 19.1% of the variation respectively (ensuring that 64.8% of variation among environmental parameters were covered). PC1 scores were positively correlated with high percentage cover of rocks (PC1 loading 0.380), steep slopes (PC1 loading 0.357), and high percentage cover of isolated pools (PC1 loading 0.291), and low water temperature (PC1 loading -0.350), low canopy openness (PC1 loading -0.293), and fewer connected pools (PC1 loading -0.302) (**Table S3.5 & Figure S3.4**). In addition, PC2 scores were correlated with high percentage cover of riffles (PC2 loading 0.461) and rapids (PC2 loading 0.217), high canopy openness (PC2 loading 0.307), and rapid flow speed (PC2 loading -0.453, the negative sign represented less time needed for a tennis ball to travel along a 2-m string), as well as low percentage cover of deadwood (PC2 loading -0.411), and low percentage cover of connected pools (PC2 loading -0.337) (**Table S3.5 & Figure S3.4**).

*Impacts of land-use change on semi-aquatic bug abundance, total biomass, richness, and community composition*

In total, 10,420 individual bugs comprising 5082 adults and 5338 juveniles were found across all streams in this study (**Table S3.8**). The collected bugs were from two families, (Gerridae and Veliidae), 12 genera, and 38 morphospecies (identifications for adults only) (**Table S3.9**). *Ptilomera* sp. and *Rhagovelia* sp.1 were the most common species, found in all and almost all streams across the disturbance gradient, respectively (**Table S3.9**). Two morphospecies in the Veliidae, *Microvelia* sp.1 and 2, were completely absent in oil palm streams both with (OPB) and without buffer strips (OP) but were

found in relatively high numbers (compared with the other morphospecies in this study) in logged- (LF) and old-growth forest (OG) streams (**Table S3.9**). In general, the average abundance of the bugs in old-growth forest was more than twice, four, and six times that in logged-forest, OPB, and OP, respectively. Average richness was higher in old-growth forest than in logged-forest, although only by two species, and more than twice and three times that in OPB and OP, respectively (mean  $\pm$  SE, abundance: OG =  $1958 \pm 1031$ , LF =  $661 \pm 170$ , OPB =  $431 \pm 59$ , OP =  $306 \pm 243$ ; richness: OG =  $13.6 \pm 2.9$ , LF =  $11.0 \pm 2.3$ , OPB =  $6.0 \pm 2.1$ , OP =  $4.0 \pm 1.0$ ).

There was lower abundance of semi-aquatic bugs in streams associated with lower CatchmentPC1, RiparianPC1, and StreamPC2 scores (**Table 3.1, Figure 3.2**). Overall, a similar pattern was seen for the richness of semi-aquatic bugs, i.e., lower richness, with lower CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2 scores (**Table 3.1, Figure 3.2**). Despite the rapid decline in abundance and richness with higher levels of degradation, there was no significant effect of catchment, riparian, or stream environmental conditions on total biomass (**Table 3.1, Figure 3.2**). This reflected the significant contribution of several species of smaller-bodied Veliidae bugs towards the total abundance in the less degraded habitats, but not to total biomass (**Figure S3.5**). This was because the larger-bodied bugs (either Veliidae or Gerridae) persisted in the more degraded habitats, resulting in the lack of significant difference in the total biomass across the disturbance gradient (**Figure S3.5**). At all scales, there was no clear difference between OPB and OP in terms of the abundance, total biomass, or richness of bugs, with both sites tending to cluster together in plots (**Figure 3.2**). Removal of Rhinopool resulted in the same trends for abundance, total biomass, and richness of bugs at both catchment and riparian scales. However, there were few changes at the stream scale,

with StreamPC1 becoming a significant predictor of abundance, but with Stream PC2 becoming insignificant (**Table S3.10 & Figure S3.6**).

At the community level, there was clustering of sites related to the similarity in the composition of bugs, with CatchmentPC1 and StreamPC2 being significant drivers of the composition (**Table 3.2, Figure 3.3**). Community composition across stream sites were largely driven by singletons or doubletons (**Table S3.9**).

*Impacts of land-use change on the proportion of juveniles/adults, winged/wingless individuals, and female/male Ptilomera sp.*

We found no significant relationship between the quality of catchment, riparian, and stream conditions on the proportion of juveniles to adults or winged to wingless individuals of semi-aquatic bugs, or in the proportion of female to male *Ptilomera* sp. (**Table 3.3, Figure 3.4**).

## **Discussion**

We found that semi-aquatic bug abundance and richness were lower in sites with lower catchment and riparian forest quality, and within streams with certain characteristics. In particular, the abundance of bugs was lower within streams which had more rapid flow speed, higher percentage cover of rapids and riffles, and higher average canopy openness, as well as those with lower percentage cover of connected pools and deadwood (StreamPC2). Finally, the richness of semi-aquatic bugs was lower within streams which had rapid flow speed, higher water temperature and average canopy

openness, as well as higher percentage cover of rapids and riffles, and those with less steep slopes, lower percentage cover of rocks, and percentage cover of isolated pools and deadwood (StreamPC1 and StreamPC2). Comparatively, average abundance of semi-aquatic bugs in old-growth forest was more than twice, four, and six times that in logged forest, oil palm with and oil palm without buffer strips, respectively. Additionally, average richness in old-growth forest was higher than logged forest, although only by two species, as well as more than twice and three times higher than in oil palm with and without buffer strips, respectively. There was clustering in the community composition of bugs associated with disturbance, with catchment forest quality as well as stream characteristics mainly associated with flow speed, canopy openness, and percentage deadwood being the significant drivers. In contrast, we found no significant differences in the total biomass of semi-aquatic bugs in relation to catchment-, riparian- or stream-scale differences in environmental conditions. We also found no effect of environmental disturbance at any scale on the proportion of juveniles to adults or winged to wingless adult individuals for all species, or female to male *Ptilomera* sp..

The significantly lower abundance and richness and differing community composition that we identified with land degradation indicates that semi-aquatic bugs are sensitive to land-use change. This result reflects findings from previous studies which found lower richness (although not abundance) and altered community composition of semi-aquatic bugs in streams surrounded by oil palm compared to those surrounded by forest in the Amazon (Cunha et. al., 2015; Cunha & Juen, 2017; Dias-Silva et al., 2020b). This result also reflects findings from other studies investigating the impact of forest logging and conversion to oil palm on other freshwater taxa, which

found lower species richness with no forest species (Kano et al., 2019; Konopik et al., 2015; Luke et al., 2017b; Mercer et al., 2014), and therefore also altered local community composition (Faruk et al., 2013).

It should be noted that one old-growth forest site (Rhinopool) had particularly high abundance and richness, and therefore had considerable impact on the overall trend. Indeed, the removal from Rhinopool in the analyses caused a change in which factors at the stream level had significant effects on bugs, although this was not the case at the catchment and riparian scales. In particular, characteristics of streams associated with flow (flow speed as well as percentage cover of riffles and rapids) that were significant contributing factors when Rhinopool was included, became insignificant after the removal of this stream site. This indicates that the abundance and richness of the bugs in Rhinopool were largely driven by flow characteristics. Therefore, the change in the trend after removal of Rhinopool could be related to higher variability in the within-stream variables and reduced overall effects. As Rhinopool was the only site that had never undergone any logging, it is difficult to be certain whether this value represents unusually high levels of diversity at this particular site or is representative of the bug assemblage across a range of pristine forest sites. However, after removal of Rhinopool from analyses, differences between the bug abundance and richness at lightly logged old growth sites and the more disturbed logged forest sites still indicated a clear relationship with forest quality, albeit over a reduced range of abundance and richness values, suggesting that the trends we detected were robust. It is important to note that this study only included 12 streams across the habitat change gradient. Therefore, it is possible that trends may not be reliable or may be heavily influenced by individual stream

characteristics. Additional studies in other oil palm streams would help to show how general are the patterns that were observed in our study.

At the catchment scale, change across habitat types could include altered inputs (e.g., nutrients, sediments, herbicides, and pesticides) to streams through runoff, together with changes in the intensity of impacts of extreme events such as heavy rain. As this study indicated and as identified in previous research, at the riparian scale, sites that had no forested margins could have experienced hotter microclimate and lower input of food sources (Hardwick et al., 2015; Luke et al., 2017b; Spence & Andersen, 1994). In particular, stream margins provide food sources for the bugs both directly (e.g., terrestrial invertebrates that accidentally fall into the water surface [Spence & Andersen, 1994]) and indirectly (provision of litter supply for aquatic macroinvertebrates which are prey items for the bugs (Chellaiah & Yule, 2018; Luke, et al., 2017b). Therefore, the loss of input from stream margins might have reduced the availability of prey items for semi-aquatic bugs. In addition, the reduced amount of litter might have reduced egg laying sites for bugs (Bush & Hu, 2005; Sweeney, 1993). Finally, at the stream-scale, changes in stream physical and chemical features may also have affected the movement of some species (Crumière et al., 2016; Ditrich et al., 2008; Spence & Andersen, 1994).

Across scales, effects of habitat disturbance were more consistent and marked at catchment and riparian scales than at stream scales. This is probably because catchment and riparian scales themselves impact stream-scale characteristics and may therefore have more profound and widespread effects. Additionally, catchment and riparian-scale characteristics were largely based on structure and factors that are unlikely to vary in the short term, while chemical and physical characteristics of streams are likely to vary with rainfall levels and short-term effects (De Pauw & Roels, 1988), potentially adding

variability to the data. A related point to this, and caveat of our study, is that sampling occurred at only a single time-period for each stream. Therefore, environmental variables and indeed bug communities that change over time may not be adequately sampled at a single time-period or be representative of longer-term trends. However, comparison of the sites where we measured more than once did not find a change in semi-aquatic bugs, indicating that this may not be an important factor.

The lack of consistent effects for stream level variables is also reflected in our sensitivity analyses. The relatively greater impact of larger scales of disturbance is also likely to be a key factor in explaining why bug communities in oil palm sites with buffers did not differ markedly from oil palm sites without buffers. Although the presence of buffers may have increased shading and reduced runoff into the streams (Luke et al., 2019), it is likely that the large-scale differences in catchment characteristics dwarfed these effects, leading to similar communities across oil palm streams (Wilkinson et al., 2018). Finally, it should be noted that we used Principal Component Analyses (PCA) to reduce the dimensionality and summarise environmental data (Jolliffe, 1986) in this study, owing to our limited number of sample points. Although commonly used in ecological studies of this kind, this approach does mean that some of the variation that is present among environmental variables is not captured, meaning that the potential impact of this variability on bug communities may not be detected. However, as the principal component axes we included covered the majority of variation in environmental data (a total of ~65%), this is unlikely to be important.

At the community level, there were two species found in all or almost all streams across the habitat disturbance gradient, i.e., *Ptilomera* sp. and *Rhagovelia* sp.1. These are both well adapted to fast-flowing water, which can be found naturally in pristine

sites, but also in degraded sites linked to higher runoff and streamflow (Hurkmans et al., 2009), perhaps explaining their commonness. Additionally, there were two species of Veliid bugs (*Microvelia* sp.1 and sp.2) which were found in relatively high abundance in only logged and old-growth forest, suggesting that they are sensitive to forest conversion. Contrastingly, several morphospecies were only found in oil palm streams (either with or without buffer strips), such as those in the genera *Cylindrothetus* and *Limnogonus*, with the latter being relatively rare (only two individuals were found in this study) (see **Table S3.9**). These results accord with those from previous studies, which have found that species in the genus *Microvelia* were associated with forest, while bugs in the genus *Cylindrothetus* were associated with degraded habitats in Brazilian streams (Cunha et al., 2015). Studies conducted in Peninsular Malaysia found *Cylindrothetus* bugs in streams close to oil palm plantations (Mohd Ishadi et al., 2014), while *Limnogonus* bugs were found in secondary forest or protected area streams but in extremely low abundance compared to the overall abundance found across taxa (eight out of 19,928 individuals in Al-Shami et al., 2011, and two individuals out of 849 individuals in Mohd Ishadi et al., 2014), in line with this study.

In contrast to abundance and richness, total biomass of semi-aquatic bugs was more robust to land-use change, with no environmental parameters being significantly associated with changes in total biomass at any scale. This lack of measurable impact of disturbance on total biomass was probably related to species turnover. Even though some species were lost in sites with lower catchment, riparian, and stream qualities, common large-bodied species (such as *Ptilomera* sp. [Gerridae]) persisted, with the highest average abundance of this morphospecies recorded in logged forest streams followed by oil palm with and without buffer strips, while old-growth forests supported the lowest

total biomass, resulting in no discernible difference in total biomass across sites. The robustness of this and other species in disturbed sites may have been due to its adaptability to environmental change, such as being able to cope with fast-flowing water (Kim *et al.*, 2022), as this study found with *Ptilomera* sp. and *Rhagovelia* sp.1. Additionally, the two old-growth sites with the highest abundance of semi-aquatic bugs, i.e., Maliau and Rhinopool streams, were dominated by Veliidae bugs, which were generally smaller than the Gerridae and would contribute less to total biomass.

The lack of impacts on the proportion of juveniles/ adults, and female/ male *Ptilomera* sp. indicates that disturbance did not affect the reproduction of populations. If disturbance had a disproportionate effect on one sex, we might expect the sex ratio to be biased in more disturbed conditions, potentially affecting reproduction. Consequently, we might expect the proportion of juveniles to adults to decline. We also detected no difference in the proportion of winged/ wingless individuals, suggesting that dispersal was also not affected by disturbance. Other studies have found that populations tend to develop wings when conditions are unfavourable or sites dry up (Spence, 1989). The lack of differences in the proportion of winged and wingless individuals in this study therefore indicates that conditions did not stimulate bugs to develop wings, perhaps because, despite changes in condition, streams in the study sites were permanent habitats. A caveat to this finding and other species-level results in this study is that, since we sorted samples only to genus and morphospecies level, it is possible that some morphospecies might have contained more than one species. If these show different or opposing trends in response to environmental changes, then this could have masked real differences. However, we were careful in our sorting, with morphospecies only being assigned to adults and all individuals in each morphospecies being highly similar, so it

is unlikely that this affected results markedly. In addition, this limitation would not affect the results obtained for the abundance and total biomass aspects of the study and should not substantially affect community-level analyses.

### **Implications for conservation and land management**

Our study has important implications for land management and conservation. We found that land-use change caused dramatic reductions in abundance and species richness of semi-aquatic bugs, as well as changes in community composition. Indeed, the sensitivity of some species in this group to habitat degradation makes them potentially valuable indicators of change. This has implications for the functioning of stream ecosystems, since semi-aquatic bugs are predators of aquatic and terrestrial invertebrates as well as being eaten by a range of animal species. In other cases, reductions in abundance or richness of a group can lead to a reduction in related functions (Marschalek & Deutschman, 2022). In contrast to abundance and richness, we found that total biomass was robust across the gradient of environmental conditions, perhaps indicating the maintenance of the amount of food resources for the predators of semi-aquatic bugs despite habitat degradation. Other studies have found that, compared to richness or abundance, total biomass can be more important in determining ecosystem functions supported by an insect group in rainforest in Southeast Asia (Slade et al., 2011). Therefore, the lack of effects of degradation on semi-aquatic bug total biomass may indicate some stability in functions supported by this group. More work is needed to confirm this, particularly in terms of the effects on the whole food web and ecosystem functions associated with semi-aquatic bugs.

Taken together, this study emphasizes the importance of protecting remaining pristine habitats for conserving the full biodiversity of this group, as has been emphasised by another recent study (Cunha et al., 2022). Outside of these areas, logged forest and oil palm could be managed in ways that support existing species, which provide functions in the ecosystem. In particular, we found that logged forest sites contained more abundant and richer communities of bugs than oil palm streams, perhaps because logging operations within the logged forests in this study were selective and therefore less damaging. In contrast, other logging practices, such as clearcutting, may not provide the same level of support for biodiversity, particularly because such practices can result in different microclimatic conditions and hence cause changes in local aquatic species. For example, previous studies have found an increase in the density of some aquatic taxa (Noel et al., 1986) or altered community composition of aquatic assemblages (Wallace & Ely, 2014) in clearcut logged streams compared to reference streams (particularly more species that are tolerant to higher levels of canopy openness and higher water temperatures), due to a loss of canopy cover on streams. Additionally, stream management can be trialled in ways that can maintain cool water temperature, canopy cover, as well as greater proportions of rocks and deadwood. However, we found that one hopeful strategy - maintaining forested river margins (buffers), which can maintain bank stability and provide more allochthonous inputs to streams, had only marginal effects on semi-aquatic bugs, although we only studied five oil palm streams in this study. We therefore call for more studies assessing factors in streams that could be manipulated to better support semi-aquatic bugs.

## Tables and Figures

**Table 3.1** Estimated regression parameters, standard error,  $z/t$  and  $p$ -values of models used to assess the effects of environmental conditions on abundance, total biomass, and richness of adult semi-aquatic bugs at catchment, riparian, and stream scales.<sup>a</sup>

Model		Estimate	Std. error	$z/t$ value <sup>b</sup>	$p$ -value
Abundance ~ CatchmentPC1	Intercept	6.500	0.171	37.919	< <b>0.001</b> ***
	CatchmentPC1	0.398	0.107	3.697	< <b>0.001</b> ***
Abundance ~ RiparianPC1	Intercept	6.558	0.195	33.568	< <b>0.001</b> ***
	RiparianPC1	0.384	0.116	3.308	< <b>0.001</b> ***
Abundance ~ StreamPC1 + StreamPC2	Intercept	6.531	0.184	35.403	< <b>0.001</b> ***
	StreamPC1	0.112	0.076	1.479	0.139
	StreamPC2	0.331	0.117	2.810	<b>0.004</b> **
Total Biomass ~ CatchmentPC1	Intercept	1512.57	244.31	6.191	< <b>0.001</b> ***
	CatchmentPC1	77.47	153.60	0.504	0.624
Total Biomass ~ RiparianPC1	Intercept	1512.6	231.0	6.547	< <b>0.001</b> ***
	RiparianPC1	165.7	136.9	1.211	0.254
Total Biomass ~ StreamPC1 + StreamPC2	Intercept	1512.57	244.90	6.176	< <b>0.001</b> ***
	StreamPC1	94.59	101.10	0.936	0.373
	StreamPC2	-89.87	156.52	-0.574	0.579
Richness ~ CatchmentPC1	Intercept	2.138	0.102	20.806	< <b>0.001</b> ***
	CatchmentPC1	0.256	0.057	4.442	< <b>0.001</b> ***
Richness ~ RiparianPC1	Intercept	2.129	0.106	20.020	< <b>0.001</b> ***
	RiparianPC1	0.290	0.082	3.526	< <b>0.001</b> ***
Richness ~ StreamPC1 + StreamPC2	Intercept	2.096	0.106	19.605	< <b>0.001</b> ***
	StreamPC1	0.114	0.039	2.874	<b>0.004</b> **
	StreamPC2	0.267	0.056	4.710	< <b>0.001</b> ***

<sup>a</sup> Environmental conditions at each scale are represented by scores obtained from the PCAs, i.e., CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2, which represent environmental conditions at catchment, riparian, and stream scales respectively. The first PC scores (PC1) at catchment and riparian scales explained most of variation among environmental parameters. For the stream scale, two PC scores (PC1 and PC2) were needed to explain most (>60%) of the variation, so both were included in the analysis.  $P$ -values in bold fonts are less than 0.05 and indicate significant effects of environmental conditions at the corresponding scale on the abundance, total biomass, or richness of semi-aquatic bugs.

<sup>b</sup>  $z$  value if the model used either Poisson or negative binomial distribution,  $t$  value if the model used Gaussian distribution.

**Table 3.2** Output of Canonical Correspondence Analysis (CCA) assessing the effects of environmental conditions at catchment, riparian, and stream scales (CatchmentPC1, RiparianPC1, StreamPC1 and StreamPC2, respectively) on the community composition of semi-aquatic bugs across stream sites in this study, with *p*-values obtained from 999 random permutation tests under reduced model.<sup>a</sup>

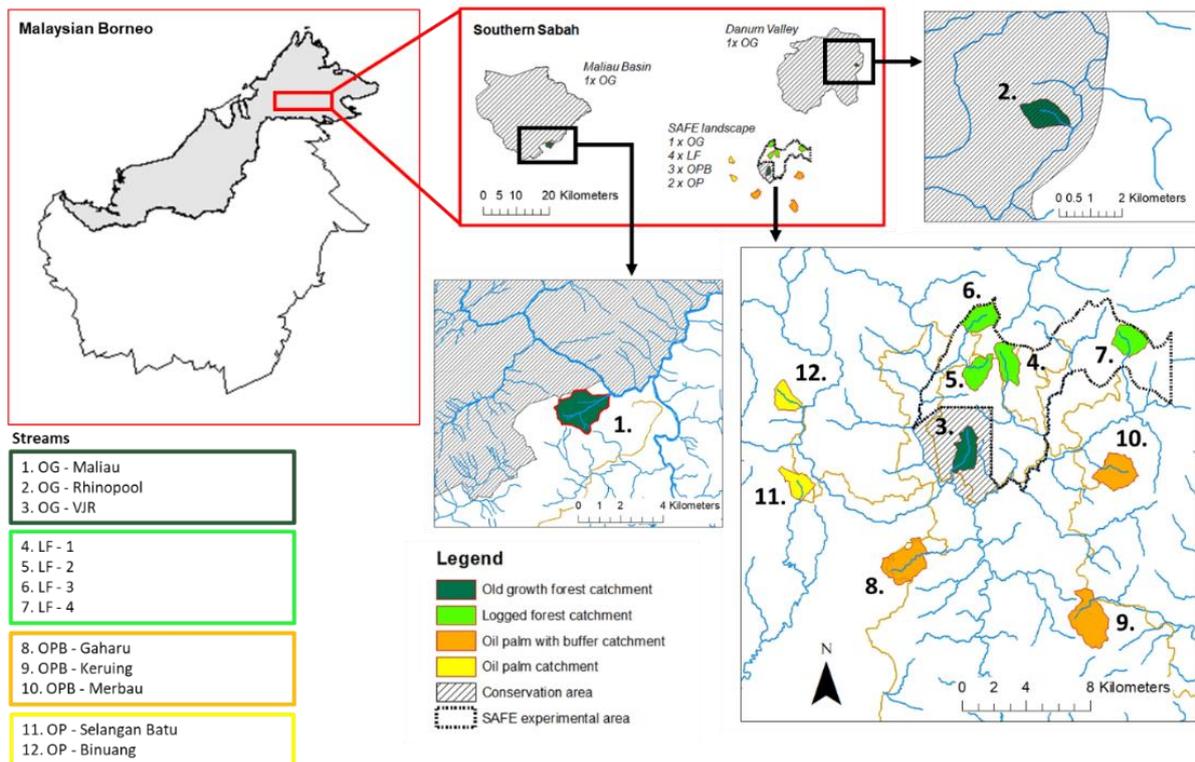
Predictor	Chi-square	F	<i>p</i> -value
CatchmentPC1	0.374	4.309	<b>0.005 **</b>
RiparianPC1	0.124	1.432	0.159
StreamPC1	0.109	1.255	0.195
StreamPC2	0.184	2.123	<b>0.029 *</b>

<sup>a</sup> Community composition used adult bug data only. *P*-values < 0.05 are shown in bold and indicate a significant effect of a particular predictor on the community composition of semi-aquatic bugs.

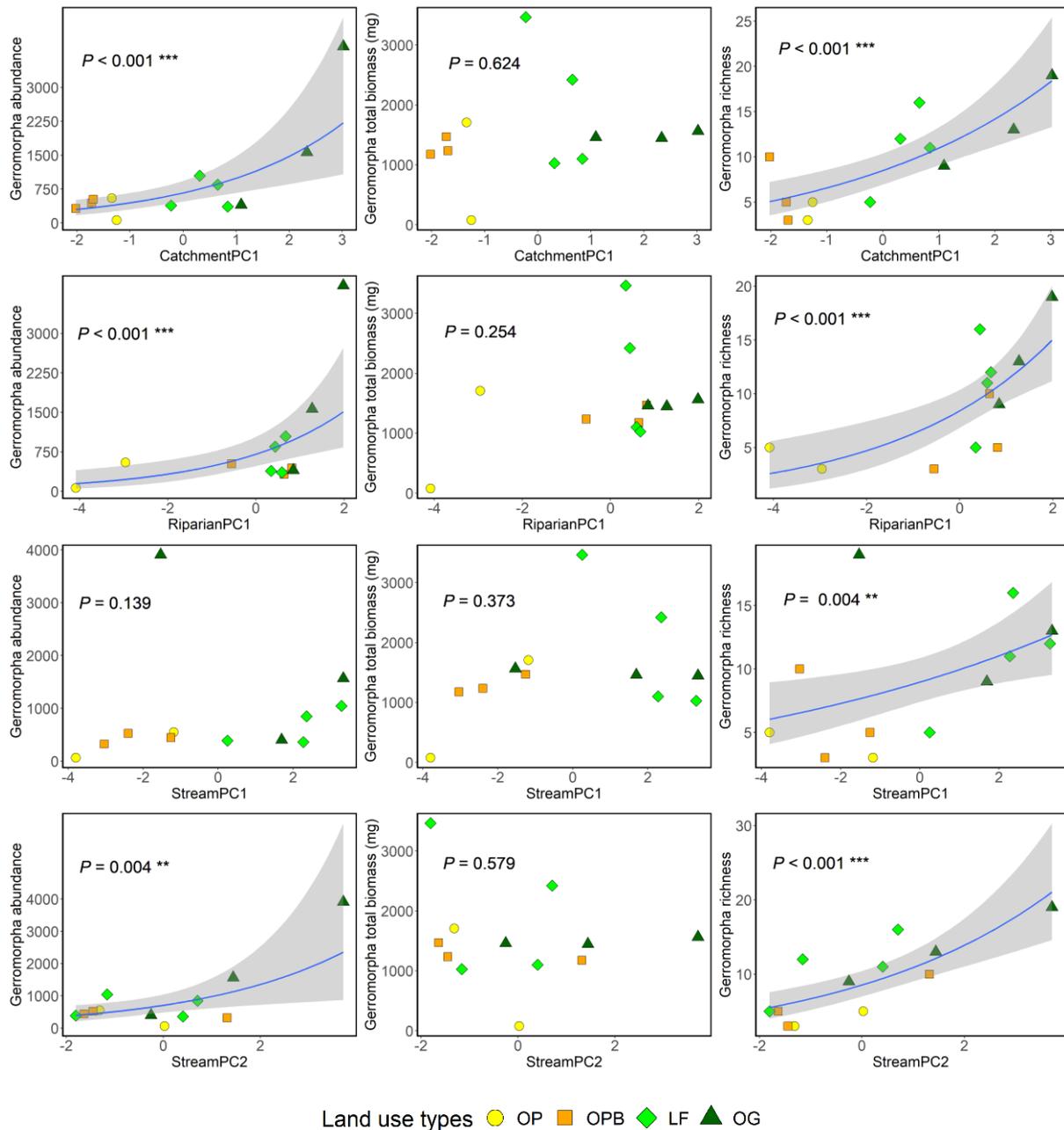
**Table 3.3** Estimated regression parameters, standard error, *z* and *p*-values of GLMs (with binomial distribution in all cases) used to assess the effects of environmental conditions at catchment, riparian, and stream scales on the proportion of juveniles to adults, winged to wingless semi-aquatic bugs, and female to male *Ptilomera* sp.<sup>a</sup>

Model		Estimate	Std. error	<i>z</i> value	<i>p</i> -value
Proportion of juveniles ~ CatchmentPC1	Intercept	0.427	0.597	0.715	0.475
	CatchmentPC1	-0.193	0.375	-0.516	0.606
Proportion of juveniles ~ RiparianPC1	Intercept	0.517	0.657	0.788	0.431
	RiparianPC1	-0.478	0.512	-0.934	0.350
Proportion of juveniles ~ StreamPC1 + StreamPC2	Intercept	0.440	0.609	0.723	0.470
	StreamPC1	-0.103	0.248	-0.414	0.679
	StreamPC2	0.269	0.388	0.695	0.487
Proportion of winged individuals ~ CatchmentPC1	Intercept	-2.556	1.125	-2.271	<b>0.023*</b>
	CatchmentPC1	0.122	0.681	0.180	0.856
Proportion of winged individuals ~ RiparianPC1	Intercept	-2.543	1.112	-2.286	<b>0.022*</b>
	RiparianPC1	-0.053	0.624	-0.085	0.932
Proportion of winged individuals ~ StreamPC1 + StreamPC2	Intercept	-2.620	1.195	-2.193	<b>0.028*</b>
	StreamPC1	0.179	0.489	0.368	0.713
	StreamPC2	0.034	0.783	0.044	0.964
Proportion of female <i>Ptilomera</i> sp. ~ CatchmentPC1	Intercept	0.579	0.604	0.959	0.337
	CatchmentPC1	0.116	0.385	0.302	0.763
Proportion of female <i>Ptilomera</i> sp. ~ RiparianPC1	Intercept	0.579	0.604	0.959	0.338
	RiparianPC1	-0.101	0.373	-0.271	0.786
Proportion of female <i>Ptilomera</i> sp. ~ StreamPC1 + StreamPC2	Intercept	0.677	0.665	1.017	0.309
	StreamPC1	-0.197	0.277	-0.713	0.476
	StreamPC2	0.403	0.496	0.812	0.417

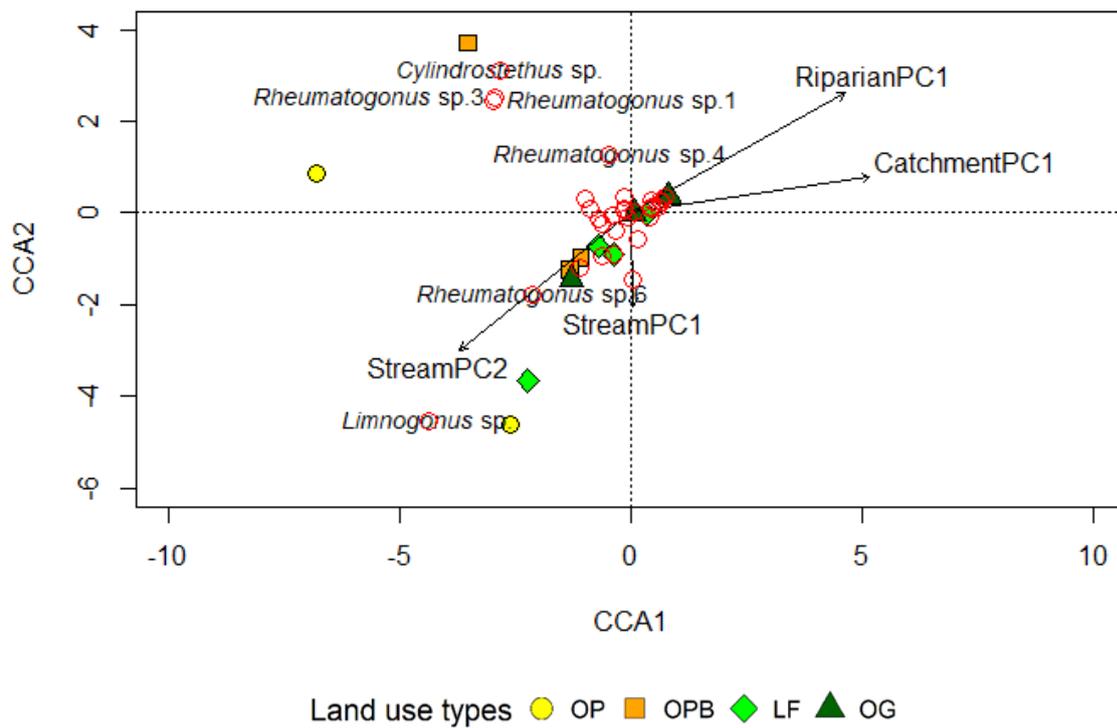
<sup>a</sup> *P*-values < 0.05 are in bold and indicate significant effects.



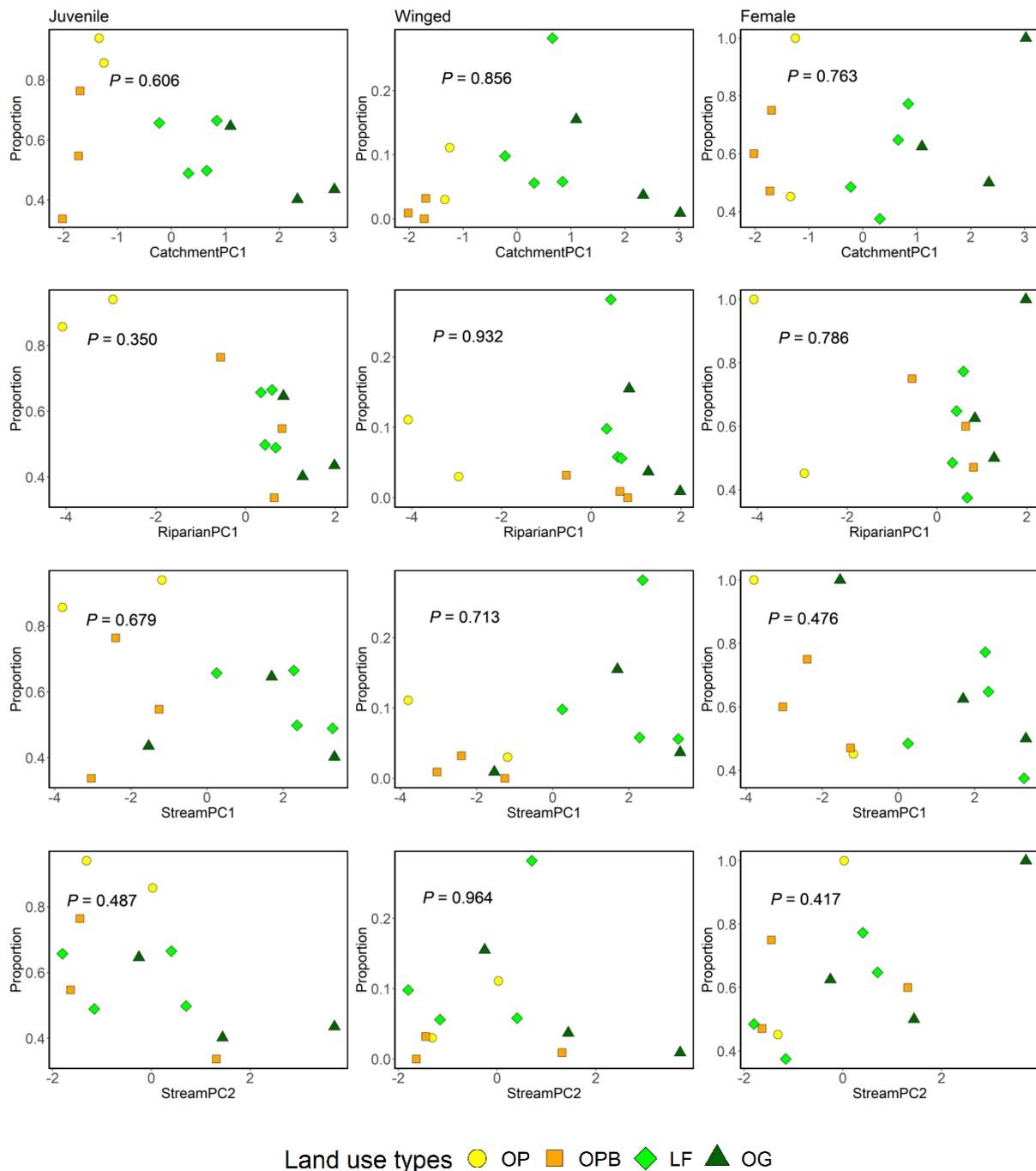
**Figure 3.1** Map of stream sites in this study. Sites were in Sabah, Malaysian Borneo and comprised stream sites surrounded by old-growth forest (OG), selectively logged forest (LF), oil palm with riparian buffer strip (OPB), and oil palm without riparian buffer strip (OP) catchments. See Luke, et al., 2017b for further details. Map is obtained from Harianja et al., 2023a (Chapter 2).



**Figure 3.2** Correlations between environmental conditions across three scales (CatchmentPC1, RiparianPC1, and StreamPC1 and StreamPC2 representing catchment, riparian, and stream scales, respectively) on the abundance, total biomass (sum of biomass of all semi-aquatic bugs in each stream site), and species richness of semi-aquatic bug communities (Gerromorpha). Abundance and total biomass included both juvenile and adult individuals. Richness included adults only. Smoothed regression lines for significant relationships are shown. Shaded areas represent confidence intervals. OP = Oil palm no buffer, OPB = Oil palm with buffer strips, LF = Logged forest, OG = Old-growth forest. Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses.



**Figure 3.3** A Canonical Correspondence Analysis (CCA) tri-plot showing the correlation between environmental conditions at catchment, riparian and stream scales (CatchmentPC1, RiparianPC1, StreamPC1 and StreamPC2, respectively) and the community composition of semi-aquatic bugs across stream sites in this study. On the plot, environmental conditions are shown as arrows. Community composition is represented by morphospecies of adult bugs, shown as circles with no colour but red borders. Stream sites are shown as coloured shapes with black borders, representing land-use types (yellow circle = Oil palm no buffer strips-OP, orange square = Oil palm with buffer strips-OPB, green diamond = Logged forest-LF, dark green triangle = Old growth forest-OG). The closer a morphospecies is to a stream site, the higher the probability of finding that species in that stream. Morphospecies that were outliers are labelled. Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses.



**Figure 3.4** Correlations between environmental conditions across three scales (catchment, riparian, and stream) on the proportion of juveniles (left-hand side panels) and winged individuals (middle panels) of semi-aquatic bugs (Gerromorpha), as well as on the proportion of female *Ptilomera* sp. (right-hand side panels). OP = Oil palm no buffer, OPB = Oil palm with buffer strips, LF = Logged forest, OG = Old growth forest. Data used for analyses in this study come from transects at each stream. Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses.

## Supplementary materials

**Table S3.1** Catchment size and physical characteristics of each stream site in this study. Catchment size was obtained from RapidEye™ satellite images taken in 2012 and 2013. Measurements of slope, channel and wetted widths, maximum depth, and flow speed were conducted every 10m along 200m transects in each stream site. OP- oil palm without riparian buffer, OPB – oil palm with riparian buffer, LF – logged forest, OG – old growth forest.

Stream	Land-use type	Catchment size (km-square)	Average slope (degree)	Average channel width (m)	Average wetted width (m)	Average maximum depth (cm)	Average flow speed (m/s)
Binuang	OP	2.049	1.9	5.977	3.262	13.447	1.518
Selangan Batu	OP	2.269	3.35	7.603	5.135	33.525	2.469
Gaharu	OPB	4.943	1.35	11.072	5.796	21.55	1.621
Keruing	OPB	5.744	1.7	11.866	6.189	35.73	1.458
Merbau	OPB	4.109	2.05	8.685	5.795	27.238	1.448
LF-1 (“0m”)	LF	2.846	4.75	11.737	6.713	35.718	1.968
LF-2 (“5m”)	LF	2.575	4.9	13.428	6.923	44.685	2.857
LF-3 (“60m”)	LF	2.811	6.05	15.708	6.020	34.421	3.267
LF-4 (“120m”)	LF	2.285	4.15	8.325	5.045	28.33	3.896
Maliau	OG	3.212	8.15	15.891	7.853	52.1	1.699
Rhinopool	OG	0.966	2.7	8.314	4.928	37.190	0.492
VJR	OG	3.225	4.45	10.214	6.876	49.523	4.846

**Table S3.2** Details regarding the collection location within each transect and date of semi-aquatic bugs in each stream in this study. <sup>a</sup>

Stream	Land-use type	Transect details	Collection dates
		0-10m, 40-50m, 80-90m,	June – August 2012
Binuang	OP	120-130m, 160-170m	
Selangan Batu	OP	0-10m, 80-90m, 120-130m	July – September 2011
		0-10m, 20-30m, 80-90m,	June – August 2012
Selangan Batu	OP	120-130m, 160-170m	
		0-10m, 20-30m, 40-50m,	July – September 2011
Gaharu	OPB	100-110m, 140-150m,	
		0-10m, 40-50m, 80-90m,	June – August 2012
Keruing	OPB	120-130m, 160-170m	
		0-10m, 40-50m, 80-90m,	June – August 2012
Merbau	OPB	120-130m, 160-170m	
		20-30m, 40-50m, 80-90m,	July – September 2011
LF-1 (“0m”)	LF	100-110m, 180-190m	
		20-30m, 40-50m, 60-70,	July – September 2011
LF-2 (“5m”)	LF	100-110m, 180-190m	
		20-30m, 80-90m, 100-110m,	July – September 2011
LF-3 (“60m”)	LF	160-170m, 180-190m	
		20-30m, 80-90m, 120-130m, 160-170m,	July – September 2011
LF-4 (“120m”)	LF	170m, 180-190m	
Maliau	OG	0-10m, 40-50m, 80-90m	July – September 2011
		0-10m, 40-50m, 80-90m,	June – August 2012
Maliau	OG	120-130m, 160-170m	
		0-10m, 40-50m, 80-90m,	May – June 2013
Rhinopool	OG	120-130m, 160-170m	
		20-30m, 40-50m, 80-90m,	July – September 2011
VJR	OG	100-110m, 180-190m	

<sup>a</sup> OP = Oil palm no buffer, OPB = Oil palm with buffer strips, LF = Logged forest, OG = Old growth forest. Data used for analyses in this study from transects at each stream.

**Table S3.3** PC1 and PC2 (Principal Component) scores of environmental parameters measured at the catchment scale, obtained using PCA (Principal Component Analysis). N = 12 streams (three, four, three, and two stream sites in old-growth forest (OG, 1. Maliau, 2. Rhinopool, and 3. VJR), logged forest (LF, 1. "0m", 2. "5m", 3. "60m", and 4. "120m"), oil palm with (OPB, 1. Gaharu, 2. Keruing, and 3. Merbau), and without riparian buffer strips (OP, 1. Binuang and 2. Selangan Batu), respectively).

Parameter	Description	PC1	PC2
AGBMean_mean	Mean above ground living biomass (AGB [t/ha])	0.552	0.824
FCOMean_mean	Mean percentage forest cover (FCO)	0.594	-0.285
LAIMean_mean	Mean leaf area index (LAI)	0.583	-0.489

**Table S3.4** PC1 and PC2 (Principal Component) scores of environmental parameters measured at the riparian scale, obtained using PCA (Principal Component Analysis). N = 12 streams (three, four, three, and two stream sites in old-growth forest (OG, 1. Maliau, 2. Rhinopool, and 3. VJR), logged forest (LF, 1. "0m", 2. "5m", 3. "60m", and 4. "120m"), oil palm with (OPB, 1. Gaharu, 2. Keruing, and 3. Merbau), and without riparian buffer strips (OP, 1. Binuang and 2. Selangan Batu), respectively).

Parameter	Description	PC1	PC2
CanopyOpenness	Mean canopy openness	-0.534	-0.048
Vine	Mean percentage vine cover	0.392	0.837
ForestQualityScore	Mean forest quality score using SAFE Project scale	0.554	-0.171
BasalArea	Mean basal area	0.503	-0.515

**Table S3.5** PC1 and PC2 (Principal Component) scores of environmental parameters measured at the stream scale, obtained using PCA (Principal Component Analysis). N = 12 streams (three, four, three, and two stream sites in old-growth forest (OG, 1. Maliau, 2. Rhinopool, and 3. VJR), logged forest (LF, 1. "0m", 2. "5m", 3. "60m", and 4. "120m"), oil palm with (OPB, 1. Gaharu, 2. Keruing, and 3. Merbau), and without riparian buffer strips (OP, 1. Binuang and 2. Selangan Batu), respectively). Relatively high loadings of each PC axis are in bold.

Parameter	Description	PC1	PC2
FlowAverage	Mean flow speed represented by time needed by a tennis ball to travel a 2-m string	-0.154	<b>-0.453</b>
CanopyAverage	Mean canopy openness	<b>-0.293</b>	<b>0.307</b>
WettedWidth	Mean wetted width of stream	0.290	-0.084
Slope	Mean slope	<b>0.357</b>	-0.070
Rocks	Mean percentage cover of rocks	<b>0.380</b>	0.001
Pebbles	Mean percentage cover of pebbles	-0.203	-0.224
DeadWood	Mean percentage cover of dead wood	0.121	<b>-0.411</b>
Rapids	Mean percentage cover of rapids	0.244	<b>0.217</b>
Riffles	Mean percentage cover of riffles	-0.179	<b>0.461</b>
ConnectedPools	Mean percentage cover of connected pools	<b>-0.302</b>	<b>-0.337</b>
IsolatedPools	Mean percentage cover of isolated pools	<b>0.291</b>	0.167
WaterTemp	Mean water temperature	<b>-0.350</b>	0.118
pH	Mean water pH	0.166	0.174
Conductivity	Mean water conductivity	0.242	-0.144

**Table S3.6** The abundance, total biomass, and richness of semi-aquatic bugs collected in Maliau and Selangan Batu streams, separated by two time blocks, i.e., year 2011 (Time Block 1) and 2012 (Time Block 2) as well as transects (Maliau: N transects = 3 for Time Block 1 and N transects = 5 for Time Block 2), Selangan Batu: N transects = 4 for Time Block 1 and N transects = 5 for Time Block 2). Data from both streams are shown for assessment of whether collection period affected the abundance, total biomass, and species richness of semi-aquatic bugs within each stream. <sup>a</sup>

Stream	Time Block	Data collection time (collection period)	Transect	Abundance	Total biomass (mg)	Species richness
Maliau	1	July – September 2011	0-10m	94	85.465	4
	1	July – September 2011	40-50m	343	244.083	9
	1	July – September 2011	80-90m	135	124.357	7
	2	June – August 2012	0-10m	332	290.043	8
	2	June – August 2012	40-50m	444	302.334	8
	2	June – August 2012	80-90m	270	236.848	8
	2	June – August 2012	120-130m	199	246.094	7
	2	June – August 2012	160-170m	320	371.262	9
Selangan Batu	1	July – September 2011	0-10m	22	168.569	1
	1	July – September 2011	40-50m	17	95.688	0
	1	July – September 2011	80-90m	99	237.984	4
	1	July – September 2011	120-130m	206	146.978	4
	2	June – August 2012	0-10m	72	224.266	1
	2	June – August 2012	20-30m	151	331.145	2
	2	June – August 2012	80-90m	97	559.001	1
	2	June – August 2012	120-130m	105	146.777	1
	2	June – August 2012	160-170m	124	445.929	2

<sup>a</sup> Both abundance and total biomass used juvenile and adult semi-aquatic bugs, while species richness was based on adults only. Species richness was based on morphospecies data from adult bugs only.

**Table S3.7** Outputs of t-tests or Wilcoxon tests assessing differences in the abundance, total biomass, and species richness of semi-aquatic bugs between time blocks, i.e., year 2011 (Time Block 1) and 2012 (Time Block 2), in Maliau (N = 3 for Time Block 1 and N = 5 for Time Block 2) and Selangan Batu (N = 4 for Time Block 1 and N = 5 for Time Block 2) streams. <sup>a</sup>

<b>Parameter</b>	<b>Stream</b>	<b><i>t</i>/<i>W</i><sup>b</sup></b>	<b><i>df</i></b>	<b><i>p</i>-value</b>
Abundance	Maliau	-1.406	3.123	0.250
	Selangan Batu	0.515	3.542	0.636
Total biomass	Maliau	-2.583	3.040	0.080
	Selangan Batu	-2.244	5.192	0.072
Species richness	Maliau	5	NA	0.536
	Selangan Batu	11.5	NA	0.796

<sup>a</sup> For abundance and total biomass data, t-tests were used because data were normally distributed and had equal variance. For species richness, morphospecies of adult bugs only were used and Wilcoxon tests were run because data were rejected for either normality or equal variance.

<sup>b</sup> *t* if the test run was *t*-test and *W* if the test run was Wilcoxon test

**Table S3.8** Summary of richness, abundance, and total biomass of semi-aquatic bugs found across the twelve streams and four land use types sampled in this study. N = 12 streams <sup>a</sup>

Category	Land-use types											Total across land use types	
	Oil palm no buffer (OP)		Oil palm with buffer (OPB)			Logged forest (LF)				Old-growth forest (OG)			
	Binuang	Selangan Batu	Gaharu	Keruing	Merbau	LF-1 ("0m")	LF-2 ("5m")	LF-3 ("60m")	LF-4 ("120m")	Maliau	Rhinopool		VJ R
Richness ( <i>Adult bugs only</i> ) <sup>b</sup>	5	3	5	10	3	16	11	12	5	13	19	9	38*
Total abundance of juveniles	54	516	243	109	401	422	240	511	255	629	1699	259	5338
Abundance of winged adults	1	1	0	2	4	120	7	30	13	35	19	22	254
Abundance of wingless adults	8	32	201	212	120	306	114	504	120	901	2190	120	4828
Total abundance of adult bugs	9	33	201	214	124	426	121	534	133	936	2209	142	5082
Abundance female <i>Ptilomera</i> sp.	1	14	16	12	18	35	17	3	47	5	1	20	189
Abundance of male <i>Ptilomera</i> sp.	0	17	18	8	6	19	5	5	50	5	0	12	145
Total biomass of adult bugs (mg)	38.194	849.687	1024.599	988.713	714.482	1831.942	683.446	632.567	2659.547	985.059	1000.947	942.11	12351.29
Total biomass of juvenile bugs (mg)	37.848	857.431	445.118	188.926	522.174	589.685	417.559	394.42	805.3	461.522	563.067	516.475	5799.525

<sup>a</sup> Richness based on adult bugs only. Abundance shown is the total number of all juvenile and adult bugs. The breakdown for juveniles and adults, winged and wingless adults, as well as female and male *Ptilomera* sp. (a semi-aquatic bug species in this study that was separated based on sex for further analysis) across streams is also shown. Biomass data were obtained from body length-biomass equations, in which

biomass of each individual bug was derived from its body length. Biomass estimation considered families and body forms (Harianja *et al.*, 2023). The breakdown of the total biomass (sums of the biomass of all semi-aquatic bugs in a stream site) for each life stage as well as for *Ptilomera* sp. (based on sex) across streams is also shown.

<sup>b</sup> See **Table S3.9** on the following page for details of all the 38 morphospecies found in streams across land use types.

**Table S3.9** The morphospecies and corresponding abundance of semi-aquatic bugs found across streams in the four land use types (oil palm without buffer/ OP, oil palm with buffer/ OPB, logged forest/ LF, and old-growth forest/ OG) sampled in this study. N = 12 streams. <sup>a</sup>

Family	Subfamily <sup>b</sup>	Morphospecies	Land-use types											Total	
			Oil palm without buffer (OP)		Oil palm with buffer (OPB)			Logged forest (LF)				Old-growth forest (OG)			
			Binuang	Selangan Batu	Gaharu	Keruing	Merbau	LF-1 (“0m”)	LF-2 (“5m”)	LF-3 (“60m”)	LF-4 (“120m”)	Maliau	Rhino-pool		VJR
Gerridae	Cylindrostethinae	<i>C. scrutator</i>	0	0	0	19	0	0	0	0	0	0	0	0	19
Gerridae	Cylindrostethinae	<i>Cylindrostethus</i> sp.	0	0	0	9	0	0	0	0	0	0	0	0	9
Gerridae	Gerrinae	<i>Limnogonus</i> sp.	2	0	0	0	0	0	0	0	0	0	0	0	2
Gerridae	Gerrinae	<i>Limnometra</i> sp.	0	0	0	0	0	0	1	1	0	2	2	3	9
Gerridae	Halobatinae	<i>Metrocoris</i> sp.1	0	1	0	1	0	1	0	0	0	0	3	1	7
Gerridae	Halobatinae	<i>Metrocoris</i> sp.2	0	0	0	0	0	0	0	2	0	0	0	0	2
Veliidae	Microveliinae	<i>Microvelia</i> sp.1	0	0	0	0	0	32	19	147	1	212	679	1	1091
Veliidae	Microveliinae	<i>Microvelia</i> sp.2	0	0	0	0	0	56	28	189	0	224	998	1	1496
Veliidae	Microveliinae	<i>Microvelia</i> sp.3	0	0	0	0	0	2	0	0	0	0	2	0	4
Veliidae	Microveliinae	<i>Microvelia</i> sp.4	0	0	0	0	0	8	6	3	0	0	12	1	30
Veliidae	Microveliinae	<i>Microvelia</i> sp.5	0	0	0	0	0	4	0	1	0	0	0	0	5
Veliidae	Microveliinae	<i>Microvelia</i> sp.6	0	0	0	0	0	0	0	1	0	0	0	0	1
Veliidae	Microveliinae	<i>Microvelia</i> sp.7	0	0	0	0	0	2	0	0	0	0	0	0	2

Family	Subfamily <sup>b</sup>	Morphospecies	Land-use types											Total	
			Oil palm without buffer (OP)		Oil palm with buffer (OPB)			Logged forest (LF)				Old-growth forest (OG)			
			Binuang	Selangan Batu	Gaharu	Keruing	Merbau	LF-1 ("0m")	LF-2 ("5m")	LF-3 ("60m")	LF-4 ("120m")	Maliau	Rhino-pool		VJR
Veliidae	Microveliinae	<i>Microvelia</i> sp.8	0	0	0	0	0	4	6	3	1	0	10	0	24
Veliidae	Microveliinae	Morphospecies30	0	0	0	0	0	0	0	0	0	0	1	0	1
Veliidae	Microveliinae	Morphospecies40	0	0	0	0	0	0	0	0	0	0	0	1	1
Gerridae	Ptilomerinae	<i>Potamometropsis</i> sp.	0	0	0	0	0	11	1	22	0	12	0	0	46
Gerridae	Ptilomerinae	<i>Ptilomera</i> sp.	1	31	34	20	24	54	22	8	97	10	1	32	334
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.1	1	0	149	107	99	240	34	155	33	435	291	101	1645
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.2	0	0	1	0	0	0	1	2	1	0	0	0	5
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.3	0	0	0	1	0	0	0	0	0	0	0	0	1
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.4	0	0	0	0	0	0	1	0	0	0	0	0	1
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.5	0	0	0	0	0	2	0	0	0	3	0	0	5
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.6	0	0	0	0	0	0	0	0	0	0	0	1	1
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.7	0	0	0	0	0	1	0	0	0	0	0	0	1
Veliidae	Rhagoveliinae	<i>Rhagovelia</i> sp.8	0	0	0	0	0	0	0	0	0	1	0	0	1
Gerridae	Ptilomerinae	<i>Rheumatogonus</i> sp.1	3	0	0	31	0	0	0	0	0	0	0	0	34
Gerridae	Ptilomerinae	<i>Rheumatogonus</i> sp.2	0	0	0	0	0	0	0	0	0	1	1	0	2
Gerridae	Ptilomerinae	<i>Rheumatogonus</i> sp.3	2	0	0	24	0	0	0	0	0	0	0	0	26

Family	Subfamily <sup>b</sup>	Morphospecies	Land-use types										Total		
			Oil palm without buffer (OP)		Oil palm with buffer (OPB)			Logged forest (LF)				Old-growth forest (OG)			
			Binuang	Selangan Batu	Gaharu	Keruing	Merbau	LF-1 (“0m”)	LF-2 (“5m”)	LF-3 (“60m”)	LF-4 (“120m”)	Maliau		Rhino-pool	VJR
Gerridae	Ptilomerinae	<i>Rheumatogonus</i> sp.4	0	0	0	1	0	0	0	0	0	0	2	0	3
Gerridae	Ptilomerinae	<i>Rheumatogonus</i> sp.5	0	0	0	0	0	0	0	0	0	1	3	0	4
Gerridae	Ptilomerinae	<i>Rheumatogonus</i> sp.6	0	0	0	0	1	0	0	0	0	0	0	0	1
Veliidae	Haloveliinae	<i>Strongylovelia</i> sp.	0	0	0	0	0	0	0	0	0	0	9	0	9
Gerridae	Gerrinae	<i>Tenagogonus</i> sp.	0	1	1	0	0	5	2	0	0	12	12	0	33
Gerridae	Halobatinae	<i>Ventidius</i> sp.1	0	0	16	1	0	3	0	0	0	9	126	0	155
Gerridae	Halobatinae	<i>Ventidius</i> sp.2	0	0	0	0	0	1	0	0	0	14	55	0	70
Gerridae	Halobatinae	<i>Ventidius</i> sp.3	0	0	0	0	0	0	0	0	0	0	1	0	1
Gerridae	Halobatinae	<i>Ventidius</i> sp.4	0	0	0	0	0	0	0	0	0	0	1	0	1
Total															5082

<sup>a</sup> In total, there were 38 morphospecies with total abundance of 5082 individuals, in the Gerridae and Veliidae families. Morphospecies were identified using adult individuals only.

<sup>b</sup> Along with families, subfamilies were used for body form assessment for the biomass estimation of semi-aquatic bugs. See Harianja et al. 2023a (Chapter 2) for further details.

**Table S3.10** Estimation regression parameters, standard error,  $z/t$  and  $p$ -values of models after removal of Rhinopool from replicates, which are used to assess the effects of environmental conditions at catchment, riparian, and stream scales on the abundance, total biomass, and species richness of semi-aquatic bugs.  $N = 11$  streams. <sup>a</sup>

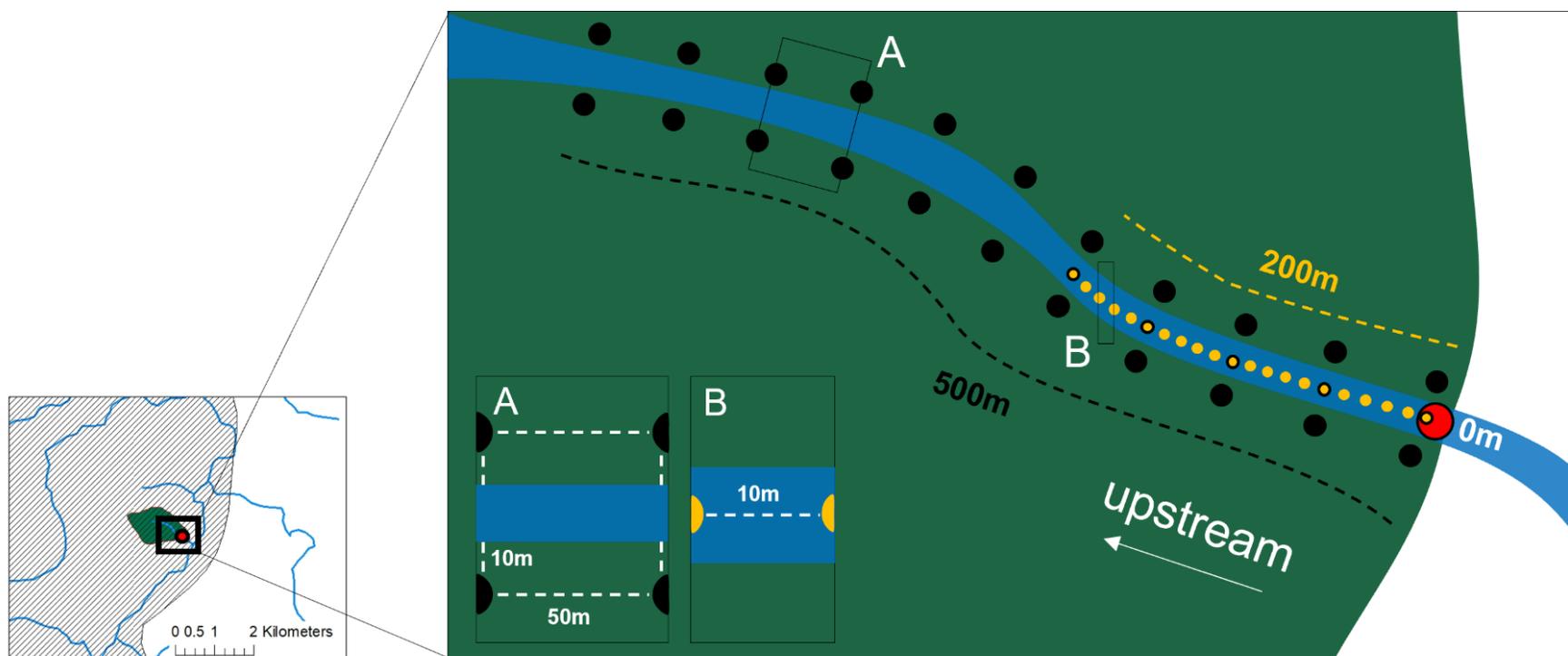
Model		Estimate	Std. error	$z/t$ value <sup>b</sup>	$p$ -value
Abundance ~ CatchmentPC1	Intercept	6.378	0.173	36.791	< <b>0.001</b> ***
	CatchmentPC1	0.273	0.124	2.191	<b>0.0284</b> *
Abundance ~ RiparianPC1	Intercept	6.358	0.175	36.294	< <b>0.001</b> ***
	RiparianPC1	0.257	0.105	2.425	<b>0.015</b> *
Abundance ~ StreamPC1 + StreamPC2	Intercept	6.224	0.154	40.298	< <b>0.001</b> ***
	StreamPC1	0.207	0.060	3.425	< <b>0.001</b> ***
	StreamPC2	-0.020	0.131	-0.156	0.875
Total Biomass ~ CatchmentPC1	Intercept	1537.3	273.3	5.624	< <b>0.001</b> ***
	CatchmentPC1	107.0	196.8	0.544	0.599
Total Biomass ~ RiparianPC1	Intercept	1541.4	254.0	6.069	< <b>0.001</b> ***
	RiparianPC1	185.7	153.1	1.213	0.256
Total Biomass ~ StreamPC1 + StreamPC2	Intercept	1406.0	269.4	5.220	< <b>0.001</b> ***
	StreamPC1	122.4	105.5	1.161	0.279
	StreamPC2	-251.3	229.3	-1.096	0.304
Richness ~ CatchmentPC1	Intercept	2.133	0.105	20.26	< <b>0.001</b> ***
	CatchmentPC1	0.247	0.074	3.30	< <b>0.001</b> ***
Richness ~ RiparianPC1	Intercept	2.104	0.107	19.594	< <b>0.001</b> ***
	RiparianPC1	0.235	0.088	2.669	<b>0.007</b> **
Richness ~ StreamPC1 + StreamPC2	Intercept	2.086	0.113	18.336	< <b>0.001</b> ***
	StreamPC1	0.120	0.045	2.669	<b>0.007</b> **
	StreamPC2	0.246	0.096	2.563	<b>0.010</b> *

<sup>a</sup> Environmental conditions at each scale are represented by scores obtained from PCA: CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2 represents catchment, riparian, and stream respectively. The first PC scores (PC1) at each catchment and riparian scale explained most of variation among environmental parameters. For stream scale, two PC scores (PC1 and PC2) were needed to explain most of the variation.  $P$ -values in bold fonts are less than 0.05 and indicate significant effects of environmental conditions at the corresponding scale on the abundance, total biomass, or richness of semi-aquatic bugs.

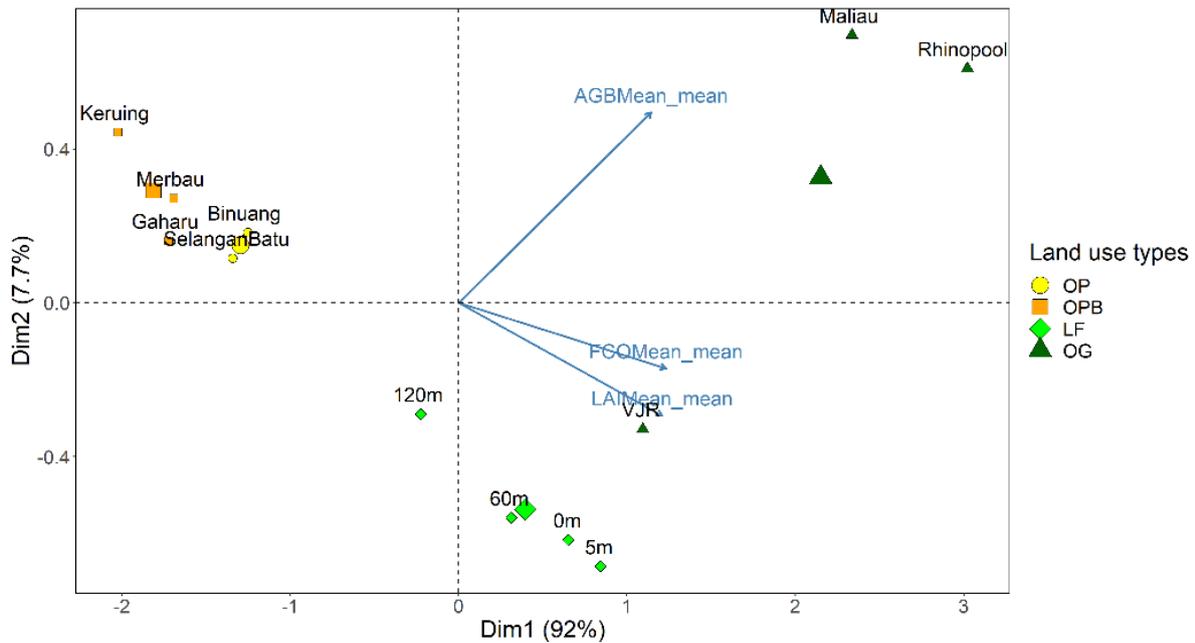
<sup>b</sup>  $z$  value states if the model used either a Poisson or negative binomial distribution,  $t$  value if the model used Gaussian distribution.

**Appendix S3.1** Details on procedures in assessing the difference in abundance, total biomass, and richness data in Maliau and Selangan Batu streams, which contained bugs collected in two time blocks (2011 and 2012).

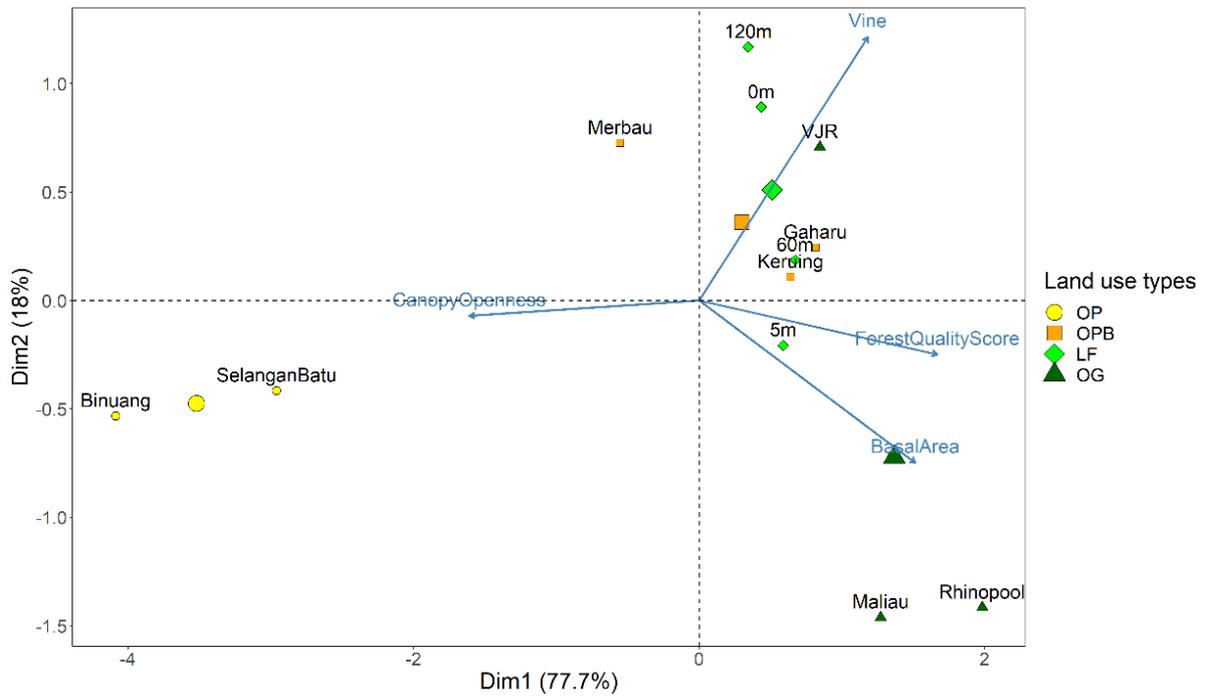
Since bugs were collected in three different time blocks, i.e., between 2011 and 2013 (**Table S3.2**), we calculated the possible effect of collection time by comparing the abundance, total biomass, and richness of the bugs for Maliau and Selangan Batu streams, where repeat collections were carried out in 2011 and 2012 (**Table S3.6 & S3.7**). Before assessing the difference in abundance, total biomass, and richness between time blocks in each of the two streams, we checked normality of data by assessing the plots of fitted and residuals as well as using Shapiro-Wilk tests. We also ran Levene's tests to check the equality of variance for abundance, total biomass, and richness data in each stream. Shapiro tests rejected non-normality in the distribution of both abundance and total biomass data. In addition, both data had equal variance. However, richness data from Maliau was not normal although had equal variance, while the richness data from Selangan Batu was normal but did not have equal variance. Since both abundance and total biomass data were not rejected for non-normality and had equal variance, we ran student *t*-tests with 95% confidence intervals to assess the difference between time blocks for the two streams for abundance and total biomass data. For richness data, we ran Wilcoxon tests. We found no significant difference in either abundance, total biomass, or richness between time blocks (**Table S3.7**), so we did not consider time block as a factor in our wider analyses. Hence, we only used data collected in 2012 in Maliau and Selangan Batu in all of our subsequent analyses (**Table S3.2 & S3.6**).



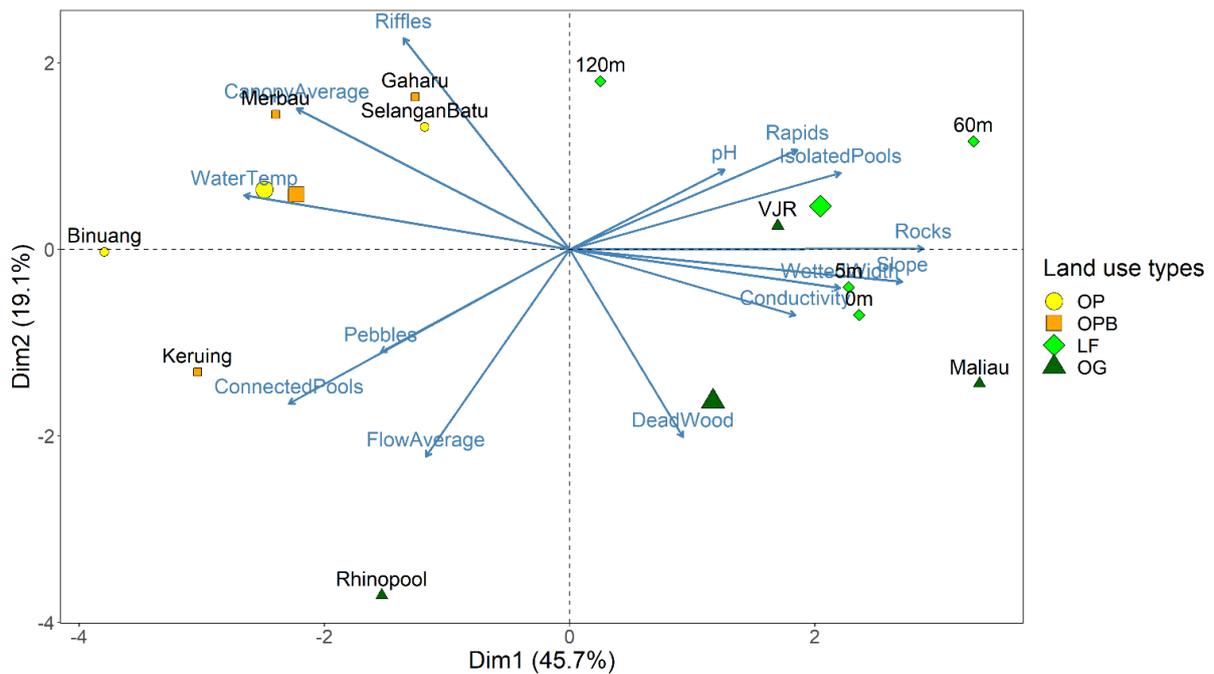
**Figure S3.1** Diagram illustrating the data collection set-up at riparian and stream scales in each site. For the riparian scale, data were collected at points at 50m intervals (box A, inset) along a 500m transect. For the stream scale, data were collected along a 200m transect, at points at both 10m intervals (box B, inset), for the measurement of stream physical characteristics and whole river channel, and 50m intervals (yellow circles with black borders), for the measurement of stream chemical characteristics. Data collection at riparian and stream scales were done by travelling upstream from “0m point” (the red circle with black border). Data collection was carried out approximately 2km downstream from the stream source. Green area represents catchment area; areas with no colour represent the same land-use type.



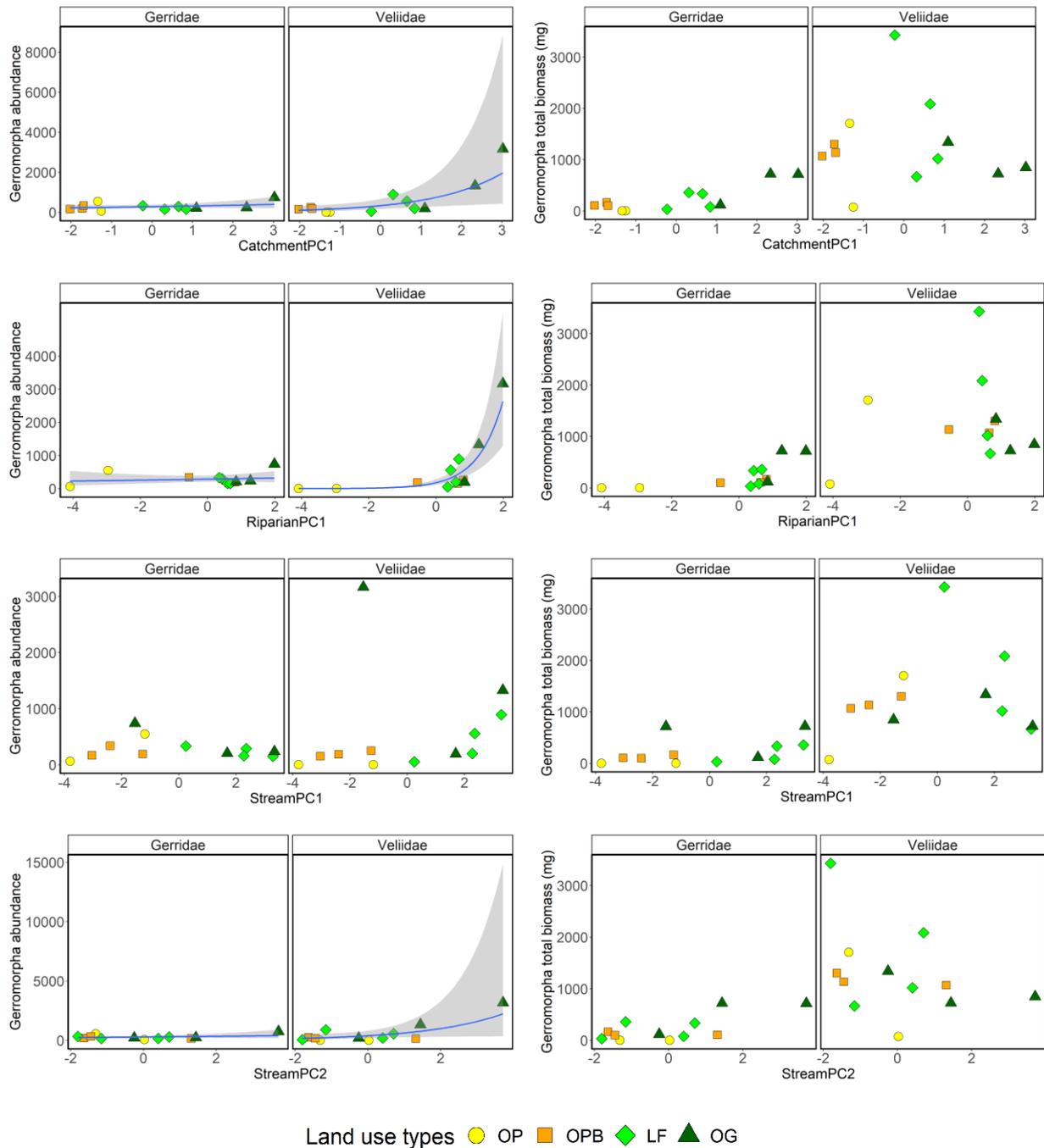
**Figure S3.2** PCA (Principal Component Analysis) biplot showing clusters of stream sites (points with differing colours and shapes representing land use types) plotted based on PC1 and PC2 site scores as well as environmental parameters measured at the catchment scale shown as arrows. Axes 1 and 2 explain 92% and 7.7% of variation in environmental parameters across stream sites. N = 12 streams (three, four, three, and two stream sites in old-growth forest (OG, 1. Maliau, 2. Rhinopool, and 3. VJR), logged forest (LF, 1. "0m", 2. "5m", 3. "60m", and 4. "120m"), oil palm with (OPB, 1. Gaharu, 2. Keruing, and 3. Merbau), and without riparian buffer strips (OP, 1. Binuang and 2. Selangan Batu, respectively).



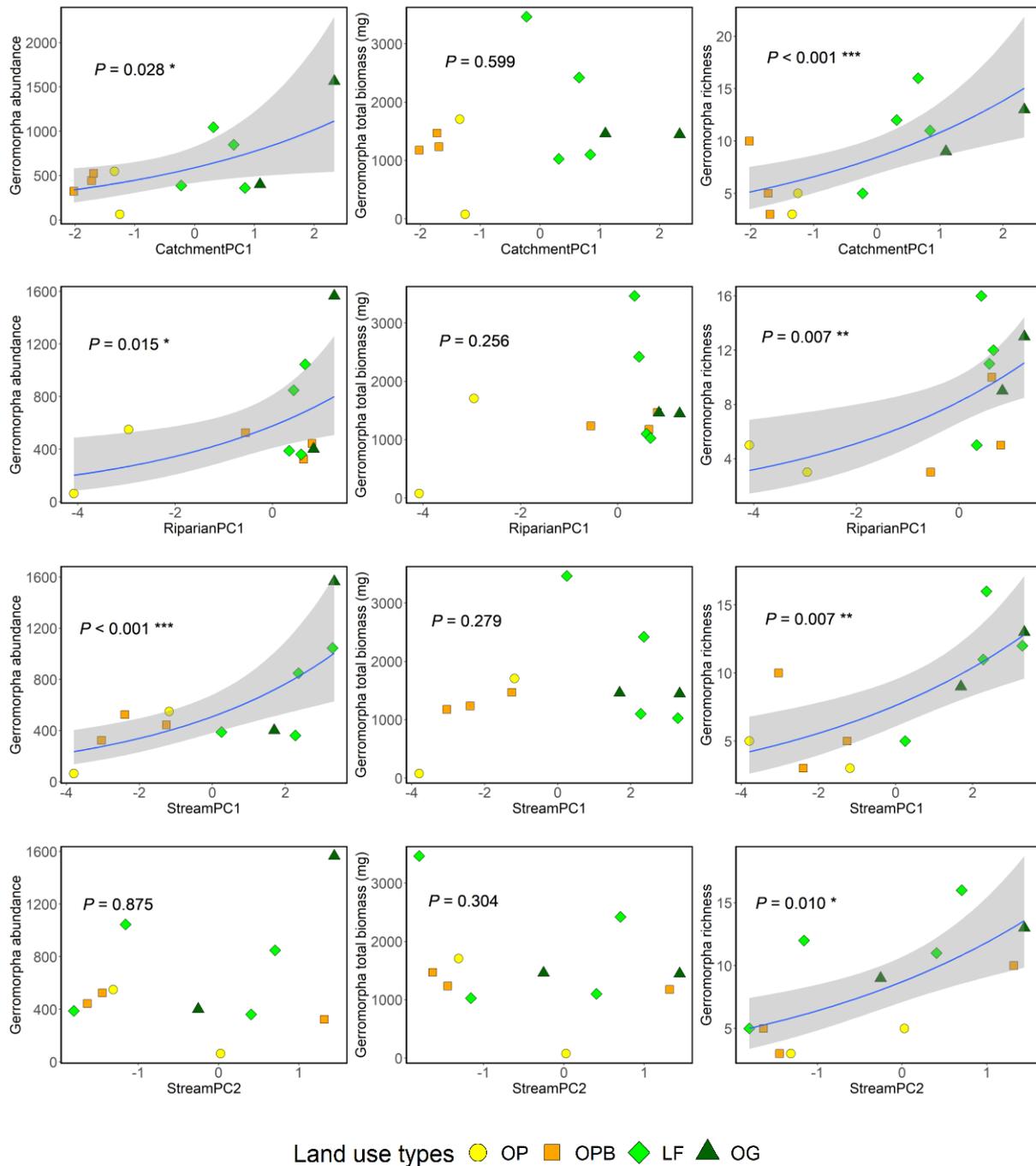
**Figure S3.3** PCA (Principal Component Analysis) biplot showing clusters of stream sites (points with differing colours and shapes representing land-use types) plotted based on PC1 and PC2 site scores as well as environmental parameters measured at the riparian scale shown as arrows. Axes 1 and 2 explain 77.7% and 18% of variation in environmental parameters across stream sites. N = 12 streams (three, four, three, and two stream sites in old-growth forest (OG, 1. Maliau, 2. Rhinopool, and 3. VJR), logged forest (LF, 1. "0m", 2. "5m", 3. "60m", and 4. "120m"), oil palm with (OPB, 1. Gaharu, 2. Keruing, and 3. Merbau), and without riparian buffer strips (OP, 1. Binuang and 2. Selangan Batu, respectively).



**Figure S3.4** PCA (Principal Component Analysis) biplot showing clusters of stream sites (points with differing colours and shapes representing land-use types) plotted based on PC1 and PC2 site scores as well as environmental parameters measured at the stream scale shown as arrows. Axes 1 and 2 explain 45.7% and 19.1% of variation in environmental parameters across stream sites. N = 12 streams (three, four, three, and two stream sites in old-growth forest (OG, 1. Maliau, 2. Rhinopool, and 3. VJR), logged forest (LF, 1. "0m", 2. "5m", 3. "60m", and 4. "120m"), oil palm with (OPB, 1. Gaharu, 2. Keruing, and 3. Merbau), and without riparian buffer strips (OP, 1. Binuang and 2. Selangan Batu, respectively).



**Figure S3.5** Total abundance and total biomass (sum of biomass of all semi-aquatic bugs in each stream site) of semi-aquatic bugs, separated by families across the gradient of environmental conditions at each catchment, riparian, and stream scale and land-use type. Regression line of significant relationships between predictors and response variables using the overall bug data is shown. Smoothed regression lines for significant relationships are shown. Shaded areas represent confidence intervals. N = 12 streams.



**Figure S3.6** Correlations between environmental variables across three scales (CatchmentPC1, RiparianPC1, and StreamPC1 and StreamPC2 representing catchment, riparian, and stream scales, respectively), after removal of Rhinopool from replicates, on the abundance, total biomass (sum of biomass of all semi-aquatic bugs in each stream site), and richness of semi-aquatic bugs (Gerromorpha).  $N = 11$  streams. Smoothed regression lines for significant relationships are shown. Shaded areas represent confidence intervals.

## **Chapter 4: The impacts of within-stream physical structure and riparian buffer strips on semi-aquatic bugs in Southeast Asian oil palm**

**Martina F. Harianja<sup>1</sup>, Sarah H. Luke<sup>2,1</sup>, Holly Barclay<sup>3,1</sup>, Vun K. Chey<sup>4</sup>, David C. Aldridge<sup>1</sup>, William A. Foster<sup>1</sup> & Edgar C. Turner<sup>1</sup>**

<sup>1</sup>Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK,

<sup>2</sup>School of Biosciences, University of Nottingham, Sutton Bonington Campus, Nr Loughborough, LE12 5RD, UK,

<sup>3</sup>School of Science, Monash University Malaysia, Jalan Lagoon Selatan, 47500 Subang Jaya, Selangor Darul Ehsan, Malaysia, and

<sup>4</sup>Forest Research Centre (Sepilok), Sabah Forestry Department, PO Box 1407, 90715 Sandakan, Sabah, Malaysia

**Key words:** riparian buffer strips, oil palm, Gerromorpha, semi-aquatic bugs, conservation management.

Under review by *Frontiers in Forests and Global Change*, section Forest Disturbance.

## Abstract

Despite the numerous ecosystem services forested stream margins (“riparian buffer strips”) can provide in agricultural landscapes, understanding of their impacts on various taxa in the tropics is lacking. Invertebrates living in streams support many ecosystem functions and several groups have been identified as valuable bioindicators of environmental conditions. Semi-aquatic bugs (insects in the order Hemiptera that inhabit the water surface) are important within the aquatic food chain, acting as predators of other invertebrates and prey for larger animals. Additionally, since they inhabit the water surface throughout their lives, semi-aquatic bugs are potentially valuable indicators of within-stream health. Focussing on the impacts of conditions at the small-scale, we investigated how within-stream physical structure and the presence of riparian buffer strips affected the abundance, total biomass, richness, and community composition of semi-aquatic bugs in oil palm plantations in Sabah, Malaysia, to identify factors affecting bug communities and whether buffer strips in oil palm (of a range of widths) might support more abundant and diverse semi-aquatic bug communities. We also assessed the effects of small-scale within-stream physical structure on the proportion of juveniles and females of *Ptilomera* sp. (a common bug species in this study). Findings from this work can be widely applied, as within-stream scale can be tailored to management practices by both industrial and smallholder plantation managers. At the small-scale (along 10-meter transect), we found higher average abundance (just less than twice as abundant) and marginally higher species richness of semi-aquatic bugs in oil palm streams with riparian buffer strips than those without (3.55 [SE ± 0.419] in streams with riparian buffer strips compared to 1.4 [SE ± 0.221] in streams without). Overall, we found a significantly different community composition between streams with and without

riparian buffer strips (out of 15 morphospecies of bugs found across streams, only seven were found in streams without buffer strips while streams with buffer strips had 14 morphospecies in total), but no difference in bug total biomass or proportion of female *Ptilomera* sp. Characteristics of within-stream physical conditions that were associated with a significantly higher abundance of semi-aquatic bugs were wider wetted width, more isolated pools, shallower slopes, and lower percentage of deadwood. Furthermore, the proportion of juveniles was higher in streams with higher canopy openness, higher percentage of deadwood, lower percentage of pebbles, and narrower wetted widths. This study demonstrates that small-scale differences in stream conditions within oil palm can influence sensitive groups, such as semi-aquatic bugs. Therefore, it opens up the possibility that management could be tailored to improve environmental conditions for stream communities in oil palm. However, the improvements we recorded were limited and our findings are based on only a few streams, and at measurements collected at a single time-point. More studies are therefore needed to validate what we have found, particularly assessments of the value of maintaining riparian buffer strips across larger oil palm areas, and whether within-plantation management practices can promote the development of favourable conditions for semi-aquatic bugs in the long-term.

**Key words:** riparian buffer strips, oil palm, Gerromorpha (Hemiptera), semi-aquatic bugs, conservation management

## **Introduction**

Globally, over 100,000 species (of plants as well as invertebrates and vertebrates) rely on freshwater systems for their habitat, but many of these systems have been degraded by land-use change, flow modification, pollution, invasive species, overharvesting, and management to collect hydropower (Carpenter et al., 2011; Cazzolla Gatti, 2016; Reid et al., 2019). The extinction or decline of freshwater species in modified systems is often driven by a change in physical and chemical environmental conditions within and around freshwater systems, as well as loss or reduction of resources (Reid et al., 2019; Tanaka et al., 2021). In terms of land-use change, forest conversion causes erosion, sedimentation, and increased inputs of pollution into waterways (Dudgeon et al., 2006). Such increase of inputs also changes the characteristics of waterways. For instance, an increased amount of sediment deposited at the bottom of streams can reduce flow rate and alter aspects of the stream physical structure (such as reducing channel width and depth [Luke et al., 2017a]). In addition, conversion can result in the loss of natural habitat margins surrounding freshwater systems, resulting in a reduction in canopy cover (which reduces litter inputs and increases water temperature), as well as an increase in erosion and nutrient enrichment (Cole et al., 2020; Tanaka et al., 2021; Wantzen & Mol, 2013).

Whilst it is estimated that 83% of global freshwater biota populations have declined between 1970 and 2014, little information is available within the tropics, particularly about how species respond to each type of threat (Reid et al., 2019; Sundar et al., 2020; WWF, 2018). Environmental impacts in the tropics are expected to be more severe than in other regions (Dudgeon et al., 2006), since they house higher levels of biodiversity (Myers et al., 2000) and experience higher precipitation (hence more flash flood events and higher erosion) (Tanaka et al., 2021). Therefore, more investigation is

needed to improve evidence-based conservation policy and management for the tropical freshwater ecosystems. Given the extensive scale of global tropical agricultural expansion, including in Southeast Asia (Halpern et al., 2022), studies addressing how land-use change affects tropical freshwater species and how conservation strategies can mitigate these impacts, are needed urgently, particularly at a scale at which land-managers can influence conditions.

Several management approaches have been proposed that could reduce impacts of habitat change on streams. These include conservation easement (leaving private land unexploited), retaining natural margins around streams (or “riparian buffer strips”), returning crop residue to the soil (reducing erosion by covering the soil surface with crop residue), reducing tillage in the surrounding catchment, and planting grass or vegetation strips around waterways and ditches. These strategies all aim to reduce erosion and sedimentation, or limit inputs of nutrients and pollutants into waterways (Blanco-Canqui et al., 2004; Cooper et al., 2004; Du et al., 2022; Farmer et al., 2015; Luke et al., 2019). Several studies have assessed the impacts of retaining riparian buffer strips on a range of freshwater species, including fishes and several groups of invertebrates, and have recorded benefits in terms of both abundance and diversity (e.g., Arnaiz et al., 2011; Ceneviva-Bastos & Casatti, 2014; Luke et al., 2017b; Pusey & Arthington, 2003).

Across tropical agricultural crops, oil palm is one of the main drivers of biodiversity loss (Foster et al., 2011; Sodhi et al., 2004), including within freshwater communities (e.g., Carvalho et al., 2018; Chellaiah & Yule, 2018; Giam et al., 2015; Luke et al., 2017b; Luiza-Andrade et al., 2017; Mercer et al., 2014). As a platform to improve the sustainability of palm-oil production, the RSPO (the Roundtable of Sustainable Palm Oil) provides guidelines for less environmentally damaging production

techniques, including for maintaining and managing riparian buffers strips. This includes recommendations on the width of buffer to be maintained as a parameter, and how to design riparian buffer strips within oil palm plantations considering the type of soil, stream, and age of the plantation (Barclay et al., 2017). Retaining riparian buffer strips in oil palm in Malaysian Borneo has been shown to support higher species richness and abundance of adult dragonflies (Luke et al., 2017b), as well as the altering the composition of benthic macroinvertebrate communities (Chellaiah & Yule, 2018). However, this strategy does not protect the diversity and abundance of larval dragonflies (Luke et al., 2017b) or other sensitive groups (such as larvae of aquatic insects, dung beetles, and large mammals [Deere et al., 2022]). Furthermore, despite the availability of such studies, there is limited research on the effects of riparian buffer strips on freshwater communities in the tropics, including Southeast Asia (Luke et al., 2019). Considering the large total area of oil palm in Southeast Asia (Pendrill et al., 2022), studies based in this region will be particularly useful for informing biodiversity conservation strategies, including platforms such as the RSPO.

Invertebrates play critical functions in freshwater systems by acting as decomposers, herbivores, predators, or prey items (Bay, 1974; Malmqvist, 2002). Semi-aquatic bugs (Gerromorpha, Hemiptera) are predator-scavengers as well as being preyed upon by other animals (Foster & Treherne, 1981; Spence & Andersen, 1994). All stages within the lifecycle of semi-aquatic bugs occur on or in the water (Spence & Andersen, 1994), making their survival highly dependent on within-stream conditions. Within each population, there can be polymorphism in terms of the presence or absence and form of wings. The proportion of winged and wingless adults can be related to the stability (Andersen, 2000) and quality of the habitat (Cunha et al., 2020), as well as breeding

seasons – although in the tropics, semi-aquatic bugs generally breed throughout the year (Andersen, 2000) – making quantification of wing forms a potentially valuable source of information on stream conditions. For instance, a study by Ditrich et al. (2008) on semi-aquatic bug communities in spring areas in the Czech Republic found that, unlike in permanent pools and streams, temporary systems were dominated by winged individuals.

Studies have reported shifts in species composition of semi-aquatic bugs between streams with and without forested riparian margins in Brazilian savanna streams (Dias-Silva et al., 2020). Furthermore, richness of semi-aquatic bugs has been found to be lower in oil palm than forest in Amazonian streams (Cunha et al., 2015), highlighting the impact of land-use change on semi-aquatic bugs. Another study found a higher number of winged individuals in forests than in oil palm in the Amazon (Cunha et al., 2020). Nevertheless, no studies have yet assessed the impacts of maintaining riparian buffer strips on this group in Southeast Asia. Studies seeking to understand how conservation strategies affect streams at a small scale within rivers could provide relevant information regarding the impacts of microhabitats on this group and could increase understanding of how microhabitat conditions affect demographic factors, such as reproduction and sex ratios, influencing population growth in semi-aquatic bugs. As an example from another insect group, a laboratory study found that the growth of mayflies (species investigated: *Eurylophella prudentalis* and *Eurylophella macdunnough*) was affected significantly by water temperature, with either an increase or decrease of five degrees Celsius causing higher mortality or a reduction in the hatch success of eggs (Sweeney, 1993). Consequently, this could affect the proportion of juveniles and adults, affecting the number of juveniles, if an increasing proportion cannot

develop into the adult stage. Additionally, differing sexes of semi-aquatic bugs may respond to environmental change differently, resulting in the proportion of males and females changing as within stream conditions alter. For instance, since female insects sometimes require more nutrition than males (Teder & Kaasik, 2023), a reduction in food resources (such as when the loss of riparian buffer strips causes a loss or reduction in food inputs from the surrounding area) could reduce the proportion of females to males and the reproductive success of the population. Work at the within-stream scale may be particularly relevant for conservation management and for informing sustainability guidelines, as this is the scale at which individual industrial or smallholder plantation managers can operate (Maddock, 1999).

In this study, we investigated the impacts of within-stream physical structure and maintaining riparian buffer strips on semi-aquatic bugs in oil palm streams in Sabah, Malaysia. We also assessed impacts on the demographic factors of the most widespread and easily sexed species in the study: *Ptilomera* sp.. We asked the following questions:

1) What is the variability in within-stream physical structure across oil palm, and do these differ between streams with and without riparian buffer strips? We hypothesised that riparian areas with buffer strips would have differing environmental conditions than those without, with streams without riparian buffer strips having a higher percentage of canopy openness, a lower percentage deadwood, as well as narrower wetted width, lower flow speed, and more homogenous flow regimes (due to a higher level of runoff and sediment deposition).

2) What is the impact of within-stream physical structure and the presence of riparian buffer strips on the richness, abundance, total biomass, and composition of semi-aquatic bugs in oil palm? Since semi-aquatic bugs live on the surface of the water and are

therefore likely to be affected by the environmental conditions in and around streams, we hypothesised that oil palm streams without forest margins would have lower species richness, abundance, and total biomass of semi-aquatic bugs, compared to streams with forested river margins. As some species are likely to be more resilient to disturbed conditions, we also hypothesised that the absence of riparian buffers, and altered environmental conditions, would result in an altered community composition, with a higher abundance of disturbance-tolerant species.

3) What is the impact of within-stream physical structure and the presence of riparian buffer strips on the proportion of juvenile semi-aquatic bugs, proportion of winged and wingless adult individuals, as well as the proportion of female *Ptilomera* sp.? As different sexes, presence of wings in adults, and juvenile and adult semi-aquatic bugs may be affected by environmental conditions to different extents, we predict significantly altered proportions, with streams without riparian buffer strips have reduced numbers of females, higher numbers of wingless adult individuals, as well as reduced numbers of juveniles.

## **Materials and methods**

### *Stream sites*

Streams within oil palm plantations were surveyed in July – September 2011 and in May – August 2012 in Sabah, Malaysia, where there is little seasonality throughout the year (tropical rainforest climate with average annual rainfall of 2455mm in the study sites) (Luke et al., 2017a). All the streams were natural channels present in established oil palm plantations (with drainage channels present in the surrounding area), either had or did not have forested riparian buffer strips, and were located within the SAFE (Stability of

Altered Forest Ecosystems) Project study system, which were near the Kalabakan Forest Reserve, 116°570E to 117°420E, 4°380N to 4°460N (Ewers et al., 2011) (**Figure 4.1**). Oil palm sites with forested riparian buffers strips (OPB) were in Gaharu, Keruing, and Merbau estates (managed by Benta Wawasan). The width of the buffer strips in each stream varied, with average widths of approximately 331m, 68m, and 26m in Gaharu, Keruing, and Merbau respectively, and buffers being continuous in all streams, but with plantation roads likely to be crossing them (Luke, et al., 2017b). Exact buffer widths varied across the lengths of the streams. Streams without forested riparian buffer strips (OP) were in Binuang and Selangan Batu estates, where oil palms were planted up to the margins of streams. Within oil palm sites without forested buffer strips, oil palm fruit bunches were managed and harvested as normal up to the stream edge.

All streams originated within oil palm catchments (see **Table S4.1** for information on the sizes of catchments surrounding stream sites, average slopes, as well as channel and wetted widths of the streams), with surrounding oil palms being planted between 1999 and 2009 and were therefore between two and thirteen years old at the time of this study (Luke et al., 2017b). At each stream, data collection was standardised to be conducted from approximately 2km downstream from the stream source. This was to ensure catchment areas across streams were comparable, and this point is termed as the “0m point” throughout this chapter.

#### *Data collection on within-stream physical structure*

Stream environmental data at each site were collected once in May – August 2012 along a 200m transect from the “0m point” and going upstream. Data were collected during non-flood conditions. Stream physical structure was recorded at points at 10m intervals

along the 200m transect and consisted of: flow speed (time needed for a tennis ball to travel along a 2m string at the fastest flowing point along each transect (at rapids or riffles), repeated three times and then averaged), canopy openness (measured using a spherical densiometer (Lemmon, 1956) in the middle of each stream facing upstream, downstream, and to the left and right sides of the stream; average calculated), and wetted width of the stream, measured using a tape measure. Due to logistical constraints in the field, it was not possible to measure specific buffer widths at each sample point. However, as riparian width is likely to affect within-stream conditions downstream of the buffer location, rather than at the location itself, measurement at this scale is unlikely to reflect conditions at the sample locations themselves.

The physical structure of the whole river channel was also measured by recording percentage cover of rocks, pebbles, sand, deadwood, rapids, riffles, connected pools, and isolated pools between the 10m intervals, and slope at each 10m along the 200m transect using a clinometer. Deadwood were large chunks of wood from trees (tree trunks or portions of them, or very large branches), with coverage of >5% over the 10m intervals. Pools, riffles, and rapids were assessed according to water speed (pools = still water, riffles = flowing water with a rippled surface, and rapids = fast-flowing white water). The average of each variable was calculated for subsequent analyses. We acknowledge that because we measured within-stream conditions at one time-period only we are unlikely to have captured the full range of conditions experienced by bugs at each location, although our measurements do reflect conditions at the time of sampling.

### *Semi-aquatic bug collection and processing*

Semi-aquatic bugs were collected once from five or ten 10m sub-transects of the 200m transects in July – September 2011 or June – August 2012, using hand-held nets (Ditrich et al., 2008) with mesh size of 1mm or less (hereafter, termed as “10m transect”) (**Table S4.2**). The bugs were collected from the same starting points as the measurements of stream environmental variables (the “0m point”). After collection, all the bugs were preserved in 70% ethanol. Juveniles were identified to family level, while adults were identified to morphospecies level, using relevant identification guides and taxonomic papers (Andersen, 1982; Chen & Nieser 1992, 1993a, 1993b; Chen & Zettel, 1998; Polhemus & Polhemus, 1988). During the identification process, advice from taxonomic experts was also obtained (see “**Statement of contribution**” [page viii] for details). However, although morphospecies were split as accurately as possible, it is possible that morphospecies in this study represent more than one species.

In addition to identification, the body length of all individuals was measured to allow biomass calculations. Body length measurement was done to the nearest 1mm using graph paper. Biomass was then calculated using power regression equations, following Harianja et al. (2023a) (derived from semi-aquatic bugs from the same study area, see Chapter 2). Family and body form of the bugs can influence the length-biomass relationship, thus we used three equations for the biomass calculations:  $y = 0.040x^{2.271}$  for Cylindrostethinae, Gerrinae, and Ptilomerinae;  $y = 0.072x^{2.218}$  for Halobatinae; and  $y = 0.041x^{2.320}$  for Veliidae, with  $y$  = the biomass and  $x$  = the body length of a bug (see Harianja et al., 2023a [Chapter 2] for further details). Total biomass was obtained by summing of all individual biomass of semi-aquatic bugs from each of the 10-m transects and were used for subsequent analyses.

For assessment of the demographic structure of semi-aquatic bugs, we grouped adults and juveniles separately. Grouping was based on tarsal segments: juveniles have only one tarsal segment, while adults have at least two. For one species, *Ptilomera* sp., we further grouped individuals into males and females. It was not feasible to distinguish sex for other species (*Ptilomera* sp. have clear sexual dimorphism, while other species in this study do not). For each adult individual, we also recorded whether they were winged or wingless. However, because of the low number of winged adult individuals (only twelve in totals across streams, with streams with riparian buffer strips having ten, while streams without buffer strips having only two winged individuals), we did not conduct further analysis on this aspect of the data.

### *Statistical analysis*

We carried out analyses and visualisations using R version 4.0.4 (R Core Team, 2021) and R Studio version 2022.07.1+554 (R Studio Team, 2022). For analysis, basic R syntax and package “dplyr” were used (Wickham et al., 2021). We used “plotrix” (Lemon, 2006) to calculate standard errors. To check for association between the presence or absence of riparian buffer strips and each of the stream environmental variables, we used “lrm” package (Rizopoulos, 2006). To summarise and visualise stream environmental variables, we used a Principal Component Analysis (PCA), run through built-in codes in R and “factoextra” (Kassambara & Mundt, 2020), respectively. For analyses on impacts of stream physical structure and the presence or absence of riparian buffer strips on semi-aquatic bugs, we used “vegan” (Oksanen et al., 2020) to run Canonical Correspondence Analysis (CCA), and “lme4” (Bates et al., 2015) to run Linear Mixed-Effect Models (LMMs) and Generalised Linear Mixed-Effect Models

(GLMMs). We used the following packages for all other visualisations in this study: “tidyverse” (Wickham et al., 2019), “cowplot” (Wilke, 2020), and “gridExtra” (Auguie, 2017).

### *Within-stream physical structure*

To reduce the dimensionality and summarise the environmental variables measured across all oil palm stream sites, we used PCA (Jolliffe, 1986), with data from each 10m transect included as a separate data point. We did not transform any variables used in the analyses, and all variables were standardised first to account for differing units (using a correlation matrix) (Jolliffe, 1986). In R this was conducted using the following function: “scaling = TRUE”. Sand was excluded from the PCA because its value was implied from the total percentages of other measured percentage cover stream variables. Since the stream environmental variables could be correlated with the presence or absence of riparian buffer strips, we assessed whether buffer strip presence was associated with environmental variables. For this, we ran a biserial correlation test and found that there was a weak to moderate correlation, suggesting that additional information was included in the environmental data and presence/absence of buffer information (**Table S4.3**). Therefore, for subsequent analyses, we included the presence of riparian buffer strips as a separate factor (hereafter “Riparian”). Finally, to assess if the stream physical structure differed between oil palm with and without riparian buffer strips, we ran separate Mann-Whitney U tests for the most influential stream Principal Component (PC) scores, obtained from PCA between the two types of streams.

*Impacts of within-stream physical structure and retaining riparian buffer strips on semi-aquatic bugs*

To assess the impacts of measured stream environmental conditions as well as the presence or absence of riparian buffer strips on semi-aquatic bugs (abundance, total biomass, and richness), we ran LMMs or GLMMs, with each data point representing a 10m transect site. For all analyses, we considered four PC scores on stream environmental variables (“StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”, obtained from the PCA) as separate predictors, because PC scores explained similar levels of variation among stream environmental variables. In all models, stream identity was included as a random factor to take into account the non-independence of points within each stream. Rather than composite biodiversity indices, we chose to focus on simple measures of our community as these allow assessments of specific impacts of environmental conditions on semi-aquatic bugs (Barrantes & Sandoval, 2009).

For abundance, we ran negative binomial models due to overdispersion. For total biomass and richness, we ran LMM and GLMM with gaussian and Poisson distribution, respectively, according to the type of data (biomass and count). To assess the importance of each predictor (“StreamPC1”/ “StreamPC2”/ “StreamPC3”/ “StreamPC4”/ “Riparian” [“Riparian” indicates the presence/ absence of riparian buffer strips]), we ran log-likelihood ratio tests. In particular, we used separate ANOVA tests to compare the full model (consisting of all predictors) with a model in which one of the predictors was dropped. To assess the effects on community composition, we ran CCA with 999 random permutation tests using stream environmental variables and buffer strip presence along with community data of adult bugs. To assess the impact of stream physical structure

and retaining riparian buffer strips on the proportion of juveniles as well as the proportion of female *Ptilomera* sp., we ran GLMM with binomial family. Similarly, for assessing the importance of each predictor on the proportion of juveniles and female *Ptilomera* sp., we ran log-likelihood ratio tests. Since there were very few winged individuals found in this study, we carried out no formal analysis on these data, but present totals in the results.

## Results

### *Variability and differences in within-stream physical structure between oil palm streams with and without riparian buffer strips*

At the stream scale, PCA scores were spread evenly between axes 1, 2, 3, and 4 (“StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”, respectively), with StreamPC1 and StreamPC2 explaining 24.5% and 18% of the variation in environmental variables measured in all stream sites, while “StreamPC3” and “StreamPC4” explained 15.3% and 11.7% respectively (**Figure 4.2**). In general, this means that multiple uncorrelated variables explained environmental differences between streams. “StreamPC1” scores were correlated with a higher percentage cover of rocks (0.387), rapids (0.366) and riffles (0.306), a steeper slope (0.374), and more rapid flow speed (-0.333, negative sign indicates that less time was needed for a tennis ball to travel the 2m string), but with lower percentage cover of connected pools (-0.471) (**Table 4.1**). “StreamPC2” scores were associated with wider wetted width (0.464) and higher percentage of pebbles (0.417), but with lower percentage of canopy openness (-0.531) and deadwood (-0.332) (**Table 4.1**). “StreamPC3” scores were associated with a steeper

slope (0.312), a higher percentage of rocks (0.475), pebbles (0.372) and isolated pools (0.359), but with lower percentage of riffles (-0.538) (**Table 4.1**). Finally, “StreamPC4” scores were correlated with a higher percentage of deadwood (0.427) and steeper slope (0.342), but with a lower percentage of isolated pools (-0.566) and narrower wetted width (-0.445) (**Table 4.1**). Streams with and without riparian buffer strips only differed significantly in “StreamPC4” scores (**Table 4.2**), with streams without riparian buffer strips having a higher percentage of deadwood and isolated pools, steeper slopes, and lower wetted widths. (**Table 4.2**).

*Impacts of within-stream physical structure and retaining riparian buffer strips on the abundance, total biomass, and richness of semi-aquatic bugs*

We found 2699 semi-aquatic bugs (including 1858 juveniles and 841 adults) across oil palm streams in this study. The bugs were from two families (Gerridae and Veliidae), eight genera, and 15 morphospecies (**Table S4.4-S4.5**). Higher “StreamPC4” scores were significantly associated with lower abundance of bugs (**Figure 4.3, Table S4.6**), and the presence of riparian buffer strips (“Riparian”) was significantly associated with higher richness of bugs (**Table S4.6**). Overall, the average abundance of semi-aquatic bugs in oil palm with and without riparian buffer strips were 104.35 (SE±11.811) and 61.2 (SE±17.408), respectively. Additionally, the average number of morphospecies of semi-aquatic bugs in oil palm streams with riparian buffer strips was 3.55 (SE±0.419), compared to 1.4 (SE±0.221) in oil palm streams without. There were no other significant effects of within-stream physical structure on the abundance, total biomass, or richness of semi-aquatic bugs (**Figure 4.3, Table S4.6**). Nor was there an effect of the presence of riparian buffer strips on the abundance or total biomass of the bugs (**Table S4.6**).

There was a differing community composition of semi-aquatic bugs associated with StreamPC1 and the presence of buffer strips, but not with other environmental variables representing stream physical structure (**Table 4.3, Figure 4.4**). In particular, the two commonest morphospecies, *Ptilomera* sp. and *Rhagovelia* sp. differed markedly in their distribution in relation to the presence of riparian buffer strips: *Ptilomera* sp. were found across sites, but *Rhagovelia* sp. were found almost exclusively in streams with buffers (**Figure 4.4, Table S4.5**). Across the 15 morphospecies of adult bugs found across streams, only seven were found in oil palm without riparian buffer strips (while 14 morphospecies in total were found in oil palm streams with riparian buffer strips) and they were generally in low abundance (**Table S4.4**). We found two genera that are known to be resilient to habitat change and pollution: *Limnogonus* and *Rheumatogonus* (Mohd Ishadi et al., 2014). On the other hand, a genus that is generally found in shaded streams only (*Metrocoris* [Polhemus, 1990]) was found at an extremely low abundance across streams in this study, with only one individual from streams without riparian buffer strips (**Table S4.4-S4.5**).

*Impacts of within-stream physical structure and retaining riparian buffer strips on the ratios of juveniles to adults and females to males in Ptilomera sp.*

We found that StreamPC2 (wider wetted width and higher percentage of pebbles, but lower percentage of canopy openness and deadwood) significantly affected the proportion of juveniles across streams, with higher StreamPC2 scores being associated with a lower proportion of juveniles. We found no other effects of within-stream physical structure or retaining riparian buffer strips on the proportion of juveniles and females of *Ptilomera* sp. (**Figure 4.5, Table S4.7**). We found a low number of winged adult

individuals across stream types, with streams with and without riparian buffer strips having ten and two winged individuals in total, respectively.

## Discussion

At the small-scale (10m transects), the lack of clear differences that we found in most of environmental variables forming stream physical structure between streams with and without riparian buffer strips indicates that, in general, the presence of riparian buffer strips does not have significant impacts on within-stream physical structure, particularly for the parameters that we measured. This could be because the influences of wider catchment properties on stream conditions are more pervasive, or because the riparian buffers in this study were not able to protect streams from the influence of chemical runoff or erosion from the surrounding agricultural landscape (Harianja et al., 2023 f [Chapter 3]; Xu et al., 2023). The characteristics of streams without riparian buffer strips that we recorded (higher percentage cover of deadwood, steeper slopes, fewer isolated pools, and lower wetted widths) could be because riparian areas around smaller streams with narrower wetted width are less likely to be protected during plantation establishment. Indeed, the RSPO (2017) advises that riparian buffer strips should be at least five meters wide for streams or rivers between one and five meters wide, and wider strips should be maintained along wider waterways. All oil palm streams in this study (both with and without riparian buffer strips) had average channel widths that were between five and twelve meters (**Table S4.1**). Hence, streams without buffer strips could have experienced more impacts of disturbance occurring on land, such as more surface runoff and erosion (Du et al., 2022). Smaller streams may also be more likely to be found on steeper slopes (Burt et al., 2023, **Table S4.1**) and therefore to have fewer isolated

pools. This higher steepness of slope could also explain the higher recorded presence of deadwood, which may be more readily exposed from sediment in such areas. However, it should be noted that buffers were variable in size and condition in this study (average widths of buffer strips were approximately 331m, 68m, and 26m in Gaharu, Keruing, and Merbau, respectively), and we only sampled two oil palm streams without buffers and three oil palm streams with buffers. Differences could therefore be heavily influenced by parameters associated with just one stream and it is important to assess these findings in a larger-scale study. Related to this, we collected data on stream physical structure once at each site. Therefore, the conditions we recorded may not be representative of the overall conditions of streams or the conditions experienced by semi-aquatic bugs over longer time periods. However, some characteristics we recorded were less likely to be impacted by this than others (for example, percentage canopy openness, percentage cover of rocks, steepness of slopes, and the presence of deadwood are less likely to vary over the year than wetted width or flow speeds).

We found only a limited range of species in our study system, consisting of 15 morphospecies, from eight genera and two families. This is much lower than previous studies within forested areas in the region (e.g., up to 30 morphospecies from all forest sites in Harianja et al., 2023f [Chapter 3]). The lower number of species we found in oil palm is most likely due to the impacts of land-use change, altering within-stream environmental conditions. On a larger scale, land-use change might have caused changes in streamflow and have increased erosion and sedimentation (Wantzen & Mol, 2013). On a finer scale, changes in the water physicochemical characteristics, such as increased water temperature and higher nutrient content, might have occurred (Horne & Hubbart, 2020; Lima et al., 2022; Tanaka et al., 2021). Furthermore, some resources provided by

forest cover (such as input of organic matter) might have been reduced or lost because of conversion to oil palm (Lima et al., 2022). As a result, microhabitats for some species of semi-aquatic bugs might have disappeared, resulting in the lower richness of bugs in oil palm compared to forests (see Harianja et al., 2023f [Chapter 3]). Other studies have also found a similar pattern, particularly that regardless of the presence of riparian buffer strips, oil palm streams cannot support species that are sensitive to anthropogenic disturbance. For instance, some insect species (including some Odonata in Carvalho et al., 2018 and Luke et al., 2017b, aquatic insect larvae and dung beetles in Deere et al., 2022) are not found in oil palm streams.

We found that oil palm streams with riparian buffer strips had more species/morphospecies of semi-aquatic bugs and the community composition in streams with and without buffers was different. This is likely to be because oil palm with riparian buffer strips provides more resources than oil palm without, such as leaf litter for invertebrates that are prey items of semi-aquatic bugs, or terrestrial invertebrates themselves, falling from the surrounding margins, that are also prey items (Maier, 1977; Mendes et al., 2019a; Popescu et al., 2021). Furthermore, the presence of the strips may buffer the microclimatic conditions within streams, so bug species with lower heat tolerance can be supported. Indeed, studies conducted on other aquatic invertebrates found that oil palm streams house more species that are more tolerant to higher water temperatures caused by the loss of canopy cover, compared to forest streams (Mendes et al., 2019b).

It is notable that only seven of the 15 morphospecies in our study were found in streams without buffers: *Limnogonus* sp., *Metrocoris* sp., *Ptilomera* sp., *Rhagovelia* sp.1, *Rheumatogonus* sp.1 and sp.3, and *Tenagogonus* sp.. Previous studies have found

*Limnogonus* species in forest as well as oil palm streams, showing this genus to be resilient to habitat change (Al-Shami et al., 2011; Mohd Ishadi et al., 2014; Moy et al., 2022). In contrast, *Metrocoris* species are known to live in shaded streams (Polhemus, 1990), which may explain their low abundance in this study: only one individual was found in oil palm streams without riparian buffer strips (although overall abundance of this genus across streams were generally extremely low; see **Table S4.4-S4.5**). *Ptilomera* and *Rhagovelia* species can tolerate fast-flowing water because of specialised structures they possess that help rowing in such habitats (Kim et al., 2022). This may explain their presence in oil palm streams, which can be highly variable in streamflow due to rapid surface runoff from surrounding agricultural land. Mohd Ishadi et al. (2014) also found *Rhagovelia* and *Rheumatogonus* bugs across stream sites with varying levels of pollutant sources (including from households, mining operations, and agriculture), demonstrating the resilience of these genera to changing stream conditions.

A notable difference in the community composition between streams with and without buffers was in the two commonest morphospecies of bugs, *Ptilomera* sp. and *Rhagovelia* sp.. *Ptilomera* sp. was found across stream types, but in contrast *Rhagovelia* sp. was largely restricted to streams with buffers. This could be owing to a marked size difference between the species: *Rhagovelia* spp. are relatively small and perhaps more vulnerable to variable climatic conditions, whereas *Ptilomera* sp. are much larger and therefore perhaps more robust (Kingsolver et al., 2011). We note that, as we only identified bugs to morphospecies level in this study, it is possible that some morphospecies may have contained more than one species. However, this is unlikely to systematically affect the results we recorded and would only be likely to reduce the chance of recording changes with environmental parameters.

Along 10m transects, the fact that we found a higher abundance of bugs in streams with higher wetted width and isolated pools, as well as shallower slopes and lower percentage cover of deadwood, is likely to be largely related to habitat availability. Streams with higher wetted width and more isolated pools are likely to have a larger surface area, providing space for more individuals, and such conditions may be more likely within streams on less steep slopes. Indeed, habitat heterogeneity in oil palm can be associated with a higher abundance of individuals across taxa, such as frogs (Kurz et al., 2016) and larval dragonflies (Luke et al., 2017b). The association with a lower percentage of deadwood is harder to explain, as some species of semi-aquatic bugs are known to lay eggs on deadwood (Sweeney, 1993). It is possible that this trend again is a feature of the limited number of stream sites sampled in this study. The altered community composition we found associated with slope, percentage cover of rocks, rapids, riffles, connected pools and flow speed is likely to be related to each of these factors altering the environmental conditions for semi-aquatic bugs (Dias-Silva et al., 2020; Moy et al., 2022), which are known to have varying requirements across species (Andersen, 1982; Andersen & Weir, 1997).

In contrast to effects on abundance, richness, and composition, we did not identify any environmental factor or presence of buffer that affected total biomass of semi-aquatic bugs. In contrast, other studies have found that the presence of riparian buffer strips is associated with a higher biomass of invertebrates (Burdon & Harding, 2008; Sargac et al., 2021). The opposite trend observed in this study could have been because of species replacement/ turnover across sites, stabilising total biomass measurements. In particular, although streams with buffer strips had a generally higher abundance of semi-aquatic bugs, this was from a combination of large- and small-bodied species across life

stages, while streams without buffer strips were dominated by larger bodied bugs for both life stages. For instance, small species (up to 4mm in body length) such as *Rhagovelia* spp. were common and abundant in streams with buffer strips, but the larger *Ptilomera* sp. (up to 19mm in body length) as well as large-bodied juveniles (up to 15mm in body length) remained abundant in streams without buffers, maintaining a high total biomass owing to their large individual size (Slade et al., 2011).

Furthermore, at the small scale (10m transects), we found that there were more juveniles in streams with higher canopy openness and deadwood, but lower wetted width and percentage cover of pebbles. This might show that juveniles can still survive and grow in streams with warmer water temperature caused by higher canopy openness, and indeed warmer conditions could result in higher growth rates for juvenile bugs, as it can (within an optimal range for growth) in other insects (Kingsolver et al., 2011). The higher incidence of deadwood could provide a substrate for egg-laying (Sweeney, 1993), potentially boosting numbers of juveniles in these streams. Finally, the lower wetted width could mean that these streams are less commonly used by adults, potentially allowing juveniles to escape competition, increasing their relative numbers (Spence & Carcamo, 1991).

We found an extremely low number of winged individuals at the small scale (10m transects) across streams and found no relationship between any environmental factors or the presence of riparian buffer strips on the sex ratio of *Ptilomera* sp.. In terms of sex ratio, this may show that neither sex is disproportionately affected by habitat disturbance, at least in *Ptilomera* species. This could be owing to this species being robust to change or could be a finding that is true across species and merits further study. As a caveat to this, since *Ptilomera* semi-aquatic bugs in this study were identified to morphospecies

level, this group might have included more than one species, so our results should be interpreted with caution.

### **Implications and conclusion**

Our study found that certain stream environmental conditions and the presence of riparian buffer strips benefited semi-aquatic bugs, particularly their abundance and richness. In particular, we found more abundant semi-aquatic bugs in streams with higher wetted width and more isolated pools, but shallower slopes and lower percentage cover of deadwood. Further studies assessing the impacts of stream characteristics on other groups of animals may provide clarity towards their effects on a wider range of species, improving conservation efforts in agricultural landscapes.

Despite the above findings, there were lower species richness and abundance of semi-aquatic bugs in oil palm streams (regardless of the presence of riparian buffer strips) when compared to forests from another study (Harianja et al., 2023 f [Chapter 3]), and the species that we found in oil palm streams were generally tolerant of disturbance. In addition, at the small-scale (10m transects), the higher richness of semi-aquatic bugs in oil palm streams with riparian buffer strips than oil palm streams without was only by two morphospecies (average number of morphospecies in oil palm streams with riparian buffer strips was 3.55 (SE  $\pm$  0.419) and was 1.4 (SE  $\pm$  0.221) in streams without), indicating that benefits of this management approach, at least for semi-aquatic bugs, are limited. This lack of a strong effect is likely because of the limited impact that buffer presence had on environmental conditions within streams (Carvalho et al., 2018; Deere et al., 2022; Luke et al., 2017b). Taken together, these findings highlight that managers should not assert that putting in a buffer strip will compensate for the wider loss of forest.

More studies, particularly at a larger scale, are needed to confirm the findings from this study, particularly because we surveyed only five streams. In addition, over time there can be variation in semi-aquatic bug communities (Fernando, 1963) and stream physical parameters, so it is also important to carry out studies over longer-time periods.

Finally, whilst abundance, richness, and composition of semi-aquatic bugs were affected by stream physical structure and the presence of riparian buffer strips, this was not the case for total biomass, number of winged individuals, or for the sex ratio of *Ptilomera* sp.. This suggests that these latter factors may not be helpful when assessing environmental change, particularly for semi-aquatic bugs in permanent lotic habitats, as in this study.

## Tables and Figures

**Table 4.1** Outputs of PCA (Principal Component Analysis) for 30 10-m transects representing streams with (OPB) and without riparian buffer strips (OP) (from three and two streams for OPB and OP, respectively), showing loading scores of each environmental variable within Principal Component (PC) axis 1 to 4 (“StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”, respectively). Variables with loading scores over 0.3 for each axis are shown in bold. Each stream consisted of five transects, but one stream (Gaharu) having ten transects.

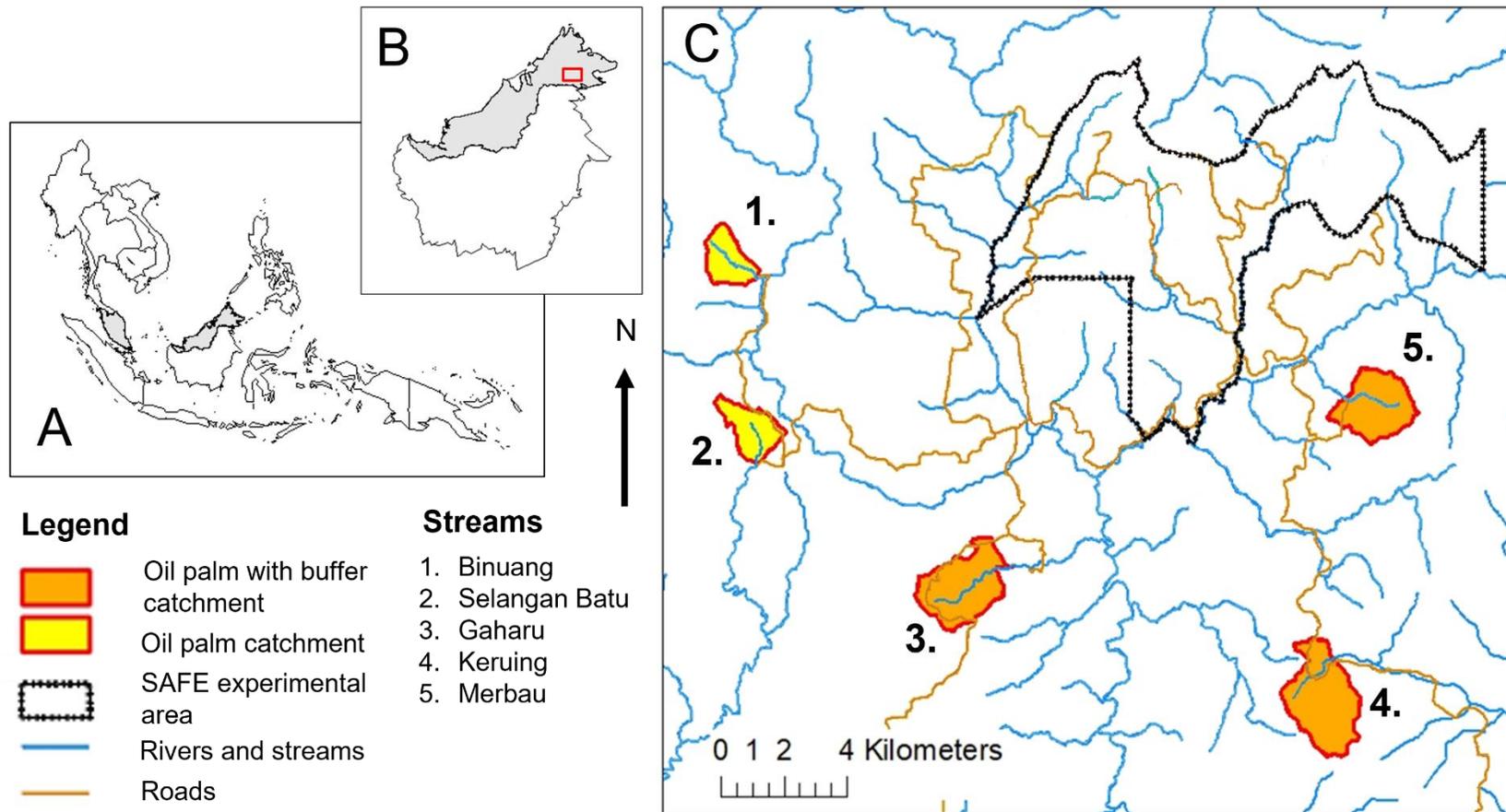
Parameter	Description	StreamPC1	StreamPC2	StreamPC3	StreamPC4
Average_FlowAverage	Average flow speed represented by time needed by a tennis ball to travel a 2-m string	<b>-0.333</b>	0.238	-0.076	-0.273
	Average canopy openness	-0.131	<b>-0.531</b>	0.176	-0.079
Average_WettedWidth	Average wetted width of stream	-0.088	<b>0.464</b>	-0.188	<b>-0.445</b>
Slope	Average slope	<b>0.374</b>	0.086	<b>0.312</b>	<b>0.342</b>
Rocks	Average percentage cover of rocks	<b>0.387</b>	-0.082	<b>0.475</b>	-0.076
Pebbles	Average percentage cover of pebbles	-0.229	<b>0.417</b>	<b>0.372</b>	0.079
DeadWood	Average percentage cover of dead wood	-0.253	<b>-0.332</b>	-0.047	<b>0.427</b>
Rapids	Average percentage cover of rapids	<b>0.366</b>	0.199	-0.202	0.154
Riffles	Average percentage cover of riffles	<b>0.306</b>	-0.240	<b>-0.538</b>	-0.206
ConnectedPools	Average percentage cover of connected pools	<b>-0.471</b>	0.186	-0.038	0.141
IsolatedPools	Average percentage cover of isolated pools	0.069	-0.116	<b>0.359</b>	<b>-0.566</b>

**Table 4.2** Outputs of Mann-Whitney U-test used to assess the difference in stream physical structure between oil palm with (OPB, three streams) and without riparian buffer strips (OP, two streams), consisting of 20 and 10 10-m transects respectively. Stream physical structure was represented by four PC scores (“StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”) obtained from a PCA, which explained most of the environmental variability between the two stream sites. *P*-values that are less than 0.05 are given in bold and indicate significant differences.

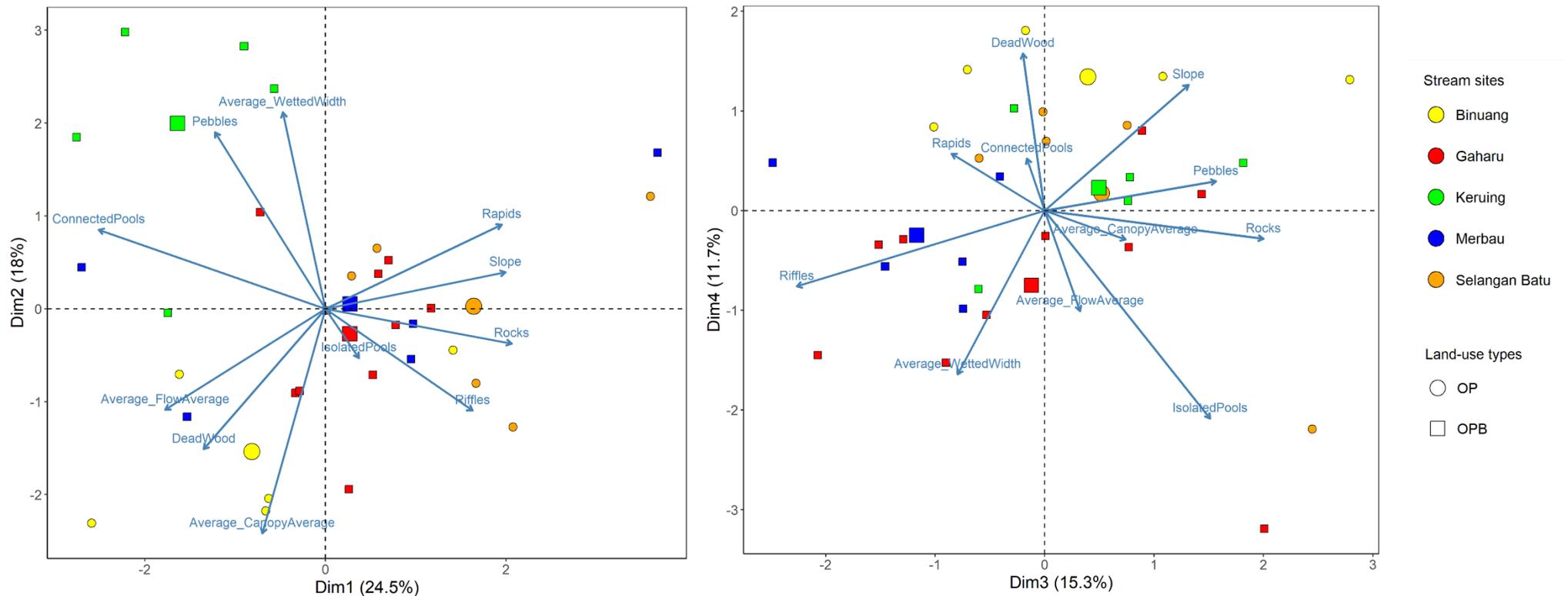
Compared PC scores	<i>W</i>	<i>P</i> -value
StreamPC1	121	0.373
StreamPC2	56	0.054
StreamPC3	129	0.213
StreamPC4	174	<b>&lt; 0.001 ***</b>

**Table 4.3** Outputs of CCA (Canonical Correspondence Analysis) used to assess the impacts of within-stream physical structure (represented by “StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”) and the presence of riparian buffer strips (Riparian) on the community composition of semi-aquatic bugs. *P*-values were obtained from 999 random permutation tests. *P*-values that are less than 0.05 are given in bold and indicate the significant impact of a particular predictor on the community composition of semi-aquatic bugs. Data included adult bugs only. N = 29 of 10m stream transects (one transect was removed from the analysis because of zero abundance of adults [Binuang transect “0-10m”]).

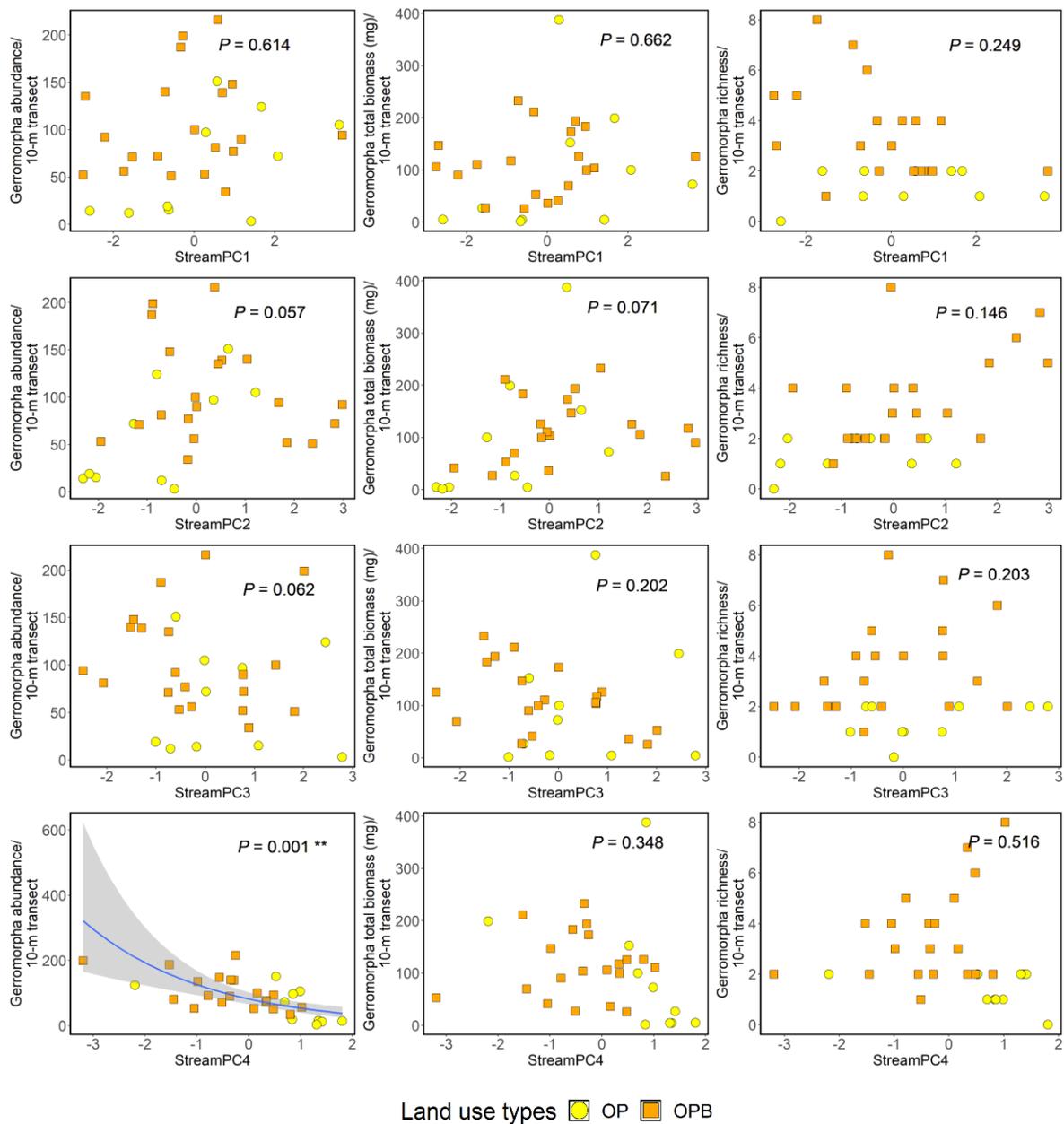
Predictor	$\chi^2$	F	<i>p</i> -value
StreamPC1	0.178	3.381	<b>0.002 **</b>
StreamPC2	0.088	1.681	0.095
StreamPC3	0.046	0.870	0.492
StreamPC4	0.045	0.860	0.472
Riparian	0.181	3.431	<b>0.004 **</b>



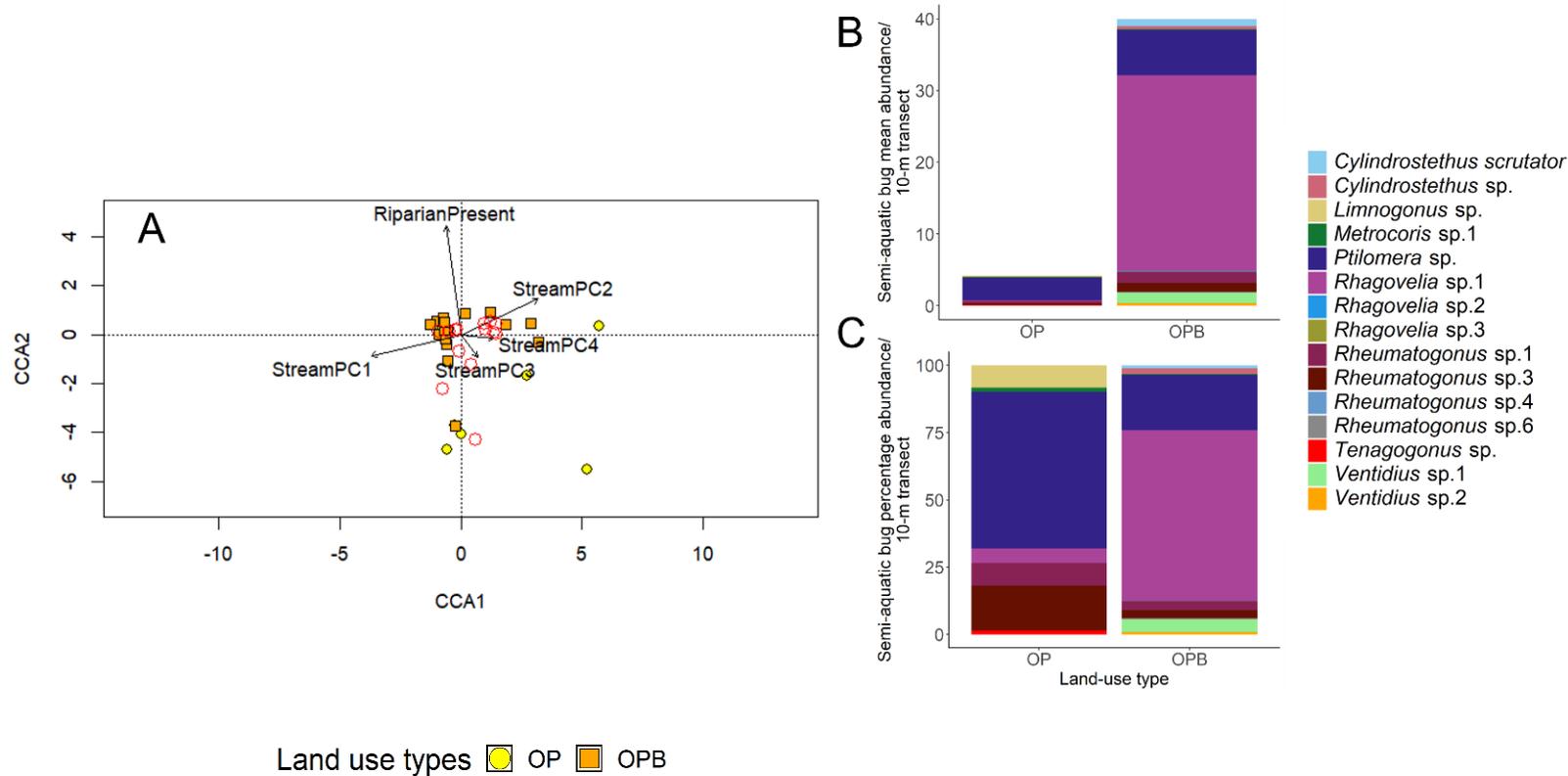
**Figure 4.1** Map of streams in oil palm with and without riparian buffer strips in the SAFE (Stability of Altered Forest Ecosystems) Project sites in Sabah, Malaysian Borneo. The SAFE Project sites consist of streams within forest areas, an experimental area (“SAFE experimental area”) nearby Kalabakan Forest Reserve, as well as oil palm streams with and without riparian buffer strips. See Luke, et al., 2017 for more details.



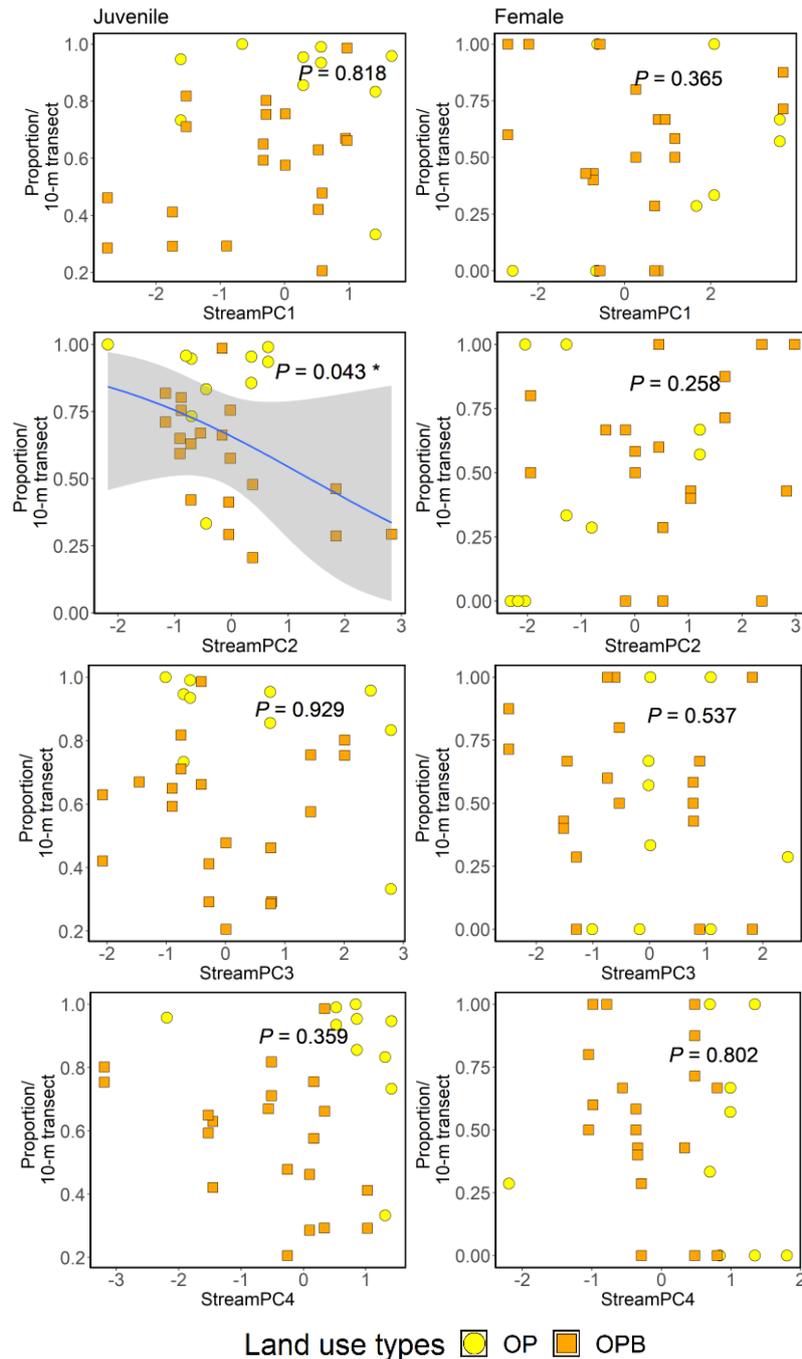
**Figure 4.2** PCA (Principal Component Analysis) biplots showing PC1 and PC2 (“Dim1” and “Dim2” respectively, left panel) as well PC3 and PC4 (“Dim3” and “Dim4” respectively, right panel) site scores of streams in oil palm with (OPB) and without buffer strips (OP). Arrows represent environmental variables (representing within-stream physical structure), while square and circle points represent streams in oil palm with and without riparian buffer strips, respectively. Differing colours represent stream sites. Axes 1 and 2 explained 24.5% and 18% of the variation in environmental variables measured in all stream sites, while axes 3 and 4 explained 15.3% and 11.7% respectively. Each smaller point represents a 10-m transect from each stream site, while larger points represent the average value for each stream site. N = 30 of 10-m stream transects.



**Figure 4.3** Impacts of within-stream physical structure (“StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”) on the abundance (left-hand side panel), total biomass (middle panel), and richness (right-hand side panel) of semi-aquatic bugs. For analyses on abundance and total biomass (sum of biomass of all semi-aquatic bugs in each 10m transect), both juvenile and adult individuals were used. For richness analyses, only adult bugs were used. *P*-values were obtained from ANOVA tests in the framework of log-likelihood ratio tests used to assess the importance of each predictor. Regression lines shown for significant associations fitted from “glm” with negative binomial family. Shaded areas show 95% confidence intervals. OP = Oil palm without buffer strips, OPB = Oil palm with buffer strips. Each point represents a 10-m transect from each stream site. N = 30 stream transects.



**Figure 4.4** Community composition of semi-aquatic bugs in stream sites in oil palm with (OPB, orange points) and without buffer strips (OP, yellow points) in relation to environmental conditions (representing within-stream physical structure) measured at stream scales, visualised by a Canonical Correspondence Analysis (CCA) tri-plot (**Panel A**). The presence of riparian buffer strips is also shown. Environmental parameters are indicated as arrows. Community composition is shown by adult bug morphospecies, indicated by circles with no colour but red borders. The position of a morphospecies represents the probability of finding that species in a stream. Mean and percentage abundance of each morphospecies in both stream types (OPB, OP) are also shown (**Panel B and C**, respectively). N = 30 stream transects (but for the CCA, one transect was removed from the analysis because of zero abundance of adults [Binuang transect “0-10m”]).



**Figure 4.5** Impacts of stream physical structure (represented by “StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”) and the presence or absence of riparian buffer strips (Riparian) on the proportion of juveniles (left-hand side panel) and female *Ptilomera* sp. (right-hand side panel). *P*-values were obtained from ANOVA tests in the framework of log-likelihood ratio tests used to assess the importance of each predictor. Regression lines shown for significant associations fitted from “glm” with binomial family. Shaded areas show 95% confidence intervals. OP = Oil palm no buffer, OPB = Oil palm with buffer strips. Each point represents 10-m transect from each stream site. N = 30 stream transects.

## Supplementary materials

**Table S4.1** Average values of several physical characteristics of the streams in this study. Streams consisted of two oil palm streams without riparian buffer strips (OP) and three with riparian buffer strips (OPB), all located within Sabah, Malaysia. RapidEye™ satellite images were taken to obtain catchment sizes. Slopes as well as channel and wetted widths were measured at 10-m transects in each stream site. N = 30 stream transects.

Stream	Land-use type	Catchment size (km-square)	Average slope (degrees)	Average channel width (m)	Average wetted width (m)
Binuang	OP	2.049	1.9	5.977	3.262
Selangan Batu	OP	2.269	3.35	7.603	5.135
Gaharu	OPB	4.943	1.35	11.072	5.796
Keruing	OPB	5.744	1.7	11.866	6.189
Merbau	OPB	4.109	2.05	8.685	5.795

**Table S4.2** Details of transects and dates of semi-aquatic bug collections in oil palm streams with (OP) and without (OPB) riparian buffer strips.

Stream	Land-use type	Transect details	Collection dates
Binuang	OP	0-10m, 40-50m, 80-90m, 120-130m, 160-170m	June – August 2012
Selangan Batu	OP	0-10m, 20-30m, 80-90m, 120-130m, 160-170m	June – August 2012
Gaharu	OPB	0-10m, 20-30m, 40-50m, 60-70m, 80-90m, 100-110m, 120-130m, 140-150m, 160-170m, 180-190m	July – September 2011
Keruing	OPB	0-10m, 40-50m, 80-90m, 120-130m, 160-170m	June – August 2012
Merbau	OPB	0-10m, 40-50m, 80-90m, 120-130m, 160-170m	June – August 2012

**Table S4.3** Outputs of biserial correlation tests used to assess the correlation between the presence of riparian buffer strips (Riparian) and stream environmental conditions (StreamPC1, StreamPC2, StreamPC3, StreamPC4) measured in oil palm streams in this study.

<b>What's tested</b>	<b>Outputs of biserial correlation test (r)</b>
Riparian & StreamPC1	0.180
Riparian & StreamPC2	-0.386
Riparian & StreamPC3	0.253
Riparian & StreamPC4	0.480

**Table S4.4.** Summaries of richness, abundance, and total biomass (sum of biomass of all semi-aquatic bugs in each 10m transect) of semi-aquatic bugs found across 10m transects in oil palm streams in this study (OPB = Oil palm with riparian buffer strips, OP = oil palm without), and breakdown for the number of juveniles, adults, female (“PtilomeraFemale”) and male (“PtilomeraMale”) of *Ptilomera* sp..<sup>a</sup>

Stream type	StreamID	Distance	Juveniles	Adults	Abundance	Total biomass (mg)	Richness <sup>b</sup>	PtilomeraMale	PtilomeraFemale	<i>Ptilomera</i> sp.
OP	Binuang	0-10m	14	0	14	4.811	0	0	0	0
OP	Binuang	120-130m	11	4	15	4.397	2	0	0	0
OP	Binuang	160-170m	18	1	19	1.325	1	0	0	0
OP	Binuang	40-50m	10	2	12	26.684	2	0	1	1
OP	Binuang	80-90m	1	2	3	4.33	2	0	0	0
	Selangang									
OP	Batu	0-10m	69	3	72	99.902	1	2	1	3
	Selangang									
OP	Batu	120-130m	104	1	105	72.469	1	0	1	1
	Selangang									
OP	Batu	160-170m	116	8	124	198.998	2	3	4	7
	Selangang									
OP	Batu	20-30m	144	7	151	152.394	2	2	4	6
	Selangang									
OP	Batu	80-90m	83	14	97	387.771	1	10	4	14
OPB	Gaharu	0-10m	43	47	90	103.624	4	3	3	6
OPB	Gaharu	100-110m	7	27	34	125.824	2	5	7	12
OPB	Gaharu	120-130m	40	13	53	41.402	4	1	0	1
OPB	Gaharu	140-150m	80	59	139	193.6	2	2	4	6
OPB	Gaharu	160-170m	59	81	140	232.597	3	10	10	20
OPB	Gaharu	180-190m	136	80	216	172.8	4	1	4	5
OPB	Gaharu	20-30m	65	35	100	36.143	3	3	0	3
OPB	Gaharu	40-50m	48	33	81	69.684	2	5	2	7
OPB	Gaharu	60-70m	150	37	187	211.077	4	4	3	7
OPB	Gaharu	80-90m	150	49	199	52.767	2	9	6	15

Stream type	StreamID	Distance	Juveniles	Adults	Abundance	Total biomass (mg)	Richness <sup>b</sup>	PtilomeraMale	PtilomeraFemale	<i>Ptilomera</i> sp.
OPB	Keruing	0-10m	27	65	92	89.998	5	0	5	5
OPB	Keruing	120-130m	21	30	51	25.511	6	0	1	1
OPB	Keruing	160-170m	21	51	72	117.274	7	0	3	3
OPB	Keruing	40-50m	16	40	56	110.694	8	4	0	4
OPB	Keruing	80-90m	24	28	52	105.902	5	4	3	7
OPB	Merbau	0-10m	63	31	94	125.533	2	1	7	8
OPB	Merbau	120-130m	96	39	135	147.015	3	2	5	7
OPB	Merbau	160-170m	121	27	148	183.237	2	2	3	5
OPB	Merbau	40-50m	70	1	71	27.101	1	0	1	1
OPB	Merbau	80-90m	51	26	77	99.469	2	1	2	3

<sup>a</sup> Richness used adult bugs only. Abundance includes the total number of all juvenile and adult bugs. The breakdown for juveniles and adults as well as female and male *Ptilomera* sp. (a semi-aquatic bug species in this study that was separated based on sex for further analysis) across streams is also shown. Biomass data were obtained from body length-biomass equations, in which biomass of each individual bug was derived from its body length (Harianja *et al.*, 2023a [Chapter 2]).

<sup>b</sup> See **Table S4.5** below for the details of all the 15 morphospecies found across oil palm streams.

**Table S4.5** The morphospecies and corresponding abundance of semi-aquatic bugs found across 10m transects (“Distance”) in oil palm streams (OPB = Oil palm with riparian buffer strips, OP = oil palm without) in this study (N = 30 of 10m stream transects).<sup>a</sup>

Types of oil palm streams	Stream	Distance	Family (G, V) <sup>b</sup>														
			G	G	G	G	G	V	V	V	G	G	G	G	G	G	
			<i>Cylindrostethus scrutator</i>	<i>Cylindrostethus</i> sp.	<i>Linnogonus</i> sp.	<i>Metrocoris</i> sp.1	<i>Ptilomera</i> sp.	<i>Rhagovelia</i> sp.1	<i>Rhagovelia</i> sp.2	<i>Rhagovelia</i> sp.3	<i>Rheumatogonus</i> sp.1	<i>Rheumatogonus</i> sp.3	<i>Rheumatogonus</i> sp.4	<i>Rheumatogonus</i> sp.6	<i>Tenagogonus</i> sp.	<i>Ventidius</i> sp.1	<i>Ventidius</i> sp.2
OP	Binuang	0-10m	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OP	Binuang	120-130m	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0
OP	Binuang	160-170m	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
OP	Binuang	40-50m	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
OP	Binuang	80-90m	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
OP	Selangan Batu	0-10m	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
OP	Selangan Batu	120-130m	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
OP	Selangan Batu	160-170m	0	0	0	0	7	0	0	0	0	0	0	0	1	0	0
OP	Selangan Batu	20-30m	0	0	0	1	6	0	0	0	0	0	0	0	0	0	0
OP	Selangan Batu	80-90m	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0
OPB	Gaharu	0-10m	0	0	0	0	6	39	1	0	0	0	0	0	1	0	0
OPB	Gaharu	100-110m	0	0	0	0	12	15	0	0	0	0	0	0	0	0	0
OPB	Gaharu	120-130m	0	0	0	0	1	8	0	0	0	0	0	0	0	3	1
OPB	Gaharu	140-150m	0	0	0	0	6	53	0	0	0	0	0	0	0	0	0
OPB	Gaharu	160-170m	0	0	0	0	20	57	0	0	0	0	0	0	0	0	4
OPB	Gaharu	180-190m	0	0	0	1	5	73	0	0	0	0	0	0	0	1	0
OPB	Gaharu	20-30m	0	0	0	0	3	16	0	0	0	0	0	0	0	16	0

			Family (G, V) <sup>b</sup>														
			G	G	G	G	G	V	V	V	G	G	G	G	G	G	G
Types of oil palm streams	Stream	Distance	<i>Cylindrostethus scrutator</i>	<i>Cylindrostethus</i> sp.	<i>Linnogonus</i> sp.	<i>Metrocoris</i> sp.1	<i>Ptilomera</i> sp.	<i>Rhagovelia</i> sp.1	<i>Rhagovelia</i> sp.2	<i>Rhagovelia</i> sp.3	<i>Rheumatogonus</i> sp.1	<i>Rheumatogonus</i> sp.3	<i>Rheumatogonus</i> sp.4	<i>Rheumatogonus</i> sp.6	<i>Tenagonus</i> sp.	<i>Ventilius</i> sp.1	<i>Ventilius</i> sp.2
OPB	Gaharu	40-50m	0	0	0	0	7	26	0	0	0	0	0	0	0	0	0
OPB	Gaharu	60-70m	0	0	0	0	7	20	0	0	0	0	0	0	0	8	2
OPB	Gaharu	80-90m	0	0	0	0	15	34	0	0	0	0	0	0	0	0	0
OPB	Keruing	0-10m	8	0	0	0	5	25	0	0	17	10	0	0	0	0	0
OPB	Keruing	120-130m	0	3	0	0	1	19	0	0	2	4	1	0	0	0	0
OPB	Keruing	160-170m	1	3	0	0	3	40	0	1	1	2	0	0	0	0	0
OPB	Keruing	40-50m	5	3	0	1	4	18	0	0	4	4	0	0	0	1	0
OPB	Keruing	80-90m	5	0	0	0	7	5	0	0	7	4	0	0	0	0	0
OPB	Merbau	0-10m	0	0	0	0	8	23	0	0	0	0	0	0	0	0	0
OPB	Merbau	120-130m	0	0	0	0	7	31	0	0	0	0	0	1	0	0	0
OPB	Merbau	160-170m	0	0	0	0	5	22	0	0	0	0	0	0	0	0	0
OPB	Merbau	40-50m	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
OPB	Merbau	80-90m	0	0	0	0	3	23	0	0	0	0	0	0	0	0	0
Total																	841

<sup>a</sup> Overall, there were 15 morphospecies with total abundance of 841. All were in the Gerridae and Veliidae families. Morphospecies were identified using adult individuals only.

<sup>b</sup> G = Gerridae, V = Veliidae.

**Table S4.6** Outputs of log-likelihood ratio tests ( $\chi^2$  and  $p$ -values) using the GLMM (Generalised Linear Mixed-Effect Models) run to assess the impacts of within-stream physical structure (represented by “StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”) and the presence or absence of riparian buffer strips (“Riparian”) on the abundance, biomass, and richness of semi-aquatic bugs.  $P$ -values that are less than 0.05 are given in bold and indicate significant impacts. N = 30 of 10m stream transects.

<b>Full model including all explanatory variables: Abundance/ Total Biomass/ Richness ~ StreamPC1 + StreamPC2 + StreamPC3 + StreamPC4 + Riparian + (1   StreamID)</b>			
<b>Response variable</b>	<b>Explanatory variables</b>	<b>Outputs of log-likelihood ratio tests</b>	
		<b><math>\chi^2</math></b>	<b><math>p</math>-value</b>
Abundance	StreamPC1	0.254	0.614
	StreamPC2	3.594	0.057
	StreamPC3	3.480	0.062
	StreamPC4	10.269	<b>0.001 **</b>
	Riparian	0.338	0.560
Total Biomass	StreamPC1	0.190	0.662
	StreamPC2	3.252	0.071
	StreamPC3	1.626	0.202
	StreamPC4	0.879	0.348
	Riparian	0.776	0.378
Richness	StreamPC1	1.328	0.249
	StreamPC2	2.107	0.146
	StreamPC3	1.619	0.203
	StreamPC4	0.420	0.516
	Riparian	6.060	<b>0.013 *</b>

**Table S4.7** Outputs of log-likelihood ratio tests ( $\chi^2$  and  $p$ -values) using the GLMM (Generalised Linear Mixed-Effect Models) run to assess the impacts of stream physical structure (represented by “StreamPC1”, “StreamPC2”, “StreamPC3”, and “StreamPC4”) and the presence of riparian buffer strips (“Riparian”) on the proportion of juveniles and female *Ptilomera* sp..  $P$ -values that are less than 0.05 are given in bold and indicate significant impacts. N = 30 of 10m stream transects.

<b>Full model including all explanatory variables: Proportion of juveniles/ Proportion of female <i>Ptilomera</i> sp. ~ StreamPC1 + StreamPC2 + StreamPC3 + StreamPC4 + Riparian + (1   StreamID)</b>			
<b>Response variable</b>	<b>Explanatory variables</b>	<b>Outputs of log-likelihood ratio tests</b>	
		<b><math>\chi^2</math></b>	<b><math>p</math>-value</b>
Proportion of juveniles	StreamPC1	0.052	0.818
	StreamPC2	4.060	<b>0.043 *</b>
	StreamPC3	0.007	0.929
	StreamPC4	0.838	0.359
	Riparian	3.546	0.059
Proportion of female <i>Ptilomera</i> sp.	StreamPC1	0.819	0.365
	StreamPC2	1.279	0.258
	StreamPC3	0.381	0.537
	StreamPC4	0.062	0.802
	Riparian	0.019	0.889

## **Chapter 5: How do management decisions impact butterfly assemblages in smallholding oil palm plantations in Peninsular Malaysia?**

**Martina F. Harianja<sup>1</sup>, Jake Stone<sup>1</sup>, Sarah H. Luke<sup>2,1</sup>, Badrul Azhar<sup>3</sup>, Wan Z.W. Mamat<sup>3</sup>, Muhammad A. Hadi<sup>3</sup>, Edgar C. Turner<sup>1</sup>**

<sup>1</sup>Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

<sup>2</sup>School of Biosciences, University of Nottingham, Sutton Bonington Campus, Nr Loughborough, LE12 5RD

<sup>3</sup>Department of Forest Management, Faculty of Forestry, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

**Key words:** butterfly assemblages, floral complexity, habitat structure, monoculture, oil palm plantations, polyculture, smallholding, tropical agriculture, understory vegetation management.

Under review by *Journal of Applied Ecology*.

## **Abstract**

1. Conversion of tropical forests to oil palm plantations has driven a reduction in populations or loss of species. Although there are a growing number of studies investigating management decisions to enhance biodiversity and ecosystem functions within oil palm, studies investigating the impacts of alternative management strategies in smallholder plantations are lacking. In the world's leading palm oil producing countries (Indonesia and Malaysia), smallholders make up about 40 percent of total oil palm plantation area. Management in smallholdings can be highly variable, ranging from intensive monoculture to polyculture systems, consisting of a variety of crop types. Currently, many plantations in the region are mature and due to be replanted, making an investigation of the effects of alternative management decisions at this point particularly timely. Butterflies are a functionally important group that pollinate wild plants, are prey for larger species, and are common in tropical systems. Butterfly species also show a range of sensitivities to habitat disturbance, with some being vulnerable to change, but others being common in plantations.

2. We investigated the impacts of replanting and choice of crop management following replanting (growing oil palm as a monoculture or polyculture) on habitat structure and complexity, and on the abundance, richness, and composition of butterfly assemblages in smallholding oil palm plantations in Banting, Selangor, Malaysia. We also assessed the direct effects of habitat structure and complexity on butterfly assemblages.

3. Across 27 plantations, we recorded 1227 butterflies from 5 families, 46 genera, and 56 species. Habitat structure and complexity differed between management decisions (mature monoculture, immature monoculture, immature polyculture), although many environmental parameters overlapped. We found no significant differences in species

richness, density, and assemblage composition of butterflies between management decisions. However, increase in the coverage of understory vegetation, including hostplants and nectar sources, increased the abundance of butterflies.

4. *Synthesis and applications*: Our findings suggest that replanting oil palm and choice of mono or polyculture have relatively few effects on butterflies, but management for specific features in plantations could benefit butterfly assemblages.

## **Introduction**

About 11% of the global land surface is used for crop production, and agricultural practices have driven the loss or reduction of biodiversity (Raven & Wagner, 2021). Agricultural intensification has resulted in the destruction of habitats for wildlife through habitat simplification in converted systems, fragmentation of remaining natural habitats, as well as negative impacts through inputs of pollutants, such as fertilizers, herbicides, and pesticides (Raven & Wagner, 2021). As a result, a wide range of terrestrial and aquatic taxa across biomes have experienced reductions in diversity, abundance, and biomass (Bar-On et al., 2018; Davison et al., 2021). Within established agricultural areas, farmlands that apply conservation management strategies can have a higher level of biodiversity than those that do not (Estrada-Carmona et al., 2022). These practices may also maintain ecosystem services that support yield. For example, plantations with higher landscape complexity can have higher species diversity, level of fruit set (Mediterranean cereal fields, Dainese et al., 2017), fruit production (Mexican coffee plantations, Vergara & Badano, 2009), and pest control (annual crop fields in South Korea, Martin et al., 2013).

A good case study for this is oil palm, which had a global cultivated area of 19.5 million hectares in 2019 (Meijaard et al., 2020), the expansion of which has resulted in widespread forest loss (Gaveau et al., 2016). However, previous studies have found that management for biodiversity in oil palm can maintain ecosystem services such as decomposition (Ashton-Butt et al., 2019), hence potentially benefitting production. Oil palm is generally replanted after 25 years, when yields begin to drop, and harvesting becomes less efficient. This long lifespan can result in the development of relatively

stable environmental conditions and resources for wildlife, potentially increasing biodiversity and abundance across taxa over time (Snaddon et al., 2013). However, removal of mature oil palm during replanting changes the structure and environmental conditions (Snaddon et al., 2013). Few studies have assessed the impacts of replanting on taxa and ecosystem functions, but these have identified a decrease in species richness and abundance of frogs (Kurz et al., 2016), and an altered assemblage composition of soil macrofauna (Ashton-Butt et al., 2019) and spiders (Pashkevich et al., 2021) following or a few years after replanting. However, other ecosystem functions, such as dung removal, soil mesofauna feeding activity (Ashton-Butt et al., 2019) and herbivory (Woodham et al., 2019), remained unaffected.

The impacts of implementing alternative management at the time of replanting are understudied, limiting the available evidence to inform more environmentally sustainable replanting practices. Research in this scope could provide a more complete understanding of the implications of management decisions, as well as informing biodiversity conservation strategies in oil palm and inform sustainability certification schemes, such as Roundtable on Sustainable Palm Oil (RSPO) (RSPO, 2018).

In Indonesia and Malaysia, the world's major palm oil producers, smallholders make up about 40 percent of the total oil palm plantation area (Wild Asia, 2012). Unlike industrial plantations, smallholders often plant other crops alongside oil palm (polyculture). Since polyculture plantations are more diverse in crop species, this could support more wildlife through provision of a more complex environment, including a wider range of food sources, nesting sites, and refuges. Alternatively, it could be that polycultures result in a larger area of understory being devoted to crops, more intensive management, and lower levels of non-crop vegetation. As other studies have found that

plantations with higher levels of understory vegetation support higher biodiversity (Ashton-Butt et al., 2019; Hood et al., 2020; Nájera & Simonetti, 2010), this could mean lower biodiversity in polyculture plantations. The few studies that have investigated the effects of mono versus polyculture oil palm on biodiversity have found varying results (e.g., Asmah et al., 2017; Syafiq et al., 2016; Yahya et al., 2017). In particular, species richness of fruit-feeding butterflies did not differ between oil palm monoculture and polyculture (Asmah et al., 2017), while species richness of birds and frugivorous bats was higher in polyculture (Syafiq et al., 2016; Yahya et al., 2017).

Within oil palm, invertebrates support a wide range of ecosystem services (e.g., nutrient cycling, biological control, and pollination, see Dislich et al. (2017). Butterflies are among the invertebrate groups that pollinate flowering weeds (which can be used to feed cattle in integrated oil palm farming [Nobilly et al., 2021]), as well as being prey items for many predators. Owing to their sensitivity to environmental conditions, they are often used as bioindicators of environmental change (Koh, 2007; Kleiman et al., 2021). In Southeast Asia, butterfly diversity has declined considerably due to land-use change (Koh, 2007). To reduce further declines, altered habitats such as agricultural landscapes should be managed in ways that maintain higher abundance and diversity of butterflies. Previous studies have shown that crop management can be tailored to increase butterfly abundance in oil palm, (Asmah et al., 2017, Reiss-Woolever, 2023a), but no study has yet studied the impacts of alternative replanting strategies on butterfly populations.

Using an existing patchwork of first- and second-generation oil palm smallholdings in Peninsular Malaysia, we assessed the effects of replanting and alternative replanting decisions (replanting with monoculture versus polyculture oil

palm plantations) on the local environment and butterfly assemblages. We asked: 1) How does mature oil palm monoculture (the previous dominant land-use in the area) differ from plots replanted with monoculture versus polyculture immature oil palm, in terms of habitat structure and complexity, as well as butterfly abundance, richness, and composition? 2) What is the impact of habitat structure and complexity across management decisions on the density, species richness, and assemblage composition of butterflies?

## **Materials and methods**

### **Study sites**

Data were collected between 21 June 2022 and 28 July 2022 from 27 smallholder oil palm plantations in Banting, Selangor, Malaysia (2.788267°N, 101.546651°E). The climate category in the region is Af (tropical wet climate), characterised by a high level of precipitation throughout the year. The average annual air temperature and rainfall in the area were 27.6°C (Vijayanathan et al., 2021) and 1822.60 mm (Yusof et al., 2021). The 27 plantations consisted of nine each of: mature oil palm monoculture (MM01-09), immature monoculture (IM01-09) and immature polyculture (IP01-09) (**Figure S5.1**). None of the mature plantations were first generation oil palm. Other crops cultivated in the immature polyculture plantations ranged from bamboo, banana, cassava, coconut, galangal, yam, jackfruit, pineapple, and torch ginger. The size of plantations in this study ranged from 0.208 to 1.290 acres (converted to acres from step counts in the field – assessed by walking the perimeter of each plantation). Plots were evenly spread and

interspersed across an area of approximately 4.5 by 3.5 km (**Figure S5.1**). Details of each plantation, comprising information about plantation size, oil palm age, and crops cultivated is available in **Table S5.1**. The plantations used in this study form part of the Ecological and Social studies in Smallholder Tropical Agriculture (ESSTA) Project. The ESSTA Project aims to explore social, ecological, and interdisciplinary dynamics, by investigating how management decisions impact biodiversity, ecosystem functions and crop yield within oil palm smallholdings.

## **Data collection**

### *Habitat structure and complexity*

As all plantations were small and surrounded by plantations or areas under different management practices, focal plantations were likely to be influenced by surrounding habitats. To account for this, we collected environmental data both within plantations, as well as from the surrounding area. Neighbouring habitat type characteristics were measured at each of the four sides of each plantation and were recorded as a percentage of surrounding area through perimeter walks. Categories included: oil palm monoculture, oil palm polyculture (any combination of crops), housing, road, empty or unused land, grassland or low natural vegetation including ferns, and cassava monoculture plantations (**Figure S5.2, Table S5.2**).

When doing the perimeter walks, we counted the number of palms on each side of the plantation, multiplying this to calculate the total number of palms. We also recorded the density of butterfly nectar sources (plants with open flowers as nectar

sources, identified using Barnes & Chan [1990]; Fee et al. [2017], Mohamed & Idris [2012], Nobilly et al. [2021], and Ya'acob et al. [2022]), following the methods of Steffan-Dewenter & Tschardtke (1997): using a scale of 0 to 5, with 0 = absent or no flower, 1= $\leq 0.5$  flowers per  $m^2$ , 2= $\leq 1$  flowers per  $m^2$ , 3= $\leq 5$  flowers per  $m^2$ , 4= $\leq 10$  flowers per  $m^2$ , 5= $> 10$  flowers per  $m^2$ . This assessment was carried out separately for each individual plant species observed and the average calculated for all flowering wild plants across the four perimeters and central path (see below for details (**Table S5.3**)). We estimated the age of oil palms (in years) at each site through interviews with the owners of the plantations.

Environmental data within plantations were collected along a central path (**Figure S5.2**), where we recorded crop types present and their total coverage, as well as the density of nectar sources, as above. We also assessed environmental parameters at four 5x5m sample squares (hereafter, “sample squares”) along the central path (**Figure S5.3**). The squares were created using two tape measures laid out in a cross shape with the top of the cross pointing north. Each contained a central sample point (hereafter, “main sample point”) and three sub-sample points, each equidistant from the centre (**Figure S5.4**).

Environmental parameters measured within “sample squares” were percentage vegetation cover (crop, bare ground, fern, other vegetation, oil palm (either a tree or a sapling), leaf litter, cut fronds, and other [any type of materials other than the previous categories]), canopy openness, height of the nearest oil palm tree to main sampling point, and epiphyte cover on the same palm. Canopy openness was measured using a spherical densiometer (Lemmon, 1956), by standing at the “main sample point” and taking a reading facing north, south, east, and west. Average canopy openness was then

calculated and multiplied by 1.04 to give percentage openness. The height of the nearest oil palm tree from the “main sample point” was measured relative to the person recording environmental parameters (how many times the palm was the height of the person, and this was multiplied by the person’s height). Epiphyte cover was estimated by eye and recorded as overall percentage cover of trunk. At each of the three sub-sample points, we measured vegetation height in centimetres, using a measuring stick and then calculated the average for each square.

### *Butterfly surveys*

Butterfly surveys were conducted on two days in all plantations between 9a.m. and 5p.m. and when it did not rain. We stratified timings of visit to each plantation type by morning, noon, and afternoon, and then selected specific plantations at random, to ensure that visit time as well as weather did not vary systematically between plantation types. During the survey, we systematically walked along the transect and recorded any butterflies with an imagined 5mx5m box in front of the recorder, covering the entire plantation area.

Each survey lasted for up to two hours. In five cases, owing to lack of time (two immature monocultures (IM01, IM03), one immature polyculture (IP05), and two mature monocultures (MM05, MM06), plantations were not sampled completely. When we saw a butterfly, we recorded its scientific name. If it could not be identified, we caught the butterfly and put it in a clear small Ziplock plastic bag, before taking photos of the upper- and underside of its wings. We identified butterflies in the field or from these photos, using guides by Kirton (2020, third edition) and Corbet and Pendlebury (2020, fifth edition). We classified the butterfly based on abundance group (common,

less common, and rare) in Peninsular Malaysia, using descriptions by Corbet and Pendlebury (2020).

### **Statistical analysis**

All analyses and visualisations were carried out with R version 4.0.4 (R Core Team, 2021) and R Studio version 2022.07.1+554 (R Studio Team, 2022). To conduct analyses, we used basic R syntax and package “dplyr” (Wickham et al., 2021). We used “performance” (Lüdecke et al., 2021) to check overdispersion. Package “see” (Lüdecke et al., (2021) and “Rcpp” (Eddelbuettel, 2013; Eddelbuettel & Balamuta, 2018; Eddelbuettel & Francois, 2011) to visualise model assumptions. For all other visualisations, we used “tidyverse” (Wickham et al., 2019), “cowplot” (Wilke, 2020), and “gridExtra” (Auguie, 2017). For specific analyses and visualisations, we used several packages with more details below.

#### *Habitat structure and complexity across plantations*

We ran a PCA to summarise and reduce the dimensionality of environmental parameters (Jolliffe, 1986), including data collected from plantation perimeters and within plantations. The parameters were: plantation size (in acres), oil palm age (in years), percentage coverage of crops other than oil palm (bamboo, banana, cassava, coconut, galangal, yam, jackfruit, pineapple, and torch ginger), percentage coverage of neighbouring habitats (monoculture oil palm, polyculture oil palm, housing, road, empty or unused land, grassland, and monoculture cassava plantation), average density of

nectar sources for butterflies (average of sums of density scales for all nectar source species from each plantation), average canopy openness, average percentage ground cover (bare ground, oil palm tree or sapling, other crop, cut frond, fern, other vegetation, and other), average understory vegetation height (from all sub-sample points), average oil palm height (average of all heights of the nearest oil palm trees to the four main sampling points within a plantation), and average epiphyte cover. Percentage leaf litter cover was removed from the analysis, because its values were directly implied by the other ground cover components. We used built-in codes in R to run PCA, and to create PCA biplots, we used “factoextra” (Kassambara & Mundt, 2020). We ran ANOVA or Kruskal-Wallis tests (depending on the distribution and equality of variance of the PC score data) to assess differences of the most influential PC scores between management types.

### *Impacts of management decisions on butterfly assemblages*

To calculate the total species richness of butterfly assemblages in each of the plantations and across all plantations in each management type, we used the Chao1 index (Gotelli & Colwell, 2011). To visualise diversity of butterflies, we created species accumulation curves, for all plots, separated by management decision type, and separated by individual plantation, allowing us to account for unequal sampling effort in later analyses, related to incomplete surveys or sub-optimal conditions at the time of sampling. In all cases, calculations and accumulation curves were created using abundance and species identity data, only including butterflies which were identified to species or morphospecies levels

(Table S5.4). To create accumulation curves and calculate the Chao1 index, we used “iNEXT” package (Chao et al., 2014; Hsieh et al., 2020).

We assessed whether alternative management decision types (mature monoculture, immature monoculture, immature polyculture) differed in density (calculated density per 500m<sup>2</sup> by calculating the density of butterflies found per surveyed area over both days) and species richness (based on Chao1 index score per plantation) of butterflies. For this, we ran separate Kruskal-Wallis tests (since the distribution of data were not normal based on Shapiro-Wilk tests), with plantation type as the explanatory variable and density and species richness as outcome variables. We ran non-metric multidimensional scaling (NMDS) and produced stacked bar charts to visualise the assemblage composition of butterflies among management decisions. Finally, we ran analysis of similarities (ANOSIM) to assess whether the composition of butterflies (only using butterflies identified to species or morphospecies level) differed between management decisions. We used “vegan” (Oksanen et al., 2020) to run non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM).

#### *Impacts of habitat structure and complexity on butterfly assemblages*

To assess the direct impacts of habitat structure and complexity associated with management decisions on butterfly assemblages, we used Generalised Linear Models (GLMs), with the most influential Principal Component (PC) scores, as a fixed factor. For all models, we multiplied PC3 with -1, so scores were always in the direction of increasing complexity. Species richness and density were used in separate models as response variables. For GLMs run on the density of butterfly assemblages, we used

negative binomial family with log link, because of overdispersion. For GLMs run on species richness, we used gaussian distribution with identity link, considering the type of response variable (decimals). For both density and species richness analyses, we used log-likelihood ratio tests to assess the significance of each predictor, in which we compared full models with all predictors to models without one of the predictors. We used “lme4” (Bates et al., 2015) to run GLMs (Generalised Linear Models) and “MASS” (Venables & Ripley, 2002) to run negative binomial models. Assumptions for all models were checked using diagnostic plots. For the models (GLMs) run on the density of butterfly assemblages, we ran sensitivity analyses by excluding sites (IM05, IP01, IP04, IP06, MM06, and MM08) that were influential to the trend in the original full model (points [oil palm sites] that fall at or beyond the Cook’s distance on Residual vs Leverage diagnostic plot).

## Results

### *Habitat structure and complexity across plantations*

The first six PC scores explained most of the variation among environmental parameters, with PC1 and PC2 explaining 17.3% and 12% of variation, PC3 and PC4 explaining 9.6% and 9.2%, and PC5 and PC6 explain 8.5% and 6.5%, respectively (so in total PC1 - PC6 explain 63.1% of variation in the variables representing environmental conditions) (**Table S5.5, Figure 5.1**). The three management decision types overlapped in terms of habitat structure and complexity, particularly for axes 2, 3, 4, 5, and 6 (**Figure 5.1**). However, environmental parameters explaining the structure and complexity of plantations differed significantly for PC1 (**Table 5.1**), with immature monoculture

sitting in between mature monoculture and immature polyculture along the first axis. Average height, age and percentage epiphyte cover of oil palms all decreased from mature monoculture to immature polyculture, while percentage of cassava, banana, and other crop types increased.

### *Impacts of management decisions on butterfly assemblages*

We recorded 1227 individual butterflies from 5 families (Nymphalidae, Papilionidae, Pieridae, Lycaenidae, and Hesperiiidae), 46 genera, and 56 species from all plantations surveyed (**Table S5.4**). The average density of butterflies per 500m<sup>2</sup> was 13 (SE ± 4.873) in mature monoculture, 10.666 (SE ± 2.881) in immature monoculture, and 18.444 (SE ± 6.646) in immature polyculture. The accumulation curves generated across plantation types seemed to reach an asymptote, indicating that sampling had recorded most of the species in our focal plantations. Using only butterflies identified to species/morphospecies levels (946 individuals), mature monoculture had an estimated species richness (based on Chao1 index) of 42 (SE ± 5.431), immature polyculture 39 (SE ± 9.138) and immature monoculture 33 (SE ± 3.231) (**Table 5.2, Figure 5.2**).

Of the 56 species/ morphospecies recorded, 50 were described as common species in Peninsular Malaysia (Corbet and Pendlebury, 2020), while four were relatively less common (*Deudorix epijarbas* [Lycaenidae], *Erionota thrax* [Hesperiiidae], *Mycalesis janardana* [Nymphalidae], and *Rapala pheretima* [Lycaenidae]), and three were relatively rare species (*Gangara thyrasis* [Hesperiiidae], *Plastingia pellationia* [Hesperiiidae], and *Taractrocera archias* [Hesperiiidae]) (**Table S5.4**). We found no endemic butterflies in this study. Across all plantations, *Amathusia*

*phidippus* (Nymphalidae), *Appias libythea* (Pieridae), *Elymnias hypermnestra* (Nymphalidae), *Leptosia nina* (Pieridae), *Potanthus omaha* (Hesperiidae), *Ypthima baldus* (Nymphalidae), and *Ypthima huebneri* (Nymphalidae) were the most abundant ( $\geq 30$  individuals), with *Elymnias hypermnestra* being found in the highest density (208 individuals across all plantations).

Although the species richness of butterflies varied substantially between individual plantations (**Table S5.6, Fig. S5.5**), there were no significant differences in the density, estimated species richness (**Table 5.3, Fig. 5.3**), or assemblage composition of butterflies between management decisions ( $R = -0.034$ ,  $p$ -value = 0.786, **Figure 5.4**).

#### *Impacts of habitat structure and complexity on butterfly assemblages*

Habitat structure and complexity significantly impacted the density, but not the species richness of butterflies (**Table 5.4, Figure 5.5**). In particular, PC2, PC3, and PC5 were significant predictors for butterfly density. Associated with PC2, butterfly density decreased with higher percentage of bare ground, percentage of polyculture plantation as a neighbouring habitat and plantation size, but increased with percentage of coconut and torch ginger in the plots, and the height of understory vegetation. Associated with PC3, butterfly density increased with percentage of monoculture plantation and road as neighbouring habitats, levels of nectar sources, and percentage of other vegetation, but decreased with more housing and polyculture plantations as neighbouring habitat types, and cover of cut fronds. Associated with PC5, butterfly density increased with higher percentage of road but lower percentage of oil palm monoculture as neighbouring habitat types, higher levels of nectar sources and yam, as well as lower percentage of fern and average height of understory vegetation. However, the observed trends were likely

driven by a few influential outliers (i.e., IM05, IP01, IP04, IP06, MM06, and MM08). Removing the outliers, resulted in PC1, PC4, and PC6 being significant drivers for butterfly density (**Table S5.7, Figure S5.6**).

## **Discussion**

### *Habitat structure and complexity across plantations*

Habitat structure and complexity generally overlapped across management types. However, there was a clear split across habitats for PC1, with average height of oil palm stands, age of oil palm, and percentage epiphyte cover all increasing from immature polyculture to immature monoculture and mature monoculture, but average percentage of other crops, and percentage of cassava and banana decreasing. These differences are in-line with the broad habitat types and demonstrate that replanting significantly affects the local environment, with immature monoculture generally appearing more similar to mature monoculture than immature polyculture. However, the high level of overlap suggests that differences in coarse habitat structure as a result of growing immature oil palm as a monoculture or polyculture, only have marginal effects on other aspects of habitat structure and complexity. It should be noted that this may also be related to the characteristics of plantations surrounding our focal sites, which also influenced habitat characteristics. The varying environmental conditions we recorded within a single management decision type could impact biodiversity, including butterfly assemblages. As such, managing oil palm plantations based on broad categories, particularly among smallholders, may still result in differing habitat structure and complexity.

### *Impacts of management decisions on butterfly assemblages*

Across all plantations, the species richness we found was below the number of butterfly species recorded in forest, and only represented a small subset of all known species in Peninsular Malaysia: 56 in this study compared to 74 species in agroforestry orchards in Negeri Sembilan, Peninsular Malaysia (Wan Zaki et al., 2023), 138 species in forest in Pahang, Peninsular Malaysia (Suhaimi et al., 2017) and 1051 species recorded in the peninsula (Corbet and Pendlebury, 2020). The 50 out of 56 species were also common lowland species, or species found at all elevations, with larvae that feed on a range of plant species or have hostplants that were present in the study areas due to introduction or cultivation by people (**Table S5.8**, Corbet and Pendlebury, 2020). Therefore, it is clear that, although relatively diverse, the butterfly assemblage we found is dominated by wider-habitat and disturbance-tolerant species, backing up findings from previous work (Reiss-Woolever et al., 2023a, b). This again highlights the importance of conserving forest habitats for butterfly diversity, especially those that are sensitive to environmental change.

There were no significant differences in the density (per 500m<sup>2</sup>), estimated species richness or composition of butterfly assemblages across management decision types. This finding might be related to the similarities in several environmental parameters between management types, or greater importance of wider habitat characteristics in determining butterfly communities, both of which could mean that butterflies did not differ greatly between plantation types.

We found that mature monoculture had marginally higher estimated species richness of butterflies across plots. This could be because the environmental conditions

in mature plantations were more stable compared to immature plantations, providing microhabitats for more species (Luskin & Potts, 2011). Indeed, mature oil palm plantations have been recorded to have a higher richness and abundance of soil macrofauna than young plantations (Ashton-Butt et al., 2019), substantiating this hypothesis. Polyculture plantations had the second highest estimated total species richness, perhaps because several of the crops, cultivated in addition to oil palm, are hostplants or food sources for butterflies (**Table S5.8**). However, despite these trends, it must be noted that confidence intervals on our accumulation curves were overlapping, so differences between management types were marginal.

#### *Impacts of habitat structure and complexity on butterfly assemblages*

Assessment of the impacts of habitat structure and complexity on butterfly assemblages identified several environmental factors that were significantly associated with the density of butterflies within plantations, although none had significant impacts on species richness. In particular, there was a higher density of butterflies (per 500m<sup>2</sup>) in smaller plantations, with lower percentage bare ground, cut frond and fern cover, but higher percentage of other vegetation, as well as lower average height of understory vegetation, higher percentage cover of coconut, torch ginger, and yam, and higher levels of nectar sources for butterflies. In addition, neighbouring habitats were also a significant factor, with lower percentage polyculture plantation and housing, but higher percentage of road being associated with a higher densities of butterflies.

These findings are likely to be related to resource availability and habitat condition. For example, smaller plantations could have had a higher density of butterflies

because all the available resources, such as hostplants, nectar sources, and surfaces for perching, were concentrated in a smaller space. The higher density of butterflies with more understory vegetation (**Table S5.8**) and higher level of nectar sources is likely to be because this habitat is used for perching, breeding, and nectaring sites. The negative association with a higher density of fern cover could be because ferns can be competitively dominant in plantation understories, so their increased cover could reduce the diversity of other resources used by butterflies. Overall, these findings are in line with previous studies which found the importance of maintaining understory vegetation within oil palm plantations to maintain more diverse and abundant butterflies (Reiss-Woolever, 2023a, b). The higher density of butterflies we found in plantations with a higher average percentage of coconut (*Cocos nucifera*) and torch ginger (*Etilingera elatior*) could also be because both these species are hostplants of several butterfly species in this study (Corbet and Pendlebury, 2020).

Environmental conditions around a plantation are also likely to influence butterfly density, due to effects on resources and conditions. For example, the higher density of butterflies in plantations surrounded by less polyculture could be because polyculture provides favourable resources that draw butterflies out of the focal plantation. Polyculture plantations and gardens in our study contained several kinds of crops and other plants which could be used by butterflies as resources (**Table S5.8**). Finally, roads might have been a barrier to butterflies (Muñoz et al., 2015), leading to relatively higher butterfly densities in the focal plantation. Our sensitivity analyses showed some differences in terms of significant drivers for the density of butterflies. This variability suggests that results were influenced by outliers, and indicates that more larger-scale studies should be carried out to assess the influence of different aspects of

smallholder variability on within-plantation biodiversity. In general, this finding could have been driven by the wide range of management decisions made by smallholders, resulting in the differing environmental conditions recorded within plantations, and subsequently affecting the density of butterflies (**Table S5.7, Figure S5.6**).

### *Management implications*

We found remarkably few differences in both habitat structure and complexity as well as butterfly species richness, density, and composition between management decision types (mature monoculture, immature monoculture and polyculture). Similar results were also found by Asmah et al. (2017) who assessed fruit-feeding butterflies in immature oil palm mono- and polyculture and suggest that overall farmer management decisions have only limited impacts on butterflies. In contrast, we identified several environmental parameters that were associated with increases in butterfly abundance in plantations. Increasing the coverage of understory vegetation, particularly of hostplants and nectar sources for butterflies, are likely to increase the abundance of butterflies and could potentially be implemented at little cost. Within a smallholder context, these approaches could be trialled by local communities to boost the positive effects on butterflies.

## Tables and Figures

**Table 5.1** Outputs of ANOVA or Kruskal-Wallis tests used to assess the difference in habitat structure and complexity between oil palm plantations across three differing management decisions (mature monoculture, immature monoculture, and immature polyculture), consisting of nine plantations for each management decision type. Habitat structure and complexity were represented by six PC scores (PC1-6) obtained from a PCA, which explained most of the variability between management decision types. *P*-values that are less than 0.05 are given in bold and indicate significant differences.

Compared PC scores	Group comparison	F/ $\chi^2$ / diff *	<i>P</i> -value
PC1	Overall	52.02	< <b>0.001</b> ***
	immature monoculture & immature polyculture	-2.966	< <b>0.001</b> ***
	immature monoculture & mature monoculture	1.935	<b>0.001</b> **
	immature polyculture & mature monoculture	4.901	< <b>0.001</b> ***
PC2	Overall	0.680	0.711
PC3	Overall	1.925	0.168
PC4	Overall	2.395	0.301
PC5	Overall	0.176	0.840
PC6	Overall	0.888	0.425

\* F value if ANOVA,  $\chi^2$  if Kruskal-Wallis test, “diff” in the case of post-hoc analyses showing value differences between two compared groups

**Table 5.2** Outputs of Chao1 index calculations (shown as “Estimator”) used to estimate species richness across habitat types (Mature monoculture, immature monoculture, immature polyculture; only butterflies identified to species/ morphospecies levels were used). Observed species richness, standard errors of the calculations, and confidence intervals are also shown.

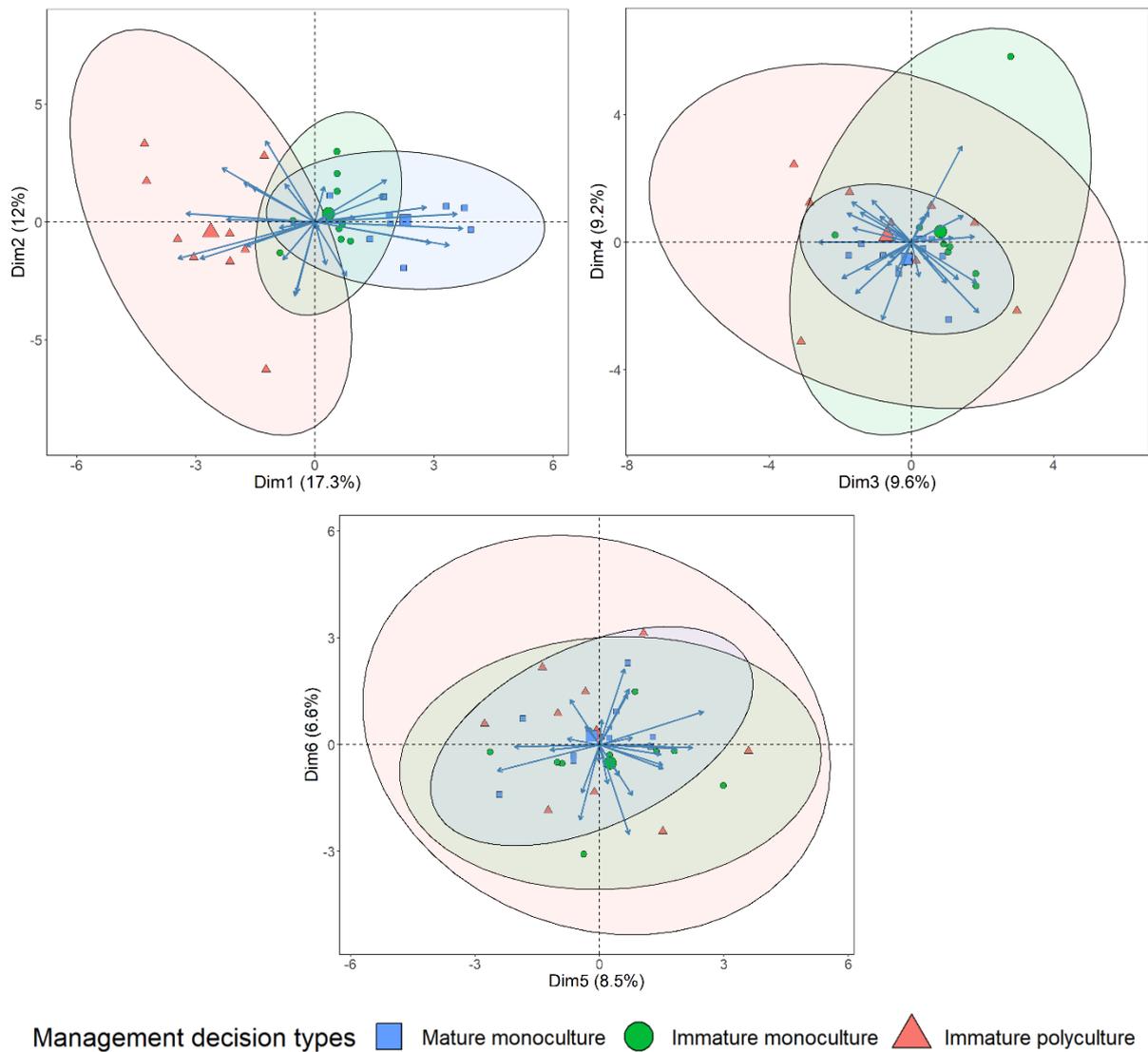
Plantation type	Observed species richness	Estimator	Estimated standard error	95% Lower confidence interval	95% Upper confidence interval
Mature monoculture	42	49.177	5.431	43.92	68.836
Immature monoculture	33	35.99	3.231	33.533	49.766
Immature polyculture	39	50.962	9.138	42.167	84.179

**Table 5.3** Outputs of Kruskal-Wallis tests run to assess differences in the density (per 500m<sup>2</sup>) and estimated species richness of butterfly assemblages between the three plantation types (MM – mature monoculture, IM – immature monoculture, IP – immature polyculture). N = 27 plantations (nine for each management decision type).

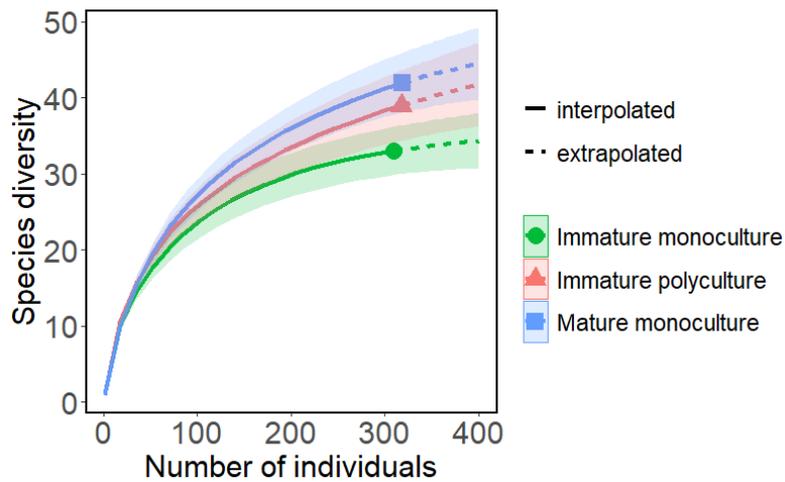
Explanatory variable	Response variable	df	$\chi^2$ value	P-value
Management decision types	Density of butterflies per 500m <sup>2</sup>	2	0.864	0.648
	Estimated species richness (Chao1)	2	0.786	0.674

**Table 5.4** Outputs of log-likelihood ratio tests ( $\chi^2$  and *p*-values) in GLMs (Generalised Linear Models) run to assess the impacts of habitat structure and complexity associated with oil palm crop management (represented by PCA axes 1-6 [PC1, PC2, PC3, PC4, PC5, and PC6]) on the density (per 500m<sup>2</sup>) and estimated species richness (represented by Chao1 index) of butterfly assemblages across the 27 plantations (nine for each mature monoculture, immature monoculture, immature polyculture). *P*-values that are less than 0.05 are given in bold and indicate significant impacts.

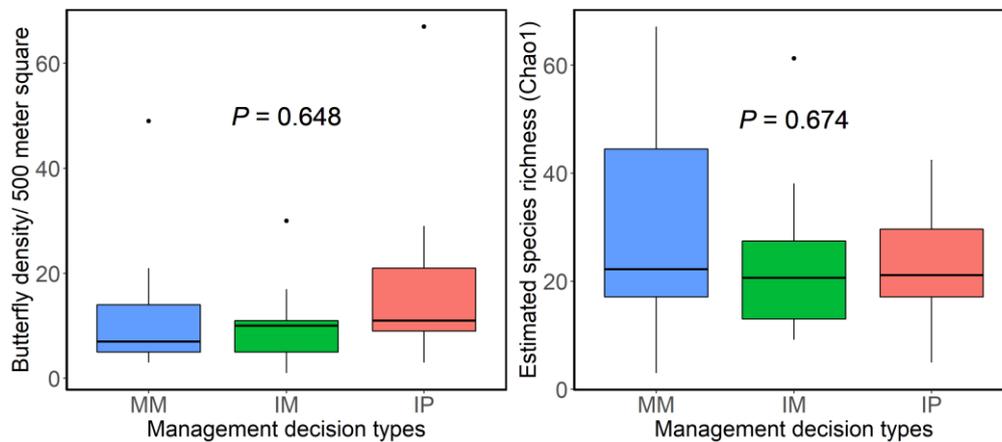
Full model including all explanatory variables: Density per 500m <sup>2</sup> / Chao1 ~ PC1 + PC2 + PC3 + PC4				
Response variable	Explanatory variables	Outputs of log-likelihood ratio tests		
		$\chi^2$	P-value	
Density of butterflies per 500m <sup>2</sup>	PC1	1.405	0.235	
	PC2	15.084	< <b>0.001</b> ***	
	PC3	11.416	< <b>0.001</b> ***	
	PC4	0.803	0.370	
	PC5	4.288	<b>0.038</b> *	
	PC6	0.239	0.624	
Estimated species richness (Chao1)	PC1	1.417	0.233	
	PC2	0.130	0.718	
	PC3	0.889	0.345	
	PC4	0.746	0.387	
	PC5	1.785	0.181	
	PC6	0.904	0.341	



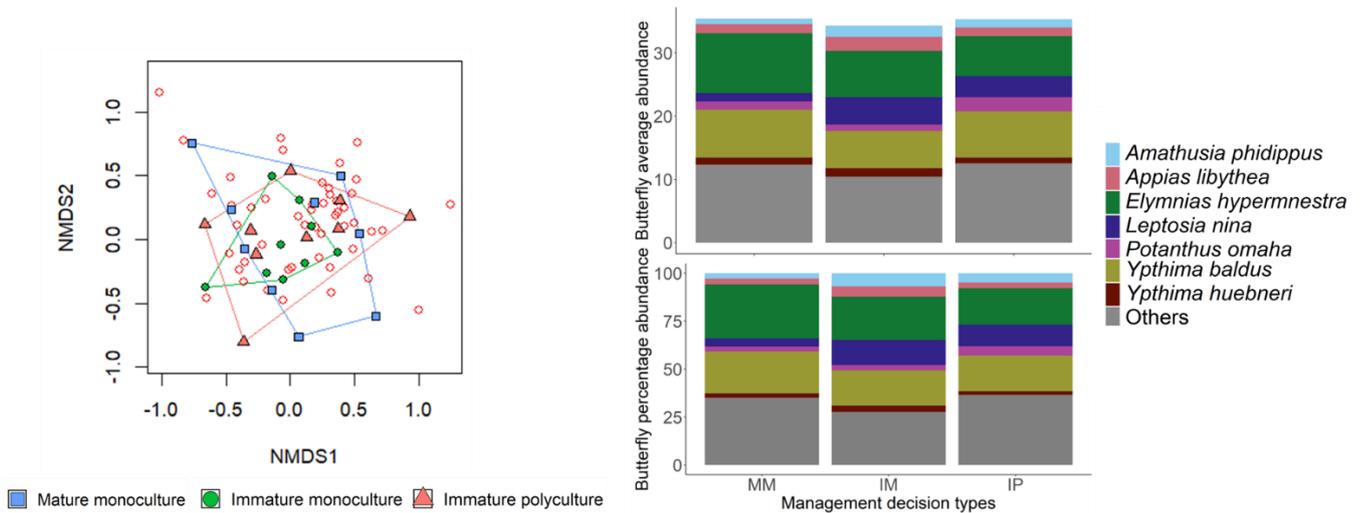
**Figure 5.1** PCA (Principal Component Analysis) biplots showing PC1 and PC2 (“Dim1” and “Dim2”, top left panel), PC3 and PC4 (“Dim3” and “Dim4”, top right panel), and PC5 and PC6 (“Dim5” and “Dim6”, bottom panel) loading scores of plantations (coloured points) as well as environmental variables (arrows). Axes 1 and 2 explained 17.3% and 12% of the variation in environmental variables. Axes 3 and 4 explained 9.6% and 9.2%. Axes 5 and 6 explained 8.5% and 6.6%, respectively. In total, PC1-PC6 explain 63.1% of variation in the variables representing environmental conditions. This study used 27 plantations, consisting of nine of each of the management decision types (mature monoculture, immature monoculture, and immature polyculture). Larger points represent the average values of management decision types, while smaller points represent individual plantation. Refer to **Table S5.5** to see loadings of environmental variables assessed in the PCA.



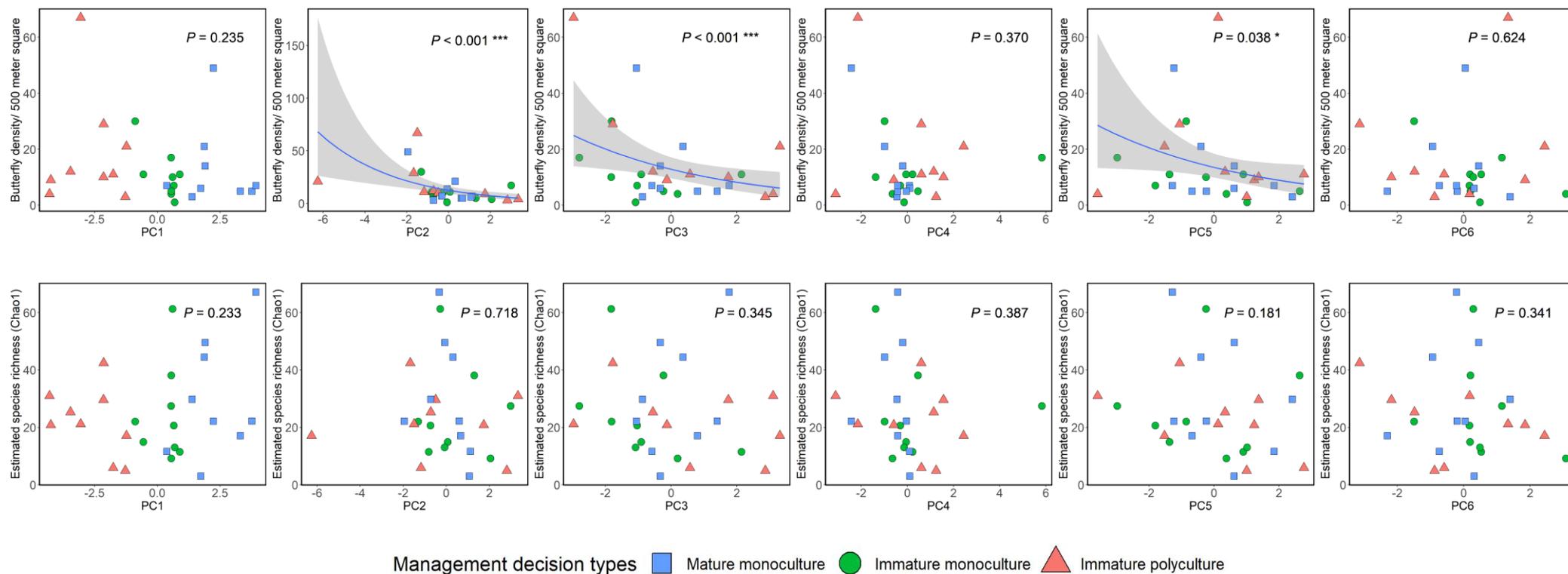
**Figure 5.2** Accumulation curves based on abundance of butterfly assemblages found in two-day surveys for up to two-hour time window each day. Curves were created using individuals identified to species or morphospecies level only. Each plantation type consisted of nine plots. Shaded areas represent 95% confidence intervals.



**Figure 5.3** Effects of management decision types (MM = mature monoculture, IM = immature monoculture, IP = immature polyculture) on the density per 500m<sup>2</sup> and estimated species richness of butterfly assemblages.



**Figure 5.4** Effects of management decision types (MM = mature monoculture, IM = immature monoculture, IP = immature polyculture) on the composition of butterfly assemblages. A – NMDS plot with coloured points showing individual plantations, and open circles species locations (species identities not labelled). Outlying site points for each management type are joined together in separate polygons to visualise overlap. B – Stacked bar chart showing average abundance (top) and percentage abundance (bottom) of the seven most abundant butterfly species in the plantations, with all other species lumped as “others”.



**Figure 5.5** Effects of habitat structure and complexity associated with management decision types (mature monoculture, immature monoculture, and immature polyculture), represented by PC1, PC2, PC3, PC4, PC5, and PC6 (obtained from PCA used to summarise parameters representing environmental conditions) on the density and estimated species richness (based on Chao1 index) of butterfly assemblages. Trend lines generated from glm fit are shown for significant relationships. Shaded areas represent 95% confidence intervals. PC3 and PC5 were multiplied by -1 so all trend lines are in the same directions.

## Supplementary materials

**Table S5.1** Plantation size, oil palm age, as well as percentage of crops cultivated other than oil palm across plantations of differing management type used in this study. Each plantation type (mature monoculture [MM], immature monoculture [IM], immature polyculture [IP]) comprised nine replicates.

Plantation replicate	Plot size (acre)	Palm age (year)	Percentage of crops cultivated other than oil palm								
			Bamboo	Banana	Cassava	Coconut	Galangal	Yam	Jackfruit	Pineapple	Torch Ginger
IM01	0.674	6	0	0	0	0	0	0	0	0	0
IM02	0.864	8	0	0	0	0	0	0	0	0	0
IM03	0.326	5	0	3	0	0	0	0	0	2	0
IM04	0.474	7	0	0	0	0	0	0	0	0	0
IM05	0.4	7	1	5	0	0	0	0	1	0	0
IM06	0.45	5	0	2	0	0	0	0	0	1	0
IM07	0.967	5	0	0	0	0	0	0	0	0	0
IM08	0.969	5	0	0	0	0	0	0	0	0	0
IM09	0.961	5	0	0	0	0	0	0	0	0	0
IP01	0.702	6	0	10	10	0	2.5	2.5	0	0	0
IP02	0.395	5	0	30	10	0	0	0	0	0	0
IP03	0.208	6	0	0	0	0	0	0	0	0	0
IP04	0.304	5	0	20	3	3	0	0	0	2	2
IP05	0.297	7	0	50	0	0	0	0	0	0	0
IP06	0.395	4	0	20	15	0	0	0	0	5	0
IP07	0.86	4	0	10	20	0	0	0	0	15	0
IP08	0.96	6	0	5	0	0	20	0	0	0	0
IP09	0.727	5	0	20	0	0	0	0	0	0	0
MM01	0.245	15	0	0	0	0	0	0	0	0	0
MM02	0.5	15	0	0	0	0	0	0	0	0	0
MM03	0.32	20	0	0	0	0	0	0	0	0	0

Plantation replicate	Plot size (acre)	Palm age (year)	Percentage of crops cultivated other than oil palm								
			Bamboo	Banana	Cassava	Coconut	Galangal	Yam	Jackfruit	Pineapple	Torch Ginger
MM04	0.524	22	0	0	0	0	0	0	0	0	0
MM05	0.578	20	0	0	0	0	0	0	0	0	0
MM06	0.617	22	0	0	0	0	0	0	0	0	0
MM07	1.273	20	0	0	0	0	0	0	0	0	0
MM08	0.904	22	0	0	0	0	0	0	0	0	0
MM09	1.29	22	0	0	0	0	0	0	0	0	0

**Table S5.2** Percentage neighbouring habitat types across plantations of differing management decisions in this study. Each plantation type (mature monoculture [MM], immature monoculture [IM], immature polyculture [IP]) comprised nine replicates.

Plantation code	Plantation perimeter	Monoculture oil palm plantations	Polyculture plantations	Housing	Road	Empty or unused land	Grassland or alike	Cassava plantations
IP01	A	0	0	0	100	0	0	0
IP01	B	0	100	0	0	0	0	0
IP01	C	0	100	0	0	0	0	0
IP01	D	0	0	90	0	10	0	0
IM01	A	0	0	0	100	0	0	0
IM01	B	0	0	0	100	0	0	0
IM01	C	100	0	0	0	0	0	0
IM01	D	0	0	100	0	0	0	0
MM01	A	0	0	100	0	0	0	0
MM01	B	100	0	0	0	0	0	0
MM01	C	100	0	0	0	0	0	0
MM01	D	100	0	0	0	0	0	0
MM02	A	100	0	0	0	0	0	0
MM02	B	0	0	50	0	0	50	0
MM02	C	100	0	0	0	0	0	0
MM02	D	100	0	0	0	0	0	0
IP02	A	50	0	50	0	0	0	0
IP02	B	100	0	0	0	0	0	0
IP02	C	0	0	0	0	100	0	0
IP02	D	0	0	0	100	0	0	0
IM02	A	0	100	0	0	0	0	0
IM02	B	100	0	0	0	0	0	0
IM02	C	100	0	0	0	0	0	0
IM02	D	0	0	0	0	0	100	0
MM03	A	100	0	0	0	0	0	0

Plantation code	Plantation perimeter	Monoculture oil palm plantations	Polyculture plantations	Housing	Road	Empty or unused land	Grassland or alike	Cassava plantations
MM03	B	0	0	0	100	0	0	0
MM03	C	100	0	0	0	0	0	0
MM03	D	100	0	0	0	0	0	0
IP03	A	0	0	0	100	0	0	0
IP03	B	50	0	50	0	0	0	0
IP03	C	0	100	0	0	0	0	0
IP03	D	100	0	0	0	0	0	0
IP04	A	0	0	100	0	0	0	0
IP04	B	70	0	30	0	0	0	0
IP04	C	0	0	100	0	0	0	0
IP04	D	0	0	0	100	0	0	0
IM03	A	0	0	0	100	0	0	0
IM03	B	0	0	0	0	100	0	0
IM03	C	100	0	0	0	0	0	0
IM03	D	40	0	60	0	0	0	0
MM04	A	0	0	0	100	0	0	0
MM04	B	100	0	0	0	0	0	0
MM04	C	100	0	0	0	0	0	0
MM04	D	100	0	0	0	0	0	0
IM04	A	0	0	100	0	0	0	0
IM04	B	10	0	90	0	0	0	0
IM04	C	100	0	0	0	0	0	0
IM04	D	0	10	90	0	0	0	0
MM05	A	0	0	0	100	0	0	0
MM05	B	100	0	0	0	0	0	0
MM05	C	100	0	0	0	0	0	0
MM05	D	0	0	100	0	0	0	0
IM05	A	100	0	0	0	0	0	0
IM05	B	0	0	0	100	0	0	0
IM05	C	0	0	0	100	0	0	0

Plantation code	Plantation perimeter	Monoculture oil palm plantations	Polyculture plantations	Housing	Road	Empty or unused land	Grassland or alike	Cassava plantations
IM05	D	100	0	0	0	0	0	0
IP05	A	0	0	0	0	100	0	0
IP05	B	0	0	0	100	0	0	0
IP05	C	0	0	0	100	0	0	0
IP05	D	100	0	0	0	0	0	0
MM06	A	0	0	0	100	0	0	0
MM06	B	0	0	60	0	0	40	0
MM06	C	100	0	0	0	0	0	0
MM06	D	0	0	100	0	0	0	0
IM06	A	100	0	0	0	0	0	0
IM06	B	0	0	0	100	0	0	0
IM06	C	0	0	0	100	0	0	0
IM06	D	0	30	70	0	0	0	0
IP06	A	100	0	0	0	0	0	0
IP06	B	100	0	0	0	0	0	0
IP06	C	0	0	0	100	0	0	0
IP06	D	0	0	40	0	0	60	0
MM07	A	0	0	0	100	0	0	0
MM07	B	90	0	10	0	0	0	0
MM07	C	40	0	60	0	0	0	0
MM07	D	100	0	0	0	0	0	0
IM07	A	0	0	0	100	0	0	0
IM07	B	100	0	0	0	0	0	0
IM07	C	100	0	0	0	0	0	0
IM07	D	100	0	0	0	0	0	0
IP07	A	100	0	0	0	0	0	0
IP07	B	0	0	0	100	0	0	0
IP07	C	100	0	0	0	0	0	0
IP07	D	0	100	0	0	0	0	0
MM08	A	0	0	100	0	0	0	0

<b>Plantation code</b>	<b>Plantation perimeter</b>	<b>Monoculture oil palm plantations</b>	<b>Polyculture plantations</b>	<b>Housing</b>	<b>Road</b>	<b>Empty or unused land</b>	<b>Grassland or alike</b>	<b>Cassava plantations</b>
MM08	B	100	0	0	0	0	0	0
MM08	C	0	0	0	100	0	0	0
MM08	D	100	0	0	0	0	0	0
IP08	A	0	0	0	100	0	0	0
IP08	B	100	0	0	0	0	0	0
IP08	C	0	100	0	0	0	0	0
IP08	D	30	0	70	0	0	0	0
IM08	A	100	0	0	0	0	0	0
IM08	B	100	0	0	0	0	0	0
IM08	C	100	0	0	0	0	0	0
IM08	D	100	0	0	0	0	0	0
IP09	A	0	0	100	0	0	0	0
IP09	B	0	0	0	0	0	0	100
IP09	C	0	0	100	0	0	0	0
IP09	D	100	0	0	0	0	0	0
IM09	A	0	0	0	100	0	0	0
IM09	B	100	0	0	0	0	0	0
IM09	C	100	0	0	0	0	0	0
IM09	D	100	0	0	0	0	0	0
MM09	A	0	0	100	0	0	0	0
MM09	B	100	0	0	0	0	0	0
MM09	C	0	0	0	100	0	0	0
MM09	D	0	20	80	0	0	0	0













**Table S5.5** Outputs of PCA (Principal Component Analysis) used to summarise parameters representing environmental conditions across plantations with varying crop management (mature monoculture, immature monoculture, and immature polyculture) in this study. The four most influential PC scores (PC1-4) explaining variabilities in the environmental conditions are shown (PC1 and PC2 explain 17.3% and 12% of variation among environmental parameters, PC3 and PC4 explain 9.6% and 9.2%, while PC5 and PC6 explain 8.5% and 6.5%, respectively, so in total PC1-PC6 explain 63.1% of the variation in the variables representing environmental conditions). The three variables with the highest loadings (in positive and negative directions) are shown in bold for each axis. Each plantation type consisted of nine plantations. \*

Parameter	Description	PC1	PC2	PC3	PC4	PC5	PC6
PlotSize_acre	The size of each plantation plot (acre)	0.166	<b>0.198</b>	-0.178	-0.119	0.003	-0.037
PalmAge	The age of oil palm in each plantation	<b>0.331</b>	0.037	-0.057	-0.122	0.008	0.121
OtherCropType_Bamboo	The percentage of bamboo as another crop type in each plantation	0.021	0.166	0.194	<b>0.422</b>	0.234	-0.116
OtherCropType_Banana	The percentage of banana as another crop type in each plantation	<b>-0.267</b>	-0.173	0.046	0.113	0.104	<b>0.245</b>
OtherCropType_Cassava	The percentage of cassava as another crop type in each plantation	<b>-0.300</b>	0.040	0.030	-0.151	0.030	-0.189
OtherCropType_Coconut	The percentage of coconut as another crop type in each plantation	-0.047	<b>-0.346</b>	-0.230	0.177	0.120	<b>-0.245</b>
OtherCropType_Galangal	The percentage of galangal as another crop type in each plantation	-0.070	0.178	-0.225	0.062	-0.044	0.086
OtherCropType_Yam	The percentage of yam as another crop type in each plantation	-0.165	0.184	-0.215	<b>-0.226</b>	<b>0.282</b>	-0.018
OtherCropType_Jackfruit	The percentage of jackfruit as another crop type in each plantation	0.021	0.166	0.194	<b>0.422</b>	0.234	-0.116
OtherCropType_Pineapple	The percentage of pineapple as another crop type in each plantation	-0.206	0.013	0.065	-0.077	-0.065	-0.234
OtherCropType_TorchGinger	The percentage of torch ginger as another crop type in each plantation	-0.047	<b>-0.346</b>	-0.230	0.177	0.120	<b>-0.245</b>
Neighbouring_MonoOilPalm	Monoculture oil palm plantation being the neighbouring habitat type	0.160	0.123	<b>0.242</b>	0.025	<b>-0.375</b>	-0.127
Neighbouring_PolyPlantations	Polyculture plantation being the neighbouring habitat type	-0.216	<b>0.254</b>	<b>-0.267</b>	-0.158	0.071	-0.150
Neighbouring_Housing	Housing being the neighbouring habitat type	0.072	-0.253	<b>-0.358</b>	0.000	0.120	0.033
Neighbouring_Road	Road being the neighbouring habitat type	-0.056	-0.011	0.199	0.116	<b>0.382</b>	0.160
Neighbouring_Other_EmptyOrUnusedLand	Empty or unused land being the neighbouring habitat type	-0.160	-0.112	0.160	0.020	0.092	<b>0.368</b>
Neighbouring_Other_GrasslandOrAlike	Grasslands or alike being the neighbouring habitat type	0.009	0.001	0.134	-0.179	-0.072	<b>-0.365</b>
Neighbouring_Other_Cassava	Monoculture cassava plantation being the neighbouring habitat type	-0.083	-0.027	-0.121	0.113	-0.108	0.218
Sum	The sum of nectar sources for butterflies	0.007	-0.036	<b>0.251</b>	-0.178	<b>0.342</b>	-0.014
CanopyAverage_percent	Average canopy openness	-0.145	0.162	-0.113	<b>-0.341</b>	0.226	-0.047
UnderstoryCover_Bare	Percentage bare ground as ground cover	-0.114	<b>0.381</b>	-0.152	<b>0.184</b>	-0.118	0.028
UnderstoryCover_Palm	Percentage oil palm tree as ground cover	0.093	0.022	0.066	0.131	0.109	<b>-0.434</b>
UnderstoryCover_OtherCrop	Percentage other crop as ground cover	<b>-0.319</b>	-0.172	-0.196	0.131	-0.051	0.088

Parameter	Description	PC1	PC2	PC3	PC4	PC5	PC6
UnderstoryCover_CutFron	Percentage cut frond as ground cover	0.270	-0.097	<b>-0.247</b>	0.127	-0.004	-0.080
UnderstoryCover_Fern	Percentage fern as ground cover	-0.074	-0.176	0.031	0.027	<b>-0.313</b>	-0.010
UnderstoryCover_OtherVeg	Percentage other vegetation as ground cover	0.025	-0.199	<b>0.259</b>	<b>-0.310</b>	0.198	-0.002
UnderstoryCover_Other	Percentage other as ground cover	0.259	0.069	-0.075	0.018	0.108	<b>0.269</b>
AverageHeight_cm	Average height of understory vegetation (cm)	-0.043	<b>-0.331</b>	0.180	-0.163	<b>-0.182</b>	-0.025
PalmHeight_m	Average height of oil palm closest to main sampling point (m)	<b>0.344</b>	-0.030	-0.093	-0.102	0.043	0.094
TotalEpiphyteCover_percent	Average percentage epiphyte cover	<b>0.312</b>	-0.109	-0.083	-0.067	0.232	-0.099

\* PC1 was mainly associated with higher height of oil palm stands (**0.344**), older age of oil palm (**0.331**), higher percentage epiphyte cover (**0.312**), and lower percentage ground cover of other crops (**-0.319**), cassava (**-0.300**) and banana (**-0.267**). PC2 was mainly associated with higher percentage bare ground (**0.381**), higher percentage of polyculture plantations as neighbouring habitat types (**0.254**), larger plantation size (**0.198**), but lower percentage cover of coconut (**-0.346**) and torch ginger (**-0.346**), and lower height of understory vegetation (**-0.331**). PC3 was mainly associated with higher percentage of monoculture oil palm plantation (**0.242**), but lower percentage of housing (**-0.358**), and polyculture plantations (**-0.267**) as neighbouring habitat types, as well as higher summed nectar sources for butterflies (**0.251**), higher percentage of other vegetation (**0.259**), but lower percentage of cut fronds (**-0.247**) as ground cover. PC4 was mainly associated with a higher percentage of bamboo (**0.422**), jackfruit (**0.422**) and bare ground (**0.184**), but lower yam (**-0.226**), and lower percentage of other vegetation (**-0.310**), and canopy openness (**-0.341**). PC5 was mainly associated with higher percentage of road (**0.382**) but lower percentage of monoculture oil palm (**-0.375**) as neighbouring habitat types, higher summed nectar sources (**0.342**), and higher percentage of yam (**0.282**), as well as lower average percentage of fern as ground cover (**-0.313**) and lower average height of understory vegetation (**-0.182**). Finally, PC6 was mainly associated with higher percentage of other substrates (either termite mound, moss, fallen palm, palm stump, dead wood, or moss and termite mound) (**0.269**) but lower percentage of oil palm tree (**-0.434**) as ground cover, higher percentage of empty or unused land (**0.368**) but lower percentage of grassland or similar habitat (**-0.365**) as neighbouring habitat types, as well as higher percentage of banana (**0.245**) but lower percentage of coconut (**-0.245**) and torch ginger (**-0.245**) as other crop types.

**Table S5.6** Chao1 index scores (“Estimator”) used to estimate species richness of butterfly assemblages across oil palm management types (only butterflies identified to species/ morphospecies levels were used for calculations). Estimated species richness are shown for individual plantation plots. Observed species richness, standard errors of the estimation, and confidence intervals are also shown.

<b>Plantation replicates</b>	<b>Observed species richness</b>	<b>Estimator</b>	<b>Estimated standard error</b>	<b>95% lower confidence interval</b>	<b>95% upper confidence interval</b>
MM01	11	49.571	20.270	11	89.300
MM02	8	29.777	11.860	8	53.024
MM03	6	11.6	4.383	6	20.191
MM04	3	3	0.492	3	3.965
MM05	20	44.479	23.395	20	90.333
MM06	16	22.166	8.235	16	38.308
MM07	10	22.195	9.163	10	40.154
MM08	11	17.066	7.761	11	32.278
MM09	18	67.137	23.866	20.360	113.915
IM01	12	20.64	8.947	12	38.177
IM02	7	9.147	4.303	7	17.583
IM03	18	21.994	9.613	18	40.836
IM04	10	11.459	3.916	10	19.135
IM05	17	27.448	16.418	17	59.627
IM06	11	14.878	5.285	11	25.238
IM07	17	61.262	23.549	17	107.418
IM08	11	38.096	13.966	11	65.470
IM09	5	13	3.665	5.816	20.183
IP01	12	30.984	18.301	12	66.855
IP02	15	25.322	10.741	15	46.376
IP03	5	5.923	1.868	5	9.585
IP04	11	17.104	7.751	11	32.297
IP05	18	42.456	19.758	18	81.182
IP06	15	21.144	13.239	15	47.092
IP07	15	20.853	9.254	15	38.991
IP08	4	4.95	0.715	4	6.352
IP09	12	29.632	16.743	12	62.450

**Table S5.7** Outputs of log-likelihood ratio tests (Deviance and *p*-values) in the GLMs (Generalised Linear Models) run to assess the impacts of habitat structure and complexity associated with management decisions (represented by PC1, PC2, PC3, PC4, PC5, and PC6 – PC3, PC5, and PC6 was multiplied by -1 before running the tests for visualisations) on the density (per 500m<sup>2</sup>) of butterfly assemblages across 21 plantations (out of 27 plantation plots in total) – *influential outliers that contributed to the observed trend (replicates that fall at or beyond the Cook’s distance on Residual vs Leverage diagnostic plot) were removed* (IM05, IP01, IP04, IP06, MM06, and MM08). *P*-values that are less than 0.05 are given in bold and indicate significant impacts.

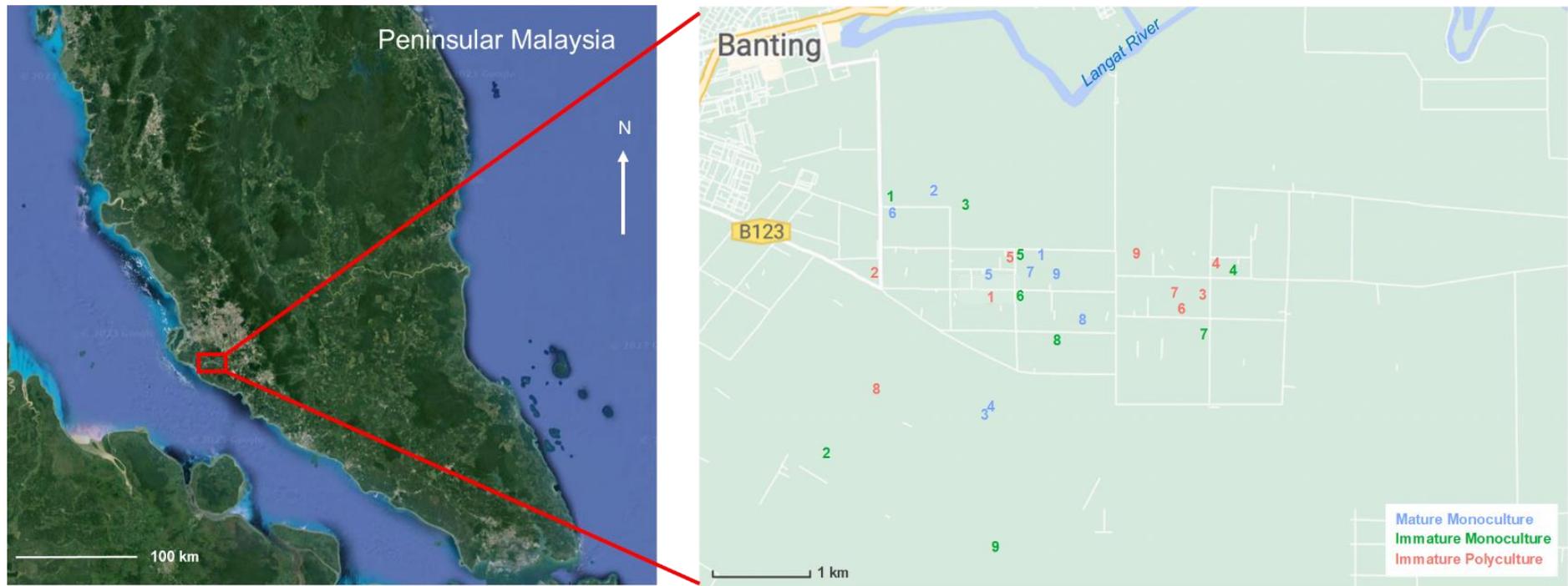
<b>Full model including all explanatory variables: Density per 500m<sup>2</sup> ~ PC1 + PC2 + PC3 + PC4 + PC5 + PC6</b>			
<b>Response variable</b>	<b>Explanatory variables</b>	<b>Outputs of log-likelihood ratio tests</b>	
		<b><math>\chi^2</math></b>	<b><i>P</i>-value</b>
Density of butterflies per 500m <sup>2</sup>	PC1	7.444	<b>0.006 **</b>
	PC2	3.429	0.064
	PC3	2.256	0.133
	PC4	11.367	<b>&lt; 0.001 ***</b>
	PC5	0.490	0.483
	PC6	11.651	<b>&lt; 0.001 ***</b>

**Table S5.8** List of butterflies surveyed in this study and their corresponding resources which were available in the study sites (except for ornamental cycad (Cycadaceae), the hostplant of *Chilades pandava*, which was found in a garden close to one of our study sites). \*

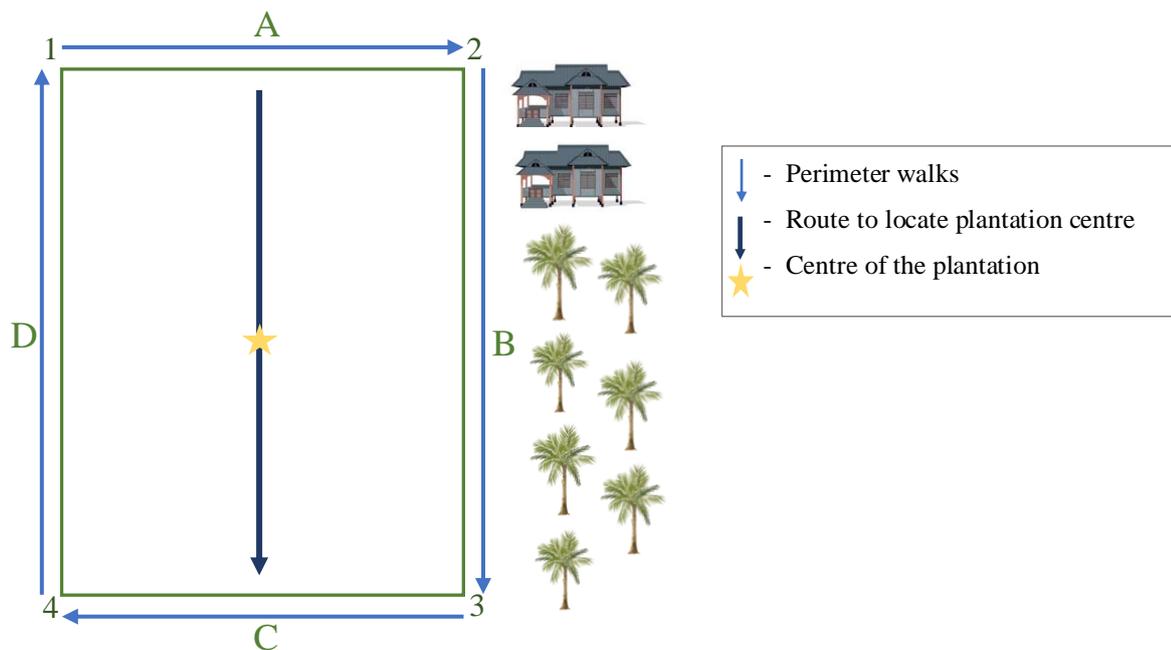
Butterfly species	Resource	Function of resource	Category of resource
<i>Ancistroides nigrita</i>	<i>Etilingera elatior</i> (Zingiberaceae) and other Zingiberaceae	Hostplant	Crop
<i>Appias libythea</i>	<i>Cleome rutidosperma</i> (Capparaceae)	Hostplant	Understory vegetation
<i>Amathusia phidippus</i>	<i>Elaeis guineensis</i> (Araceae)	Hostplant	Crop
	<i>Cocos nucifera</i> (Araceae)	Hostplant	Crop
<i>Chilades pandava</i>	Cycadaceae	Hostplant	Ornamental cycad
<i>Elymnias hypermnestra</i>	<i>Elaeis guineensis</i> (Araceae)	Hostplant	Crop
<i>Erionota thrax</i>	<i>Musa spp.</i> (Musaceae)	Hostplant	Crop
<i>Gangara thyrasis</i>	<i>Elaeis guineensis</i> (Araceae)	Hostplant	Crop
	<i>Cocos nucifera</i> (Araceae)	Hostplant	Crop
<i>Graphium agamemnon</i>	<i>Lantana</i> (Verbenaceae)	Hostplant	Understory vegetation
<i>Hypolimnas bolina</i>	<i>Asystasia gangetica</i> (Acanthaceae)	Hostplant	Understory vegetation
<i>Iambrix salsala</i>	Poaceae	Hostplant	Understory vegetation
<i>Junonia almana</i>	<i>Lindernia</i> (Linderniaceae)	Hostplant	Understory vegetation
<i>Leptosia nina</i>	<i>Cleome rutidosperma</i> (Capparaceae)	Hostplant	Understory vegetation
<i>Mycalesis anapita</i>	Poaceae	Hostplant	Understory vegetation
<i>Mycalesis janardana</i>	Poaceae	Hostplant	Understory vegetation
<i>Mycalesis mineus</i>	Poaceae	Hostplant	Understory vegetation
<i>Neptis hylas</i>	<i>Musa spp.</i> (Musaceae)	Food plant	Crop
	<i>Psophocarpus tetragonolobus</i> (Fabaceae)	Hostplant	Understory vegetation
<i>Oriens gola</i>	Poaceae	Hostplant	Understory vegetation
<i>Orsotriaena medus</i>	Poaceae	Hostplant	Understory vegetation
<i>Pelopidas mathias</i>	Poaceae	Hostplant	Understory vegetation
<i>Plastigia naga</i>	Araceae	Hostplant	Crop
<i>Plastingia pellationia</i>	Araceae	Hostplant	Crop

<b>Butterfly species</b>	<b>Resource</b>	<b>Function of resource</b>	<b>Category of resource</b>
<i>Potanthus omaha</i>	<i>Axonopus compressus</i> (Poaceae) and other Poaceae	Hostplant	Understory vegetation
<i>Psolos fuligo</i>	Araceae	Hostplant	Crop
<i>Pyronaura latoia</i>	Araceae	Hostplant	Crop
<i>Rapala pheretima</i>	<i>Mallotus paniculatus</i> (Euphorbiaceae)	Hostplant	Understory vegetation
<i>Spindasis lohita</i>	<i>Melastoma malabathricum</i> (Melastomataceae)	Hostplant	Understory vegetation
<i>Taractrocera archias</i>	Poaceae	Hostplant	Understory vegetation
<i>Telicota colon</i>	Poaceae	Hostplant	Understory vegetation
<i>Ypthima baldus</i>	<i>Axonopus compressus</i> (Poaceae)	Hostplant	Understory vegetation
<i>Ypthima horsfieldii</i>	Poaceae	Hostplant	Understory vegetation
<i>Ypthima huebneri</i>	Poaceae	Hostplant	Understory vegetation
<i>Zizina otis</i>	<i>Mimosa pudica</i> (Fabaceae)	Hostplant	Understory vegetation

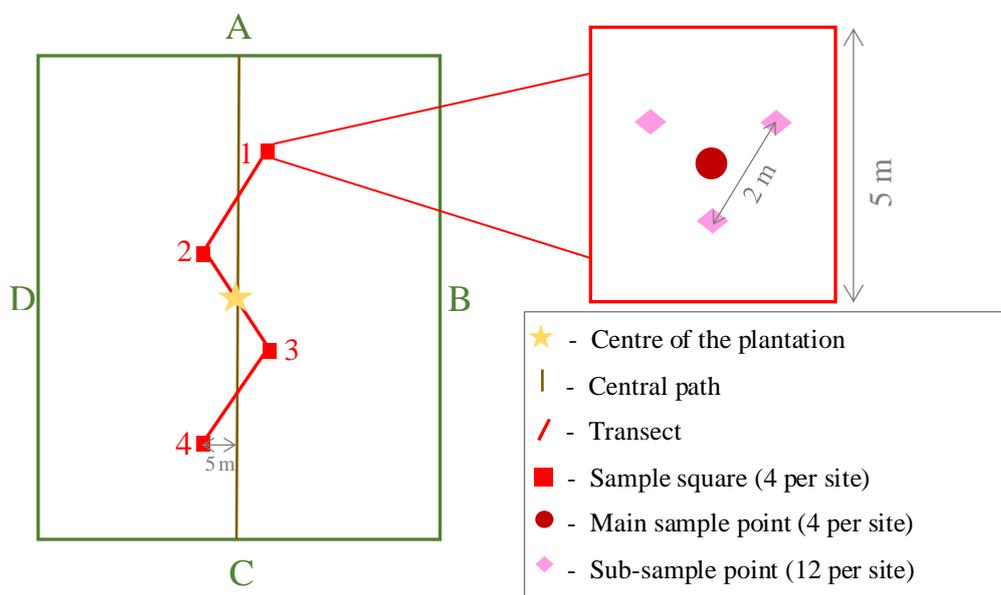
\* Information on food plants (food sources for adult butterflies) and hostplants (food sources for caterpillars) for the butterflies were obtained from Corbet and Pendlebury (2020).



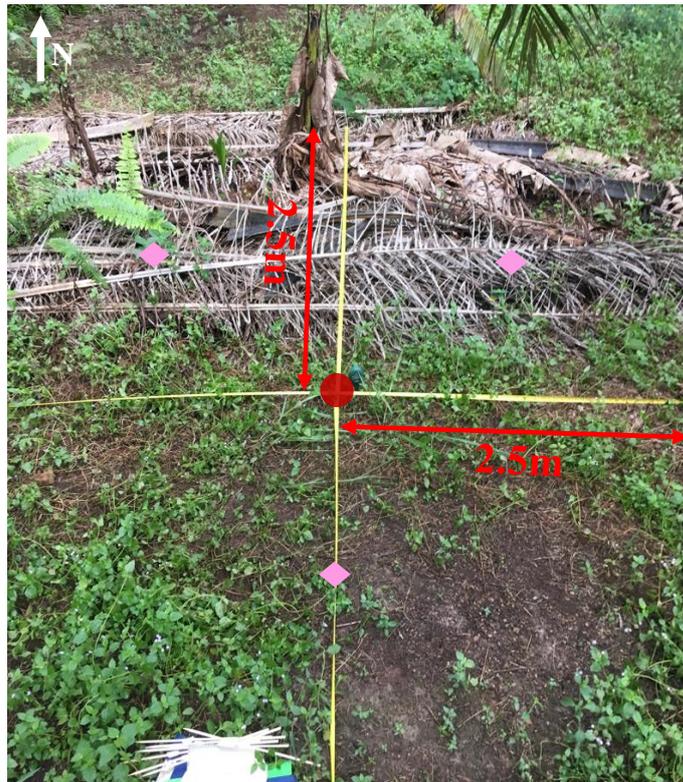
**Figure S5.1** Study sites in Banting, Selangor, Peninsular Malaysia; comprising of nine smallholder-managed oil palm plantations of mature monoculture, immature monoculture, and immature polyculture. Map of Peninsular Malaysia: Google Earth.



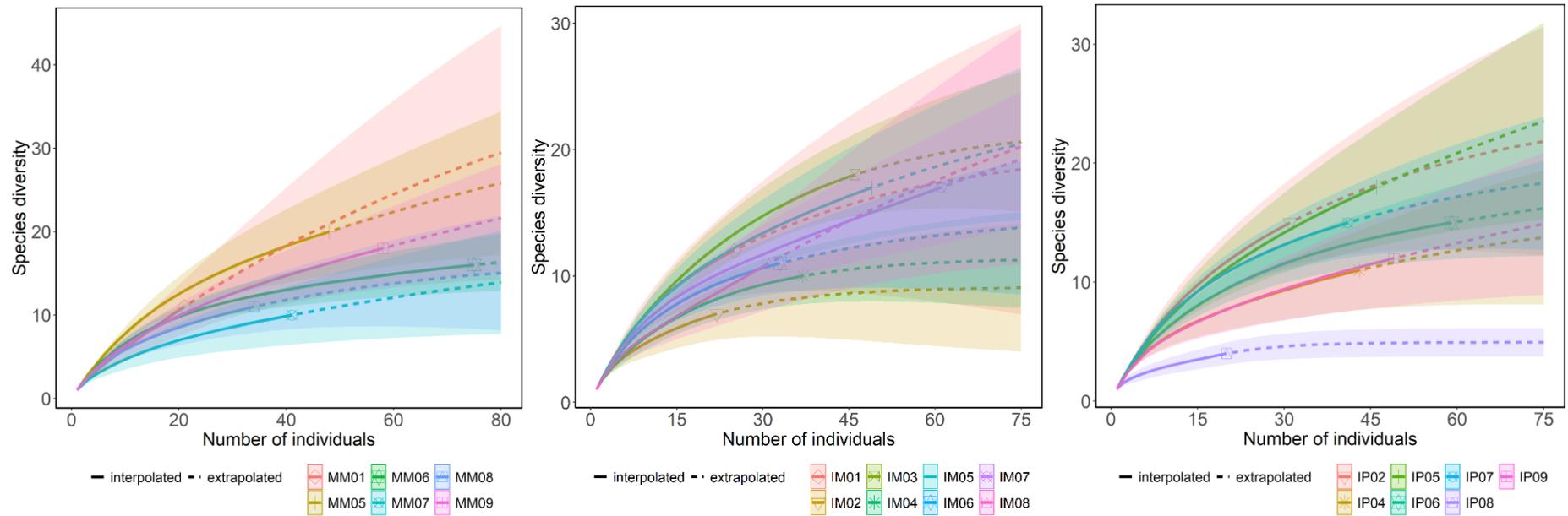
**Figure S5.2** Schematic illustrating a single study site and how perimeter (blue arrows) and central walks (black arrows) were conducted. Perimeter walks were done to assess neighbouring habitat types and the density of food sources for butterflies. Central walks were to assess the types of crops cultivated as well as the density of food sources for butterflies. Green square represents the perimeter of the plantation.



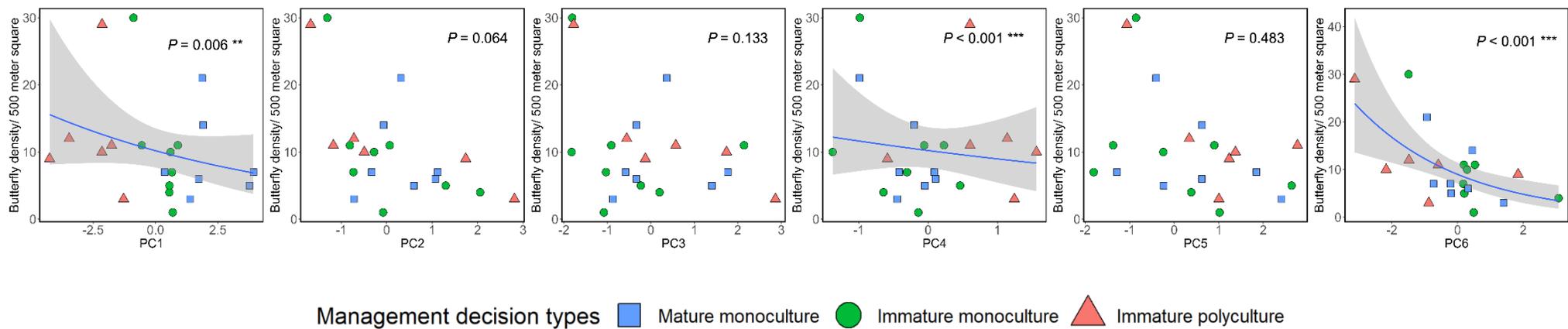
**Figure S5.3** Schematic illustrating the set-up of measurements of environmental parameters within plantations done along the central line of each plantation. Each 5 x 5 m sample square (red square) contained one main central sample point (dark red circle) and three sub-sample points (pink diamonds). Green square represents the perimeter of the plantation.



**Figure S5.4** 5m x 5m sampling square (“sample squares”) for environmental parameter measurements within each plantation, created using two tape measures laid out in a cross shape with the central sample point at the centre of the cross. Main central sample point (“main sample point”) shown with red circle and three sub sample points with pink diamonds.



**Figure S5.5** Accumulation curves of butterfly assemblages from mature monoculture (MM, left), immature monoculture (IM, middle), and immature polyculture (IP, right) (plantations that consisted of fewer than 20 individuals were excluded for visualization: MM02, MM03, MM04, IM09, IP01, and IP03).



**Figure S5.6** Effects of habitat structure and complexity associated with crop management (mature monoculture immature monoculture, and immature polyculture) represented by PC1, PC2, PC3, PC4, PC5, and PC6 (obtained from PCA used to summarise parameters representing environmental conditions) on the density of butterfly assemblages. Only 21 out of 27 plantation plots were used – *influential outliers that contributed to the observed trend (replicates that fall at or beyond the Cook’s distance on Residual vs Leverage diagnostic plot) were removed* (IM05, IP01, IP04, IP06, MM06, and MM08). PC6 was multiplied by -1 so all trend lines are in the same directions. Trend line generated from glm fit is shown for the significant relationship. Shaded areas represent 95% confidence intervals.

## **Chapter 6: Direct observation to assess the effects of habitat structure and complexity on resource-use behaviour of butterflies: a study case in smallholding oil palm plantations in Peninsular Malaysia**

**Martina F. Harianja<sup>1</sup>, Wan Z. W. Mamat<sup>2</sup>, Muhammad A. Hadi<sup>2</sup>, Jake Stone<sup>1</sup>, Badrul Azhar<sup>2</sup>, Sarah H. Luke<sup>3,1</sup>, Edgar C. Turner<sup>1</sup>**

<sup>1</sup>Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

<sup>2</sup>Department of Forest Management, Faculty of Forestry, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

<sup>3</sup>School of Biosciences, University of Nottingham, Sutton Bonington Campus, Nr Loughborough, LE12 5RD

**Key words:** direct observation, habitat structure and complexity, resource-use behaviours, butterflies, *Leptosia nina*, *Ypthima* spp., oil palm.

*In preparation.*

## **Abstract**

Current studies investigating the effects of habitat change and management on populations generally use metrics such as abundance, richness, biomass, and community/ assemblage composition. Most studies are also carried out at relatively large scales, with small-scale studies of how individuals use specific features of habitats being rare. Assessing this aspect of habitat change and management can increase understanding of how differing structure and complexity affect the behaviour of a species in using resources and, therefore, why some systems support more individuals and species than others. Using a small-scale case-study approach, we investigated how two tropical butterfly species (*Leptosia nina* [Pieridae] and *Ypthima* spp. [Nymphalidae]), commonly found in oil palm plantations, used the habitat, in terms of movement and accessing resources (resource-use behaviours). Using novel direct-observation methods, we followed seven and nine individuals of each species respectively (numbers were low due to the limited availability of butterflies and time constraints during the study period), for three minutes in smallholder-owned oil palm plantations in Banting, Selangor, Malaysia. Observations were pragmatically made across plantations of three main management types: immature monoculture, immature polyculture, and mature monoculture plantations, representing a range of habitat conditions and complexities. We compared the distance travelled and characteristics of locations used by butterflies and paired control points (generated by pairing observed distances travelled but selecting the direction for each movement after a stop at random). We assessed how individuals in the two species used the local environment and whether this differed with habitat structure and complexity. Due to the low number of observations, we did not have enough evidence to explain how habitat structure and

complexity affect the resource-use behaviours of the two butterfly species. However, we did find that a higher proportion of *L. nina* butterflies landed on vegetation compared to controls, while *Ypthima* spp. butterflies selected higher average heights of substrate than controls. In conclusion, we demonstrated that butterflies display fine-scale habitat choice and choose specific features of a habitat to land on, even within fairly homogenous plantation habitats, and with a limited sample size in this study. This highlights the importance of maintaining resources that are used by butterflies within plantations, although conclusions need to be investigated further due to the low number of individuals we observed. We note that the methods used in this study, while time-consuming, yielded detailed information on each species at a fine scale. We call for more studies to trial related methods in other habitats.

## Introduction

Studies investigating the impacts of environmental change on biodiversity are commonly done through usage of metrics such as abundance, species richness, composition, and biomass (e.g., Elek et al., 2022; Turner & Foster, 2009; Wan Zaki et al., 2023). Despite providing a big picture of the outcomes of environmental change on the studied species, how resources within a habitat are used (“resource-use” behaviours) cannot be measured directly using these metrics. Studying resource-use behaviours is important, since the behaviours of animals can alter when natural conditions change (Wilson & Fox, 2020) and are often the first response recorded towards changes in the environment (Tuomainen & Candolin, 2011). Changes in behaviour can have consequences on the fitness of individuals, as well as on their survival and reproduction (Tuomainen & Candolin, 2011). For example, change in habitat structure in a cloud forest in Kenya altered the mate-locating strategy of an Afrotropical butterfly species (*Salamis parhassus*), from perching to patrolling (Bonte & Dyck, 2009). However, the behavioural change observed in this butterfly species did not affect their population, perhaps because they are a disturbance-tolerant species (Bonte & Dyck, 2009). However, behavioural changes in other species or taxa may have detrimental consequences on their populations, particularly if they are sensitive to environmental change. Furthermore, it is often loss of habitat complexity and resources at the small scale (e.g., microclimate, food- and hostplants) that drive losses of species across the wider area (Bladon et al., 2020).

In Southeast Asia, where the level of biodiversity and endemism is relatively high compared to many other regions (Myers et al., 2000), oil palm expansion has been one

of the major drivers for declines in abundance and species losses (Foster et al., 2011; Meijaard et al., 2020). However, once plantations are established, the negative impacts of ongoing cultivation on biodiversity can be reduced through conservation management within oil palm, which can maintain a higher richness and abundance of certain taxa, as well as improving ecosystem functions (Ashton-Butt et al., 2018; Hood et al., 2020; Slade et al., 2011; Tao et al., 2016; Woodham et al., 2019) compared to traditional management approaches. Among animals, a wide range of invertebrates persist and can support numerous ecosystem functions within oil palm. For instance, butterflies are common in the system, and act as generalist pollinators, as well as food sources for other species. Several studies have assessed how butterfly assemblages can be better supported within oil palm plantations. In general, it has been demonstrated that increasing the number of crop species and maintaining understory vegetation, which are used as hostplants and/ or nectar sources by butterflies, can increase butterfly richness or abundance (Asmah et al., 2017; Harianja et al., 2023g [Chapter 5]; Reiss-Woolever et al., 2023a, b). Despite this, how habitat structure and complexity within oil palm plantations affect resource-use behaviours of butterflies is not yet known.

Butterflies are ectotherms which rely on the temperature of the environment to adjust their body temperature. Active sunbathing to warm up is often done by butterflies to prepare for flight, which is needed to find resources (nectar, breeding site, and shelter) and for reproduction (Naik et al., 2022). In contrast, when the weather is hot, butterflies seek shaded areas to cool down (Kemp & Krockenberger, 2004). All these behaviours require the availability of variable microclimatic conditions within a system (Kuefler & Haddad, 2006). Management within agricultural landscapes can therefore determine whether the resources needed by wildlife, such as butterflies, are provided.

In an oil palm context, habitat structure and complexity within plantations can change dramatically over the oil palm life cycle, particularly after replanting (which usually occurs when oil palm stands reach 25 years of age (Snaddon et al., 2013), creating a hotter and drier environment because of the loss of canopy cover, as well as reduction of plant transpiration (Luskin & Potts, 2011; Pashkevich et al., 2021). Microclimatic conditions can become more equable as the crop grows, although it takes several years for the canopy to reclose, shading the understory (Luskin & Potts, 2011). Following replanting, plantation managers may also decide to alter their management, such as replanting with all oil palm (monoculture) or a mixture of oil palm and other crops (polyculture) (Harianja et al., 2023g [Chapter 5]). Growers can also be highly variable in terms their understory vegetation management, with some removing the vegetation completely by spraying and manual cutting, but others leaving vegetation to grow (Luke et al., 2020). All these approaches may affect resource-use behaviour by butterflies. Hence, investigating the effects of varying habitat structure and complexity (associated with management decisions) on resource-use behaviours of butterflies may provide evidence on whether certain aspects of structure and complexity better support butterfly assemblages (Azhar et al., 2015; Kuefler & Haddad, 2006). Such information could inform strategies to better support butterfly assemblages in plantations, which in turn could maintain higher butterfly numbers.

Based within smallholder plantations in Selangor, Malaysia, our study is the first that assesses the resource-use behaviours of two common butterfly species (*Leptosia nina* [Pieridae] and *Ypthima* spp. [Nymphalidae]), and whether these differ with oil palm habitat complexity. We flag that this represents a small-scale case study to trial our methodological approaches for studying fine-scale butterfly habitat choices. We

conducted direct observations to assess resource-use behaviours of the butterflies as they moved through plantations and compared these to paired controls, where direction of travel was randomised after each stop. We addressed the following questions: 1) What are the effects of habitat structure and complexity on butterfly resource-use behaviour (total distance flown, start to finish distance flown, number of hops, and the proportion of time spent flying) of the two species? 2) How do observed butterflies differ from their paired controls in use of resources (i.e., proportion perching on vegetation, height of perching substrates chosen, and start-to-finish distance flown) for each species?

## **Materials and methods**

### *Study sites*

Data were collected from 11 smallholder oil palm plantations between 20 June and 3 August 2022 in Banting, Selangor, Malaysia (2.788267°N, 101.546651°E). The average annual rainfall and air temperature and were 1822.60 mm (Yusof et al., 2021) and 27.6°C (Vijayanathan et al., 2021) in the area. The choice of specific plantations was pragmatic, based on the presence of suitable butterflies, and intended to represent a range of habitat structure and complexity, rather than for formal comparisons across different types of management. The 11 plantations consisted of three management decision types: five mature monocultures, two immature monocultures, and four immature polycultures, and all sized between 0.4 and 1.29 acres (**Table S6.1, Figure 6.1**). Other crops that were cultivated in the immature polycultures were banana, cassava, coconut, galangal, pineapple, torch ginger, and yam (**Table S6.1**). The study plantations therefore represented a wide range of habitat structure and complexity, allowing us to assess the

effects of varying structure and complexity on butterfly small-scale movement and resource use. In general, the range of annual usage of fertilisers and herbicides by smallholders in this study (excluding MM03 due to missing data) was 62.5 – 1000 kg/ha and 0 – 32 l/ha, respectively (based on unpublished self-reported data from smallholders). All other relevant information regarding the age of the oil palm stands, understory cover and level of shelter, as well as butterfly replicates, are available in **Table S6.1** and **S6.2**.

#### *Direct observation of butterflies*

We followed the movement of individual butterflies at all plantations for a subset of two common species: *Leptosia nina* and *Ypthima* spp.. Observed butterflies were chosen pragmatically (based on presence and to fit with data collection during a larger study), across the three plantation management types, and some plantations contained more than one butterfly observation (**Table S6.1**). We did not aim to achieve equal numbers of observations in each management type, but rather included observations from across management types to ensure a range of conditions were represented, and to allow us to assess whether understory structure and complexity affected results.

*Leptosia nina* is distributed across the Oriental region, can be found at moderate elevations and is abundant in Peninsular Malaysia (Corbet and Pendlebury, 2020). Its hostplants are *Capparis heyneana*, *Crateva religiosa*, and *Cleome rutidopsperma* (Corbet and Pendlebury, 2020). *L. nina* are found in open areas and known to fly slowly (“bobbing flight”) and low near substrates (rarely more than one meter from the ground) (Corbet and Pendlebury, 2020 and personal observation). *Ypthima* is a genus that is

distributed across Africa as well as the Indo-Australian region and can be found in high abundance at all elevations (Corbet and Pendlebury, 2020). Its larvae feed on grasses (Poaceae) (Corbet and Pendlebury, 2020). In terms of behaviour, *Ypthima* spp. are found commonly around grasses, either perching or flying short distances (“skipping” flight pattern) (Osozawa et al., 2017; Sugiura et al., 2010; and personal observation).

We selected these species, as they were locally common in all plantation types and therefore represented a tractable choice for this project. The second species could consist of several different species (other surveys taking place in the area found three species of *Ypthima* butterfly (Harianja et al., 2023g [Chapter 5]). However, confirming to the species level was not always feasible, because it was not possible to catch all butterflies after the three minutes of direct observations (caught butterflies at IP03, MM0-03, 04, and 05 were all *Ypthima baldus*, but other individuals were not caught). As all species in this genus show similar behaviour (Osozawa et al., 2017; Sugiura et al., 2010; and personal observation), we chose to lump data for this study, but acknowledge that this represents a caveat to our findings, as behaviour could differ between related species in the genus.

For each individual encountered, we waited for one minute before starting observations, to make sure that the behaviour of the observed butterfly was not influenced by our presence. Directly after this, we recorded the date, time, and weather condition (overcast/ sunny), as well as the species of the observed butterfly, the identity of the plant on which they were found (if perching), and their activity by audio-recording the different activities on a smartphone as we followed the individual for three minutes. This allowed us to calculate the duration of different activities and location of perching points post-hoc. Activity categories recorded were flying, interacting (chasing another

butterfly), nectaring, sunning (perching on substrate with wings angled towards the sun, and at least some forewing exposed above the hindwing), and resting (perching on substrate with wings not angled to the sun). If a butterfly perched for too-brief an interval to assess its behaviour, this was categorised as resting. We set up flags and recorded the GPS position wherever a butterfly landed, enabling us to calculate the exact distance travelled and how circuitous the route taken was. Butterflies that were recorded for less than three minutes, either because we lost sight of them, or because they flew outside of the surveyed plantation, were excluded from analyses. Throughout the three-minute observations, we did not chase the butterflies (but followed where they moved) and kept our distance (at least ~2 meters or more from the butterfly), to minimise any chance of disturbance. Occasionally, the butterfly flew past us, and during such events, which we could not control, we stood still and made no movements. No butterflies were obviously disturbed by our presence during observations.

For each butterfly recorded, we then manually simulated a control flight of equal distance and number of stops, beginning from where each butterfly recording began. For the control flights, we conducted the measurements immediately after the three-minute observations on the butterflies. After each “perching point”, we generated a random bearing to enable us to determine direction of flight using <https://www.random.org> (Haahr, 2020), prepared in advance, and paired length of each flight, until all movements within the three-minute recording period had been replicated. The website enabled us to generate random numbers, which we used as the degrees on a hand-held compass as the random bearings. The GPS locations of all control “perching points” where butterflies landed, were recorded using a handheld GPS unit (Garmin GPS Map 64S, with an accuracy of 3.05 – 3.66 meters). Any bearings which created a point beyond the

plantation were noted, and then regenerated. This ensured all control movements were constrained within the plantation, in line with the observed butterfly movements themselves. Our calculated movements provided us with controls to compare with movement patterns of the observed butterflies, hence making the only difference the direction of each movement (set by the random bearings).

Direct observations on butterflies were carried out between 09.00 and 17.00. The day of data collection in each type of plantation with differing management decisions was done in a randomized way to ensure that there were no systematic differences in day of collection between management types. However, due to weather, herbicide spraying activities by the plantation owners, and logistics, three of the mature monoculture plantations were surveyed on three consecutive days. We also recorded the time window of collections (morning/ noon/ afternoon) for each survey.

#### *Environmental data collection*

Environmental data were collected at all perching points for butterfly and control collections. We collected data within a 5m x 5m square surrounding the individual perching point. Measurements were only taken at points that were separated by at least 1m in distance. If the observed butterfly made a perch and moved to a point that was less than 1m, environmental parameter measurements were only taken at the first point, and the values were used for both points. This was done to save time during observations and because points at distances of less than one metre were likely to have the same environmental conditions.

Environmental parameters measured were percentage ground cover of different substrates and shelter, as well as whether the butterfly landed on vegetation or another substrate, and the height of substrate that the butterfly landed on. Ground cover categories were grass, ferns, herbs, dead oil palm fronds, bare ground, and other (any substrates that were not classified in any of the previous categories). Shelter was assessed by recording whether there was any substrate taller than waist height in the cardinal directions, north, east, south, west, and summing values to give a single shelter reading (0 if no shelter present, and 4 if all directions had a barrier). For recording identity of substrate and height of substrate at control points, we measured the highest substrate present using the drop-disk method, wherever the point landed, particularly if the points fell on a clump of understory vegetation. To do this, we used a 1.5 m pipe and a disk with a hole at its centre. At each of the points, where the observed butterflies made perches, the pipe was set vertically, then the disk was inserted from the top of the pipe and dropped. The substrate height was measured by recording the height from the ground to where the disk fell. However, if the point fell on an individual substrate (e.g., an individual stick of vegetation, or a stack of oil palm dead fronds), we used a measuring stick to directly record the height. This was done because the disk's weight could press the individual vegetation to the ground and therefore would have made it difficult to measure its real height.

### *Data processing*

Prior to running statistical analyses on parameters used in this study, we carried out data processing first to standardise inputs. In particular, total distance flown was calculated by summing the distance travelled by the butterflies between perches during the three-

minute observations (in cm). Start to finish distance flown was obtained by calculating the distance between first and last perching points of the observed butterflies and their paired controls using GPS coordinates (calculation from the “geosphere” package in R (Hijmans, 2022), and converted to cm). There were some clear cases of overestimations by the package in calculating the start to finish distance (when calculations were larger than the total distance flown). However, in all cases this amounted to less than 15m and was likely due to inaccurate coordinate measurements by the GPS unit. As this inaccuracy should not bias the results, since there could also be errors in the other direction (i.e., straight line distances being shorter than they really were), we did not adjust calculated values for analyses. Number of hops were obtained from sums of hops made by the butterflies during the three-minute observations. Finally, the proportion of time spent flying was calculated by dividing 180 seconds (three minutes of direct observation) by time spent flying in seconds. An activity was considered as flying only if it was at least one second in duration, so very quick movements between close substrates were not included. For both number of hops and proportion of time spent flying, we used audio recordings to extract detailed information on the observations.

### *Statistical analysis*

Analyses and visualisations were run using R version 4.0.4 (R Core Team, 2021) and R Studio version 2023.03.0-386 (R Studio Team, 2023). We used basic R syntax and package “dplyr” for general analyses (Wickham et al., 2021). We used “plotrix” (Lemon, 2006) to calculate standard errors. The following packages were used for visualisations: “tidyverse” (Wickham et al., 2019), “cowplot” (Wilke, 2020), and “gridExtra” (Auguie, 2017). We provide details below on packages we used for specific analyses.

### *Habitat structure and complexity across management decisions*

We used PCA (Principal Component Analysis) to summarise environmental parameters collected from butterfly perching points across all plantation management types, therefore representing complexity in habitat features at the local scale chosen by butterflies (during three-minute observations) within plantations across mature and immature oil palm monoculture as well as immature polyculture sites (**Table S6.1** and **S6.2**). We included all management types together, to ensure that a wide range of habitat conditions were present. For *Leptosia nina*, environmental parameters we analysed using PCA were percentage cover of 1) grass, 2) herb, 3) bare ground, 4) oil palm dead frond, and 5) other, as well as 6) shelter. We excluded ferns from the percentage ground cover because its values were implied from the other parameters forming ground cover. For *Ypthima* spp., we analysed the same parameters, but did not include shelter, due to several missing values (four missing values out of nine replicates/ individual butterflies in the group).

### *The effects of habitat structure and complexity on resource-use behaviour*

We used the most influential PC scores from the PCA as summary variables of habitat structure and complexity in separate generalised linear models (GLMs), which were used to assess the impact of habitat structure and complexity on resource-use behaviours of the two butterfly species. In particular, the resource-use behaviours were represented by the following: 1) total distance flown, 2) start to finish distance flown, 3) number of

hops, and 4) the proportion of time spent flying. To summarise environmental parameters shaping habitat structure and complexity, we used a Principal Component Analysis (PCA) with available (built-in) codes in R, and “factoextra” for visualisations through PCA biplots (Kassambara & Mundt, 2020).

For total and start to finish distance flown, we used gaussian distribution with identity link in separate models. We used poisson distribution with log link for the analyses on number of hops. Finally, we used binomial distribution with logit link for the models on the proportion of time spent flying. To assess the importance of each predictor, we use log-likelihood ratio tests. We compared full models consisting of all predictors with models with one of the predictors dropped. For all the analyses, we validated model assumptions. We used “performance” to check overdispersion in the GLMs (Generalised Linear Models) with poisson distribution (Lüdecke et al., 2021), as well as “see” (Lüdecke et al., (2021) with “Rcpp” (Eddelbuettel, 2013; Eddelbuettel & Balamuta, 2018; Eddelbuettel & Francois, 2011) to check model assumptions.

We were aware that time windows (morning/ noon/ afternoon) and weather (overcast/ sunny) might have influenced the behaviours of the observed butterflies. To check if there was any pattern, we ran separate ANOVA or Kruskal-Wallis tests to assess whether there was any difference in the resource-use behaviours of butterflies (particularly: 1) total distance flown, 2) start to finish distance, 3) number of hops, and 4) the proportion of time spent flying) across time windows and weather. In each case, we checked the distribution of the values of outcome variables as well as their equality of variance before deciding to use either ANOVA or Kruskal-Wallis tests, using the package “car” (Fox & Weisberg, 2019) to check the equality of variance with Levene’s test. In most cases, there were no significant patterns, although weather was a significant

factor in the start to finish distance flown by the *Ypthima* spp. butterflies (**Table S6.3&S6.4, Figure S6.1&S6.2**). We then ran a biserial correlation test to assess whether weather correlated with the use of habitat by *Ypthima* spp. butterflies.

To assess the effect of habitat structure and complexity on *Ypthima* spp. butterflies, we used PC1 and PC2, which are the first and the second axis generated by PCA. We found that there was a weak correlation between weather and PC1, but a strong correlation with PC2 (**Table S6.5**). We therefore excluded time window and weather from most later analyses to keep models simple, given our low replicate number. However, for the analysis on start to finish distance flown, we incorporated weather in the model used to assess the effect of habitat structure and complexity (represented by PC1 and PC2).

*Differences between butterflies and paired controls in using resources within plantations across habitat structure and complexity*

To assess how butterflies used resources within plantations, we compared observed butterflies with their paired controls. We compared the following: 1) proportion of perches on vegetation, 2) the height of substrates being perched on, and 3) start-to-finish distance flown. For these, we used separate paired Wilcoxon tests for each butterfly species group. For the first and the second analyses, we used data from the second to the last “perching points”. This was because the first points of both butterflies and their paired controls had the same values (because we used the first “perching points” of the butterflies as the first “perching points” of the paired controls). As with previous analyses, we used the “geosphere” package to calculate the start and finish distance

flown by the butterflies and their paired controls, using the coordinates measured by the GPS units.

## Results

### *Habitat structure and complexity across management decisions*

For *Leptosia nina* points, we found that PC1 and PC2 scores contributed most to the variation (43.3 and 30%, respectively) in habitat structure and complexity across plantations, particularly in terms of understory cover and level of shelter (**Figure S6.3**). PC1 scores were associated with lower percentage cover of bare ground but higher cover of oil palm dead fronds, while PC2 scores were associated with lower percentage cover of grass but higher cover of oil palm dead fronds (**Table 6.1**).

For *Ypthima* spp. points, PC1 and PC2 scores were also the most important in explaining variation (48% and 30.7%, respectively) in habitat structure and complexity across plantations, particularly in terms of understory cover (**Figure S6.5**). PC1 scores were mainly associated with lower percentage cover of herbs but higher cover of grass, while PC2 scores were mainly associated with lower percentage cover of oil palm dead fronds but higher cover of other substrates (**Table 6.2**). These other substrates included banana plants, climbing plants, dead leaves, debris, ditches, dead wood (of oil palm), mango trees, moss, mature or young oil palm trees, and pineapples.

### *The effects of habitat structure and complexity on resource-use behaviour*

Overall, *Leptosia nina* butterflies flew further during direct observations than *Ypthima* spp. butterflies, as well as making more hops and spending a higher proportion of time in flight. Average of total distance flown, start-to-finish distance flown, number of hops, and proportion of time spent flying (compared to other activities) during the three-minute direct observations on *L. nina* butterflies were 1808.93 (SE  $\pm$  458.9) cm, 1327.30 (SE  $\pm$  408.8) cm, 6.57 (SE  $\pm$  1.3), and 0.42 (SE  $\pm$  0.1), respectively, while for *Ypthima* spp. butterflies, they were 201.62 (SE  $\pm$  61.5) cm, 225.46 (SE  $\pm$  51.9) cm, 1.63 (SE  $\pm$  0.3), and 0.06 (SE  $\pm$  0.02), respectively. When perching on vegetation, the plant species selected were *Ageratum conyzoides* and *Asystasia gangetica* (plus one unidentified species) for *Leptosia nina*, and *Ageratum conyzoides*, *Asystasia gangetica*, *Brachiaria milliformis*, *Centotheca lappacea*, *Melastoma* sp., and *Melastoma malabatricum* for *Ypthima* spp.. We found that there were no significant effects of habitat structure and complexity within plantations on either total or start to finish distance flown, number of hops, or proportion of time spent flying for *L. nina* butterflies (**Table 6.3, Figure 6.2**). We found the same patterns for the *Ypthima* spp. butterflies (**Table 6.4, Figure 6.3**).

### *Differences between butterflies and paired controls in using resources within plantations across habitat structure and complexity*

There were significant differences between *Leptosia nina* and their paired controls in proportion landing on vegetation (**Table 6.5**), with *L. nina* butterflies always landing on vegetation, but this not being the case for control points (**Figure 6.4**). However, there were no significant differences between *L. nina* butterflies and their paired controls in

average height of substrates landed on or start to finish distance. There was a significant difference between *Ypthima* spp. butterflies and their paired controls in average height of substrates being landed on (**Table 6.6**), with *Ypthima* spp. butterflies almost always landing on substrates with higher heights than their paired controls (**Figure 6.5**). There were no significant differences between *Ypthima* spp. butterflies and their paired controls in proportion landing on vegetation or start to finish distance.

## **Discussion**

Due to the low numbers of individual butterflies observed in this study, we did not have enough evidence to show any particular association between habitat structure and complexity and resource-use behaviours of butterflies. However, we did find that *Leptosia nina* butterflies were more likely to land on vegetation than their control points. This indicates that *L. nina* butterflies specifically select vegetation as a landing site within plantations, either for nectaring or resting, as we directly observed in this study. In particular, most perching points of the butterflies were understory vegetation (particularly *Ageratum conyzoides* and *Asystasia gangetica*), which are both common nectar sources for the butterflies. The lack of difference in the average height of substrates landed on between butterflies and controls could be because *L. nina* butterflies tend to fly low near substrates (Corbet and Pendlebury, 2020), and may have little preference for vegetation of differing heights. In addition, the lack of difference could be related to the choice of habitat structure and complexity available within plantations. For example, in our observations, the possible perching locations at control points were bare ground, debris, herbs, and ferns, the heights of which only ranged from zero to

several centimetres. In other words, although we observed that the butterflies made choices, as has been found in other studies (Azhar et al., 2015), in this case height alone cannot be used to indicate substrate preferences of the butterflies.

In contrast, we found that *Ypthima* spp. butterflies chose significantly higher vegetation than their paired controls. One of the reasons that butterflies chose higher substrates could be to intercept more energy from sunlight to warm up (Dennis & Sparks, 2005). Indeed, whenever we observed the butterflies sunning, their chosen substrates were always higher than their paired controls. In contrast, we did not observe any difference between the proportion of butterflies landing on vegetation and control points. This could be due to the habitat structure and complexity within plantations. In particular, most of the plantations used by the *Ypthima* spp. butterflies had a variety of understory vegetation, and only five out of seventeen perching points were on bare ground or debris, driving the lack of significant difference observed. In addition, the short distance flown between individual perching points by *Ypthima* spp. butterflies (also observed by other studies, e.g., Osozawa et al., 2017; Sugiura et al., 2010), compared to *L. nina* butterflies, increased the chance that paired controls fell within the same or similar substrate type (although with different heights) to butterfly points, making it less likely for us to detect a difference with the methods used in this study.

Finally, for both butterfly species there was a lack of significant difference in terms of start to finish distance flown between butterflies and controls. This could be because of the relatively small size of plantations used in this study, which effectively constrained the total distances recorded for both butterfly and control measurements. However, it could also mean that these species were not specifically associating with a certain area of the plantation, but moving at random (Kareiva & Shigesada, 1983).

Indeed, both species are generalists (Corbet and Pendlebury, 2020), so it could be that resources are equally available across all areas of the plantation (Kuefler & Haddad, 2006). In addition, neither are reported to form territories or defend an area as adults (Corbet and Pendlebury, 2020), which could result in more limited movements in other species that carry out these behaviours.

It is important to acknowledge the low sample size in this study, which reduces the chance of detecting real impacts of habitat structure on butterfly movement. Indeed, we found that weather as well as the presence of oil palm dead frond and other substrates (mainly grasses) significantly affected the start to finish distance flown by *Ypthima* spp. butterflies. Regarding the presence of grasses, this might have been driven by the reliance of *Ypthima* butterflies on grasses (Poaceae) as their host plants (Corbet and Pendlebury, 2020; Osozawa et al., 2017; Sugiura et al., 2010). However, when all factors were included in the same model (weather as well as PC1 and PC2 representing habitat structure and complexity), there was no significant relationship, despite the clear pattern seen. It is also possible that other habitat characteristics not recorded in our study, such as distance from surrounding habitats or roads, affected our observations. However, as comparisons between butterflies and controls were paired, these larger-scale effects are unlikely to have affected this component of our study. We call for more work to employ these methods more widely to verify our findings.

### **Implications of the direct observation methods used in this study**

We found that plantations across management decision types overlapped in terms of habitat structure and complexity, likely partly explaining the lack of effects on resource-

use behaviours by both *L. nina* and *Ypthima* spp. butterflies. However, we directly observed that both butterflies used a range of substrates during the three-minute observations, which were mainly understory vegetation, for either resting, sunning, or nectaring. This may emphasize the importance of maintaining complexity within plantations (Azhar et al., 2015), particularly understory vegetation (Reiss-Woolever et al., 2023a, b, Wan Zaki et al., 2023), to support the resource-use behaviours of butterflies. Indeed, all the butterfly activities we observed (resting, sunning, or nectaring) have direct consequences on the population number of butterflies.

The conclusions we draw in this study, particularly in terms of the association between resource-use behaviours of the butterflies and habitat structure and complexity, should be investigated further, due to the low number of individual butterflies that we observed. Additionally, the possibility that our observations include more than one species within *Ypthima* butterflies, also means that these results should be interpreted with caution, as different species could display different preferences. However, this may not be a strong effect, since we found that all the individuals observed behaved very similarly, as noted in other studies (Osozawa et al., 2017; Sugiura et al., 2010).

We also demonstrated that the methodological approach with direct observations that we employed in this study can be effective in assessing fine scale factors within a system that are important for target species. We have shown that by direct observations, it is possible to quantify how individuals use the existing resources. This method could help to identify resources and habitat characteristics that are important for maintaining populations of butterfly species (Naik et al., 2022), as well as informing the design of habitats that facilitate resource-use behaviours.

## Tables and Figures

**Table 6.1.** PCA (Principal Component Analysis) outputs showing scores of principal components (PC) 1 and 2 explaining the variation in habitat structure and complexity (measured by several environmental parameters) within oil palm plantations, taken from sites used by *Leptosia nina* butterflies (N = 7). The two highest scores for both axes are shown in bold.

Environmental parameter	Description	PC1	PC2
Grass	Average percentage ground cover that was grass	0.073	<b>-0.602</b>
Herb	Average percentage ground cover that was herb	0.310	-0.521
BareGround	Average percentage ground cover that was bare ground	<b>-0.572</b>	0.238
OilPalmDeadFronD	Average percentage ground cover that was dead fronds of oil palm	<b>0.512</b>	<b>0.295</b>
Other	Average percentage ground cover that was not any of the above categories	-0.413	-0.043
Shelter	Average of any substrate that had height at least the waist level of the observer	-0.369	-0.468

**Table 6.2.** PCA (Principal Component Analysis) outputs showing scores of principal components (PC) 1 and 2 explaining the variation in habitat structure and complexity (measured by several environmental parameters) within oil palm plantations, taken from sites used by *Ypthima* spp. butterflies (N = 9). The two highest scores for both axes are shown in bold.

Environmental parameter	Description	PC1	PC2
Grass	Average percentage ground cover that was grass	<b>0.598</b>	-0.297
Herb	Average percentage ground cover that was herb	<b>-0.535</b>	0.378
BareGround	Average percentage ground cover that was bare ground	-0.402	-0.193
OilPalmDeadFronD	Average percentage ground cover that was dead fronds of oil palm	-0.403	<b>-0.434</b>
Other	Average percentage ground cover that was not any of the above categories	0.173	<b>0.736</b>

**Table 6.3.** Outputs of log-likelihood ratio tests (Deviance and *p*-values) in the GLMs (Generalised Linear Models) run to assess the effects of habitat structure and complexity (represented by PC1 and PC2) on resource-use behaviours of *Leptosia nina* butterflies (N = 7).

<b>Full model including all explanatory variables: Total distance flown/ Start to finish distance flown/ Number of hops/ Proportion of time spent flying ~ PC1 + PC2</b>			
Response variable	Explanatory variables	Outputs of log-likelihood ratio tests	
		Deviance	<i>P</i> -value
Total distance flown (cm)	PC1	-856523	0.449
	PC2	-1996442	0.248
Start to finish distance flown (cm)	PC1	-1295298	0.328
	PC2	-298149	0.639
Number of hops	PC1	-2.144	0.143
	PC2	-0.568	0.451
Proportion of time spent flying	PC1	-0.005	0.943
	PC2	-0.528	0.467

**Table 6.4.** Outputs of log-likelihood ratio tests (Deviance and *p*-values) in the GLMs (Generalised Linear Models) run to assess the effects of habitat structure and complexity (represented by PC1 and PC2) on resource-use behaviours of *Ypthima* spp. butterflies (N = 9). For the analysis on start to finish distance flown, weather was incorporated into the model, due to a significant relationship found with both start to finish distance flown and PC2.

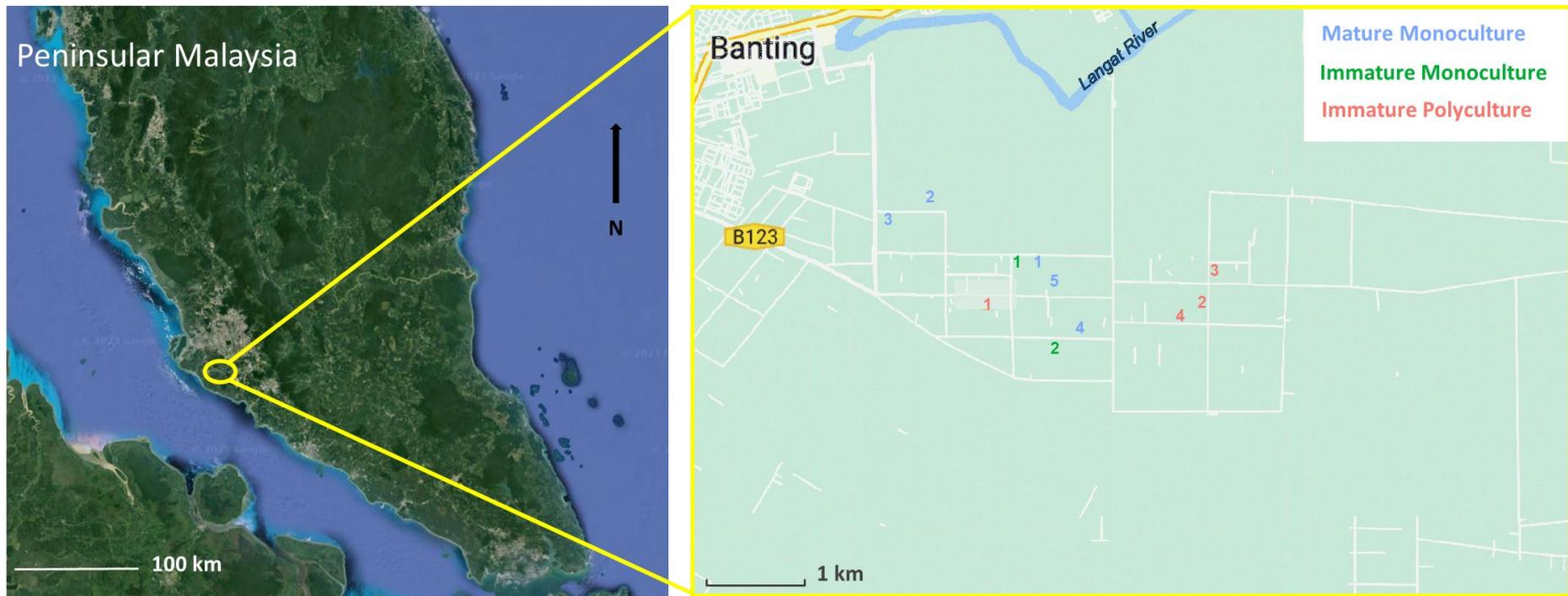
<b>Full model including all explanatory variables: Total distance flown/ Start to finish distance flown/ Number of hops/ Proportion of time spent flying ~ PC1 + PC2</b>			
Response variable	Explanatory variables	Outputs of log-likelihood ratio tests	
		Deviance	<i>P</i> -value
Total distance flown (cm)	PC1	-32487	0.323
	PC2	-39796	0.274
Start to finish distance flown (cm)	PC1	-186.7	0.918
	PC2	-6488.8	0.546
	Weather	-16995	0.328
Number of hops	PC1	-0.511	0.474
	PC2	-0.174	0.675
Proportion of time spent flying	PC1	-0.009	0.921
	PC2	-0.023	0.877

**Table 6.5.** Outputs of paired Wilcoxon tests, run to assess the difference in proportion of perches on vegetation, average heights of substrates landed on, and start to finish distance flown by *Leptosia nina* butterflies and their paired controls (N = 7). Significant differences are shown in bold.

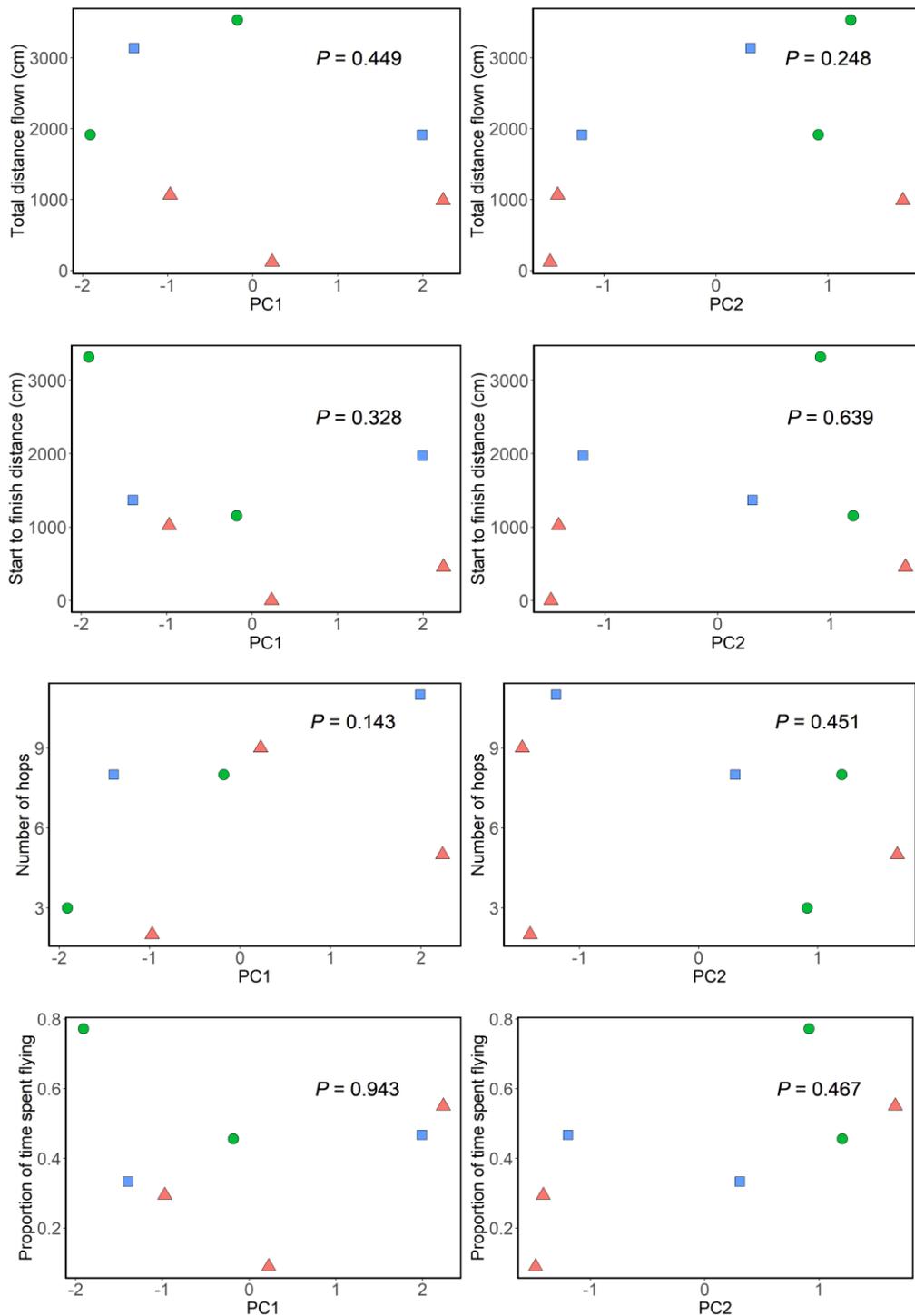
Compared parameters	V	P-value
Proportion of landing on vegetation	27	<b>0.031</b> *
Average heights of substrates being landed on (cm)	22	0.218
Average start to finish distance flown (cm)	15	0.401

**Table 6.6.** Outputs of paired Wilcoxon tests, run to assess the difference in proportion of perches on vegetation, average heights of substrates landed on, and start to finish distance flown by *Ypthima* spp. butterflies and their paired controls (N = 9). Significant differences are shown in bold.

Compared parameters	V	P-value
Proportion of landing on vegetation	10	0.097
Average heights of substrates being landed on (cm)	36	<b>0.014</b> *
Average start to finish distance flown (cm)	7.5	0.309

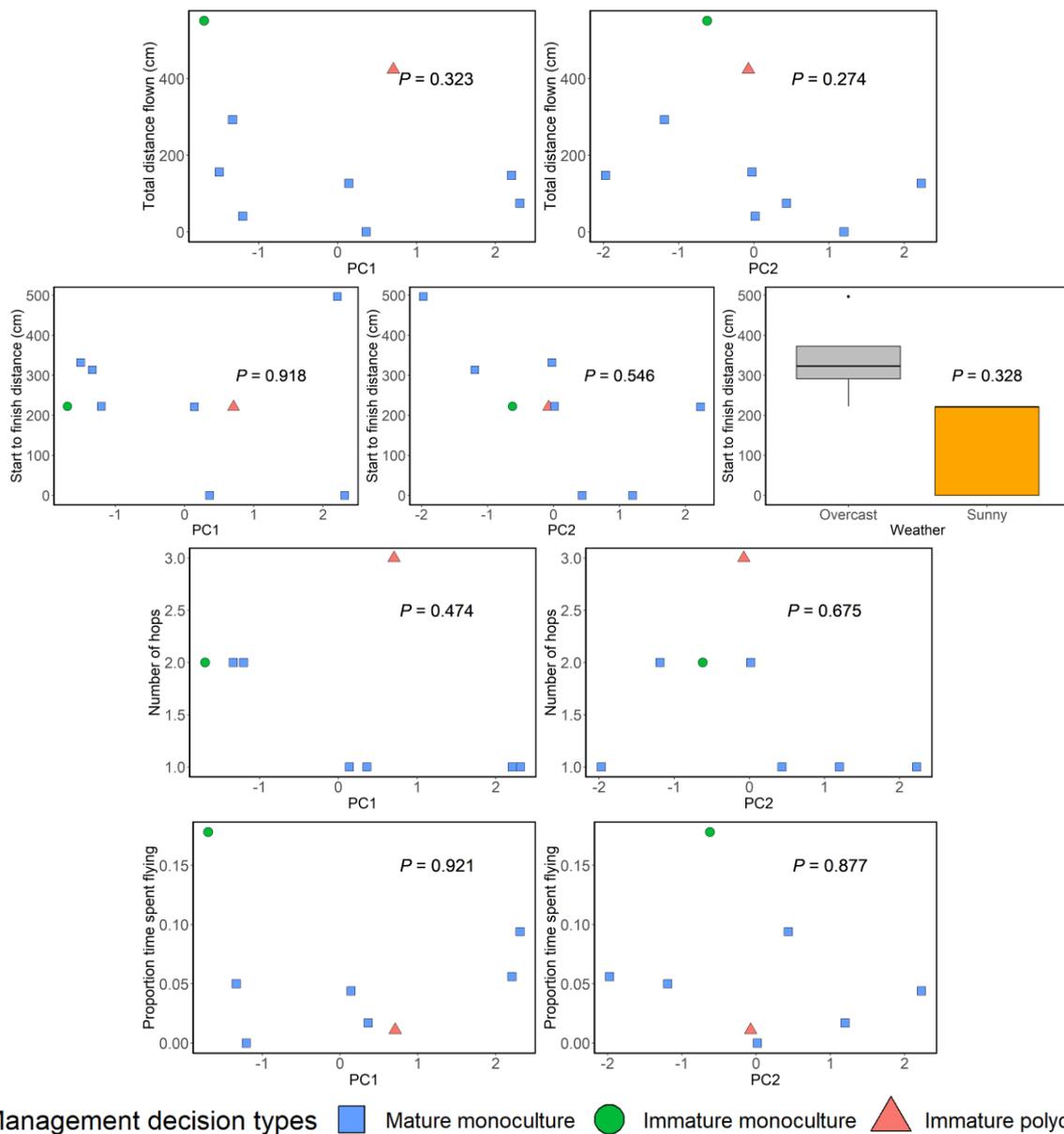


**Figure 6.1** Map showing data collection sites in smallholding oil palm plantations in Banting, Selangor, Peninsular Malaysia, which consisted of five mature monocultures, two immature monocultures, and four immature polycultures. Map source: Google Earth (showing Peninsular Malaysia).

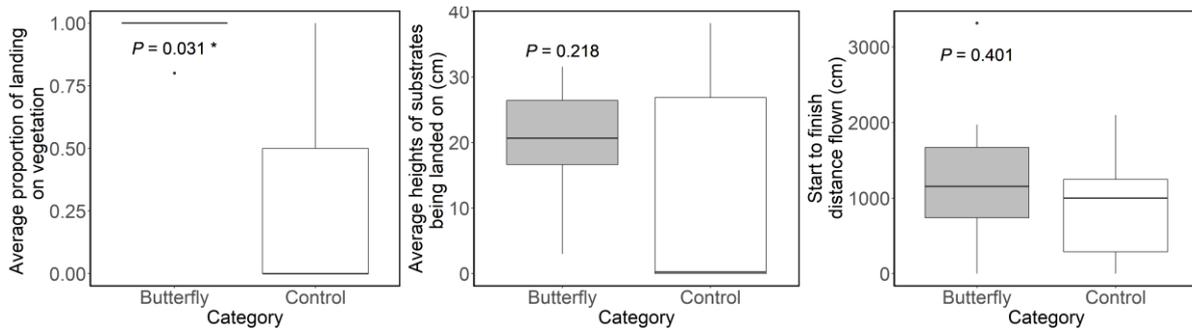


Management decision types ■ Mature monoculture ● Immature monoculture ▲ Immature polyculture

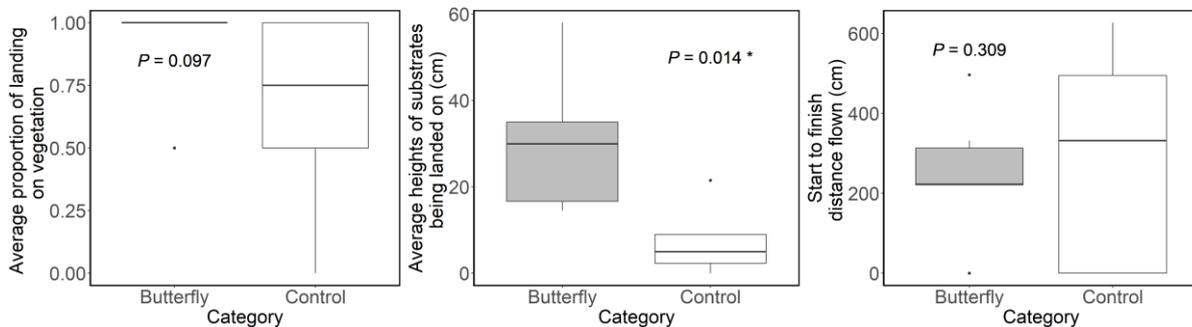
**Figure 6.2** Scatter plots showing relationship between habitat structure and complexity (PC1 & PC2) on the total distance flown (cm), start to finish distance flown (cm), number of hops, and proportion of time spent flying of *Leptosia nina* butterflies. N = 7 individuals. Different plantation types are shown with different symbols and colour for visual comparison only.



**Figure 6.3** Scatter plots showing relationship between habitat structure and complexity (PC1 & PC2) on the total distance flown (cm), start to finish distance flown (cm), number of hops, and proportion of time spent flying of *Ypthima* spp. butterflies. N = 9 individuals (with the exception for number of hops and proportion of time spent flying, for which N = 8). Different plantation types are shown with different symbols and colour for comparison only. For the boxplot showing the association between weather and start to finish distance, all the plantations across management decision types are lumped together. The lines in the middle of boxplots show median values, while the top and bottom of boxplots indicate upper and lower quartiles, respectively. Upper and lower tails indicate maximum and minimum values. Individual points outside of boxplots show outliers.



**Figure 6.4** Comparisons between *Leptosia nina* butterflies (“Butterfly”) and their paired controls in terms of average proportion landing on vegetation (left), average height of substrates landed on (cm) (middle), and average distances between start and finish points (cm) (right). The lines in the middle of boxplots show median values, while the top and bottom of boxplots indicate upper and lower quartiles, respectively. Upper and lower tails indicate maximum and minimum values. Individual points outside of boxplots show outliers. N = 7 individuals.



**Figure 6.5** Comparisons between *Ypthima* spp. butterflies (“Butterfly”) and their paired controls in terms of average proportion landing on vegetation (left), average height of substrates landed on (cm) (middle), and average distances between start and finish points (cm) (right). The lines in the middle of boxplots show median values, while the top and bottom of boxplots indicate upper and lower quartiles, respectively. Upper and lower tails indicate maximum and minimum values. Individual points outside of boxplots show outliers. N = 9 individuals.

## Supplementary materials

**Table S6.1** The characteristics of plantations where butterflies were observed in this study (plantation size, oil palm age, and percentage of crops cultivated other than oil palm) across three types of management (mature monoculture, immature monoculture, and immature polyculture), as well as details of the individual butterflies observed in each. Immature monocultures (IM01&02) consisted of two replicates, immature polycultures (IP01-04) of four, and mature monocultures (MM01-05) of five. Number of replicates across management types was based on the availability of the butterflies which could be surveyed during the sampling period (20 June – 3 August 2022), and while a larger-scale study was taking place.

Plantation replicate	Observation dates	Plot size (acre)	Palm age (year)	Percentage of crops cultivated other than oil palm									Observed butterfly
				Bamboo	Banana	Cassava	Coconut	Galangal	Yam	Jackfruit	Pineapple	Torch ginger	
IM01	14 July 2022	0.4	7	1	5	0	0	0	0	1	0	0	<i>Ypthima</i> spp.4 <i>Leptosia nina</i> 3
IM02	26 July 2022	0.969	5	0	0	0	0	0	0	0	0	0	<i>Leptosia nina</i> 5
IP01	20 June 2022	0.702	6	0	10	10	0	2.5	2.5	0	0	0	<i>Leptosia nina</i> 1
IP02	4 July 2022	0.208	6	0	0	0	0	0	0	0	0	0	<i>Leptosia nina</i> 2
IP03	15 July 2022	0.304	5	0	20	3	3	0	0	0	2	2	<i>Leptosia nina</i> 4
IP04	18 July 2022	0.395	4	0	20	15	0	0	0	0	5	0	<i>Ypthima</i> spp.5
MM01	3 August 2022	0.245	15	0	0	0	0	0	0	0	0	0	<i>Leptosia nina</i> 7
MM02	27 June 2022	0.5	15	0	0	0	0	0	0	0	0	0	<i>Ypthima</i> spp.1
MM03	14 July 2022	0.617	22	0	0	0	0	0	0	0	0	0	<i>Ypthima</i> spp.2 <i>Ypthima</i> spp.3
MM04	2 August 2022	0.904	22	0	0	0	0	0	0	0	0	0	<i>Ypthima</i> spp.7 <i>Ypthima</i> spp.8 <i>Ypthima</i> spp.9 <i>Leptosia nina</i> 6
MM05	28 July 2022	1.29	22	0	0	0	0	0	0	0	0	0	<i>Ypthima</i> spp.6

**Table S6.2** Characteristics of understory complexity in each of the surveyed plantations in this study. Percentage cover of understory complexity was assessed from 5x5m areas surrounding each of perching points of the surveyed butterflies. Level of shelter was assessed by counting the number of times a substrate was present within 5m at a researcher’s waist height, in each of the directions north, south, west, and east surrounding a perching point. Because most values of shelters in the observations on *Ypthima* spp. butterflies were not available (NA/ missing data), shelter was not included in the analyses on *Ypthima* spp. butterflies.

Plantation replicate	Observed butterfly	Observation date	Average percentage cover of understory complexity					Average level of shelter (0-4)
			Grass	Herb	Bare ground	Oil palm dead frond	Other *	
IP01	<i>Leptosia nina</i> 1	20 June 2022	7	18	26.5	21.5	21.5	0.625
IP02	<i>Leptosia nina</i> 2	4 July 2022	5	19	39	11	20	1.2
IM01	<i>Leptosia nina</i> 3	14 July 2022	10	40	20	10	20	1
IP03	<i>Leptosia nina</i> 4	15 July 2022	0	30	20	25	2.5	0
IM02	<i>Leptosia nina</i> 5	26 July 2022	10	30	30	10	10	2.5
MM04	<i>Leptosia nina</i> 6	3 August 2022	7.222	24.444	35	11.111	21.666	1
MM01	<i>Leptosia nina</i> 7	4 August 2022	17.272	32.272	13.636	24.545	12.272	0.818
MM02	<i>Ypthima</i> spp.1	27 June 2022	1.666	45	33.333	11.666	6.666	NA
MM03	<i>Ypthima</i> spp.2	14 July 2022	42.5	41.25	8.75	0	7.5	NA
MM03	<i>Ypthima</i> spp.3	14 July 2022	60	10	0	5	25	NA
IM01	<i>Ypthima</i> spp.4	14 July 2022	80	5	0	10	0	1.666
IP04	<i>Ypthima</i> spp.5	18 July 2022	12.5	50	7.5	27.5	2.5	3
MM05	<i>Ypthima</i> spp.6	28 July 2022	0	60	10	20	10	NA
MM04	<i>Ypthima</i> spp.7	2 August 2022	20	50	0	5	20	NA
MM04	<i>Ypthima</i> spp.8	2 August 2022	5	60	5	20	10	0
MM04	<i>Ypthima</i> spp.9	2 August 2022	10	60	2.5	0	27.5	NA

\* “Other” category was any type of substrate, but not any of the other categories. From all the observations, “Other” category was either a banana, mango, oil palm, or pineapple tree, or dead leaves, debris, or a dead oil palm trunk.

**Table S6.3** Outputs of ANOVA tests run to assess the effects of time window and weather on the resource-use behaviours of *Leptosia nina* butterflies.

Explanatory variable	Response variable	df	F value	P-value
Time window (morning/ noon/ afternoon)	Total distance flown (cm)	2	0.196	0.829
	Start to finish distance flown (cm)	2	0.407	0.691
	Number of hops	2	1.129	0.408
	Proportion of time spent flying	2	0.189	0.835
Weather (Sunny/ Overcast)	Total distance flown (cm)	2	1.462	0.293
	Start to finish distance flown (cm)	2	0.494	0.521
	Number of hops	2	0.419	0.553
	Proportion of time spent flying	2	2.572	0.184

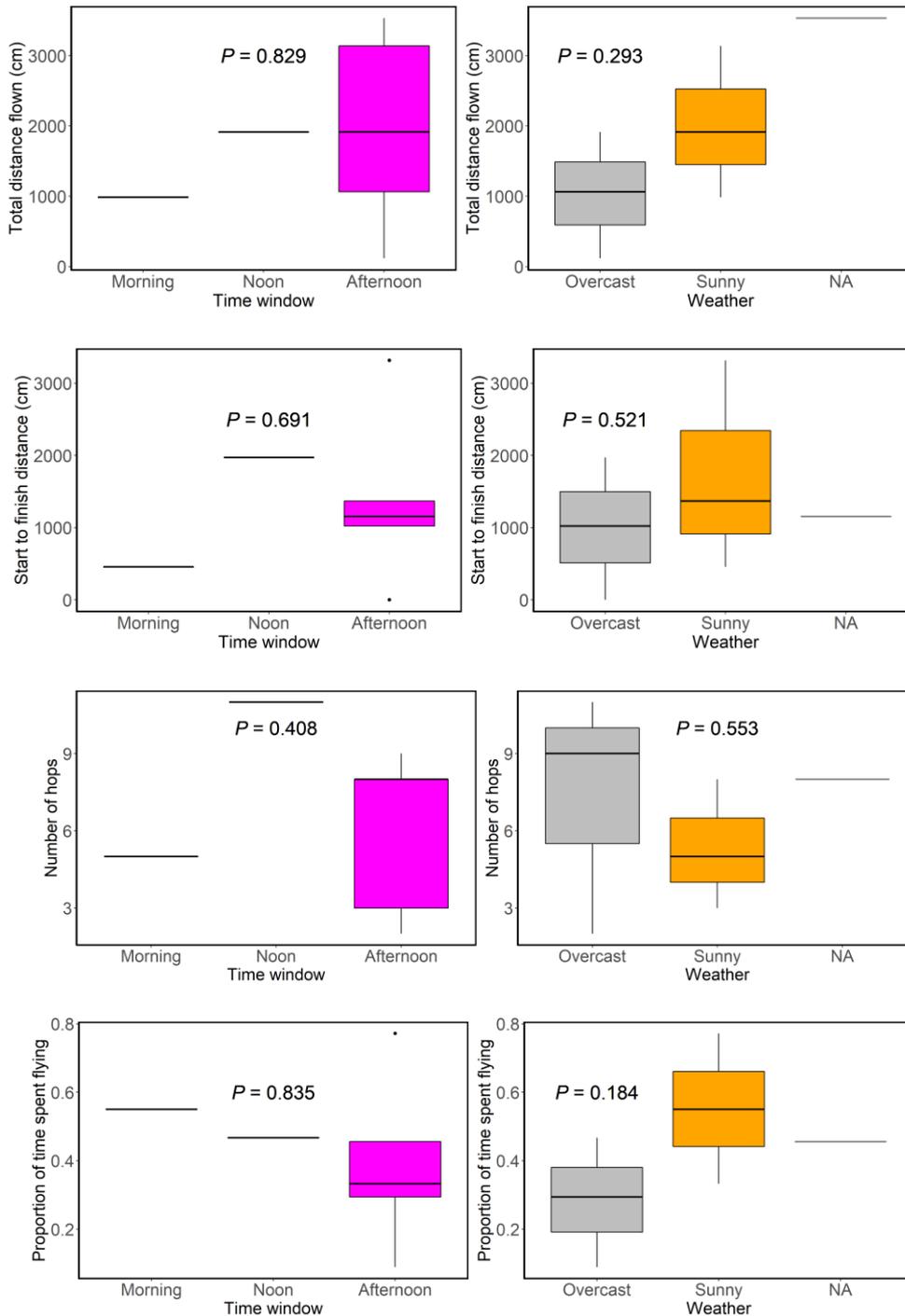
**Table S6.4** Outputs of ANOVA/ Kruskal-Wallis tests run to assess the effects of time window and weather on the resource-use behaviours of *Ypthima* spp. butterflies. Significant differences between time windows and weather categories are given in bold.

Explanatory variable	Response variable	df	F/ Chi-square value*	P-value
Time window (morning/ noon/ afternoon)	Total distance flown (cm)	2	0.099	0.907
	Start to finish distance flown (cm)	2	2.83	0.136
	Number of hops	2	0.3	0.860
	Proportion of time spent flying	2	0.011	0.989
Weather (Sunny/ Overcast)	Total distance flown (cm)	2	1.665	0.238
	Start to finish distance flown (cm)	2	6.875	<b>0.034 *</b>
	Number of hops	2	0.106	0.744
	Proportion of time spent flying	2	2.639	0.155

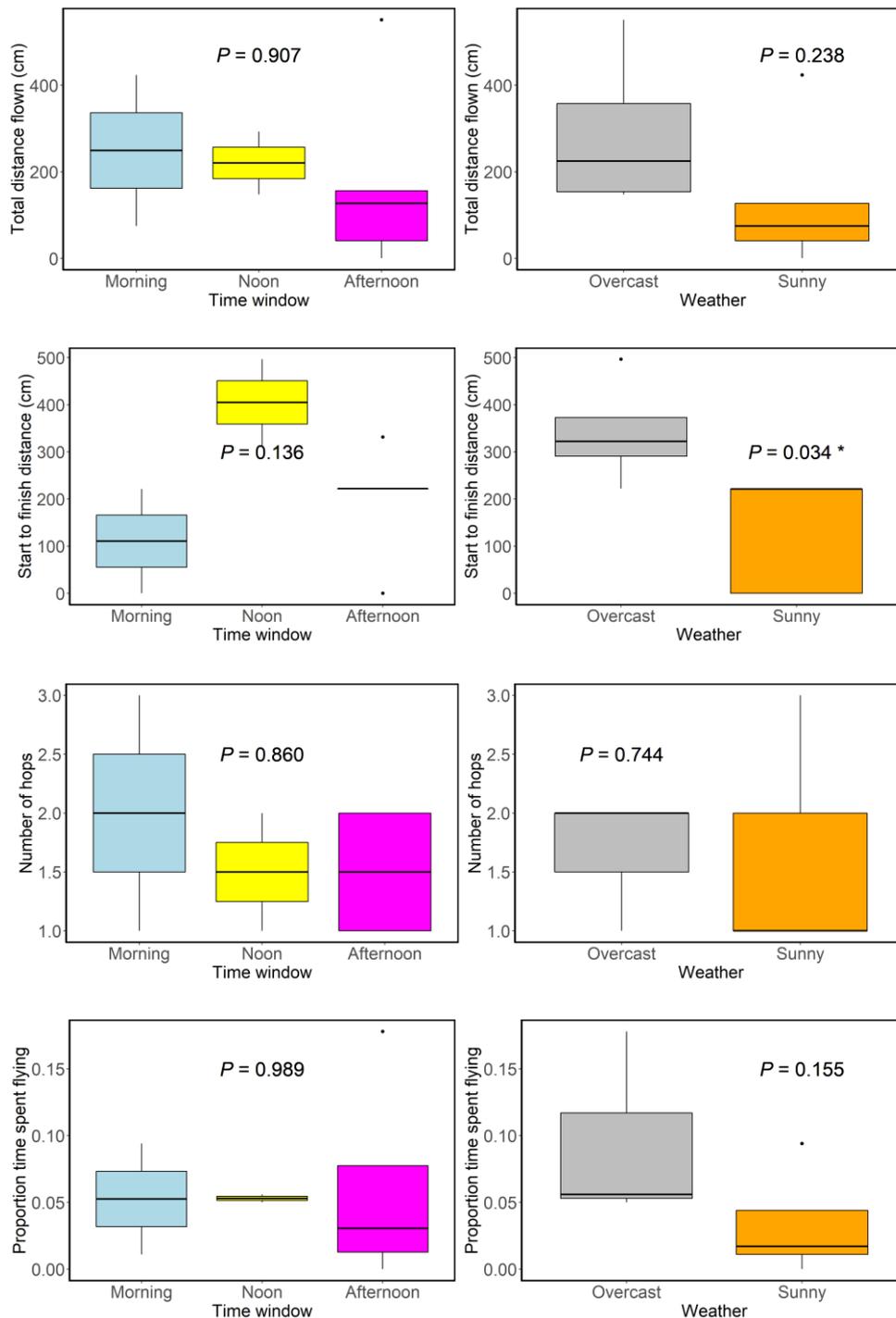
\*F if ANOVA, Chi-square if Kruskal-Wallis

**Table S6.5** Outputs of biserial correlation test to assess whether weather correlated with the habitat use by *Ypthima* spp. butterflies. PC1 and PC2 represented environmental variables forming habitat structure and complexity. Weather was either sunny or overcast.

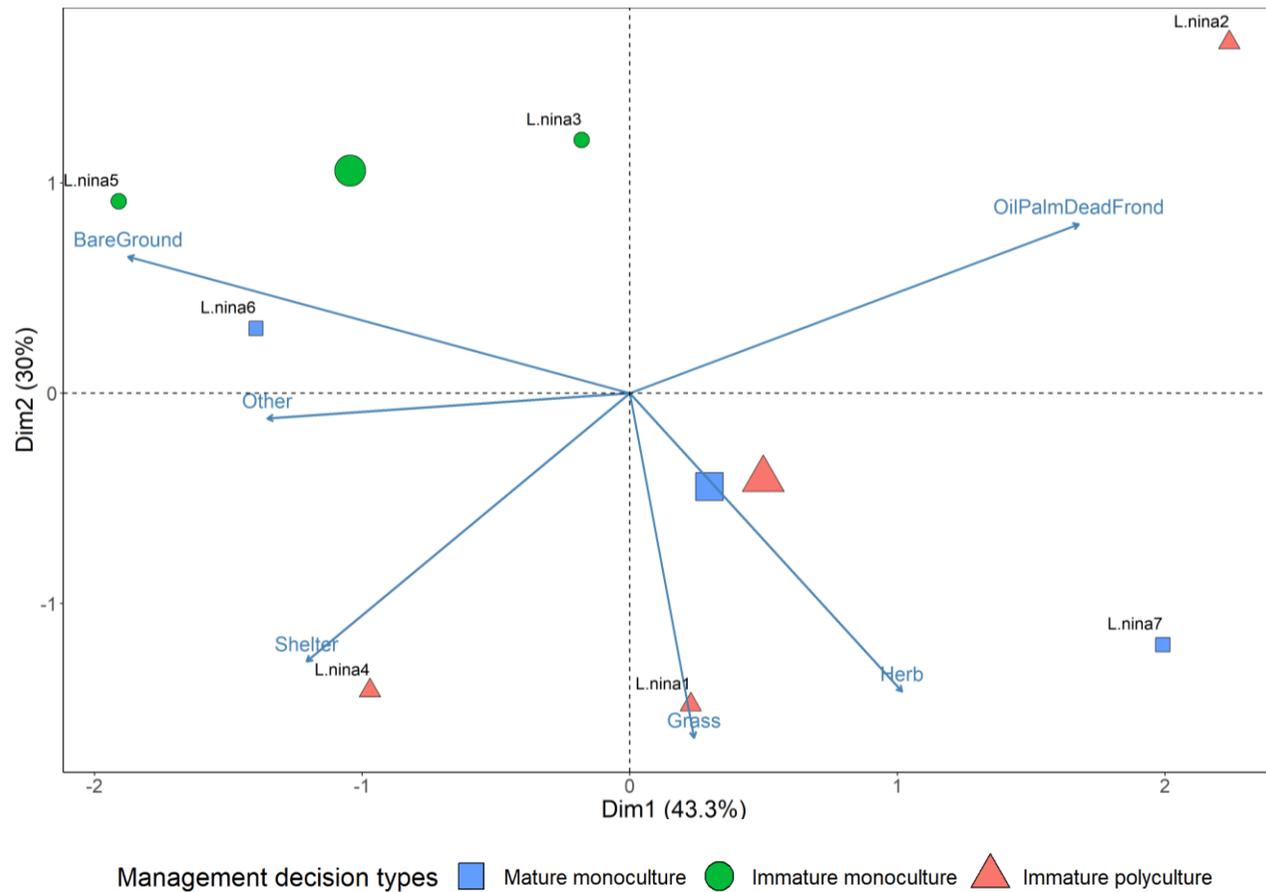
Variables assessed for correlations	Outputs of biserial correlation test
PC1 & weather	-0.354
PC2 & weather	-0.728



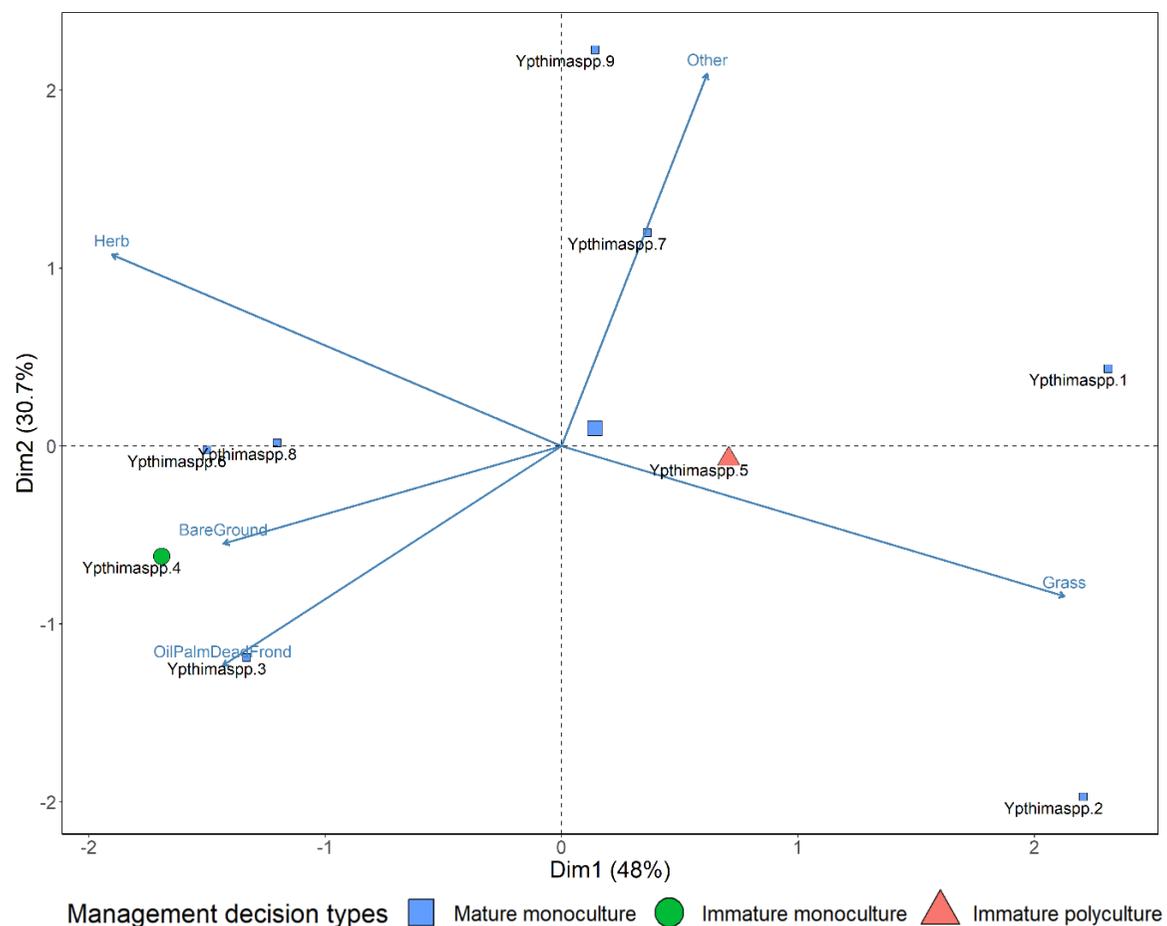
**Figure S6.1** Box plots showing time window (morning, noon, or afternoon) and weather (overcast or sunny) against the total distance flown (cm), start to finish distance flown (cm), number of hops, and proportion of time spent flying of *Leptosia nina* butterflies across plantations with differing structure and complexity. The lines in the middle of boxplots show median values, while the top and bottom of boxplots indicate upper and lower quartiles, respectively. Upper and lower tails indicate maximum and minimum values. Individual points outside of boxplots show outliers. NA indicates missing data. N = 7 individuals.



**Figure S6.2** Box plots showing time window (morning, noon, or afternoon) and weather (overcast or sunny) against total distance flown (cm), start to finish distance flown (cm), number of hops, and proportion of time spent flying of *Ypthima* spp. butterflies across plantations with differing structure and complexity. The lines in the middle of boxplots show median values, while the top and bottom of boxplots indicate upper and lower quartiles, respectively. Upper and lower tails indicate maximum and minimum values. Individual points outside of boxplots show outliers. N = 9 individuals.



**Figure S6.3** PCA plot summarising environmental parameters shaping habitat structure and complexity within oil palm plantations associated with management decision types, based on observations of *Leptosia nina* butterflies. Axes show measured environmental parameters, representing habitat structure and complexity within plantations, which were based on points on which *L. nina* butterflies made perches. Smaller points represent individual observations on *L. nina* butterflies. Larger points represent average values of habitat structure and complexity per management decision types.



**Figure S6.4** PCA plot summarising the environmental parameters shaping habitat structure and complexity within oil palm plantations associated with management types based on observations of *Ypthima* spp. butterflies. Axes show measured environmental parameters, representing habitat structure and complexity, which were based on points on which *Ypthima* spp. butterflies perched. Smaller points represent individual observations on *Ypthima* spp. butterflies. Larger points represent average values of habitat structure and complexity. There is only one point for each of the two immature plantations, because there is only one replicate for each of the immature plantations.

## **Chapter 7: General discussion**

### **7.1 | Objectives of this thesis**

Logging and oil palm expansion are two major drivers of rainforest degradation in Southeast Asia, including Peninsular Malaysia and Borneo, making studies aiming to understand their impacts on biodiversity and how management within altered habitats can be improved, an important part of biodiversity conservation in the region. Despite the growing number of ecological studies investigating this, there are many understudied taxa and unanswered ecological questions around how differing management options affect local wildlife. This research is particularly important because rainforests in Southeast Asia contain an extremely high level of biodiversity, including many sensitive taxa (compared to Africa, Central and South America [Gibson et al., 2011]), and a high level of endemism (Myers et al., 2000). Additionally, agricultural landscapes can support persisting (tolerant to anthropogenic disturbance) taxa that can sometimes be important for supporting production or are crop pests. Therefore, understanding how management can be tailored to the requirements of these organisms can improve biodiversity conservation and support ecosystem functions within altered systems. This thesis investigated the impacts of land-use change and management decisions by industrial oil palm growers (in terms of maintaining riparian buffer strips) on semi-aquatic bugs (Gerromorpha, Hemiptera) in Borneo, and smallholders (in terms of replanting and crop choice post replanting) on butterflies (Rhopalocera, Lepidoptera) in Peninsular Malaysia.

Semi-aquatic bugs, particularly in Southeast Asia, are extremely understudied, making research in this thesis the first to investigate the impacts of land-use change and

associated environmental conditions on this group in the region. Despite numerous ecological studies on butterflies, questions around the effects of varying management approaches within agricultural landscapes in Southeast Asia remain understudied for this group. For instance, we are only aware of three other studies that have investigated how management decisions (crop choice in terms of poly vs monoculture or understory vegetation management within plantations) within oil palm smallholdings affect butterflies, and how plantations can be tailored to increase the abundance or richness of butterflies (Asmah et al., 2017; Azhar et al., 2015; Sunkar et al., 2019). Such studies are of great importance, since 40% of oil palm plantations in Southeast Asia are cultivated by smallholders (Wild Asia, 2012). This means that if better approaches for biodiversity conservation within oil palm smallholding plantations are identified and implemented, they could create a considerable positive change for biodiversity conservation, particularly for butterflies, in altered habitats in the region.

In addition to the above main questions, this thesis has contributed to developing methods which can help assessments of environmental impacts on semi-aquatic bugs, particularly on their biomass, as well as increasing understanding of how butterflies use fine-scale resources within habitats through direct observations. The developed methods to estimate the biomass of semi-aquatic bugs from their body lengths can save time and resources needed to weigh individual samples and provide a higher accuracy of estimation of biomass for this group. Finally, direct observation methods to assess the behaviour of butterflies in using resources within habitats can help to identify parameters and characteristics that are directly important to support butterflies, hence increasing their numbers.

## 7.2 | Synthesis

### 7.2.1 Preventing conversion of remaining primary forest is likely to be the top priority for conservation of biodiversity

This thesis demonstrated the importance of primary (old-growth) forests for conservation of biodiversity, represented by findings on semi-aquatic bugs and butterflies. I found that the average richness of semi-aquatic bugs and butterflies are lower in altered habitats than in primary forests (semi-aquatic bugs: old-growth forest = 13.6, SE  $\pm$  2.9, logged forest = 11.0, SE  $\pm$  2.3, oil palm with riparian buffer strips = 6.0, SE  $\pm$  2.1, oil palm without riparian buffer strips = 4.0, SE  $\pm$  1.0, **Chapter 3**; butterflies (estimated species richness based on Chao1 index): mature monoculture = 42, SE  $\pm$  5.431, immature polyculture = 39, SE  $\pm$  9.138, and immature monoculture = 34, SE  $\pm$  5.905, compared to 138 species in forest in Pahang, Peninsular Malaysia (Suhaimi et al., 2017), **Chapter 5**). This thesis therefore has added novel evidence to the existing findings on how land-use change affects wildlife in Southeast Asia. In particular, the steep decline observed for semi-aquatic bugs following rainforest conversion may indicate that this group is particularly sensitive to disturbance.

Generally, the loss of species following forest conversion is caused by a change in microclimatic conditions and microhabitats, as well as loss of key resources (e.g., substrates for laying eggs, hostplants, nectar sources, or refuges), and loss of connectivity between suitable habitats. In this thesis, the reduction of semi-aquatic bug species due to forest conversion (for logging and oil palm) was associated with changes in environmental conditions at catchment, riparian, and stream scales. At the catchment and riparian scales, reduction in species richness of semi-aquatic bugs was associated with reduced forest cover and quality, basal and leaf area, aboveground biomass, canopy

cover, and vine cover. At the stream scale, associated parameters were reduction in percentage cover of rocks, steep slopes, percentage cover of isolated pools, and flow speed, but increase in water temperature, canopy openness, percentage cover of riffles, rapids, connected pools, and deadwood.

Many other studies have indicated that protection of remaining primary forests should be a priority for biodiversity conservation (e.g., Barlow et al., 2007; Gardner et al., 2009; Kosmos et al., 2018; Spitzer et al., 1993). One of the reasons is that species losses as a result of habitat change are not always immediate, with declines continuing for many years (Angeler et al., 2014; Dumbrell & Hill, 2005), and changes persisting for centuries (Edwards et al., 2014; Rubin et al., 2017). In addition, habitat restoration can take a long time (decades or centuries, for example) and a large investment to return conditions and functions to pre-disturbance levels (Edwards et al., 2014; Ong & Vandermeer, 2018; Poff, 2009). For instance, even though canopy cover in forests can recover when logging is relaxed, one study found that after 53 years, canopy height was still not equivalent to that in primary forests (a study based in logged forests in Peninsular Malaysia, Okuda et al., 2019). Furthermore, the costs of conducting evaluation on a restoration project can be more expensive than running the project itself (Rubin et al., 2017). Protection of intact forest landscapes in Southeast Asia is also crucial due to the need of connectivity for some sensitive species (such as some damselfly species in Carvalho et al., 2018, as well as larvae of aquatic insects and dung beetles in Deere et al., 2022). This is because tropical species can have longer lifespans (e.g., Beck & Fiedler, 2008) and generation times (e.g., Coffman & de la Rosa, 1998), as well as lower local and regional population densities, and patchier distributions (Edwards et al., 2014;

Stratford & Robinson, 2005), compared to temperate species. Considering all the above, protection of primary forests, must be prioritised, before it is too late.

### **7.2.2 Connectivity: the impacts of edge effects on terrestrial species and the importance of land and water linkage for conservation of aquatic species**

In the context of terrestrial systems, the conditions surrounding a single habitat (edge effects) can have significant implications for the populations of local species, particularly mobile species. This thesis found that the conditions surrounding smallholding oil palm plantations had a significant influence on the abundance of butterflies (**Chapter 5**). Plantations that were surrounded by road had a higher abundance of butterflies, indicating isolation due to the presence of roads (Muñoz et al., 2015). On the other hand, plantations that were surrounded by polyculture plantations and housings had a lower butterfly abundance, indicating movement from within plantations to surrounding habitats, potentially due to the presence of resources nearby (e.g., polyculture plantations can consist of crops that can be food plants for butterflies, and houses can have gardens that contain nectar sources). Considering these results, management by stakeholders, particularly oil palm smallholders in this case, should take spatial effect (“connectivity”) into account. Since smallholding plantations are commonly smaller (e.g., between 0.245 and 1.29 acres, **Chapter 5 & 6**; less than 50 hectares in Shuhada et al., 2020) than industrial plantations (that can cover thousands of hectares, e.g., Shuhada et al., 2020) and owners often live close to each other as neighbours, it is possible that smallholders could work together to support local biodiversity.

The connection between land and water means that any modification occurring on land has impacts on both terrestrial and aquatic ecosystems. For example, studies have demonstrated that land-use change alters many aspects of waterways, including its morphological characteristics and features (e.g., Luke et al., 2017a) and aquatic assemblages (e.g., Chellaiah & Yule, 2018; Dias-Silva et al., 2020a). When forest is converted into a plantation, there is often runoff of soil particulates as well as nutrients, and chemicals (herbicides and pesticides), particularly if crops are grown to the edge of waterways (Williamson et al., 2008). Such runoff disrupts the natural state of the water chemistry and alters channel physical structure. Additionally, modifications that occur in the area surrounding water bodies can alter the microclimatic conditions in and around the water (**Chapter 3 & 4**) and reduce inputs from riparian habitats (Lo et al., 2020). This in turn, can cause the loss of some taxa whose preferred microhabitats are lost, reduced, or altered due to shifts in stream conditions.

Finally, habitat disturbance and change on land affecting aquatic ecosystems also represents potential threats to human health and wellbeing. For instance, inputs from the catchment surrounding waterways can pollute water, making it unsafe for humans to use. In addition, if waterways are polluted, consumption of freshwater species, such as fish, might also impact the health of people who eat them (Al-Mamun et al., 2018; Williamson et al., 2008). In the longer term, the loss of sensitive taxa might disrupt the stability of an aquatic system, resulting in declines of taxa of direct benefits to people (Feio et al., 2023). Since a high number of people in Southeast Asia live in rural areas (The World Bank, 2023) or rely on farming, and use waterways in this way for drinking (Ismail & Go, 2021), change in the water quality could impact a very large number of people.

### **7.2.3 Importance of taking large- and small-scale approaches to understand habitat change and incorporate biodiversity conservation into altered habitats**

As a complement to preventing further conversion of primary forests, conservation efforts should also be conducted outside of protected areas. Such approaches can support persisting (tolerant) taxa through provision of habitats and resources. This approach will not protect disturbance intolerant or forest specialist taxa (Atkinson et al., 2022), but can support a higher level of biodiversity in the surrounding landscape, as well as associated functions. Studies have shown the importance of incorporating both landscape (large) and local (small) scale biodiversity conservation approaches in altered habitats (e.g., Ashton-Butt et al., 2018; Kurz et al., 2016; Luke et al., 2017b), and this thesis has also demonstrated this. Indeed, management that considers key requirements of target taxa often has a higher success rate for effective conservation (e.g., Kolkman et al., 2022). This is because effective management for biodiversity conservation provides the conditions and resources that targeted taxa need to feed and reproduce (Kolkman et al., 2022; Samways et al., 2020), such as nest and egg laying sites, food resources, shelter, and connectivity (Samways et al., 2020).

At the large scale, in **Chapters 3 and 5**, this thesis identified several environmental parameters that significantly impacted semi-aquatic bugs (in terms of abundance, species richness, and community composition) and butterflies (abundance) within oil palm landscapes. We found higher richness and abundance of semi-aquatic bugs in streams with forested margins (riparian buffer strips) and within streams which had less rapid flow speed, lower water temperature and average canopy openness, as well as lower percentage rapids and riffles, and those with steeper slopes, and higher percentage cover of rocks, isolated pools, and deadwood (**Chapter 3**). For butterflies,

there was a higher density of butterflies with more understory vegetation (particularly species that are hostplants for larvae) and more abundant nectar sources (**Chapter 5**). These findings therefore can inform plantation managers on factors that are likely to increase the abundance of both taxa.

At the small scale (10-meter transects), **Chapter 4** found that the presence of riparian buffer strips was significantly associated with a higher number of semi-aquatic bugs, and impacted community composition. Within-stream physical structure was also associated with more abundant semi-aquatic bugs at the small scale (particularly wider wetted width, more isolated pools, shallower slopes, and lower percentage of deadwood). Additionally, streams with forested riparian buffer strips supported a higher richness of semi-aquatic bugs than streams without (although still considerably lower than streams with a forested catchment, i.e., only by two species in this thesis). Furthermore, streams with higher canopy openness, higher percentage cover of deadwood, lower percentage cover of pebbles, and narrower wetted width were associated with a higher proportion of juvenile bugs (**Chapter 4**). Finally, in **Chapter 6**, understory vegetation characteristics affected the behaviours of two common butterfly species (*Leptosia nina* and *Ypthima* spp.). From the direct observations, I found that understory vegetation within plantations supported the resource-use behaviours of the two butterfly species, particularly by providing nectar sources and substrates for resting and sunning. Similar with the large-scale effects, tailoring management to the requirements of target taxa at the small scale could potentially provide better support for such taxa within altered habitats (Reiss-Woolever et al., 2023a, b).

#### **7.2.4 Working with varied stakeholders with differing management decisions**

Findings from this thesis (**Chapters 3 – 6**) and other studies from the existing literature (e.g., King & Brown, 2010; Reed et al., 2008) indicate that management to support biodiversity conservation should be tailored to the type of stakeholders. Industrial plantations and smallholders differ in size and in how they manage plantations. Firstly, industrial plantations are generally larger in size than smallholdings (Shuhada et al., 2020). Secondly, unlike industrial plantations, smallholding plantations tend to be located among other types of land-use, such as habitation (**Chapter 5**). Such an arrangement will have different impacts on local wildlife, when compared to industrial plantations. For instance, this thesis found that differing neighbouring habitat types surrounding a plantation significantly affected the abundance of butterflies (**Chapter 5**). Thirdly, industrial plantations and smallholdings also differ in their management (Comte et al., 2012; Shuhada et al., 2020), again resulting in different impacts on the environment. For example, industrial oil palm has more extensive research and development to improve production, such as leaf and soil analyses, whilst smallholdings commonly do not have access to such sophisticated approaches. As a result, industrial plantations are often much more targeted in their application of pesticides and fertilisers (Comte et al., 2012). Additionally, as shown in this thesis, some smallholders cultivated oil palm with other crops (polyculture), unlike industrial plantations. Although we found no significant effects of practicing such polyculture on the diversity and abundance of butterflies (**Chapter 5**), oil palm polyculture plantations could provide food resources for local butterflies, such as fruit-producing crops that can be food resources for fruit-feeding butterflies (Asmah et al., 2017), opening up a possibility of enhancing the number of local butterflies within smallholding plantations.

Considering the above, to provide better habitats and resources for biodiversity, recommendations for optimum agricultural practices should be tailored to the type of estate under consideration. Although current policies have been established according to the type of stakeholders (RSPO, 2018), understanding on how differing layouts of plantations and management practices can impact wildlife differently is still lacking (Luke et al., 2019b; Popkin et al., 2022). Therefore, this thesis has provided new evidence of how current management in industrial and smallholding plantations affect local biodiversity.

#### **7.2.5 The pervading effects of climate change**

Climate change can exacerbate existing threats from forest conversion and associated impacts (pollution as well as altered chemical and physical structures of habitats) in terrestrial (Habel et al., 2021; Molina-Martínez et al., 2016) and freshwater systems (to Bühne et al., 2021; Carpenter et al., 2011). Impacts resulting from climate change, such as warming average temperatures, changes in the lengths of seasons, as well as increased extreme weather events, can drive extinction of species, particularly those that are temperature sensitive. Habitat change can also alter microclimatic conditions within a system (Lembrechts & Nijs, 2020), potentially making habitats more susceptible to climate change-induced warming. For instance, the loss of canopy cover in oil palm streams without riparian buffer strips, that I found in this study, as well as the hotter air temperature within oil palm plantations than forests (Hardwick et al., 2015) can be even higher with a warming climate, potentially causing more loss of sensitive species. To avoid further loss of biodiversity, conservation management within altered habitats

should be tailored to facilitate organisms to get the resources they need, such as access to shelter and breeding sites, food plants, or prey items.

In this thesis, I identified several factors that are associated with a higher abundance or richness of semi-aquatic bugs (**Chapter 3 & 4**) as well as abundance of butterflies (**Chapter 5**) and their behaviours (**Chapter 6**), and those factors are potentially related to the resources these two taxa need to survive and reproduce. Therefore, more research investigating the potential dual benefits of these approaches (for guarding against habitat loss effects and climate change effects) is needed. Some studies predict that species in the tropics may be more vulnerable to climate change, due to their narrower tolerance to environmental temperature variation (Bonacina et al., 2023). Despite existing studies assessing how tropical communities respond to a warming climate, studies answering how differing taxa, such as macroinvertebrates, respond to such change is lacking, meriting further investigation (Bonacina et al., 2023).

### **7.3 | Directions for future research**

This thesis has identified several environmental parameters associated with the richness, abundance, and community composition of semi-aquatic bugs, as well as the density of butterfly assemblages. Future research could be directed to investigate the effects of those parameters further and assess whether they benefit these two taxa, in terms maintaining similar community/ assemblage composition to forest sites. Paired to this, future research could investigate how these factors affect the food web in a local system, to quantify any cascading effects through the ecosystem. Such research could provide clarity in how the population size of a taxon affects other taxa and higher trophic levels.

For semi-aquatic bugs, further research could also include assessments of the effects of differing buffer widths on semi-aquatic bug communities. This thesis has demonstrated that the loss of riparian buffer strips alters the community composition of semi-aquatic bugs, indicating the importance of maintaining forested riparian margins. However, it is still not known if differing buffer size will have different effects on semi-aquatic bugs. In addition, since findings in this thesis are based on studies in industrial plantations, it is not certain if the same results would be obtained for smallholdings. Hence, another potential scope of research is assessing the effect of forest buffers in a smallholding context. This is particularly relevant, since characteristics and management of industrial and smallholding plantations differ (Comte et al., 2012; Shuhada et al., 2020). Assessing the effects of alternative riparian margin restoration on semi-aquatic bugs is also another potential area for further study, particularly regarding the type of vegetation forming the buffer strips.

For butterflies, research could also be carried out to assess the efficiency of conservation efforts, if local smallholders work together. I found that the population of wildlife in a plantation is significantly affected by the conditions of its surrounding area. Hence, there is potential scope for research to assess whether tailoring efforts within and around plantations could benefit butterfly assemblages. Since butterflies are a popular animal group among smallholders in the study sites (from surveys conducted by a colleague in our research group), their popularity could be used as a tool to garner further conservation efforts within smallholding plantations. For example, during my studies, I corresponded about butterflies with smallholders through a WhatsApp group, which could represent a tool for supporting coordinated smallholder management. Finally, the

behavioural methods that I developed in **Chapter 6** could be applied to a wider range of butterfly species and study systems.

At a broader level, future research should also consider incorporating the impacts of inputs from multiple systems on biodiversity, since human actions often cause widespread effects (Ormerod et al., 2010). In an oil palm context, there are many aspects of management that were not directly assessed in this study, but could potentially affect freshwater communities, such as how wastewater from oil palm mills is treated and how this affects waterways and local species. There are also very few studies that assess how interactions between land-use change and climate change affect dynamics within freshwater systems, such as streamflow, water temperature (due to global warming), habitat structure, aquatic species, and ecosystem processes (Taniwaki et al., 2017).

Finally, in terms of restoring degraded systems for biodiversity conservation, it is important to identify and quantify specific targets for restoration (Rubin et al., 2017). Such targets should be tailored to differing priorities in different systems, particularly in terms of what functions or services should be prioritised. For polluted urban streams, for example, restoring water quality may be the top priority, rather than restoring habitats to meet the requirements of certain taxa. In contrast, in other less-degraded areas, more targeted interventions, such as adding dead wood into water bodies, may be more appropriate to benefit taxa with these requirements, but which may not be heavily influenced by water quality (Rubin et al., 2017).

## 7.4 | Conclusion

This thesis has provided novel evidence about the impacts of rainforest logging and conversion to oil palm on semi-aquatic bugs in Sabah, Borneo as well as effects of replanting and management decisions within oil palm smallholdings on butterfly assemblages in Banting, Peninsular Malaysia. Rainforest conversion reduces species richness and abundance of semi-aquatic bugs in Borneo, while differing management decision of oil palm smallholders do not have significant impacts on butterfly assemblages in Peninsular Malaysia. In addition, I have demonstrated that tailoring management at large and small scales can improve biodiversity conservation in altered systems, particularly for semi-aquatic bugs and butterflies. I also developed length-biomass equations that can be used to estimate the biomass of semi-aquatic bugs from their body lengths, facilitating future ecological studies to consider assessment on biomass of semi-aquatic bugs. Additionally, the developed methods for direct observations on butterflies can be used to understand how different butterfly species use resources within habitats. As habitat change continues to accelerate worldwide, and the impacts of climate change on taxa become more marked, it is more important than ever that conservation approaches are developed to efficiently target conservation protection to the most biodiverse areas, while also supporting functionally important taxa in the wider landscape. My thesis has added to the body of knowledge supporting these approaches for understudied taxa and ecosystems.

## References

- Al-Mamun, M., Chowdhury, T., Biswas, B., & Absar, N. (2018). *Chapter 11 - Food Poisoning and Intoxication: A Global Leading Concern for Human Health in Food Safety and Preservation (Modern Biological Approaches to Improving Consumer Health)*. 307–352. <https://doi.org/10.1016/B978-0-12-814956-0.00011-1>.
- Al-Shami, S.A., Md Rawi, C.S., Ahmad, A.H., Hamid, S.A., Mohd Nor, S.A. (2011). Influence of agricultural, industrial, and anthropogenic stresses on the distribution and diversity of macroinvertebrates in Juru River Basin, Penang, Malaysia. *Ecotoxicology and Environmental Safety*, 74, 1195–1202. <https://doi.org/10.1016/j.ecoenv.2011.02.022>.
- Alias, M.A. (1995). An introduction to tropical rainforests in Malaysia. *Eco-Habitat*, 2(1), 53–54. [https://doi.org/10.24600/ecohabitat.2.1\\_App3](https://doi.org/10.24600/ecohabitat.2.1_App3).
- Allan, J.D. (2004). Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 35, 257–284. <https://doi.org/10.1146/annurev.ecolsys.35.120202.110122>.
- Allen, K., Corre, M.D., Tjoa, A., & Veldkamp, E. (2015). Soil nitrogen-cycling responses to conversion of lowland forests to oil palm and rubber plantations in Sumatra, Indonesia. *Public Library of Sciences (PLOS) One*, 10(7), e0133325. <https://doi.org/10.1371/journal.pone.0133325>.
- Andersen, N.M. (1997). A phylogenetic analysis of the evolution of sexual dimorphism and mating systems in water striders (Hemiptera: Gerridae). *Biological Journal of the Linnean Society*, 61, 345–368. <https://doi.org/10.1111/j.1095-8312.1997.tb01796.x>.
- Andersen, N.M. (1993). The evolution of wing polymorphism in water striders (Gerridae): a phylogenetic approach. *Oikos*, 67(3), 433–443. <https://doi.org/10.2307/3545355>.
- Andersen, N.M. (1982). *The Semiaquatic Bugs (Hemiptera, Gerromorpha): Phylogeny, Adaptations, Biogeography and Classification*. Entomonograph Volume 3. Scandinavian Science Press Ltd. Klampenborg, Denmark.

- Andersen, N.M. & Weir, T.A. (1997). The Gerrinae water striders of Australia (Hemiptera: Gerridae): taxonomy, distribution, and ecology. *Invertebrate Taxonomy* 11, 203–299. <https://doi.org/10.1071/IT95047>.
- Andersen, N.M., Yang, C.M., & Zettel, H. (2002). Guide to the aquatic Heteroptera of Singapore and Peninsular Malaysia. *The Raffles Bulletin of Zoology*, 50(1), 231–249.  
[https://www.researchgate.net/publication/297273170\\_Guide\\_to\\_the\\_aquatic\\_Heteroptera\\_of\\_Singapore\\_and\\_Peninsular\\_Malaysia\\_-\\_2\\_Veliidae](https://www.researchgate.net/publication/297273170_Guide_to_the_aquatic_Heteroptera_of_Singapore_and_Peninsular_Malaysia_-_2_Veliidae).
- Angeler, D.G., Allen, C.R., Birge, H.E., Drakare, S., McKie, B.G., & Johnson, R.K. (2014). Assessing and managing freshwater ecosystems vulnerable to environmental change. *Ambio*, 43, 113–125. <https://doi.org/10.1007/s13280-014-0566-z>.
- Armisen, D., Refki, P.N., Crumière, A.J.J., Viala, S., Toubiana, W., & Khila, A. (2015). Predator strike shapes antipredator phenotype through new genetic interactions in water striders. *Nature Communications*, 6, 8153. <https://doi.org/10.1038/ncomms9153>.
- Arnaiz, O.L., Wilson, A.L., Watts, R.J., & Stevens, M.M. (2011). Influence of riparian condition on aquatic macroinvertebrate communities in an agricultural catchment in south-eastern Australia. *Ecological Research*, 26(1), 123–131. <https://doi.org/10.1007/s11284-010-0767-2>.
- Ashton-Butt, A., Willcock, S., Purnomo, D., Suhardi, Aryawan, A.A.K., Wahyuningsih, R., Naim, M., Poppy, G.M., Caliman, J.-P., Peh, K.S.H., & Snaddon, J.L. (2019). Replanting of first-cycle oil palm results in a second wave of biodiversity loss. *Ecology and Evolution*, 9(11), 6433–6443. <https://doi.org/10.1002/ece3.5218>.
- Ashton-Butt, A., Aryawan, A.A.K., Hood, A.S.C., Naim, M., Purnomo, D., Suhardi, Wahyuningsih, R., Willcock, S., Poppy, G.M., Caliman, J.-P., Turner, E.C., Foster, W.A., Peh, K.S.-H., & Snaddon, J.L. (2018). Understory vegetation in oil palm plantations benefits soil biodiversity and decomposition rates. *Frontiers in Forests and Global Change*, 1. <https://doi.org/10.3389/ffgc.2018.00010>.

- Asmah, S., Ghazali, A., Syafiq, M., Yahya, M.S., Peng, T.L., Norhisham, A.R., Puan, C.L., Azhar, B., & Lindenmayer, D.B. (2017). Effects of polyculture and monoculture farming in oil palm smallholdings on tropical fruit-feeding butterfly diversity. *Agricultural and Forest Entomology*, 19(1), 70–80. <https://doi.org/10.1111/afe.12182>.
- Asner, G.P., Rudel, T.K., Mitchell Aide, T., Defries, R., & Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. *Conservation Biology*, 23(6), 1386–1395. <https://doi.org/10.1111/j.1523-1739.2009.01333.x>.
- Atkinson, J., Brudvig, L.A., Mallen-Cooper, M., Nakagawa, S., Moles, A.T., & Bonser, S.P. (2022). Terrestrial ecosystem restoration increases biodiversity and reduces its variability, but not to reference levels: A global meta-analysis. *Ecology Letters*, 25(7), 1725–1737. <https://doi.org/10.1111/ele.14025>.
- Auguie, B. (2017). *gridExtra: Miscellaneous Functions for 'grid' Graphics*. R package v.2.3. <https://CRAN.R-project.org/package=gridExtra>.
- Azevedo-Santos, V.M., Brito, M.F.G., Manoel, P.S., Perroca, J.F., Rodrigues-Filho, J.L., Paschoal, L.R.P., Gonçalves, G.R.L., Wolf, M.R., Blettler, M.C.M., Andrade, M.C., Nobile, A.B., Lima, F.P., Ruocco, A.M.C., Silva, C.V., Perbiche-Neves, G., Portinho, J.L., Giarrizzo, T., Arcifa, M.S., & Pelicice, F.M. (2021). Plastic pollution: A focus on freshwater biodiversity. *Ambio*, 50, 1313–1324. <https://doi.org/10.1007/s13280-020-01496-5>.
- Azhar, A., Hartke, T.R., Böttges, L., Lang, T., Larasati, A., Novianti, N., Tawakkal, I., Hidayat, P., Buchori, D., Scheu, S. & Drescher, J. (2022). Rainforest conversion to cash crops reduces abundance, biomass and species richness of parasitoid wasps in Sumatra, Indonesia. *Agricultural and Forest Entomology*, 24(4), 506–515. <https://doi.org/10.1111/afe.12512>.
- Azhar, B., Puan, C.L., Aziz, N., Sainuddin, M., Adila, N., Samsuddin, S., Asmah, S., Syafiq, M., Razak, S.A., Hafizuddin, A., Hawa, A. & Jamian, S. (2015). Effects of in situ habitat quality and landscape characteristics in the oil palm agricultural matrix on tropical understory birds, fruit bats and butterflies. *Biodiversity and Conservation*, 24, 3125–3144. <https://doi.org/10.1007/s10531-015-1005-6>.

- Bar-On, Y.M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America*, 115(25), 6506–6511. <https://doi.org/10.1073/pnas.1711842115>.
- Barclay, H., Gray, C.L., Luke, S.H., Nainar, A., Snaddon, J.L., & Turner, E.C. (2017). *RSPO manual on best management practices (BMPs) for the management and rehabilitation of riparian reserves. Guidance*. Endorsed by the RSPO Biodiversity and High Conservation Values Working Group. <https://doi.org/10.13140/RG.2.2.17011.22561>.
- Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., & Peres, C.A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, 104(47), 18555-18560. <https://doi.org/10.1073/pnas.0703333104>.
- Barnes, D.E. & Chan, L.G. (1990). *Common weeds of Malaysia and their control*. Ancom Berhad.
- Barrantes, G. & Sandoval, L. (2009). Conceptual and statistical problems associated with the use of diversity indices in ecology. *Revista de Biología Tropical*, 57(3), 451–457. <https://www.scielo.sa.cr/pdf/rbt/v57n3/art01v57n3.pdf>.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://arxiv.org/pdf/1406.5823.pdf>.
- Batty, L.C., Auladell, M., & Sadler, J. (2010). *The impacts of metalliferous drainage on aquatic communities in streams and rivers*, Chapter 4 in *Ecology of Industrial Pollution*, edited by L.C. Batty & K.B. Hallberg. Cambridge University Press.
- Bay, E.C. (1974). Predator-prey relationships among aquatic insects. *Annual Review of Entomology*, 19, 441–453. <https://doi.org/10.1146/annurev.en.19.010174.002301>.

- Beck, J. & Fidler, K. (2008). Adult life spans of butterflies (Lepidoptera: Papilionoidea + Hesperioidea): broadscale contingencies with adult and larval traits in multi-species comparisons. *Biological Journal of the Linnean Society*, 96(1), 166–184. <https://doi.org/10.1111/j.1095-8312.2008.01102.x>.
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., & Harrison, P.A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19, 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>.
- Birnie-Gauvin, K., Lynch, A.J., Franklin, P.A., Reid, A.J., Landsman, S.J., Tickner, D., Dalton, J., Aarestrup, K., & Cooke, S.J. (2023). The RACE for freshwater biodiversity: Essential actions to create the social context for meaningful conservation. *Conservation Science and Practice*, 5, e12911. <https://doi.org/10.1111/csp2.12911>.
- Bitterlich, W. (1984). *The Relascope Idea: Relative Measurements in Forestry*. Farnham Royal, Slough, UK.
- Bladon, A.J., Lewis, M., Bladon, E.K., Buckton, S.J., Corbett, S., Ewing, S.R., Hayes, M.P., Hitchcock, G.E., Knock, R., Lucas, C., McVeigh, A., Menéndez, R., Walker, J.M., Fayle, T.M., & Turner, E.C. (2020). How butterflies keep their cool: Physical and ecological traits influence thermoregulatory ability and population trends. *Journal of Animal Ecology*, 89(11), 2440–2450. <https://doi.org/10.1111/1365-2656.13319>.
- Blanco-Canqui, H., Gantzer, C.J., Anderson, S.H., Alberts, E.E., & Thompson, A.L. (2004). Grass barrier and vegetative filter strip effectiveness in reducing runoff, sediment, nitrogen, and phosphorus loss. *Soil Science Society of America Journal*, 68(5), 1670–1678. <https://doi.org/10.2136/sssaj2004.1670>.
- Bonacina, L., Fasano, F., Mezzanotte, V., & Fornaroli, R. (2023). Effects of water temperature on freshwater macroinvertebrates: a systematic review. *Biological Reviews*, 98(1), 191–221. <https://doi.org/10.1111/brv.12903>.
- Bonte, D., & Dyck, H. Van. (2009). Mate-locating behaviour, habitat-use, and flight morphology relative to rainforest disturbance in an Afrotropical butterfly.

*Biological Journal of the Linnean Society*, 96(4), 830–839.  
<https://doi.org/10.1111/j.1095-8312.2008.01125.x>.

Borgelt, J., Dorber, M., Høiberg, M.A., & Verones, F. (2022). More than half of data deficient species predicted to be threatened by extinction. *Communications Biology*, 5, 679. <https://doi.org/10.1038/s42003-022-03638-9>.

Börschig, C., Klein, A.-M., von Wehrden, H., & Krauss, J. (2013). Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic and Applied Ecology*, 14(7), 547–554. <https://doi.org/10.1016/j.baae.2013.09.002>.

Brown, N.D. & Whitmore, T.C. (1992). Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 335(1275), 369–378. <https://doi.org/10.1098/rstb.1992.0028>.

to Bühne, H.S., Tobias, J.A., Durant, S.M., & Pettorelli, N. (2021). Improving predictions of climate change–land use change interactions. *Trends in Ecology & Evolution*, 36(1), 29–38. <https://doi.org/10.1016/j.tree.2020.08.019>.

Burdon, F.J. & Harding, J.S. (2008). The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshwater Biology*, 53, 330–346. <https://doi.org/10.1111/j.1365-2427.2007.01897.x>.

Bush, J.W.M., & Hu, D.L. (2005). Walking on water: biolocomotion at the interface. *Annual Review of Fluid Mechanics*, 38, 339–69. <https://doi.org/10.1146/annurev.fluid.38.050304.092157>.

Carpenter, S.R., Stanley, E.H., & vander Zanden, M.J. (2011). State of the world's freshwater ecosystems: Physical, chemical, and biological changes. *Annual Review of Environment and Resources*, 36, 75–99. <https://doi.org/10.1146/annurev-environ-021810-094524>.

Carvalho, F.G., de Oliveira Roque, F., Barbosa, L., de Assis Montag L.F., & Juen L. (2018). Oil palm plantation is not a suitable environment for most forest specialist species of Odonata in Amazonia. *Animal Conservation*, 21, 526–533. <https://doi.org/10.1111/acv.12427>.

- Cazzolla Gatti, R. (2016). Freshwater biodiversity: a review of local and global threats. *International Journal of Environmental Studies*, 73(6), 887–904. <https://doi.org/10.1080/00207233.2016.1204133>.
- Ceneviva-Bastos, M<sup>o</sup>., & Casatti, L. (2014). Shading effects on community composition and food web structure of a deforested pasture stream: Evidences from a field experiment in Brazil. *Limnologica*, 46, 9–21. <https://doi.org/10.1016/j.limno.2013.11.005>.
- Chao, A. & Chiu, C.H. (2016). *Species richness: estimation and comparison*. Wiley StatsRef: Statistics Reference Online. 1-26. <https://doi.org/10.1002/0471667196.ess5051>.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67. <https://doi.org/10.1890/13-0133.1>.
- Chaturvedi, S. & Mansi. (2022). Types of biomass burning in South East Asia and its impact on health. *EQA - International Journal of Environmental Quality*, 50, 55–79. <https://doi.org/10.6092/issn.2281-4485/15539>.
- Chellaiah, D. & Yule, C.M. (2018). Riparian buffers mitigate impacts of oil palm plantations on aquatic macroinvertebrate community structure in tropical streams of Borneo. *Ecological Indicators*, 95(1), 53–62. <https://doi.org/10.1016/j.ecolind.2018.07.025>.
- Chen, P.P., Nieser, N., & Zettel, H. (2021). *The aquatic and semi-aquatic bugs (Heteroptera: Nepomorpha & Gerromorpha) of Malesia*, 5. Brill.
- Chen, P.P. & Nieser, N. (2002). Taxonomic characters of the male endosomal structure in the genus *Rheumatogonus* Kirkaldy (Hemiptera: Gerridae), with descriptions of four new species from Borneo and Sri Lanka. *Zoologische Mededelingen*, 76, 371–409. [https://repository.naturalis.nl/pub/217480/ZM76\\_371-410.pdf](https://repository.naturalis.nl/pub/217480/ZM76_371-410.pdf).
- Chen, P.P. & Nieser, N. (1992). Gerridae, mainly from Sulawesi and Pulau Buton (Indonesia). Notes on Malesian aquatic and semiaquatic bugs (Heteroptera), III. *Tijdschrift Voor Entomologie*, 135(2), 145–162. <https://archive.org/details/biostor-50004>.

- Chen, P.P. & Nieser, N. (1993a). A taxonomic revision of the Oriental water strider Genus *Metrocoris* Mayr (Hemiptera, Gerridae). Part I. *Steenstrupia Zoological Museum, University of Copenhagen*, 19(1), 1–43.
- Chen, P.P. & Nieser, N. (1993b). A taxonomic revision of the Oriental water strider genus *Metrocoris* Mayr (Hemiptera, Gerridae). Part II. *Steenstrupia*, 19, 45–82.
- Chen, P.P. & Zettel, H. (1998). A taxonomic revision of the Oriental water strider Genus *Ventidius* Distant (Hemiptera, Gerromorpha, Gerridae). *Tijdschrift voor Entomologie*, 141(1–2), 137–208. [https://brill.com/view/journals/tve/141/1-2/article-p137\\_10.xml](https://brill.com/view/journals/tve/141/1-2/article-p137_10.xml).
- Cheng, L. (1973). Marine and freshwater skaters: differences in surface fine structures. *Nature*, 242, 132–133. <https://doi.org/10.1038/242132a0>.
- Cheng, L., Yang, C.M., & Andersen, N.M. (2001). Guide to the aquatic Heteroptera of Singapore and Peninsular Malaysia.I. Gerridae and Hermatobatidae. *The Raffles Bulletin of Zoology*, 49(1), 129–148. <https://escholarship.org/uc/item/5jh4r6wc>.
- Chopra, A.K., Sharma, M.K., & Chamoli, S. (2011). Bioaccumulation of organochlorine pesticides in aquatic system-an overview. *Environmental Monitoring and Assessment*, 173(1–4), 905–916. <https://doi.org/10.1007/s10661-010-1433-4>.
- Coffman, W.P. & de la Rosa, C.L. (1998). Taxonomic composition and temporal organization of tropical and temperate species assemblages of lotic Chironomidae. *Journal of the Kansas Entomological Society*, 71(4), 388–406. <https://www.jstor.org/stable/25085856>.
- Cole, L.J., Stockan, J., & Helliwell, R. (2020). Managing riparian buffer strips to optimise ecosystem services: A review. *Agriculture, Ecosystems and Environment* 296. <https://doi.org/10.1016/j.agee.2020.106891>.
- Comte, I., Colin, F., Whalen, J.K., Grünberger, O., & Caliman, J.-P. (2012). Agricultural practices in oil palm plantations and their impact on hydrological changes, nutrient fluxes and water quality in Indonesia: A review. *Advances in Agronomy*, 116. <https://doi.org/10.1016/B978-0-12-394277-7.00003-8>.
- Cooper, C.M., Moore, M.T., Bennett, E.R., Smith, S., Farris, J.L., Milam, C.D., & Shields, Jr., F.D. (2004). Innovative uses of vegetated drainage ditches for

- reducing agricultural runoff. *Water Science and Technology*, 49(3), 117–123. <https://doi.org/10.2166/wst.2004.0176>.
- Corbacho, C., Sánchez, J.M., & Costillo, E. (2003). Patterns of structural complexity and human disturbance of riparian vegetation in agricultural landscapes of a Mediterranean area. *Agriculture, Ecosystems and Environment*, 95(2–3), 495–507. [https://doi.org/10.1016/S0167-8809\(02\)00218-9](https://doi.org/10.1016/S0167-8809(02)00218-9).
- Corbet, A.S & Pendlebury, H.M. (2020). *The butterflies of the Malay Peninsula*. Fifth edition revised by G.M. van der Poorten & N.E. van der Poorten. Malaysian Nature Society. Kuala Lumpur.
- Covich, A.P., Palmer, M.A., & Crowl, T.A. (1999). The role of benthic invertebrate species in freshwater ecosystem: Zoobenthic species influence energy flows and nutrient cycling. *BioScience*, 49(2), 119–127. <https://doi.org/10.2307/1313537>.
- Crumière, A.J.J., Santos, M.E., Sémon, M., Armisen, D., Moreira, F.F.F., & Khila, A. (2016). Diversity in morphology and locomotory behavior is associated with niche expansion in the semi-aquatic bugs. *Current Biology*, 26(24), 3336–3342. <https://doi.org/10.1016/j.cub.2016.09.061>.
- Cunha, E.J., Cruz, G.M., Faria, A.P.J., De Oliveira, J.N., & Juen, L. (2022). Urban development and industrialization impacts on semiaquatic bugs diversity: A case study in eastern Amazonian streams. *Water Biology and Security*. <https://doi.org/10.1016/j.watbs.2022.100061>.
- Cunha, E.J., Guterres, A.P.M., Godoy, B.S., & Juen, L. (2020). Wing dimorphism in semiaquatic bugs (Hemiptera, Heteroptera, Gerromorpha) as a tool for monitoring streams altered by oil palm plantation in the Amazon. *Ecological Indicators*, 117, 106707. <https://doi.org/10.1016/j.ecolind.2020.106707>.
- Cunha, E.J. & Juen, L. (2020). Environmental drivers of the metacommunity structure of insects on the surface of tropical streams of the Amazon. *Austral Ecology*, 45, 586–595. <https://doi.org/10.1111/aec.12873>.
- Cunha, E.J. & Juen, L. (2017). Impacts of oil palm plantations on changes in environmental heterogeneity and Heteroptera (Gerromorpha and Nepomorpha) diversity. *Journal of Insect Conservation*, 21, 111–119. <https://doi.org/10.1007/s10841-017-9959-1>.

- Cunha, E.J., De Assis Montag, L.F., & Juen, L. (2015). Oil palm crops effects on environmental integrity of Amazonian streams and Heteropteran (Hemiptera) species diversity. *Ecological Indicators*, 52, 422–429. <https://doi.org/10.1016/j.ecolind.2014.12.024>.
- Damgaard, J. (2008). Evolution of the semi-aquatic bugs (Hemiptera: Heteroptera: Gerromorpha) with a re-interpretation of the fossil record. *Acta Entomologica Musei Nationalis Pragae*, 48(2), 251–268. <https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=64d61f5686b47dc063541de083c1a4aa4e6dfceb>.
- Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., & Marini, L. (2017). High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. *Journal of Applied Ecology*, 54(2), 380–388. <https://doi.org/10.1111/1365-2664.12747>.
- Darras, K.F.A., Corre, M.D., Formaglio, G., Tjoa, A., Potapov, A., Brambach, F., Sibhatu, K.T., Grass, I., Rubiano, A.A., Buchori, D., Drescher, J., Fardiansah, R., Hölscher, D., Irawan, B., Kneib, T., Krashevskaya, V., Krause, A., Kreft, H., Li, K., Maraun, M., Polle, A., Ryadin, A.R., Rembold, K., Stiegler, C., Scheu, S., Tarigan, S., Valdés-Urbe, A., Yadi, S., Tschardtke, T., & Veldkamp, E. (2019). Reducing fertilizer and avoiding herbicides in oil palm plantations—ecological and economic valuations. *Frontiers in Forests and Global Change*, 2. <https://doi.org/10.3389/ffgc.2019.00065>.
- Davison, C.W., Rahbek, C., & Morueta-Holme, N. (2021). Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature. *Global Change Biology*, 27(21), 5414–5429. <https://doi.org/10.1111/gcb.15846>.
- Daisuke, H., Tanaka, K., Jawa, K.J., Ikuo, N., & Katsutoshi, S. (2013). Rehabilitation of degraded tropical rainforest using dipterocarp trees in Sarawak, Malaysia. *International Journal of Forestry Research*. <https://doi.org/10.1155/2013/683017>.
- De Pauw, N. & Roels, D. (1988). Relationship between biological and chemical indicators of surface water quality. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen*, 23, 1553–58. <https://doi.org/10.1080/03680770.1987.11898061>.

- Deere, N.J., Bicknell, J.E., Mitchell, S.L., Afendy, A., Baking, E.L., Bernard, H., Chung, A.Y.C., Ewers, R.M., Heroin, H., Joseph, N., Lewis, O.T., Luke, S.H., Milne, S., Fikri, A.H., Parrett, J.M., Payne, M., Rossiter, S.J., Vairappan, C.S., Vian, C.V., Wilkinson, C.L., Williamson, J., Wong, A.B.H, Slade, E.M., Davies, Z.G., & Struebig, M.J. (2022). Riparian buffers can help mitigate biodiversity declines in oil palm agriculture. *Frontiers in Ecology and the Environment*. <https://doi.org/10.1002/fee.2473>.
- Dennis, R.L.H. & Sparks, T.H. (2005). Landscape resources for the territorial Nymphalid butterfly *Inachis io*: Microsite landform selection and behavioral responses to environmental conditions. *Journal of Insect Behavior*, 18(5), <https://doi.org/10.1007/s/0905-05-7022-7>.
- Dias-Silva, K., Brasil, L.S., Juen, L., Cabette, H.S.R., Costa, C.C., Freitas, P.V., & De Marco Jr., P. (2020a). Influence of local variables and landscape metrics on Gerromorpha (Insecta: Heteroptera) assemblages in savanna streams, Brazil. *Neotropical Entomology*, 49, 191–202. <https://doi.org/10.1007/s13744-019-00748-8>.
- Dias-Silva, K., Brasil, L.S., Veloso, G.K.O., Cabette, H.S.R., & Juen, L. (2020b). Land use change causes environmental homogeneity and low beta-diversity in Heteroptera of streams. *Annales de Limnologie*, 56, 9. <https://doi.org/10.1051/limn/2020007>.
- Dislich, C., Keyel, A.C., Salecker, J., Kisel, Y., Meyer, K.M., Auliya, M., Barnes, A.D., Corre, M.D., Darras, K., Faust, H., Hess, B., Klasen, S., Knohl, A., Kreft, H., Meijide, A., Nurdiansyah, F., Otten, F., Pe'er, G., Steinebach, S., Tarigan, S. Tölle, M.H., Tschardtke, T., & Wiegand, K. (2017). A review of the ecosystem functions in oil palm plantations, using forests as a reference system. *Biological Reviews*, 92(3), 1539–1569. <https://doi.org/10.1111/brv.12295>.
- Ditrich, T., Papáček, M., & Broum, T. (2008). Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohořský Potok stream spring area (Novohradské Hory Mts.). *Silva Gabreta*, 14(3), 173–178. [https://www.researchgate.net/publication/267200310\\_Spatial\\_distribution\\_of\\_semiaquatic\\_bugs\\_Heteroptera\\_Gerromorpha\\_and\\_their\\_wing\\_morphs\\_in\\_a\\_s](https://www.researchgate.net/publication/267200310_Spatial_distribution_of_semiaquatic_bugs_Heteroptera_Gerromorpha_and_their_wing_morphs_in_a_s)

[mall scale of the Pohorsky Potok stream spring area Novohradske Hory Mts.](#)

- Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, McGlade, J.J., Mooney, H., Rusak, J.A., Sala, O., Wolters, V., Wall, D., Winfree, R., & Xenopoulos, M.A. (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87, 1915–1924. [https://doi.org/10.1890/0012-9658\(2006\)87\[1915:HLTCAT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2).
- Douglas, I. (2022). Impact of logging on interception and soil water. In: Water and the Rainforest in Malaysian Borneo. *Ecological Studies*, 242. Springer, Cham. [https://doi.org/10.1007/978-3-030-91544-5\\_14](https://doi.org/10.1007/978-3-030-91544-5_14).
- Du, X., Jian, J., Du, C., & Stewart, R.D. (2022). Conservation management decreases surface runoff and soil erosion. *International Soil and Water Conservation Research*, 10(2), 188–196.
- Duchelle, A.E., Simonet, G., Sunderlin, W.D., & Wunder, S. (2018). What is REDD+ achieving on the ground? *Current Opinion in Environmental Sustainability*, 32, 134–140. <https://doi.org/10.1016/j.cosust.2018.07.001>.
- Dudgeon, D. (2000). The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Review of Ecology and Systematics*, 31, 239–263. <https://doi.org/10.1146/annurev.ecolsys.31.1.239>.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., & Sullivan, C.A. (2006). Freshwater biodiversity: Importance, threats, status, and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, 81(2), 163–182. <https://doi.org/10.1017/S1464793105006950>.
- Dumbrell, A.J. & Hill, J.K. (2005). Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: Implications for sampling. *Biological Conservation*, 125(1), 123–131. <https://doi.org/10.1016/j.biocon.2005.02.016>.
- Eddelbuettel, D. (2013). *Seamless R and C++ Integration with Rcpp*. Springer, New York. <https://doi.org/10.1007/978-1-4614-6868-4>.

- Eddelbuettel, D. & Balamuta, J.J. (2018). Extending R with C++: A brief Introduction to Rcpp. *The American Statistician*, 72(1). <https://doi.org/10.1080/00031305.2017.1375990>.
- Eddelbuettel, D., & Romain F. (2011). Rcpp: Seamless R and C++ integration. *Journal of Statistical Software*, 40(8), 1–18. <https://doi.org/10.18637/jss.v040.i08>.
- Elek, Z., Růžičková, J., & Ódor, P. (2022). Functional plasticity of carabids can presume better the changes in community composition than taxon-based descriptors. *Ecological Applications*, 32(1). <https://doi.org/10.1002/eap.2460>.
- Estrada-Carmona, N., Sanchez, A.C., Remans, R., & Jones, S.K. (2022). Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. *Proceedings of the National Academy of Sciences of the United States of America*, 119(38), e2203385119. <https://doi.org/10.1073/pnas.2203385119>.
- Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., & Laurance, W.F. (2014). Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, 29(9), 511–520. <http://dx.doi.org/10.1016/j.tree.2014.07.003>.
- Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., & Turner, E.C. (2011). A large-scale forest fragmentation experiment: The stability of altered forest ecosystems project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582), 3292–3302. <https://doi.org/10.1098/rstb.2011.0049>.
- Farmer, J.R., Meretsky, V., Knapp, D., Chancellor, C., & Fischer, B.C. (2015). Why agree to a conservation easement? Understanding the decision of conservation easement granting. *Landscape and Urban Planning*, 138, 11–19. <https://doi.org/10.1016/j.landurbplan.2015.01.005>.
- Faruk, A., Belabut, D., Ahmad, N., Knell, R.J., & Garner, T.W.J. (2013). Effects of oil-palm plantations on diversity of tropical anurans. *Conservation Biology*, 27(3), 615–624. <https://doi.org/10.1111/cobi.12062>.
- Fee, C.G., Tui, L.C., Bin, C.S., & Hoy, C.K. (2017). *Pictorial guide to common weeds of plantations and their control (No. L-0987)*, 2nd ed. Agricultural Crop Trust, ACT, Bonn.

- Feio, M.J., Hughes, R.M., Serra, S.R.Q., Nichols, S.J., Kefford, B.J., Lintermans, M., Robinson, W., Odume, O.N., Callisto, M., Macedo, D.R., Harding, J.S., Yates, A.G., Monk, W., Nakamura, K., Mori, T., Sueyoshi, M., Mercado-Silva, N., Chen, K., Baek, M.J., Bae, Y.J., Tachamo-Shah, R.D., Shah, D.N., Campbell, I., Moya, N., Arimoro, F.O., Keke, U.N., Martins, R.T., Alves, C.B.M., Pompeu, P.S. & Sharma, S. (2023). Fish and macroinvertebrate assemblages reveal extensive degradation of the world's rivers. *Global Change Biology*, 29(2), 355–374. <https://doi.org/10.1111/gcb.16439>.
- Ficke, A.D., Myrick, C.A. & Hansen, L.J. (2007). Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries*, 17, 581–613. <https://doi.org/10.1007/s11160-007-9059-5>.
- Finet, C., Decaras, A., Armise'n, D., & Khila, A. (2018). The achaete–scute complex contains a single gene that controls bristle development in the semi-aquatic bugs. *Proc. R. Soc. B.*, 285, 20182387. <https://dx.doi.org/10.1098/rspb.2018.2387>.
- Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Farnon Ellwood, M.D., Broad, G.R., Chung, A.Y.C., Eggleton, P., Khen, C.V., & Yusah, K.M. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582), 3277–3291. <https://doi.org/10.1098/rstb.2011.0041>.
- Foster, W.A. & Treherne, J.E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293, 466–467. <https://doi.org/10.1038/293466a0>.
- Fox, J. & Weisberg, S. (2019). *An {R} Companion to Applied Regression*, Third Edition. Thousand Oaks CA: Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Freitag, H. & Zettel, H. (2012). Aquatic Heteroptera of the Lake Manguao catchment, Palawan and new rank of *Rhagovelia kawakamii hoberlandti* Hungerford & Matsuda 1961. *Philippine Journal of Systematic Biology*, 6, 54–80. <https://archium.ateneo.edu/biology-faculty-pubs/14/>.

- Ganihar, S.R. (1997). Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences*, 22, 219–224. <https://doi.org/10.1007/BF02704734>.
- Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., & Sodhi, N.S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, 12(6), 561–582. <https://doi.org/10.1111/j.1461-0248.2009.01294.x>.
- Gaveau, D.L.A., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M., Pacheco, P., & Meijaard, E. (2016). Rapid conversions and avoided deforestation: Examining four decades of industrial plantation expansion in Borneo. *Scientific Reports*, 6. <https://doi.org/10.1038/srep32017>.
- Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N., & Meijaard, E. (2014). Four decades of forest persistence, clearance, and logging on Borneo. *Public Library of Sciences (PLOS) One*. <https://doi.org/10.1371/journal.pone.0101654>.
- Giam, X., Hadiaty, R.K., Tan, H.H., Parenti, L.R., Wowor, D., Sauri, S., Chong, K.Y., Yeo, D.C.J., Wilcove, D.S. (2015). Mitigating the impact of oil-palm monoculture on freshwater fishes in Southeast Asia. *Conservation Biology*, 29(5), 1357–1367. <https://doi.org/10.1111/cobi.12483>.
- Giam, X., Ng, T.H., Yap, V.B. & Tan, H.T.W. (2010). The extent of undiscovered species in Southeast Asia. *Biodiversity and Conservation*, 19, 943–954. <https://doi.org/10.1007/s10531-010-9792-2>.
- Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., & Foley, J.A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America*, 107(38), 16732–16737. <https://doi.org/10.1073/pnas.0910275107>.
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A, Laurance, W.F., Lovejoy, T.E., & Sodhi, N.S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381. <https://doi.org/10.1038/nature10425>.

- Giustini, M., Miccoli, F.P., De Luca, G., & Cicolani, B. (2008). Length-weight relationships for some Plecoptera and Ephemeroptera from a carbonate stream in central Apennine (Italy). *Hydrobiologia*, 605, 183–191. <https://doi.org/10.1007/s10750-008-9353-9>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022a). *Limnogonus* Stål, 1868 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/2020455>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022b). *Limnometra* Mayr, 1865 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4773644>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022c). *Metrocoris* Mayr, 1865 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4773687>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022d). *Microvelia* Westwood, 1834 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/2020348>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022e). *Ptilomera* Amyot & Serville, 1843 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4773658>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022f). *Potamometropsis* Lundblad, 1933 in Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4773676>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022g). *Rheumatogonus* Kirkaldy, 1909 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4772602>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022h). *Strongylovelia* Esaki, 1924 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4774615>.
- GBIF (Global Biodiversity Information Facility) Secretariat. (2022i). *Tenagogonus* Stål, 1853 in GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2023-07-12. <https://www.gbif.org/species/4780471>.

- Gómez, A.M., Parra, A., Pavelsky, T.M., Wise, E., Villegas, J.C. & Meijide, A. (2023). Ecohydrological impacts of oil palm expansion: a systematic review. *Environ. Res. Lett.*, 18, 033005. <https://doi.org/10.1088/1748-9326/acbc38>.
- Gotelli, N.J. & Colwell, R.K. (2011). *Estimating species richness*. Chapter 4 of *Biological Diversity: Frontiers in Measurement and Assessment*, edited by Anne E. Magurran & Brian J. McGill. Oxford University Press.
- Gowing, G. & Recher, H.F. (1985). Further comments on length-weight relationships of invertebrates. *Australian Journal of Ecology*, 10, 195. [https://www.researchgate.net/publication/240654030\\_Further\\_comments\\_on\\_length-weight\\_relationships\\_of\\_invertebrates](https://www.researchgate.net/publication/240654030_Further_comments_on_length-weight_relationships_of_invertebrates).
- Greenshields, B., von der Lühe, B., Hughes, H.J., Stiegler, C., Tarigan, S., Tjoa, A., & Sauer, D. (2023). Oil-palm management alters the spatial distribution of amorphous silica and mobile silicon in topsoils. *Soil*, 9, 169–188. <https://doi.org/10.5194/soil-9-169-2023>.
- Grizzetti, B., Pretato, U., Lassaletta, L., Billen, G., & Garnier, J. (2013). The contribution of food waste to global and European nitrogen pollution. *Environmental Science & Policy*, 33, 186–195. <https://doi.org/10.1016/j.envsci.2013.05.013>.
- Gruner, D.S. (2003). Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. *Pacific Science*, 57, 325–336. <https://doi.org/10.1353/psc.2003.0021>.
- Guterres, A.P.M., Cunha, E.J., Godoy, B.S., Silva, R.R., & Juen, L. (2020). Co-occurrence patterns and morphological similarity of semiaquatic insects (Hemiptera: Gerromorpha) in streams of Eastern Amazonia. *Ecological Entomology*, 45, 155–166. <https://doi.org/10.1111/een.12785>.
- Guterres, A.P.M., Cunha, E.J., & Juen, L. (2021). Tolerant semiaquatic bugs species (Heteroptera: Gerromorpha) are associated to pasture and conventional logging in the Eastern Amazon. *Journal of Insect Conservation*, 25, 555–567. <https://doi.org/10.1007/s10841-021-00316-9>.
- Haahr, M. (2020). RANDOM.ORG - True random number service. <https://www.random.org>.

- Habel, J.C., Teucher, M., Gros, P., Schmitt, T., & Ulrich, W. (2021). Land use and climate change affects butterfly diversity across northern Austria. *Landscape Ecology*, 36, 1741–1754. <https://doi.org/10.1007/s10980-021-01242-6>.
- Hall, R.J., Driscoll, C.T., & Likens, G.E. (1985). Physical, chemical, and biological consequences of episodic aluminum. *Limnology and Oceanography*, 30(1), 212–220. <https://doi.org/10.4319/lo.1985.30.1.0212>.
- Halpern, B.S., Frazier, M., Verstaen, J., Rayner, P.E., Clawson, G., Blanchard, J.L., Cottrell, R.S., Froehlich, H.E., Gephart, J.A., Jacobsen, N.S., Kuempel, C.D., McIntyre, P.B., Metian, M., Moran, D., Nash, K.L., Többen, J. & Williams, D.R. (2022). The environmental footprint of global food production. *Nature Sustainability*. <https://doi.org/10.1038/s41893-022-00965-x>.
- Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. (2003). Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, 40, 150–162. <https://doi.org/10.1046/j.1365-2664.2003.00783.x>.
- Hancock, P.J. (2002). Human impacts on the stream-groundwater exchange zone. *Environmental Management*, 29(6), 763–781. <https://doi.org/10.1007/s00267-001-0064-5>.
- Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., & Ewers, R.M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201, 187–195. <https://doi.org/10.1016/j.agrformet.2014.11.010>.
- Harianja, M.F., Luke, S.H., Barclay, H., Chey, V.K., Aldridge, D.C., Foster, W.A., & Turner, E.C. (2022). *Data set and analytic codes supporting "Length-biomass equations to allow rapid assessment of semi-aquatic bug biomass in tropical streams"* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.6659535>.
- Harianja, M.F., Luke, S.H., Barclay, H., Chey, V.K., Aldridge, D.C., Foster, W.A., & Turner, E.C. (2023a). Length–biomass equations to allow rapid assessment of semi-aquatic bug biomass in tropical streams. *Entomologia Experimentalis et Applicata*, 171, 102–115. <https://doi.org/10.1111/eea.13247>.

- Harianja, M.F., Turner, E.C., Barclay, H., Chey, V.K., Aldridge, D.C., Foster, W.A., & Luke, S.H. (2023b). *Data set and analytic codes supporting "The effects of land-use change on semi-aquatic bugs (Gerromorpha, Hemiptera) in rainforest streams in Sabah, Malaysia"* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.7516680>.
- Harianja, M.F., Luke, S.H., Barclay, H., Chey, V.K., Aldridge, D.C., Foster, W.A., & Turner, E.C. (2023c). *Data set and analytic codes supporting "The impacts of within-stream physical structure and riparian buffer strips on semi-aquatic bugs in Southeast Asian oil palm"* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.7813514>.
- Harianja, M.F., Stone, J., Mamat, W.Z.W., Hadi, M.A., Luke, S.H., Azhar, B., & Turner, E.C. (2023d). *Data set and analytic codes supporting "How do management decisions impact butterfly assemblages in smallholding oil palm plantations in Peninsular Malaysia?"* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.7973718>.
- Harianja, M.F., Mamat, W.Z.W., Hadi, M.A., Stone, J., Azhar, B., Luke, S.H., & Turner, E.C. (2023e). *Data set and analytic codes supporting "Direct observation to assess the effects of habitat structure and complexity on resource-use behaviour of butterflies: a study case in smallholding oil palm plantations in Peninsular Malaysia"* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.8014109>.
- Harianja, M.F., Turner, E.C., Barclay, H., Chey, V.K., Aldridge, D.C., Foster, W.A., & Turner, E.C. (2023f). The effects of land-use change on semi-aquatic bugs (Gerromorpha, Hemiptera) in rainforest streams in Sabah, Malaysia. *Freshwater Biology*. Under review.
- Harianja, M.F., Stone, J., Mamat, W.Z.W., Hadi, M.A., Luke, S.H., Azhar, B., & Turner, E.C. (2023g). How do management decisions impact butterfly assemblages in smallholding oil palm plantations in Peninsular Malaysia? *Journal of Applied Ecology*. Under review.
- Herring, J.L. (1951). The aquatic and semiaquatic Hemiptera of Northern Florida. Part 4: Classification of habitats and keys to the species. *The Florida Entomologist*, 34(4), 146–161. <https://www.jstor.org/stable/3492445>.

- Hester, E.T. & Gooseff, M.N. (2010). Moving beyond the banks: hyporheic restoration is fundamental to restoring ecological services and functions of streams. *Environmental Science & Technology*, 44, 1521–1525. <https://doi.org/10.1021/es902988n>.
- Hewitt, C.N., Lee, J.D., MacKenzie, A.R., Barkley, M.P., Carslaw, N., Carver, G.D., Chappell, N.A., Coe, H., Collier, C., Commane, R., Davies, F., Davison, B., DiCarlo, P., Di Marco, C.F., Dorsey, J.R., Edwards, P.M., Evans, M.J., Fowler, D., Furneaux, K.L., Gallagher, M., Guenther, A., Heard, D.E., Helfter, C., Hopkins, J., Ingham, T., Irwin, M., Jones, C., Karunaharan, A., Langford, B., Lewis, A.C., Lim, S.F., MacDonald, S.M., Mahajan, A.S., Malpass, S., McFiggans, G., Mills, G., Misztal, P., Moller, S., Monks, P.S., Nemitz, E., Nicolas-Perea, V., Oetjen, H., Oram, D.E., Palmer, P.I., Phillips, G.J., Pike, R., Plane, J.M.C., Pugh, T., Pyle, J.A., Reeves, C.E., Robinson, N.H., Stewart, D., Stone, D., Whalley, L.K., & Yin, X. (2010). Overview: oxidant and particle photochemical processes above a South-east Asian tropical rainforest (the OP3 project): introduction, rationale, location characteristics and tools. *Atmospheric Chemistry and Physics*, 10, 169–199. <http://www.atmos-chem-phys.net/10/169/2010/>.
- Hijmans, R.J. (2022). *geosphere: Spherical Trigonometry*. R package version 1.5-18. <https://CRAN.R-project.org/package=geosphere>.
- Hood, A.S.C, Advento A.D., Stone J., Fayle T.M., Fairnie A.L.M., Waters H.S., Foster W.A., Snaddon J.L., Sudharto ps., Caliman J.P., Naim M., & Turner E.C. (2020) Removing understorey vegetation in oil palm plantations reduces ground-foraging ant abundance but not species richness. *Basic and Applied Ecology*, 48, 26–36. <https://doi.org/10.1016/j.baae.2020.07.002>.
- Horne, J.P. & Hubbart, J.A. (2020). A spatially distributed investigation of stream water temperature in a contemporary mixed-land-use watershed. *Water*, 12, 1756. <https://doi.org/10.3390/w12061756>.
- Hosonuma, N., Herold, M., De Sy, V., De Fries, R.S., Brockhaus, M., Verchot, L., Angelsen, A., & Romijn, E. (2012). An assessment of deforestation and forest degradation drivers in developing countries. *Environmental Research Letters*, 7, 044009. <https://doi.org/10.1088/1748-9326/7/4/044009>.

- Hsieh, T.C., Ma, K.H. & Chao, A. (2020). *iNEXT: iNterpolation and EXTrapolation for species diversity*. R package version 2.0.20. <https://chao.stat.nthu.edu.tw/wordpress/software-download/suh>.
- Hughes, A.C. (2017). Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere*, 8(1), 1–33. <https://doi.org/10.1002/ecs2.1624>.
- Hurkmans, R.T.W.L., Terink, W., Uijlenhoet, R., Moors, E.J., Troch, P.A., & Verburg, P.H. (2009). Effects of land use changes on streamflow generation in the Rhine basin. *Water Resources Research*, 45, 1–15. <https://doi.org/10.1029/2008WR007574>.
- Ismail, Z. & Go, Y.I. (2021). Fog-to-water for water scarcity in climate-change hazards hotspots: pilot study in Southeast Asia. *Global Challenges*, 5(5), 2000036. <https://doi.org/10.1002/gch2.202000036>.
- IUCN. (2022). *IUCN red list of threatened species*. [www.iucnredlist.org/search?taxonomies](http://www.iucnredlist.org/search?taxonomies). Accessed on 24 December 2022.
- Izah, S.C., Angaye, T.C.N., & Ohimain, E.I. (2016). Environmental impacts of oil palm processing in Nigeria. *Biotechnol. Res.*, 2(3), 132–141. <https://br.biomedpress.org/index.php/br/article/view/724>.
- Jabiol, J., Mckie, B.G., Bruder, A., Bernadet, C., Gessner, M.O., & Chauvet, E. (2013). Trophic complexity enhances ecosystem functioning in an aquatic detritus-based model system. *Journal of Animal Ecology*, 82, 1042–1051. <https://doi.org/10.1111/1365-2656.12079>.
- Jehamalar, E.E., Chandra, K., Basu, S., & Selvakumar, C. (2018). Review of *Ptilomera* (*Ptilomera*) (Hemiptera: Heteroptera: Gerridae) from India, with description of a new species. *Zootaxa*, 4370(5), 501–518. <https://doi.org/10.11646/zootaxa.4370.5.3>.
- Jha, V., Garcia-Garcia, G., Iseki, K., Li, Z., Naicker, S., Plattner, B., Saran, R., Wang, A.Y-M., & Yang, C-W. (2013). Chronic kidney disease: global dimension and perspectives. *The Lancet*, 382(9888), 260–272. [https://doi.org/10.1016/S0140-6736\(13\)60687-X](https://doi.org/10.1016/S0140-6736(13)60687-X).
- Jolliffe, I.T. (1986). *Principal Component Analysis*. Springer. New York.

- Juen, L., Cunha, E.J., Carvalho, F.G., Ferreira, M.C., Begot, T.O., Andrade, A.L., Shimano, Y., Leão, H., Pompeu, P.S., & Montag, L.F.A. (2016). Effects of oil palm plantations on the habitat structure and biota of streams in Eastern Amazon. *River research and Applications*, 32(10), 2081–2094. <https://doi.org/10.1002/rra.3050>.
- Kan, S., Chen, B., Persson, U.M., Chen, G., Wang, Y., Li, J., Meng, J., Zheng, H., Yang, L., Li, R., Du, M., & Kastner, T. (2023). Risk of intact forest landscape loss goes beyond global agricultural supply chains. *One Earth*, 6, 55–65. <https://doi.org/10.1016/j.oneear.2022.12.006>.
- Kano, Y., Hon, J., Sulaiman, M.K., Aizu, M., Noshita, K. & Samejima, H. (2019). Stream fish biodiversity and the effects of plantations in the Bintulu Region, Sarawak. *Advances in Asian Human-Environmental Research*, 235–274. [https://doi.org/10.1007/978-981-13-7513-2\\_13](https://doi.org/10.1007/978-981-13-7513-2_13).
- Kareiva, P.M. & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. *Oecologia*, 56, 234-238. <https://doi.org/10.1007/BF00379695>.
- Kassambara, A. (2020). *ggpubr: 'ggplot2' Based Publication Ready Plots*. R package v.0.4.0. <https://CRAN.R-project.org/package=ggpubr>.
- Kassambara, A. & Mundt, F. (2020). *factoextra: Extract and visualize the results of multivariate data analyses*. R package version 1.0.7. <https://CRAN.R-project.org/package=factoextra>.
- Kemp, D.J., & Krockenberger, A.K. (2004). Behavioural thermoregulation in butterflies: The interacting effects of body size and basking posture in *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae). *Australian Journal of Zoology*, 52(3), 229–236. <https://doi.org/10.1071/ZO03043>.
- Kingsolver, J.G., Woods, H.A., Buckley, L.B., Potter, K.A., MacLean, H.J., & Higgins, J.K. (2011). Complex life cycles and the responses of insects to climate change. *Integrative and Comparative Biology*, 51(5), 719–732. <https://doi.org/10.1093/icb/ucr015>.
- Kim, W., Pham, T.H., Nguyen, P.D., Tran, A.D., Ha, J., Jablonski, P.G., & Lee, S.-I. (2022). Locomotion and flow speed preferences in natural habitats by large

- water striders, *Ptilomera tigrina*, with micro-morphological adaptations for rowing. *Journal of Ethology*. <https://doi.org/10.1007/s10164-022-00749-y>.
- King, J. & Brown, C. (2010). Integrated basin flow assessments: concepts and method development in Africa and South-east Asia. *Freshwater Biology*, 55(1), 127–146. <https://doi.org/10.1111/j.1365-2427.2009.02316.x>.
- Kinsella, R.S., Thomas, C.D., Crawford, T.J., Hill, J.K., Mayhew, P.J., & Macgregor, C.J. (2020). Unlocking the potential of historical abundance datasets to study biomass change in flying insects. *Ecology and Evolution*, 10, 8394–8404. <https://doi.org/10.1002/ece3.6546>.
- Kirton, L.G. (2020). *A Naturalist's Guide to the Butterflies of Peninsular Malaysia, Singapore, and Thailand*, Third Edition. John Beaufoy Publishing Limited. Oxford, Singapore, and Thailand.
- Kishimoto-Yamada, K. & Itioka, T. (2015). How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? *Entomological Science*, 18(4), 407–419. <https://doi.org/10.1111/ens.12134>.
- Kleiman, B.M., Koptur, S., & Jayachandran, K. (2021). Weeds enhance pollinator diversity and fruit yield in mango. *Insects*, 12, 1114. <https://doi.org/10.3390/insects12121114>.
- van Klink, R., Bowler, D.E., Gongalsky, K.B., & Chase, J.M. (2021). Revisiting global trends in freshwater insect biodiversity: A reply. *Wiley Interdisciplinary Reviews: Water*, 8(2). <https://doi.org/10.1002/wat2.1501>.
- Koh, L.P. (2007). Impacts of land use change on South-east Asian forest butterflies: A review. *Journal of Applied Ecology*, 44(4), 703–713. <https://doi.org/10.1111/j.1365-2664.2007.01324.x>.
- Koh, L.P., & Wilcove, D.S. (2008). Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters*, 1(2), 60–64. <https://doi.org/10.1111/j.1755-263X.2008.00011.x>.
- Kolkman, A., Dopagne, C., & Piqueray, J. (2022). Sown wildflower strips offer promising long term results for butterfly conservation. *Journal of Insect Conservation*, 26, 387–400. <https://doi.org/10.1007/s10841-021-00347-2>.

- Konopik, O., Steffan-Dewenter, I., & Grafe, T.U. (2015). Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. *Biotropica*, 47(5), 636–643. <https://doi.org/10.1111/btp.12248>.
- Kosmos, C.F., Mackey, B., DellaSala, D.A., Kumpe, N., Jaeger, T., Mittermeier, R.A. & Filardi, C. (2018). Primary Forests: Definition, Status and Future Prospects for Global Conservation. In: Dominick A. DellaSala, & Michael I. Goldstein (eds.) *The Encyclopedia of the Anthropocene*, 2, 31-41. Elsevier. Oxford. [https://www.researchgate.net/profile/Cyril-Kormos-2/publication/313150421\\_Primary\\_forests\\_biodiversity\\_and\\_ecosystem\\_services/links/5b29e543aca27209f374d5ce/Primary-forests-biodiversity-and-ecosystem-services.pdf](https://www.researchgate.net/profile/Cyril-Kormos-2/publication/313150421_Primary_forests_biodiversity_and_ecosystem_services/links/5b29e543aca27209f374d5ce/Primary-forests-biodiversity-and-ecosystem-services.pdf).
- Kovac, D. & Yang, C.M. (2000). Revision of the oriental bamboo-inhabiting semiaquatic bug Genus *Lathriovelia* Andersen, 1989 (Heteroptera: Veliidae) with description of *l. rickmersi*, new species, and notes on the Genus *Baptista* Distant, 1903. *The Raffles Bulletin of Zoology*, 48(1), 153–165. <https://lkcnhm.nus.edu.sg/wp-content/uploads/sites/10/app/uploads/2017/04/48rbz153-165.pdf>.
- Krishnapillay, B. (2004). *Dipterocarps*, a chapter in Tropical Ecosystems. Elsevier Ltd. [PII: B0121451607001939 \(sciencedirectassets.com\)](https://doi.org/10.1016/B0121451607001939).
- Kumagai, T., Saitoh, T.M., Sato, Y., Takahashi, H., Manfroi, O.J., Morooka, T., Kuraji, K., Suzuki, M., Yasunari, T., & Komatsu, H. (2005). Annual water balance and seasonality of evapotranspiration in a Bornean tropical rainforest. *Agricultural and Forest Entomology*, 182(1–2), 81–92. <https://doi.org/10.1016/j.agrformet.2004.08.006>.
- Kuefler, D. & Haddad, N.M. (2006). Local versus landscape determinants of butterfly movement behaviors. *Ecography*, 29, 549–560. <https://doi.org/10.1111/j.0906-7590.2006.04574.x>.
- Kunin, W.E. (2019). Robust evidence of insect declines. *Nature*, 574, 641–642. <https://doi.org/10.1038/d41586-019-03241-9>.
- Kurz, D.J., Turner, E.C., Aryawan, A.A.K., Barkley, H.C., Caliman, J.P., Konopik, O., Ps, S., & Foster, W.A. (2016). Replanting reduces frog diversity in oil palm. *Biotropica*, 48(4), 483–490. <https://doi.org/10.1111/btp.12320>.

- Laird-Hopkins, B.C., Ashe-Jepson, E., Basset, Y., Cobo, S.A., Eberhardt, L., Freiberga, I., Hellon, J., Hitchcock, G.E., Kleckova, I., Linke, D., Lamarre, G.P.A., McFarlane, A., Savage, A.F., Turner, E.C., Zamora, A.C., Sam, K., & Bladon, A.J. (2023). Thermoregulatory ability and mechanism do not differ consistently between neotropical and temperate butterflies. *Global Change Biology*, 29(15), 4180–4192. <https://doi.org/10.1111/gcb.16797>.
- Lang, H.H. (1980). Surface wave discrimination between prey and nonprey by the back swimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). *Behavioral Ecology and Sociobiology*, 6, 233–246. <https://doi.org/10.1007/BF00569205>.
- Lansbury, I. (1993). *Strongylovelia* (Veliidae) and *Metrobatopsis* (Gerridae) and associated pleuston Hemiptera of West New Britain. *Tijdschrift voor Entomologie*, 136, 15–22. <https://www.biodiversitylibrary.org/partpdf/67059>.
- Lansbury, I. & Zettel, H. (1997). New species and subspecies of the genus *Strongylovelia* Esaki (Insecta, Heteroptera, Veliidae) from Borneo and the Philippines. *Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie*, 99B, 51–77. <https://www.jstor.org/stable/41767051>.
- Lembrechts, J.J. & Nijs, I. (2020). Microclimate shifts in a dynamic world. *Science*, 368(6492), 711–712. <https://www.science.org/doi/10.1126/science.abc1245>.
- Lemmon, P.E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science*, 2, 314–320. <https://doi.org/10.1093/forestscience/2.4.314>.
- Lemon, J. (2006). Plotrix: a package in the red light district of R. *R-News* 6: 8–12. [https://www.researchgate.net/publication/260171541\\_Plotrix\\_A\\_package\\_in\\_the\\_red\\_light\\_district\\_of\\_R](https://www.researchgate.net/publication/260171541_Plotrix_A_package_in_the_red_light_district_of_R).
- Lima, M., Firmino, V.C., de Paiva, C.K.S., Juen, L., & Brasil, L.S. (2022). Land use changes disrupt streams and affect the functional feeding groups of aquatic insects in the Amazon. *Journal of Insect Conservation*. <https://doi.org/10.1007/s10841-022-00375-6>.
- Lo, M., Reed, J., Castello, L., Steel, E.A., Frimpong, E.A., & Ickowitz, A. (2020). The influence of forests on freshwater fish in the tropics: a systematic review. *BioScience*, 70(5), 404–414. <https://doi.org/10.1093/biosci/biaa021>.

- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60), 3139. <https://doi.org/10.21105/joss.03139>.
- Lüdecke, D., Patil, I., Ben-Shachar, M.S., Wiernik, B.M., Waggoner, P. & Makowski, D. (2021). see: An R package for visualizing statistical models. *Journal of Open Source Software*, 6(64), 3393. <https://doi.org/10.21105/joss.03393>.
- Luiza-Andrade, A., Brasil, L.S., Benone, N.L., Shimano, Y., Farias, A.P.J., Montag, L.F., & Dolédec, S., & Juen, L. (2017). Influence of oil palm monoculture on the taxonomic and functional composition of aquatic insect communities in eastern Brazilian Amazonia. *Ecological Indicators*, 82, 478–483. <https://doi.org/10.1016/j.ecolind.2017.07.006>.
- Luke, S.H., Roy, H.E., Thomas, C.D., Tilley, L.A.N., Ward, S., Watt, A., Carnaghi, M., Jaworski, C.C., Tercel, M.P.T.G., Woodrow, C., Aown, S., Banfield-Zanin, J.A., Barnsley, S.L., Berger, I., Brown, M.J.F., Bull, J.C., Campbell, H., Carter, R.A.B., Charalambous, M., Cole, L.J., Ebejer, M.J., Farrow, R.A., Fartyal, R.S., Grace, M., Hight, F., Hill, J.K., Hood, A.S.C., Kent, E.S., Krell, F.-T., Leather, S.R., Leybourne, D.J., Littlewood, N.A., Lyons, A., Matthews, G., Mc Namara, L., Menéndez, R., Merrett, P., Mohammed, S., Murchie, A.K., Noble, M., Paiva, M.-R., Pannell, M.J., Phon, C.-K., Port, G., Powell, C., Rosell, S., Sconce, F., Shortall, C.R., Slade, E.M., Sutherland, J.P., Weir, J.C., Williams, C.D., Zielonka, N.B., & Dicks, L.V. (2023). Grand challenges in entomology: Priorities for action in the coming decades. *Insect Conservation and Diversity*, 16(2), 173–189. <https://doi.org/10.1111/icad.12637>.
- Luke, S.H., Advento, A.D., Aryawan, A.A.K., Adhy, D.N., Ashton-Butt A., Barclay H., Dewi J.P., Drewer J., Dumbrell A.J., Edi, Eycott A.E., Harianja M.F., Hinsch J.K., Hood A.S.C., Kurniawan C., Kurz D.J., Mann D.J., Matthews Nicholass K.J., Naim M., Pashkevich M.D., Prescott G.W., Ps S., Pujianto, Purnomo D., Purwoko R.R., Putra S., Rambe T.D.S., Soeprapto, Spear D.M., Suhardi, Tan D.J.X., Tao H-H., Tarigan R.S., Wahyuningsih R., Waters H.S., Widodo R.H., Whendy, Woodham C.R., Caliman J-P., Slade E.M., Snaddon J.L., Foster W.A. and Turner E.C. (2020). Managing oil palm plantations more sustainably: large-scale experiments within the Biodiversity and Ecosystem Function in Tropical

- Agriculture (BEFTA) Programme. *Frontiers in Forests and Global Change*, 2, 75. <https://doi.org/10.3389/ffgc.2019.00075>.
- Luke, S.H., Purnomo, D., Advento, A.D., Aryawan, A.A.K., Naim, M., Pikstein, R.N., Ps, S., Rambe, T.D.S., Soeprapto, Caliman, J.-P., Snaddon, J.L., Foster, W.A. & Turner, E.C. (2019a). Effects of understory vegetation management on plant communities in oil palm plantations in Sumatra, Indonesia. *Frontiers in Forests and Global Change*, 2, 33. <https://doi.org/10.3389/ffgc.2019.00033>.
- Luke, S.H., Slade, E.M., Gray, C.L., Annammala, K.V., Drewer, J., Williamson, J., Agama, A. L., Ationg, M., Mitchell, S.L., Vairappan, C.S., & Struebig, M.J. (2019b). Riparian buffers in tropical agriculture: Scientific support, effectiveness, and directions for policy. *Journal of Applied Ecology*, 56(1), 85–92. <https://doi.org/10.1111/1365-2664.13280>.
- Luke, S.H., Barclay, H., Bidin, K., Chey, V.K., Ewers, R.M., Foster, W.A., Nainar, A., Pfeifer, M., Reynolds, G., Turner, E.C., Walsh, R.P.D., & Aldridge, D.C. (2017a). The effects of catchment and riparian forest quality on stream environmental conditions across a tropical rainforest and oil palm landscape in Malaysian Borneo. *Ecohydrology*, 10(4). <https://doi.org/10.1002/eco.1827>.
- Luke, S.H., Dow, R.A., Butler, S., Vun K.C., Aldridge, D.C., Foster, W.A., & Turner, E.C. (2017b). The impacts of habitat disturbance on adult and larval dragonflies (Odonata) in rainforest streams in Sabah, Malaysian Borneo. *Freshwater Biology*, 62(3), 491–506. <https://doi.org/10.1111/fwb.12880>.
- Luke, S.H., Fayle, T.M., Eggleton, P., Turner, E.C., & Davies, R.G. (2014). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation*, 23, 2817–2832. <https://doi.org/10.1007/s10531-014-0750-2>.
- Luskin, M.S., & Potts, M.D. (2011). Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology*, 12(6), 540–551. <https://doi.org/10.1016/j.baae.2011.06.004>.
- Macadam, C.A. & Stockan, J.A. (2015). More than just fish food: ecosystem services provided by freshwater insects. *Ecological Entomology*, 40(S1), 113–123. <https://doi.org/10.1111/een.12245>.

- Maddock, I. (1999). The importance of physical habitat assessment for evaluating river health. *Freshwater Biology*, 41, 373–391. <https://doi.org/10.1046/j.1365-2427.1999.00437.x>.
- Maier, C.T. (1977). The behavior of *Hydrometra championana* (Hemiptera: Hydrometridae) and resource partitioning with *Tenagogonus quadrilineatus* (Hemiptera: Gerridae). *Journal of the Kansas Entomological Society*, 50(2), 263–271. <https://www.jstor.org/stable/25082933>.
- Maino, J.L. & Kearney, M.R. (2015). Testing mechanistic models of growth in insects. *Proceedings of the Royal Society B.*, 282, 20151973. <https://doi.org/10.1098/rspb.2015.1973>.
- Mohamed, M.S. & Idris, A.S. (2012). Occurrence of common weeds in immature plantings of oil palm plantations in Malaysia. *The Planter*, 88(1037), 537–547. [https://www.researchgate.net/publication/260078910\\_MAIZATUL\\_S\\_M\\_and\\_IDRIS\\_A\\_S\\_2012\\_Occurrence\\_of\\_Common\\_Weeds\\_in\\_Immature\\_Plantings\\_of\\_Oil\\_Palm\\_Plantations\\_In\\_Malaysia\\_The\\_Planter\\_Vol\\_88\\_1037](https://www.researchgate.net/publication/260078910_MAIZATUL_S_M_and_IDRIS_A_S_2012_Occurrence_of_Common_Weeds_in_Immature_Plantings_of_Oil_Palm_Plantations_In_Malaysia_The_Planter_Vol_88_1037).
- Malmqvist, B. (2002). Aquatic invertebrates in riverine landscapes. *Freshwater Biology*, 47(4), 679–694. <https://doi.org/10.1046/j.1365-2427.2002.00895.x>.
- Maltby, L., Paetzold, A., & Warren, P. (2010). *Sustaining industrial activity and ecological quality: the potential role of an ecosystem services approach*, Chapter 16 in *Ecology of Industrial Pollution*, edited by L.C. Batty & K.B. Cambridge University Press. Hallberg.
- Marschalek, D.A. & Deutschman, D.H. (2022). Differing insect communities and reduced decomposition rates suggest compromised ecosystem functioning in urban preserves of southern California. *Global Ecology and Conservation*, 33, e01996. <https://doi.org/10.1016/j.gecco.2021.e01996>.
- Martin, E.A., Reineking, B., Seo, B., & Steffan-Dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 110(14), 5534–5539. <https://doi.org/10.1073/pnas.1215725110>.
- Md Rawi, C.S., Al-Shami, S.A., Madrus, M.R., & Ahmad, A.H. (2013). Local effects of forest fragmentation on diversity of aquatic insects in tropical forest streams:

- Implications for biological conservation. *Aquatic Ecology*, 47(1), 75–85. <https://doi.org/10.1007/s10452-012-9426-8>.
- Meijaard, E., Brooks, T. M., Carlson, K. M., Slade, E. M., Garcia-Ulloa, J., Gaveau, D. L. A., Lee, J.S.H., Santika, T., Juffe-Bignoli, D., Struebig, M.J., Wich, S.A., Ancrenaz, M., Koh, L.P., Zamira, N., Abrams, J.F., Prins, H.H.T, Sendashonga, C.N., Murdiyarso, D., Furumo, P.R., Macfarlane, N., Hoffmann, R., Persio, M., Descals, A., Szantoi, Z., & Sheil, D. (2020). The environmental impacts of palm oil in context. *Nature Plants*, 6(12), 1418–1426. <https://doi.org/10.1038/s41477-020-00813-w>.
- Mendes, T.P., Amado, L.L., Ribeiro, R.A.B., & Juen, L. (2020). Morphological diversity of Odonata larvae (Insecta) and abiotic variables in oil palm plantation areas in the Eastern Amazon. *Hydrobiologia*, 847, 161–175. <https://doi.org/10.1007/s10750-019-04079-y>.
- Mendes, T.P., Benone, N.L., & Juen, L. (2019). To what extent can oil palm plantations in the Amazon support assemblages of Odonata larvae? *Insect Conservation and Diversity*, 12, 448–458. <https://doi.org/10.1111/icad.12357>.
- Mercer, E.V., Mercer, T.G., & Sayok, A.K. (2014). Effects of forest conversions to oil palm plantations on freshwater macroinvertebrates: a case study from Sarawak, Malaysia. *Journal of Land Use Science*, 9(3), 260–277. <https://doi.org/10.1080/1747423X.2013.786149>.
- Miettinen, J., Shi, C., & Liew, S.C. (2011). Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology*, 17, 2261–2270. <https://doi.org/10.1111/j.1365-2486.2011.02398.x>.
- Mohd Ishadi, N.A., Md Rawi, C.S., Ahmad, A.H., & Abdul, N.H. (2014). The influence of heavy metals and water parameters on the composition and abundance of water bugs (Insecta: Hemiptera) in the Kerian River Basin, Perak, Malaysia. *Tropical Life Sciences Research*, 25(2), 61–79. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4814147/>.
- Molano, F., Moreira, F.F.F., & Morales, I. (2016). New species and records of Microveliinae and Veliinae (Hemiptera: Heteroptera: Veliidae) from Colombia. *Zootaxa*, 4171(3), 575–585. <https://doi.org/10.11646/zootaxa.4171.3.11>.

- Molina-Martínez, A., León-Cortés, J.L., Regan, H.M., Lewis, O.T., Navarrete, D., Caballero, U., & Luis-Martínez, A. (2016). Changes in butterfly distributions and species assemblages on a Neotropical mountain range in response to global warming and anthropogenic land use. *Diversity and Distributions*, 22(11), 1085–1098. <https://doi.org/10.1111/ddi.12473>.
- Moy, K.M., Brasil, L.S., Oliveira-Junior, J.M.B., Juen, L., Vieira, T.B., & Dias-Silva, K. (2022). Effects of environmental changes on Gerromorpha (Heteroptera: Hemiptera) communities from Amazonian streams. *Hydrobiology*, 1, 111–121. <https://doi.org/10.3390/hydrobiology1010008>.
- Muñoz, P.T., Torres, F.P., & Megías, A.G. (2015). Effects of roads on insects: a review. *Biodiversity and Conservation*, 24, 659–682. <https://doi.org/10.1007/s10531-014-0831-2>.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>.
- Naik, D., Rao, R.SP., Kunte, K., & Mustak, M.S. (2022). Ecological monitoring and indicator taxa: butterfly communities in heterogeneous landscapes of the Western Ghats and Malabar coast, India. *Journal of Insect Conservation*, 26, 107–119. <https://doi.org/10.1007/s10841-022-00368-5>.
- Nájera, A. & Simonetti J.A. (2010) Can oil palm plantations become bird friendly? *Agroforestry Systems*, 80, 203–209. <https://doi.org/10.1007/s10457-010-9278-Y>.
- Nakasuji, F. & Dyck, V.A. (1984). Evaluation of the role of *Microvelia douglasi atrolineata* (Bergroth) (Heteroptera: Veliidae) as predator of the brown planthopper *Nilaparvata lugens* (Stal) (Homoptera: Delphacidae). *Res. Popul. Ecol.*, 28, 134–149. <https://doi.org/10.1007/BF02515513>.
- Nazarreta, R., Hartke, T.R., Hidayat, P., Scheu, S., Buchori, D. & Drescher, J. (2020). Rainforest conversion to smallholder plantations of rubber or oil palm leads to species loss and community shifts in canopy ants (Hymenoptera: Formicidae). *Myrmecol. News*, 30, 175–186. [https://doi.org/10.25849/myrmecol.news\\_030:175](https://doi.org/10.25849/myrmecol.news_030:175).

- Nieser, N. & Chen, P.P. (1992). Revision of *Limnometra* Mayr (Gerridae) in the Malay Archipelago. Notes on Malesian aquatic and semiaquatic bugs (Heteroptera), II. *Tijdschrift Voor Entomologie*, 135(1), 11–26. <https://www.biodiversitylibrary.org/partpdf/66397>.
- Nobilly, F., Atikah, S.N., Yahya, M.S., Jusoh, S., Maxwell, T.M.R., Norhisham, A.R., Tohiran, K.A., Zulkifli, R. & Azhar, B. (2023). Do silvopastoral management practices affect biological pest control in oil palm plantations? *BioControl*. <https://doi.org/10.1007/s10526-023-10196-4>.
- Nobilly, F., Atikah, S.N., Yahya, M.S., Jusoh, S., Cun, G.S., Norhisham, A.R., Tohiran, K.A., Zulkifli, R., & Azhar, B. (2021). Rotational cattle grazing improves understory vegetation biodiversity and structural complexity in oil palm plantations. *Weed Biology and Management*, 22(1), 13-26. <https://doi.org/10.1111/wbm.12246>.
- Nummelin, M., Lodenius, M., Tulisalo, E., Hirvonen, H., & Alanko, T. (2007). Predatory insects as bioindicators of heavy metal pollution. *Environmental Pollution*, 145, 339–347. <https://doi.org/10.1016/j.envpol.2006.03.002>.
- Okolle, J.N., Mansor, M., & Ahmad, A.H. (2006). Seasonal abundance of the banana skipper, *Erionota thrax* (Lepidoptera: Hesperidae) and its parasitoids in a commercial plantation and a subsistence farm in Penang, Malaysia. *International Journal of Tropical Insect Science*, 26(3), 197–206. <https://doi.org/10.1079/IJT2006116>.
- Okuda, T., Yamada, T., Hosaka, T., Miyasaku, N., Hashim, M., Lau, A.M.S., & Saw, L.G. (2019). Canopy height recovery after selective logging in a lowland tropical rain forest. *Forest Ecology and Management*, 442, 117–123. <https://doi.org/10.1016/j.foreco.2019.03.045>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2020). *vegan: Community Ecology Package*. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>.
- Ong, T.W.Y. & Vandermeer, J. (2018). Multiple hysteretic patterns from elementary population models. *Theoretical Ecology*. <https://doi.org/10.1007/s12080-018-0376-1>.

- Ormerod, S.J., Dobson, M., Hildrew, A.G., & Townsend, C.R. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55(1), 1–4. <https://doi.org/10.1111/j.1365-2427.2009.02395.x>.
- Osozawa, S., Takáhashi, M., & Wakabayashi, J. (2017). Quaternary vicariance of *Ypthima* butterflies (Lepidoptera, Nymphalidae, Satyrinae) and systematics in the Ryukyu Islands and Oriental region. *Zoological Journal of the Linnean Society*, 180, 593–602. <https://academic.oup.com/zoolinnean/article/180/3/593/2967157>.
- Otsuka, K. (2001). *A field guide to the butterflies of Borneo and South East Asia*. Hornbill Books. <https://myagric.upm.edu.my/id/eprint/5600/>.
- de Paiva, C.K.S., de Faria, A.P.J., Calvão, L.B., & Juen, L. (2017). Effect of oil palm on the Plecoptera and Trichoptera (Insecta) assemblages in streams of eastern Amazon. *Environmental Monitoring and Assessment*, 189, 393. <https://doi.org/10.1007/s10661-017-6116-y>.
- Pashkevich, M.D., Aryawan, A.A.K., Luke, S.H., Dupérré, N., Waters, H.S., Caliman, J.P., Naim, M., & Turner, E.C. (2021). Assessing the effects of oil palm replanting on arthropod biodiversity. *Journal of Applied Ecology*, 58(1), 27–43. <https://doi.org/10.1111/1365-2664.13749>.
- Pasternack, R., Wishnie, M., Clarke, C., Wang, Y., Belair, E., Marshall, S., Gu, H., Nepal, P., Dolezal, F., Lomax, G., Johnston, C., Felmer, G., Morales-Vera, R., Puettmann, M., & Van den Huevel, R. (2022). What is the impact of mass timber utilization on climate and forests? *Sustainability*, 14(2), 758. <https://doi.org/10.3390/su14020758>.
- Pendrill, F., Gardner, T.A., Meyfroidt, P., Persson, U.M., Adams, J., Azevedo, T., Lima, M.G.B., Baumann, M., Curtis, P.G., De Sy, V., Garrett, R., Godar, J., Goldman, E.D., Hansen, M.C., Heilmayr, R., Herold, M., Kuemmerle, T., Lathuilière, M.J., Ribeiro, V., Tyukavina, A., Weisse, M.J., & West, C. (2022). Disentangling the numbers behind agriculture-driven tropical deforestation. *Science*, 377, 1168. <https://doi.org/10.1126/science.abm9267>.
- Pfeifer, M., Kor, L., Nilus, R., Turner, E.C., Cusack, J., Lysenko, I., Khoo, M., Chey, V.K., Chung, A.C., & Ewers, R.M. (2016). Mapping the structure of Borneo's

- tropical forests across a degradation gradient. *Remote Sensing of Environment*, 176, 84–97. <https://doi.org/10.1016/j.rse.2016.01.014>.
- Poff, N.L. (2009). Managing for variability to sustain freshwater ecosystems. *Journal of Water Resources Planning and Management*, 135(1), 1–4. [https://doi.org/10.1061/\(ASCE\)0733-9496\(2009\)135:1\(1\)](https://doi.org/10.1061/(ASCE)0733-9496(2009)135:1(1)).
- Polhemus, D.A. (1994). Taxonomy, phylogeny, and zoogeography of the Genus *Cylindrostethus* Fieber in the paleotropical region (Heteroptera: Gerridae). *Bishop Museum Occasional Paper*, 38, 1–34.
- Polhemus, D.A. (1990). A revision of the genus *Metrocoris* Mayr (Heteroptera: Gerridae) in the Malay Archipelago and the Philippines. *Entomologica Scandinavica*, 21(1), 1–26. [https://brill.com/view/journals/ise/21/1/article-p1\\_1.xml](https://brill.com/view/journals/ise/21/1/article-p1_1.xml).
- Polhemus, D.A. & Polhemus, J.T. (2001). A revision of the Genus *Ptilomera* (Heteroptera: Gerridae) on New Guinea and nearby islands. *Journal of the New York Entomological Society*, 109(1), 81–166. [https://doi.org/10.1664/0028-7199\(2001\)109\[0081:AROTGP\]2.0.CO;2](https://doi.org/10.1664/0028-7199(2001)109[0081:AROTGP]2.0.CO;2).
- Polhemus, J.T. & Polhemus, D.A. (1988). Zoogeography, ecology, and systematics of the Genus *Rhagovelia* Mayr (Heteroptera: Veliidae) in Borneo, Celebes, and the Moluccas. *Insecta Mundi*, 2(3–4), 161–230. <https://digitalcommons.unl.edu/insectamundi/492/>.
- Polhemus, J.T. & Zettel, H. (1997). Five new *Potamometropsis* species (Insecta: Heteroptera: Gerridae) from Borneo. *Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie*, 99B, 21–40. <https://www.jstor.org/stable/41767049>.
- Popescu, C., Oprina-Pavelescu, M., Dinu, V., Cazacu, C., Burdon, F.J., Forio, M.A.E., Kupilas, B., Friberg, N., Goethals, P., McKie, B.G., & Rîşnoveanu, G. (2021). Riparian vegetation structure influences terrestrial invertebrate communities in an agricultural landscape. *Water*, 13(2), 188. <https://doi.org/10.3390/w13020188>.
- Popkin, M., Reiss-Woolever, V.J., Turner, E.C. & Luke, S.H. (2022). A systematic map of within-plantation oil palm management practices reveals a rapidly growing

- but patchy evidence base. *Public Library of Sciences (PLOS) Sustainability and Transformation*, 1(7), e0000023.. <https://doi.org/10.1371/journal.pstr.0000023>.
- Pusey, B.J., & Arthington, A.H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: A review. *Marine and Freshwater Research*, 54(1), 1–16. <https://doi.org/10.1071/MF02041>.
- R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- R Studio Team (2022). *RStudio: integrated development for R*. RStudio, PBC, Boston, MA. <https://www.rstudio.com/>.
- R Studio Team. (2020). *RStudio: Integrated Development for R*. RStudio, Boston, MA, USA. <https://www.rstudio.com/>.
- Raffaelli, D. & White, P.C.L. (2013). Ecosystems and their services in a changing world: an ecological perspective. *Advances in Ecological Research*, 48. <http://dx.doi.org/10.1016/B978-0-12-417199-2.00001-X>.
- Raven, P.H., & Wagner, D.L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2). <https://doi.org/10.1073/PNAS.2002548117>.
- Reed, M.S. (2008). Stakeholder participation for environmental management: A literature review. *Biological Conservation*, 141(10), 2417–2431. <https://doi.org/10.1016/j.biocon.2008.07.014>.
- Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., & Cooke, S.J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. <https://doi.org/10.1111/brv.12480>.
- Reiss-Woolever, V.J., Advento, A.D., Aryawan, A.A.K., Caliman, J-P., Foster, W.A., Naim, M., Pujianto, Purnomo, D., Snaddon, J.L., Soeprapto, Suhardi, Tarigan, R.S., Wahyuningsih, R., Rambe, T.D.S., Ps, S., Widodo, R.H., Luke, S.H., & Turner, E.C. (2023a). Habitat heterogeneity helps support day-flying

- Lepidoptera biodiversity in oil palm plantations. *Journal of Tropical Ecology*, 39, E24. <https://doi.org/10.1017/S0266467423000111>.
- Reiss-Woolever, V.J., Advento, A.D., Aryawan, A.A.K., Caliman, J-P., Foster, W.A., Naim, M., Pujianto, Purnomo, D., Snaddon, J.L., Soeprapto, Suhardi, Tarigan, R.S., Wahyuningsih, R., Rambe, T.D.S., Ps, S., Widodo, R.H., Luke, S.H., & Turner, E.C. (2023b). Understory vegetation can support more abundant and diverse butterfly communities in oil palm plantations. *Frontiers in Forests and Global Change*, 6. <https://doi.org/10.3389/ffgc.2023.1205744>.
- Riutta, T., Malhi, Y., Kho, L.P., Marthews, T.R., Huasco, W.H., Khoo, M.S., Tan, S., Turner, E.C., Reynolds, G., Both, S., Burslem, D.F.R.P., Teh, Y.A., Vairappan, C.S., Majalap, N. & Ewers, R.M. (2018). Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biology*, 24(7), 2913–2928. <https://doi.org/10.1111/gcb.14068>.
- Rizopoulos, D. (2006). ltm: An R package for latent variable modelling and item response theory analyses. *Journal of Statistical Software*, 17(5), 1–25. <https://doi.org/10.18637/jss.v017.i05>.
- Rogers, L.E., Buschbom, R.L., & Watson, C.R. (1977) Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, 70, 51–53. <https://doi.org/10.1093/aesa/70.1.51>.
- Rojas-Castillo, O.A., Kepfer-Rojas, S., Vargas, N., & Jacobsen, D. (2023). Forest buffer-strips mitigate the negative impact of oil palm plantations on stream communities. *Science of The Total Environment*, 873, 162259. <https://doi.org/10.1016/j.scitotenv.2023.162259>.
- Rousk, J. (2016). Biomass or growth? How to measure soil food webs to understand structure and function. *Soil Biology and Biochemistry*, 102, 45–47. <https://doi.org/10.1016/j.soilbio.2016.07.001>.
- Rubin, Z., Mathias Kondolf, G., & Rios-Touma, B. (2017). Evaluating stream restoration projects: what do we learn from monitoring? *Water*, 9, 174. <https://doi.org/10.3390/w9030174>.
- RSPO (Roundtable on Sustainable Palm Oil). 2018. Principles and criteria for the production of sustainable palm oil. <https://rspo.org/resources/>.

- Sackett, T.E., Classen, A.T., & Sanders, N.J. (2010). Linking soil food web structure to above and belowground ecosystem processes: a meta-analysis. *Oikos*, 119, 1984–1992. <https://doi.org/10.1111/j.1600-0706.2010.18728.x>.
- Saha, A. & Gupta, S. (2019). Nepomorpha and Gerromorpha (Hemiptera) community in the agricultural fields of Barak Valley, Assam, North East India. *Asian Journal of Conservation Biology*, 8, 149–158. [https://www.ajcb.in/journals/full\\_papers\\_dec\\_2019/AJCB-Vol8-No2-Saha-Gupta.pdf](https://www.ajcb.in/journals/full_papers_dec_2019/AJCB-Vol8-No2-Saha-Gupta.pdf).
- Sample, B.E., Cooper, R.J., Greer, R.D., & Whitmore, R.C. (1993). Estimation of insect biomass by length and width. *American Midland Naturalist*, 129, 234–240. <https://www.jstor.org/stable/2426503>.
- Samways, M.J., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kaila, L., Kwak, M.L., Maes, D., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C., & Cardoso, P. (2020). Solutions for humanity on how to conserve insects. *Biological Conservation*, 242, 108427. <https://doi.org/10.1016/j.biocon.2020.108427>.
- Sargac, J., Johnson, R.K., Burdon, F.J., Truchy, A., Rîşnoveanu, G., Goethals, P., & McKie, B.G. (2021). Forested riparian buffers change the taxonomic and functional composition of stream invertebrate communities in agricultural catchments. *Water*, 13(8), 1028. <https://doi.org/10.3390/w13081028>.
- Savilaakso, S., Garcia, C., Garcia-Ulloa, J., Ghazoul, J., Groom, M., Guariguata, M.R., Laumonier, Y., Nasi, R., Petrokofsky, G., Snaddon, J. & Zrust, M. (2014). Systematic review of effects on biodiversity from oil palm production. *Env. Evidence*, 3, 4. <https://doi.org/10.1186/2047-2382-3-4>.
- Schoener, T.W. (1980). Length-weight regressions in tropical and temperate forest-understory insects. *Annals of the Entomological Society of America*, 73, 106–109. <https://doi.org/10.1093/aesa/73.1.106>.
- Scott, D.T., Gomez-Velez, J.D., Nathan Jones, C., & Harvey, J.W. (2019). Floodplain inundation spectrum across the United States. *Nature Communications*, 10, 5194. <https://doi.org/10.1038/s41467-019-13184-4>.

- Sharpley, A.N. & Syers, J.K. (1979). Phosphorus inputs into a stream draining an agricultural watershed II: amounts contributed and relative significance of runoff types. *Water, Air, and Soil Pollution*, 11, 417-428. <https://doi.org/10.1007/BF00283433>.
- Shearman, P., Bryan, J., & Laurance, W.F. (2012). Are we approaching 'peak timber' in the tropics? *Biological Conservation*, 151(1), 17–21. <https://doi.org/10.1016/j.biocon.2011.10.036>.
- Shuhada, S.N., Salim, S., Nobilly, F., Lechner, A.M., & Azhar, B. (2020). Conversion of peat swamp forest to oil palm cultivation reduces the diversity and abundance of macrofungi. *Global Ecology and Conservation*, 23, e01122. <https://doi.org/10.1016/j.gecco.2020.e01122>.
- Sidle, R.C., Ziegler, A.D., Negishi, J.N., Nik, A.R., Siew, R., & Turkelboom, F. (2006). Erosion processes in steep terrain - Truths, myths, and uncertainties related to forest management in Southeast Asia. *Forest Ecology and Management*, 224(1–2), 199–225. <https://doi.org/10.1016/j.foreco.2005.12.019>.
- da Silva Giehl, N.F., Cabette, H.S.R., Dias-Silva, K., Juen, L., Moreira, F.F.F. de Castro, L.A., Ferreira, V.R.S., & Batista, J.D. (2020). Variation in the diversity of semiaquatic bugs (Insecta: Heteroptera: Gerromorpha) in altered and preserved veredas. *Hydrobiologia*, 847, 3497–3510. <https://doi.org/10.1007/s10750-020-04364-1>.
- Slade, E.M., Mann, D.J. & Lewis, O.T. (2011). Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biological Conservation*, 144, 166–174. <https://doi.org/10.1016/j.biocon.2010.08.011>.
- Smock, L.A. (1980). Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, 10, 375–383. <https://doi.org/10.1111/j.1365-2427.1980.tb01211.x>.
- Snaddon, J.L., Willis, K.J., & Macdonald, D.W. (2013). Oil-palm replanting raises ecology issues. *Nature (Correspondence)*, 502, 170–171. <http://dx.doi.org/10.1038/502170d>.

- Sodhi, N.S., Koh, L.P., Brook, B.W., & Ng, P.K.L. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*, 19(12), 654–660. <https://doi.org/10.1016/j.tree.2004.09.006>.
- Spence, J.R. (1989). The habitat templet and life history strategies of pond skaters (Heteroptera: Gerridae): reproductive potential, phenology, and wing dimorphism. *Canadian Journal of Zoology*, 67, 2432–2477. <https://doi.org/10.1139/z89-344>.
- Spence, J.R. (1983). Pattern and process in co-existence of water-striders (Heteroptera: Gerridae). *Journal of Animal Ecology*, 52, 497–511. <https://www.jstor.org/stable/4568>.
- Spence, J.R. & Andersen, N.M. (1994). Biology of water striders: interactions between systematics and ecology. *Annual Review of Entomology*, 39, 101–128. <https://doi.org/10.1146/annurev.en.39.010194.000533>.
- Spence, J.R. & Carcamo, H.A. (1991). Effects of cannibalism and intraguild predation on pondskaters (Gerridae). *Oikos*, 62, 333–341. <https://www.jstor.org/stable/3545498>.
- Spitzer, K., Novotny, V., Tonner, M., & Leps, J. (1993). Habitat preferences, distribution, and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *Journal of Biogeography*, 20(1), 109–121. <http://www.jstor.com/stable/2845744>.
- Steffan-Dewenter, I. & Tschardt, T. (1997). Early succession of butterfly and plant communities on set-aside fields. *Oecologia*, 109, 294–302. <https://doi.org/10.1007/s004420050087>.
- Stork, N.E. (2018). How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, 63, 31–45. <https://doi.org/10.1146/annurev-ento-020117-043348>.
- Stratford, J.A. & Robinson, W.D. (2005). Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and the Environment*, 3(2), 85–92. [https://doi.org/10.1890/1540-9295\(2005\)003\[0085:GTTTFT\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0085:GTTTFT]2.0.CO;2).

- Straus, S. & Aviles, L. (2017). Estimating consumable biomass from body length and order in insects and spiders. *Ecological Entomology*, 43, 69–75. <https://doi.org/10.1111/een.12471>.
- Strayer, D.L. (2006). Challenges for freshwater invertebrate conservation. *J. of the North American Benthological Society*, 25(2), 271-287. [https://doi.org/10.1899/0887-3593\(2006\)25\[271:CFFIC\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2006)25[271:CFFIC]2.0.CO;2).
- Strayer, D.L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1), 344–358. <https://www.journals.uchicago.edu/doi/abs/10.1899/08-171.1>.
- Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., & Bell, D. (2013). Quantifying the biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from Borneo. *Advances in Ecological Research*, 48. <http://dx.doi.org/10.1016/B978-0-12-417199-2.00003-3>.
- Sugiura, M., Imafuku, M., & Ohtani, T. (2010). Skipping flights in *Ypthima* butterflies (Lepidoptera: Nymphalidae). *Entomological Science*, 13(2), 183–190. <https://doi.org/10.1111/j.1479-8298.2010.00382.x>.
- Suhaimi, S., Zakaria, A., Sulaiman, A., Mohd Yaakob, M.Z., Juhary, M.A.A., & Sulaiman, N. (2017). Species diversity and abundance of butterfly (Lepidoptera: Rhopalocera) at different altitudes along the raub corridor to Fraser’s Hill, Pahang, Malaysia. *Serangga*, 22(1), 123–145. <http://journalarticle.ukm.my/13041/1/22878-66117-1-SM.pdf>.
- bin Sulaiman, S.K., Ibrahim, Y., & Jeffree, M.S. (2019). Evaluating the perception of farmers towards pesticides and the health effect of pesticides: A cross-sectional study in the oil palm plantations of Papar, Malaysia. *Interdiscip Toxicol.*, 12(1), 15–25. <https://sciendo.com/downloadpdf/journals/intox/12/1/article-p15.xml>.
- Sundar, S., Silva, D.P., de Oliveira Roque, F., Simião-Ferreira, J., & Heino, J. (2021). Predicting climate effects on aquatic true bugs in a tropical biodiversity hotspot. *Journal of Insect Conservation*, 25, 229–241. <https://doi.org/10.1007/s10841-021-00298-8>.

- Sundar, S., Heino, J., Roque, F. de O., Simaika, J.P., Melo, A.S., Tonkin, J.D., Nogueira, D.G., & Silva, D.P. (2020). Conservation of freshwater macroinvertebrate biodiversity in tropical regions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(6), 1238–1250. <https://doi.org/10.1002/aqc.3326>.
- Sunkar, A., Santosa, Y., Masyithoh, G., & Erniwati (2019). Policy advocacy: the potential role of independent smallholding oil palm plantation in biodiversity conservation. *IOP Conf. Series: Earth and Environmental Science*, 285, 012012. <https://iopscience-iop-org/article/10.1088/1755-1315/285/1/012012/meta>.
- Sweeney, B.W. (1993). Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in Eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 144, 291-340. <https://www.jstor.org/stable/4065013>.
- Syafiq, M., Nur Atiqah, A.R., Ghazali, A., Asmah, S., Yahya, M.S., Aziz, N., Puan, C.L., & Azhar, B. (2016). Responses of tropical fruit bats to monoculture and polyculture farming in oil palm smallholdings. *Acta Oecologica*, 74, 11–18. <https://doi.org/10.1016/j.actao.2016.06.005>.
- Tanaka, Y., Minggat, E., & Roseli, W. (2021). The impact of tropical land-use change on downstream riverine and estuarine water properties and biogeochemical cycles: a review. *Ecological Processes*, 10(1). <https://doi.org/10.1186/s13717-021-00315-3>.
- Tang, T., R. Stevenson, J., & Grace, J.B. (2020). The importance of natural versus human factors for ecological conditions of streams and rivers. *Science of The Total Environment*, 704. <https://doi.org/10.1016/j.scitotenv.2019.135268>.
- Tank, J.L., Rosi-Marshall, E.J., Griffiths, N.A., Entekin, S.A., & Stephen, M.L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*, 29(1), 118–146. <https://www.journals.uchicago.edu/doi/abs/10.1899/08-170.1>.
- Tao, H.H., Slade, E.M., Willis, K.J., Caliman, J.P., & Snaddon, J.L. (2016). Effects of soil management practices on soil fauna feeding activity in an Indonesian oil palm plantation. *Agriculture, Ecosystems and Environment*. <https://doi.org/10.1016/j.agee.2015.11.012>.

- Thompson, R.M., Brose, U., Dunne, J.A., Hall Jr., R.O., Hladysz, S. Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., & Tylianakis, J.M. (2012). Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*, 27, 689–697. <https://doi.org/10.1016/j.tree.2012.08.005>.
- Tohiran, K.A., Nobilly, F., Zulkifli, R., Ashton-Butt, A., & Azhar, B. (2019). Cattle-grazing in oil palm plantations sustainably controls understory vegetation. *Agriculture, Ecosystems and Environment*, 278, 54–60. <https://doi.org/10.1016/j.agee.2019.03.021>.
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151(1), 53–59. <https://doi.org/10.1016/j.biocon.2012.01.068>.
- Turner, E.C. & Foster, W.A. (2009). The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology*, 25, 23–30. <https://doi.org/10.1017/S0266467408005658>.
- Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, 86(3), 640–657. <https://doi.org/10.1111/j.1469-185X.2010.00164.x>.
- Venables, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*. Fourth Edition. Springer, New York. <http://www.stats.ox.ac.uk/pub/MASS4/>.
- Vergara, C.H., & Badano, E.I. (2009). Pollinator diversity increases fruit production in Mexican coffee plantations: The importance of rustic management systems. *Agriculture, Ecosystems and Environment*, 129(1–3), 117–123. <https://doi.org/10.1016/j.agee.2008.08.001>.
- Vieira, T.B., Dias-Silva, K. & Pacífico, E.S. (2015). Effects of riparian vegetation integrity on fish and Heteroptera communities. *Applied Ecology and Environmental Research*, 13, 53–65. [https://doi.org/10.15666/aeer/1301\\_053065](https://doi.org/10.15666/aeer/1301_053065).
- Vijaynathan, J., Ishak, M.F., Parlan, I., Omar, H., Haruna, A.O., Lion, M., Hassan, M.G., Jong, R.M., & Samah, A.K.A. (2021). Temporal patterns control carbon balance

- in forest and agricultural tropical peatlands in North Selangor, Malaysia. *iForest - Biogeosciences and Forestry*, 14(4), 362–369. <https://doi.org/10.3832/ifor3700-014>.
- Wagner, D.L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>.
- Wallace, J.B. & Webster, J.R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, 41, 115-139. <https://doi.org/10.1146/annurev.en.41.010196.000555>.
- Wan Zaki, W.M., Yahya, M.S., Norhisham, A.R., Sanusi, R., van der Meer, P.J., & Azhar, B. (2023). Agroforestry orchards support greater butterfly diversity than monoculture plantations in the tropics. *Oecologia*. <https://doi.org/10.1007/s00442-023-05348-3>.
- Wantzen, K.M., & Mol, J. H. (2013). Soil erosion from agriculture and mining: A threat to tropical stream ecosystems. *Agriculture (Switzerland)*, 3(4), 660–683. <https://doi.org/10.3390/agriculture3040660>.
- Wardhaugh, C.W. (2013). Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. *Australian Journal of Entomology*, 52, 291–298. <https://doi.org/10.1111/aen.12032>.
- Weijters, M.J., Janse, J.H., Alkemade, R., & Verhoeven, J.T.A. (2009). Quantifying the effect of catchment land use and water nutrient concentrations on freshwater river and stream biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19(1), 104–112. <https://doi.org/10.1002/aqc.989>.
- Welcomme, R.L. (1979). *Fisheries ecology of floodplain rivers*. Longman, London. <https://archive.org/details/fisherieecology0000welc/page/n9/mode/2up>.
- Whitmore, T.C. (1984). *Tropical rain forests of the Far East*, 2nd edition. Oxford University Press. Oxford.
- Wickham, H., François, R., Henry, L., & Müller, K. (2021). *dplyr: A grammar of data manipulation*. R package version 1.0.4. <https://CRAN.R-project.org/package=dplyr>.

- Wickham, H., Averick, M., Bryan, J., Chang, W., & McGowan, L.D., François, R., Golemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seide, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., & Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software* 4: 1686. <https://doi.org/10.21105/joss.01686>.
- Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., & Koh, L.P. (2013). Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology and Evolution*, 28(9), 531–540. <https://doi.org/10.1016/j.tree.2013.04.005>.
- Wild Asia. (2012). *A Review of Smallholder Oil Palm Production Challenges and Opportunities for Enhancing Sustainability: A Malaysian Perspective*. A white paper. p.5. <http://oilpalm.wildasia.org/1627/review-smallholder-projects-palm-oil-malaysian-perspective/>.
- Wilke, C.O. (2020). cowplot: Streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.1.1. <https://CRAN.R-project.org/package=cowplot>.
- Willott, S.J., Lim, D.C., Compton, S.G., & Sutton, S.L. (2000). Effects of selective logging on the butterflies of a Bornean rainforest. *Conservation Biology*, 14(4), 1055–1065. <https://doi.org/10.1046/j.1523-1739.2000.98427.x>.
- Wilkinson, C.L., Yeo, D.C.J., Hui, T.H., Fikri, A.H., & Ewers, R.M. (2018). Land-use change is associated with a significant loss of freshwater fish species and functional richness in Sabah, Malaysia. *Biological Conservation*, 222, 164–171. <https://doi.org/10.1016/j.biocon.2018.04.004>.
- Williamson, C.E., Dodds, W., Kratz, T.K., & Palmer, M.A. (2008). Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. *Frontiers in Ecology and the Environment*, 6(5), 247–254. <https://doi.org/10.1890/070140>.
- Wilson, R.J., & Fox, R. (2020). Insect responses to global change offer signposts for biodiversity and conservation. *Ecological Entomology*. <https://doi.org/10.1111/een.12970>.

- Woodham, C.R., Aryawan, A.A.K., Luke, S.H., Manning, P., Caliman, J.P., Naim, M., Turner, E.C., & Slade, E.M. (2019). Effects of replanting and retention of mature oil palm riparian buffers on ecosystem functioning in oil palm plantations. *Frontiers in Forests and Global Change*, 2. <https://doi.org/10.3389/ffgc.2019.00029>.
- The World Bank. (2023). *Rural population, percent - Country rankings*. [https://www.theglobaleconomy.com/rankings/rural\\_population\\_percent/South-East-Asia/](https://www.theglobaleconomy.com/rankings/rural_population_percent/South-East-Asia/). Accessed on 28 June 2023.
- WWF (World Wildlife Fund). (2018). *Living Planet Report 2018: Aiming Higher* (Eds M. Grooten & R.E.A. Almond). WWF International. Gland, Switzerland. <https://www.worldwildlife.org/pages/living-planet-report-2018>.
- Wourms, M.K. & Wasserman, F.E. (1985). Bird predation on Lepidoptera and the reliability of beak-marks in determining predation pressure. *Journal of the Lepidopterists' Society*, 39, 239–261. [https://images.peabody.yale.edu/lepsoc/jls/1980s/1985/1985-39\(4\)239-Wourms.pdf](https://images.peabody.yale.edu/lepsoc/jls/1980s/1985/1985-39(4)239-Wourms.pdf).
- Wu, C., Maurer, C., Wang, Y., Xue, S., & Davis, D.L. (1999). Water pollution and human health in China. *Environmental Health Perspectives*, 107(4), 251–256. <https://doi.org/10.1289/ehp.99107251>.
- Xu, Q., Yan, T., Wang, C., Hua, L., & Zhai, L. (2023). Managing landscape patterns at the riparian zone and sub-basin scale is equally important for water quality protection. *Water Research*, 229, 119280. <https://doi.org/10.1016/j.watres.2022.119280>.
- Ya'acob, M.E., Lu, L., Nobilly, F., Che'Ya, N.N., Aziz, A.A., Dupraz, C., Yahya, M.S., Atikah, S.N. & Mamun, M.A.A. (2022). Analysis of weed communities in solar farms located in tropical areas—the case of Malaysia. *Agronomy*, 12(12), 3073. <https://doi.org/10.3390/agronomy12123073>.
- Yahya, M.S., Syafiq, M., Ashton-Butt, A., Ghazali, A., Asmah, S., & Azhar, B. (2017). Switching from monoculture to polyculture farming benefits birds in oil palm production landscapes: Evidence from mist netting data. *Ecology and Evolution*, 7(16), 6314–6325. <https://doi.org/10.1002/ece3.3205>.

- Yang, C.M., Wong, T.C.M., Lua, H.K., & Koh, L.M. (1999). A checklist of aquatic and semi-aquatic bugs (Insecta: Hemiptera: Heteroptera) from Pulau Tioman, Peninsular Malaysia. *The Raffles Bulletin of Zoology*, 6, 277–288.
- Yang, C.M., Lua, H.K., & Yeo, K.L. (1997). Semi-aquatic bug (Heteroptera: Gerromorpha) fauna in the Nature Reserves of Singapore. Proceedings of the Nature Reserves Survey Seminar. *Gardens' Bulletin Singapore*, 49, 313–319. <https://www.nparks.gov.sg/sbg/research/publications/gardens'-bulletin-singapore/-/media/sbg/gardens-bulletin/4-4-49-2-08-y1997-v49p2-gbs-pg-313.pdf>.
- Ye, Z., Zhen, Y., Zhou, Y., & Bu, W. (2017). Out of Africa: Biogeography and diversification of the pantropical pond skater genus *Limnogonus* Stål, 1868 (Hemiptera: Gerridae). *Ecology and Evolution*, 7, 793–802. <https://doi.org/10.1002/ece3.2688>.
- Ye, Z., Chen, P., & Bu, W. (2015). A review of the *Strongylovelia* Esaki, 1924 (Hemiptera: Heteroptera: Veliidae) from China, with descriptions of three new species. *Zootaxa*, 3920(4), 534–544. <https://dx.doi.org/10.11646/zootaxa.3920.4.2>.
- Yusof, N.F., Lihan, T., Idris, W.M.R, Rahman, Z.A., Mustapha, M.A., & Yusof, M.A.W. (2021). Spatially distributed soil losses and sediment yield: A case study of Langat watershed, Selangor, Malaysia. *Journal of Asian Earth Sciences*, 212, 104742. <https://doi.org/10.1016/j.jseae.2021.104742>.
- Zettel, H. (2014). Annotated catalogue of the semi-aquatic bugs (Hemiptera: Heteroptera: Gerromorpha) of Luzon Island, the Philippines, with descriptions of new species). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, 66, 85–140. [https://www.zobodat.at/pdf/ZAOE\\_66\\_0085-0140.pdf](https://www.zobodat.at/pdf/ZAOE_66_0085-0140.pdf).
- Zettel, H. & Chen, P.P. (2000). *Limnometra palawanensis* spec. nov. (Heteroptera: Gerridae), and a synopsis of the species of *Limnometra*. *Entomologische Berichten*, 60(5), 73–83. <https://natuurtijdschriften.nl/pub/1012057/EB2000060005001.pdf>.

Zimmermann, M. & Spence, J.R. (1989). Prey use of the fishing spider *Dolomedes triton* (Pisauridae, Araneae): an important predator of the neuston community. *Oecologia*, 80, 187–194. <https://doi.org/10.1007/BF00380149>.