

**The effects of replanting and restoration of riparian  
buffers on arthropods in oil palm systems**

Michael David Pashkevich, Jr.  
Jesus College

July 2021

This thesis is submitted for the degree of Doctor of Philosophy at the  
University of Cambridge



## **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

### The effects of replanting and restoration of riparian buffers on arthropods in oil palm systems

Michael David Pashkevich, Jr.

Oil palm is a widely grown tropical crop, and its product – palm oil – has international economic importance. The expansion of oil palm plantations has caused substantial declines in biodiversity and changes in ecosystem processes. Protecting natural habitats is a conservation priority. However, once oil palm plantations are established, it is important to investigate how changes in management can affect oil palm systems, which can be relatively ecologically complex. Despite this, there is limited understanding of how most management strategies – such as those used to replant oil palms when they have reached the end of their commercial life cycle, and to maintain and restore areas around rivers in plantations (“riparian buffers”) – can affect oil palm systems.

This PhD was based primarily at the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme in Sumatra, Indonesia, within oil palm plantations that received different levels of management. Across these plantations, we sampled arthropods in the canopy, understory, and ground microhabitats using insecticide fogging; sticky traps and hand collections; and pitfall traps, respectively. We sampled in different ages of oil palm, and in sites that were within, near, and far from riparian buffers undergoing different restoration management, in order to investigate the effects of replanting and restoration of riparian buffers on arthropod biodiversity. This thesis has four data chapters:

**Chapter 2:** By surveying arthropods across an oil palm chronosequence that spanned a replanting event, we showed that replanting using recommended strategies did not affect total arthropod abundance, but had effects on order-level community composition, and the biodiversity of functionally important groups, including spiders.

**Chapter 3:** Sampling the same chronosequence as in Chapter 2, we found that riparian buffers that were made of mature oil palms and being passively restored did not have consistent

impacts on environmental conditions and arthropod biodiversity across the oil palm commercial life cycle.

**Chapter 4:** Working in the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project, we used an experimental approach to show that passive and active restoration of riparian buffers did not benefit arthropod biodiversity within two years of restoration treatments being implemented. Longer-term observations are needed before the full impacts of this experiment can be determined.

**Chapter 5:** Using systematic review and meta-analysis, we showed that anthropogenic disturbance reduced spider abundance and species richness, and restoration initiatives did not consistently benefit spiders in the tropics. We also demonstrated that spider responses to disturbance and restoration varied substantially, and were therefore context-dependent.

This thesis shows that replanting has substantial impacts on environmental conditions and biodiversity in oil palm plantations, but the effects of replanting are variable across microhabitats and taxonomic groups. It also shows that restoration of riparian buffers in oil palm systems is possible through tractable changes in management, but longer-term observations are needed to demonstrate whether there are consistent benefits of restored buffers to biodiversity, and to determine the comparative benefits of passive and active approaches to riparian restoration. Further, this thesis demonstrates that there is no “silver bullet” to restoring degraded tropical landscapes, and highlights the importance of conducting large-scale, long-term experiments to improve knowledge of how restoration can benefit degraded tropical systems.

## Statement of Contributions

**Chapter 1:** Most of this chapter was reproduced from a commentary paper that is currently in review in *Journal of Applied Ecology* (Pashkevich, d'Albertas, et al., In Review). I made minor formatting changes, and did not include three case studies that were featured as boxes of text in the manuscript. I wrote the manuscript, and all co-authors (Francisco d'Albertas, Anak Agung Ketut Aryawan, Damayanti Buchori, Jean-Pierre Caliman, Adrian González Chaves, Purnama Hidayat, Holger Kreft, Mohammad Naim, Appolinaire Razafimahatratra, Edgar Turner, Delphine Clara Zemp, and Sarah Luke) commented on it.

**Chapter 2:** This chapter was reproduced from a paper that has been published in *Journal of Applied Ecology* (Pashkevich et al., 2021). I made minor edits, changed the formatting, and did not include all supplementary materials. Edgar Turner, Sarah Luke, Helen Waters, and I conceived the study. Nadine Dupérré advised on identification of spiders. I led data collection, carried out the statistical analyses, and wrote the paper. All co-authors (Anak Agung Ketut Aryawan, Sarah Luke, Nadine Dupérré, Helen Waters, Jean-Pierre Caliman, Mohammad Naim, and Edgar Turner) and two reviewers (Jochen Drescher, and one anonymous reviewer) commented on the manuscript.

**Chapter 3:** This chapter was reproduced from a paper that is currently in review in *Ecological Applications* (Pashkevich, Luke, et al., In Review). I made minor edits, changed the formatting, and did not include all supplementary materials. Edgar Turner, Sarah Luke, Helen Waters, and I conceived the study. Nadine Dupérré advised on identification of spiders. I led data collection, carried out the statistical analyses, and wrote the paper. All co-authors (Sarah Luke, Anak Agung Ketut Aryawan, Helen Waters, Jean-Pierre Caliman, Nadine Dupérré, Mohammad Naim, Anton Potapov, and Edgar Turner) and two anonymous reviewers commented on the manuscript.

**Chapter 4:** The RERTA Project was designed by Edgar Turner, Sarah Luke, Jake Snaddon, Anak Agung Ketut Aryawan, Mohammad Naim, Jean-Pierre Caliman, Ribka Sionita Tarigan, Suhardi, Resti Wahyuningsih, Dedi Purnomo, Soeprapto, Dwi Nugroho Adhy, Edi, Pujianto, Syafrisar Putra, Whendy, William Foster, and Eleanor Slade. Anak Agung Ketut Aryawan (RERTA Project Field Manager) and I collected the data. Anak Agung Ketut Aryawan and I

led order-level identification of all arthropods. I led species-level identification of all spiders, with assistance from Nadine Dupérré. I carried out all statistical analyses, and wrote the chapter. Edgar Turner and Sarah Luke commented on the chapter.

**Chapter 5:** Edgar Turner and I conceived this study. I carried out the data collection, statistical analyses, and wrote the chapter. Thomas Kemenes reviewed all data that I extracted from the 91 studies that were included in the meta-analysis. Edgar Turner and Sarah Luke commented on the chapter.

**Chapter 6:** I wrote this chapter, with comments from Edgar Turner and Sarah Luke.

Please see my acknowledgements for information on funding and additional assistance that I received whilst completing my PhD. Please note that, although I led all research in this thesis, I mostly use “we” throughout, owing to the highly collaborative nature of this research.

## Acknowledgements

First, I thank my supervisor, Ed Turner, who has made my last four years an incredible learning experience. I have truly enjoyed my PhD, in large part owing to Ed's constant support and guidance. I cannot imagine a more kind and helpful supervisor.

I am so grateful to Sarah Luke, who has been an immense source of support, patient feedback, and friendship across my PhD, and also my frequent running companion whilst I was on fieldwork. Also, thanks to Millie Hood for helping to show me how to be a serious researcher without taking myself too seriously. I want to thank the Insect Ecology Group for their friendship and support, particularly Jake Stone, Matt Hayes, Kate Howlett, and Valentine Reiss-Woolever. Additionally, thank you to my advisors David Aldridge and William Sutherland. Thanks to Lily Bentley, Cansu Karabiyik, Melanie Sferrazza, and Francesca Vaccaro for their friendship. I also want to thank the residents of 7 Pelham Court, especially Francisco d'Albertas, Anoushka Handa, Dan Potter, and Simon Stephenson for helping me to stay sane during Lockdown One. I am so grateful to Aimée Thomas, Bob Thomas, and Naomi Yavneh-Klos for their constant guidance over the years.

I spent about 15 months of my PhD on fieldwork, and received a huge amount of support during this time. I thank PT Ivo Mas Tunggal, Golden Agri Resources, Sinar Mas Agro Resources and Technology Research Institute (SMARTRI), RISTEK (Permit number: 1068/FRP/E5/Dit.KI/II/2018; EXT: 7/EXT/FRP/E.5/Dit.KI/1/2019; EXT: 7/EXT/FRP/E.5/Dit.KI/I/2020), and KSDA (Collect permit #SK. 377/KSDAE/SET/KSA.2/9/2019) for allowing me to conduct research in Indonesian oil palm plantations. At SMARTRI, I particularly thank Jean-Pierre Caliman, Mohammad Naim, Anak Agung Ketut Aryawan, Joni Jupesta, Yan, Aby, and Hasbullah and his lovely family. I also thank Victor Barron, Julia Drewer, Amy Eycott, William Foster, Martina Faika Harianja, Eva Haentjens, Helen Waters, and Stella White for their wonderful company and support whilst I was on fieldwork.

My PhD was funded by the Gates Cambridge Trust. Support for my fieldwork costs was provided by Jesus College, Cambridge; the Department of Zoology, Cambridge; School of Biological Sciences, Cambridge; Tim Whitmore Fund; and Cambridge Global Food Security.

I am grateful to The Isaac Newton Trust and Cambridge University for helping fund the larger Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme.

Lastly, I thank my family. Mom, Dad, Marie, Katherine, Michael G., David, Elizabeth, and Clare (who was born the week prior to my hand-in!): you remain my greatest support system, and make me smile every day.

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# Chapter 1

## Introduction

This introductory chapter outlines the underlying theory for the studies in this thesis, and places the studies into a wider context. Section 1.1 represents a submitted commentary piece, ‘Time to restore tropical agriculture’, for which I led authorship (hereafter referred to in this thesis as Pashkevich, d’Albertas, et al., In Review). It has been modified slightly for this thesis. Sections 1.2 and 1.3 provide information on oil palm agriculture, which is the system from which most data were collected for this thesis. Sections 1.4 and 1.5 outline the objectives and methods of my four data chapters.

### 1.1 Time to restore tropical agriculture

#### 1.1.1 | Abstract

Ecological restoration – including management that enhances the structural and ecological complexity of human-modified landscapes – has great potential to halt and reverse the negative impacts of anthropogenic disturbance on Earth’s ecosystems by increasing biodiversity and levels and resilience of ecosystem functioning, mitigating the effects of climate change, and improving livelihoods within degraded landscapes. The United Nations Decade on Ecosystem Restoration, 2021-2030, has shone a spotlight on global restoration efforts. Whilst there is growing engagement with restoration as a promising conservation strategy, and the evidence base for its benefits and for best practices is developing fast, knowledge is still patchy. A key knowledge gap is how to practically restore biodiversity and functioning within tropical agricultural systems. Restoring these systems could be particularly valuable, as the spread and intensification of agriculture is a leading contributor to ecosystem degradation worldwide, and the tropics offer large socioenvironmental benefits relative to the costs of implementing restoration actions.

We identify eight key actions to improve understanding of ‘who’ should be involved in, and benefit from, restoration of tropical agriculture, and ‘where’, ‘what’, and ‘how’ restoration initiatives should occur: (1) Involve a diverse network of stakeholders, at all stages and in all parts of restoration initiatives; (2) Collect more empirical data from observational studies; (3) Use new technologies to accelerate data collection; (4) Inform algorithms to identify restoration

priority areas; (5) Implement large-scale, long-term experiments to test restoration strategies; (6) Include traditional ecological knowledge and local farming practices in restoration initiatives; (7) Develop techniques for assessing and improving restoration over time; and (8) Share results and data openly and widely. Actions (2)–(7) fall into three broad categories – ecological understanding, social and economic understanding, and capacity building – all of which are underpinned by increased stakeholder engagement, collaboration, and sharing of knowledge and resources in actions (1) and (8). The increased attention and access to financial resources associated with the UN Decade on Ecosystem Restoration provide a unique opportunity to improve understanding of successful restoration in tropical agriculture. The time for simply discussing restoration is over; now is the time to capitalise on existing knowledge and resources, develop focussed strategies to fill knowledge gaps, and take ambitious action to restore tropical agricultural systems.

In this thesis, we use large-scale experiments and observational studies to determine the effects of disturbance and restoration on environmental conditions and biodiversity in oil palm agriculture. We focus on oil palm as a model system, as it is a widely grown vegetable oil crop (Davis et al., 2020) that has international economic importance. Management strategies that provide benefits to oil palm ecosystems could therefore affect large areas of land, and be implemented and financially supported within plantations across the tropics.

### **1.1.2 | Restoring Earth’s terrestrial systems**

Approximately 75% of terrestrial ecosystems are modified by humans, and this percentage is increasing (Williams et al., 2020). Habitat change is causing severe losses of biodiversity and has associated impacts on ecosystem functioning (Butchart et al., 2010). If we are to prevent mass extinctions and safeguard human wellbeing, these losses not only need to be halted, but must also be reversed (Díaz et al., 2019; Leclère et al., 2020). An approach focussed on protecting pristine areas alone is not sufficient to achieve conservation and ecosystem service delivery goals, and so more environmentally-friendly management within human-modified lands is needed (Leclère et al., 2020).

Ecological restoration (hereafter, “restoration”) is a promising management strategy for conservation in human-modified habitats. Human-modified habitats often have simplified habitat structure, including fewer layers and types of vegetation; consequent changes in microclimate, resource availability and processes; and higher prevalence of introduced and

invasive species (Dislich et al., 2017; Drescher et al., 2016; Wagner, 2020). Restoration aims to enhance the structural and ecological complexity of human-modified landscapes to direct them towards a target state, which is usually either a historical baseline or a desired, more ecologically complex system (Brancalion & Chazdon, 2017; Gann et al., 2019; Rey Benayas & Bullock, 2012; Strassburg et al., 2020; Uriarte & Chazdon, 2016). Meta-analyses indicate that restoration provides benefits to biodiversity (Barral et al., 2015; Crouzeilles et al., 2016, 2017; De Beenhouwer et al., 2013; Jones et al., 2018; Meli et al., 2017; Rey Benayas et al., 2009; Tamburini et al., 2020) and ecosystem functions and services (Barral et al., 2015; De Beenhouwer et al., 2013; Jones et al., 2018; Meli et al., 2017; Rey Benayas et al., 2009; Shimamoto et al., 2018; Tamburini et al., 2020), often over relatively short periods of time (Jones & Schmitz, 2009; Meli et al., 2017). As restoration often results in greater plant diversity and coverage, which can sequester more carbon, such strategies can also help mitigate the effects of climate change (Strassburg et al., 2019, 2020). Importantly, restoration can also be profitable, and therefore result in win-win solutions for natural and social systems. Economic returns can often outweigh the costs of implementation (Bradbury et al., 2021; De Groot et al., 2013) and, accordingly, provide economic benefits to local communities (Bradbury et al., 2021), although this can depend on how lands are being used prior to restoration and the scale at which costs and benefits accrue (Brancalion et al., 2019). There is also substantial potential for restoration to provide social benefits, such as improving health and equity, if the correct context-dependent strategies are developed (Chazdon & Brancalion, 2019).

Approaches to restoration are diverse and occur across broad spatial and temporal scales. For instance, restoration includes everything from small-scale increases in habitat complexity (e.g. planting strips of annual wildflowers to improve habitat complexity and provide resources for a wide range of species in crop monocultures; Ponisio et al., 2016) to wholesale regeneration of systems to desired alternative or undisturbed states (Ghazoul & Chazdon, 2017; Moreno-Mateos et al., 2020). Restoration can be passive or active. Passive restoration (also called natural regeneration) allows abandoned ecosystems to recover on their own or with little human intervention (Crouzeilles et al., 2017; Ghazoul & Chazdon, 2017). In contrast, active restoration involves the input of resources to accelerate recovery towards a target state. This often involves planting trees (whether across large areas of land, or in smaller stands within a larger area, i.e., ‘applied nucleation’ or ‘tree island’ approaches; Rey Benayas & Bullock, 2012; Teuscher et al., 2016), but can also include other management strategies such as transferring

soil with beneficial bacteria or nutrients from one area to another (Wubs et al., 2016) or reintroducing keystone species to facilitate rewilding (Corlett, 2016).

In certain circumstances, passive restoration is preferable to active approaches, as it can be done at lower cost, can allow a more ecologically diverse successional community to develop as local species colonise (Arroyo-Rodríguez et al., 2017), and is often equally (Barral et al., 2015; Jones et al., 2018; Meli et al., 2017), or more (Crouzeilles et al., 2017), successful at meeting restoration objectives. However, passive restoration may be insufficient when ecosystems are heavily degraded, or transformed to the extent that their biotic and abiotic conditions no longer resemble those found in natural systems (i.e. ‘novel ecosystems’; Hobbs, Higgs, & Harris, 2009). In these cases, active restoration towards a more desirable, ecologically complex state may be required (Crouzeilles et al., 2017; Holl et al., 2020). In addition to ecological status, social, economic, and political considerations can play a large role in determining what might be the most feasible or beneficial strategy for a site (Chazdon, Lindenmayer, et al., 2020; Holl, 2017b). Although the success of restoration varies between individual studies (Chazdon, Lindenmayer, et al., 2020; Crouzeilles et al., 2016, 2017; Jones et al., 2018; Meli et al., 2017) and misguided restoration initiatives can cause more harm than good (Holl & Brancalion, 2020), the collective evidence is clear: restoration can help meet global conservation goals and benefit society.

### **1.1.3 | The potential for restoring tropical agricultural systems**

Agriculture is a dominant land use worldwide and is continuing to expand globally. Agricultural production is necessary for food security and livelihoods (Tilman et al., 2011), but also contributes towards declines in biodiversity (Gibson et al., 2011), losses of ecosystem functions and services (Shimamoto et al., 2018), rises in greenhouse gas emissions (Tilman et al., 2017), and increases in economic inequity and frequency of social conflict (Santika et al., 2019, 2020). Restoration can help mitigate these adverse effects and, depending on the approach to restoration, can also allow high-yielding agricultural production.

Restoring agriculture can involve large-scale transformation of abandoned farmlands and low-yielding areas into more natural habitat, but also small-scale restoration within intensely cultivated landscapes. These smaller scale restoration options often form part of ‘ecological intensification’ methods to boost or maintain production. With this approach, yields are enhanced by increasing biodiversity and harnessing ecosystem services (Bommarco et al.,

2013; Garibaldi et al., 2017, 2019), rather than through more chemical-dependent ‘green revolution’ options, therefore providing a win-win for conservation and crop production (Barral et al., 2015; Tamburini et al., 2020; Wanger et al., 2020). For instance, agroforestry systems (here considered as a form of ecological intensification where native trees are planted amongst crops) can host forest-dwelling species that are otherwise absent or rare in the crop matrix (Bhagwat et al., 2008), and enhance the abundance and diversity of faunal communities at both the local (Udawatta et al., 2019) and farm (Lichtenberg et al., 2017) scales. In comparison to more simplified crop systems, agroforestry systems have higher levels of ecosystem functions and services, including pest and weed control, soil health, carbon sequestration, regulation of the hydrological cycle, and increased yield stability (De Beenhouwer et al., 2013; Maas et al., 2020; Marsden et al., 2020; Martin, Wurz, et al., 2020; Pumariño et al., 2015; Rosa-Schleich et al., 2019; Santos et al., 2019).

Restoring agriculture can also provide benefits beyond farm boundaries. For example, planting tree islets within abandoned pastures or cultivated or abandoned croplands can accelerate reforestation in surrounding habitat (Holl et al., 2020; Rey Benayas & Bullock, 2012); restoring riparian buffers — areas of land that surround waterways in agricultural areas — can improve water quality for communities downstream (Luke, Slade, et al., 2019); and incorporating management strategies informed by traditional ecological knowledge can benefit local biodiversity whilst conserving aspects of indigenous culture (Falkowski et al., 2020).

Although restoration is needed urgently across all ecosystems (Strassburg et al., 2020), restoring tropical agricultural systems may result in particularly large and immediate benefits to ecosystems and society. This is partly because ecosystems at lower latitudes have the potential for faster and more complete recovery than those at higher latitudes (Jones et al., 2018). This is driven by fast plant growth rates, which allow rapid recovery of floral structural complexity and diversity (Crouzeilles et al., 2017), and possibly by the inherently high levels of diversity that are found in the tropics (Gaston, 2000). In addition, although large parts of the tropics have been degraded, substantial areas of intact natural habitat remain (Pugh et al., 2019). This habitat can assist the recovery of surrounding degraded areas (César et al., 2021), through spillover of biodiversity (e.g. increased propagule pressure) and ecosystem services (e.g. pollination) (Rey Benayas & Bullock, 2012).

Further, restoring tropical agriculture may be particularly feasible, as agricultural production in many tropical areas has only recently increased in intensity and scale (Ramankutty et al., 2018; Song et al., 2018). Many local communities have traditionally practiced intercropping, agroforestry, and homegarden-style approaches to agriculture, which can allow for relatively high levels of biodiversity and structural complexity within the crop matrix (Abebe et al., 2010; Ashraf et al., 2018; Maas et al., 2020). It is only relatively recently that a ‘green revolution’ approach to intensifying tropical agriculture has become widely implemented, possibly making it easier to reduce its use and reverse its impacts (César et al., 2021; Chazdon, Lindenmayer, et al., 2020), either towards more ecologically intensive farming approaches or removal of land from production and restoration towards natural habitat (Bommarco et al., 2013). For example, low levels of damage to soils or seed banks might make restoration more achievable through either passive or active restoration (Skoglund, 1992).

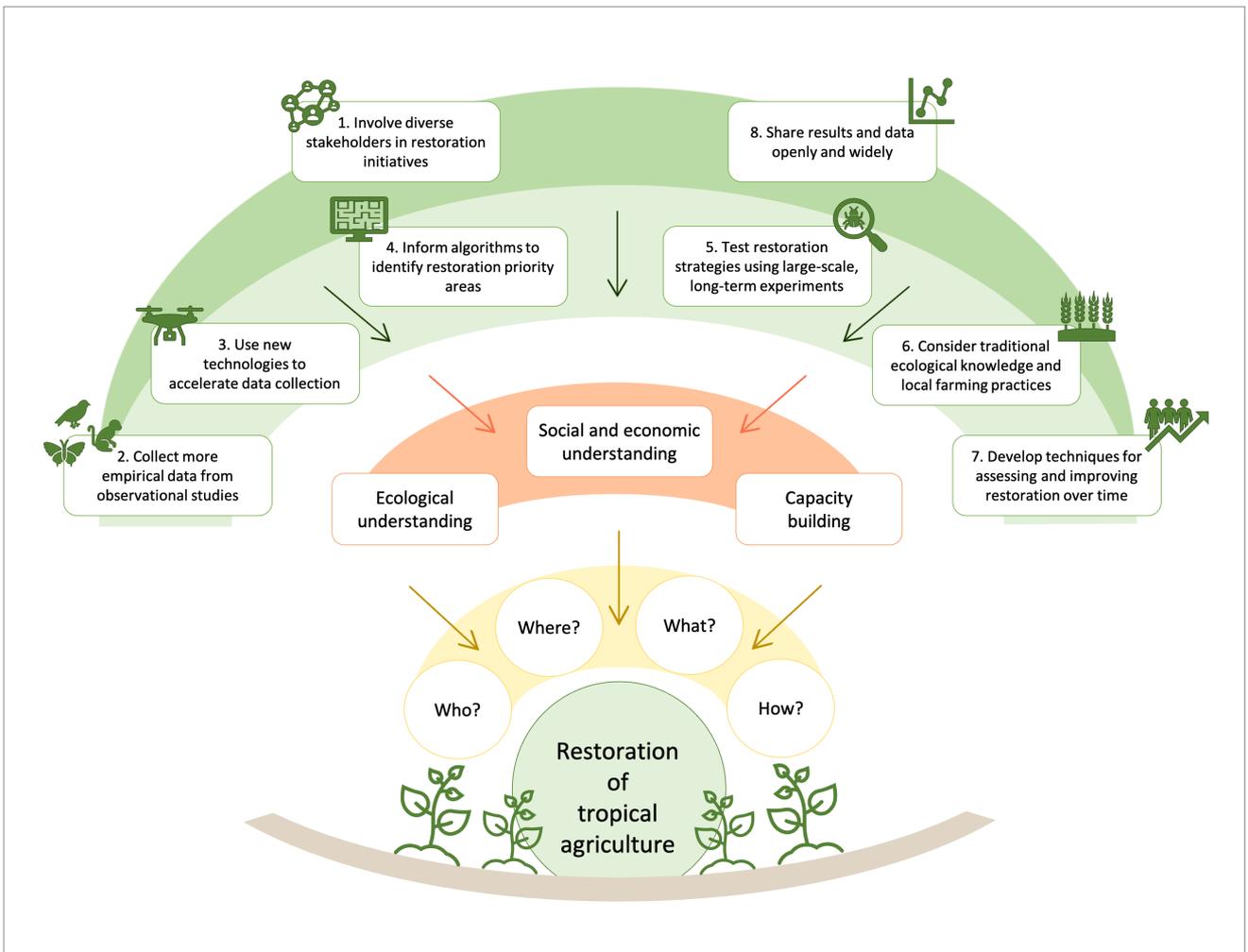
Lastly, it is noteworthy that the most recent assessments have shown that restoring tropical landscapes can offer the highest socioenvironmental returns on restoration investment globally (Strassburg et al., 2020). Dependent on having the necessary social, economic, and political structures in place to distribute benefits locally, restoration could therefore provide important economic benefits to communities within tropical countries, many of which are low-income and lower-middle-income economies (Erbaugh et al., 2020) and have amongst the highest rates of population growth (Tilman et al., 2017).

#### **1.1.4 | What is required to restore tropical agriculture?**

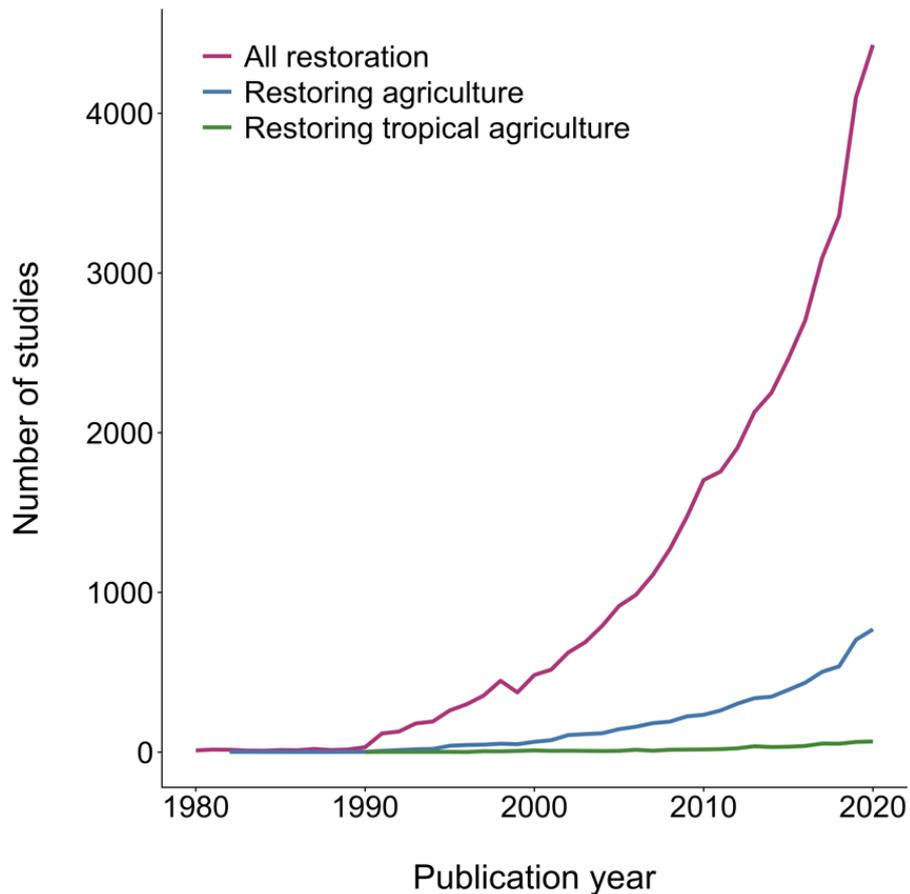
As the benefits of restoration become more widely recognised, and the number of restoration projects increase, there is a growing understanding of what is required for restoration projects to meet their target objectives, within a timeframe that satisfies stakeholders, and can thus be judged as successful. For instance, a recent review identified key rules for successful reforestation, including selecting suitable sites (e.g. ‘Protecting existing forest first’; ‘Select appropriate areas’); choosing appropriate targets for what to restore (e.g. ‘Aim to maximise biodiversity recovery’; ‘Make it pay’); and using tractable and efficient methods to achieve these targets (e.g. ‘Work together’; ‘Use natural regeneration wherever possible’; ‘Plan ahead’; ‘Learn by doing’) (Di Sacco et al., 2021). This study and other recommendations from the restoration literature (e.g. Cooke et al., 2019; Holl, 2017a; Holl & Brancalion, 2020; Kollmann et al., 2016; Suding, 2011; Uriarte & Chazdon, 2016) indicate that restoration is more likely to be successful when key questions relating to ‘who’ should be involved in, and benefit from,

restoration initiatives, and ‘where’, ‘what’, and ‘how’ to restore are addressed. We believe that answering these questions requires three broad categories of knowledge and activities: (1) ecological understanding, (2) social and economic understanding, and (3) capacity building; all of which are underpinned by increased stakeholder engagement, collaboration, and sharing of knowledge and resources (Figure 1.1).

Despite an established framework for successful restoration, there is currently a dearth of knowledge about where, what, and how to restore tropical agriculture and who to engage with in this process, owing to limited understanding of many ecological, social, and economic contexts within these systems. For instance, in a global meta-analysis on the benefits of agricultural restoration to biodiversity and ecosystem services, only 4 out of 54 studies were in the tropics (Barral et al., 2015). Similarly, a search of the ISI Web of Science Core Collection on 11 February 2021 showed that, although the frequency of studies focussed on restoration has increased rapidly over the last three decades, studies focussed on the restoration of agriculture, and particularly tropical agriculture, are occurring at far lower rates (Figure 1.2). In addition, even studies that focus exclusively on restoring tropical agriculture often have knowledge gaps. For example, a meta-analysis on the benefits of agroforestry to tropical cacao and coffee ecosystems found only limited studies from tropical Africa, despite Africa producing 65% of global cacao supply and being the continent where coffee evolved (De Beenhouwer et al., 2013). Further, most restoration-focussed studies concentrate on forest landscapes (Temperton et al., 2019) and, in comparison, there is much less known about how to restore other tropical systems, such as grasslands and savannahs. The limited understanding of many ecological and social contexts within tropical systems may be partially attributed to lack of investment in local capacity building. Capacity building is needed to successfully implement and monitor restoration initiatives (Bloomfield et al., 2019; Erbaugh et al., 2020; Mansourian et al., 2018), and to ensure that restoration benefits local communities.



**Figure 1.1.** Restoration of tropical agriculture is more likely to be successful when key questions relating to ‘who’ should be involved in, and benefit from, restoration initiatives, and ‘where’, ‘what’, and ‘how’ to restore these systems are addressed. Answering these key questions requires improving ecological understanding, social and economic understanding, and capacity building. We identify eight key actions that are particularly promising for improving these understandings, all of which are underpinned by increased stakeholder engagement, collaboration, and sharing of knowledge and resources (i.e. actions 1 and 8 that are in the overarching dark green band).



**Figure 1.2.** Number of academic studies from 1980 - 2020 that focus on ecological restoration, ecological restoration in all agriculture, and ecological restoration in tropical agriculture. We obtained results from three independent searches of the ISI Web of Science Core Collection with the following search strings: 1) Restoration; 2) Restoration AND agri\* OR agro\* OR farm\*; 3) Restoration AND agri\* OR agro\* OR farm\* AND tropic\*. Our searches occurred on 11 February 2021. In all searches, we filtered for papers only in these Web of Science Research Areas: agriculture, biodiversity and conservation, environmental sciences and ecology, forestry, plant sciences, and zoology. Although “regeneration” is a common synonym of “restoration”, we did not include it in our search string, as a preliminary search suggested that its addition did not uncover more studies and risked including studies that were focussed on anatomical regeneration.

Within the broad framework shown in Figure 1.1, and drawing on examples from across the tropics and our personal experience of restoring tropical agricultural landscapes, we identify key steps that should be taken to improve understanding of how to restore tropical agricultural systems. We identify eight actions – including two (actions 1 and 8) that underpin all others – that are particularly promising for determining ‘who’ should be involved in, and benefit from, restoration of tropical agriculture, and ‘where’, ‘what’, and ‘how’ restoration should occur. Although these actions are ordered and somewhat sequential, we emphasise that they do not form a mechanistic roadmap, and may need to be used interchangeably and in tandem.

*1) Involve a diverse network of stakeholders, at all stages and in all parts of restoration initiatives*

When restoring tropical agriculture, stakeholders may include farmers, land owners, community leaders, activists, conservation NGOs, members of agricultural industries, sustainability certification organisations, academics, consumers of agricultural goods, and governments (Chazdon & Brancalion, 2019; Cooke et al., 2019; Holl, 2017a). Stakeholders should be engaged from the start of restoration initiatives, as having meaningful engagement with a wide range of stakeholders in decision-making increases the views that are considered and therefore the likely long-term appropriateness of target objectives, methodologies, and chances of achieving direct socioenvironmental benefits (Bloomfield et al., 2019; Holl, 2017b). One way to involve local communities in decision-making is to encourage and respect their traditional communication styles. For instance, local communities participating in the Fandriana-Marolambo Forest Landscape Restoration Project (started by the World Wild Fund for Nature (WWF) in 2005, and one of the longest-running tropical restoration projects) provide feedback on proposed restoration initiatives during the “kabary”, a traditional communication style during which elders lead discussions, present the problem, and make decisions at the community level (Mansourian et al., 2016). Taking a highly collaborative approach to restoration is particularly important when members from outside communities (e.g. researchers from Europe and the USA) establish tropical restoration experiments, helping to decolonise the process (Baker et al., 2019; Trisos et al., 2021).

As well as ensuring that a range of views are considered, diverse stakeholder engagement throughout a project can also improve access to more facilities and equipment (e.g. (Luke, Advento, Aryawan, et al., 2020; Rochmyaningsih, 2019), funding (e.g. Mansourian et al., 2018), and allow exchange of knowledge and expertise to increase the chances of long-term

success. For example, local people can teach scientists from outside areas about local floral and faunal diversity, methods for effectively growing native tree seedlings, or local socioeconomic considerations; whilst externally-led projects can provide local people with employment, funding, and training in new skills such as project management (Bloomfield et al., 2019; Jack et al., 2008; Metzger et al., 2021). We suggest that additional steps should be taken within academia and funding schemes to incentivise highly collaborative restoration projects, and to recognise and reward existing restoration initiatives that collaboratively build capacity in local communities. A notable example of successful engagement of diverse stakeholders and local capacity building is the Atlantic Forest Restoration Pact (AFRP), through which policymakers, NGOs, and universities have united to create an ambitious restoration plan to protect and restore Brazil's socio-environmentally invaluable Atlantic Rainforest (Crouzeilles et al., 2019).

### *2) Collect more empirical data from observational studies*

Across the tropics, empirical data on ecological and socioeconomic conditions are lacking. Socioecological data from areas that are relatively free from human disturbance, or more structurally and ecologically complex (e.g. traditional agroforestry systems) than intensively managed farmlands, are needed to inform restoration target objectives, and to assess recovery completeness. Data are also needed from within tropical agricultural systems, so that practitioners can assess the extent to which systems are degraded (i.e. to avoid “shifting baseline syndrome”, which is when human perceptions of “normal” ecological conditions change due to lack of experience or knowledge of past conditions; Papworth et al., 2009), and monitor the progress of ongoing restoration initiatives (Di Sacco et al., 2021). In addition, there are limited data on what local communities want outcomes of restoration to be, and what capacity-building support might be needed to help communities achieve their goals and derive maximum benefits from planned restoration projects (Bloomfield et al., 2019).

### *3) Use new technologies to accelerate data collection*

Advances in technology are increasingly improving our ability to rapidly collect, and process, data across vast spatial and temporal scales, both in terms of resolution and extent. For example, increasing availability of high resolution satellite imagery and other remote sensing technology (Pettorelli et al., 2018; Turner, 2014), coupled with rapid and detailed ground-truthing of differences in stand structural complexity (Ehbrecht et al., 2021), offer the exciting possibility for monitoring vegetation structure and growth. These techniques have been used effectively

in the Sabah Biodiversity Experiment in Malaysia (Wu et al., 2020), and the EFForTS-BEE restoration experiment in Indonesia (Khokthong et al., 2019; Zemp, Gérard, et al., 2019) to monitor changes in structural complexity and canopy cover after planting native tree seedlings in degraded tropical rainforest landscapes. To extend the reach of data collection, and to build capacity and engagement, we advocate for continued uptake of applications that encourage citizen science initiatives (e.g. iNaturalist, <https://www.inaturalist.org>; and iRecord, <https://www.brc.ac.uk/irecord/>) (Silvertown, 2009) as well as large-scale digital surveys to collect socioeconomic data, as access to mobile phones and internet increases across the tropics. Advances in sequencing technology also offer great potential to support restoration efforts worldwide. High throughput DNA sequencing may allow rapid understanding (at increasingly low costs; Reuter et al., 2015) of how restoration treatments affect interspecies relationships (Lamarre et al., 2020), functional traits (Perring et al., 2015), or taxa, such as bacteria and fungi (Ballauff et al., 2020), that are often omitted from restoration studies but are critical to the functioning and stability of agricultural systems (Turley et al., 2020). High throughput DNA sequencing data can also be coupled with recently developed phylogenetic mixed models to quantify phylogenetic and functional responses to environmental changes (Hadfield, 2010; Lamarre et al., 2020).

#### *4) Inform algorithms to identify restoration priority areas*

In recent years, algorithms based on linear programming (a mathematical approach that quickly finds high-quality solutions to optimisation problems; Beyer et al., 2016) have allowed identification of restoration priority areas (i.e. areas where restoration will maximise socioenvironmental benefits whilst minimising restoration implementation costs, and loss of agricultural productivity) across various spatial scales (e.g. Brancalion et al., 2019; Strassburg et al., 2019, 2020). These algorithms are informed by known spatial data on biodiversity, ecosystem services, and socioeconomic conditions, and have great potential to combine multiple lines of evidence into tractable recommendations for restoration policy. For instance, the Brazilian Ministry of Environment is developing a strategic plan to restore the Atlantic Rainforest, which has largely been degraded by agriculture, using restoration prioritisation algorithms (Strassburg et al., 2019). However, the ability of algorithms to accurately detect restoration priority areas across broad contexts is often limited by the data that are available. Data are often collected from just a few locations and taxa, and there has been limited development of strategies to include social data. Efforts should therefore be made to collect and inform algorithms with standardised data from a larger number of regions, biomes, socio-

political and environmental contexts and, importantly, farm (e.g. industrial versus smallholder farmlands) and crop systems, since restoration success can vary across crop types (Lichtenberg et al., 2017).

#### *5) Implement large-scale, long-term experiments to test restoration strategies*

We currently lack an established evidence base of case studies that demonstrate how to successfully restore abandoned and cultivated farmlands in the tropics (Figure 1.2). An experimental approach is required to disentangle how restoration activities affect the large numbers of interactions that characterise tropical ecological (Fayle, Turner, et al., 2015) and social (e.g. Bradbury et al., 2021) networks. We therefore need more field experiments – which should be robust in design to reduce study bias (Christie et al., 2020), and replicated across space and time using standardised methodology – to account for variation in the effects of restoration treatments across regions, climatic conditions, socio-political contexts, land use histories, and crop systems (Barral et al., 2015; Holl & Kappelle, 1999; Holl et al., 2011; Holl, 2017b; Jones et al., 2018; Martin, Osen, et al., 2020; Rey Benayas et al., 2009). Experiments should not only be multidisciplinary (i.e. involving several disciplines at the same time), but also interdisciplinary (i.e. using transferrable methodologies across disciplines, to improve understanding of a research topic) and transdisciplinary (i.e. integrating findings from across disciplines, to better view a system as a whole rather than a sum of parts) (Nicolescu, 2014), although this may not be possible across all restoration initiatives depending on context and resource availability. Multidiversity and multifunctionality indices may be helpful to assess the effects of experimental treatments on a range of different stakeholder interests (Manning et al., 2018) although, for interpretation of these indices to be meaningful, data collection in experiments must be standardised (Trogisch et al., 2017). Experiments should also involve and build capacity within local communities (Chazdon, Cullen, et al., 2020; Erbaugh et al., 2020). As large-scale, long-term restoration experiments are often hindered by the short-term nature of ecological-focussed research grants (Hughes et al., 2017; Simons, 2011), we advocate for more long-term funding opportunities. When long-term funding is not available, alternative funding should be sought, such as coupling short-term funding with support from agricultural industries (e.g. Luke, Advento, Aryawan, et al., 2020; Rochmyaningsih, 2019).

#### *6) Include traditional ecological knowledge and local farming practices in restoration initiatives*

For millennia, communities across the tropics have maintained a close relationship with natural systems to protect and improve their livelihoods (Flores & Levis, 2021), resulting in a wealth of traditional ecological knowledge (TEK) that has helped shape modern-day farming practices (Falkowski et al., 2020). For instance, in rural Java (Indonesia), traditional agricultural practices are informed by ‘Pranamatangsa’, a calendar that is based on the changing of the seasons and other aspects of local ecology, such as plant growth and animal migration patterns (Daldjoeni, 1984). Restoration practitioners should include TEK and local farming practices as experimental treatments when testing the efficacy of alternative restoration options. In comparison to recent ‘green revolution’ approaches to agriculture, management that incorporates TEK – such as agroforests (e.g. Falkowski et al., 2020; Maas et al., 2020) and homegardens (e.g. Abebe et al., 2010) – can create more ecologically and structurally complex crop systems. These have the potential to help support ecosystem services (Maas et al., 2020), which are key to an ecological intensification approach to maintaining yields, whilst also being a promising strategy for meeting restoration target objectives. To incorporate TEK into restoration experiments, practitioners should develop close working relationships with members of local communities, to assess what TEK and local farming practices exist and how these can be integrated into experimental frameworks. Such relationships can help emphasise the importance of local people when restoring landscapes, preserve aspects of indigenous culture, and ensure that restoration management represents ‘real-world’ practices that can be adopted more widely across tropical landscapes.

#### *7) Develop techniques for assessing and improving restoration over time*

Restoration projects should be assessed regularly and empirically to determine that target objectives are reached; or whether projects are failing to meet their targets, and therefore changes in management are needed. Assessments should measure both ecological and socioeconomic changes, and focus on multiple aspects of biodiversity and socioeconomic status in order to give a representative view of how restoration is affecting systems (Audino et al., 2014; Le et al., 2012). However, it is usually unfeasible or impossible to measure all impacts, and so it can be valuable to develop key indicator taxa or metrics that can be surveyed easily, but are correlated with other variables (Audino et al., 2014; Lawes et al., 2017; Viani et al., 2017; Wortley et al., 2013). It can also be helpful to identify key time points when assessment is critical, for instance, whilst planted trees are still seedlings and therefore vulnerable (Le et al., 2012), or when seedlings are well-established but in danger of being destroyed by herbivores (e.g. Holl & Quiros-Nietzen, 1999).

Increased efforts are needed to develop assessment plans when restoring tropical agriculture. Restoration practitioners should make use of valuable indicator taxa that have already been identified in tropical ecosystems (e.g. Andersen, 1993; Audino et al., 2014; Lawes et al., 2017; Ruiz-Jaén & Aide, 2005a; Viani et al., 2017), and existing protocols that provide best practices for developing restoration assessment plans (e.g. the SER International Primer on Ecological Restoration describes nine attributes that characterise successful restoration initiatives; (Ruiz-Jaén & Aide, 2005b). However, it is unlikely that these will be transferrable across all tropical agricultural contexts, as many ecological indicators may be limited to specific spatial or temporal scales (although taxon-free indicators, such as water quality, are likely to be more widely applicable; National Research Council, 2000), and most studies on restoration assessment have occurred in North America (Wortley et al., 2013). We therefore recommend that existing indicators and assessment protocols are tested in ongoing tropical agricultural restoration projects, and their fitness for measuring success within these systems is assessed. If existing protocols are found to be inadequate, work should be undertaken to modify them to improve their fit across tropical agricultural systems. In particular, socioeconomic assessments may need to be adapted, as the priorities of local communities are very likely to be context-specific. Partnering with local governments can help ensure appropriate long-term monitoring of restoration projects in tropical agriculture. For instance, in São Paulo, Brazil, the Secretariat for the Environment has provided resources to ensure that ongoing restoration projects are assessed periodically using a tripartite system, which indicates whether projects have reached, partially reached, or failed to reach their target objectives (Chaves et al., 2015). Assessments are based on three indicators ('Ground coverage with native vegetation', 'Density of native plants spontaneously regenerating', and 'Number of spontaneously regenerating native plant species'), and occur 3, 5, 10, 15, and 20 years after restoration has started (Chaves et al., 2015).

#### *8) Share results and data openly and widely*

It is critical that the findings from restoration projects are communicated widely, and in a form that allows long-term engagement and education – both for current farmers and future generations – in order to maximise their uptake and impact. This may require separate funding or partnership with public engagement specialists – such as zoos, botanical gardens or museums – that are additional to those needed for implementation of restoration initiatives. Findings should be communicated to all stakeholders, but it is especially important that they

are communicated effectively to policymakers, land managers, local community members, and sustainability certification organisations.

If restoration teams successfully engage with policymakers, they can incorporate restoration findings into legal frameworks, and therefore increase the scope and uptake of restoration efforts. For instance, in Colombia, restoration is largely driven by the government, which has initiated and funded more than 60% of ongoing restoration initiatives in the country (Murcia et al., 2016). In Indonesia, national law requires that land managers protect and restore riparian areas in agricultural systems (Barclay et al., 2017). In addition to government policy, sustainability certification organisations can help to ensure that larger numbers of farmers take up restoration actions (Millard, 2011; Tschardt et al., 2015). Sustainability organisations have been developed for many farming systems (e.g. Roundtable on Sustainable Palm Oil, <https://rspo.org>; Cotton Made in Africa, <https://cottonmadeinafrica.org/>; Rainforest Alliance, <https://www.rainforest-alliance.org>) and work on the basis of farmers voluntarily agreeing to follow more-sustainable production practices in return for receiving a price premium for their goods, funded by consumers who are willing to pay more for increased sustainability. Certification schemes have successfully led to increased uptake of agroforestry practices within coffee and cocoa farms (Millard, 2011).

To successfully carry out restoration activities, it is critical that land managers have access to evidence and information in an accessible form. Initiatives such as Conservation Evidence (<https://www.conservationevidence.com/>; Sutherland et al., 2019), the Cool Farm Tool (<https://coolfarmtool.org/>), PARTNERS ([partners-rcn.org](https://partners-rcn.org)), and Conservation International's Applied Nucleation Report (<https://www.conservation.org/research/applied-nucleation-report>) provide free online and print summaries of scientific evidence for management actions that can support conservation, and methods of assessing current practices. These tools should be developed further to ensure that they cover tropical agricultural restoration actions as fully as possible. Additionally, results and data from restoration experiments should be made freely accessible through online databases, and shared with restoration syntheses (e.g. Restor; <https://restor.eco/>). This will broaden the impact and global relevance of individual experiments (Ladouceur & Shackelford, 2020).

Communicating findings to the general public should occur both in consumer communities and within local communities that are affected by restoration, and can be achieved through a range

of methods. For example, demonstration field sites have been used successfully in Brazil to teach both local and outside communities about restoration initiatives (Chazdon, Cullen, et al., 2020). Blog posts and social media can be useful tools for communicating findings to the general public more widely. Once informed, members of the public can also place pressure on governments or agricultural industries to invest in restoration or conservation action (e.g. Tschardt et al., 2015). Public pressure can also help ensure that restoration findings are able to withstand changes in political structure and leadership, as these can threaten restoration initiatives depending on the attitudes of the new government. Additionally, members of the public can contribute actively to restoration at small and large scales, for instance by planting trees on their own land. Successful communication of findings to all of these groups can therefore lead to developing a community of local- and broad-level stakeholders who can act as restoration advocates.

### **1.1.5 | Now is the time to develop solutions**

The last decade has seen increased creation of legal, social, financial, and theoretical frameworks to protect and restore tropical landscapes. For instance, there are existing international (e.g. The Bonn Challenge, <https://www.bonnchallenge.org/>; New York Declaration on Forests, <https://forestdeclaration.org/>; and the Paris Agreement, <https://www.un.org/en/climatechange/paris-agreement>) and regional (e.g. the Atlantic Forest Restoration Pact, Crouzeilles et al., 2019; Reflorestar Program, Latawiec et al., 2015; and Regreening Africa, <https://regreeningafrica.org>) agreements, global conferences (e.g. Conference of the Parties to the Convention on Biological Diversity, <https://www.cbd.int/cop/>; and the 26<sup>th</sup> UN Climate Change Conference, <https://ukcop26.org>), and recommendations from academia (e.g. Di Sacco et al., 2021; Holl, 2017b; Maas et al., 2020) to support restoration efforts worldwide. All of this is now supported by the UN Decade on Ecosystem Restoration (2021 – 2030; [www.decadeonrestoration.org](http://www.decadeonrestoration.org)), which has put a renewed focus on global restoration efforts, creating additional research funding and capacity to test restoration initiatives and, ultimately, to inspire a large-scale movement to restore ecosystems globally. We should take advantage of these opportunities, and utilise the UN Decade to improve understanding relating to ‘who’ should be involved in, and benefit from, restoring tropical agriculture, and ‘where’, ‘what’, and ‘how’ restoration should occur, with the eight sets of strategies we have outlined as key starting points for action. The time to commit to restoration action within tropical agriculture – and indeed all global systems – is now.

## 1.2 Oil Palm Agriculture

This thesis uses oil palm agriculture as a case study in which to investigate the impacts of anthropogenic disturbance and restoration management on tropical ecosystems. Oil palm (*Elaeis guineensis*) is a crop that is grown across the tropics (Davis et al., 2020). Its product, palm oil, can be found in a range of commercial goods, such as biodiesel, lipstick, and biscuits (Sheil et al., 2009). This versatility has contributed to palm oil becoming the most traded vegetable oil worldwide (USDA, 2021). Additionally, the high productivity of oil palm has driven booms in palm oil production over the last 30 years. In comparison to other vegetable oil crops, such as soybean and rapeseed, oil palm can produce up to twelve times more oil per hectare (Meijaard, Brooks, et al., 2020), making oil palm highly profitable relative to its alternatives.

Oil palm evolved in West Africa (Corley & Tinker, 2016), but growth and production are now concentrated in Southeast Asia (Davis et al., 2020), where Indonesia and Malaysia are the top producing countries (USDA, 2021). Oil palm is most often grown in plantations, which in Southeast Asia can be classified broadly as industrial, smallholder, or assisted smallholder (also called, “plasma” or “nucleus” system) plantations (Bennett et al., 2019; Reiss-Woolever et al., 2021). Industrial plantations are owned by large corporations. They are spatially large (e.g. one industrial plantation can occupy more than 15000 hectares; Luke, Advento, Aryawan, et al., 2020), and typically managed as monoculture systems (i.e. no other crops are grown amongst the oil palms). Smallholder plantations are owned by individuals or families, and generally occupy a far smaller area (Reiss-Woolever et al., 2021). Assisted smallholder plantations partner with companies to improve their production, for instance, by receiving technical advice on plantation management from large-scale industry (Reiss-Woolever et al., 2021). In comparison to industrial plantations and depending on their management, smallholder and assisted smallholder plantations are often more structurally and ecologically complex. For instance, smallholder oil palm plantations in Malaysia that were intercropped with pineapple, bamboo, black pepper, cacao, and bactris (another palm crop) had higher levels of structural diversity and associated arthropod biodiversity than monoculture systems (Ashraf et al., 2018). However, it is also noteworthy that smallholder and assisted smallholder oil palm plantations typically have lower yields than industrial plantations, and therefore may require more land to produce similar amounts of palm oil (Meijaard et al., 2018).

The expansion of industrial, smallholder, and assisted smallholder oil palm plantations in Southeast Asia has resulted in widespread habitat loss. For instance, in Sumatra (Indonesia), oil palm plantations occupy more than 1 million hectares of land, the majority of which was rainforest until the 1990s (Miettinen et al., 2016). Loss of habitat is accompanied by changes in structural complexity and environmental conditions. In comparison to forests, oil palm plantations are hotter, less humid, and have lower levels of plant diversity and structural complexity (Drescher et al., 2016; Foster et al., 2011; Hardwick et al., 2015; Luskin & Potts, 2011). These changes have caused substantial declines in biodiversity. Taxonomic groups with relatively lower levels of biodiversity in oil palm plantations include birds, insects, and small mammals (Foster et al., 2011), as well as culturally important species such as Sumatran tigers and orangutans (Sheil et al., 2009). Loss of biodiversity as forests are converted to oil palm plantations has also changed the functioning of ecosystems and reduced the delivery of key ecosystem services including erosion prevention and waste removal (Dislich et al., 2017). In some cases, expansion of oil palm agriculture has led to decreases in human wellbeing, for instance, by increasing the frequency of social conflicts and contributing to higher social inequity in local communities (Santika et al., 2019, 2020).

Oil palm agriculture is expanding rapidly (Davis et al., 2020), and plantations already occupy more than 21 million hectares of land across the tropics (FAO, 2019). Oil palm plantations are, therefore, now the dominant habitat in some regions (Ramdani & Hino, 2013). Conserving remaining forest habitats represents the only tractable method of conserving global biodiversity (Gibson et al., 2011). However, once oil palm plantations are established, one way to help increase structural and ecological complexity within existing oil palm plantations, and therefore to address their longer-term ecological impacts, is through changes in management. In recent years, academics and members of the palm oil industry have co-designed experiments to test the environmental effects of different management options on oil palm systems. Management strategies that have been assessed within oil palm plantations include passive and active restoration of riparian buffers (i.e. strips of land around plantation waterways) (Luke, Advento, Aryawan, et al., 2020), planting diverse tree islands (Teuscher et al., 2016), reducing fertiliser use to mitigate runoff of nutrients into local water sources (Darras et al., 2019), manipulating application of herbicides to increase understory vegetation complexity (Ashton-Butt et al., 2018; Darras et al., 2019; Hood, Advento, et al., 2020; Hood, Pashkevich, et al., 2020, Hood et al., 2019; Luke, Advento, Dow, et al., 2020; Luke, Purnomo, et al., 2019; Nájera & Simonetti, 2010; Spear et al., 2018), and intercropping oil palms with other cash crops

(Amoah et al., 1995; Ashraf et al., 2018; Asmah et al., 2017; Ghazali et al., 2016; Jezeer & Pasiecznik, 2019; Syafiq et al., 2016; Yahya et al., 2017). These experiments have shown that small- and large-scale changes in oil palm management can benefit a wide range of taxa (Ashraf et al., 2018; Ashton-Butt et al., 2018; Hood, Advento, et al., 2020; Hood et al., 2019; Luke, Advento, Aryawan, et al., 2020; Luke, Purnomo et al., 2019; Spear et al., 2018; Syafiq et al., 2016; Teuscher et al., 2016; Yahya et al., 2017; Zemp, Ehbrecht, et al., 2019), ecosystem functions (Ashton-Butt et al., 2018; Darras et al., 2019; Eycott et al., 2019), and crop yields (Gérard et al., 2017), therefore delivering benefits for the livelihoods and wellbeing of farmers (Zemp, Ehbrecht, et al., 2019; Zemp, Gérard, et al., 2019). As oil palm is being farmed at increasingly large scales across the tropics (Davis et al., 2020), further collaboration between academics and members of the palm oil industry is needed to better evaluate the impacts of management on oil palm systems. Identifying management strategies that lead to win-win situations for conservation, crop production, and the livelihoods and wellbeing of farmers can help to improve the overall sustainability of palm oil production.

### **1.3 Study site**

The oil palm studies in this thesis were based in industrial oil palm plantations at the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme (see Figure 2.1 in Chapter 2 for a map of the BEFTA Programme plantations). BEFTA is a research collaboration between international academics and the palm oil industry that is testing how different levels of management affect environmental conditions, biodiversity, ecosystem processes, and yields in oil palm systems (Luke, Advento, Aryawan, et al., 2020). Ultimately, BEFTA aims to identify management strategies that provide win-win or win-neutral solutions for conservation and palm oil production. BEFTA is based in Riau (Sumatra, Indonesia), which is a large province (~ 8.9 million ha) with a natural habitat of lowland rainforest (Ramdani & Hino, 2013). Today, Riau has one of the highest coverages of oil palm agriculture worldwide, with plantations occupying more than 20% of the province (Ramdani & Hino, 2013).

Broadly, BEFTA has four main objectives (Luke, Advento, Aryawan, et al., 2020). First, BEFTA is assessing existing variability within oil palm plantations, and characterising oil palm ecosystems under “business-as-usual” management. Second, in the Understory Vegetation Project (UVP), BEFTA is manipulating levels of herbicide management in mature oil palm plantations to test how understory vegetation complexity affects oil palm ecosystems. Third,

in the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project, BEFTA is testing how different riparian restoration strategies affect replanted oil palm ecosystems. Fourth, BEFTA offers opportunities for additional research to be conducted within industrial oil palm plantations, for instance, the ability to assess how cattle grazing affects local levels of biodiversity and delivery of ecosystem services (Slade et al., 2014). The studies in this thesis characterise oil palm ecosystems under business-as-usual management (BEFTA Objective 1), provide first findings from the RERTA Project (BEFTA Objective 3), and examine the effects of management on ecological conditions within the wider BEFTA Programme landscape (BEFTA Objective 4).

#### **1.4 Objectives and framework of project**

In this thesis, we investigated the effects of replanting and restoration of riparian buffers on oil palm ecosystems at the BEFTA Programme sites. We view BEFTA and the studies in this thesis as a prototype that embodies the eight actions we identified to help improve understanding of ‘who’ should be involved in, and benefit from, restoration of tropical agriculture, and ‘where’, ‘what’, and ‘how’ restoration initiatives should occur (Pashkevich, d’Albertas, et al., In Review). The Programme is highly collaborative (Action 1) and, from its start, has involved various stakeholders, including members of the palm oil industry, sustainability certification organisations, and international academics, including in the design, data collection, analysis and write-up of results. The UVP and RERTA Project are large-scale, long-term experiments that test the effects of restoration strategies on oil palm ecosystems (Action 5). Assessing the effects of the UVP and RERTA Project experimental treatments relies on the use of recently developed technologies (Action 3), such as remote sensing. Some of the experimental treatments in the UVP and RERTA Project incorporate aspects of local farming practices (Action 6). For instance, active restoration treatments in the RERTA Project include planted tree species that are traditionally grown in Riau for fruit production and consumption (Luke, Advento, Aryawan, et al., 2020). All components of BEFTA are assessed regularly through meetings between plantation managers, and local and international researchers (Action 7). Findings from BEFTA are communicated widely (Action 8). For instance, findings have been, or will be, submitted to sustainability certification organisations, such as the Roundtable on Sustainable Palm Oil (RSPO, 2018), which is the largest certifier of sustainable palm oil worldwide. Additionally, findings from BEFTA are shared at the International Conference on Oil Palm and the Environment (ICOPE; [21](https://icope-</a></p></div><div data-bbox=)

series.com/ICOPE/), which is a biennial meeting attended by those working in oil palm plantations, including members of the palm oil industry, international academics, and conservation NGOs. Through outreach and public engagement events, BEFTA has also communicated its findings to members of local communities in Riau, as well as in the UK and USA. For instance, findings from BEFTA are featured in exhibitions at the University Museum of Zoology in Cambridge. Ultimately, BEFTA and the studies in this thesis demonstrate the potential for collaborative research projects to empirically test the effects of management on ecological conditions in human-modified systems.

Our primary aim (Chapters 2 – 4) was to determine the impacts of replanting and restoration of riparian buffers – areas of land that surround rivers within agriculture – on oil palm systems. We achieved this through a multi-year field campaign, during which we sampled environmental conditions and arthropods in industrial oil palm plantations in Riau (Indonesia). We sampled arthropods because they are abundant in oil palm systems across different microhabitats (Ashraf et al., 2018; Ashton-Butt et al., 2018; Hood, Pashkevich, et al., 2020; Spear, 2016; Turner & Foster, 2009); affect profitability by helping to deliver ecosystem services (such as pollination and pest control) that boost palm oil production (Li et al., 2019; Nurdiansyah et al., 2016; Tuner & Hinsch, 2017), or by being pests that damage crop yields (Corley & Tinker, 2016); and have previously been shown to be responsive to changes in oil palm management (e.g. Ashraf et al., 2018; Ashton-Butt et al., 2018; Ghazali et al., 2016; Hood, Advento, et al., 2020; Spear et al., 2018). When sampling arthropods, we particularly focussed on spiders, as they are abundant predators that affect functioning in terrestrial systems worldwide (Nyffeler & Birkhofer, 2017) and provide pest control services in agricultural landscapes, including oil palm (Michalko et al., 2019). Building upon this focus on spiders, a secondary aim of this thesis was to use systematic review and meta-analysis approaches to determine whether anthropogenic disturbance and restoration affected spider abundance and species richness in the tropics (Chapter 5). The findings of this thesis will help inform more-sustainable management of oil palm plantations, and improve understanding of how anthropogenic disturbance and restoration processes affect tropical systems.

## 1.5 Outline of data chapters

### Chapter 2

#### **Assessing the effects of oil palm replanting on arthropod biodiversity**

In this chapter, we use canopy fogging, sticky traps, hand collections, and pitfall traps to assess how replanting of oil palm affects environmental conditions, arthropods (order-level biodiversity), and spiders (morphospecies-level biodiversity).

### Chapter 3

#### **Riparian buffers made of mature oil palms have inconsistent impacts on oil palm ecosystems**

In this chapter, we use the same sampling techniques as in Chapter 2 to assess the impacts of riparian buffers made of mature oil palms on environmental conditions, arthropods (order-level biodiversity) and spiders (morphospecies-level biodiversity). Buffers were in the process of being passively restored, through relaxed management that included no use of pesticides, herbicides, or fertilisers.

### Chapter 4

#### **Riparian restoration within replanted oil palm plantations does not benefit arthropod biodiversity within two years**

In this chapter, we test the impacts of different riparian restoration strategies on arthropods (order-level biodiversity) and spiders (morphospecies-level biodiversity) in replanted oil palm plantations. This chapter provides first insights from the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project: a large-scale, before-after control-impact experiment that is testing different strategies for restoring riparian buffers in oil palm agriculture.

### Chapter 5

#### **Anthropogenic disturbance reduces spider abundance and species richness, and restoration does not consistently benefit spiders in the tropics: A meta-analysis**

In this chapter, we use systematic review and meta-analysis approaches to investigate the effects of anthropogenic disturbance and restoration on the abundance and species richness of spiders in the tropics, and to explain variation in how spiders respond to disturbance and restoration initiatives.

## Chapter 2

### Assessing the effects of oil palm replanting on arthropod biodiversity

#### 2.1 Abstract

Palm oil is the most traded vegetable oil worldwide. Production is concentrated in Southeast Asia, where established oil palm plantations dominate the landscape in many regions. Although levels of biodiversity are much lower than in forest, mature oil palm plantations can support a wide range of generalist species. However, these species may be threatened, as large areas of plantation have already been, or will soon be, replanted as they near the end of their productive life (20 – 30 years). Replanting changes vegetation complexity and microclimate, but short- and long-term effects on biodiversity are largely unstudied. We surveyed an oil palm chronosequence (first-generation mature palms, and replanted second-generation palms aged one, three, and eight years) in an industrial plantation in Riau, Indonesia to assess the impacts of replanting over an 8-year period on arthropods in the ground, understory, and canopy microhabitats. Replanting was carried out using current recommended strategies, which included staggering replanting events to promote landscape-level heterogeneity, retaining mature oil palm riparian buffers, planting a cover crop immediately after replanting, and using chopped mature palms as mulch after clearance. We assessed changes in total arthropod abundance and order-level community composition, as well as specific changes in spider communities. We observed no significant declines in total arthropod abundance after replanting, but arthropod order-level community composition varied across the chronosequence in all microhabitats. These findings were replicated, or more pronounced, in spider-specific analyses. Spider abundance and species richness decreased in the understory in the first year after replanting (although these returned to pre-replanting levels after 3 years), and spider species-level community composition in all microhabitats differed significantly across the chronosequence. Our findings indicate that total arthropod abundance is resilient to replanting of oil palm, but that replanting changes total arthropod and spider community composition and decreases spider abundance and species richness in some microhabitats. Whilst it is somewhat encouraging from a management perspective that recommended replanting strategies maintain overall arthropod abundance, the changes in composition and spider biodiversity that we observed may impact ecosystem processes, such as pest control, in second-generation oil palm plantations, with potential implications for yield. Additional studies

that focus on other taxonomic groups and assess the effects of individual replanting strategies are needed before the long-term ecological impacts of replanting on existing oil palm plantations can be fully determined.

## 2.2 Introduction

Palm oil — derived from oil palm fruits — is the most traded vegetable oil worldwide (> 70 million metric tons traded in the 2019/20 fiscal year; USDA, 2021), and oil palms are the most productive vegetable oil crop (5.5 tons / ha oil output; Zimmer, 2010). Oil palms grow on 21.3 million hectares across the tropics (FAO, 2019), with production led by Indonesia and Malaysia, which together account for > 80% of global supply (USDA, 2021). Here, oil palm plantations have often replaced natural habitat (Brooks et al., 2006; Koh et al., 2011; Myers et al., 2000; Sodhi et al., 2004; Vijay et al., 2016). Converting forests to oil palm reduces biodiversity across a wide range of taxa (Barnes et al., 2017; Drescher et al., 2016; Edwards et al., 2014; Fitzherbert et al., 2008; Foster et al., 2011; Savilaakso et al., 2014), and causes changes in ecosystem functions, including soil fertility and water quality (Dislich et al., 2017).

Retaining natural habitats is paramount to mitigating biodiversity losses (Gibson et al., 2011), but steps should also be taken to improve biodiversity within existing oil palm plantations (Luke, Advento, Aryawan, et al., 2020). Managing for biodiversity in plantations is important to both conservation and profitability, owing to the essential ecosystem services that many taxa provide (Dislich et al., 2017; Foster et al., 2011). Oil palm plantations have the potential to support more biodiversity than many other crops – particularly annuals such as rice – owing to their 20 – 30 year commercial life cycle (Corley & Tinker, 2016; Meijaard et al., 2018; USDA, 2012). Oil palms reach peak production after 6 – 10 years and, after this time, plantations can develop stable microclimates (Luskin & Potts, 2011), structurally complex vegetation (Luke, Purnomo, et al., 2019), and increased soil organic carbon (Hamilton et al., 2016; Pauli et al., 2014), increasing habitat stability and providing resources for biodiversity. For instance, mature oil palm plantations have been found to support abundant and relatively diverse communities of plants (Luke, Purnomo, et al., 2019), fungi (Brinkmann et al., 2019), birds (Azhar et al., 2011), dragonflies (Luke, Advento, Dow, et al., 2020), and mammals (Pardo et al., 2019), amongst other taxonomic groups.

Terrestrial arthropods are some of the most diverse and functionally important taxa within oil palm plantations. They facilitate a wide range of ecosystem functions (Dislich et al., 2017), which include reducing pest activity (Turner & Hinsch, 2017), recycling waste (Gray et al., 2014), and pollinating oil palm inflorescences (Li et al., 2019; Vaknin, 2012). However, arthropods can also be oil palm pests, causing ecological and economic damage (Corley & Tinker, 2016; Dislich et al., 2017). Changes to routine plantation management, for instance intercropping with other crops (Ashraf et al., 2018; Ghazali et al., 2016) or enhancing understory vegetation complexity (Ashton-Butt et al., 2018; Spear et al., 2018), have the potential to increase arthropod abundance and diversity. Employing management strategies that boost populations of beneficial arthropods, such as predatory spiders, while suppressing pests can lead to more productive, as well as more biodiverse, oil palm systems (Turner & Hinsch, 2017).

The relatively high levels of biodiversity that can develop within oil palm plantations are potentially threatened by replanting (Ashton-Butt et al., 2019; Snaddon et al., 2013). Oil palms are replanted once they pass peak yields, at around 20 – 30 years old (Corley & Tinker, 2016). The process of replanting mature plantations with young palms is highly destructive and results in substantial soil disturbance, vegetation loss, and a much hotter and drier microclimate (Ashton-Butt et al., 2019; Luskin & Potts, 2011; Snaddon et al., 2013). Across Southeast Asia, large swathes of first-generation mature oil palms (i.e. palms that replaced forest during large-scale oil palm expansion in the 1990s) have already been replanted, or are likely to be replanted in the near future, presenting a novel phase for the palm oil industry (Snaddon et al., 2013).

Despite the substantial environmental changes that occur as oil palm is replanted, we know of only four published studies that have examined the effects of replanting on oil palm biodiversity and functions, and these have found no consistent ecosystem responses (Ashton-Butt et al., 2019; Kurz et al., 2016; Waters, 2018; Woodham et al., 2019). Furthermore, these studies focus on only one microhabitat (Ashton-Butt et al., 2019; Kurz et al., 2016; Waters, 2018), or taxonomic group (Kurz et al., 2016; Waters, 2018). Therefore, there is still substantial uncertainty about the short- and long-term impacts of replanting on oil palm ecosystems. This has led stakeholders to identify the development of sustainable replanting strategies as a top priority for oil palm research (Padfield et al., 2019). Current recommended strategies that may benefit oil palm ecosystems include staggering replanting events within large-scale plantations to promote landscape-level heterogeneity (Luskin & Potts, 2011), retaining riparian buffers

(Barclay et al., 2017), planting a cover crop immediately (< 2 months) after replanting to protect soil (Corley & Tinker, 2016), and using chopped palm trunks as mulch in second-generation plantations (Corley & Tinker, 2016).

This study investigates the effects of oil palm replanting on terrestrial arthropods in industrial plantations in Riau, Indonesia. We sampled a chronosequence of first-generation mature oil palm, and second-generation oil palms aged one, three, and eight years, which had been replanted using recommended replanting strategies. We quantified the environmental conditions and arthropod community (all arthropods identified to order level and spiders to family and morphospecies level) in ground, understory, and canopy microhabitats to answer the following questions: 1) How does microclimate and vegetation complexity change after replanting? 2) Does within-microhabitat total arthropod abundance and order-level community composition change after replanting? We then conducted focussed analyses on spiders – a key predatory group within oil palm – to investigate whether order-level trends were replicated at higher taxonomic resolution, asking: 3) Does within-microhabitat spider abundance, species richness, and morphospecies-level community composition change after replanting?

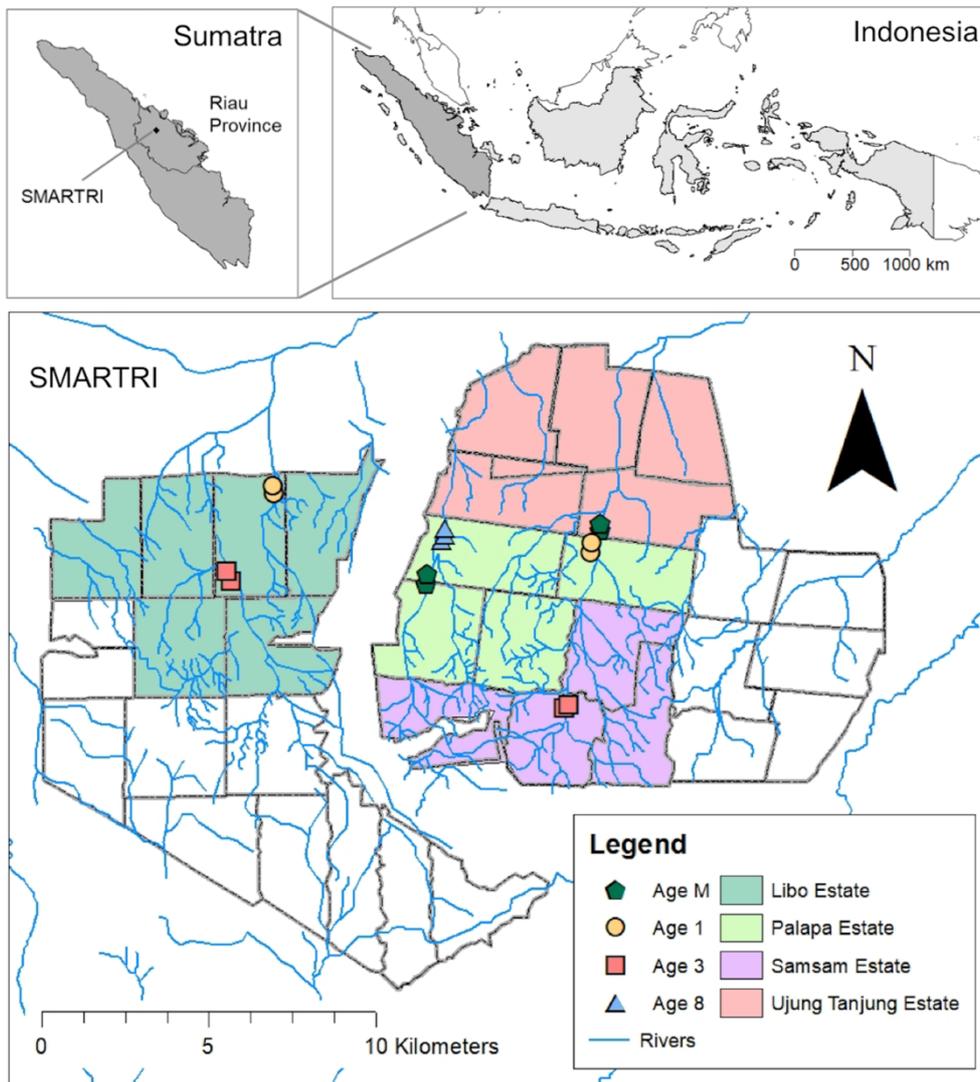
## 2.3 Methods

### 2.3.1 | Study sites

Fieldwork was based in industrial oil palm plantations at the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme in Riau, Sumatra, Indonesia (N0 55.559, E101 11.619; Figure 2.1). The plantations are owned by PT Ivo Mas Tunggal (a subsidiary company of Golden Agri Resources (GAR)), and run with management advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI), the research and development centre of GAR. Historically, the region was lowland rainforest but, after logging in the 1970s, it was converted to oil palm monoculture (1985 - 1995). The closest forest network (> 5000 ha) is now nearly 30 km away. The area is composed of seven oil palm estates, which are split into divisions and further divided into 300 x 1000 m blocks, intersected with roads. Estates are managed following standard industry practices (see Table S2.1 and Luke, Advento, Aryawan, et al. (2020) for more details) and in line with Roundtable on Sustainable Palm Oil (RSPO; <http://rspo.org>), Indonesian Sustainable Palm Oil (ISPO; <http://ispo-org.or.id>), and International Sustainability & Carbon Certification (ISCC; <http://iscc-system.org>) guidelines. Regional temperature is an average of 26.8 °C and mean annual rainfall

is 2350 mm (see Tao et al., (2016)). Climate and rainfall is influenced by the El Niño Southern Oscillation (see Eycott et al. (2019)).

Replanting of first-generation oil palms across the estates began in 2010, in areas that were identified as being more than 25 years old, having fewer than 100 palms / ha, and yielding less than 14 tons of oil / ha each year. Replanting occurred using a suite of recommended replanting strategies (Figure S2.1). These included retaining mature oil palm riparian buffers (50m in width on both sides of the river) (Barclay et al., 2017), planting a leguminous cover crop (primarily *Mucuna bracteata* but also *Pueraria javanica* and *Calopogonium mucuroides*) immediately (< 2 months) after clearance of mature palms to maintain soil health (Corley & Tinker, 2016), and using large diggers to uproot and then chop mature palms, which were later used as mulch (Corley & Tinker, 2016). SMARTRI has also staggered replanting events in approximate one-yearly intervals (each estate replants no more than 4% of its planted area each year and ensures that immature palms, which cannot be harvested, are never more than 12% of its total planted area) to increase landscape-level heterogeneity across the plantation (Luskin & Potts, 2011). Over time, this has resulted in a landscape mosaic of differently-aged oil palm.



**Figure 2.1.** Maps showing the location of study sites in the BEFTA Programme landscape (Riau, Sumatra, Indonesia). Estates used in this study (Libo, Palapa, Samsam, and Ujung Tanjung) are shown in colour. Study sites in *Ages M, 1, 3, and 8* are represented, respectively, by pentagons, circles, squares, and triangles. At each site, we established a 100 m transect with sampling points at the start, middle, and end. Due to spatial constraints, two *Age 1* transects were within 100 m of each other, and two *Age 8* transects were only 135 m apart. All other transects were at least 300 m apart. All sites were 125 m from riparian buffers, consisting of 50 m-wide areas of mature palm on each riverbank. We made maps using ArcMap 10.5.1 (ESRI, 2017), and package *maps* (Brownrigg, 2016), with reference to maps supplied by SMARTRI.

We established study sites across this chronosequence in four age cohorts (hereafter, “cohorts”) in a space-for-time design, to investigate the impacts of replanting over an 8-year post-replanting period (Figure 2.1). We chose cohorts that differed from each other environmentally and were of industry importance (Figure S2.1):

- First-generation mature palms (31 - 33 years old; “*Age M*”). These palms were established on previously forested land. Palms were still being harvested but were past peak yields and had closed canopies and a well-developed understory of shade-tolerant plants, particularly ferns (mostly *Nephrolepis biserrata*, *Asplenium longissimum*, and *Dicranopteris linearis*). Understory vegetation along access paths and within a 1.5 m radius of palm trunks was cleared using herbicide to facilitate access. Palms were ~15 - 18 m tall.
- Second-generation one-year-old palms (“*Age 1*”). These palms were before yielding age, had open canopies, and were surrounded by leguminous cover crop. Palms were ~2 m tall.
- Second-generation three-year-old palms (“*Age 3*”). These palms had just reached yielding age, and harvesting paths (~3 m wide) had been made between every other row of palms in areas that were not on steep slopes or prone to flooding. Herbicides were used to clear understory vegetation around palm trunks. Canopies were more extensive than those in *Age 1* but remained open. Palms were surrounded by leguminous cover crop and were ~4 m tall.
- Second-generation eight-year-old palms (“*Age 8*”). These palms had reached fruiting maturity and had closed canopies. Shade-tolerant understory plants had replaced the leguminous cover crop. Heavy equipment used for harvesting had flattened or cleared some vegetation between palms, and vegetation was cleared manually around palm trunks. Palms were ~7 m tall.

We established four study sites in each cohort and split sites within a cohort across two estates (except in *Age 8*, where availability only allowed three sites within one estate; Figure 2.1). We interviewed estate managers to ensure that management was broadly consistent across sites within a cohort (Table S2.1). At each of the 15 sites, we established a 100 m transect with three independent sampling points, each located 50 m apart. Due to spatial constraints, two *Age 1* transects were within 100 m of each other, and two *Age 8* transects were only 135 m apart, but all other transects were at least 300 m apart. All transects were 125 m from retained riparian buffers.

## 2.3.2 | Data collection

### 2.3.2.1 | Environmental conditions

Data collection occurred from February - May 2018, during the regional rainy season. We measured environmental conditions along 12 transects ( $n_{Age\ M} = 2$ ,  $n_{Age\ 1} = 3$ ,  $n_{Age\ 3} = 4$ ,  $n_{Age\ 8} = 3$ ) to characterise changes in vegetation complexity and microclimate across the chronosequence. We measured understory vegetation height, understory vegetation composition, and canopy openness at 10 m intervals along transects (11 data points per transect) (Vegetation and Canopy:  $n_{Age\ M} = 22$ ,  $n_{Age\ 1} = 33$ ,  $n_{Age\ 3} = 44$ ,  $n_{Age\ 8} = 33$ ). We measured vegetation height using a drop disc (30 cm diameter and 231 g, dropped from an initial height of 170 cm), as similar methods have previously proven successful for measuring vegetation height in oil palm (Luke, Purnomo, et al., 2019). We classified the dominant understory vegetation type(s) touching the disc into four categories: fallen oil palm frond, herbaceous plant, bare ground, and fern. We measured canopy openness using a spherical densiometer (Lemmon, 1956), alternating facing left and right as we measured along each transect. We also measured soil temperature using iButton dataloggers (DS1922L-F5 thermochrons at high capacity). We set dataloggers to record for 24 hours at three-hourly intervals, placing them in mesh bags that were buried 5 cm below the soil surface at the first sampling point in each transect. Each datalogger recorded 8 temporal data points. One datalogger in *Age 3* overheated, and therefore no soil temperatures were obtained at this transect (Temperature:  $n_{Age\ M} = 16$ ,  $n_{Age\ 1} = 24$ ,  $n_{Age\ 3} = 24$ ,  $n_{Age\ 8} = 24$ ).

### 2.3.2.2 | Order-level arthropod sampling

We sampled arthropods across all 15 transects in three microhabitats: ground, understory, and canopy. To sample ground arthropods, we placed a single pitfall trap (19.5 cm diameter at mouth) at each sampling point. Pitfall traps were partially filled with 70% ethanol and covered with a plastic plate to prevent rainfall dilution and flooding. To sample understory arthropods, we placed a brown sticky trap (sticky on both sides, with a total sticky area of 19 cm x 27 cm) adjacent to each pitfall trap, and hung approximately 1.5 m from the ground using string. All traps along a transect were set on the same day. We collected both pitfall and sticky traps after 72 hours (Ground and understory arthropods:  $n_{Age\ M} = 12$ ,  $n_{Age\ 1} = 12$ ,  $n_{Age\ 3} = 12$ ,  $n_{Age\ 8} = 9$ ).

After pitfall and sticky traps were collected, we sampled canopy arthropods using insecticide fogging. To fog, we suspended six trays (each 1 m in diameter) under a single focal palm at the

start of each transect and tessellated trays, such that half were flush against the trunk and half were under the canopy. Although the distance between trays and canopies varied between cohorts, we kept fogging methods constant so that samples from all cohorts were comparable and each represented a consistent area of vertical space sampled per palm. We fogged each focal palm (Canopy arthropods:  $n_{Age M} = 4$ ,  $n_{Age 1} = 4$ ,  $n_{Age 3} = 4$ ,  $n_{Age 8} = 3$ ) using a Pulsfog K-10-SP Portable Thermal Fogger filled with a solution of 4.950 L diesel and 50 mL insecticide (Matador 25 EC, 25 g/L lambda-cyhalothrin). We fogged for 60 seconds after making sure that the fog had completely enveloped the oil palm canopy, as it was previously shown that similar fogging times collected large numbers of arthropods in oil palm plantations (Turner & Foster, 2009), and we sought to limit the impact on the wider environment. We collected arthropods from trays after 2 hours. All fogging was completed before 09:45 and during periods of minimal wind and no rain.

We identified all arthropods using stereomicroscopes in labs at SMARTRI research centre. We identified most arthropods to order-level, although we identified Chilopoda and Diplopoda to class and separated Formicidae (family) and Isoptera (infraorder) to their own groups, owing to their distinctive ecology and to be consistent with a comparable previous study (Ashton-Butt et al., 2019). We also placed endopterygote larvae in their own group. Hereafter, we collectively refer to all groups as orders. Identifying to order-level allowed all samples to be identified with the resources available and provided an overview of the responses of the total arthropod community to replanting.

### **2.3.2.3 | Species-level spider sampling**

We conducted focussed analyses on spiders in all microhabitats, in order to determine whether arthropod-level trends were replicated when taxonomic resolution was increased. We focussed on spiders, in part due to their contributions to pest control in croplands (Michalko et al., 2019) and also because adults could be reliably identified to morphospecies. We collected ground and canopy spiders during pitfall trapping and canopy fogging, as described above (Ground spiders:  $n_{Age M} = 12$ ,  $n_{Age 1} = 12$ ,  $n_{Age 3} = 12$ ,  $n_{Age 8} = 9$ ; Canopy spiders:  $n_{Age M} = 4$ ,  $n_{Age 1} = 4$ ,  $n_{Age 3} = 4$ ,  $n_{Age 8} = 3$ ). Understory spiders caught on sticky traps were often partially damaged and difficult to identify. We, therefore, collected understory spiders by walking each transect and collecting all spiders located above the ground and within 1 m of the observer (Understory spiders:  $n_{Age M} = 4$ ,  $n_{Age 1} = 4$ ,  $n_{Age 3} = 4$ ,  $n_{Age 8} = 3$ ). We walked all transects during the day between 07:00 and 14:00 and when it was not raining. In the lab, we separated juveniles from

adults (dissecting when necessary to differentiate haplogyne adult females and juveniles), and identified adults to family and morphospecies (hereafter, “species”) using dissecting microscopes and relevant keys (<http://ecotaxonomy.org/ecokeys>; Deeleman-Reinhold, 2000; Jocqué & Dippenaar-Schoeman, 2006). It was not possible to match males and females for all species, and therefore we counted each unique male and female as its own species. The spiders are preserved in 75% ethanol at SMARTRI research centre.

### 2.3.3 | Statistical analyses

All statistical analyses were performed in R version 3.5.1 (R Core Team, 2018) within R Studio version 1.1.456 (R Studio Team, 2018). We used *readxl* (Wickham et al., 2019), *tidyverse* (Wickham, 2017), *zoo* (Zeileis et al., 2019), *data.table* (Dowle et al., 2019), *plyr* (Wickham, 2016), *ggsignif* (Ahlmann-Eltze, 2019), *lemon* (Edwards et al., 2019), *car* (Fox et al., 2020), and *cowplot* (Wilke, 2019) for data wrangling, exploration, and visualisation. Exploration followed Zuur, Ieno, and Elphick (2010). We fitted generalized additive models (GAMs) using *mgcv* (Wood, 2019), generalized linear models (GLMs) using *MASS* (Ripley et al., 2019), generalized linear mixed models (GLMMs) using *glmmTMB* (Magnusson et al., 2019), Kruskal-Wallis tests using *stats* (R Core Team, 2018), and multivariate generalized linear models (mGLMs) using *mvabund* (Wang et al., 2019).

Unless otherwise stated, we fitted models to negative binomial distributions using log links, included cohort as a fixed effect (levels: *Age M*, *Age 1*, *Age 3*, *Age 8*) and, for mixed models, Transect ID as a random intercept effect to account for potential spatial autocorrelation. We validated models by plotting Pearson residuals against fitted values, covariates, and random effect levels (to verify that no spatial autocorrelation remained) and verifying no patterns were present. To ensure our models fitted the observed data, we simulated 10000 datasets from each model, calculated dispersion statistics for each simulated dataset, and verified that the dispersion statistic from our model was within the range of dispersion statistics calculated from our simulations (Zuur & Ieno, 2016). Our simulations indicated that there were no issues in model fit. We determined the significance of cohort to each model by comparing fitted models with null models using likelihood ratio tests (LRTs). If mixed models suggested a moderately significant effect of cohort ( $0.01 < p < 0.07$ ), we re-calculated *p*-values based on parametric bootstrapping using *DHARMA* (Bates et al., 2015; Hartig, 2019). If cohort was confirmed to be significant, we used *multcomp* (Hothorn et al., 2020) to conduct post-hoc analyses (Tukey all-

pair comparisons, adjusting  $p$ -values using the Bonferroni correction) to identify cohorts between which significant differences occurred.

### **2.3.3.1 | Impacts of replanting on the environment**

We analysed vegetation height and canopy openness using GLMMs, to account for non-independence of measurements along the same transect. We fitted the canopy openness GLMM to a normal distribution (identity link), after applying a logit transformation to the data in order to meet model assumptions (Warton & Hui, 2011). During data exploration, we noticed *Age 3* had high variability in canopy openness, owing to several data points that were collected near palm trunks (i.e. areas with unusually low canopy openness, in comparison to the majority of the *Age 3* landscape). We therefore eliminated *Age 3* data that were more than one standard deviation away from the mean ( $n_{\text{eliminated}} = 9$  data points) and, as a sensitivity analysis, re-ran our model on the adjusted dataset to explore the impact of the eliminated *Age 3* data on our initial model findings. We described understory vegetation composition along transects using stacked bar charts that conveyed percent vegetation occurrence by vegetation category. We analysed soil temperature using a GAM fitted to a gaussian distribution (identity link). We fitted a smoothing function (using cyclic penalized cubic regression splines and multiplied by the fixed effect) to the time of day at which recording occurred, and used an F-test to determine the significance of cohort.

### **2.3.3.2 | Impacts of replanting on all arthropods**

We analysed total arthropod abundances separately for the ground, understory, and canopy microhabitats. Prior to analysing understory data, we eliminated ant abundance from one sample due to an extremely high abundance of winged ants that had emerged from one nest and flown into the trap. When fogging, five sample trays across two palms overturned before collection and so samples were lost. We therefore standardised abundance data for each palm prior to analysis by calculating mean abundance per tray and multiplying by 6 (the number of trays set per palm). We also rounded to the nearest integer to meet model assumptions. We analysed ground and understory abundances using GLMMs, to account for non-independence of traps along the same transect. We analysed canopy abundances using a GLM, but model validation indicated patterns in the residuals. For this reason, and due to the small sample size, we re-analysed these data using a Kruskal-Wallis test.

We used mGLMs (Warton et al., 2012; Warton & Hui, 2017) to analyse arthropod order-level community composition. In these analyses, we excluded endopterygote larvae and individuals that could not be identified to order. After removals, 97.2% of all collected arthropods still remained and were used in analyses. We included Transect ID as a blocking variable in ground and understory models, to account for non-independence of traps along the same transect. We validated mGLMs by plotting Dunn-Smyth residuals against fitted values, covariate cohort, and blocking variable levels (to verify that no spatial autocorrelation remained) (Wang et al., 2012; Wang et al., 2019). We determined a significant effect of cohort using LRTs and by bootstrapping probability integral transform (PIT) residuals using 10000 resampling iterations (Warton et al., 2017). If cohort was significant ( $p < 0.05$ ), we ran univariate analyses on individual arthropod orders. We adjusted univariate  $p$ -values to correct for multiple testing using a step-down resampling algorithm (Wang et al., 2012), but otherwise our statistical approach remained unchanged from the multivariate parent models.

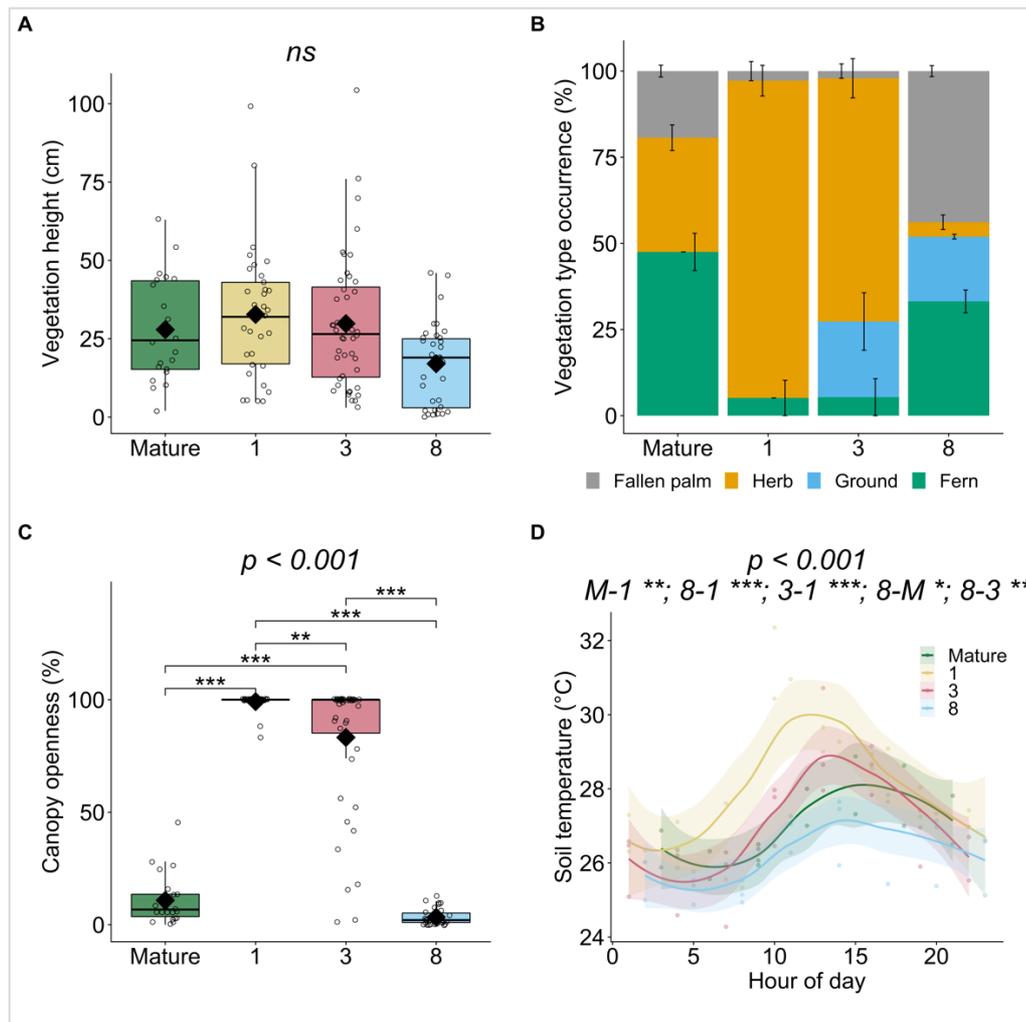
### **2.3.3.3 | Impacts of replanting on spiders**

To better understand the spider assemblage within the plantation, and to assess our sampling completeness, we calculated interpolated and extrapolated species richness, based on adult data only, within each microhabitat (using the richness estimators derived by Chao et al. (2014) and *iNEXT* (Hsieh et al., 2016; Hsieh, Ma, & Chao, 2019) and plotted these as species accumulation curves. We extrapolated to double the number of observed individuals. We separately analysed spider abundance and species richness for the ground, understory, and canopy microhabitats. We used all collected spiders in abundance analyses, but we only included adults in species richness analyses. We analysed ground spider abundance and species richness using GLMMs, to account for non-independence of traps along the same transect. We analysed understory and canopy spider abundance and species richness using GLMs but, due to patterns in residual plots and our small sample size, we re-analysed these data using Kruskal-Wallis tests. We, therefore, could not account for potential spatial autocorrelation in these analyses. When cohort was significant, we used *dunn.test* (Dinno, 2017) to conduct post-hoc analyses (Dunn's Test for Multiple Comparisons, adjusting  $p$ -values using the Bonferroni correction). We used mGLMs to analyse spider species-level community composition, based on adults only. We included Transect ID as a blocking variable in the ground model, to account for non-independence of traps along the same transect. If cohort was significant ( $p < 0.05$ ), we ran univariate analyses on individual spider species. Our statistical approach otherwise remained unchanged from our arthropod order-level community composition analyses.

## 2.4 Results

### 2.4.1 | Impacts of replanting on the environment

Replanting affected vegetation composition, canopy openness (Canopy openness: LRT = 43.015,  $p < 0.001$  (Sensitivity analysis: LRT = 63.628,  $p < 0.001$ )), and soil temperature (Soil temperature:  $F = 18.100$ ,  $p < 0.001$ ), but not vegetation height (Vegetation height: LRT = 5.199,  $p = 0.158$ ; Figure 2.2A). Compared to *Age M*, vegetation composition in *Ages 1* and *3* had higher densities of herbaceous plants and lower densities of ferns (Figure 2.2B). Vegetation composition in *Ages M* and *8* was similar, although more fallen palm fronds and bare ground were present in the latter. Canopy openness in *Ages 1* and *3* was greater than in *Ages M* and *8* ( $p < 0.001$  for all). *Age 1* had a more open canopy than *Age 3* ( $p = 0.004$ ), although this difference was dependent on the 9 extreme values in *Age 3*, as our sensitivity analysis indicated no difference in openness between these cohorts ( $p = 0.334$ ). This indicated that, away from palm trunks (i.e. the majority of the *Age 3* landscape), openness in *Ages 1* and *3* was not different. Openness was not different between *Ages M* and *8* ( $p = 0.417$ ; Figure 2.2C), although this lack of difference was dependent on the 9 extreme values in *Age 3*. After eliminating these *Age 3* values in our sensitivity analysis, the standard errors around all model estimates shrunk, leading to our post-hoc comparisons indicating that *Age 8* had a more closed canopy than *Age M* ( $p < 0.001$ ). Soils in *Age 1* were hotter than in *Age M* ( $p = 0.002$ ), *Age 3* ( $p < 0.001$ ), and *Age 8* ( $p < 0.001$ ). Soils in *Age 8* were cooler than in *Age 3* ( $p = 0.009$ ) and *Age M* ( $p = 0.030$ ; Figure 2.2D). Temperature varied across the day in all cohorts ( $p < 0.002$  for all), but the degree of variability was not the same. Cross-day variability in *Age 1* (25.3 – 32.4 °C) and *Age 3* (24.3 – 30.7 °C) was approximately double that in *Age M* (25.6 – 28.9 °C) and *Age 8* (24.9 – 27.8 °C). This was also indicated by the smoothing functions for *Ages 1* and *3* being more non-linear than those for *Ages M* and *8* (Figure S2.2).



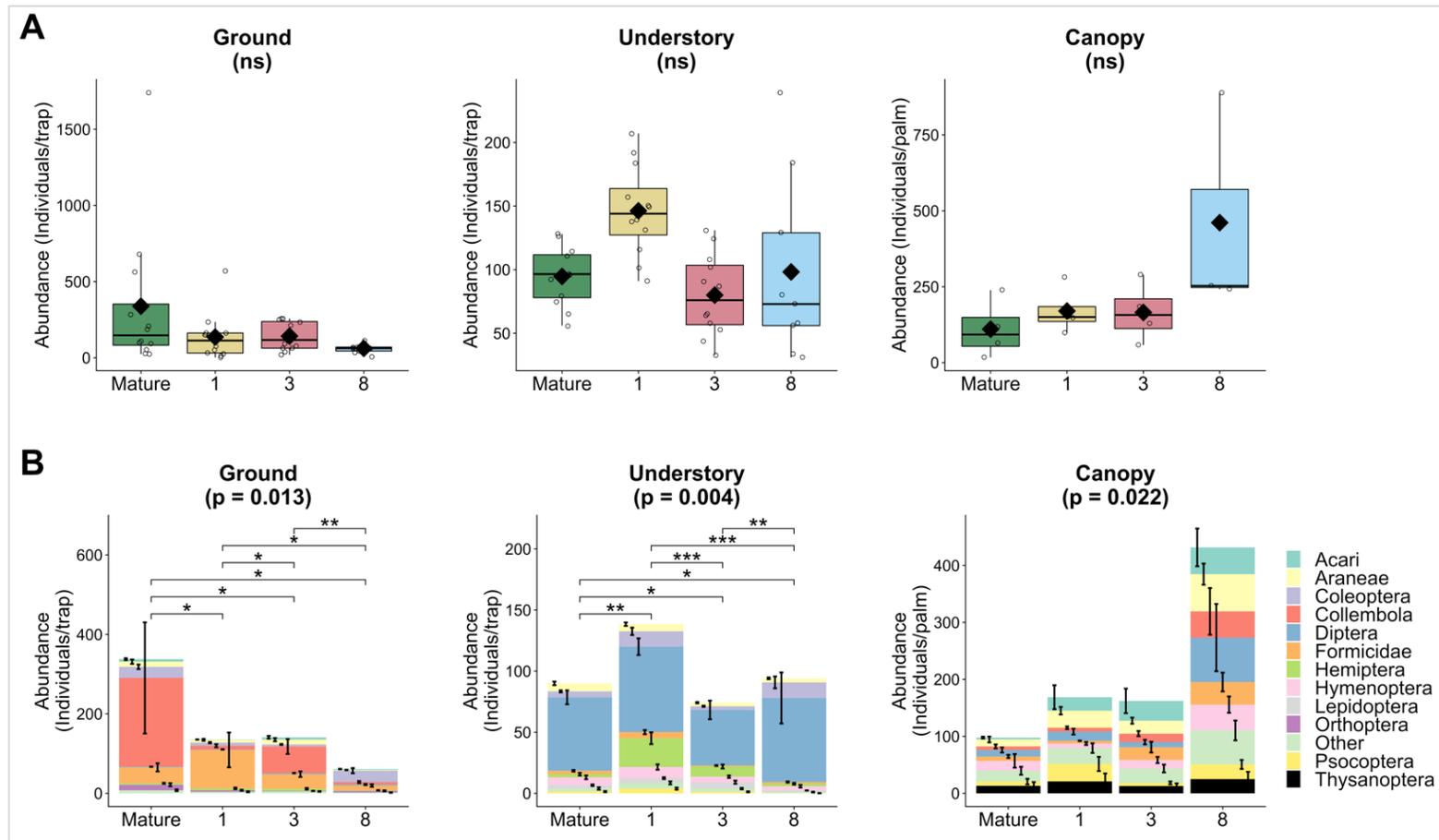
**Figure 2.2.** Differences in understory vegetation height (A), understory vegetation composition (B), canopy openness (C), and soil temperature (D) across studied oil palm age cohorts (*Mature, Age 1, Age 3, Age 8*). For A and C, boxplots display median and interquartile ranges, raw data are shown in grey circles, and black diamonds indicate observed means. For B, error bars represent the standard errors of means. For D, lines represent outputs from the generalised additive model (with 95% confidence intervals), and raw data are shown as circles with colours indicating the associated cohort. The significance of cohort in each model (A, C, D) is indicated above the plots in text and, when cohort was significant, we indicate cohorts between which significant differences occurred: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ , *ns* = cohort not significant in the model. For C, we present significance as per our initial model (i.e. we do not present significance as indicated by our sensitivity analysis, in which we tested the influence of 9 extreme canopy openness data points in *Age 3* on our initial model findings).

## 2.4.2 | Impacts of replanting on all arthropods

We collected 15854 arthropods, of which 7955 were from pitfall traps, 4736 were from sticky traps, and 3163 were from canopy fogging (after correcting for overturned fogging trays). Replanting did not affect ground arthropod abundance (Ground arthropod abundance: LRT = 3.317,  $p = 0.345$ ; Figure 2.3A-Left), although abundance was highly variable in *Age M* (owing to large variation in numbers of Collembola and – to a lesser extent – Araneae and Coleoptera) and less variable in *Age 8* compared to other cohorts. Understory arthropod abundance increased in the first year after replanting (*Age M* to *Age I*) but returned to pre-replanting levels by *Age 3*. The conditional model suggested cohort was a significant predictor of this effect (Understory arthropod abundance: LRT = 9.024,  $p = 0.029$ ); however, parametric bootstrapping indicated that the effect was not significant (Understory arthropod abundance:  $p_{10000\text{ iter}} = 0.077$ ; Figure 2.3A-Centre). Similarly, canopy arthropod abundance did not differ after replanting (Canopy arthropod abundance:  $\chi^2 = 5.392$ ;  $p = 0.145$ ; Figure 2.3A-Right), but abundance in *Age 8* was highly variable (owing to large variation in numbers of Acari, Araneae, Collembola, Diptera, and Formicidae), with one palm having more than triple the arthropod abundance of any other palm.

We identified 15596 of the 15854 arthropods (98.4%) to 24 orders, including 7955 from pitfall traps (100%), 4479 from sticky traps (94.6%), and 3162 from canopy fogging (99.9%). The majority of non-identifiable arthropods were damaged individuals. Of the identified arthropods, 15405 were used in order-level community composition analyses, including 7916 from pitfall traps, 4479 from sticky traps, and 3010 from canopy fogging. Collembola ( $n = 3649$ ), Formicidae ( $n = 2191$ ), and Coleoptera ( $n = 751$ ) were dominant on the ground; Diptera ( $n = 2727$ ), Hemiptera ( $n = 432$ ), and Coleoptera ( $n = 360$ ) were dominant in the understory; and Araneae ( $n = 456$ ), Acari ( $n = 388$ ), and Diptera ( $n = 379$ ) were dominant in the canopy. Ground (LRT = 186.1,  $p = 0.013$ ), understory (LRT = 177.0,  $p = 0.004$ ), and canopy (LRT = 124.0,  $p = 0.022$ ) order-level community composition differed significantly after replanting. On the ground, arthropod order-level community composition in all post-replanted cohorts differed significantly from *Age M* and from each other ( $p < 0.05$  for all post-hoc comparisons; Figure 2.3B-Left). Univariate analyses indicated that reduced coleopteran abundances (LRT = 30.668,  $p = 0.011$ ) in *Ages 1* and *3* were the primary drivers of these differences (Figure S2.3). A similar effect was observed in the understory ( $p < 0.05$  for all post-hoc comparisons; Figure 2.3B-Centre), with increased abundances in Coleoptera (LRT = 21.435,  $p = 0.029$ ), Hemiptera (LRT = 38.596,  $p = 0.001$ ), and Psocoptera (LRT = 20.331,  $p = 0.029$ ) in *Age 1* driving these

differences (Figure S2.4). Although our analyses indicated that cohort significantly influenced canopy order-level community composition, post-hoc comparisons did not indicate significant pairwise differences between cohorts ( $p > 0.05$  for all; Figure 2.3B-Right). Univariate analyses indicated that lowered abundances in Dermaptera (LRT = 17.331,  $p = 0.050$ ) and Lepidoptera (LRT = 25.449,  $p = 0.008$ ) in *Ages 1* and *3* were the primary drivers of the overall significant difference (Figure S2.5).



**Figure 2.3.** Differences in total abundance (A) and order-level community composition (B) for ground (Left), understory (Centre), and canopy (Right) arthropods across studied age cohorts (*Mature*, *Age 1*, *Age 3*, *Age 8*). The significance of cohort in each model is indicated above the plots in text and, when cohort was significant, we indicate cohorts between which significant differences occurred: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ , *ns* = cohort not significant in the model. In A, boxplots display medians and interquartile ranges, raw data are shown in grey circles, and black diamonds indicate observed means. In B, only the 8 most abundant orders in each microhabitat are plotted, for ease of interpretation. Orders are plotted as they are sequenced in the legend. Error bars indicate one standard error from the mean.

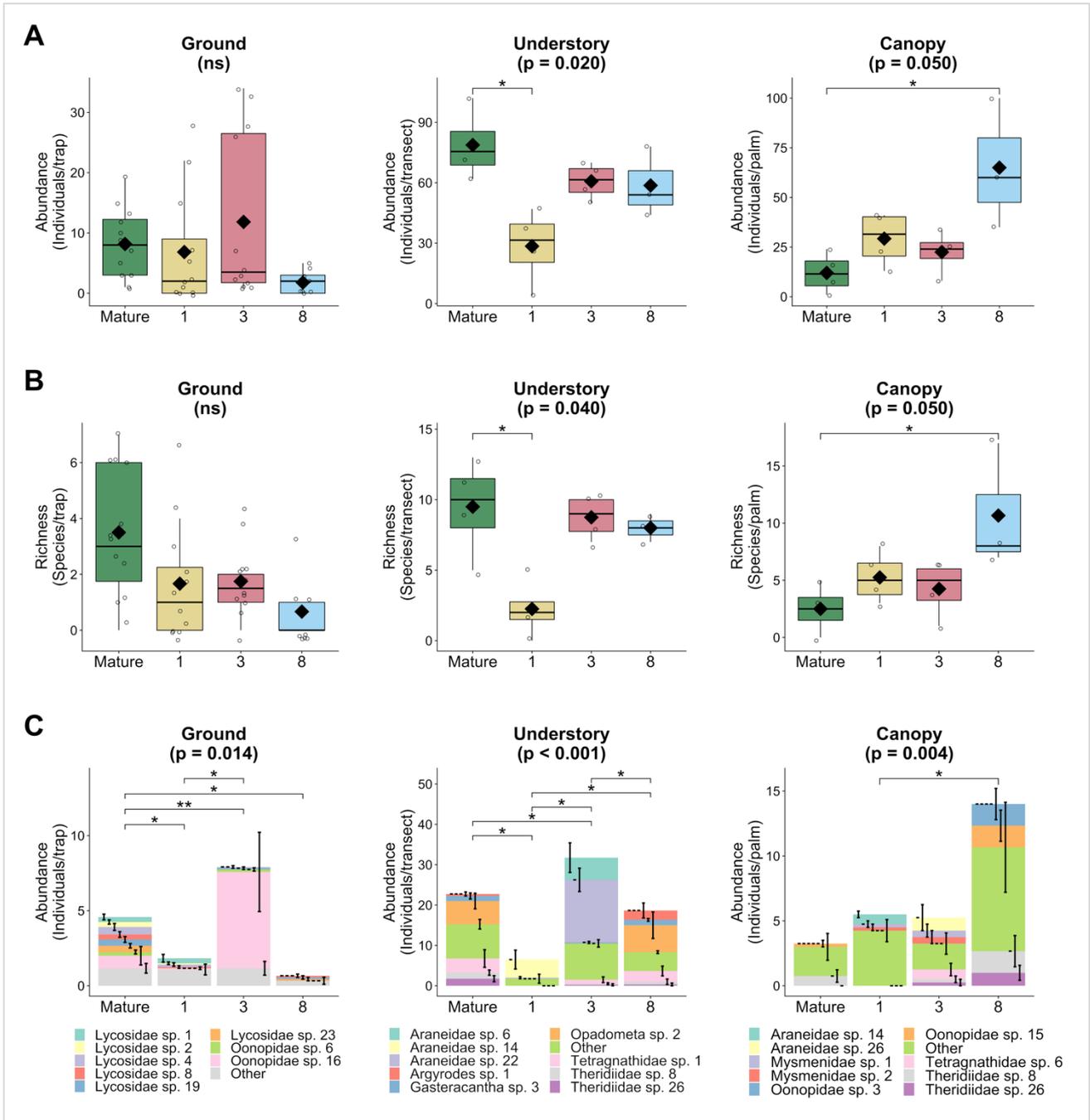
### 2.4.3 | Impacts of replanting on spiders

We collected 338 spiders from the ground ( $n_{\text{adults}} = 178$ ;  $n_{\text{species}} = 38$ ; Table S2.2), 848 spiders from the understory ( $n_{\text{adults}} = 300$ ;  $n_{\text{species}} = 52$ ; Table S2.2), and 450 spiders from the canopy ( $n_{\text{adults}} = 98$ ;  $n_{\text{species}} = 52$ ; Table S2.2). Species accumulation curves in all microhabitats were starting to asymptote, indicating that our sampling of species was nearing completion within each microhabitat (Figure S2.6).

Replanting did not affect ground spider abundance (Ground spider abundance: LRT = 4.473,  $p = 0.215$ ; Figure 2.4A-Left) or species richness (Ground spider species richness: LRT = 6.880,  $p = 0.076$ ; Figure 2.4B-Left). Replanting affected both understory spider abundance ( $\chi^2 = 9.675$ ;  $p = 0.020$ ; Figure 2.4A-Centre) and species richness ( $\chi^2 = 8.507$ ;  $p = 0.040$ ; Figure 2.4B-Centre; Tables S2.10-11). Per transect, *Age 1* had ~50 fewer understory spider individuals ( $p = 0.006$ ) and ~7 fewer understory spider species ( $p = 0.023$ ) than *Age M*. Replanting also impacted canopy spider abundance ( $\chi^2 = 7.787$ ;  $p = 0.050$ ; Figure 2.4A-Right) and species richness ( $\chi^2 = 7.870$ ;  $p = 0.050$ ; Figure 2.4B-Right). Per palm, *Age 8* had ~50 more canopy spider individuals ( $p = 0.019$ ) and ~8 more canopy spider species ( $p = 0.017$ ) than *Age M*.

Ground (LRT = 163.5,  $p = 0.014$ ), understory (LRT = 275.8,  $p < 0.001$ ), and canopy (LRT = 195.3,  $p = 0.004$ ) species-level community composition changed significantly after replanting. On the ground, community composition in all post-replanted cohorts differed significantly from *Age M*, and the community composition in *Age 1* differed from that in *Age 3* (Figure 2.4C-Left). Univariate analyses indicated that four spider species (two species each of Oonopidae and Lycosidae) were the primary drivers of these differences ( $p < 0.05$  for univariate analyses; Table S2.2). In the understory, species-level community composition in *Ages 1* and *3* differed significantly from *Age M*, although *Age M* did not differ significantly from *Age 8*. Species-level community composition in all post-replanted cohorts differed significantly from each other (Figure 2.4C-Centre). Univariate analyses indicated that nine spider species (five species of Araneidae, three species of Tetragnathidae, and one species of Theridiidae) were the primary drivers of these differences ( $p < 0.05$  for univariate analyses; Table S2.2). In the canopy, community composition in *Age 1* differed significantly from *Age 8*, but there were no other significant differences between cohorts (Figure 2.4C-Right). Univariate analyses indicated that eleven spider species (three species of Araneidae, one species of Linyphiidae, three species of Oonopidae, one species of Tetragnathidae, two species of Theridiidae, and one species of

Thomisidae) were the primary drivers of these differences ( $p < 0.05$  for univariate analyses; Table S2.2).



**Figure 2.4.** Differences in abundance (A), species richness (B), and species-level community composition (C) for ground (Left), understory (Centre), and canopy (Right) spiders across age cohorts (*Mature, Age 1, Age 3, Age 8*). The significance of cohort in each model is indicated above the plots in text and, when cohort was significant, we indicate cohorts between which significant differences occurred: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ , ns = cohort not significant in the model. In A and B, boxplots display medians and interquartile ranges, raw data are shown in grey circles, and black diamonds indicate observed means. In C, only the 9

most abundant species in each microhabitat are plotted, for ease of interpretation. Only the 8 most abundant species are plotted in C-Left, owing to several species having equal abundances after the 8<sup>th</sup> most abundant species. Species are plotted as they are sequenced in their respective legends. Error bars indicate one standard error from the mean.

## 2.5 Discussion

In this study, we investigated changes in environmental conditions and arthropod communities across an oil palm chronosequence, to determine the impacts of replanting on oil palm landscapes over an 8-year period following replanting. Replanting in our study area was carried out using recommended industry replanting strategies, and is therefore likely to be comparable to how replanting has happened, or will soon happen, in industrial oil palm estates across Southeast Asia. Across the chronosequence, we found substantial changes in understory vegetation composition, canopy openness, and soil temperature, but we did not find changes in understory vegetation height. We also found differences in arthropod order-level community composition, spider abundance and species richness in the understory and canopy, and spider species-level community composition in all microhabitats. We found no significant differences in total arthropod abundance, or ground spider abundance and species richness.

### 2.5.1 | Impacts of replanting on the environment

Replanting of oil palm changed microclimate and understory vegetation, with some changes still present even 8-years after replanting. The largest environmental differences occurred in two phases: between *Ages M* and *I*, and between *Ages 3* and *8*. Between *Age M* and *Age I* (i.e. the period when first-generation mature palms were replaced by young replanted palms), an understory vegetation community dominated by ferns was replaced by cover crop, a closed canopy became almost fully open, and soil temperatures increased and became more variable across the day. It is likely that replanting also changed other aspects of the ecosystem that were beyond the scope of this study, such as soil humidity and compaction. Between *Age 3* and *Age 8* (i.e. the period when young replanted palms grew into maturity), environmental conditions shifted back towards pre-replanting conditions. In comparison to the other cohorts, the environmental conditions in *Age 8* resembled those in *Age M* and, even where differences occurred, *Age 8* was more similar to *Age M* than to *Ages 1* and *3*. We note that, in comparison to our initial canopy openness model, our sensitivity analysis indicated that, away from palm

trunks (i.e. the majority of the *Age 3* landscape), openness in *Ages 1* and *3* was similar. Additionally, our sensitivity analysis found that *Age 8* had a more closed canopy than *Age M* (our initial model found no differences in openness between these cohorts). This difference may be partially explained by variation in management between *Ages M* and *8*. For example, canopy fronds in *Age M* are often cut so that palm fruits can be more easily harvested, creating small gaps in the canopy, but this is not done in *Age 8*. Additionally, as a result of being older, occasional palms in *Age M* are more likely to be dead or dying than in *Age 8*, leading to gaps in the canopy at larger scales. Replanting did not affect understory vegetation height. We attribute this to changes in vegetation composition related to replanting, which enabled different types of plants to produce similar vegetation height across the chronosequence. It is also likely that replanting changed other aspects of vegetation. For example, a previous study found that plant species richness and percent vegetation coverage increased in the first year after replanting before returning to pre-replanting levels within three years (Ashton-Butt et al., 2019). Our findings reflect previous research that documented changes in environmental conditions and processes across the oil palm life cycle (Hamilton et al., 2016; Luskin & Potts, 2011; Pauli et al., 2014; Röhl et al., 2015). This indicates that, as second-generation oil palms age, environmental conditions may follow similar patterns of development as has previously been documented in first-generation plantations.

### **2.5.2 | Impacts of replanting on arthropods**

We recorded 24 arthropod orders or other groups, and 131 spider morphospecies from 20 families, across ground, understory, and canopy microhabitats within oil palm. Our findings show that, although significantly less biodiverse than natural forests (Drescher et al., 2016; Foster et al., 2011; Potapov et al., 2020), oil palm plantations can harbour a broad range of taxa. Encouragingly, we found that replanting had little short-term (i.e. 1-3 years) or long-term (i.e. 8 years) negative impacts on total arthropod abundance in any microhabitat, as we found no significant differences in total arthropod abundance across the studied chronosequence and found relatively high arthropod abundances in all cohorts. This is likely to be explained by oil palm being primarily populated by generalist arthropod taxa that adapt easily to changes in microclimate and vegetation complexity (Chey, 2006; Chung et al., 2000; Fayle, Edwards, et al., 2015). However, we also found that replanting changed arthropod order-level composition, altered spider species-level composition, and decreased spider abundance and species richness in some microhabitats.

### **2.5.2.1 | Impacts of replanting on the ground**

On the ground, we found that replanting did not affect total arthropod abundance but changed arthropod order-level composition, owing to significant decreases in Coleoptera abundance after replanting. Our spider-focussed analyses showed similar trends, as replanting did not affect ground spider abundance or species richness, but changed species-level composition. Our findings reflect those of another study that occurred over a similar replanting period and focussed on soil macrofauna (Ashton-Butt et al., 2019), a community that is likely to exhibit similar patterns to surface-dwelling ground arthropods. This study found that replanting caused short-term (i.e. one month) declines in soil macrofauna abundance, although abundance recovered to pre-replanting levels within one year after replanting. Similar to our study, Ashton-Butt et al. (2019) also found that replanting caused long-term (i.e. 7 years after replanting) changes in soil arthropod order-level composition.

Coleoptera was the only ground-dwelling taxon affected by replanting, with decreases in Coleoptera abundance in the first 3 years after replanting. This could be due to a lack of dead palm fronds on the ground during this time period. Dead palm fronds are abundant on the ground in mature plantations, but not in young plantations, and can be an important habitat for ground-dwelling invertebrates (Wong et al., 2016). We suggest that the otherwise limited impacts of replanting on other ground arthropods may be attributed to management decisions that are implemented immediately after replanting. For instance, a cover crop was planted within 2 months of replanting in the plantations in which we sampled. Cover crops are primarily planted to reduce soil erosion after replanting, but they may also benefit arthropod biodiversity within agricultural systems. For instance, a previous study occurring in maize found that planting a cover crop increased soil macrofauna diversity and biomass (Blanchart et al., 2006). It is also noteworthy that the established management practice in the plantations in which we worked was to chop mature palms after clearance and leave them as mulch in the post-replanting landscape. This practise provides additional habitat for ground arthropods, may provide more suitable microclimatic conditions than surrounding replanted areas, and may partially compensate for the loss of palm fronds.

### **2.5.2.2 | Impacts of replanting in the understory**

We found that replanting did not affect total arthropod abundance in the understory but changed arthropod order-level composition (owing to significant increases in Coleoptera, Hemiptera, and Psocoptera in the first year after replanting). We also found that replanting significantly

decreased the abundance and species richness of understory spiders in the first year after replanting, and additionally changed spider species-level community composition.

The post-replanting changes in understory arthropods that we observed are likely to be related to differences in vegetation composition across the chronosequence. Replanting resulted in a fern-dominated understory being replaced by cover crop and other herbaceous plants, which may have benefited some arthropods. For instance, the post-replanting rise in Hemiptera and Coleoptera abundance could be related to the increased density of herbaceous plants in *Age 1*, which could provide additional food sources for plant and insect-feeding species within these groups. Understory vegetation that was killed during replanting and is decomposing in *Age 1* could be an important food source for Psocoptera, possibly explaining their post-replanting rise in abundance. The majority of understory spiders that we collected were orb-weavers (Araneidae and Tetragnathidae), which depend on structurally complex and stable vegetation in order to build their webs (Greenstone, 1984; Rypstra, 1983). In comparison to cover crop, ferns have greater structural integrity and complexity, potentially affecting the ability or proclivity of orb-weavers to inhabit them. It is also noteworthy that fern fronds curl distally, and we observed during our fieldwork that orb-weavers often retreated to these distal spaces whilst not feeding or when threatened. By comparison, we did not observe spiders in retreats under cover crop leaves. Although we did not quantify the association between understory vegetation composition and orb-weavers, our hypothesis is supported by a previous study that found that areas of mature palm with standard or enhanced levels of understory vegetation supported more understory spiders, and a different assemblage of understory spiders, to areas with reduced levels of vegetation (Spear, 2016). We do not attribute the changes in understory spider abundance or species richness that we observed to altered prey availability, since we found that total arthropod abundance in the understory did not change significantly after replanting.

### **2.5.2.3 | Impacts of replanting in the canopy**

As in the ground and understory, replanting did not affect total arthropod abundance in the canopy, but changed arthropod order-level composition, owing to reduced abundances of Dermaptera and Lepidoptera in the first 3 years after replanting. We also found that replanting significantly changed canopy spider species-level composition, and that canopy spider abundance and species richness was significantly higher in *Age 8* than *Age M*. However, our

canopy spider abundance and species richness findings were only weakly significant ( $p = 0.050$ ). Therefore, we recommend caution in interpreting these results.

The significant declines in Dermaptera and Lepidoptera after replanting may be attributed to reduced trunk and canopy complexity in young palms. For example, previous studies have found that frond axils, which are only found on mature palm trunks, can host abundant arthropod communities (Ganser et al., 2017; Potapov et al., 2020). We found that the abundance of canopy arthropods was particularly high 8-years after replanting, although trends were not always significant. This could be attributed to epiphytes, which are only found on the trunks of mature oil palms (i.e. they are not present on the trunks of *Age 1* and *Age 3* palms), but gradually decline in abundance as oil palms pass peak yields and the bases of fallen fronds rot away on the trunk. Such epiphytes can support high densities of arthropods in oil palm (Ganser et al., 2017; Turner & Foster, 2009), potentially explaining the high numbers of arthropods found in *Age 8* palms in this study.

We found relatively few ants in our canopy samples compared to other studies, particularly prior to replanting (i.e. *Age M*, where we found ~7 ants per fogging sample, representing ~7% of all arthropods that were collected). For instance, Turner & Foster (2009) found ~200 ants per fogging sample (~41% of all arthropods that were collected) in mature oil palm in Malaysia, and Hood (2019) found ~120 ants per fogging sample (~40% of all arthropods that were collected) in mature palms in the same plantation in which we sampled. Had ants been similarly abundant in our sites as they were in these studies, we could have observed more substantial changes in arthropod order-level community composition in the canopy, and possibly observed decreases in total canopy arthropod abundance after replanting. It is possible that the fewer ants that we found were due to differences in climate between our study and others. For instance, a previous study found that prolonged rainfall could reduce the abundance of ants in tropical forest canopies (Adis, 1988), and our canopy sampling occurred towards the end of the regional rainy season.

### **2.5.3 | Overall impacts of replanting, and implications for ecosystem functioning**

Our analyses show that some aspects of arthropod biodiversity, such as total arthropod abundance, showed consistent trends across microhabitats. However, other aspects of biodiversity showed microhabitat-specific trends, suggesting that replanting differently impacted arthropods within the ground, understory, and canopy. For instance, immediately (i.e.

1 year) after replanting, the abundance of spiders in the understory declined, but spider abundance on the ground and in the canopy remained unchanged. These findings demonstrate that some aspects of the ground, understory, and canopy are differently impacted by replanting and subsequent management decisions in second-generation plantations. This can partially be explained by some management decisions specifically targeting a single microhabitat, for instance, herbicides that are applied to understory vegetation will have a greater impact on understory arthropods than arthropods in the canopy. Collectively, our microhabitat-specific analyses demonstrate that a single-microhabitat approach could offer a limited, or possibly biased, understanding of oil palm ecosystems. Our findings therefore underscore the importance of taking a whole-ecosystem approach when assessing the impacts of management on biodiversity within oil palm plantations.

The changes in composition, and declines in abundance of ground-inhabiting coleopterans, canopy-inhabiting lepidopterans and dermapterans, and declines in abundance and species richness of understory spiders that we observed in this study could result in changes in a range of ecosystem functions. These include functions that impact growth and production of oil palms such as pollination, predation, decomposition and nutrient recycling, for which arthropods play key roles. For instance, some ground-inhabiting beetles contribute to dung removal (Gray et al., 2014) in oil palm plantations, and web-building spiders are important predators of pests in various agricultural systems (Michalko et al., 2019). It is also noteworthy that some arthropods are pests, such as caterpillars that eat the fronds of oil palms (Corley & Tinker, 2016). However, the impacts of replanting on ecosystem functioning in oil palm plantations may be limited, as a previous study found no short-term (i.e. 1-4 years) impacts of replanting on dung removal, soil mesofauna feeding activity, herbivore predation, seed predation, or average multifunctionality (Woodham et al., 2019). To date, herbivory is the only ecosystem function that is known to change after replanting, and has been found to increase in the first four years after replanting but to return to pre-replanting levels within eight years (Waters, 2018; Woodham et al., 2019). It is possible that this lack of difference is related to the lack of overall change in arthropod number that we found in this study and that, despite individual differences within orders, the arthropod community is relatively robust and able to deliver associated ecosystem functions across replanting events.

#### **2.5.4 | Relevance to oil palm management**

The oil palm estates in which this study occurred were replanted using recommended strategies, which included staggering replanting events to promote landscape-level heterogeneity across the plantation, retaining mature oil palm riparian buffers, planting a cover crop < 2 months after replanting, and using chopped mature palms as mulch for young second-generation palms. After replanting, the estates were managed in accordance with sustainable growth guidelines from three independent certification bodies: Roundtable on Sustainable Palm Oil (RSPO), Indonesian Sustainable Palm Oil (ISPO), and International Sustainability & Carbon Certification (ISCC). Compliance with these strategies and growth guidelines is likely to be comparable to how replanting and regrowth will happen, or has already happened, in industrial oil palm estates across Southeast Asia. To these ends, the findings of this study give valuable information about the effects of current sustainable growth guidelines, such as those provided by the RSPO, ISPO, and ISCC. Importantly, we did not test the impacts of any singular strategy, and we highlight that this research is urgently required. Examples of such research initiatives are the *Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project*, which is testing how riparian buffer quality affects biodiversity, ecosystem processes, and yields across oil palm replanting events (Luke, Advento, Arywan, et al., 2020) and the *Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (EFForTS) Project*, which is testing the impacts of different fertilizer and herbicide regimes on oil palm ecosystems (Darras et al., 2019).

### **2.6 Conclusions**

Across our sampled chronosequence, we found no differences in total ground, understory, or canopy arthropod abundance or the abundance and species richness of ground spiders, which assuages previously raised concerns (e.g. Snaddon et al., 2013) that replanting could devastate arthropod communities in oil palm ecosystems. However, we also found changes in arthropod order-level community composition and spider species-level community composition in all microhabitats, and differences in spider abundance and species richness in the understory and canopy. Owing to these latter findings, our results are only somewhat encouraging for the long-term persistence of arthropods in oil palm plantations, and of the functions they can support. To these ends, this study is a useful baseline in determining how replanting using recommended strategies impacts oil palm ecosystems. We highlight that future research is needed, such as assessing the impacts of replanting on other taxonomic groups and quantifying the effects of

individual replanting strategies, before the full long-term impacts of replanting on existing oil palm plantations can be understood.

## Chapter 3

### **Riparian buffers made of mature oil palms have inconsistent impacts on oil palm ecosystems**

#### **3.1 Abstract**

Expansion of oil palm has caused widespread declines in biodiversity and changes in ecosystem functioning across the tropics. A major driver of these changes is loss of habitat heterogeneity as forests are converted into oil palm plantations. Therefore, one strategy to help support biodiversity and functioning in oil palm is to increase habitat heterogeneity, for instance, by retaining forested buffers around rivers when new plantations are established, or maintaining buffers made of mature oil palms (“mature palm buffers”) when old plantations are replanted. Whilst forested buffers are known to benefit oil palm systems, the impacts of mature palm buffers are less certain. In this study, we assessed the benefits of mature palm buffers, which were being passively restored (in this case, meaning that buffers were treated with no herbicides, pesticides, or fertilisers) by sampling environmental conditions and arthropods within buffers and in surrounding non-buffer areas (i.e. areas that were 25 m and 125 m from buffers, and receiving normal business-as-usual management) across an 8-year chronosequence in industrial oil palm plantations (Sumatra, Indonesia). We ask: 1) Do environmental conditions and biodiversity differ between buffer and non-buffer areas? 2) Do buffers affect environmental conditions and biodiversity in adjacent non-buffer areas (i.e. areas that were 25 m from buffers)? 3) Do buffers become more environmentally complex and biodiverse over time? We found that buffers can have environmental conditions (canopy openness, variation in openness, vegetation height, ground cover, and soil temperature) and levels of arthropod biodiversity (total arthropod abundance and spider abundance in the understory, and spider species-level community composition in all microhabitats) that are different from those in non-buffer areas, but that these differences are inconsistent across the oil palm commercial life cycle. We also found that buffers might contribute to small increases in vegetation height and changes in ground cover in adjacent non-buffer areas, but do not increase levels of arthropod biodiversity in these areas. Finally, we found that canopy openness, variation in openness, and ground cover—but no aspects of arthropod biodiversity—change within buffers over time. Collectively, our findings indicate that mature palm buffers that are being passively restored can have greater environmental complexity and higher levels of

arthropod biodiversity than non-buffer areas, particularly in comparison to recently replanted oil palm, but these benefits are not consistent across the crop commercial life cycle. If the goal of maintaining riparian buffers is to consistently increase habitat heterogeneity and improve biodiversity, an alternative to mature palm buffers or a move towards more active restoration of these areas is, therefore, probably required.

### 3.2 Introduction

Agriculture is expanding rapidly across the tropics (Gibbs et al., 2010; Tilman et al., 2001). One of the crops showing among the largest expansions in recent years is oil palm (*Elaeis guineensis*), which is grown to produce palm oil: the most widely traded vegetable oil worldwide (> 70 million metric tons traded in the 2019/20 fiscal year; USDA, 2021). The majority of palm oil production occurs in Southeast Asia, where oil palm plantations are the dominant landscape in some regions (Ramdani & Hino, 2013). Although expansion of oil palm plantations can bring socioeconomic benefits, such as improved food security (e.g. Edwards, 2019), the conversion of natural habitat to oil palm also leads to widespread declines in biodiversity (Drescher et al., 2016; Foster et al., 2011) and alters a range of ecosystem functions, such as predation and soil fertility (Barnes et al., 2017; Dislich et al., 2017).

The relatively low levels of biodiversity and reduced ecosystem functioning within oil palm plantations are driven, in part, by reduction of habitat heterogeneity that occurs as natural landscapes are converted to oil palm systems (e.g. Drescher et al., 2016; Luskin and Potts, 2011). Therefore, one strategy to support biodiversity and functioning in oil palm plantations is to increase habitat heterogeneity within the crop landscape (Foster et al., 2011; Luke, Advento, Aryawan, et al., 2020; Luskin & Potts, 2011; Sirami et al., 2019). In comparison to other crops—particularly annuals, such as rice and soybean—oil palm plantations are an ideal system in which to enhance habitat heterogeneity through changes in management practice (Beyer et al., Unpublished). Oil palm is a perennial tree crop with a long commercial life cycle (20 – 30 years, although palms can live for more than a century; Corley & Tinker, 2016), providing ample time for heterogeneous habitat to develop. The crop is also grown over vast swathes of land (Descals et al., 2020), across which large areas of heterogeneous habitat can be established. Additionally, oil palm growers are incentivized to maintain heterogeneous habitat, as such practices are often a requirement for sustainability certification schemes (such as the Roundtable on Sustainable Palm Oil; RSPO, 2018).

Increasing habitat heterogeneity in oil palm plantations can be achieved at various scales. For instance, at a local scale, structural complexity can be increased by applying empty oil palm fruit bunches (EFBs) to the bases of mature palms (Tao et al., 2018), by retaining epiphytes on palm trunks (Prescott et al., 2015), or by enhancing the structural complexity of understory vegetation (e.g. Darras et al., 2019; Hood, Advento, et al., 2020; Luke, Purnomo, et al., 2019; Luke, Advento, Aryawan, et al., 2020; Luke, Advento, Dow, et al., 2020; Spear et al., 2018). At a landscape-scale, habitat heterogeneity within plantations can be increased by intercropping palms with other cash crops (Ashraf et al., 2018; Asmah et al., 2017; Yahya et al., 2017), retaining rainforest fragments within plantations at the time of establishment (Lucey et al., 2014; Lucey & Hill, 2012), establishing diverse tree islands within plantations (Teuscher et al., 2015; Zemp, Ehbrecht, et al., 2019; Zemp, Gérard, et al., 2019), and maintaining riparian buffers along plantation waterways (Luke, Slade, et al., 2019). Collectively, strategies to increase habitat heterogeneity in oil palm plantations have been demonstrated to benefit a wide variety of taxa, including spiders (Spear et al., 2018), insects (Ashraf et al., 2018; Ashton-Butt et al., 2018; Hood, Advento, et al., 2020; Lucey et al., 2014; Lucey & Hill, 2012), and birds (Teuscher et al., 2016; Yahya et al., 2017).

Increasing landscape-scale heterogeneity through maintaining or restoring riparian buffers has particularly high potential to bring a wide range of environmental benefits in oil palm agriculture. Buffers—also called riparian reserves, corridors, strips, margins, and zones—border plantation waterways and are managed less intensely than surrounding cultivated areas. They can provide terrestrial habitat, freshwater protection, and landscape connectivity (Luke, Slade, et al., 2019), but require relatively little land area (Bicknell, Unpublished). Within oil palm systems, buffers are typically formed from either (1) remnant patches of rainforest that were retained during plantation establishment (hereafter, “forested buffers”) or (2) zones of mature oil palm that are managed less intensely than surrounding cultivated areas, and are maintained when mature oil palm is replanted with young palms at the end of its commercial life cycle (hereafter, “mature palm buffers”). These mature palm buffers are often allowed to passively restore; an approach to restoration in which ecosystems recover on their own, or with minimal human intervention (Ghazoul & Chazdon, 2017), and which allows succession within buffers to occur.

Most research to date has focussed on forested buffers, and has shown that they provide multiple benefits to oil palm systems. For instance, forested buffers can mitigate soil erosion, improve stream water quality (Chellaiah & Yule, 2018a; Luke, Barclay, et al., 2017), and act as microclimate refugia in oil palm landscapes (Williamson et al., 2021). In comparison to surrounding oil palm areas, forested buffers support more species of ants (Gray et al., 2015), birds (Mitchell et al., 2018), adult dragonflies (Luke, Dow, et al., 2017), and dung beetles (Gray et al., 2014). Birds (Knowlton et al., 2017) and moths (Gray et al., 2019) can move through forested buffers to cross oil palm landscapes and, in some circumstances, invertebrates can move from forested buffers into adjacent oil palm plantations (Gray et al., 2016). In comparison to forested buffers, the impacts of mature palm buffers on oil palm systems are less known. Only two studies to date, occurring in industrial plantations in Sumatra (Indonesia), have focussed on mature palm buffers, finding that they do little to support different environmental conditions or levels of ecosystem functioning or multifunctionality (Luke, Advento, Aryawan, et al., 2020; Woodham et al., 2019), in comparison to cultivated areas. It is unknown whether mature palm buffers have levels of biodiversity that are different from those in cultivated areas, or whether buffers affect environmental conditions and levels of biodiversity in adjacent cultivated areas (i.e. just outside mature palm buffers). This knowledge gap exists despite mature palm buffers becoming increasingly widespread as plantations across Southeast Asia are replanted, and because maintaining mature palm buffers during replanting is a requirement for major sustainability certifications (Barclay et al., 2017; RSPO, 2018; Indonesian Sustainable Palm Oil, <http://ispo-org.or.id>).

Oil palm is a long-lived crop with a 20-30 year commercial life cycle. The impacts of mature palm buffers on oil palm systems are expected to vary across this period, as conditions in the surrounding cultivated areas change. As cultivated areas age, they become cooler and more humid (Luskin and Potts, 2011; Pashkevich et al., 2021) and, depending on management, trunk epiphytes can become more abundant, depth of leaf litter can increase, and soil quality and nutrient cycling can fluctuate over time (Hamilton et al., 2016; Luskin and Potts, 2011; Pauli et al., 2014). These changes in environmental conditions may cause cultivated areas to have different levels of biodiversity, relative to mature palm buffers. For instance, the species-level composition of ground-foraging ants was found to differ between young (4 – 7 years), mature (10 – 13 years), and old (15 – 26 years) oil palm plantations (Wang & Foster, 2016). In addition, we previously demonstrated that the order-level community composition of arthropods, and species-level community composition of spiders, changed as second-generation oil palm

plantations aged (Pashkevich et al., 2021). Further, it is likely that conditions within mature palm buffers themselves will change over time as succession occurs although, to our knowledge, this has not yet been investigated.

This study investigated whether mature palm buffers that were being passively restored affected habitat heterogeneity and biodiversity within oil palm systems and, if so, whether the effects were consistent across the oil palm commercial life cycle. We focussed our biodiversity surveys on arthropods, as they are abundant within oil palm plantations; facilitate important ecosystem processes such as waste management (Gray et al., 2016), pollination (Li et al., 2019), decomposition (Eycott et al., 2019), and pest control (Nurdiansyah et al., 2016); and affect other animals as both prey and predators (Barnes et al., 2014). We aimed to: 1) Quantify differences in environmental conditions and biodiversity between buffers and surrounding non-buffer areas (i.e. areas that were 25 m and 125 m from buffers), and determine whether differences were consistent across the oil palm commercial life cycle; 2) Evaluate whether buffers affected environmental conditions and levels of biodiversity in adjacent non-buffer areas (i.e. areas that were 25 m from buffers) across the oil palm commercial life cycle; 3) Assess whether buffers became more environmentally complex and biodiverse over time.

### **3.3 Methods**

#### **3.3.1 | Study design**

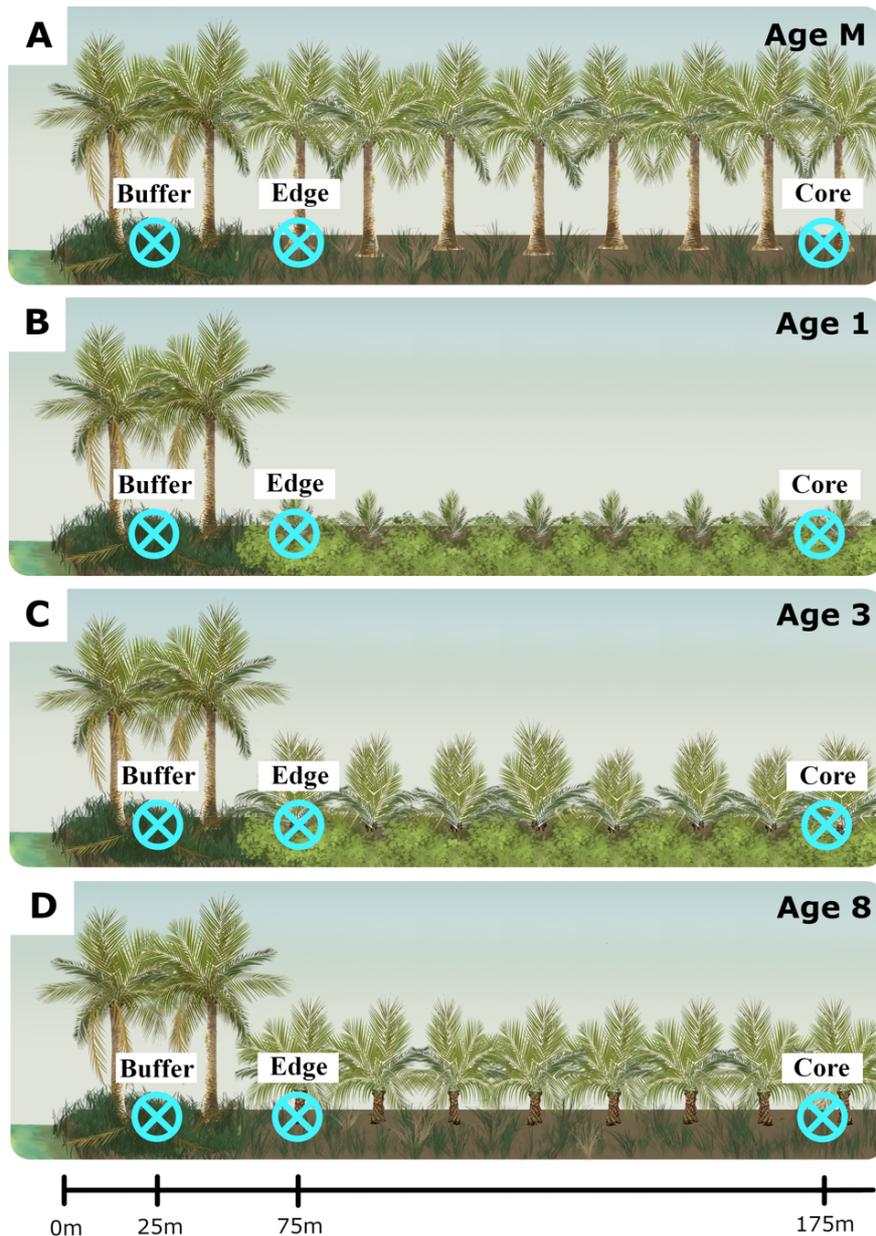
Data were collected in industrial oil palm plantations in Riau, Sumatra, Indonesia (N0 55.559, E101 11.619) as part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme (Luke, Advento, Aryawan, et al., 2020) (see Figure 2.1 in Chapter 2 for the location of the BEFTA Programme). The plantations are owned and managed by PT Ivo Mas Tunggal (a subsidiary of Golden Agri Resources (GAR)), and run with technical input from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI). The area is divided into seven estates, which are managed semi-independently. The natural habitat in the region is lowland rainforest, but oil palm plantation is now the dominant land use type (Ramdani & Hino, 2013). Mean annual temperature and rainfall at SMARTRI is 26.8 °C and 2350 mm, respectively, with the rainy season occurring between October and April (Tao et al., 2016).

SMARTRI is managed in accordance with guidelines from three independent certification bodies: the Roundtable on Sustainable Palm Oil (RSPO; <http://rspo.org>), Indonesian Sustainable Palm Oil (ISPO; <http://ispo-org.or.id>), and International Sustainability and Carbon Certification (ISCC; <http://iscc-system.org>). SMARTRI plantations were chartered before recommendations and laws were in place that required retaining forested buffers during plantation establishment, and therefore all buffer areas in SMARTRI are currently made of mature oil palms. These mature palm buffers occupy ~ 200 hectares of land (although we did not consider topography when we calculated this estimate), which corresponds to 1.36% of all area in SMARTRI plantations. Following guidelines, buffers are 50 m wide and managed less intensely than surrounding cultivated areas (i.e. they are treated with no herbicides, pesticides, or fertilisers). Therefore, buffers are managed according to a passive restoration strategy – an approach to restoration that allows ecosystems to recover on their own or with little human intervention (Ghazoul & Chazdon, 2017) – and with no enrichment planting, although bamboo is sometimes planted along riverbanks to reduce erosion. As in cultivated areas, palms within buffers are harvested by hand using scythe-like tools (“egreks”). Buffers are maintained when old plantations are replanted, creating remnant strips of mature palms in a landscape of young palms (Figure S3.1). SMARTRI began replanting first-generation palms in 2010 following recommended replanting strategies, which represent how replanting is likely to occur, or has already occurred, across most industrial estates in Southeast Asia (Pashkevich et al., 2021). Over time, this has resulted in a chronosequence of differently aged areas of oil palm (hereafter, “*Cohorts*”), which contain mature palm buffers. We previously demonstrated that these cohorts differ from each other environmentally – in their vegetation composition, canopy openness, and soil temperature – and in terms of their management, including application of herbicides, pesticides, and fertilisers (Pashkevich et al., 2021).

To understand the impacts of mature palm buffers on oil palm systems across the crop commercial life cycle, we assessed differences in environmental conditions and biodiversity between buffers and surrounding cultivated areas across four cohorts in a space-for-time study design. Cohorts were: First-generation mature oil palms that were nearing the end of their commercial life cycle (aged 31 – 33; “*Age M*”), and second-generation replanted oil palms aged one, three, and eight years (“*Age 1*”, “*Age 3*”, “*Age 8*”; Figure 3.1). We established four study sites (hereafter, “*Sites*”) in each cohort. Every site was located near a river with a neighbouring mature palm buffer (i.e. no sites were located on rivers without buffers). We split sites within a cohort across two estates to account for differences in local management (see

Pashkevich et al. (2021) for details on differences in estate management across the sites). However, spatial constraints allowed only three *Age 8* sites within one estate, resulting in 15 sites in total (see Figure 2.1 in Chapter 2 for a map of the study sites). Also due to spatial constraints, two *Age 1* sites were located within 100 m of each other, and two *Age 8* sites were 135 m apart. All other sites were at least 300 m apart.

We established three 100 m-long transects within each site that followed the course of the adjacent river (Figure 3.1). Transects were located at three distances from the river edge (hereafter, “*Distance*”): within riparian buffers (“*Buffer*”; 25 m from riverbanks), just outside buffers within the surrounding cultivated area (“*Edge*”; 75 m from riverbanks and 25 m from buffers; and receiving typical levels of management), and far from buffers in the core of the plantation landscape (“*Core*”; 175 m from riverbanks and 125 m from buffers; and receiving typical levels of management). Hereafter, we collectively refer to *Edge* and *Core* as non-buffer areas. We included *Edge* as a sampling area to assess whether buffers affected environmental conditions and arthropod biodiversity in non-buffer areas immediately adjacent to mature palm buffers. We inferred that buffers affected *Edge* if, in comparison to *Core*, environmental conditions and arthropod biodiversity in *Edge* were more similar to those in *Buffer*. We assumed no influence of mature palm buffers on *Core* areas, as a previous study indicated that 125 m from buffers was an appropriate distance at which any impacts of buffers would no longer be detected (Gray et al., 2016).



**Figure 3.1.** Schematic of the experimental design (Riau, Sumatra, Indonesia). We established study sites across four oil palm age cohorts: *Age M* (A), *Age 1* (B), *Age 3* (C), *Age 8* (D). All study sites were located near rivers and neighbouring mature oil palm riparian buffers. We established a triplet of 100 m long transects within each site that followed the course of the adjacent river and along which data collection occurred. Transects were located at three distances from rivers: within riparian buffers (*Buffer*), just outside buffers within adjacent oil palm crop (*Edge*), and far from riparian buffers within oil palm crop (*Core*). All *Buffer* areas were composed of mature first-generation oil palms and were managed less intensely than the surrounding non-buffer area.

### 3.3.2 | Data collection

#### 3.3.2.1 | Environmental conditions

All fieldwork occurred between February – May 2018. Mean weekly rainfall ( $\pm 1$  standard error) during the study period was  $25.9 \pm 2.3$  mm (collected from nine rainfall gauges across SMARTRI).

Within each of the *Buffer*, *Edge*, and *Core* transects we measured canopy openness, vegetation height, and ground cover at 10 m intervals. This corresponded to 11 data points per transect. We recorded canopy openness using a spherical densiometer (Lemmon, 1956). We alternated pointing the densiometer to the left and right of each transect as we measured. We recorded vegetation height using a drop disc (30 cm diameter and 231 g, dropped from 170 cm above the ground). Where the drop disc fell, we categorised the type(s) of ground cover touching the disc as: fallen palm frond, herbaceous plant, fern, bare ground, or water-filled ditch. Openness, vegetation height, and ground cover data from two sites (one each in *Age M* and *Age 1*) could not be collected so, in order to retain statistical power, we included data from a comparable *Age M* site that were collected during the same study period (data from an additional *Age 1* site were not available). Canopy openness, vegetation height, and ground cover data were therefore recorded at 14 sites in total. We used iButton dataloggers (DS1922L-F5 thermochrons set at high capacity and programmed to record at three-hourly intervals) to record soil temperatures at *Buffer* and *Core* transects. We did not sample in *Edge* owing to limited availability of dataloggers, and because canopy openness data suggested that soil temperatures between *Edge* and *Core* would not differ. We buried one datalogger at 5 cm depth at the start of each transect, retrieving both dataloggers at a site after 24 hours. Each datalogger recorded 8 temporal data points. Soil temperature data from two *Age M* sites could not be collected, and three dataloggers overheated in the field (two in *Age 1* and one in *Age 3*). To retain statistical power, we included soil temperature data from a comparable *Age M* site that were collected during the same study period (data from additional *Age 1* and *Age 3* sites were not available), and therefore soil temperature was recorded at 11 sites in total.

#### 3.3.2.2 | Order-level arthropod sampling

We collected arthropods along *Buffer*, *Edge*, and *Core* transects at all sites in canopy, understory, and ground microhabitats. We collected canopy arthropods by fogging one palm at the start of each transect (Pulsfog K-10-SP Portable Thermal Fogger filled with 4.950 L diesel and 50 ml lambda-cyhalothrin insecticide). We fogged for 60 seconds after the canopy was

completely covered with insecticide, and then waited two hours before collecting arthropods from six trays that were systematically suspended  $\sim 1$  m above the ground under each palm (the total tray area under each sampled palm was  $4.74 \text{ m}^2$ ). We kept fogging methods consistent across cohorts so that samples were comparable, and to ensure that a consistent area of vertical space was sampled for each palm (for more details of the fogging protocol see Pashkevich et al. (2021)). To collect understory arthropods, we suspended sticky traps (each brown in colour, sticky on both sides, and having a total sticky area of  $513 \text{ cm}^2$ )  $\sim 1.5$  m above the ground at the start, middle, and end of each transect. To sample ground arthropods, we placed a single pitfall trap (19.5 cm diameter at mouth, filled with 70% ethanol, and covered with a plastic sheet to shield from rainfall) adjacent to each sticky trap. We set all sticky traps and pitfall traps at a *Site* on the same day, and collected them after 72 hours.

In the lab, we used dissecting microscopes to separate and identify arthropods to order-level. However, to be consistent with comparable studies (Ashton-Butt et al., 2019; Pashkevich et al., 2021) and due to their distinctive ecology, we identified the following to groups of their own: Chilopoda (class), Diplopoda (class), Formicidae (family) and Isoptera (infraorder). Endopterygote larvae were also placed in their own group. We hereafter refer to all groups as orders, for brevity.

### **3.3.2.3 | Species-level spider sampling**

We also conducted focussed surveys of spiders along *Buffer*, *Edge*, and *Core* transects at all sites in canopy, understory, and ground microhabitats. We sampled canopy and ground spiders by separating them from other arthropods in fogging and pitfall samples. As sticky traps often damaged understory spiders and did not collect a high number of individuals, we collected understory spiders by walking the length of each transect and hand-collecting all spiders within 1 m of the observer. We walked all transects at a *Site* on the same day and sampled between 07:00 and 14:00 in dry conditions.

In the lab, we separated juvenile spiders from adults (dissecting when necessary to differentiate haplogyne adult females and juveniles), and used morphological traits and the relevant keys (<http://ecotaxonomy.org/ecokeys>; Deeleman-Reinhold, 2001; Jocqué and Dippenaar-Schoeman, 2006) to identify adults to family and morphospecies (hereafter, “species”). Since it was not possible to match males and females for all species, we counted each unique male

and female as its own morphospecies. All arthropods are preserved in 75% ethanol at SMARTRI research station (Siak Regency, Riau, Indonesia).

### 3.3.3 | Statistical analyses

We conducted all analyses in R version 3.5.1 (R Core Team, 2018) using R Studio version 1.1.456 (R Studio Team, 2018). We used *readxl* (Wickham et al., 2019), *tidyverse* (Wickham, 2017), *zoo* (Zeileis et al., 2019), *data.table* (Dowle et al., 2019), *lattice* (Sarkar, 2018), and *plyr* (Wickham, 2016) for data wrangling and exploration, following the data exploration procedure outlined by Zuur, Ieno, & Elphick (2010). Visualising our results required packages *gridExtra* (Auguie & Antonov, 2017), *cowplot* (Wilke, 2019), and *lemon* (Edwards et al., 2019). We analysed our data using the following techniques (additional details on individual models are described below):

**Bayesian regression models (hereafter, GLMMs).** We fitted GLMMs using *brms* (Bürkner & Gabry, 2020) and the No-U-Turn sampler (NUTS) algorithm in Stan (Carpenter et al., 2017). We fitted five candidate models for each response: a parent model (*Cohort\*Distance*), and four derivative models (*Cohort + Distance*, a *Cohort*-only model, a *Distance*-only model, and a null model). Unless otherwise stated, we included *Site* as a random intercept effect in all models, to account for site-specific differences in environmental conditions and timing of sampling in our modelling, and to account for potential spatial autocorrelation. After generating and validating each set of models (see Supplementary Text 1 for full details of model fit and validation), we calculated their exact leave-one-out cross-validation information criterion (LOOIC) and selected the model with the lowest LOOIC as the optimal model, unless the standard errors of the difference in expected log pointwise predictive density (ELPD) of other models exceeded the difference in ELPD between these models and the model with the lowest LOOIC (Gabry et al., 2019). In this case, we chose the simplest model. We calculated a Bayesian version of R-squared for each optimal model in order to approximate the percent variance in the response that each model explained. If the null model was not the optimal model, we used *emmeans* (Lenth et al., 2020) to conduct post-hoc analyses by computing estimated marginal means for each factor level and comparing these in a pairwise fashion. We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero.

**Bayesian generalised linear latent variable model (hereafter, GLLVM).** We fitted a pure (i.e. no covariates included) GLLVM using *boral* (Hui & Blanchard, 2020) (see Supplementary Text 1). We included *Site* as a random row effect, in order to account for site-specific differences in environmental conditions in our modelling and to account for potential spatial autocorrelation, and two latent variables (LVs). We plotted a two-dimensional ordination from the posterior medians of the LVs in order to visualise the results of our analysis. To aid visualisation, we drew polygons around each *Cohort\*Distance* combination of points (e.g. *Age I-Buffer*). To determine factor levels that were meaningfully different, we compared the spatial positions of polygons in a pairwise fashion. We concluded that meaningful differences existed when polygons did not overlap.

**Multivariate generalised linear models (hereafter, mGLMs).** We fitted mGLMs using *mvabund* (Wang et al., 2019), with the interaction of *Cohort\*Distance*. After validating models (see Supplementary Text 3.1), we used likelihood ratio tests (LRTs) and bootstrapped probability integral transform (PIT) residuals (using 10000 resampling iterations; Warton et al., 2017) to determine any significant effects of covariates. We included *Site* as a blocking variable when calculating *p*-values, in order to account for site-specific differences in environmental conditions and timing of sampling and to account for potential spatial autocorrelation. We followed a backwards-stepwise model selection procedure to determine whether the interaction of *Cohort\*Distance*, or either covariate independently, was significant ( $p < 0.05$ ). When covariates were significant, we conducted post-hoc analyses to determine factor levels that were significantly different.

### 3.3.3.1 | Impacts of mature palm buffers across cohorts on the environment

We used GLMMs to analyse changes in canopy openness, variation in openness, and vegetation height. We did not include *Site* as a random effect in our canopy openness and variation in openness analyses, as there was no reason to expect that these data would be non-independent, and sensitivity analyses showed that models fitted without *Site* performed equally well. The vast majority (82.5%) of canopy openness values were from mostly open (i.e. > 80% openness) or mostly closed (i.e. <20% openness) areas, resulting in a bimodal distribution. We therefore transformed these data into a binary variable (Open canopy: “1”, or > 50% openness; Closed canopy: “0”, or <50% openness), summed values along each transect, and modelled canopy openness using a binomial distribution. Our models were overdispersed, and so we re-fitted models using beta-binomial distributions (logit links; Parent model: *Canopy openness* ~

*Cohort\*Distance*). We analysed variation in openness by calculating the standard deviation in raw openness data for each transect and modelling these data using a normal distribution (identity links), after applying a logit transformation in order to meet model assumptions (Parent model: *Variation in openness* ~ *Cohort\*Distance*). We analysed mean vegetation height per transect using a Gaussian distribution (identity links), after applying a logit transformation in order to meet model assumptions (Parent model: *Vegetation height* ~ *Cohort\*Distance* + (1 | *Site*)). We used a GLLVM (poisson distribution, log link) to analyse changes in ground cover (Parent model: *Ground cover* ~ *LV1* + *LV2* + (1 | *Site*)). We analysed ground cover using a GLLVM so that we could visualise differences in this multivariate dataset as ordinations. We analysed changes in soil temperature using a GLMM, which included smoothing functions (using cyclic penalized cubic regression splines) fitted to the time of day at which recording occurred (Parent model: *Temperature* ~ *Cohort* + *Distance* + *s(Time, by = interaction(Cohort, Distance) + (1 | Site))*).

### 3.3.3.2 | Impacts of mature palm buffers across cohorts on all arthropods

Whilst conducting fieldwork, three sticky traps (*Age 8-Edge*, *Age 8-Buffer*, *Age M-Buffer*) and one pitfall trap (*Age 8-Edge*) were damaged in the field and removed from analyses. We also eliminated Formicidae from an additional sticky trap sample because a high number (n = 278) of winged ants had emerged from their nest and flown into the trap. When fogging, we lost data from seven sample trays across three palms because they were overturned before collection. We therefore standardised total canopy arthropod abundance data prior to analysis by calculating mean abundance per tray and multiplying by 6 (the number of trays originally set under each palm). To meet model assumptions, we then rounded the standardised data to the nearest integer.

We used GLMMs (negative binomial distributions, log links) to separately analyse changes in total arthropod abundance in the canopy, understory, and ground microhabitats (Parent models: *Abundance* ~ *Cohort\*Distance* + (1 | *Site*)). We included all collected arthropods in our total abundance analyses. We used mGLMs (negative binomial distributions, log links) to separately analyse changes in arthropod order-level community composition in the canopy, understory, and ground microhabitats (Parent models: *Composition* ~ *Cohort\*Distance* + (1 | *Site*)). In these analyses, we excluded endopterygote larvae and individuals that could not be identified to order (together representing about 3% of all collected arthropods). We separately aggregated understory and ground data at the transect level prior to fitting mGLMs. We aggregated these

data because otherwise *mvabund* would not allow us to fit *Site* as a blocking variable in our analyses, and we wanted to account for site-specific differences in environmental conditions and timing of sampling that could have impacted arthropod composition. We aggregated these data in a standardised way by calculating mean abundance per trap, multiplying by 3 (the number of pitfall traps and sticky traps originally set along each transect), and rounding to the nearest integer, in order to meet model assumptions and account for the sticky traps and pitfall trap that were damaged during fieldwork. If the interaction term (i.e. *Cohort\*Distance*) or either covariate was significant in our community composition analyses, we ran univariate analyses to determine how the abundance of individual taxa changed across study areas. Univariate *p*-values were adjusted to correct for multiple testing using a step-down resampling algorithm (Wang et al., 2012). We visualised the results of our community composition analyses using stacked bar charts.

### 3.3.3.3 | Impacts of mature palm buffers across cohorts on spiders

To better understand the spider assemblage within the plantation, and to assess our sampling completeness, we used *iNEXT* (Hsieh et al., 2016) to calculate interpolated and extrapolated species richness within each microhabitat (using the richness estimators derived by Chao et al. (2014)) and plotted these as species accumulation curves. We extrapolated to double the number of observed individuals (Chao et al., 2014; Gotelli & Colwell, 2001). We also assessed species evenness within each microhabitat by plotting rank abundance curves. We included only adult spiders in both analyses.

We used GLMMs to separately analyse changes in spider abundance (negative binomial distributions, log links) and species richness (poisson distributions, log links) in the canopy, understory, and ground microhabitats (Parent models: *Abundance* ~ *Cohort\*Distance*+ (*I* | *Site*); *Richness* ~ *Cohort\*Distance*+ (*I* | *Site*)). We included juveniles and adults in abundance analyses but only adults in species richness analyses. We adjusted canopy abundance and species richness data to account for overturned trays, as previously described. We eliminated juvenile wolf spiders (Lycosidae) from one pitfall sample (*Age M-Core*) prior to analysing ground abundance data, due to an unusually high abundance of juveniles ( $n = 61$ ) that were likely to have been on the abdomen of their mother when she fell into the trap. We assessed changes in spider species-level composition within each microhabitat in two ways, including only adult spiders in these analyses. First, using *betapart* (Baselga et al., 2020), we calculated overall incidence-based beta diversity (Sørensen index) across *Cohort\*Distance* groups within

each microhabitat, partitioning this value into nestedness (i.e. species loss or gain) and turnover (i.e. species replacement) components (Baselga & Orme, 2012). Data from different sites within a *Cohort\*Distance* group (e.g. all sites within *Age 1-Buffer*) were pooled for this analysis. We then used mGLMs (negative binomial distributions, log links) to separately analyse changes in species-level community composition in the canopy, understory, and ground microhabitats (Parent models: *Composition* ~ *Cohort\*Distance* + (*1* | *Site*)). Prior to analysis, and as previously described, we aggregated ground spider data at the transect level so that *Site* could be fitted as a blocking variable. We did not aggregate canopy or understory spider data, since these were collected at the transect level. Our spider community composition analyses otherwise were unchanged from our arthropod community composition analyses.

### 3.4 Results

#### 3.4.1 | Impacts of mature palm buffers across cohorts on the environment

All environmental conditions differed between buffer and non-buffer areas, but the magnitude of these differences changed across cohorts. The model that included an interaction between *Cohort* and *Distance* best explained differences in canopy openness ( $R^2 = 90.9 \pm 2.1\%$ ; Table 3.1) and variation in openness ( $R^2 = 67.1 \pm 5.8\%$ ; Table 3.1). Post-hoc analyses from the canopy openness model showed that openness differed between buffer and non-buffer areas in *Ages 1* and *3*, with openness per transect in *Age 1-Edge* and *Age 1-Core* being more than 400% higher than in *Age 1-Buffer*, and openness per transect in *Age 3-Edge* and *Age 3-Core* being more than 180% higher than in *Age 3-Buffer* (Figure 3.2A; Table S3.1). Post-hoc analyses from the variation in openness model showed that variation differed between buffer and non-buffer areas in *Age 1*, with variation per transect in *Age 1-Buffer* being more than 570% higher than in *Age 1-Edge* and *Age 1-Core* (Figure 3.2B; Table S3.2).

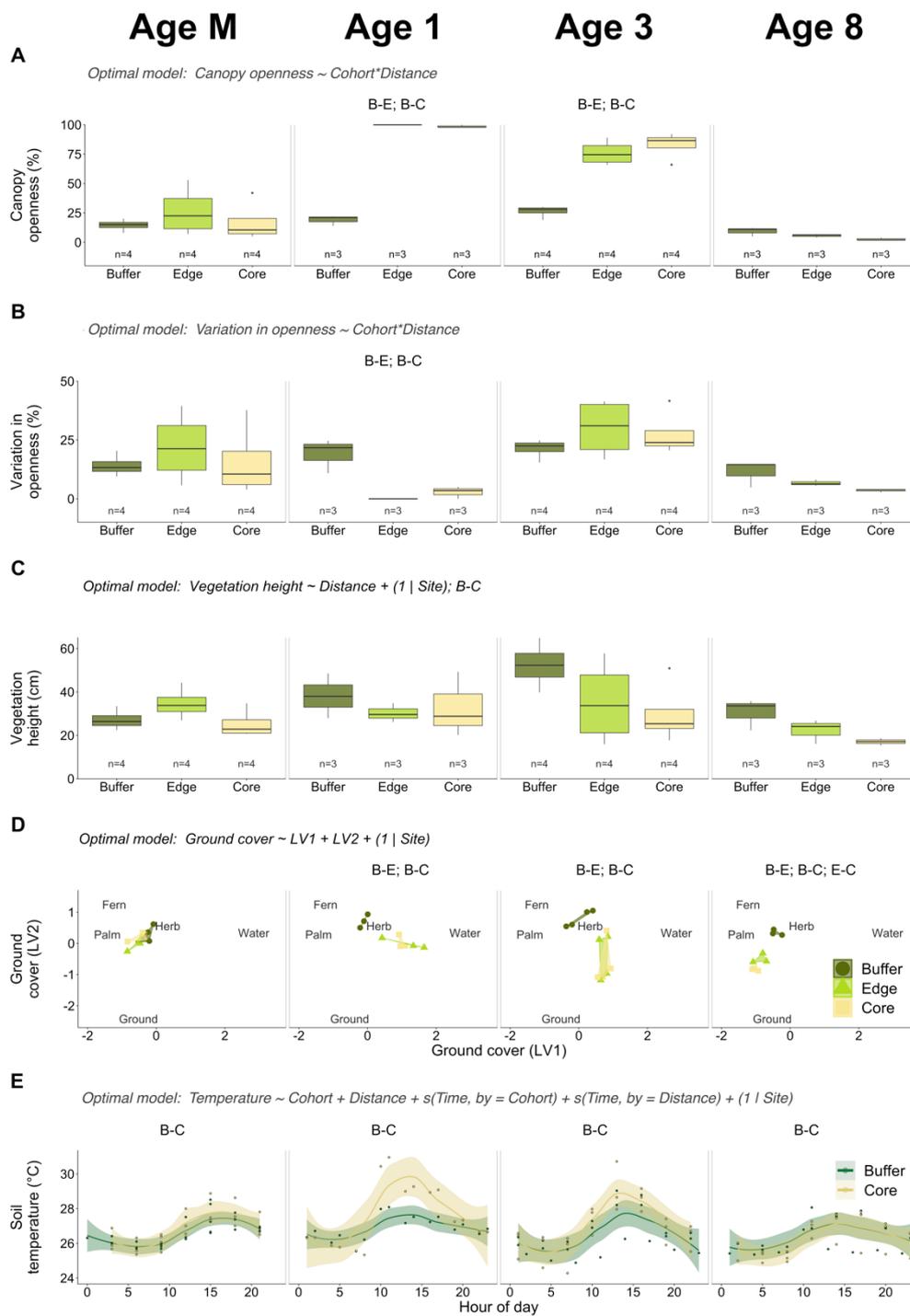
The *Distance*-only model best explained differences in vegetation height, indicating that vegetation height differed between buffer and non-buffer areas independently of cohort ( $R^2 = 39.8 \pm 12.8\%$ ; Table 3.1). Post-hoc analyses showed that vegetation height differed between *Buffer* and *Core*, with vegetation in *Buffer* being 11% higher than in *Core* (Figure 3.2C; Table S3.3). Ground cover was different between buffer and non-buffer areas in *Ages 1*, *3*, and *8*. This was indicated by the spatial separation of polygons in these cohorts in the ordination generated from our GLLVM. In *Ages 1* and *3*, *Buffer* was consistently dominated by ferns (mostly *Nephrolepis biserrata*, *Asplenium longissimum*, and *Dicranopteris linearis*), which

represented ~ 50% of all vegetation type occurrences. However, in *Edge* and *Core*, herbaceous plants (mostly the leguminous cover crop) represented ~ 70–95% of all vegetation type occurrences. *Age 8-Edge* and *Age 8-Core* differed from *Age 8-Buffer*, and from each other, owing to higher occurrences of bare ground (Figure 3.2D).

The additive model best explained changes in soil temperature ( $R^2 = 74.1 \pm 2.2\%$ ; Table 3.1). This indicated that soil temperature exhibited consistent trends between *Buffer* and *Core* in all cohorts. Post-hoc analyses showed that soil temperatures in *Core* were consistently hotter than in *Buffer*. This was most pronounced in *Age 1*, where soil temperatures in *Age 1-Core* were ~ 2 °C hotter at midday than in *Age 1-Buffer* (Figure 3.2E; Table S3.4).

**Table 3.1.** Effects of *Cohort* and *Distance* on environmental conditions (canopy openness, variation in openness, vegetation height, ground cover, and soil temperature) and arthropod biodiversity (total arthropod abundance, arthropod order-level community composition, and spider abundance, species richness, and species-level community composition) in the canopy, understory, and ground microhabitats. For each model, we present its Bayesian R<sup>2</sup> value and associated standard error. No R<sup>2</sup> values are given for our ground cover and community composition analyses, as this is not a feature supported by the packages that facilitated these analyses.

<b>Response</b>	<b>Optimal model</b>	<b>Bayesian R<sup>2</sup> ± Est. Err.</b>
<i>Environmental conditions</i>		
Canopy openness	~ Cohort*Distance	90.9 ± 2.1%
Variation in openness	~ Cohort*Distance	67.1 ± 5.8%
Vegetation height	~ Distance + (1   Site)	39.8 ± 12.8%
Ground cover	~ 1 + LV1 + LV2 + (1   Site)	-
Soil temperature	~ Cohort*Distance + s(Time, by = Cohort) + s(Time, by = Distance) + (1   Site)	74.1 ± 2.2%
<i>All arthropods abundance</i>		
Canopy	~ 1 + (1   Site)	40.8 ± 10.1%
Understory	~ Cohort*Distance + (1   Site)	51.0 ± 4.6%
Ground	~ 1 + (1   Site)	34.9 ± 10.9%
<i>All arthropods composition</i>		
Canopy	~ 1 + (1   Site)	-
Understory	~ Cohort + (1   Site)	-
Ground	~ Cohort + (1   Site)	-
<i>Spider abundance</i>		
Canopy	~ 1 + (1   Site)	31.4 ± 14.8%
Understory	~ Cohort*Distance + (1   Site)	71.4 ± 4.9%
Ground	~ 1 + (1   Site)	23.6 ± 7.7%
<i>Spider species richness</i>		
Canopy	~ 1 + (1   Site)	51.3 ± 7.8%
Understory	~ Cohort + (1   Site)	48.1 ± 9.7%
Ground	~ 1 + (1   Site)	26.2 ± 6.0%
<i>Spider composition</i>		
Canopy	~ Cohort*Distance + (1   Site)	-
Understory	~ Cohort*Distance + (1   Site)	-
Ground	~ Cohort*Distance + (1   Site)	-



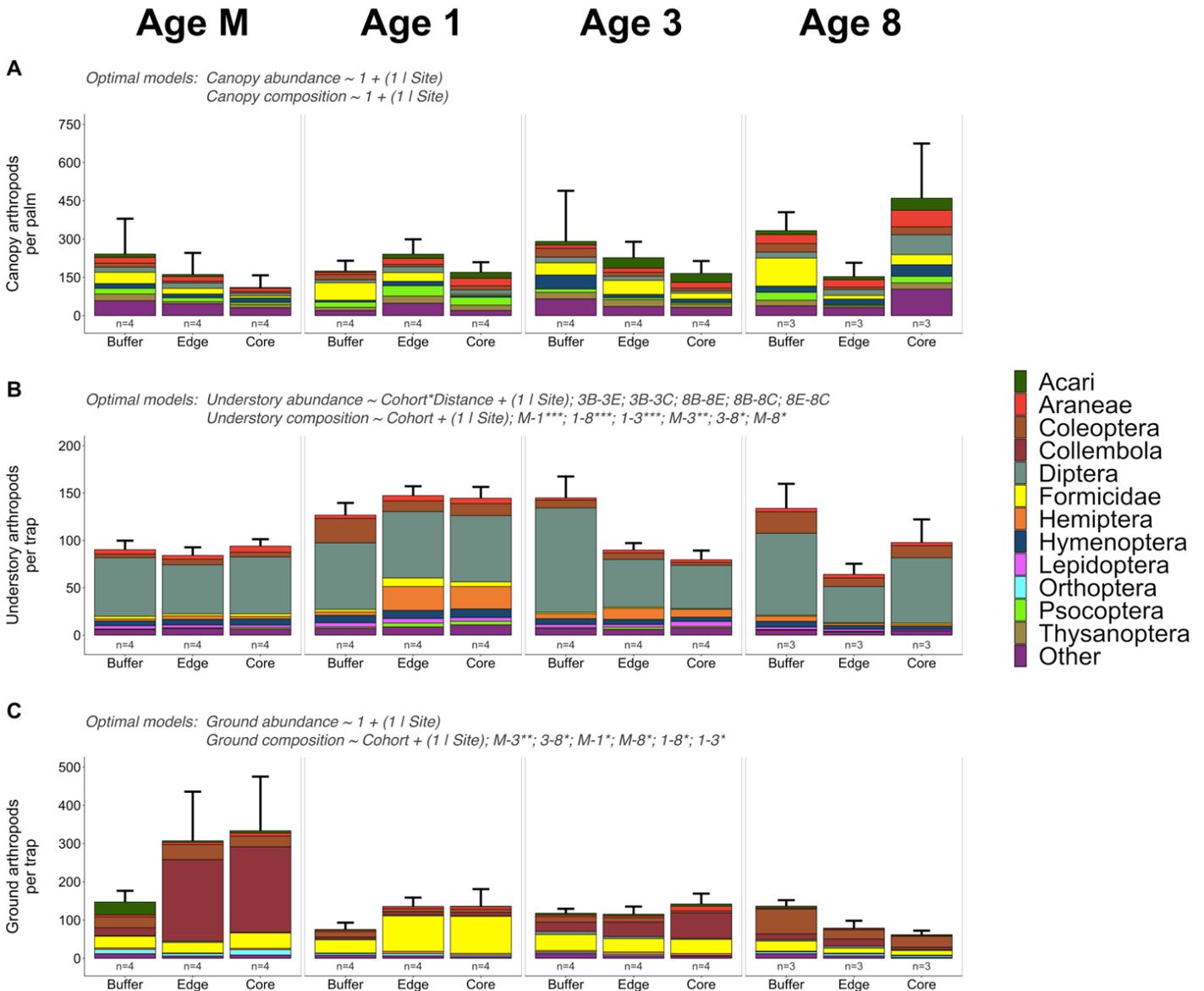
**Figure 3.2.** Differences in canopy openness (A), variation in openness (B), vegetation height (C), ground cover (D), and soil temperature (E) across cohorts (*Age M*, *Age 1*, *Age 3*, *Age 8*) and distances to riparian buffers (*Buffer*, *Edge*, *Core*). Posterior distributions from all GLMMs tracked to their underlying datasets. We indicate the optimal model (determined using LOOIC) in text above each subplot. The optimal model for D was not determined using LOOIC, as we

did not follow a model selection procedure for our ground cover analyses. In A, B, D, and E, differences between *Buffer* (B), *Edge* (E), and *Core* (C) within each cohort (as determined by our post-hoc analyses) are indicated in text above each facet. In C, differences between *Buffer*, *Edge*, and *Core* across cohorts (as determined by our post-hoc analyses) are provided after the optimal model, since the optimal model included only *Distance*. See supplementary materials (Tables S3.1-4) for a full list of post-hoc comparisons between *Buffer*, *Edge* and *Core* areas across cohorts. In A, B, and C, boxplots display the median and interquartile ranges of the data, and lettering below boxplots indicates the number of independent replicates per *Cohort\*Distance* (e.g. *Age 1-Buffer*). In D, points indicate the posterior medians of the latent variables from the pure GLLVM that we fitted to analyse ground cover data (Fern = ferns; Herb = herbaceous plants; Palm = dead and fallen palm fronds; Ground = bare ground; Water = water-filled ditch). Polygons are drawn around outlying points from the same *Cohort\*Distance* combination, in order to aid visualisation. In E, lines are visualisations of differences in soil temperature (generated using loess smoothers in *ggplot*; Wickham et al., 2020), shaded regions around lines indicate 95% credible intervals, and black circles indicate raw data points. Soil temperatures were only recorded in *Buffer* and *Core*.

### 3.4.2 | Impacts of mature palm buffers across cohorts on all arthropods

In our order-level sampling (canopy fogging, sticky traps, and pitfall traps), we collected 44,984 arthropods that were identified to 26 orders or other taxonomic groups. These included 9,970 arthropods from the canopy (after correcting for overturned fogging trays), 14,473 arthropods from the understory, and 20,541 arthropods from the ground. Total arthropod abundance in the canopy and on the ground differed little between buffer and non-buffer areas across cohorts, with the null model being the optimal model for both ( $R^2 = 40.8 \pm 10.1\%$  in the canopy;  $R^2 = 34.9 \pm 10.9\%$  on the ground) (Figure 3.3A; Figure 3.3C; Table 3.1). In the understory, the interaction model best explained differences in total arthropod abundance ( $R^2 = 51.0 \pm 4.6\%$ ; Table 3.1). Post-hoc analyses showed that total understory arthropod abundance differed between buffer and non-buffer areas in *Ages 3* and *8*, with arthropods per trap in *Age 3-Buffer* being 61% and 81% more abundant than in *Age 3-Edge* and *Age 3-Core*, respectively, and arthropods per trap in *Age 8-Buffer* being 108% and 36% more abundant than in *Age 8-Edge* and *Age 8-Core*, respectively (Figure 3.3B; Table S3.5).

Different arthropod orders were dominant within each microhabitat. Formicidae ( $n = 1,717$ ), Araneae ( $n = 1,056$ ), and Diptera ( $n = 976$ ) were numerically dominant in the canopy; Diptera ( $n = 8,865$ ), Coleoptera ( $n = 1,384$ ), and Hemiptera ( $n = 1,132$ ) were dominant in the understory (after aggregating data at the per-transect level); and Collembola ( $n = 7,677$ ), Formicidae ( $n = 5,751$ ), and Coleoptera ( $n = 2,932$ ) were dominant on the ground (after aggregating data at the per-transect level). Arthropod order-level composition in the canopy did not differ across buffer and non-buffer areas or across cohorts, as no model terms were significant ( $p > 0.05$ ; Figure 3.3A; Table 3.1). The optimal model for order-level composition of understory arthropods included only cohort (Cohort: LRT = 224.0,  $p < 0.001$ ; Figure 3.3B; Table 3.1), indicating that order-level composition differed significantly across cohorts in the chronosequence but did not differ significantly between buffer and non-buffer areas. Post-hoc analyses indicated that all cohorts differed significantly in order-level composition from each other ( $p < 0.05$ ; Table S3.6), and univariate analyses showed that these trends were driven by changed abundances of Blattodea (LRT = 24.185,  $p = 0.016$ ), Coleoptera (LRT = 22.685,  $p = 0.022$ ), Formicidae (LRT = 22.852,  $p = 0.022$ ), Hemiptera (LRT = 31.013,  $p = 0.004$ ), Lepidoptera (LRT = 15.632,  $p = 0.039$ ), and Psocoptera (LRT = 30.112,  $p = 0.005$ ). A similar trend was found on the ground, as the optimal model for order-level composition of ground arthropods included only cohort (Cohort: LRT = 228.1,  $p = 0.008$ ; Figure 3.3C; Table 3.1). Post-hoc analyses indicated that all cohorts differed significantly in order-level composition from each other ( $p < 0.05$ ; Table S3.7), and univariate analyses indicated that these trends were driven by different abundances of Acari (LRT = 27.704,  $p = 0.027$ ), Coleoptera (LRT = 33.463,  $p = 0.010$ ), Collembola (LRT = 25.463,  $p = 0.042$ ), Formicidae (LRT = 22.686,  $p = 0.042$ ), and Orthoptera (LRT = 24.278,  $p = 0.042$ ).



**Figure 3.3.** Differences in total arthropod abundance and arthropod order-level community composition in the canopy (A), understory (B), and ground (C) microhabitats across cohorts (*Age M*, *Age 1*, *Age 3*, *Age 8*) and distances to riparian buffers (*Buffer*, *Edge*, *Core*). Posterior distributions from all GLMMs tracked to their underlying datasets. We indicate the optimal model for total abundance (determined using LOOIC) and order-level composition (determined using backwards stepwise selection) in text above each subplot. If the null model was not the optimal model, we list factor levels within each cohort between which significant differences occurred (as determined by our post-hoc analyses): *Age M* (*M*), *Age 1* (*1*), *Age 3* (*3*) *Age 8* (*8*), *Buffer* (*B*), *Edge* (*E*), and *Core* (*C*). For order-level community composition analyses, we also list the magnitude of significance for post-hoc comparisons: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ . See supplementary materials (Tables S3.5-7) for a full list of post-hoc comparisons

between *Buffer*, *Edge* and *Core* areas across cohorts. Arthropods are plotted as they are sequenced in the legend. Error bars indicate one standard error from the mean. Lettering below stacked bars indicates the number of independent replicates per *Cohort\*Distance* (e.g. *Age 1-Buffer*). Data for (B) and (C) are plotted at the trap-level, but note that data were aggregated at the transect-level for order-level community composition analyses.

### 3.4.3 | Impacts of mature palm buffers across cohorts on spiders

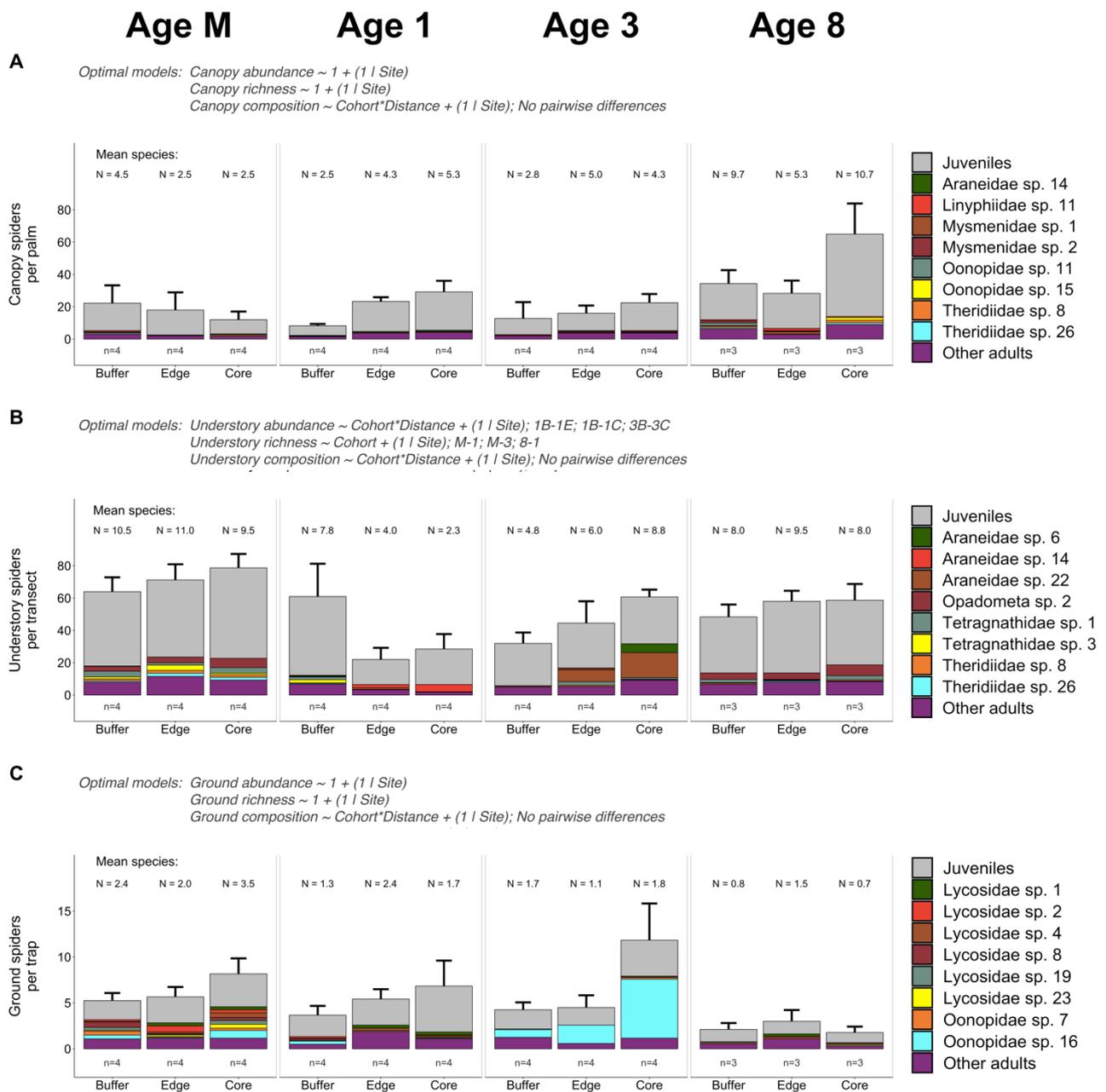
We collected 4,112 spiders that were identified to 22 families and 219 species. These included 1,040 spiders from the canopy ( $n_{\text{adults}} = 245$ ;  $n_{\text{species}} = 98$ ), 2,346 spiders within the understory ( $n_{\text{adults}} = 713$ ;  $n_{\text{species}} = 80$ ), and 726 spiders on the ground ( $n_{\text{adults}} = 374$ ;  $n_{\text{species}} = 73$ ) (Table S3.8). Species accumulation curves in all microhabitats were starting to asymptote, indicating that we had sampled a high proportion of all species within each microhabitat (an estimated 56.2% of species in the canopy, 67.1% of species in the understory, and 70.9% of species on the ground; Figure S3.2). Rank abundance curves indicated that species evenness in all microhabitats was low, with a few numerically dominant species representing the majority of individuals within each microhabitat. Species evenness was lowest on the ground (one species of Oonopidae represented 35.3% of all adult individuals) and highest in the canopy (no single species represented more than 7% of all adult individuals) (Figure S3.2).

Spider abundance in the canopy and on the ground did not differ between buffer and non-buffer areas, with the null model being the optimal model for both ( $R^2 = 31.4 \pm 14.8\%$  in the canopy;  $R^2 = 23.6 \pm 7.7\%$  on the ground) (Figure 3.4A; Figure 3.4C; Table 3.1). In the understory, the interaction model best explained differences in spider abundance ( $R^2 = 71.4 \pm 4.9\%$ ; Table 3.1). Post-hoc analyses showed that understory spider abundance differed between buffer and non-buffer areas in *Ages 1* and *3*. Spider abundance per transect in *Age 1-Buffer* was 177% higher than in *Age 1-Edge* and 114% higher than in *Age 1-Core*, and spider abundance per transect in *Age 3-Core* was 90% higher than in *Age 3-Buffer* (Figure 3.4B; Table S3.9).

Spider species richness in the canopy and on the ground did not differ between buffer and non-buffer areas, with the null model being the optimal model for both ( $R^2 = 51.3 \pm 7.8\%$  in the canopy;  $R^2 = 26.2 \pm 6.0\%$  on the ground) (Figure 3.4A; Figure 3.4C; Table 3.1). In the understory, the *Cohort*-only model best explained differences in spider species richness ( $R^2 = 48.1 \pm 9.7\%$ ; Table 3.1). Post-hoc analyses showed that understory spider species richness

differed between *Age M* and *Ages 1* and *3*, and *Age 1* and *Age 8*. Species richness per transect in *Age M* was 120% higher than in *Age 1* and 58% higher than in *Age 3*, and species richness per transect in *Age 8* was 78% higher than in *Age 1* (Figure 3.4B; Table S3.10).

Different spider species were dominant within each microhabitat. A theridiid (*Theridiidae sp. 8*,  $n = 16$ ), mysmenid (*Mysmenidae sp. 2*,  $n = 15$ ), and linyphiid species (*Linyphiidae sp. 11*,  $n = 14$ ) were numerically dominant in the canopy; an araneid (*Araneidae sp. 22*,  $n = 96$ ), and two species of tetragnathid (*Opadometa sp. 2*,  $n = 95$ ; *Tetragnathidae sp. 1*,  $n = 70$ ) were numerically dominant in the understory, and an oonopid (*Oonopidae sp. 16*,  $n = 132$ ) and three lycosid species (*Lycosidae sp. 1*,  $n = 18$ ; *Lycosidae sp. 2* and *Lycosidae sp. 6*, each  $n = 17$ ) were numerically dominant on the ground (after aggregating data at the per-transect level). Total dissimilarity across *Cohort\*Distance* groups (e.g. *Age 1-Buffer*) in all microhabitats was relatively high (Sørensen index = 91.2% in the canopy, 85.5% in the understory, and 88.6% on the ground). In all microhabitats, the turnover (i.e. species replacement) component was higher than the nestedness (i.e. species loss or gain) component. Turnover was 88.7% in the canopy, 80.0% in the understory, and 84.6% on the ground, whilst nestedness was < 6% in all microhabitats. This indicates that the relatively high dissimilarity within each microhabitat was due to substitution of species rather than species loss or gain across *Cohort\*Distance* groups. Spider species-level composition differed between buffer and non-buffer areas in multiple cohorts, as the optimal model for canopy (Interaction term: LRT = 70.3,  $p = 0.002$ ; Table S3.11), understory (Interaction term: LRT = 166.4,  $p < 0.001$ ; Table S3.12), and ground (Interaction term: LRT = 79.5,  $p = 0.002$ ; Table S3.13) spider species-level composition included the interaction of *Cohort\*Distance* (Table 3.1). Post-hoc analyses indicated that no *Cohort\*Distance* groups differed significantly in morphospecies-level composition from each other ( $p > 0.05$ ). Univariate analyses indicated that overall trends were driven by changed abundances of 6 species (1 araneid, 1 linyphiid, 2 oonopids, and 2 theridiids) in the canopy, 15 species (9 araneids, 5 tetragnathids, and 1 theridiid) in the understory, and 5 species (4 lycosids and 1 oonopid) on the ground ( $p < 0.05$  for all species) (Figure 3.4A-C; Table S3.8).



**Figure 3.4.** Differences in spider abundance, species richness, and species-level community composition in the canopy (A), understory (B), and ground (C) microhabitats across cohorts (*Age M*, *Age 1*, *Age 3*, *Age 8*) and distances to riparian buffers (*Buffer*, *Edge*, *Core*). Posterior distributions from all GLMMs tracked to their underlying datasets. We indicate the optimal model for spider abundance and species richness (determined using LOOIC) and species-level community composition (determined using backwards stepwise selection) in text above each subplot. If the null model was not the optimal model, we list factor levels within each cohort between which differences occurred (as determined by our post-hoc analyses): *Age M* (*M*), *Age 1* (*I*),

*Age 3 (3) Age 8 (8), Buffer (B), Edge (E), and Core (C)*. See supplementary materials (Tables S3.9-13) for a full list of post-hoc comparisons between *Buffer*, *Edge* and *Core* areas across cohorts. Spiders are plotted as they are sequenced in the legend. Error bars indicate one standard error from the mean. Lettering below stacked bars indicates the number of independent replicates per *Cohort\*Distance* (e.g. *Age 1-Buffer*). Data for (C) are plotted at the trap-level, but note that data were aggregated at the transect-level for species-level community composition analyses.

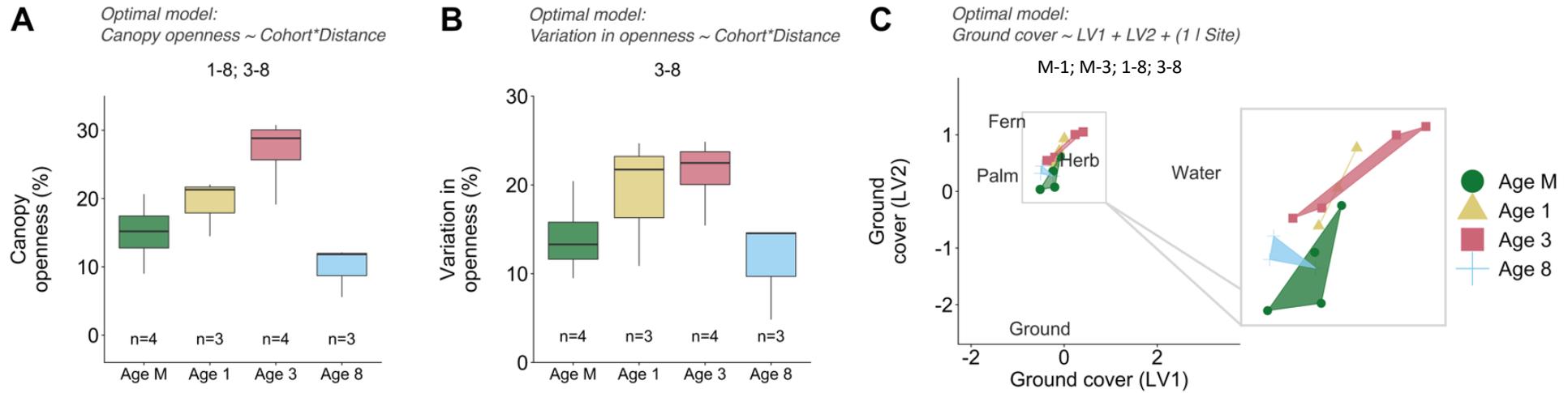
#### **3.4.4 | Impacts of mature palm buffers on adjacent *Edge* areas**

We found some evidence that buffers affected environmental conditions in adjacent non-buffer areas (i.e. *Edge*). The optimal model for vegetation height (i.e. the *Distance*-only model) indicated that vegetation in *Buffer* was taller than that in *Core*, and that vegetation height in *Buffer* and *Edge* was similar (Figure 3.2C). Ground cover in *Age 8-Buffer* and *Age 8-Edge* was more similar than ground cover in *Age 8-Buffer* and *Age 8-Core*. This was indicated by the *Age 8-Buffer* and *Age 8-Edge* polygons generated from our GLLVM being spatially closer than the *Age 8-Buffer* and *Age 8-Core* polygons; however, we note that the difference in spatial proximities was small (Figure 3.2D). We found no evidence that buffers affected levels of arthropod biodiversity in adjacent *Edge* areas, as arthropod abundance and composition in all microhabitats in *Edge* was no more similar to *Buffer* than *Core* arthropod abundance and composition.

#### **3.4.5 | Changes within mature palm buffers over time**

We found changes in canopy openness, variation in openness, and ground cover within mature palm buffers over time, but we did not find changes in other environmental conditions or any aspects of arthropod biodiversity. Post-hoc analyses from the canopy openness optimal model showed that openness in buffers differed between *Age 8* and *Ages 1* and *3*, with openness per transect in *Age 1* and *Age 3* buffers being 96% and 173% higher, respectively, than *Age 8* buffers (Figure 3.5A). Post-hoc analyses from the variation in openness optimal model showed that variation in buffers differed between *Ages 3* and *8*, with variation per transect in *Age 3* buffers being 88% higher than *Age 8* buffers (Figure 3.5B). Our ground cover analysis indicated that there were changes in ground cover within buffers over time. This was visualised by no spatial overlap of *Buffer* polygons between these respective ages (Figure 3.5C). Buffers in *Ages 1* and *3* were different from those in *Ages M* and *8* by having a higher occurrence of

ferns. However, we note that all *Buffer* polygons that were generated from our GLLVM were close in proximity, indicating that between-cohort differences in ground cover within buffers was limited.



**Figure 3.5.** Differences in canopy openness (A), variation in openness (B), and ground cover (C) between *Buffer* areas across cohorts (*Age M*, *Age 1*, *Age 3*, *Age 8*). Posterior distributions from all GLMMs tracked to their underlying datasets. We indicate the optimal model (determined using LOOIC) in text above each subplot. The optimal model for C was not determined using LOOIC, as we did not follow a model selection procedure for our ground cover analyses. Differences between cohorts (as determined by our post-hoc analyses) are indicated in text above each subplot: *Age M* (*M*), *Age 1* (*I*), *Age 3* (*3*) *Age 8* (*8*). In A and B, boxplots display the median and interquartile ranges of the data, and lettering below boxplots indicates the number of independent replicates per *Cohort*. In C, points indicate the posterior medians of the latent variables from the pure GLLVM that we fitted to analyse ground cover data (Fern = ferns; Herb = herbaceous plants; Palm = dead and fallen palm fronds; Ground = bare ground; Water = water-filled ditch). Polygons were drawn around outlying points from the same *Cohort* combination, in order to aid visualisation. We magnify polygons in the pop-out window, in order to better show their spatial orientation.

## 3.5 Discussion

### 3.5.1 | Differences between mature palm buffers and surrounding habitats

This study is the first to investigate the ecology of riparian buffers made of mature oil palms that are being passively restored (“mature palm buffers”)—a widespread, but little studied management strategy used within plantations—across the oil palm commercial life cycle. We found that mature palm buffers can have greater environmental complexity and higher levels of arthropod biodiversity than non-buffer areas (i.e. *Edge* and *Core*), particularly in recently replanted plantations, but these benefits are not consistent across the crop commercial life cycle. To some extent, our findings reflect broadly similar patterns that have been reported on heterogeneity and biodiversity for riparian buffers across various tropical agricultural landscapes (Luke, Slade, et al., 2019) and specifically for forested buffers in oil palm (Gray et al., 2015; Mitchell et al., 2018). However, in contrast to studies on forested buffers, our findings are less consistent and vary with the environmental condition and taxon being measured, suggesting that this management approach is not currently delivering the full range of environmental benefits that can result from buffer areas.

In mature plantations (i.e. *Age M*), we found no differences in environmental conditions and arthropod biodiversity between buffer and non-buffer areas. This suggests that mature palm buffers, managed in a less intensive way than the surrounding plantation (Luke, Advento, Aryawan, et al., 2020), provide limited additional benefits within mature oil palm ecosystems. As the only difference between buffer and non-buffer areas in *Age M* was the level of herbicide, fertiliser, and pesticide application, this suggests that the amount of chemicals applied under normal (non-riparian) management within mature plantations has only limited impacts on the environmental conditions and arthropod community, at least at the scale of this study. In contrast, in young plantations (i.e. *Ages 1* and *3*), which differed from mature palm buffers in terms of structure as well as chemical application, we found instances where environmental conditions and arthropod biodiversity were substantially different between buffer and non-buffer areas.

Mature palm buffers had lower canopy openness, a ground cover more dominated by ferns, and cooler soil temperatures than non-buffer areas in *Ages 1* and *3*. Buffers also had lower variation in openness than non-buffer areas in *Age 1*. These differences in environmental

conditions almost certainly resulted from the recent replanting of non-buffer areas in these cohorts, as replanting of oil palm has previously been shown to change vegetation complexity and microclimate substantially (Pashkevich et al., 2021). In regards to biodiversity, mature palm buffers had more understory arthropods than non-buffer areas in *Ages 3* and *8*, and had more understory spiders than non-buffer areas in *Age 1*. Also, spider species-level community composition in all microhabitats varied between buffer and non-buffer areas across cohorts. However, we also found evidence that buffers could have lower levels of biodiversity than non-buffer areas, as buffers had fewer understory spiders than *Core* areas in *Age 3*. We suggest that these differences in biodiversity are due to differences in environmental conditions between buffer and non-buffer areas in *Ages 1* and *3*. For instance, in *Age 1*, buffers may have had more understory spiders than non-buffer areas, because the canopy in non-buffer areas was almost entirely open and spiders are prone to desiccation (Danks, 2002). Buffers may have had fewer understory spiders than non-buffer areas in *Age 3* due to differences in vegetation complexity. *Age 3* buffers were dominated by a dense understory, primarily consisting of ferns, which contributed to these buffers having the highest vegetation height of any cohort. It is possible that these ferns were so dense that understory spiders—the majority of which were web-weavers in the families Araneidae and Tetragnathidae—were less able to build their webs, therefore reducing their abundance in these areas.

Differences in arthropod biodiversity between buffer and non-buffer areas across the oil palm commercial life cycle could affect functioning, as arthropods facilitate important ecosystem functions within oil palm plantations, including waste management (Gray et al., 2016), pollination (Li et al., 2019), decomposition (Eycott et al., 2019), and pest control (Nurdiansyah et al., 2016). Woodham et al. (2019) previously studied the impacts of mature palm buffers on ecosystem functioning, and found few differences in individual functions or multifunctionality between buffer and non-buffer areas in second-generation oil palm plantations (Woodham et al., 2019). These findings are congruous with ours, since we found inconsistent differences in arthropod biodiversity across the oil palm commercial life cycle, although it is possible that the differences we observed were not marked enough to alter rates of functioning. Our findings therefore indicate that mature palm buffers that are being passively restored have few impacts on functioning in second-generation oil palm plantations.

The differences in arthropod biodiversity that we observed between buffer and non-buffer areas could be indicative of changes in the biodiversity of a wider range of taxonomic groups. We

found that mature palm buffers increased habitat heterogeneity in recently replanted oil palm plantations. Previous studies have shown that maintaining heterogeneity in oil palm landscapes can improve the biodiversity and structural complexity of plants (Luke, Purnomo, et al., 2019), and the abundance or biodiversity of a wide range of invertebrate and vertebrate taxa, including birds (Teuscher et al., 2016; Yahya et al., 2017), bats (Syafiq et al., 2016), soil invertebrates (Ashton-Butt et al., 2018), and leopard cats (Hood et al., 2019). Additionally, as arthropods influence existing trophic networks in oil palm systems (Barnes et al., 2014), and otherwise interact ecologically with non-arthropod groups (for instance, termite mounds are valuable nesting sites for snakes in oil palm plantations; Hood, Pashkevich, et al. (2020)), differences in arthropod biodiversity between buffer and non-buffer areas could affect the biodiversity of non-arthropod biota. Future studies are needed to determine the impacts of mature palm buffers on non-arthropod taxonomic groups, and potential knock-on effects on ecosystem functioning.

### **3.5.2 | Impacts of mature palm buffers on adjacent *Edge* areas**

We found some evidence that mature palm buffers that are being passively restored affect environmental conditions in adjacent non-buffer areas (i.e. *Edge*). For example, vegetation height decreased with distance from mature palm buffers and, in comparison to areas far from buffers (i.e. *Core*), ground cover in *Edge* was more similar to that within buffers in *Age 8*. These impacts on environmental conditions could be attributed to buffers contributing to higher levels of plant biodiversity in *Edge* areas, possibly by acting as sources of seeds or by influencing soil or microclimatic conditions in adjacent areas. However, despite buffers affecting environmental conditions in *Edge*, we found no evidence for mature palm buffers contributing to higher levels of arthropod biodiversity in *Edge* areas. This suggests that the impacts of mature palm buffers on environmental conditions in *Edge* were not sufficient to enhance levels of arthropod biodiversity outside of buffers. These findings are broadly consistent with research on the effects of forested areas within oil palm plantations (Gray et al., 2016; Lucey & Hill, 2012), which found that forested habitat can affect environmental conditions in the adjacent oil palm, but that effects on biodiversity only occur across limited distances (Gray et al., 2016) and are often confined to certain taxonomic groups (Gray et al., 2016; Lucey & Hill, 2012). Similarly, Woodham et al. (2019) found that mature palm buffers do not affect levels of ecosystem functioning in adjacent non-buffer areas of plantation. Taken together, these findings indicate that areas of greater habitat complexity within oil palm plantations have only limited ability to alter the environmental conditions and biodiversity of the surrounding landscape.

### 3.5.3 | Changes in mature palm buffers over time

To our knowledge, this is the first study that has examined whether mature palm buffers that are being passively restored become more environmentally complex and biodiverse over time. We found that canopies within buffers steadily opened and became more variable (from *Age M* to *Age 3*) before becoming more closed and less variable over time (i.e. *Age 8*). Opening of buffer canopies could have been caused by pests or diseases. Outbreaks of pests (such as the rhinoceros beetle, *Oryctes rhinoceros*, and moths in the family Psychidae) and diseases (most notably basal stem rot disease, caused by *Ganoderma* fungi) often occur in oil palm plantations and can result in the defoliation or death of palms, causing the oil palm canopy to become more open (Corley & Tinker, 2016). The lower canopy openness and variation in openness that we observed in buffers in *Age 8* could be attributed to other vegetation, such as epiphytic figs, growing amongst palms and closing the canopy. We also found changes in ground cover within buffers over time, with buffers in *Ages 1* and *3* having a higher occurrence of ferns than buffers in *Ages M* and *8*. However, these changes were only slight, suggesting that ground cover within buffers changed little, and reinforcing our vegetation height and soil temperature findings, which indicated no changes within buffers over time.

Although environmental conditions changed within the passively restoring buffers over time, we observed no concurrent changes in arthropod biodiversity (total arthropod abundance; arthropod order-level composition; spider abundance, species richness, and species-level composition). This could be attributed to the limited changes in ground cover and no change in vegetation height that we observed, since the biodiversity of arthropods, such as spiders, is dependent on variation in vegetation complexity (Greenstone, 1984; Stenchly et al., 2011). However, it should be noted that the oldest mature palm buffers that we sampled were in 8-year-old second generation plantations (i.e. *Age 8*). It is likely that older mature palm buffers exist in other plantations in Southeast Asia, and it is possible that habitat complexity and arthropod biodiversity could improve or decline within these older buffers over time.

## 3.6 Conclusions and management implications

In this study, we asked whether 1) environmental conditions and levels of arthropod biodiversity differ between mature oil palm riparian buffers that are being passively restored and surrounding areas of plantation; 2) mature oil palm riparian buffers affect environmental

conditions and biodiversity in adjacent non-buffer areas; and 3) mature palm buffers become more environmentally complex and biodiverse over time. Mature palm buffers occupied ~ 200 hectares of land, and represented about 1.36% of all cultivated area within the plantations in which we sampled (not accounting for topographical differences across the landscape), and therefore any environmental or biodiversity benefits that they provide would have occurred at the expense of relatively little cultivated area. Our findings have clear management implications regarding the maintenance of riparian buffers in oil palm landscapes. First, we show that mature palm buffers that are being passively restored (meaning, in this case, that buffers were treated with no herbicides, pesticides, or fertilisers) can increase habitat heterogeneity and benefit biodiversity within oil palm systems, and maintain some pre-planting environmental conditions and aspects of arthropod biodiversity within recently replanted oil palm landscapes (i.e. *Ages 1* and *3*). However, the comparative benefit of these passively restored mature palm buffers to the surrounding non-buffer area varies across the oil palm commercial life cycle. Although maintaining mature palm buffers cannot mitigate the substantial declines in biodiversity (Drescher et al., 2016; Foster et al., 2011) and functioning (Dislich et al., 2017) that occur when forest is converted to oil palm, buffers may offer real environmental benefits within established oil palm systems. We also found that mature palm buffers that are being passively restored have some impacts on environmental conditions in adjacent non-buffer areas (i.e. *Edge*), but do not contribute to higher levels of arthropod biodiversity. However, it is noteworthy that we only assessed the effects of mature palm buffers on the order-level biodiversity of most taxa. Species-level analyses may indicate that mature palm buffers do contribute to higher levels of biodiversity, although this was not the case in our spider analyses. Further, our findings may be attributed to a lack of source populations in the surrounding landscape, as the closest forest to the plantations we sampled is > 30 km away. Previous studies have shown that proximity to forest is an important predictor of successful recovery of biodiversity in degraded tropical landscapes (César et al., 2021). Lastly, we demonstrate that canopy openness and ground cover change within passively restored mature palm buffers over time, but that buffers do not show increases in arthropod biodiversity, at least over the ~ 8-year timeframe represented by the chronosequence in this study. It is possible that, over time, levels of biodiversity within buffers will also increase, as time elapsed since restoration began is a key predictor of restoration success (César et al., 2021; Crouzeilles et al., 2016, 2017). Other potential benefits of mature palm buffers, such as supporting other taxa, preventing soil erosion, and improving stream water quality (Luke, Slade, et al., 2019), could make them valuable to conservation and palm oil production for other reasons, but were beyond

the scope of this study. We acknowledge that our relatively small sample size may have masked some significant differences between buffer and non-buffer areas, although we were limited in increasing our sampling size in SMARTRI plantations owing to spatial constraints.

If the goal of maintaining riparian buffers within oil palm systems is to consistently increase habitat heterogeneity and improve biodiversity in all microhabitats and across the oil palm commercial life cycle, our findings indicate that more active management of mature palm buffers or adjustments to their design are needed. A possible management strategy could be to enrich mature palm buffers by planting forest tree species. This could increase vegetation complexity within buffers and provide resources for a wider range of biodiversity within oil palm plantations. Managers should consider planting forest trees within mature palm buffers several years before the life span (which can be more than a century) of the oil palms within buffers is reached. This will allow native trees to grow amongst and eventually replace the mature palms, helping to maintain structural and ecological complexity within riparian areas. However, before strategies such as this are carried out across plantations, studies are needed to determine the costliness and effectiveness of such an approach. One such study is the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project, which is currently testing the value of enrichment planting within riparian buffers to biodiversity, ecosystem processes, and yields in replanted oil palm plantations (Luke, Advento, Aryawan, et al., 2020). As results from studies such as this become available, it will be possible to identify tractable strategies that maximise the benefits of riparian buffers on the environment and biodiversity within oil palm systems. These strategies can then inform best practice guidance within certification schemes, such as the Roundtable on Sustainable Palm Oil, and ultimately promote more-sustainable development of the global palm oil industry.

## Chapter 4

### **Riparian restoration within replanted oil palm plantations does not benefit arthropod biodiversity within two years**

#### 4.1 Abstract

Oil palm is a widely grown crop whose product, palm oil, is the most traded vegetable oil worldwide. In comparison to natural habitat, oil palm plantations have lower levels of structural complexity, biodiversity, and ecosystem functioning. However, when managed sustainably, oil palm plantations support conditions that can be suitable for a wide range of generalist species, some of which increase palm oil yields through the ecosystem services they deliver. Managing for biodiversity within oil palm systems could, therefore, provide win-win solutions for conservation and crop production. Ecological restoration, here defined as management strategies that enhance the structural and ecological complexity of human-modified landscapes, is one approach to support biodiversity and ecosystem functioning in oil palm. Due to their scale and ecological importance, restoration of riparian buffers (areas of land that border waterways in agricultural systems) represents a particularly promising focus for restoration, especially during replanting events, when mature oil palm plantations are felled and replaced with young palms. Such replanting can have substantial impacts on existing levels of biodiversity and functioning, as well as affecting downstream conditions, such as water quality. Despite this, there is a lack of understanding of how to restore riparian buffers in oil palm plantations, and the relative benefits of different riparian restoration strategies. For instance, there have been no comparisons of the ecological benefits of passive (e.g. maintaining mature oil palms within buffers when plantations are replanted, and stopping the application of herbicides, pesticides, and fertilisers within riparian buffers) and active (e.g. planting native tree seedlings within buffers) approaches to riparian restoration. In this study, we present early findings from the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project: a large-scale experiment that is testing the efficacy of riparian restoration strategies in replanted oil palm plantations in Sumatra, Indonesia. Prior to RERTA, the experimental landscape was mature oil palm. After replanting, we have implemented three restoration treatments (one passive, and two active) and one no-restoration control treatment. We sampled arthropods from long-term monitoring plots both before and after implementation of treatments (i.e. a before-after control-impact, or BACI, experimental design), assessing changes in arthropod

biodiversity in the canopy, understory, and ground microhabitats; and spider biodiversity in the canopy and ground microhabitats. Within two years of treatment implementation, we asked: 1) What is the impact of different riparian restoration strategies on the abundance and order-level composition of arthropods in replanted oil palm plantations? 2) What is the impact of different riparian restoration strategies on the abundance, morphospecies richness, and species-level composition of spiders in replanted oil palm plantations? 3) Do different riparian restoration strategies affect arthropod and spider biodiversity in adjacent areas (25 m outside of riparian buffers) of replanted oil palm that received business-as-usual management? After the RERTA treatments were implemented, planted tree species in our active restoration treatments established and grew quickly. However, we found that, 2 years after restoration treatments had begun, none of the RERTA treatments affected total arthropod abundance in any microhabitat, or spider abundance and species richness in the canopy and ground microhabitats, including the biodiversity of arthropods and spiders in adjacent areas of oil palm that received business-as-usual management. Although we found changes in arthropod order-level composition in the understory, and spider morphospecies-level composition in the canopy and ground microhabitats across sampling periods, RERTA treatments, and distances from riparian buffers, our analyses did not indicate that these changes in composition were caused by riparian restoration. However, the changes we recorded could indicate forthcoming benefits to arthropod biodiversity as the RERTA treatments continue to establish. Our findings suggest that, although restoration of riparian buffers in oil palm plantations can be done through tractable changes in management, restored riparian buffers do not seem to benefit arthropod communities and spiders in particular within a 2-year time period. Our findings indicate that the effects of the RERTA treatments need to be monitored over a longer time period, to determine if treatments provide benefits to biodiversity. Should benefits to biodiversity be found over time, it may be advantageous to start riparian restoration several years prior to replanting, in order to help maintain pre-replanting ecological conditions within replanted oil palm landscapes. Our findings therefore have important implications for guiding future restoration initiatives in established oil palm plantations.

## **4.2 Introduction**

Oil palm is a widely grown tropical crop (FAO, 2019) that is being farmed increasingly across tropical landscapes (Davis et al., 2020). It is highly productive relative to other vegetable oil crops, such as soybean, rapeseed, and sunflower (Meijaard, Brooks, et al., 2020), and its

product (i.e. palm oil) has a myriad of commercial uses. The expansion of oil palm has led to the degradation of vast areas of tropical rainforest and peatland landscapes (Koh et al., 2011; Ramdani & Hino, 2013). This has caused changes in environmental conditions such as structural complexity, vegetation diversity, and macro- and microclimate (Drescher et al., 2016; Foster et al., 2011; Hardwick et al., 2015; Mejjide et al., 2018; Sabajo et al., 2017), resulting in substantial declines in biodiversity (e.g. Beyer et al., Unpublished; Drescher et al., 2016; Foster et al., 2011) and shifts in ecosystem functioning (Dislich et al., 2017). However, when managed sustainably, oil palm plantations can develop suitable conditions for a relatively large number of generalist species (e.g. Azhar et al., 2011; Brinkmann et al., 2019; Luke, Purnomo, et al., 2019; Luke, Advento, Dow, et al., 2020; Pardo et al., 2019; Pashkevich et al., 2021), which can help crop production through delivering important ecosystem services such as pest control and pollination (Li et al., 2019; Nurdiansyah et al., 2016; Turner & Hinsch, 2017). Therefore, implementing management strategies within oil palm plantations that support more complex ecosystems can provide win-win solutions for conservation and production.

Ecological restoration, here defined as management that enhances the structural and ecological complexity of human-modified landscapes, is one way to manage oil palm plantations more sustainably (Luke, Advento, Aryawan, et al., 2020). In tropical agricultural systems, such as oil palm, restoration can increase levels of biodiversity and delivery of ecosystem services (De Beenhouwer et al., 2013; Rey Benayas & Bullock, 2012; Shimamoto et al., 2018), and sometimes contribute to higher crop yields (Gérard et al., 2017). Owing to the potential for restoration to benefit conservation and productivity, efforts have been made in recent years to test the efficacy of different restoration strategies within oil palm systems. Importantly, these research initiatives are the result of collaborations between the palm oil industry, academics, and NGOs, ensuring that findings inform tractable management practices that can be implemented across oil palm landscapes (Luke, Advento, Aryawan, et al., 2020). Restoration strategies that have been shown to benefit structural complexity, biodiversity, and functioning in plantations include intercropping oil palms with other cash crops (Ashraf et al., 2018; Ghazali et al., 2016; Syafiq et al., 2016; Yahya et al., 2017), enhancing the diversity and structural complexity of understory vegetation (Ashton-Butt et al., 2018; Hood et al., 2019; Hood, Advento, et al., 2020; Luke, Purnomo, et al., 2019; Luke, Advento, Aryawan, et al., 2020; Luke, Advento, Dow, et al., 2020; Spear et al., 2018), and planting diverse tree islands within existing oil palm systems (Gérard et al., 2017; Teuscher et al., 2016; Zemp, Ehbrecht, et al., 2019).

A particularly promising restoration strategy that could improve structural and ecological complexity within oil palm systems is the restoration of riparian buffers (Luke, Advento, Aryawan, et al., 2020). Riparian buffers (also called riparian margins, zones, reserves, and strips) are areas of land that surround waterways in agricultural systems that are managed less intensely than surrounding crop habitat (Luke, Slade, et al., 2019). Riparian buffers in oil palm have been shown to improve water quality (Chellaiah & Yule, 2018a; Luke, Barclay, et al., 2017), landscape connectivity (Gray et al., 2019; Knowlton et al., 2017; Luke, Slade, et al., 2019), and terrestrial and aquatic biodiversity (Gray et al., 2015; Gray & Lewis, 2014; Luke, Dow, et al., 2017; Mitchell et al., 2018; Pashkevich, Luke, et al., In Review), depending on the quality of vegetation found within buffers. Studies in other tropical agricultural systems (such as coffee, sugarcane, and pastures) have shown that riparian buffers can provide similar benefits, and possibly help store carbon and improve the delivery of ecosystem services, such as pest control and decomposition (Luke, Slade, et al., 2019). Owing to these benefits, sustainability certification organisations (e.g. the Roundtable on Sustainable Palm Oil, 'RSPO'; RSPO, 2018) and, in some countries, national law (e.g. Indonesia Sustainable Palm Oil, 'ISPO', <http://www.ispo-org.or.id/>) require that riparian buffers are protected in oil palm plantations. Although some oil palm plantations have riparian buffers formed from remnant patches of rainforest that were retained during plantation establishment (e.g. Williamson et al., 2021), many plantations were established before the ratification of laws and regulations that required such areas to be protected (Luke, Advento, Aryawan, et al., 2020). In such plantations, riparian buffers must therefore be restored to re-establish areas of valuable natural habitat that can provide ecological benefits within oil palm systems (Barclay et al., 2017).

Replanting is a key management period during the oil palm commercial life cycle, during which mature palms are replaced with young palms and adjustments in management occur, leading to substantial changes in environmental conditions and short-term declines in biodiversity (Ashton-Butt et al., 2019; Kurz et al., 2016; Pashkevich et al., 2021). For instance, Kurz et al. (2016) found that replanting oil palm caused declines in frog abundance and species richness, and changes in community composition within two years of replanting. Similarly, we have found that replanting caused short-term (i.e. 1 year after replanting) declines in the abundance and species richness of spiders living in understory vegetation (Pashkevich et al., 2021). Maintaining heterogeneous habitat within plantations could mitigate some of the ecological changes caused by replanting (Pashkevich, Luke, et al., In Review). Restoring riparian buffers

at the time of replanting could help support pre-replanting levels of biodiversity and ecosystem functioning in replanted systems, and possibly increase ecological complexity in replanted plantations over time. Further, as replanting is accompanied by changes in management that often require additional resources in the form of labour or machinery, it can be more tractable to restore riparian buffers during this period.

Despite the potential for restoring riparian buffers during replanting to benefit oil palm systems, there is a lack of understanding of how to practically achieve this, and the cost-benefit trade-offs of different restoration strategies are almost entirely unknown (Luke, Advento, Aryawan, et al., 2020). Some industrial oil palm plantations (i.e. plantations that are owned by large-scale corporations, making up about 33% of oil palm plantations worldwide; Descals et al., 2020) have taken a passive approach to restoring riparian buffers (Luke, Advento, Aryawan, et al., 2020; Pashkevich, Luke, et al., In Review; Woodham et al., 2019). In Sumatra, riparian buffers have been passively restored by keeping mature oil palms in place when plantations are replanted; stopping the use of herbicides, fertilisers, and pesticides within buffer boundaries; and allowing the succession of woody plants (Luke, Advento, Aryawan, et al., 2020; Pashkevich, Luke, et al., In Review; Woodham et al., 2019). Existing studies indicate that this approach to passively restoring riparian buffers offers few benefits to oil palm systems. For instance, we found that, although passively restored buffers can have different environmental conditions and levels of arthropod biodiversity than surrounding areas of replanted oil palm, these benefits usually disappear within three years of replanting as areas outside of buffers age and become more structurally complex (Pashkevich, Luke, et al., In Review). Similarly, when comparing passively restored buffers and adjacent areas of replanted oil palm plantation, Woodham et al. (2019) found few differences in ecosystem functioning and multifunctionality.

Although the ecological effects of passively restored buffers have only been observed in a few context-specific studies, and it is likely that they offer some environmental and ecological benefits (for instance, passively restored buffers probably improve water quality in oil palm plantations; Luke, Slade, et al. (2019)), the available research suggests that a more active approach to riparian buffer restoration may be needed. Active approaches to restoring riparian buffers include planting native tree seedlings underneath mature palms, or in place of mature palms (Luke, Advento, Aryawan, et al., 2020). Once grown, these tree seedlings can contribute to higher levels of structural complexity and plant diversity within oil palm plantations (Gérard et al., 2017; Zemp, Ehbrecht, et al., 2019). Higher levels of complexity could translate into

benefits for biodiversity. For instance, planting fruit trees within riparian buffers could increase floral diversity and structural complexity whilst also increasing the biodiversity of frugivorous fauna, such as bats (Syafiq et al., 2016). To our knowledge, there have been no studies that have assessed the ecological effects of actively restoring riparian buffers in oil palm plantations, or comparing the benefits of passive and active restoration approaches within this habitat.

The ecological impacts of passive and active approaches to riparian restoration on oil palm systems may be best understood using an experimental approach, owing to the complex ecological networks that are inherent in tropical systems (Fayle, Turner, et al., 2015). In this study, we make use of a large-scale, before-after control-impact (BACI) experiment ('The Riparian Ecosystem Restoration in Tropical Agriculture', or 'RERTA' Project) to test the efficacy of different riparian restoration strategies on arthropod biodiversity in replanted oil palm plantations. We focus on arthropods, as they are abundant, influence existing trophic relationships (Barnes et al., 2014), and contribute to important ecosystem services such as pollination (Li et al., 2019), pest control (Nurdiansyah et al., 2016; Turner & Hinsch, 2017), and resource removal (Gray et al., 2015) in oil palm landscapes. Further, arthropods have previously been shown to be responsive to changes in oil palm management (Ashraf et al., 2018; Ashton-Butt et al., 2018; Ghazali et al., 2016; Hood, Advento, et al., 2020; Spear et al., 2018), and can be an indicator for wider changes occurring across taxonomic groups in tropical forest systems (Edwards et al., 2014). Within two years of implementing our riparian restoration strategies, we ask: 1) What is the impact of different riparian restoration strategies on the abundance and order-level composition of arthropods in replanted oil palm plantations? 2) What is the impact of different riparian restoration strategies on the abundance, morphospecies richness, and morphospecies-level composition of spiders – abundant predators that eat pests in agricultural systems (Michalko et al., 2019) and are sensitive to environmental changes (Pashkevich et al., 2021; Pashkevich, Luke, et al., In Review; Spear et al., 2018) – in replanted oil palm plantations? 3) Do different riparian restoration strategies affect arthropod and spider biodiversity in nearby (i.e. < 30 m from buffers) areas of replanted oil palm that receive business-as-usual management, and therefore can riparian restoration benefit the ecology of the surrounding oil palm landscape?

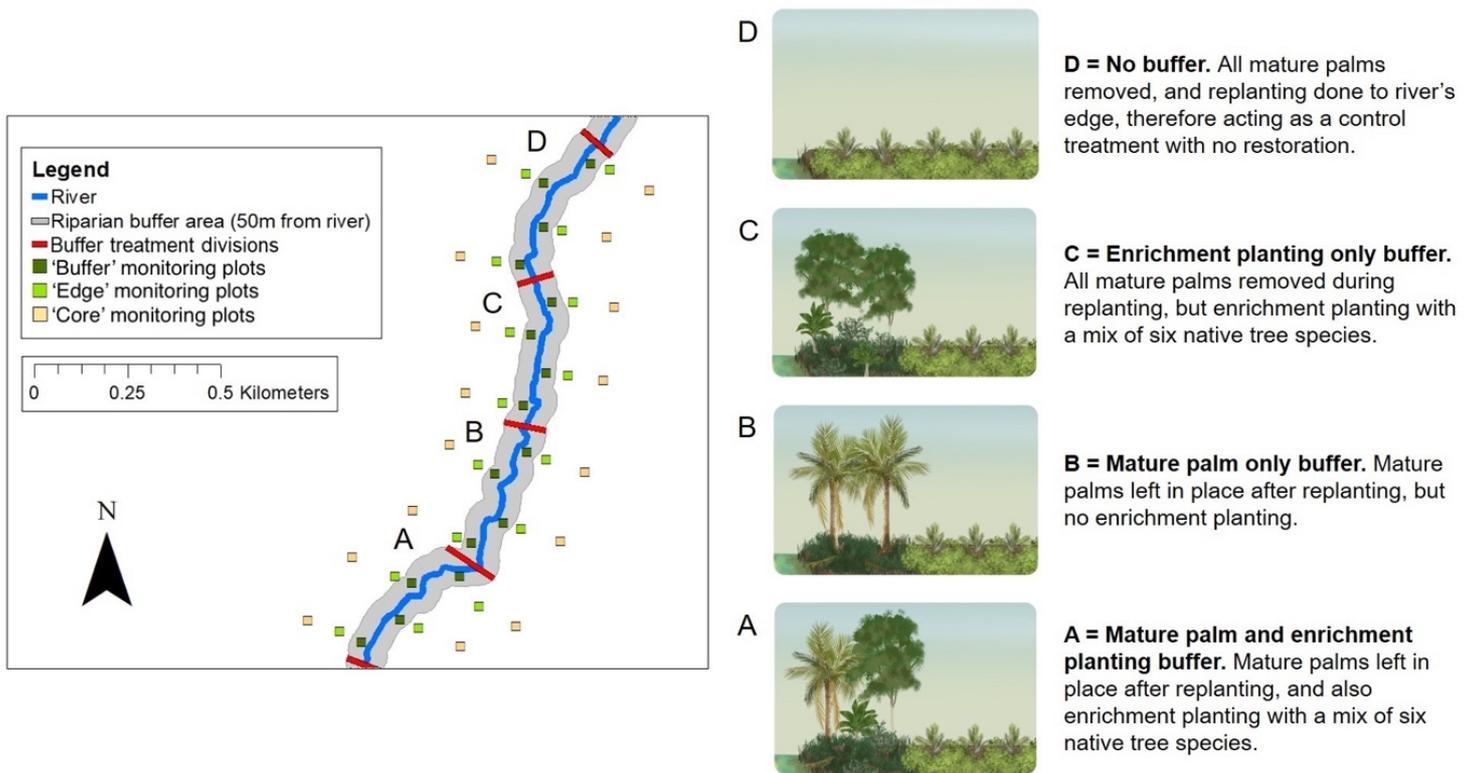
## 4.3 Methods

### 4.3.1 | Study design

This study was conducted at the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme's Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project, in industrial oil palm estates that are owned and managed by Sinar Mas Agro Resources and Technology Research Institute (SMARTRI; Riau, Sumatra, Indonesia; see Figure 2.1 in Chapter 2 for a map of the study area). RERTA is a large-scale experiment that is making use of scheduled replanting of mature oil palm plantations (i.e. > 30 years old) to test different strategies for restoring riparian buffers. The Project consists of three riparian restoration treatments, and one no-restoration control (hereafter, collectively referred to as '*Treatment*'), all of which were implemented at the time of replanting and represent viable options for riparian management in oil palm systems. Treatments are replicated across two rivers, RERTA 1 and RERTA 2, which have similar physical characteristics (Luke, Advento, Aryawan, et al., 2020). Each treatment occupies a space of 50 x 400 m on either side of each river. Treatments include (Figure 4.1):

- **Mature palm and enrichment planting buffer** ('*Mature enriched*'; Figure 4.1A) – Mature oil palms were left in place at the time of replanting and, amongst these palms, six native tree species were planted.
- **Mature palm only buffer** ('*Mature only*'; Figure 4.1B) – Mature oil palms were left in place at the time of replanting, and passive restoration was allowed.
- **Enrichment planting only buffer** ('*Enriched only*'; Figure 4.1C) – Mature oil palms were removed at the time of replanting and, in their place, six native tree species were planted at the same density as in the '*Mature enriched*' treatment.
- **No buffer** ('*No buffer*'; Figure 4.1D) – Mature oil palms were removed at the time of replanting and, in their place, young palms were planted.

No herbicides, pesticides, or chemical fertilisers were applied within buffer areas in any treatments, although organic fertilisers and manual weeding took place in '*No buffer*' to support the establishment of young palms.



**Figure 4.1.** Experimental set-up of the RERTA Project. The experiment is replicated across two rivers (RERTA 1 and RERTA 2), although only one river is shown in the figure. The map shows a birds-eye view of the relative placement of the river (dark blue line), riparian buffer (shaded grey area), divisions between restoration treatments (red lines), and long-term monitoring plots ('*Buffer*' = dark green, '*Edge*' = light green, '*Core*' = yellow). Within a treatment (A – D), the area occupied by a riparian buffer measures 50 x 400 m from either riverside. '*Buffer*' plots are in the middle of riparian buffers (25 m from the river), '*Edge*' plots are 28.5 m from riparian buffers (78.5 m from the river), and '*Core*' plots are 130 m from riparian buffers (180 m from the river). A 100 m transect starts from each '*Buffer*', '*Edge*', and '*Core*' plot, following the course of the river. Figure adapted from Luke, Advento, Aryawan, et al. (2020).

Treatments were implemented in RERTA 1 in August 2018 and in RERTA 2 in August 2019. Prior to implementation of treatments, all riparian areas consisted of mature oil palms and did not receive herbicide, pesticide or chemical fertiliser input during the previous ten years (i.e. were under passive restoration) (Barclay et al., 2017; Pashkevich, Luke, et al., In Review). However, manual cutting of vegetation sometimes occurred, to improve access for harvesting and to suppress woody vegetation growth. Bamboo and vetiver grass were intermittently planted along riverbanks, to reduce erosion.

The six tree species planted in ‘*Mature enriched*’ and ‘*Enriched only*’ were: Sungkai, (*Peronema canescens*), Meranti (*Shorea leprosula*), Pulai (*Alstonia scholaris*), Cempedak (*Artocarpus integer*), Bintagur (*Calophyllum inophyllum*), and Sengon (*Albizia chinensis*). These trees are commonly found in the geographic region surrounding SMARTRI, and represent a variety of fruiting, leguminous, and pioneer species. Tree seedlings were planted in a 4 x 4 m grid design across ‘*Mature enriched*’ and ‘*Enriched only*’. The seedling species that was planted at each grid point was determined randomly, except in specific areas where neighbouring grid points were planted with the same species to facilitate experiments to test the effects of neighbour identity on growth, diversity, and function (not analysed as part of this study). After planting, seedlings were monitored for growth and survival, and weeds around seedlings were removed manually. Seedlings were replaced if they died. We hereafter refer to the 50 x 400 m RERTA treatment areas as “buffer areas”, and the surrounding croplands as “cultivated areas”. Seedlings had a high rate of survival and grew quickly (Unpublished data).

Replicated long-term monitoring plots (25 x 25 m) and transects (100 m length) were set-up across the RERTA landscape prior to replanting and establishment of the treatments. The centres of plots are located at three distances from riverbanks (hereafter, ‘*Distance*’): within buffer areas (‘*Buffer*’; 25 m from riverbanks), just outside buffer areas in the cultivated landscape (‘*Edge*’; 78.5 m from riverbanks and 28.5 m from buffer areas), and deep within the cultivated landscape (‘*Core*’; 180 m from riverbanks and 125 m from buffer areas). We use ‘*Edge*’ to determine whether the RERTA treatments affect conditions in nearby cultivated areas. ‘*Core*’ should not be affected ecologically by ‘*Buffer*’, as previous studies have found that the impacts of buffers do not extend to 125 m from their edge (Gray et al., 2016; Pashkevich, Luke, et al., In Review). Transects begin from the centre of each plot, and track the course of the adjacent river. Plots and transects are arranged in triplets (hereafter, ‘*Triplet*’), which are alternated across riversides and are spaced at least 100 m apart (Figure 4.1). There

are four triplets within a treatment on each river (N = 8 plots for each *Distance* within a *Treatment* across both rivers). ‘*Buffer*’, ‘*Edge*’, and ‘*Core*’ areas varied minimally in their ecology prior to replanting and implementation of treatments (see Luke, Advento, Aryawan, et al. (2020) for further details on the RERTA Project experimental design).

#### 4.3.2 | Data collection

##### 4.3.2.1 | Order-level arthropod sampling

We sampled arthropods across triplets in three microhabitats: canopy, understory, and ground, enabling us to assess whether arthropods exhibited any microhabitat-specific responses to management, as has been found in other studies (Pashkevich et al., 2021; Pashkevich, Luke, et al., In Review). We sampled canopy and ground arthropods once before and once after implementation of treatments (hereafter, ‘*PrePost*’: levels ‘*Pre*’ and ‘*Post*’), and understory arthropods once before (‘*Pre*’) and twice after (‘*Post 1*’ and ‘*Post 2*’) implementation of treatments, in a before-after control-impact (BACI) experimental design. See Figure S4.1 for sampling periods.

We sampled each ‘*Distance*’ within a ‘*Triplet*’ on the same day. To sample canopy arthropods, we used insecticide fogging, as described in Chapters 2 and 3. Pre-treatment, we fogged a randomly selected mature palm in each plot. Post-treatment in buffer areas, we fogged either a randomly selected mature palm (‘*Mature enriched*’, ‘*Mature only*’), native tree (‘*Enriched only*’), or young palm (‘*No buffer*’) in each plot. Post-treatment in cultivated areas (i.e. ‘*Edge*’ and ‘*Core*’), we fogged a randomly selected young palm in each plot. Although the distance between trays and canopies varied between mature palms, native trees, and young palms, we kept fogging methods the same so that samples were comparable (Pashkevich et al., 2021; Pashkevich, Luke, et al., In Review). To sample understory arthropods, we used string to hang a brown sticky trap (sticky on both sides, with a total sticky area of 19 cm x 27 cm) approximately 1.5 m above the ground at the start, middle, and end of each 100 m transect. We were only able to set sticky traps in 6 plots (2 triplets) prior to the implementation of treatments in RERTA 1, and therefore most of our pre-treatment data for understory arthropods came from RERTA 2. To sample ground arthropods, we placed a pitfall trap (19.5 cm diameter at mouth) at the centre of each plot. We filled traps with 70% ethanol, and covered them with a plastic plate that was raised on sticks to prevent rainfall dilution or flooding. Sticky traps and pitfall traps were collected after 72 hours.

We identified all arthropods using microscopes at SMARTRI field station. We identified arthropods to the same groups as in Chapters 2 and 3.

#### 4.3.2.2 | Species-level spider sampling

We conducted focussed analyses on spiders in the canopy and ground microhabitats, to assess whether the effects of the RERTA treatments on arthropods were consistent when taxonomic resolution was increased. We collected canopy and ground spiders using insecticide fogging and pitfall traps, as described above. We separated juveniles from adults, and used dissecting microscopes and relevant keys (<http://ecotaxonomy.org/ecokeys>; Deeleman-Reinhold, 2000; Jocqué & Dippenaar-Schoeman, 2006) to identify adults to family and morphospecies (hereafter, “species”). We counted each unique male and female as its own species, since it was not possible to match males and females. The spiders are preserved in 75% ethanol at SMARTRI field station.

#### 4.3.3 | Statistical analyses

We did all analyses in R version 4.0.5 (R Core Team, 2018) using RStudio version 1.4.1106 (RStudio Team, 2018). We used *readxl* (Wickham et al., 2019), *tidyverse* (Wickham, 2017), *zoo* (Zeileis et al., 2019), *data.table* (Dowle et al., 2019), *lattice* (Sarkar, 2018), and *plyr* (Wickham, 2016) for data wrangling and exploration, and explored our data using the methods of Zuur, Ieno, & Elphick (2010). We visualised our results using *gridExtra* (Auguie & Antonov, 2017), *cowplot* (Wilke, 2019), and *lemon* (Edwards et al., 2019). We analysed our data using the following techniques (additional details on individual models are described below):

**Bayesian regression models (hereafter, GLMMs).** We used *brms* (Bürkner & Gabry, 2020) and the No-U-Turn sampler (NUTS) algorithm in Stan (Carpenter et al., 2017) to fit GLMMs. For each response, we first fitted a parent model, which had a triple-interaction of ‘*PrePost\*Treatment\*Distance*’ as a fixed effect. We then fitted fourteen derivative models (Table S4.1), which had reduced parameters, relative to the parent model. The most simple model we fitted was a null model, which included no fixed effects. We included ‘*Triplet*’ as a random intercept effect in all models, to account for potential spatial autocorrelation, repeated measurements within a ‘*Triplet*’, and site-specific differences in environmental conditions and timing of sampling. After generating and validating our models (Supplementary Text 4.1), we determined an optimal model and calculated its Bayesian R-squared value (Bürkner & Gabry,

2020). If the optimal model was not the null model, we conducted post-hoc analyses, as described in Supplementary Text 4.1.

**Multivariate generalised linear models (hereafter, mGLMs).** We used *mvabund* (Wang et al., 2019) to fit mGLMs. For each response, we fitted a parent model with the interaction of ‘*PrePost\*Treatment\*Distance*’. We validated models and determined the significance of covariates ( $P < 0.05$ ), as described in Chapters 2 and 3. We did not include ‘*Triplet*’ as a blocking variable when calculating P-values, as we did not have an equal number of observations across triplets owing to lost and damaged samples, and *mvabund* required balanced datasets to fit blocking variables. We acknowledge that we therefore could not account for potential spatial and temporal autocorrelation of samples. If the interaction of ‘*PrePost\*Treatment\*Distance*’ was not a significant covariate, we used a backwards-stepwise model selection procedure to determine whether double-interactions or individual fixed effects were significant and – when covariates were significant – conducted post-hoc analyses, as described in Chapters 2 and 3.

For both GLMMs and mGLMs, we inferred that the RERTA treatments affected arthropod and spider biodiversity when optimal models included the interaction of ‘*PrePost\*Treatment*’, and post-hoc analyses indicated that biodiversity within a ‘*Treatment*’ differed between ‘*Pre*’ and ‘*Post*’ sampling periods. We inferred that ‘*Buffer*’ affected arthropod biodiversity in ‘*Edge*’ when optimal models included the interaction of ‘*PrePost\*Treatment\*Distance*’, and post-hoc analyses indicated that biodiversity within a ‘*Treatment*’ in ‘*Buffer*’ and ‘*Edge*’ was more similar than that in ‘*Buffer*’ and ‘*Core*’.

#### **4.3.3.1 | Impacts of the RERTA riparian restoration treatments on all arthropods**

During fieldwork, several sticky traps were damaged in the field and consequently removed from our dataset. We, therefore, standardised understory arthropod data prior to analysis by aggregating undamaged trap data at the transect level, calculating mean abundance per undamaged trap, and multiplying by 3 (the number of traps originally set along each transect). To meet model assumptions, we rounded these standardised data to the nearest integer. When analysing understory arthropod data, we identified one outlier (‘*Post 1*’-‘*Mature enriched*’-‘*Edge*’) during data exploration. We eliminated this outlier, which had a particularly high abundance of Diptera, as it caused issues with model fit.

We used GLMMs (negative binomial distributions, log links) to quantify changes in total arthropod abundance in the canopy, understory, and ground microhabitats (Parent models:  $Abundance \sim PrePost * Treatment * Distance + (1 | Triplet)$ ). We included all arthropods in these analyses. We used mGLMMs (negative binomial distributions, log links) to quantify changes in arthropod order-level community composition in the canopy, understory, and ground microhabitats (Parent models:  $Composition \sim PrePost * Treatment * Distance + (1 | Triplet)$ ). We did not include endopterygote larvae and arthropods that could not be identified to order in our composition analyses. These represented 5.2% of individuals collected in the canopy (all endopterygote larvae), < 0.2% of individuals in the understory, and 1.0% of individuals on the ground. If any covariates were significant, we conducted univariate analyses to determine how the abundance of individual orders changed across study areas, as in Chapters 2 and 3. We visualised the results of our community composition analyses using stacked bar charts.

#### **4.3.3.2 | Impacts of the RERTA riparian restoration treatments on spiders**

Prior to analysis, we eliminated Lycosidae spiders (n = 46) from one pitfall trap ('Post'- 'Enriched only'- 'Edge'). These individuals were spiderlings that were likely to have been on the back of their mother when she fell into the trap. We assessed our sampling completeness by using *iNEXT* (Hsieh et al., 2016) to calculate the interpolated and extrapolated (to double the number of observed individuals; Gotelli & Colwell, 2001) species richness of spiders within the canopy and ground microhabitats, as per Chao et al. (2014). We assessed species evenness within the canopy and ground microhabitats by plotting rank abundance curves. Only adult spiders were included in these analyses.

We used GLMMs to separately quantify changes in spider abundance and species richness in the canopy and ground microhabitats (Parent models:  $Abundance \sim PrePost * Treatment * Distance + (1 | Triplet)$ ;  $Richness \sim PrePost * Treatment * Distance + (1 | Triplet)$ ). In the canopy, we fitted our abundance models to negative binomial distributions (log links), and our species richness models to zero-inflated negative binomial distributions (log links), owing to a high proportion of zeroes in the dataset. On the ground, we fitted both abundance and species richness models to zero-inflated negative binomial distributions. All models were fitted using log links. We included all spiders in our abundance analyses, but only adults were included in our species richness analyses.

We separately quantified changes in spider species-level composition (adult spiders only) in the canopy and ground microhabitats in two ways. First, we used *betapart* (Baselga & Orme, 2012) to calculate incidence-based beta-diversity across ‘*PrePost\*Treatment\*Distance*’ groups, as described in Chapter 3. We then used mGLMs (negative binomial distributions, log links) to quantify changes in species-level community composition (Parent models: *Composition ~ PrePost\*Distance\*Treatment*). Although our ground spider dataset had a relatively high proportion of zeroes, we did not fit our ground spider composition models to zero-inflated negative binomial distributions, as this distribution is not supported by *mvabund* (Wang et al., 2019), and we did not detect issues when validating our models. Our spider species-level composition analyses were otherwise identical in methodology to our arthropod order-level composition analyses.

When identifying spiders, we found that some individuals in pitfall traps (set after implementation of treatments) from four triplets were severely degraded, possibly owing to excess water within sample tubes. We, therefore, conducted sensitivity analyses that excluded these traps from all of our ground spider analyses, in order to investigate whether these samples influenced our initial findings. We did not conduct these analyses in our overall arthropod analyses, as we found no evidence that arthropods with hardened exoskeletons (which comprised the vast majority of remaining individuals) were degraded.

## 4.4 Results

### 4.4.1 | Impacts of the RERTA riparian restoration treatments on all arthropods

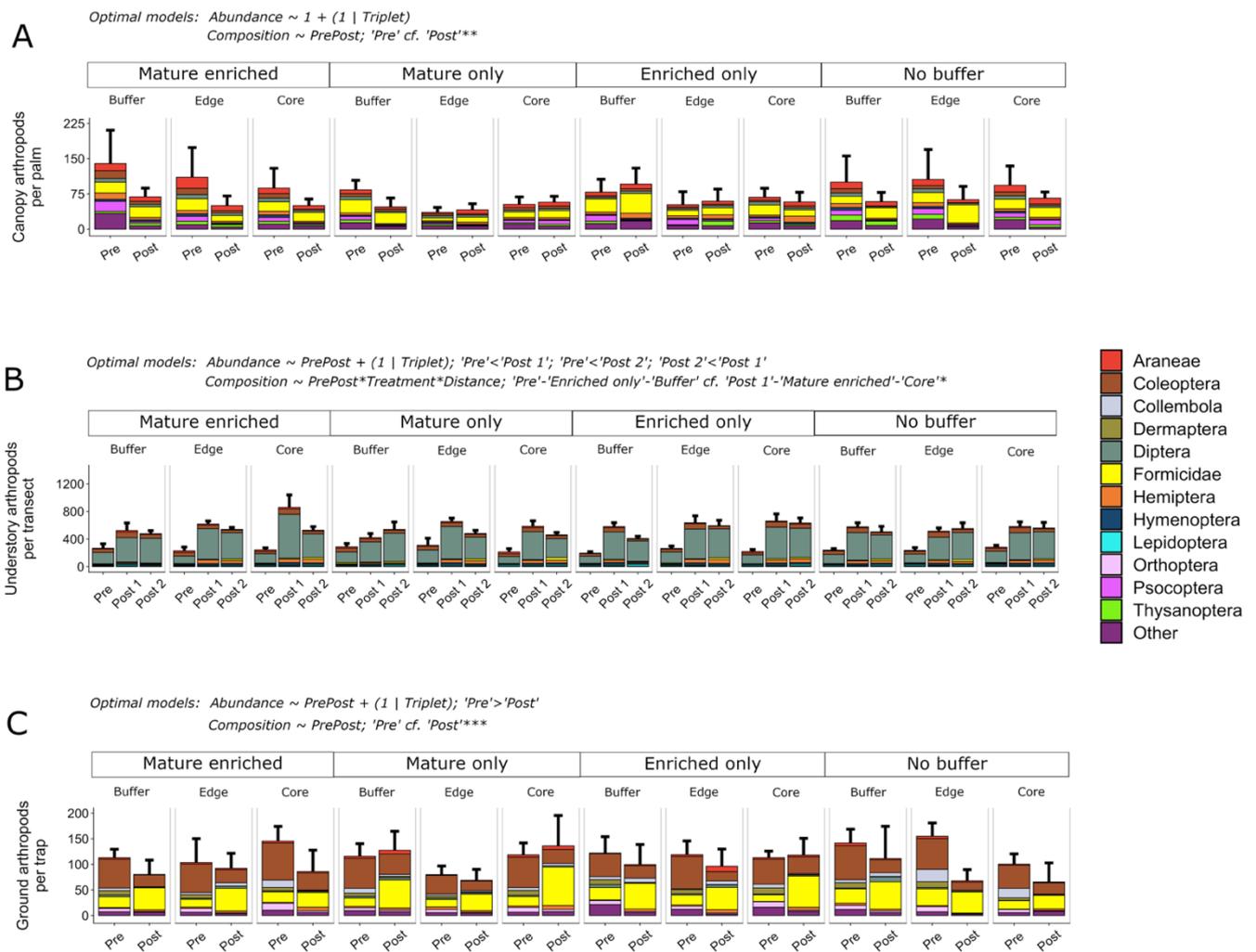
We collected 153,898 arthropods (from 23 orders) in our order-level sampling. These included 13,775 arthropods from canopy fogging, 119,622 arthropods from sticky traps, and 20,501 arthropods from pitfall traps.

Within two years of implementing the RERTA riparian restoration treatments, we found little evidence that the treatments affected the total abundance of arthropods in the canopy, understory, or ground microhabitats. The optimal model for total arthropod abundance in the canopy was the null model ( $R^2 = 19.9 \pm 7.4\%$ ; Figure 4.2A; Table S4.2). The optimal models for total arthropod abundance in the understory and on the ground included only ‘*PrePost*’ ( $R^2 = 41.7 \pm 3.7\%$  for understory;  $R^2 = 25.2 \pm 7.9\%$  on the ground; Figure 4.2B; Figure 4.2C; Table S4.2), indicating that arthropod abundances changed over time but not due to the RERTA

treatments. In the understory, post-hoc analyses showed that, per transect, 'Post 1' (Mean arthropods ( $\bar{X}$ ) = 600) and 'Post 2' ( $\bar{X}$  = 524) had 142% and 111% more arthropods than 'Pre' ( $\bar{X}$  = 248); and 'Post 1' had 15% more arthropods than 'Post 2' (Figure 4.2B). On the ground, post-hoc analyses showed that, per trap, 'Pre' ( $\bar{X}$  = 120) had 22% more arthropods, on average, than 'Post' ( $\bar{X}$  = 98.5) (Figure 4.2C).

In the canopy and ground microhabitats, we found little evidence that the RERTA riparian restoration treatments affected arthropod order-level composition, within two years of their implementation. The optimal models for both included only 'PrePost' (LRT = 148.200,  $P < 0.001$  in the canopy; LRT = 316.000,  $P < 0.001$  on the ground; Figure 4.2A; Figure 4.2C; Table S4.2), indicating that composition in these microhabitats changed over time but not with restoration treatment. Trends in the canopy were driven by decreased abundances over time of Dermaptera (LRT = 20.503,  $P = 0.003$ ), Isoptera (LRT = 19.359,  $P = 0.004$ ), Lepidoptera (LRT = 13.051,  $P = 0.032$ ), Pseudoscorpiones (LRT = 20.196,  $P = 0.003$ ), and Psocoptera (LRT = 14.975,  $P = 0.016$ ). Trends on the ground were driven by increased abundances over time of Formicidae (LRT = 32.740,  $P < 0.001$ ), Hemiptera (LRT = 10.486,  $P = 0.040$ ), and Isopoda (LRT = 13.529,  $P = 0.011$ ), but decreased abundances over time of Acari (LRT = 27.365,  $P < 0.001$ ), Coleoptera (LRT = 21.805,  $P < 0.001$ ), Dermaptera (LRT = 98.357,  $P < 0.001$ ), and Orthoptera (LRT = 56.864,  $P < 0.001$ ).

In the understory, the optimal model for order-level composition included the interaction of 'PrePost\*Treatment\*Distance' (LRT = 238.9,  $P = 0.020$ ; Figure 4.2B; Table S4.2), indicating that order-level composition differed significantly with time, RERTA treatments, and distances from riparian buffers, within two years of treatment implementation. However, post-hoc analyses indicated that the only significant difference in composition was between 'Pre'- 'Enriched only'- 'Buffer' and 'Post 1'- 'Mature enriched'- 'Core' (LRT = 103.60,  $P = 0.049$ ). As this difference was not between 'Pre' and 'Post' within a 'Treatment', it was probably not caused by the RERTA treatments. Univariate analyses indicated that overall trends across 'PrePost\*Treatment\*Distance' groups resulted from changes in the abundances of Araneae (LRT = 96.076,  $P < 0.001$ ), Coleoptera (LRT = 64.042,  $P = 0.025$ ), Dermaptera (LRT = 95.065,  $P < 0.001$ ), Diptera (LRT = 170.315,  $P < 0.001$ ), Formicidae (LRT = 112.994,  $P < 0.001$ ), Hemiptera (LRT = 339.680,  $P < 0.001$ ), Hymenoptera (LRT = 124.240,  $P < 0.001$ ), Psocoptera (LRT = 85.122,  $P < 0.001$ ), and Thysanoptera (LRT = 147.580,  $P < 0.001$ ).



**Figure 4.2.** Differences in total arthropod abundance and arthropod order-level community composition in the canopy (top; “A”), understory (middle; “B”), and ground (bottom; “C”) microhabitats in ‘Buffer’, ‘Edge’, and ‘Core’ areas both before (‘Pre’) and after (‘Post’) implementation of RERTA project treatments (‘Mature enriched’, ‘Mature only’, ‘Enriched only’, ‘No buffer’). For understory, we include data from before (‘Pre’) and twice after (‘Post 1’, ‘Post 2’) implementation of treatments. Our posterior predictive checks indicated that models for total arthropod abundance tracked to their underlying datasets. We list the optimal model for total arthropod abundance (determined using LOOIC) and order-level community composition (determined using backwards stepwise selection) above each subplot. If the optimal model included fixed effects, we list factor levels between which differences occurred (as indicated by our posthoc analyses). We list the significance for post-hoc comparisons for our order-level community composition analyses (\* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ ). Arthropod orders are plotted as they are sequenced in the legend. Error bars display one standard error from the mean.

#### 4.4.2 | Impacts of the RERTA riparian restoration treatments on spiders

We collected 2328 spiders, which we identified to 29 families and 196 species (Table S4.3). These included 1724 spiders from canopy fogging ( $n_{\text{adults}} = 468$ ;  $n_{\text{species}} = 113$ ), and 604 spiders from pitfall traps ( $n_{\text{adults}} = 332$ ;  $n_{\text{species}} = 103$ ). In both microhabitats, species accumulation curves were beginning to asymptote, and indicated that we sampled an estimated 70% and 77% of species from the canopy and ground microhabitats, respectively (Figure S4.2). Rank abundance curves indicated that spider communities in both microhabitats were dominated by a few highly abundant species. 12 species represented 53% of all adult individuals in the canopy, and 10 species represented 50% of all adult individuals on the ground (Figure S4.2).

Within two years of implementing the RERTA riparian restoration treatments, we found little evidence that the treatments affected spider abundance in the canopy or on the ground, as the null model was the optimal model for both ( $R^2 = 20.8 \pm 8.1\%$  in the canopy;  $R^2 = 9.42 \pm 6.1\%$  on the ground; Figure 4.3; Table S4.2). The null model was also the optimal model for spider species richness in both microhabitats ( $R^2 = 16.6 \pm 7.8\%$  in the canopy;  $R^2 = 4.2 \pm 4.3\%$  on the ground; Figure 4.3; Table S4.2). Our findings on the ground were upheld by our sensitivity analyses, which tested for impacts of potentially damaged samples on our initial findings.

Total dissimilarity across ‘*PrePost\*Treatment\*Distance*’ groups (e.g. ‘*Pre*’-‘*Enriched only*’-‘*Buffer*’) in both the canopy and on the ground was relatively high (Sørensen index = 93.4% in the canopy and 94.0% on the ground). The turnover (i.e. species replacement) component was 91.6% in the canopy and 91.5% on the ground. The nestedness (i.e. species loss or gain) component was 2.2% in the canopy, and 2.5% on the ground. Therefore, across ‘*PrePost\*Treatment\*Distance*’ groups, the overall dissimilarity within each microhabitat resulted from the substitution of species more than species loss or gain. In both microhabitats, the optimal model for spider species-level composition included the interaction of ‘*PrePost\*Treatment\*Distance*’ (LRT = 12.500,  $P = 0.009$  in the canopy; LRT = 32.770,  $P < 0.001$  on the ground; Figure 4.3; Table S4.2), indicating that species-level composition differed significantly across time, RERTA treatments, and distances from riparian buffer treatments, within two years of treatment implementation. However, post-hoc analyses indicated that no ‘*PrePost\*Treatment\*Distance*’ groups differed significantly in species-level composition from each other in either microhabitat ( $P > 0.05$ ), suggesting that the differences we found reflected small changes in species-level composition between all factor combinations, rather than differences caused explicitly by the RERTA treatments. Univariate analyses indicated that

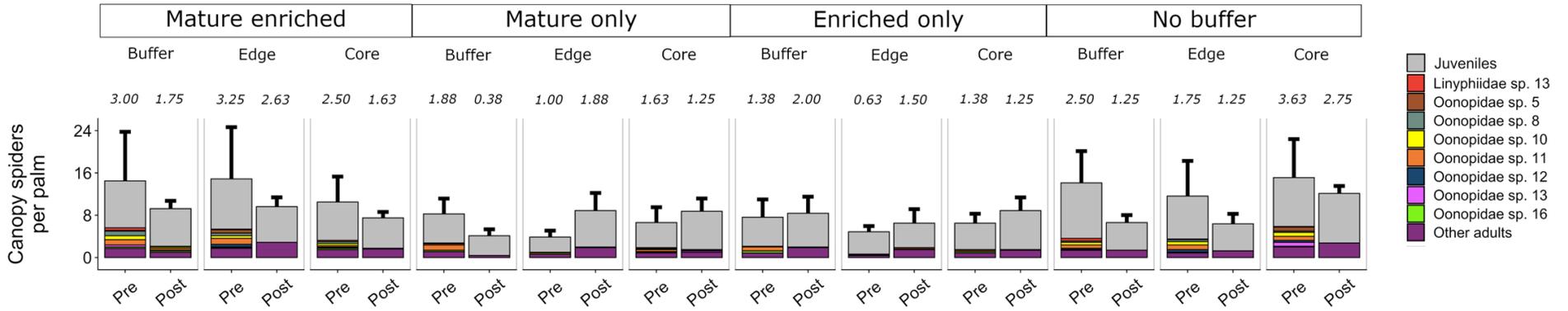
overall trends resulted from different abundances of all species in the canopy ( $P < 0.05$  for all species), and two species (*Lycosidae sp. 4*, *Lycosidae sp. 8*) on the ground ( $P < 0.05$ ), although our ground model indicated that changes in the abundance of all other ground species were marginally significant ( $P < 0.06$ ). Our sensitivity analysis, which tested for impacts of potentially damaged pitfall trap samples on our initial findings, upheld our findings on the ground ( $LRT_{\text{sensitivity}} = 24.550$ ,  $P_{\text{sensitivity}} = 0.001$ ), although univariate analyses indicated that overall trends were driven by significant changes in the abundance of all spider species ( $P_{\text{sensitivity}} < 0.05$  for all species).

#### **4.4.3 | Impacts of the RERTA riparian restoration treatments on *Edge* areas**

Within two years of implementing the RERTA riparian restoration treatments, we found no evidence that the treatments had any effect on the biodiversity of nearby cultivated areas (i.e. ‘*Edge*’), as – within a ‘*Treatment*’ – the abundance and order-level composition of all arthropods, and abundance, species richness, and species-level composition of spiders did not differ between ‘*Buffer*’, ‘*Edge*’, and ‘*Core*’ in any microhabitat.

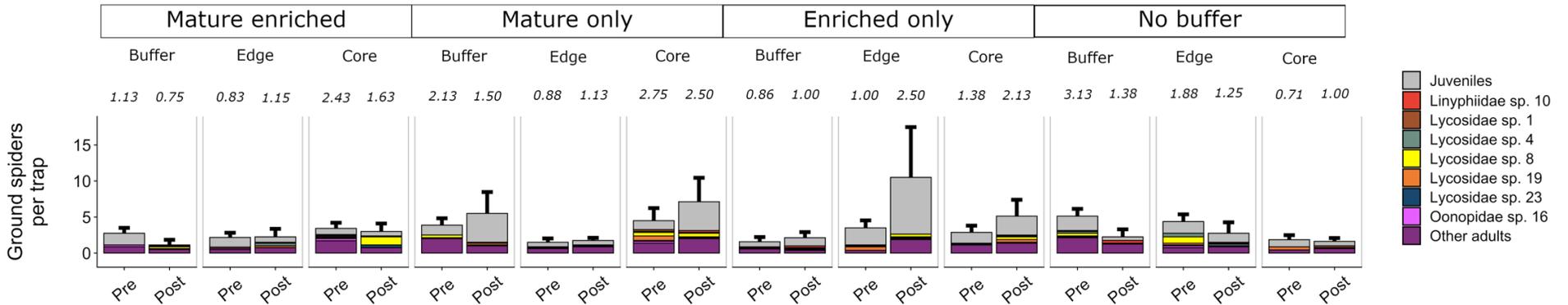
**A**

Optimal models:  $Abundance \sim 1 + (1 | Triplet)$   
 $Species\ richness \sim 1 + (1 | Triplet)$   
 $Composition \sim PrePost * Treatment * Distance; No\ pairwise\ differences$



**B**

Optimal models:  $Abundance \sim 1 + (1 | Triplet)$   
 $Species\ richness \sim 1 + (1 | Triplet)$   
 $Composition \sim PrePost * Treatment * Distance; No\ pairwise\ differences$



**Figure 4.3.** Differences in spider abundance, species richness, and species-level community composition in the canopy (top; “A”) and ground (bottom; “B”) microhabitats in ‘*Buffer*’, ‘*Edge*’, and ‘*Core*’ areas both before (‘*Pre*’) and after (‘*Post*’) implementation of RERTA project treatments (‘*Mature enriched*’, ‘*Mature only*’, ‘*Enriched only*’, ‘*No buffer*’). Our posterior predictive checks indicated that models for spider abundance and species richness tracked to their underlying datasets. We list the optimal model for spider abundance and species richness (determined using LOOIC) and species-level community composition (determined using backwards stepwise selection) above each subplot. If the optimal model included fixed effects, we list factor levels between which differences occurred (as indicated by our posthoc analyses), or ‘No pairwise differences’ if our posthoc analyses indicated that no factor levels were significantly different. Juvenile spiders and adult spider species are plotted as they are sequenced in the legend. Error bars display one standard error from the mean. Mean spider species richness is listed above each bar plot.

## 4.5 Discussion

### 4.5.1 | Impacts of the RERTA riparian restoration treatments on arthropods

Within two years of the RERTA riparian restoration treatments being implemented, we found no effects of the treatments on the biodiversity of arthropods (total abundance and order-level composition) or of spiders in particular (abundance, species richness, and species-level composition) in any microhabitat studied. We did find differences in arthropod order-level composition in the understory, and spider species-level composition in the canopy and ground microhabitats, across ‘*PrePost\*Treatment\*Distance*’ groups (e.g. ‘*Post-Mature enriched-Edge*’), but our modelling did not indicate that these changes in biodiversity were caused by the RERTA treatments. Shifts in arthropod and spider composition were caused by changes in abundance across orders and species that represented a wide range of life history strategies, indicating that arthropod biodiversity is changing broadly across the RERTA landscape.

We find it surprising that we did not observe any effects of the RERTA treatments on arthropod and spider biodiversity, as seedlings in our active restoration treatments had a high rate of survival and grew quickly, and other studies in oil palm have demonstrated clear links between plant diversity, structural complexity, and arthropod and spider biodiversity (Ashraf et al.,

2018; Ashton-Butt et al., 2018; Ghazali et al., 2016; Hood, Advento, et al., 2020; Pashkevich et al., 2021; Pashkevich, Luke, et al., In Review; Spear et al., 2018). This lack of effect may be attributed to our study occurring within a relatively short time frame after treatment implementation (i.e. within two years), therefore minimising the time allowed for the RERTA treatments to establish, and not allowing enough time to escape the effects of oil palm replanting. Also, the lack of effect may be explained by local- and landscape-level factors in the larger RERTA Project study region, and the dominance of generalist species in oil palm systems. We further unpack these explanations throughout this discussion.

We sampled arthropods once before, and within two years after, implementation of the RERTA treatments. It is possible that not enough time elapsed for the RERTA treatments to fully establish, and for their benefits to arthropods to be measurable. Indeed, although planted seedlings in our active restoration treatments grew quickly, they were still not fully grown trees at the time of our post-treatment sampling. It is noteworthy that meta-analyses have shown that the time elapsed since restoration began is an important predictor of the success of restoration initiatives in the tropics (Crouzeilles et al., 2016, 2017) and other experiments in degraded tropical landscapes have demonstrated the importance of observing changes over long time periods after implementing restoration management (e.g. Holl et al., 2020). One study in the American tropics found that it took 20 years for secondary forests being passively restored to reach 80% and 34% of the species richness and species composition found in primary forests, respectively (Rozendaal et al., 2019). We may, therefore, simply need a longer post-treatment sampling interval before effects of the RERTA treatments on arthropod biodiversity become existent or detectable. The changes in arthropod order-level composition and spider species-level composition that we observed in this study could be indicative of forthcoming effects of the RERTA treatments on arthropod biodiversity, as the experiment becomes more established over time. For instance, spider biodiversity in the RERTA landscape may increase in ‘*Mature enriched*’ and ‘*Enriched only*’ once planted seedlings are fully grown. Previous studies have shown that the biodiversity of spiders in tropical agricultural systems increases with availability of structurally complex vegetation that can be used for web-building (Spear, 2018; Stenchly et al., 2011, 2012), which is essential to spider prey capture and reproduction (Diehl et al., 2013; Greenstone, 1984). Future studies in the RERTA Project experimental framework that are based on longer-term post-treatment data will explicitly investigate the association between changes in structural complexity, plant diversity, and biodiversity brought about by the RERTA

treatments, to identify the mechanisms interrelating these components of the oil palm ecosystem.

It is also possible that we observed no effects of the RERTA treatments on arthropod biodiversity, owing to the effects of replanting. Replanting occurred within a relatively short time period (i.e. two years) prior to our post-treatment sampling, and therefore could have outweighed any effects of the RERTA treatments. We found some evidence for this, as ‘*PrePost*’ (i.e. the model term indicating changes over time, and therefore suggesting an effect of replanting) was included in optimal models in several cases. We found that replanting increased the total abundance of arthropods in the understory microhabitat, decreased the total abundance of arthropods in the ground microhabitat, shifted the order-level composition of arthropods in all microhabitats, and changed the species-level composition of spiders in the canopy and ground microhabitats. These differences in arthropod biodiversity were likely to have been caused by changes in structural complexity and environmental conditions that resulted from replanting. Before treatment implementation, ‘*Buffer*’, ‘*Edge*’, and ‘*Core*’ areas across our study sites consisted of mature oil palm. Mature oil palm plantations are relatively homogenous in their structural complexity and environmental conditions (Luke, Advento, Aryawan, et al., 2020; Pashkevich et al., 2021). In contrast, ‘*Edge*’ and ‘*Core*’ areas (and ‘*Buffer*’ in ‘*Replant only*’) across our study sites changed substantially after replanting, owing to the replacement of mature palms with young palms. In comparison to mature palms, young palms are shorter and have a smaller frond surface area (Luskin & Potts, 2011). Additionally, young oil palm plantations have different understory vegetation composition, greater canopy openness, and higher and more variable soil temperatures (Pashkevich et al., 2021). These structural and environmental changes have previously been shown to substantially affect the biodiversity of terrestrial arthropods in the microhabitats we sampled in this study (Pashkevich et al., 2021). For instance, we previously showed that replanting increased the density of herbaceous plants in oil palm plantations, in part owing to a leguminous cover crop (*Mucuna bracteata*, in the RERTA plantations) that is planted to help maintain soil health after mature palms are cleared (Pashkevich et al., 2021). This cover crop could be an important food source for understory arthropods such as Hemiptera and Coleoptera (Blanchart et al., 2006), possibly explaining the increases in total arthropod abundance that we observed in the understory microhabitat after replanting.

Further, other local- and landscape-level factors not related to replanting may explain why we did not detect an effect of the RERTA treatments on arthropod biodiversity. At the local level, it is possible that the impacts of management occurring outside ‘*Buffer*’ may have reduced any benefits of the treatments to arthropods. For instance, although herbicides, pesticides, and chemical fertilisers were no longer applied to ‘*Buffer*’ areas after implementation of the RERTA treatments, the application of these chemicals in areas of oil palm just outside riparian buffers could have spilled over into ‘*Buffer*’ areas and affected arthropod biodiversity. Previous studies in oil palm have shown that arthropods can be sensitive to changes in fertiliser and herbicide management (Darras et al., 2019). At the landscape level, it is possible that the dominance of oil palm in the wider landscape around the RERTA Project may also have reduced the ability of arthropods to respond positively to restoration, by limiting the pool of species that could move in and respond to restoration. For example, a study in the Atlantic Forest of Brazil found that the percent of natural habitat in the surrounding landscape was a critical predictor of restoration success in tropical agricultural landscapes (César et al., 2021), likely owing to the spillover of biodiversity from natural habitat to areas being restored. The RERTA Project is based more than 30 km from the nearest large patch (> 5,000 ha) of natural habitat, and therefore there is no natural habitat near it that could contribute ecologically to restoration by acting as a source of colonising species.

We also may not have detected an effect of the RERTA treatments on arthropod biodiversity owing to limitations in our study design. First, we had relatively limited replication within this study, as the RERTA treatments are replicated across only two rivers in SMARTRI plantations. Replicating the RERTA treatments across additional rivers would increase statistical power, potentially indicating that riparian restoration affects arthropod biodiversity within a two-year period. Future work in RERTA is expected to expand the experimental design to at least another river, and we will re-assess the effects of RERTA on arthropod biodiversity after this expansion has occurred. Second, it is noteworthy that we assessed the effects of the RERTA treatments on arthropods mostly at the order-level. This may have masked species-level increases in arthropod biodiversity, although our spider analyses did not suggest this was the case. Additional species-level analyses across a wider range of taxa are therefore needed to determine effects of the RERTA treatments on arthropod biodiversity over a two-year period.

Lastly, it is noteworthy that oil palm plantations are populated primarily by generalist species that can survive in disturbed habitats (Kurz et al., 2016; Pardo et al., 2019; Wang & Foster,

2015). For instance, a study in Borneo found that ant communities in oil palm plantations were characterised by generalist species (Wang & Foster, 2015). Generalist arthropod taxa in tropical systems can often readily adapt to changes in environmental conditions (Chey, 2006; Chung et al., 2000; Fayle, Edwards, et al., 2015), and may therefore be resilient to changes in oil palm management, including restoration of riparian buffers, potentially explaining the lack of clear differences in levels of arthropod biodiversity observed in this study.

#### **4.5.2 | Impacts of the RERTA riparian restoration treatments on *Edge* areas**

We found no evidence that the RERTA treatments affected the biodiversity of arthropods in ‘*Edge*’ areas within two years. This is explained partially by the lack of increase in levels of arthropod and spider biodiversity in ‘*Buffer*’ areas after the RERTA treatments were implemented. Also, it is possible that riparian buffers do not affect ecological conditions in adjacent, cultivated areas within oil palm plantations. This is supported by the results of previous studies that assessed the effects of riparian buffers on surrounding cultivated areas of oil palm. For instance, we previously showed that passively restored riparian buffers (i.e. ‘*Mature only*’ buffers) did not affect the biodiversity of arthropods or spiders in nearby cultivated areas across the oil palm commercial life cycle (Pashkevich, Luke, et al., In Review). Similarly, another study in the same plantations showed that passively restored riparian buffers (i.e. ‘*Mature only*’ buffers) did not affect levels of ecosystem functioning or multifunctionality in nearby, recently replanted cultivated areas (Woodham et al., 2019). Over time, improving the quality of vegetation within riparian buffers may increase their likelihood of affecting biodiversity in nearby cultivated areas. For example, a study in Malaysia found that riparian buffers made of remnant rainforest habitat had weak impacts on the biodiversity of dung beetles in adjacent oil palm plantations (Gray et al., 2016). A different study in Malaysia found that the abundance and species richness of butterflies in oil palm plantations decreased with distance from adjacent areas of rainforest (Lucey & Hill, 2012). Owing to this, there could be an increased chance of the RERTA treatments influencing biodiversity in nearby cultivated areas, as the planted tree species in enriched buffers (‘*Mature enriched*’ and ‘*Enriched only*’) continue to grow. However, it is noteworthy that two studies in Malaysia found that areas of rainforest did not affect the biodiversity of small mammals (Chapman et al., 2019) or ants (Lucey & Hill, 2012) in adjacent oil palm plantations. Further investigation is needed before the impacts of more-complex habitat, such as restored riparian buffers, on biodiversity in adjacent areas of oil palm plantation can be determined.

## 4.6 Conclusions and management implications

In this study, we present early before-after findings from the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project: a large-scale experiment that is testing the efficacy of different riparian restoration strategies in recently replanted oil palm plantations. Whilst we did not find that restoration treatments increased the biodiversity of arthropods and spiders in particular within two years, we did find some changes in the order-level composition of arthropods in the understory microhabitat, and species-level composition of spiders in the canopy and ground microhabitats, across time, treatments, and distances from riparian buffer treatments, suggesting possible forthcoming effects of riparian restoration on some arthropod taxa. These changes in community composition could have implications for productivity in the RERTA project landscape, as arthropods influence delivery of ecosystem services. For instance, ants influence soil fertility (Evans et al., 2011), resource removal (Griffiths et al., 2018), and decomposition and herbivory (Eycott et al., 2019); a single introduced species of weevil (*Elaeidobius kamerunicus*) is principally responsible for pollination of oil palms in Southeast Asia (Li et al., 2019); and spiders are important predators of invertebrate pests in agricultural landscapes globally (Michalko et al., 2019). The changes in arthropod order-level composition and spider species-level composition that we observed could also have knock-on consequences for the biodiversity of other groups, since arthropods affect the ecology of non-arthropod groups both by consuming them as prey, and being consumed by predators (Barnes et al., 2014). Further, shifts in arthropod community composition could indicate changes in the biodiversity of non-arthropod taxa in response to riparian restoration, since arthropod groups such as ants, beetles, aerial hymenopterans, flies, and true bugs are indicator taxa in tropical forest systems (Edwards et al., 2014).

At this point and with the available data on arthropod biodiversity, it is too early to identify whether passive or active approaches to riparian restoration provide greater ecological benefits to biodiversity in oil palm systems. However, previous studies have indicated that passive approaches to riparian restoration in oil palm systems offer limited benefits to biodiversity and ecosystem functions, and therefore it is likely more active approaches to restoring riparian buffers will be needed (Pashkevich, Luke, et al., In Review; Woodham et al., 2019). Regardless, we note that natural riparian buffers, made of rainforest that is preserved when oil palm plantations are established, must be protected whenever possible.

The RERTA riparian restoration treatments were only established within two years prior to our post-treatment sampling, and therefore the Project is still in its early days. We conclude that a longer time interval may be needed for riparian restoration to affect arthropod and spider biodiversity. If riparian restoration does prove to benefit arthropod biodiversity over time and as the RERTA treatments become more established, it may be advantageous to start riparian restoration several years before replanting so that their benefits are in full effect prior to replanting. This may better enable riparian restoration to be a tractable management strategy that can help support pre-replanting ecological conditions in replanted oil palm landscapes.

We are currently in a UN Decade on Ecosystem Restoration (<https://www.decadeonrestoration.org>), which has shone a spotlight on how restoration can benefit biodiversity, functioning, and socioeconomic conditions globally. The RERTA Project is one of only a few restoration experiments occurring in tropical agriculture (Pashkevich, d'Albertas, et al., In Review), and we believe it is a prime example of how academics and agricultural industries can collaborate to investigate tractable methods of restoring degraded tropical systems, such as oil palm. Although we found few effects of the RERTA Project on arthropods within two years, it is noteworthy that the Project is still in its early days. Future longer-term studies are needed to evaluate the effects of the RERTA Project riparian restoration treatments on oil palm ecosystems.

## Chapter 5

### **Anthropogenic disturbance reduces spider abundance and species richness, and restoration does not consistently benefit spiders in the tropics:**

#### **A meta-analysis**

##### **5.1 Abstract**

Humans are increasingly transforming natural systems globally. Human disturbance usually reduces biodiversity and changes levels of ecosystem functioning, while restoration can halt and reverse these declines by enhancing structural and ecological complexity. However, individual disturbance events and restoration initiatives are not all the same, leading to variable effects of disturbance and restoration across ecological and socio-political contexts. For example, intense and frequent disturbance can more adversely affect ecosystems, and different approaches to restoration (e.g. actively planting trees to restore forests or passively allowing native plant species to recolonise an area) can affect the speed and completeness of recovery. Understanding how ecosystems respond variably to disturbance and restoration is essential to determining the extent to which disturbed systems have changed, forecasting the impacts of future disturbance events and restoration initiatives, and identifying restoration strategies that are effective at low implementation costs. In this study, we use systematic review and meta-analysis approaches to quantify the effects of disturbance and restoration on the abundance and species richness of spiders – abundant predators that are key components of food webs in nearly all terrestrial habitats – in tropical landscapes, and identify factors influencing variation in spider responses. Our meta-analysis included 91 studies (548 individual datapoints) located across the American, African, Asian, and Australasian tropics, and were based primarily in tropical forest, savannah, and cropland habitats. Across studies, we found that disturbance reduced spider abundance and species richness. Variation in responses was related to the habitat in which studies were based. Spider abundance declined in tropical forest and savannah habitats, but not croplands. Spider species richness declined in tropical forest habitats (we lacked sufficient replication to assess variation in species richness in other habitats). Within each habitat, trends in spider abundance and species richness were sometimes affected by the type of disturbance, microhabitat in which spiders were sampled, and biome in which studies occurred. We also found that restoration did not consistently benefit tropical spiders, and variation in spider responses to restoration was not explained by any of the factors we

considered. The widespread loss of abundance and richness of spiders following disturbance in the tropics is likely to be linked to changes in structural complexity, microclimate, and prey abundance that come with disturbance. This indicates that this speciose taxon, like many others, is likely to be declining at a global scale with the continued increase of conversion of natural habitat to human-modified landscapes, such as tropical agriculture. The lack of consistent impacts of restoration is likely due to idiosyncratic responses across species and communities and variable approaches to and levels of restoration. More work is needed to identify management strategies that can help offset losses in spider biodiversity that are caused by disturbance, and to restore spider biodiversity and the ecosystem functions that spiders provide.

## 5.2 Introduction

Anthropogenic change has affected about three-quarters of terrestrial systems, and its impact on global ecosystems is increasing (Song et al., 2018; Williams et al., 2020). Human-caused habitat disturbance (hereafter, “disturbance”) is diverse, and affects systems across spatial and temporal scales. For instance, disturbance includes small-scale and immediate actions, such as mowing lawns in urban areas (Watson et al., 2020), and also large-scale changes over time, such as converting vast areas of natural habitat into agriculture (e.g. Davis et al., 2020). Although intermediate levels of disturbance can create habitat conditions that are beneficial to some groups, particularly species relying on early or mid-successional habitats (e.g. Molino & Sabatier, 2001), large-scale disturbance and consequent loss of structural complexity is usually associated with loss of biodiversity. For instance, a meta-analysis with data on nearly 27000 species from more than 11000 sites globally estimated that disturbance reduced within-site abundance and species richness by 10.7% and 13.6%, respectively (Newbold et al., 2015). In many cases, the loss of biodiversity that results from disturbance has also changed functioning of ecosystems (Newbold et al., 2020). This includes the maintenance of food webs (e.g. Barnes et al., 2017), resilience of ecosystems over time and in response to changing environmental conditions (Scheffer et al., 2001), and delivery of important ecosystem services, such as prevention of erosion and maintenance of soil fertility (Dislich et al., 2017), which can contribute to human wellbeing.

We are currently in the United Nations Decade on Ecosystem Restoration, which aims to halt and reverse the impacts of disturbance, to avoid severe consequences for natural ecosystems and people (<https://www.decadeonrestoration.org>). Restoration describes land management

strategies that enhance the structural and ecological complexity of human-modified systems, to direct them towards a historical baseline or more favourable target state (Brancalion & Chazdon, 2017; Gann et al., 2019; Rey Benayas & Bullock, 2012; Strassburg et al., 2020; Uriarte & Chazdon, 2016). Approaches to restoration are diverse and can have different objectives and benefits (for examples, see Chazdon & Brancalion, 2019; Ghazoul & Chazdon, 2017; Pashkevich, d'Albertas, et al., In Review; Suding, 2011). Restoration can be large-scale (e.g. allowing vast areas of abandoned land to recover over time; Ghazoul & Chazdon, 2017) or small-scale (e.g. minimising application of herbicides in croplands to maintain diverse and structurally complex understory vegetation communities; Luke, Advento, Aryawan, et al., 2020). When the appropriate context-dependent actions are implemented, restoration can increase biodiversity (Barral et al., 2015; Crouzeilles et al., 2016, 2017; De Beenhouwer et al., 2013; Gann et al., 2019; Jones et al., 2018; Rey Benayas et al., 2009; Tamburini et al., 2020), enhance ecosystem processes (Barral et al., 2015; De Beenhouwer et al., 2013; Gann et al., 2019; Jones et al., 2018; Shimamoto et al., 2018; Rey Benayas et al., 2009; Tamburini et al., 2020), and be financially profitable (Bradbury et al., 2021; De Groot et al., 2013; Gann et al., 2019). Restoration therefore has the capacity to improve ecological and socioeconomic conditions across degraded landscapes (Strassburg et al., 2020).

Although it is well documented that disturbance frequently affects ecosystems adversely and restoration can improve biodiversity and functioning, ecological responses to disturbance and restoration are variable across ecological, social, and political contexts. For instance, global meta-analyses have shown that ecological responses to disturbance vary across time (van Klink et al., 2020), location (Newbold et al., 2015; van Klink et al., 2020), climates and biomes (Gibb et al., 2018; Williams et al., 2020), types and intensities of disturbance (Gibb et al., 2018; Newbold et al., 2015), broad-level habitats (Newbold et al., 2015; Williams et al., 2020), microhabitats (Biswas et al., 2019; Gibb et al., 2018), and taxonomic and functional groups (Gibb et al., 2018; Newbold et al., 2020). Ecological responses to restoration can vary in a similar way (Barral et al., 2015; Crouzeilles et al., 2016, 2017; De Beenhouwer et al., 2013; Jones et al., 2018; Meli et al., 2017; Rey Benayas et al., 2009; Shimamoto et al., 2018; Tamburini et al., 2020), as well as with the restoration approach that is taken (Barral et al., 2015; Crouzeilles et al., 2017; Jones et al., 2018). Approaches to restoration fall into two broad categories (Ghazoul & Chazdon, 2017). Passive restoration (also called natural regeneration) involves abandoning active management of ecosystems and allowing them to recover over time. Active restoration involves the investment of resources (most often planting trees) to

accelerate recovery of degraded landscapes towards a target state. We urgently need to improve our understanding of how ecosystems respond variably to disturbance and restoration, in order to better quantify how systems have already changed, to forecast how future disturbance and restoration will shape global ecosystems, and to identify effective restoration strategies.

Understanding the impacts of disturbance and restoration in the tropics is particularly important, as these systems are inherently more biodiverse than temperate systems (Gaston, 2000), but are currently experiencing higher rates of habitat loss (Song et al., 2018). This is largely due to agricultural expansion (Song et al., 2018), which has caused substantial declines in tropical biodiversity and changes in ecosystem functioning (e.g. Dislich et al., 2017; Drescher et al., 2016; Foster et al., 2011). In addition, there is currently a lack of information on what restoration strategies could halt and reverse these losses (Pashkevich, d'Albertas, et al., In Review), with studies from tropical regions either missing or under-represented in many global meta-analyses of disturbance and restoration impacts (e.g. Barral et al., 2015; Prieto-Benítez & Méndez, 2011). In comparison to temperate regions, restoration of tropical landscapes could result in larger and more immediate benefits to natural systems and human societies (Strassburg et al., 2020), in part owing to the tropics having faster plant growth rates (Crouzeilles et al., 2017) and larger remaining expanses of intact habitat (Pugh et al., 2019), which could facilitate spillover of biodiversity and ecosystem services into degraded systems (Rey Benayas & Bullock, 2012).

Spiders (Arachnida, Araneae) are abundant in nearly all terrestrial ecosystems (Nyffeler & Birkhofer, 2017). They contribute to ecosystem functioning as meso-predators and provide pest control services in agricultural landscapes (Michalko et al., 2019; Nyffeler & Birkhofer, 2017). They, therefore, have both ecological and economic importance. Previous studies have shown that spiders, like other understudied arthropods (Edwards et al., 2014), can be useful indicators of environmental changes across habitats. For instance, spiders have been used as ecological indicators when assessing the impacts of cattle grazing in Australia (Churchill & Ludwig, 2004; Churchill, 1998; Houston & Melzer, 2018; Woinarski et al., 2002); expansion of rubber plantations in China (Zheng et al., 2015, 2017); and restoration of coastal sage scrub habitats in the USA (Longcore, 2003). Assessing spider responses to disturbance and restoration therefore represents a promising approach for understanding the broader impacts of disturbance on ecosystems and for identifying effective restoration approaches (Maleque et al., 2009;

Nyffeler & Sunderland, 2003; Pashkevich et al., 2021; Pashkevich, Luke, et al., In Review; Prieto-Benítez & Méndez, 2011)

This study uses systematic review and meta-analysis approaches to quantify and explain variation in the effects of disturbance and restoration on spiders in tropical landscapes. We answer the following questions: 1) What is the overall effect of disturbance and restoration on the abundance and species richness of spiders across the tropics? 2) Do trends change between three broad-level habitats ('Forest', 'Savannah', 'Cropland')? Focusing on studies within each habitat, we then ask: 3) Do trends change across types of disturbance *or* approaches to restoration (i.e. passive and active), microhabitats in which spiders were sampled, and biomes in which studies occurred?

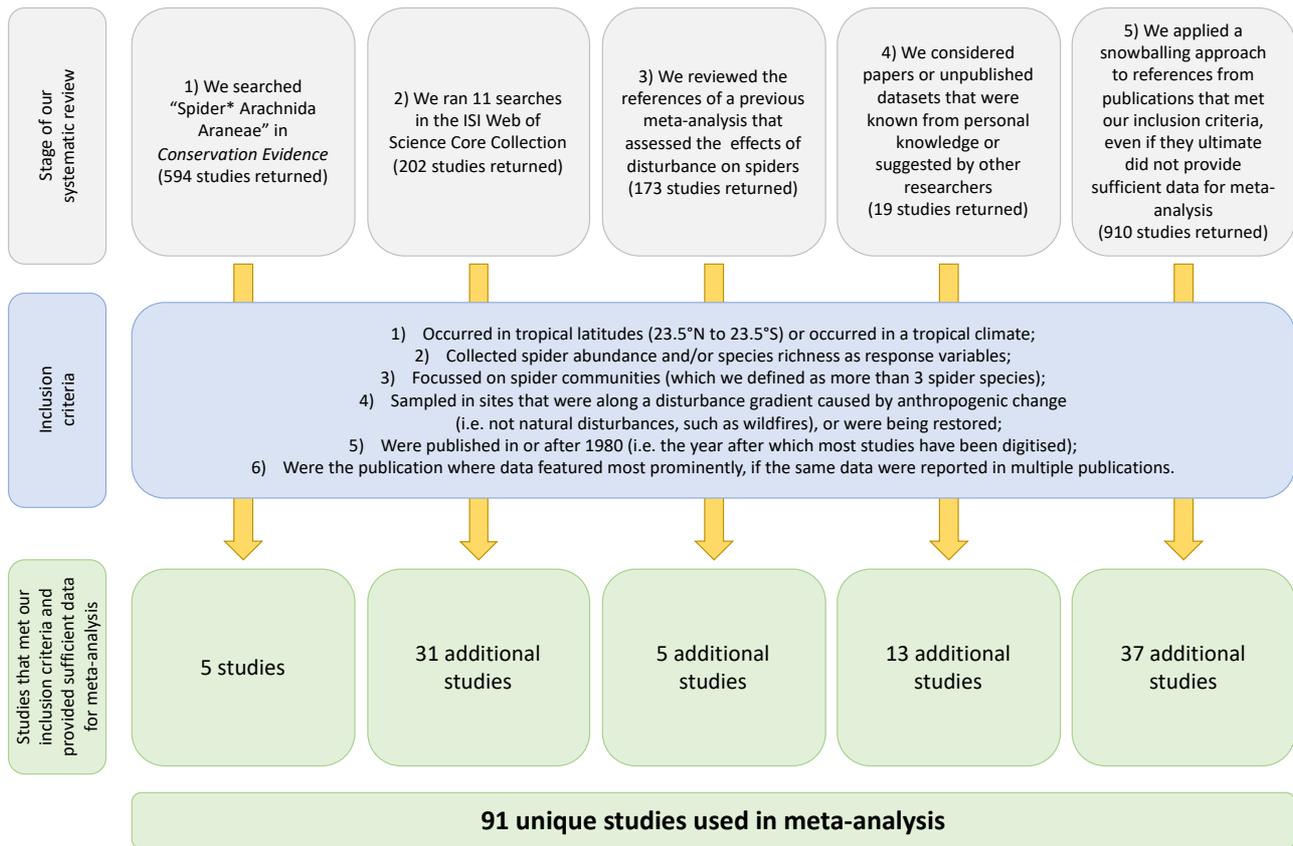
## 5.3 Methods

### 5.3.1 | Finding studies

We searched for studies with data on the effects of anthropogenic disturbance (i.e. not natural disturbance, such as wildfires) or restoration on spider abundance or species richness in the tropics, and that also met other inclusion criteria relating to study location and design (Figure 5.1). We searched for studies that focussed on disturbance and restoration across various spatial and temporal scales, including small-scale restoration actions such as planting beneficial plants within croplands (e.g. Koji et al., 2007). We focussed on abundance and species richness as response variables, as these metrics are commonly reported in the spider literature, and were the focus of a previous meta-analysis that assessed the effects of land management on spiders (Prieto-Benítez & Méndez, 2011). We acknowledge that species richness is not an ideal metric to compare biodiversity across different sites, as estimates of species richness can be affected by stochastic occurrences of rare individuals, or factors such as sampling intensity. However, it remains a tractable approach to compare effects of disturbance and restoration across studies (Fleishman et al., 2006).

We used a five-stage systematic review to identify studies to include (Figure 5.1). First, on 24 June 2020, we searched "Spider\* Arachnida Araneae" in the English databases of *Conservation Evidence*, an established online database of studies focussed on conservation interventions (Sutherland et al., 2019). Second, on 4 March 2021, we ran 11 searches in the ISI Web of Science Core Collection, which we designed to focus on tropical spiders and a variety of land

management strategies including agriculture, logging, and fire (Table S5.1). Third, we reviewed the references of a previous meta-analysis that assessed the effects of land management on spiders (Prieto-Benítez & Méndez, 2011). Fourth, we included papers or unpublished datasets that were already known by the authors in this study or were suggested to us by other researchers. Lastly, we snowballed the studies that met our inclusion criteria in stages 1-4 (Figure 5.1). This approach has previously been shown to yield high proportions of relevant studies (Greenhalgh & Peacock, 2005), and involved reviewing the references cited by a study to identify additional studies that met our inclusion criteria. We continued snowballing the references that were cited by studies that met our inclusion criteria until no more relevant studies were found. We snowballed studies even if they ultimately did not provide sufficient data for use in meta-analysis (e.g. a study that assessed the effects of disturbance on spider abundance but did not report sample sizes associated with means, therefore preventing us from calculating an effect size; see ‘*Data extraction*’ and ‘*Effect size*’ below), to maximise the number of studies captured by our systematic review. Of 1226 studies identified as being potentially relevant based on their title, we were not able to access 52 (4.2%) as full text. Many of these were conference proceedings or theses. In all stages of our systematic review, we screened studies for relevance by reading the study title and abstract, and, if we were still unsure whether a study met our inclusion criteria, by reading it in full. We included studies in all languages (translating studies as needed using Google Translate; <https://translate.google.co.uk>), as ignoring non-English studies can bias the findings of systematic reviews (Konno et al., 2020). However, as our initial search strings were only in English, we acknowledge that there was still language bias. We included studies from both the published and grey literature.



**Figure 5.1.** We systematically searched for studies that assessed the effects of disturbance or restoration on spider abundance or species richness in the tropics, and that met other inclusion criteria relating to study location and design. Our search occurred in five stages. First, on 24 June 2020, we searched “Spider\* Arachnida Araneae” in the English databases of Conservation Evidence (Sutherland et al., 2019). Second, on 4 March 2021, we ran 11 searches in the Web of Science Core Collection. Third, we reviewed the references of a previous meta-analysis that focussed on the effects of disturbance on spiders (Prieto-Benítez & Méndez, 2011). Fourth, we included some studies and unpublished datasets that were known from personal knowledge, or suggested by other researchers. Finally, we applied a snowballing approach to references from publications found in phases 1–4 that met our inclusion criteria (including studies that ultimately did not provide sufficient data to be included in our meta-analysis). We continued snowballing until we found no more studies that met our inclusion criteria. We found 91 unique studies with data that could be used in meta-analysis.

### 5.3.2 | Data extraction

We aimed to extract data on how spiders were sampled in all sites within studies that met our inclusion criteria (Table 5.1). For each study, we recorded the publication year; location (continent, country, and spatial coordinates); Whittaker biome (calculated from spatial coordinates); broad-level habitat; type of disturbance or approach to restoration being studied; and the season, methodology, and microhabitat from which spiders were sampled. We also recorded the study design (according to Christie et al., 2020), as this can bias the findings of conservation-focussed research (Christie et al., 2020). Further, for studies on restoration, we recorded the time elapsed since restoration began, as this can predict completeness of recovery in areas that are being restored (Crouzeilles et al., 2016, 2017; Meli et al., 2017). We used Plot Digitizer Version 2.6.8 (Huwaldt, 2015) to extract means, sample sizes, and standard deviations from plots if these data were not published in text or tables. We contacted authors when we could not find data within studies, or if published data were unclear. When authors shared their raw data, we calculated means, standard deviations, and sample sizes ourselves, splicing data by season, sampling method, and microhabitat, or as directed by the authors based on their knowledge of the study system. We partially excluded data from studies that occurred within experimental frameworks that did not focus wholly on disturbance or restoration. For example, Maas et al. (2013) sampled spiders within sites along a disturbance gradient, but also within an experimental framework that excluded birds and bats from set areas. In this case, we did not extract data from sites affected by the exclusions, but instead extracted control data from habitats along the disturbance gradient. When studies reported data along a time series and where possible, we aggregated data into independent samples. Lastly, we assigned a score, either “1” or “2”, for each study based on the spatial and temporal distancing and replication of its samples. “2” indicated studies with samples that were spatially and/or temporally independent and replicated, and “1” indicated otherwise. We used these scores to conduct assessments of whether initial findings from our meta-analysis held true when differences in sampling designs were considered (see ‘*Statistical analyses*’ below). One author (Pashkevich) initially extracted all data, with a second author (Kemenes) subsequently reading all studies in full and independently extracting data, to allow checking for consistency in data extraction. We found 91 unique studies with data that could be used in meta-analysis (Figure 5.1; Table S5.2-5; Supplementary Text 5.1).

Studies that focussed on disturbance often did not sample in pristine sites, but rather in less-disturbed and more-disturbed areas. We hereafter collectively refer to pristine and least-

disturbed sites within disturbance-focussed studies as ‘control sites’, and more-disturbed sites as ‘treatment sites’. For studies that focussed on restoration, we refer to unrestored areas as ‘control sites’ and restored areas as ‘treatment sites’. We refer to comparisons of treatment and control sites within a study as ‘treatment-control comparisons’. Individual studies often sampled in multiple control and treatment sites. Some studies assessed the effects of both disturbance and restoration. For instance, Spear (2016) studied how degradation (i.e. disturbance) and enhancement (i.e. restoration) of understory vegetation affected spiders in oil palm plantations. In these cases, data were included accordingly in both our disturbance and restoration analyses. Other studies sampled in areas that were pristine, continuously disturbed, and undergoing natural regeneration. In these cases, to maintain independence and ensure the same sites did not feature in both our disturbance and restoration analyses, we selected the pairwise comparison for our analyses based on the main question being considered in the studies. For example, in the case of Mathieu et al. (2005), where the main study aim was to consider the effects of disturbance, we treated both sites that were continuously disturbed and sites undergoing natural regeneration as treatment sites, and primary forest as the control site.

**Table 5.1.** Data types that were extracted from all sites within the 91 studies that were included in our meta-analysis. The type of data is listed on the left ('Variable'), and values within each variable that were found across studies are listed on the right ('Found values'). We classified 'Study design' according to Christie et al. (2020). We determined 'Whittaker biome' from the spatial coordinates of each study. Studies in the 'Temperate seasonal forest' biome either occurred in tropical latitudes, or were listed by their authors as being in a tropical climate. We found that most studies were based in three broad-level habitats ('Forest', 'Savannah', and 'Cropland'). We classified other broad-level habitats ('Dryland', 'Grassland', 'Pasture', and 'Rupestrian field', which is a specialised montane habitat in Brazil) as 'Other', owing to low sample size.

<b>Variable</b>	<b>Found values</b>
Publication year	1980 - 2021
Continent	'Africa', 'Asia', 'Australia', 'North America', 'South America'
Country	'Australia', 'Bolivia', 'Brazil', 'Cameroon', 'China', 'Colombia', 'Costa Rica', 'Côte d'Ivoire', 'Ecuador', 'Ethiopia', 'Honduras', 'India', 'Indonesia', 'Kenya', 'Malaysia', 'Martinique', 'Mexico', 'Nicaragua', 'Philippines', 'Senegal', 'Taiwan', 'Trinidad & Tobago', 'United States', 'Vietnam'
Spatial coordinates	EPSG: 4326 coordinates
Whittaker biome	'Temperate seasonal forest', 'Tropical rainforest', 'Tropical seasonal forest/savannah', 'Subtropical desert'
Broad-level habitat	'Forest', 'Savannah', 'Cropland', 'Other'
Type of disturbance	'Conversion to cropland', 'Multiple disturbances', 'Clearance of landscapes', 'Conversion to pasture', 'Logging', 'Fire', 'Forest fragmentation', 'Intensification of agricultural management', 'Increased application of pesticides'
Approach to restoration	'Active', 'Passive'
Time elapsed since restoration began	Ranged from < 1 month to > 10 years. Some studies did not report the time elapsed since restoration began.
Sampling season	'Dry', 'Wet', 'Both'
Sampling methodology	'Pitfall trap', 'Soil extraction', 'Litter extraction', 'Visual survey', 'Hand collection', 'Beat stick', 'Multiple methods', 'Sweep net', 'Insecticide fogging', 'Vacuum suctioning', 'Vegetation extraction', 'Sticky trap'
Sampling microhabitat	'Aerial', 'Understory', 'Ground', 'Soil', 'Multiple microhabitats'
Study design	'Control-Impact', 'Before-After Control Impact', 'Randomised Control-Impact'
Response	Mean spider abundance and/or richness in control and treatment sites, and associated sample sizes and standard deviations
Sampling design score	'1' (samples not spatially or temporally independent or replicated), '2' (samples spatially and/or temporally independent and replicated)

### 5.3.3 | Effect size

We used *Hedges' D* as an effect size measure to assess differences in spider abundance and species richness between control and treatment sites. *Hedges' D* quantifies differences in means, and weights differences by the standard deviation and sample size contributing to each mean (Supplementary Equation 5.1). In practice, this means that datasets with larger sample sizes and less variation are given more weight in analyses. We used *Hedges' D* because it is a standardised effect size measure that allows meaningful comparisons across studies that sample in different ways (Borenstein et al., 2009), as was the case in our meta-analysis. We interpreted *Hedges' D* using the framework of Cohen (1988): 0 is no effect;  $\pm 0.2$  is a small effect;  $\pm 0.5$  is a medium effect;  $\pm 0.8$  is a large effect that is immediately obvious. As studies often reported data from multiple control and treatment sites, we calculated *Hedges' D* for each treatment-control comparison within a study. In two treatment-control comparisons of spider abundance (one each from Cabra-García et al. (2010) and Franco et al. (2016)) and one treatment-control comparison of spider species richness (from Cabra-García et al. (2010)), the mean and standard deviation in control and treatment sites was zero. We, therefore, could not calculate *Hedges' D* for these datapoints, owing to zeroes in the denominator (see Supplementary Equation 5.1), but interpolated *Hedges' D* and variance values as zero.

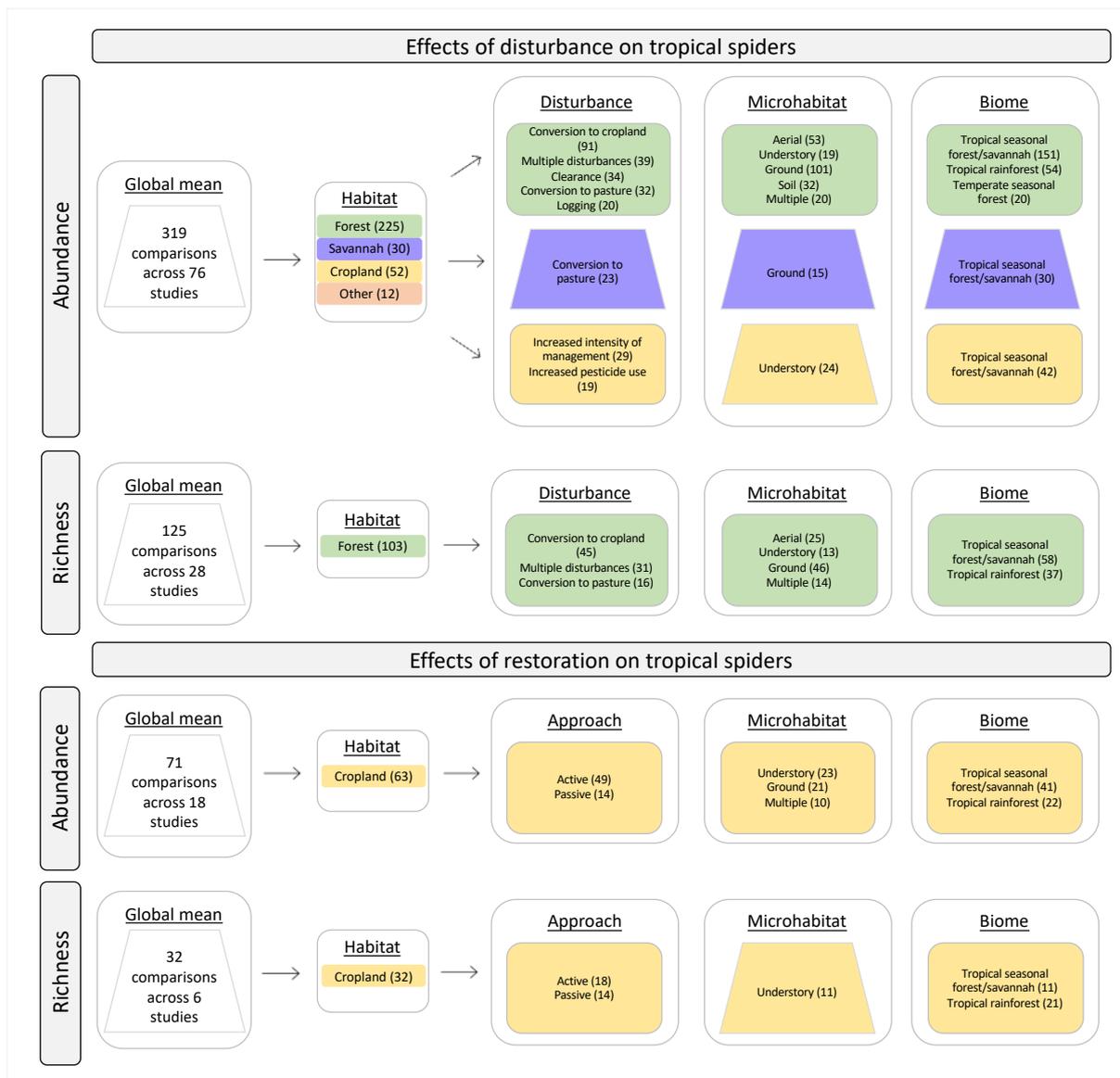
### 5.3.4 | Statistical analyses

All statistical analyses were conducted in R version 4.0.5 (R Core Team, 2018) in RStudio Version 1.4.1106 (R Studio Team, 2018). We used the packages *readxl* (Wickham et al., 2019), *tidyverse* (Wickham, 2017), *zoo* (Zeileis et al., 2019), *data.table* (Dowle et al., 2019), *plyr* (Wickham, 2016), and *cowplot* (Wilke, 2019) for data wrangling, exploration, and visualisation. Exploration followed Zuur, Ieno, and Elphick (2010). We fitted all models using *metafor* (Viechtbauer, 2020).

#### 5.3.4.1 | Effects of disturbance on spiders in the tropics

We constructed meta-analytic models to separately assess the effects of disturbance on spider abundance and species richness, using *Hedges' D* as our response variable. We fitted all models to normal distributions using restricted maximum likelihood (REML), and included a nested random effect of control site ('*Control*') within study ('*Study*'), as intra-study comparisons were more likely to be similar, and to account for those studies that sampled in multiple control and/or treatment sites. We first constructed a random effects model (function *rma.mv*;

Viechtbauer, 2020) to calculate an overall effect of disturbance on spider abundance and species richness across sites ( $Hedges \sim 1 + (1 | Study/Control)$ ). We then used meta-regression to explore whether broad-level habitat explained variation in each response ( $Hedges \sim Habitat + (1 | Study/Control)$ ). Within each broad-level habitat, we conducted further meta-regression analyses to explore the influence of three factors – broad-level type of disturbance ( $Hedges \sim Disturbance + (1 | Study/Control)$ ), microhabitat in which spiders were sampled ( $Hedges \sim Microhabitat + (1 | Study/Control)$ ), and biome in which the study was based ( $Hedges \sim Biome + (1 | Study/Control)$ ) – on each response. We chose these three factors, as they have previously been shown to influence ecological responses to disturbance (Biswas et al., 2019; Gibb et al., 2018; Newbold et al., 2015; Williams et al., 2020), and are also widely reported across studies in the relevant literature. Our meta-regression analyses were designed to calculate a mean effect of disturbance for each factor level within the covariate in our model, and therefore we included factor levels in our models only if they had sufficient replication for meaningful interpretation ( $n \geq 10$  treatment-control comparisons; Harrell (2001); Figure 5.2). We suppressed the intercept in all models so that we could determine which factor levels had estimated effect sizes that differed significantly from zero (i.e. to identify factor levels where spider abundance or species richness differed significantly across control and treatment sites).



**Figure 5.2.** We conducted four series of analyses to separately assess the effects of disturbance (upper panel) and restoration (lower panel) on the abundance and species richness of tropical spiders. Within each analysis, we first constructed a random effects model to estimate an overall effect (‘Global mean’) across studies. We then used meta-regression to determine whether broad-level habitat (‘Habitat’) affected each response. Within each broad-level habitat, we conducted further analyses to explore whether type of disturbance (‘Disturbance’) or approach to restoration (‘Approach’), microhabitat in which spiders were sampled (‘Microhabitat’), or biome (‘Biome’) affected each response. For these analyses, we only included factor levels in our models only if they had sufficient replication for meaningful interpretation ( $n \geq 10$  treatment-control comparisons; Harrell (2001)). Factor levels that had sufficient replication to be included in the model are noted within each trapezium (random

effects model) and rectangle (mixed effects model) shape on the figure. Trapezia and rectangles are coloured according to the broad-level habitat in which studies occurred: ‘All data’ (white), ‘Forest’ (green), ‘Savannah’ (purple), ‘Cropland’ (yellow), and ‘Other’ (orange). We did not explore how type of disturbance, microhabitat, or biome affected responses in ‘Other’, as this category included studies from widely differing habitat types and was, therefore, excluded from our broad-level habitat meta-regression analyses. Numbers in brackets indicate the number of treatment-control comparisons within each factor level in an analysis.

We conducted up to three sensitivity analyses for each model, to determine the robustness of our original findings. First, we re-ran each model after eliminating any outliers that were identified during data exploration (hereafter, “*No outliers*” sensitivity analysis). We then re-ran models using only studies that emphasised spatial and temporal independence in their sampling design (i.e. studies that had a sampling design score of ‘2’; hereafter, “*Studies*” sensitivity analysis). Finally, we re-ran models after eliminating outliers, and using datapoints from studies that emphasised spatial and temporal independence in their sampling design (hereafter, “*No outliers and studies*” sensitivity analysis). In the text, we only report findings from our sensitivity analyses when they differed from the findings of the original model.

When applicable (Figure 5.2), we determined the significance of broad-level habitat, type of disturbance, microhabitat, and biome to each meta-regression model, by comparing fitted models with null models using omnibus tests (reported as ‘*QM*’; Viechtbauer, 2020). If omnibus tests indicated that a factor significantly affected the response ( $P < 0.05$ ), we classed factor levels as having significant changes in spider biodiversity if the 95% confidence intervals around their estimated effect sizes differed significantly from zero.

We validated our models by plotting histograms of their raw, standardised, and student residuals, and ensuring a normal distribution was present. We also plotted residuals against covariates that were included in the model to verify that no patterns were present. We determined whether *Control* should be included as a nested random effect in each model by constructing profiles of the restricted log-likelihood (function *profile*; Viechtbauer, 2020). We updated models so that they did not include *Control* when profile plots did not peak at the corresponding REML estimate (Viechtbauer, 2020). We did not use funnel plots to test for

publication bias, as our models had random and mixed-effect model structures (Lajeunesse, 2009).

#### **5.3.4.2 | Effects of restoration on spiders in the tropics**

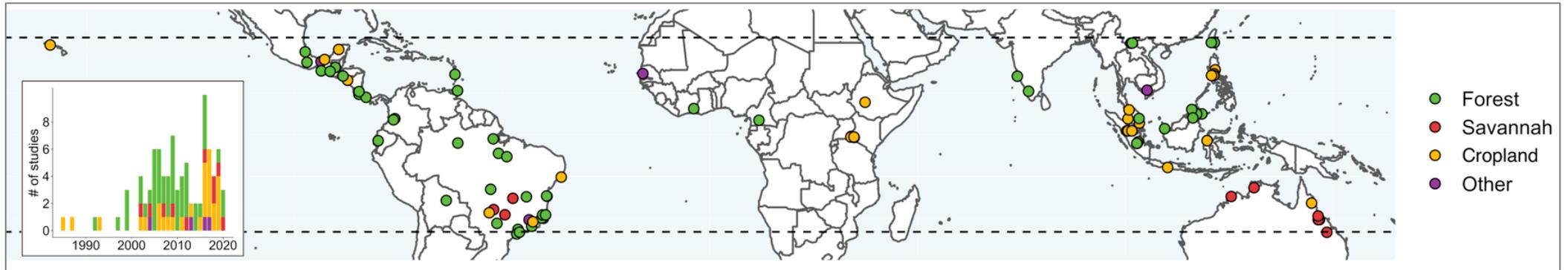
We assessed the effects of restoration on spider abundance and species richness using a comparable methodology to our disturbance analyses (Figure 5.2). However, our meta-regression analyses within each broad-level habitat focussed on the approach to restoration (i.e. active or passive restoration,  $Hedges \sim Approach + (1 | Study/Control)$ ), microhabitat in which spiders were sampled ( $Hedges \sim Microhabitat + (1 | Study/Control)$ ), and biome ( $Hedges \sim Biome + (1 | Study/Control)$ ). Although the time elapsed since restoration began is an important predictor of successful restoration (Crouzeilles et al., 2016, 2017; Meli et al., 2017), we did not include this covariate in our modelling since it was not reported in several studies.

### **5.4 Results**

#### **5.4.1 | Descriptive analysis**

The 91 studies we found mostly occurred in the American and Asian tropics, and were mostly published after the year 2000 (Figure 5.3; Table 5.2). 71 studies had control-impact designs, 13 had randomised control-impact designs, and 7 had before-after control-impact designs. The majority assessed spider responses to disturbance, and a smaller number of studies focussed on restoration (Table 5.2). Studies that focussed on disturbance mostly occurred in ‘Forest’, with ‘Cropland’ and ‘Savannah’ being the next most studied habitats (Table 5.2). Across habitats, ‘Conversion to cropland’, ‘Multiple disturbances’, ‘Conversion to pasture’, and ‘Clearance of landscapes’ were the most studied types of disturbance; ‘Ground’, ‘Aerial’, and ‘Understory’ were the most studied microhabitats; and ‘Tropical seasonal forest / savannah’ and ‘Tropical rainforest’ were the most studied biomes (Table 5.2).

Studies that focussed on restoration mostly occurred in ‘Cropland’, with remaining studies in ‘Savannah’ (Table 5.2). Across ‘Cropland’ and ‘Savannah’ habitats, ‘Active’ approaches to restoration were most studied; ‘Understory’ and ‘Ground’ were the most studied microhabitats; and ‘Tropical seasonal forest / savannah’ and ‘Tropical rainforest’ were the most studied biomes (Table 5.2). Studies assessed the effects of restoration across various time scales, as the time elapsed since restoration began varied from less than one month (Koji et al., 2007) to more than 10 years (Pashkevich et al., Unpublished).



**Figure 5.3.** Map showing the location of the 91 studies that were included in our meta-analysis. Studies occurred within 24 countries located across the American, African, Asian, and Australasian tropics. The dotted horizontal lines indicate the Tropic of Cancer (top) and Tropic of Capricorn (bottom). Point colour indicates the broad-level habitat ('Forest', 'Savannah', 'Cropland', 'Other') in which studies occurred. The inset map shows the year in which studies were published. Bars in the inset map are stacked, and therefore the height of the stack of bars indicates the number of published studies per year that were used in our meta-analysis. Three unpublished studies – Pashkevich, Luke, et al. (In Review), Pashkevich et al. (Unpublished), and Ramos et al. (Unpublished) – are not represented in the inset chart.

**Table 5.2.** Treatment-control comparisons from all sites within the 91 studies in our meta-analysis. We have aggregated these data in the table by their broad-level habitat, type of disturbance, approach to restoration, microhabitat, and biome (left-most column). Dashes indicate that type of disturbance was not relevant to our restoration analyses, and approach to restoration was not relevant to our disturbance analyses.

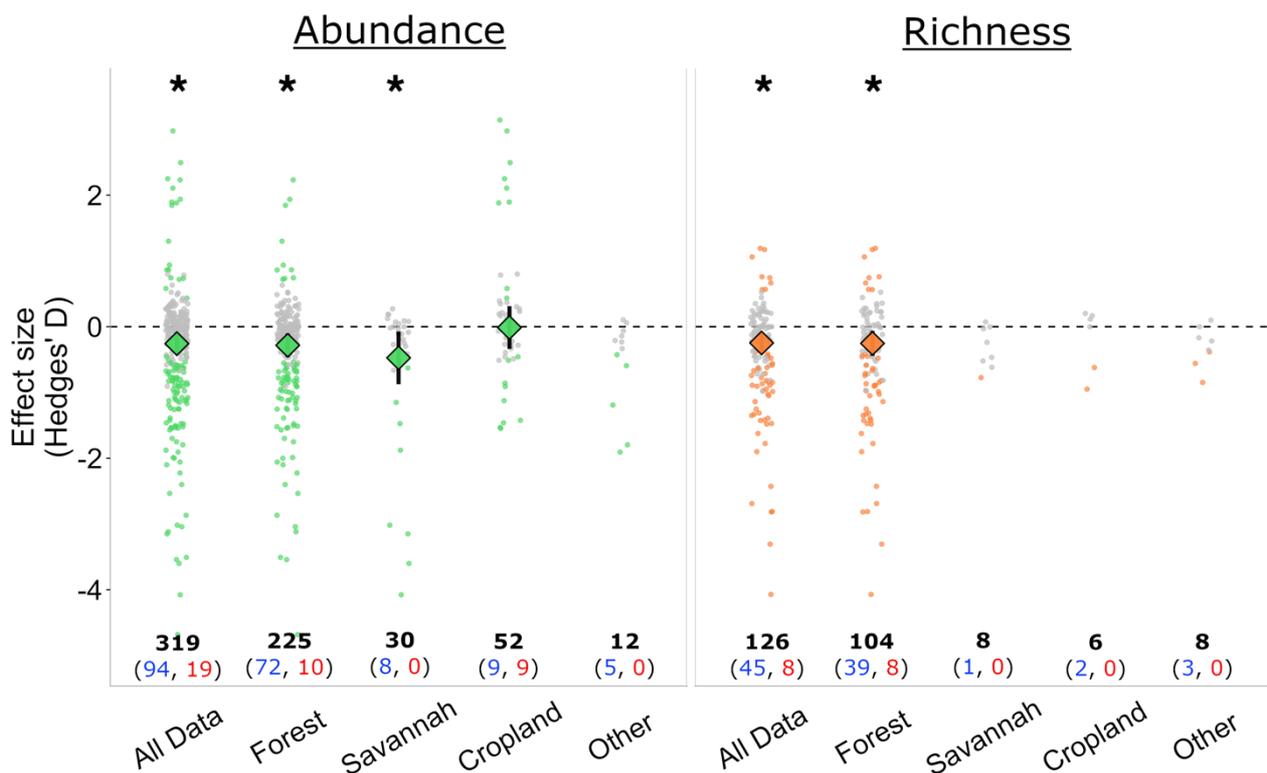
	<b>Disturbance</b>		<b>Restoration</b>	
	<b>Abundance</b>	<b>Richness</b>	<b>Abundance</b>	<b>Richness</b>
<b>Total</b>	319	126	71	32
<b>Habitat</b>				
Forest	225	104	0	0
Savannah	30	8	8	0
Cropland	52	6	63	32
Other	12	8	0	0
<b>Type of disturbance</b>				
Conversion to cropland	94	47	-	-
Multiple disturbances	47	41	-	-
Conversion to pasture	55	20	-	-
Logging	20	2	-	-
Clearance of landscapes	41	8	-	-
Fire	9	0	-	-
Forest fragmentation	5	2	-	-
Intensification of crop management	29	5	-	-
Increased application of pesticides	19	1	-	-
<b>Approach to restoration</b>				
Active	-	-	49	18
Passive	-	-	22	14
<b>Microhabitat</b>				
Aerial	59	26	8	8
Understory	49	17	29	11
Ground	132	63	23	8
Soil	44	6	1	0
Multiple microhabitats	35	14	10	5
<b>Biome</b>				
Temperate seasonal forest	24	11	0	0
Tropical rainforest	64	40	22	21
Tropical seasonal forest/savannah	225	69	49	11
Subtropical desert	6	6	0	0

## 5.4.2 | Effects of disturbance on spiders in the tropics

### 5.4.2.1 | Overall effects of disturbance, and effects of broad-level habitat

Disturbance of tropical landscapes caused small declines in spider abundance (Model estimate ( $D$ ) =  $-0.257 \pm 0.075$  (SE),  $P < 0.001$ ) and species richness ( $D = -0.250 \pm 0.076$ ,  $P = 0.001$ ) (Figure 5.4). There was large variation across treatment-control comparisons, with *Hedges' D* ranging from  $-9.26 - 3.14$  and  $-4.07 - 1.19$  for abundance and species richness, respectively.

Broad-level habitat affected trends in abundance ( $QM$  (df = 3) = 13.558,  $P = 0.004$ ), with small declines in abundance in 'Forest' ( $D = -0.282 \pm 0.092$ ,  $P = 0.002$ ) and medium declines in 'Savannah' ( $D = -0.474 \pm 0.205$ ,  $P = 0.021$ ), but no changes in 'Cropland' ( $D = -0.012 \pm 0.167$ ,  $P = 0.941$ ) (Figure 5.4). We could only calculate a mean effect for species richness in 'Forest', owing to limited number of datapoints from other habitats. In 'Forest', disturbance caused small declines in richness ( $D = -0.254 \pm 0.097$ ,  $P = 0.009$ ) (Figure 5.4).



**Figure 5.4.** Effects of disturbance on the abundance and species richness of tropical spiders in all habitats ('All Data') and the four broad-level habitats in which spiders were sampled: 'Forest', 'Savannah', 'Cropland, and 'Other'. Diamonds and corresponding error bars indicate the mean effect size across all treatment-control comparisons. Diamonds over which asterisks

are placed indicate significant changes in spider abundance and species richness, as indicated by our modelling. We only calculated mean effect sizes when there was sufficient replication ( $n \geq 10$  treatment-control comparisons). In our abundance analysis, although there was  $n = 12$  for ‘Other’, no mean effect size is shown, as this category included studies from widely differing habitat types that were not comparable. ‘Other’ was, therefore, excluded from our broad-level habitat meta-regression analyses. ‘Other’ is included here for comparative purposes only. Individual points represent a single treatment-control comparison within a study. Grey points are treatment-control comparisons with a non-significant difference in means (i.e. where the standard deviation of *Hedges’ D*, which is not shown, overlapped with zero, which is represented by the horizontal dotted line), and green and orange points are treatment-control comparisons with significantly different means for abundance and richness, respectively. Numbers in bold indicate the total numbers of treatment-control comparisons, blue numbers indicate the number of treatment-control comparisons with a significantly negative value of *Hedges’ D* (i.e. fewer spiders or fewer spider species in treatment sites), and red numbers indicate the number of treatment-control comparisons with a significantly positive value of *Hedges’ D* (i.e. more spiders or more spider species in treatment sites). One treatment-control comparison of spider abundance in ‘Forest’ (Calvi et al., 2010) is not shown, as its *Hedges’ D* value was -9.3, and therefore its inclusion on plots did not allow good visualisation of mean effect sizes.

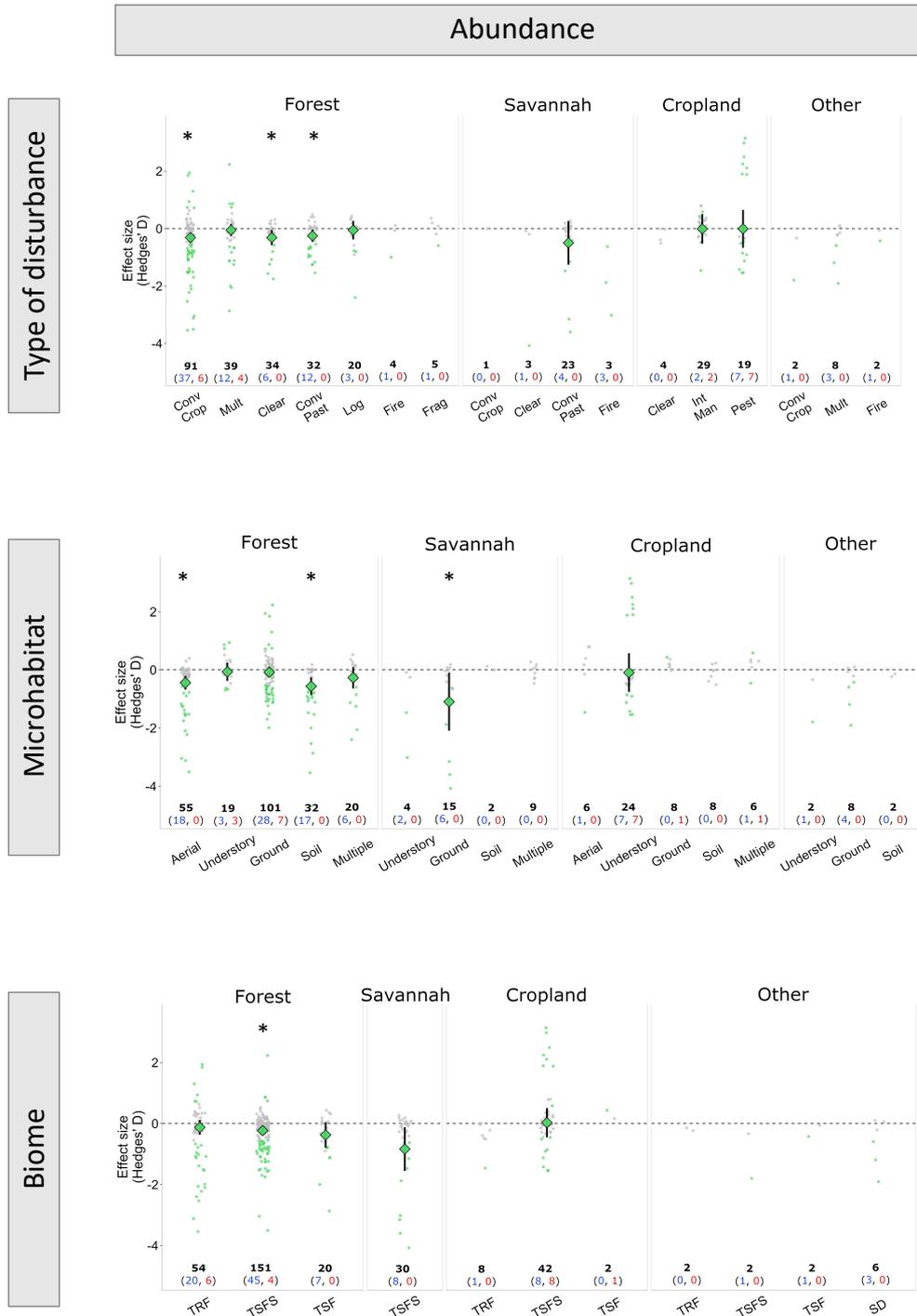
#### 5.4.2.2 | Effects of type of disturbance, microhabitat, and biome

Type of disturbance affected trends in spider abundance in ‘Forest’ ( $QM (df = 5) = 16.079, P = 0.007$ ) but not in ‘Cropland’ ( $QM (df = 2) = 0.002, P = 0.999$ ) (Figure 5.5). In ‘Forest’, ‘Conversion to cropland’ ( $D = -0.313 \pm 0.091, P < 0.001$ ), ‘Clearance of landscapes’ ( $D = -0.315 \pm 0.135, P = 0.020$ ), and ‘Conversion to pasture’ ( $D = -0.251 \pm 0.110, P = 0.022$ ) caused small declines in spider abundance, but ‘Logging’ and ‘Multiple disturbances’ had no effect (‘Logging’:  $D = -0.054 \pm 0.166, P = 0.742$ ; ‘Multiple disturbances’:  $D = -0.051 \pm 0.111, P = 0.644$ ). In ‘Savannah’, owing to low sample sizes in other disturbance types, we could only calculate a mean effect for abundance after ‘Conversion to pasture’, which had no effect on spider abundance ( $D = -0.498 \pm 0.389, P = 0.200$ ). Type of disturbance also affected trends in spider species richness in ‘Forest’ ( $QM (df = 3) = 10.887, P = 0.012$ ), with ‘Conversion to cropland’ causing a small to medium decline in species richness ( $D = -0.382 \pm 0.122, P =$

0.002), but ‘Multiple disturbances’ ( $D = -0.095 \pm 0.132, P = 0.474$ ) and ‘Conversion to pasture’ ( $D = -0.272 \pm 0.144, P = 0.058$ ) having no effect (Figure 5.6).

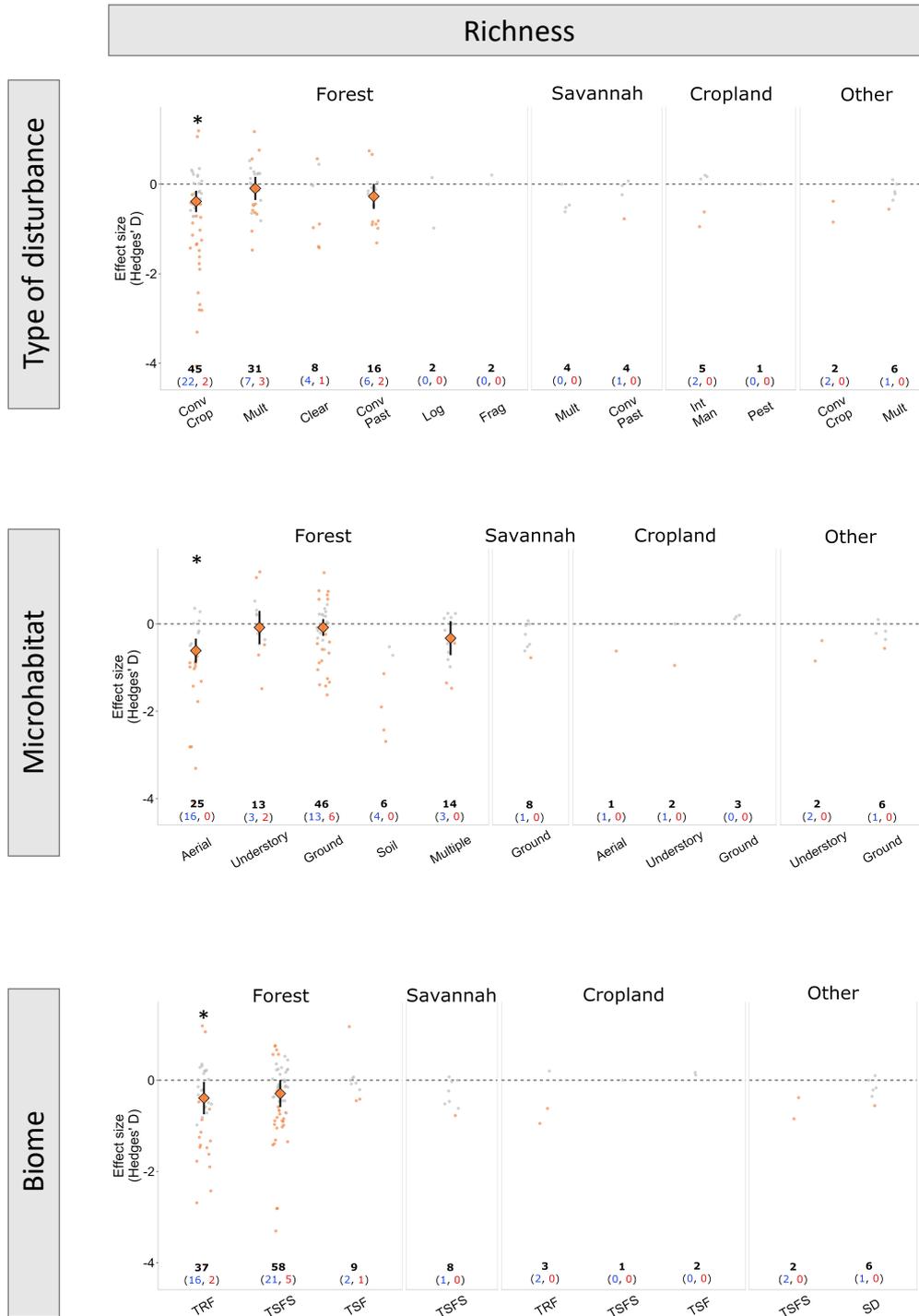
Microhabitat affected trends in spider abundance in ‘Forest’ ( $QM(df = 5) = 28.304, P < 0.001$ ), with medium declines in abundance in ‘Aerial’ ( $D = -0.444 \pm 0.120, P < 0.001$ ) and ‘Soil’ ( $D = -0.563 \pm 0.153, P < 0.001$ ), but no changes in ‘Understory’ ( $D = -0.066 \pm 0.161, P = 0.680$ ), ‘Ground’ ( $D = -0.078 \pm 0.083, P = 0.344$ ), or ‘Multiple’ ( $D = -0.269 \pm 0.189, P = 0.156$ ) (Figure 5.5). In ‘Savannah’, owing to low sample sizes in other microhabitats, we could only calculate a mean effect for abundance in ‘Ground’, where disturbance caused large declines in abundance ( $D = -1.098 \pm 0.508, P = 0.031$ ). In ‘Cropland’, we could only explore trends in abundance in ‘Understory’, where there were no changes ( $D = -0.092 \pm 0.341, P = 0.787$ ). Microhabitat also affected trends in spider species richness in ‘Forest’ ( $QM(df = 4) = 21.798, P < 0.001$ ), with disturbance causing medium declines in species richness in ‘Aerial’ ( $D = -0.611 \pm 0.142, P < 0.001$ ), but no changes in ‘Understory’ ( $D = -0.080 \pm 0.194, P = 0.679$ ), ‘Ground’ ( $D = -0.080 \pm 0.099, P = 0.418$ ), or ‘Multiple’ ( $D = -0.323 \pm 0.199, P = 0.101$ ) (Figure 5.6).

Biome affected trends in spider abundance in ‘Forest’ ( $QM(df = 3) = 11.400, P = 0.010$ ), with disturbance causing small declines in abundance in ‘Tropical seasonal forest/savannah’ ( $D = -0.233 \pm 0.083, P = 0.005$ ), but no changes in ‘Temperate seasonal forest’ ( $D = -0.375 \pm 0.213, P = 0.079$ ) or ‘Tropical rainforest’ ( $D = -0.125 \pm 0.124, P = 0.312$ ) (Figure 5.5). Our *Studies* and *No outliers and studies* sensitivity analyses both indicated that biome did not affect trends (*Studies*:  $QM(df = 3) = 7.433, P = 0.059$ ; *No outliers and studies*:  $QM(df = 3) = 5.119, P = 0.163$ ). In ‘Savannah’, due to low sample sizes in other biomes, we could only calculate a mean effect for abundance in ‘Tropical seasonal forest/savannah’, where disturbance caused medium to large declines in abundance ( $D = -0.837 \pm 0.366, P = 0.022$ ). In ‘Cropland’, we could only calculate a mean effect for abundance in ‘Tropical seasonal forest/savannah’, where abundance did not change ( $D = 0.027 \pm 0.246, P = 0.911$ ). Biome affected trends in spider species richness in ‘Forest’ ( $QM(df = 2) = 8.381, P = 0.015$ ), with disturbance causing small to medium declines in species richness in ‘Tropical rainforest’ ( $D = -0.392 \pm 0.182, P = 0.031$ ) but no changes in ‘Tropical seasonal forest/savannah’ ( $D = -0.294 \pm 0.152, P = 0.053$ ) (Figure 5.6).



**Figure 5.5.** Effects of type of disturbance (top), microhabitat in which spiders were sampled (middle), and biome (bottom) on the abundance of tropical spiders in disturbed habitats. Each plot is faceted by the broad-level habitat in which studies occurred: ‘Forest’, ‘Savannah’, ‘Cropland, and ‘Other’. Diamonds and corresponding error bars indicate the mean effect size across all treatment-control comparisons. Diamonds over which asterisks are placed indicate significant changes in spider abundance, as indicated by our modelling. We only calculated

mean effect sizes when there was sufficient replication ( $n \geq 10$  treatment-control comparisons). Individual points represent a single treatment-control comparison within a study. Grey points are treatment-control comparisons with a non-significant difference in means (i.e. where the standard deviation of *Hedges' D*, which is not shown, overlapped with zero, which is represented by the horizontal dotted line), and green points are treatment-control comparisons with significantly different means. Numbers in bold indicate the total numbers of treatment-control comparisons, blue numbers indicate the number of treatment-control comparisons with a significantly negative value of *Hedges' D* (i.e. fewer spiders in treatment sites), and red numbers indicate the number of treatment-control comparisons with a significantly positive value of *Hedges' D* (i.e. more spiders in treatment sites). In (top), 'Conv Crop' = 'Conversion to cropland'; 'Mult' = 'Multiple disturbances'; 'Clear' = 'Clearance of landscapes'; 'Conv Past' = 'Conversion to pasture'; 'Log' = 'Logging'; 'Fire' = 'Fire'; 'Frag' = 'Forest fragmentation'; 'Int Man' = 'Intensification of agricultural management'; 'Pest' = 'Increased application of pesticides'. In (bottom), 'TRF' = 'Tropical rainforest'; 'TSFS' = 'Tropical seasonal forest/savannah'; 'TSF' = 'Temperate seasonal forest'; 'SD' = 'Subtropical desert'. One treatment-control comparison in 'Forest' ('Multiple disturbances', 'Ground', 'Tropical seasonal forest/savannah'; Calvi et al., 2010) is not shown, as its *Hedges' D* value was -9.3, and therefore its inclusion on plots did not allow good visualisation of mean effect sizes.



**Figure 5.6.** Effects of type of disturbance (top), microhabitat in which spiders were sampled (middle), and biome (bottom) on the species richness of tropical spiders in disturbed habitats. Each plot is faceted by the broad-level habitat in which studies occurred: ‘Forest’, ‘Savannah’, ‘Cropland, and ‘Other’. Diamonds and corresponding error bars indicate the mean effect size across all treatment-control comparisons. Diamonds over which asterisks are placed indicate significant changes in spider species richness, as indicated by our modelling. We only

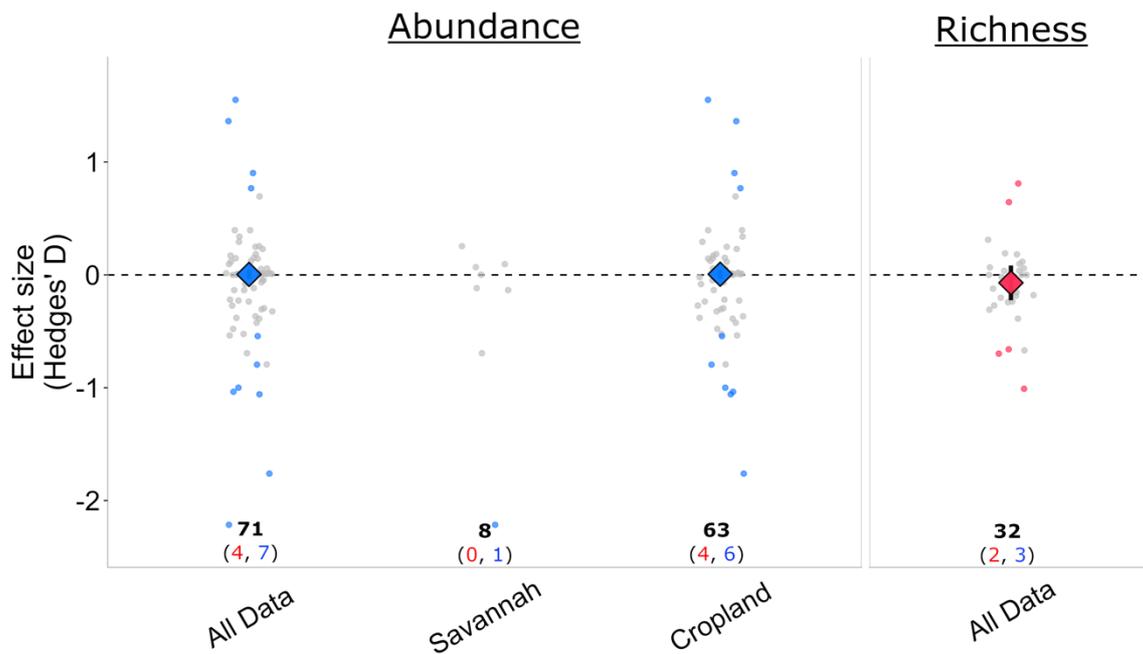
calculated mean effect sizes when there was sufficient replication ( $n \geq 10$  treatment-control comparisons). Individual points represent a single treatment-control comparison within a study. Grey points are treatment-control comparisons with a non-significant difference in means (i.e. where the standard deviation of *Hedges' D*, which is not shown, overlapped with zero, which is represented by the horizontal dotted line), and orange points are treatment-control comparisons with significantly different means. Numbers in bold indicate the total numbers of treatment-control comparisons, blue numbers indicate the number of treatment-control comparisons with a significantly negative value of *Hedges' D* (i.e. fewer spider species in treatment sites), and red numbers indicate the number of treatment-control comparisons with a significantly positive value of *Hedges' D* (i.e. more spider species in treatment sites). In (top), 'Conv Crop' = 'Conversion to cropland'; 'Mult' = 'Multiple disturbances'; 'Clear' = 'Clearance of landscapes'; 'Conv Past' = 'Conversion to pasture'; 'Log' = 'Logging'; 'Fire' = 'Fire'; 'Frag' = 'Forest fragmentation'; 'Int Man' = 'Intensification of agricultural management'; 'Pest' = 'Increased application of pesticides'. In (bottom), 'TRF' = 'Tropical rainforest'; 'TSFS' = 'Tropical seasonal forest/savannah'; 'TSF' = 'Temperate seasonal forest'; 'SD' = 'Subtropical desert'.

### 5.4.3 | Effects of restoration on spiders in the tropics

#### 5.4.3.1 | Overall effects of restoration, and effects of broad-level habitat

Restoring tropical landscapes had no effect on spider abundance ( $D = 0.004 \pm 0.020$ ,  $P = 0.830$ ) or species richness ( $D = -0.070 \pm 0.079$ ,  $P = 0.373$ ) (Figure 5.7). There was large variation across treatment-control comparisons, with *Hedges' D* ranging from  $-2.21 - 1.55$  and  $-1.01 - 0.81$  for abundance and species richness, respectively.

Owing to low sample sizes in other habitats, we could only calculate a mean effect for abundance in ‘Cropland’, where restoration had no effect ( $D = 0.006 \pm 0.020$ ,  $P = 0.767$ ). All studies that reported spider species richness occurred in ‘Cropland’ (Figure 5.7).

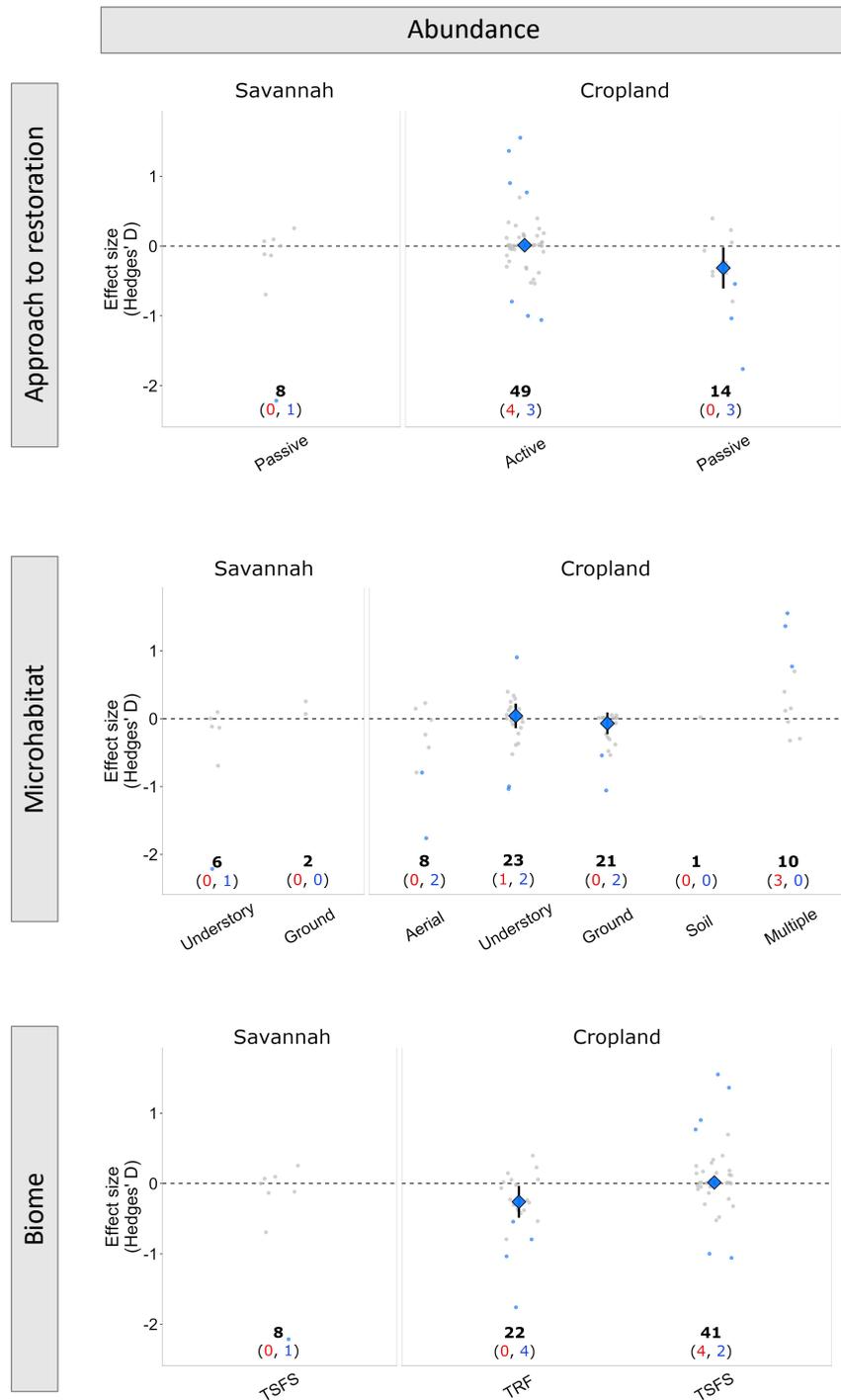


**Figure 5.7.** Effects of restoration on the abundance and species richness of tropical spiders in all habitats (‘All Data’) and the broad-level habitats in which spiders were sampled: ‘Savannah’ and ‘Cropland’. Diamonds and corresponding error bars indicate the mean effect size across all treatment-control comparisons. Diamonds over which asterisks are placed indicate significant changes in spider abundance and species richness, as indicated by our modelling. We only calculated mean effect sizes when there was sufficient replication ( $n \geq 10$  treatment-control comparisons). Individual points represent a single treatment-control comparison within a study. Grey points are treatment-control comparisons with a non-

significant difference in means (i.e. where the standard deviation of *Hedges' D*, which is not shown, overlapped with zero, which is represented by the horizontal dotted line), and blue and pink points are treatment-control comparisons with significantly different means for abundance and richness respectively. Numbers in bold indicate the total numbers of treatment-control comparisons, red numbers indicate the number of treatment-control comparisons with a significantly positive value of *Hedges' D* (i.e. more spiders or more spider species in treatment sites), and blue numbers indicate the number of treatment-control comparisons with a significantly negative value of *Hedges' D* (i.e. fewer spiders or fewer spider species in treatment sites). Only 'All Data' is included in 'Richness', as all studies reporting species richness occurred in 'Cropland'.

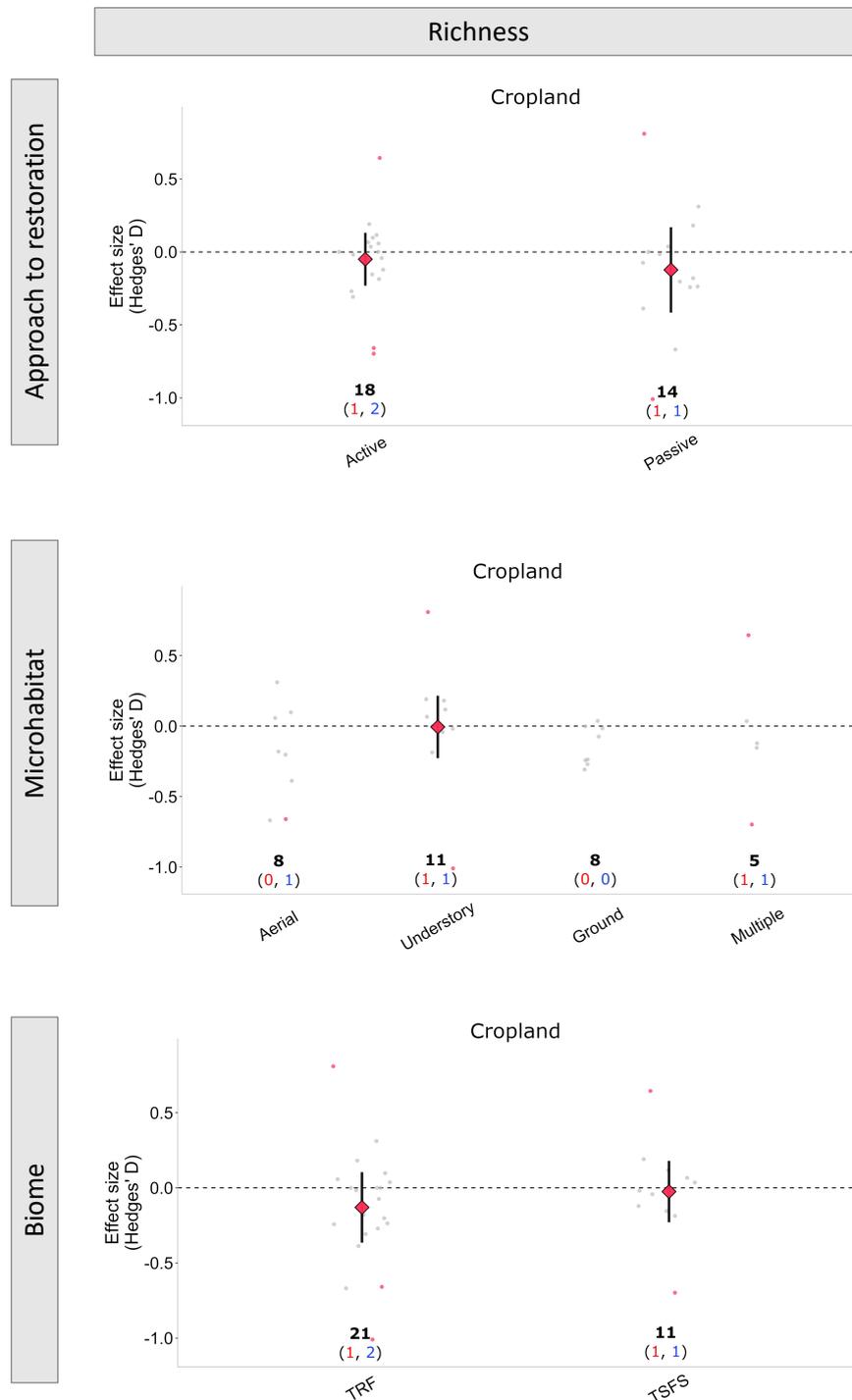
#### **5.4.3.2 | Effects of passive and active restoration approaches, microhabitat, and biome**

Spider abundance and species richness in 'Cropland' was not affected by the approach to restoration (Abundance:  $QM(df = 2) = 4.666, P = 0.097$ ; Richness:  $QM(df = 2) = 0.968, P = 0.616$ ), microhabitat (Abundance:  $QM(df = 3) = 2.325, P = 0.508$ ; Richness ('Understory' only):  $D = -0.006 \pm 0.113, P = 0.960$ ), or biome (Abundance:  $QM(df = 2) = 5.580, P = 0.061$ ; Richness:  $QM(df = 2) = 1.234, P = 0.540$ ) (Figures 5.8-9).



**Figure 5.8.** Effects of approach to restoration (A), microhabitat in which spiders were sampled (B), and biome (C) on the abundance of tropical spiders in restored habitats. Plots are faceted by the broad-level habitat in which studies occurred: ‘Savannah’ and ‘Cropland’. Diamonds and corresponding error bars indicate the mean effect size across all treatment-control comparisons. Diamonds over which asterisks are placed indicate significant changes in spider abundance, as indicated by our modelling. We only calculated mean effect sizes when there was sufficient replication ( $n \geq 10$  treatment-control comparisons). Individual points represent

a single treatment-control comparison within a study. Grey points are treatment-control comparisons with a non-significant difference in means (i.e. where the standard deviation of *Hedges' D*, which is not shown, overlapped with zero, which is represented by the horizontal dotted line), and blue points are treatment-control comparisons with significantly different means. Numbers in bold indicate the total numbers of treatment-control comparisons, red numbers indicate the number of treatment-control comparisons with a significantly positive value of *Hedges' D* (i.e. more spiders in treatment sites), and blue numbers indicate the number of treatment-control comparisons with a significantly negative value of *Hedges' D* (i.e. fewer spiders in treatment sites). In (bottom), 'TRF' = 'Tropical rainforest'; 'TSFS' = 'Tropical seasonal forest/savannah'.



**Figure 5.9.** Effects of approach to restoration (top), microhabitat in which spiders were sampled (middle), and biome (bottom) on the species richness of tropical spiders in restored habitats. All studies reporting species richness occurred in ‘Cropland’. Diamonds and corresponding error bars indicate the mean effect size across all treatment-control comparisons. Diamonds over which asterisks are placed indicate significant changes in spider species richness, as indicated by our modelling. We only calculated mean effect sizes when there was

sufficient replication ( $n \geq 10$  treatment-control comparisons). Individual points represent a single treatment-control comparison within a study. Grey points are treatment-control comparisons with a non-significant difference in means (i.e. where the standard deviation of *Hedges' D*, which is not shown, overlapped with zero, which is represented by the horizontal dotted line), and pink points are treatment-control comparisons with significantly different means. Numbers in bold indicate the total numbers of treatment-control comparisons, red numbers indicate the number of treatment-control comparisons with a significantly positive value of *Hedges' D* (i.e. more spider species in treatment sites), and blue numbers indicate the number of treatment-control comparisons with a significantly negative value of *Hedges' D* (i.e. fewer spider species in treatment sites). In (bottom), 'TRF' = 'Tropical rainforest'; 'TSFS' = 'Tropical seasonal forest/savannah'.

## 5.5 Discussion

In this meta-analysis, we used data from 91 studies to assess how anthropogenic disturbance and restoration has affected spiders in the tropics. We found that disturbance reduced spider abundance and species richness in tropical landscapes, while restoration did not consistently benefit spiders. In addition to these overall trends, we found that spider responses to disturbance and restoration varied substantially from study to study, and were therefore context-dependent. Variation in response to disturbance was affected by the broad-level habitat in which sampling occurred, with additional variation being related to the type of disturbance, microhabitat in which spiders were sampled, and biome in which studies occurred. In contrast, variation in response to restoration was not affected by broad-level habitat, approach to restoration, microhabitat in which spiders were sampled, or biome in which studies occurred.

### 5.5.1 | Effects of disturbance on spiders in the tropics

Across studies, we found that disturbance of tropical landscapes caused small declines in spider abundance and species richness, indicating that this speciose taxon, like many others (Newbold et al., 2015), is likely to be declining at a global scale with the continued modification of natural habitats. The negative effects of disturbance on spider biodiversity that we observed were likely driven by changes in environmental conditions that resulted from disturbance. For instance, disturbance can reduce the structural complexity and diversity of plants (e.g. Rembold et al., 2017), which many spiders rely on for habitat (e.g. web-building; Diehl et al., 2013;

Greenstone, 1984; Rypstra, 1983), reproduction (e.g. Spear et al., 2018; Zanatta, 2013) and, for some species, food (Nyffeler et al., 2016). Changes in plant communities that limit canopy cover may further harm spiders, by increasing the risk of desiccation in high sun exposure (Main, 1976). For instance, when comparing tropical rainforests to oil palm plantations in two regions in Sumatra, Potapov et al. (2020) found that rainforests had, on average, 25.25 and 9.25 more spiders than oil palm. Previous studies have shown that oil palm plantations are significantly drier than rainforests (Hardwick et al., 2015). Further, disturbance of tropical systems can reduce the abundance and biomass of insects, and change insect community composition. For instance, studies in Sumatra have shown that tropical rainforests can contain roughly twice the density of litter invertebrates than oil palm plantations (Mumme et al., 2015), with impacts on food web structure (Barnes et al., 2017). As spiders predominantly feed on insects, declines in insect abundance could have detrimental impacts on spider communities and potentially disrupt spider food webs.

Prieto-Benítez & Méndez (2011) previously used a meta-analysis approach to assess the effects of land management on spiders globally, and found that land use change caused medium declines in spider abundance and species richness. As we found that disturbance caused only small declines in the abundance and species richness of tropical spiders, findings across both studies indicate that disturbance in the tropics may have more muted impacts on spiders than that in other parts of the world. The differences in our findings could be explained in part by differences in disturbance patterns in tropical and temperate systems, particularly in ‘Forest’ habitats. Large-scale disturbance of tropical forest systems has increased substantially only in recent decades (Song et al., 2018), whilst disturbance of temperate forests has occurred over centuries, leaving relatively few areas of temperate forest habitat intact (Bergmeier et al., 2010). It is possible that the long-term impacts of disturbance in temperate systems caused the relatively larger declines in spider biodiversity observed by Prieto-Benítez & Méndez (2011). In addition, tropical ecosystems have the capacity to recover faster and more completely than systems at higher latitudes (Jones et al., 2018). Several of the studies in our disturbance analyses (e.g. Mathieu et al., 2005) compared spiders in pristine habitat and recovering habitats, and it is possible that recovery of these habitats was already fairly complete, mitigating the effects of disturbance observed. Differences in our findings could additionally be explained by the available studies that were included in our meta-analyses. Although Prieto-Benítez & Méndez (2011) and our current study covered a similar range of broad-level habitats and types of disturbance, the relative proportion of treatment-control comparisons across habitats and

types of disturbance was not the same. For instance, treatment-control comparisons in ‘Cropland’ represented ~ 38% of all comparisons of spider abundance in Prieto-Benítez & Méndez (2011), but only ~ 16% of all comparisons of abundance in our current study.

Although we found an overall negative effect of disturbance on the abundance and species richness of tropical spiders, we found variation in spider responses to disturbance between and within studies, with some studies finding a large positive effect on spiders, or no discernible effect on spiders at all. Our findings therefore indicate that, although disturbance usually causes losses in tropical spider biodiversity, its effects are context-dependent. Similar to other meta-analyses that have assessed ecological responses to disturbance (Newbold et al., 2015; Prieto-Benítez & Méndez, 2011; Williams et al., 2020), we found that the broad-level habitat in which studies occurred sometimes explained some of the variation in how disturbance affected spiders. Most studies that were included in our meta-analysis occurred in tropical forests (‘Forest’), where we found that disturbance caused small declines in the abundance and species richness of spiders. However, as tropical forest habitats are home to a large portion of global biodiversity (Gaston, 2000), including that of spiders (Piel, 2018), these declines could indicate large losses in spiders and changes in spider communities with disturbance. Our modelling also indicated that disturbance caused medium declines in spider abundance in ‘Savannah’, and no effect on spider abundance in ‘Cropland’. Trends in spider abundance between broad-level habitats therefore suggest that, in comparison to croplands, spiders in tropical forests and savannahs are more severely affected by disturbance. This is likely due to the more pronounced structural and ecological differences between control and treatment sites in ‘Forest’ and ‘Savannah’, relative to those in ‘Cropland’. For instance, in Baretta et al. (2007), a ‘Forest’ study, the control site was native forest, and one treatment site was a pasture area that had been accidentally exposed to intense fire prior to sampling. In comparison, in Dominik et al. (2017), a ‘Cropland’ study, both control and treatment sites were rice fields, which differed in the complexity of their surrounding landscapes. Further, spiders in ‘Cropland’ are likely generalists that survived the initial conversion of natural habitat to agricultural landscape, and therefore may be less sensitive to further disturbance effects (Potapov et al., 2020).

Within broad-level habitats, we found that the type of disturbance and microhabitat in which spiders were sampled sometimes affected spider responses to disturbance. These findings mirror the results of previous meta-analyses, which also found variability in ecological responses to disturbance due to type of disturbance and microhabitat sampled (Biswas et al.,

2019; Gibb et al., 2018; Newbold et al., 2015; Williams et al., 2020). Variation in spider abundance across types of disturbance and microhabitats was most noticeable in ‘Forest’, where we found small declines in spider abundance due to ‘Conversion to cropland’, ‘Clearance of landscapes’, and ‘Conversion to pasture’; and medium declines in spider abundance in the ‘Aerial’ and ‘Soil’ microhabitats. We also found small or medium declines in the species richness of ‘Forest’ spiders due to ‘Conversion to cropland’, and in the ‘Aerial’ microhabitat’. We found no significant changes in spider abundance or species richness due to other types of disturbance or in the remaining microhabitats we studied. In ‘Forest’, variation in spider responses to different types of disturbance may be attributed to the magnitude of difference in structural and ecological complexity between control and treatment sites across different disturbance types. Control sites in ‘Forest’ were areas of primary or secondary forest. However, depending on the type of disturbance, treatment sites ranged from being relatively minimally disturbed (e.g. in Yanoviak et al. (2003), a ‘Multiple disturbances’ study, a treatment site was areas of secondary forest that had last been disturbed 30 – 50 years prior to sampling, but had not yet reached a climax state) to highly disturbed (e.g. in several ‘Conversion to cropland’ studies, the treatment sites were intensively managed coffee plantations; Goehring et al., 2002; Marín et al., 2016; Méndez-Castro & Rao, 2014; Pellens & Garay, 1999b; Pinkus-Rendón et al., 2006; Teodoro et al., 2011). Studies in ‘Forest’ that were focussed on ‘Conversion to cropland’ could also explain why disturbance particularly affected spiders in the ‘Aerial’ and ‘Soil’ microhabitats. Croplands often have less complex canopies than tropical forests (e.g. Foster et al., 2011; Rembold et al., 2017), and many ‘Aerial’ spiders – for instance, those in web-building families such as Araneidae, Tetragnathidae, and Theridiidae – rely on structurally complex vegetation for nest construction, prey capture and shelter (Diehl et al., 2013; Greenstone, 1984; Rypstra, 1983). Similarly, croplands can have hotter, drier, and more compact soils than tropical rainforests (Hardwick et al., 2015), therefore making it more likely that ‘Soil’ spiders or their prey will desiccate, and reducing the amount of space available for hunting. In comparison, aspects of understory vegetation habitat in rainforests can be maintained or increased in croplands (Rembold et al., 2017), providing structurally complex understory vegetation for web-attachment, and contributing to small-scale heterogeneity at the surface level, possibly explaining why disturbance did not affect spiders in ‘Ground’ and ‘Understory’.

We also found that the biome in which studies occurred sometimes affected spider responses to disturbance. For instance, in ‘Forest’, disturbance caused small declines in spider abundance

in ‘Tropical seasonal forest/savannah’, and small to medium declines in spider species richness in ‘Tropical rainforest’. However, it is noteworthy that our *Studies* and *No outliers and studies* sensitivity analyses in ‘Forest’ indicated that biome was not significant to our spider abundance model. Therefore, we recommend caution in interpreting whether spider abundance responses to disturbance varied across biomes in tropical forest habitats. The similar effects of disturbance across biomes in ‘Forest’ may be driven by spider communities in different tropical regions having similar functional diversity (Cardoso et al., 2011), perhaps resulting in all communities being similarly affected by disturbance events (Tilman et al., 1997), despite differences in species identities. As “biome” is a broad classification category, further research is needed to understand how spider responses to disturbance vary with finer-scale climate and vegetative patterns.

Some treatment-control comparisons indicated that disturbance increased spider abundance (19 treatment-control comparisons) and species richness (8 treatment-control comparisons), although the frequency of these ‘positive’ comparisons was about five times less than comparisons that showed declines in spiders (94 comparisons for abundance, and 45 comparisons for species richness). Several of these ‘positive’ comparisons sampled in treatment sites that had relatively low levels of management, for instance, coffee (Marín et al., 2016; Pinkus-Rendón et al., 2006) and cacao (Maas et al., 2013) agroecosystems with a high local density of shade trees, and 50-year-old secondary forest that had previously been used for cassava production (Calvi et al., 2010). This suggests that a low level of disturbance could lead to higher levels of tropical spider biodiversity in some instances, in accordance with the intermediate disturbance hypothesis (Connell, 1978). However, we note that this effect was not supported across studies and so may be context-dependent. Additional efforts to identify conditions in which disturbance can benefit spider biodiversity could help to inform management to reduce the negative impacts of disturbance on spider communities long-term.

### **5.5.2 | Effects of restoration on spiders in the tropics**

Across studies, we found that restoration of tropical landscapes did not consistently benefit spider abundance and species richness. Further, in studies occurring in ‘Cropland’, we found no effect of restoration on spiders regardless of approach to restoration (i.e. passive or active), microhabitat in which spiders were sampled, or biome in which studies occurred. Several factors could explain why restoration is not benefitting tropical spiders. First, restoration in several studies in our meta-analysis was relatively recently initiated. For instance, working in

rice fields in the Philippines, Horgan et al. (2019) found few differences in spider abundance or species richness in areas of rice that were near clean bunds or bunds that had been planted with weedy plants or mixtures of sesame and okra. However, spiders were sampled only 60 days after treatments were implemented (Horgan et al., 2019). Previous meta-analyses have found that the time elapsed since restoration started was a principal factor in predicting successful restoration initiatives in forest habitats globally (Crouzeilles et al., 2016, 2017; Meli et al., 2017). Although we attempted to identify the time elapsed since restoration began for each study in our meta-analysis, we were not able to gather these data for several studies and therefore could not formally analyse whether this factor affected spider responses to restoration. We recommend that future studies continue to monitor the effectiveness of restoration initiatives on tropical spiders across longer time periods. Second, some studies in our meta-analysis occurred in landscapes that were largely devoid of natural habitat. For instance, Pashkevich, Luke, et al. (In Review) and Pashkevich et al. (Unpublished) sampled spiders in Indonesian oil palm plantations after restoring riparian areas using passive and active approaches. However, the sampled plantations were part of a larger matrix of oil palm, with the nearest natural habitat being > 30 km away. The proportion of natural habitat that surrounds degraded landscapes has previously been shown to be a driver of successful restoration in the tropics (César et al., 2021; Crouzeilles et al., 2016), in part owing to spillover of biodiversity and ecosystem functions from natural habitat into degraded landscapes. Restoration of highly-modified systems with little remaining natural habitat in the surrounding landscape may be less likely to produce a measurable change in spider communities. Third, many restoration initiatives are not designed specifically with invertebrates in mind, but are instead focussed on improving the biodiversity of charismatic vertebrate groups, such as mammals and birds. Whilst such restoration initiatives could have trickle-down benefits to spiders, as spider and vertebrate ecology in tropical systems is linked through multi-trophic interactions (Barnes et al., 2017), these benefits may be less pronounced, if existent at all.

Although most treatment-control comparisons indicated that restoration did not benefit spiders, some comparisons did report significant benefits. Restoration approaches that benefitted spider abundance or species richness included using push-pull methods in croplands (i.e. where crops are intercropped with plant species that deter pests; Midega et al., 2008; Midega et al., 2006), growing mahogany trees in polycultures rather than monocultures (Esquivel-Gómez et al., 2017), and maintaining mature oil palm riparian buffers in oil palm systems that had been replanted one year previously (Pashkevich, Luke et al., In Review). On the other hand, some

treatment-control comparisons indicated that restoration caused declines in spider abundance or species richness. These comparisons included maintaining mature oil palm riparian buffers in oil palm plantations that had been replanted three years previously (Pashkevich, Luke, et al., In Review), limiting pesticide and herbicide use in rice and oil palm systems, respectively (Horgan et al., 2017; Spear, 2016), intercropping broccoli and cowpea with other crops (Hooks & Johnson, 2006; Kyamanywa et al., 1993), and destocking pastures (Houston & Melzer, 2018). Our findings collectively indicate that restoration can be effective for spiders, but may also produce negative impacts. Our findings do not indicate whether passive or active approaches to restoration provide larger benefits to tropical spider communities. We recommend that further research is carried out to replicate and refine restoration strategies that have already proved effective, and to trial such approaches in a wider range of systems.

### **5.5.3 | Knowledge gaps**

The studies in our meta-analysis indicated the presence of several trends and biases in the tropical spider literature, and highlight knowledge gaps that future studies should address. First, most studies (71% of treatment-control comparisons) in our disturbance analyses occurred in ‘Forest’. These studies exhibited a fairly uniform pattern, which showed that disturbance of tropical forest typically has a small negative impact on spider abundance and species richness. In comparison, far fewer studies occurred in ‘Savannah’ and ‘Cropland’ (9% and 16% of treatment-control comparisons, respectively), and the overall effect of disturbance within these broad-level habitats was more variable. We therefore recommend that more studies are carried out in ‘Savannah’, ‘Cropland’, or other broad-level habitats that were entirely, or nearly, absent from the literature (e.g. tropical drylands and grasslands), and therefore where the effects of disturbance on spiders are relatively unknown. Additional studies in tropical savannahs may be particularly useful as, of the broad-level habitats in our meta-analysis, spider abundance in ‘Savannah’ declined most substantially, and recent increases in human pressure have disproportionately affected tropical savannah and grassland systems (Williams et al., 2020). If future studies occur in ‘Forest’, we recommend that they include types of disturbance, microhabitats, or biomes that are currently underrepresented in the literature. For instance, within ‘Forest’, the effects of fragmentation and fires started by humans on spiders are largely unstudied, and yet these disturbances are increasingly affecting mega-biodiverse tropical systems such as the Amazon rainforest (Cardil et al., 2020; Escobar, 2019). Future studies in ‘Cropland’ should assess the effects of disturbance in a variety of different crop systems, as the quality of disturbance can be related to crop type (e.g. annual crops such as soybean are

replanted yearly, but perennial crops such as oil palms are replanted only once every commercial cycle), and the functional diversity of spider assemblages has been demonstrated to vary across crop systems (Uetz et al., 1999).

Second, we found that fewer studies assessed the effects of restoration on tropical spiders, in comparison to studies focussed on disturbance. Our meta-analysis indicated that existing restoration initiatives do not consistently benefit spider biodiversity and, in some cases, have even led to declines in spider abundance and species richness. It is noteworthy that ~ 30% and ~ 65% of treatment-control comparisons in our abundance and species richness restoration analyses, respectively, occurred in one oil palm plantation site in Riau, Sumatra, Indonesia (Ashton-Butt et al., 2018; Pashkevich, Luke, et al., In Review; Pashkevich et al., Unpublished; Spear, 2016). Therefore, our findings are biased towards restoration initiatives in oil palm systems, rather than restoration of tropical landscapes as a whole. Our findings highlight the need for more research to investigate the effects of restoration strategies on a wider range of tropical systems (Di Sacco et al., 2021; Holl, 2017b; Holl & Kappelle, 1999; Pashkevich, d'Albertas, et al., In Review). Studies on restoration of tropical landscapes and, particularly, tropical agricultural landscapes (i.e. a commonly found degraded habitat across the tropics; Song et al., 2018) are relatively rare (Pashkevich, d'Albertas, et al., In Review), and less common than restoration studies in temperate systems (Barral et al., 2015). Restoring tropical landscapes with spider biodiversity in mind will require additional field experiments (Holl, 2017b; Holl & Kappelle, 1999; Holl et al., 2011; Pashkevich, d'Albertas, et al., In Review), to empirically test the effects of individual restoration strategies on spiders. As the tropics are home to a large portion of global biodiversity and have immense social, economic, and cultural value (Gaston, 2000), yet are being degraded increasingly (Song et al., 2018), increased efforts are needed to improve understanding of how to restore tropical landscapes (Holl, 2017b; Holl & Kappelle, 1999; Pashkevich, d'Albertas, et al., In Review).

Third, we found spatial (i.e. geographic) bias across studies. Most studies in our meta-analysis occurred in Central America, Brazil's Atlantic Rainforest, and the Indo-Malayan archipelago. Noticeably, and similar to most other meta-analyses focussed on the effects of disturbance and restoration globally (e.g. Crouzeilles et al., 2016, 2017; De Beenhouwer et al., 2013; Jones et al., 2018; Prieto-Benítez & Méndez, 2011), we found fewer studies occurring in the African tropics, in comparison to the American, Asian, and Australasian tropics. Global assessments show that human pressure is increasing more substantially in tropical Africa than most other

world regions (Williams et al., 2020). Therefore, we recommend that future studies focus on spider responses to disturbance and restoration in tropical Africa, to determine the extent of the declines that have already occurred, to estimate the impacts of future disturbance, and to inform restoration efforts in this biodiverse and socioeconomically and culturally important region.

Fourth, additional research that focusses on the effects of disturbance and restoration on aspects of spider biodiversity other than abundance and species richness may be useful. For instance, Potapov et al. (2020) assessed changes in spider functional ecology across a tropical land use gradient; Spear et al. (2018) studied shifts in the relationship between *Nephila* sp. and the cleptoparasites (*Argyrodes* sp.) that inhabit their webs across different vegetation complexity regimes in oil palm plantations; and González-Tokman & Martínez-Garza (2015) quantified shifts in the body condition (body size and mass, and lipid and muscle content) of *Nephila clavipes* in restoration plots where cattle had been excluded and native trees had been planted. Such work can provide a more nuanced understanding of the effects of disturbance and restoration, including impacts on species interactions and the long-term health of spider populations.

Finally, we emphasise that more consistent, long-term monitoring of spiders is needed across the tropics. Long-term monitoring is essential to understanding changes in spider communities across tropical landscapes that have been disturbed or are undergoing restoration (van Klink et al., 2020). This is particularly noteworthy for future restoration studies, as the time elapsed since restoration began varied extensively across studies in our meta-analysis, with some studies assessing the effects of restoration less than one month after implementation of restoration (e.g. Koji et al., 2007), and other studies examining the effects of restoration after more than 10 years (Pashkevich et al., Unpublished). Further, the effects of restoration can vary over time within a single study (Holl et al., 2020). We also emphasise that robust study designs, such as before-after control-impact (BACI) experiments, that maintain spatial and temporal independence of samples are critical to mitigating bias in the findings of all future studies that assess the impacts of disturbance and restoration on spiders in the tropics (Christie et al., 2020). More than three-quarters of studies in our meta-analysis had control-impact study designs, which are more likely to give biased estimates of the effects of conservation focussed research, relative to more-robust randomised control-impact and before-after control-impact designs (Christie et al., 2020).

## 5.6 Overall management implications and conclusions

The changes in spider abundance and richness caused by disturbance of tropical landscapes that we recorded in this study could have large impacts on ecosystem functions that are provided by spiders in these systems. Spiders are abundant across terrestrial habitats (Nyffeler & Birkhofer, 2017), and are important meso-predators that are key components of existing trophic networks (Barnes et al., 2014; Spear et al., 2018). Declines in spider biodiversity could, therefore, disrupt functioning of tropical habitats, including existing food webs. Within productive habitats, such as tropical agricultural systems, declines in spider biodiversity could lower crop yields and profitability, as spiders provide pest control services. A global meta-analysis found that spiders in croplands suppressed pest communities in 79% of cases, which correlated to increases in crop productivity (Michalko et al., 2019). Maintaining pest control services within farmlands will be increasingly valuable to social and natural systems as global food demands continue to rise and the amount of tropical habitat converted to agriculture continues to increase (Song et al., 2018; Tilman et al., 2017).

Our findings indicate that increased efforts are needed to conserve spiders in the tropics. Although this is true across habitats, we particularly highlight that additional conservation action may be needed in tropical savannahs, as we found that disturbance caused medium declines in spider abundance in this habitat (corresponding to the largest declines in spider abundance of any habitat), and a recent global assessment of human pressure on natural environments found that, in recent decades, human pressure has increased most substantially in tropical savannah habitats (Williams et al., 2020). Similarly, as most studies in our restoration analyses were in ‘Cropland’, additional studies that assess the effects of restoration across other degraded habitats are needed.

Ultimately, further research on the context-dependent drivers of spider responses to disturbance and restoration is needed, to improve knowledge of how disturbance and restoration has historically affected tropical spider communities; and to forecast how these communities, and the important ecosystem functions they provide, may respond to disturbance and restoration in the future. This is one of only a few meta-analyses (but see Crouzeilles et al., 2016, 2017; De Beenhouwer et al., 2013; Shimamoto et al., 2018 as exceptions) to focus on tropical ecosystem responses to restoration, and the first meta-analysis to assess the effects of restoration on tropical spider biodiversity. Importantly, as we found that restoration of tropical landscapes did

not consistently benefit spiders, this study also underscores the importance of identifying restoration initiatives that improve levels of spider biodiversity in degraded tropical landscapes. As we enter the UN Decade on Ecosystem Restoration (<https://www.decadeonrestoration.org>), we urge spider researchers and enthusiasts globally, and especially in the tropics, to commit to improving understanding of how restoration initiatives can halt and reverse the impacts of disturbance on spider communities.

## **Chapter 6**

### **General discussion**

#### **6.1 | Objectives**

In this thesis, we investigated the effects of anthropogenic disturbance and restoration on tropical landscapes. We primarily aimed to determine the effects of oil palm replanting and passive and active restoration of riparian buffers on oil palm systems (Chapters 2 – 4). We did this by sampling environmental conditions and arthropods in industrial oil palm plantations in Riau, Indonesia, that are part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme. In addition to our oil palm studies, we used systematic review and meta-analysis approaches to assess the effects of anthropogenic disturbance and restoration on spiders in the tropics (Chapter 5).

We found that replanting of mature oil palm plantations with young palms affected the biodiversity of arthropods, but these effects were microhabitat-specific, affected only some arthropod groups, and were confined to certain periods of the oil palm commercial life cycle (Chapter 2). We also found that maintaining riparian buffers made of mature palms provided inconsistent ecological benefits across the oil palm commercial life cycle (Chapter 3), and that restoration of riparian buffers using both passive and active approaches did not affect arthropod biodiversity within two years (Chapter 4). Finally, we found that habitat disturbance had negative impacts on spider biodiversity, whilst restoration did not consistently benefit spiders in the tropics, but the effects of disturbance and restoration varied across studies and were therefore context-specific (Chapter 5). Collectively, our studies have implications for restoration across tropical landscapes and show that there is no “silver bullet” to restoring degraded tropical landscapes. Our studies also demonstrate the importance of large-scale, long-term collaborative experiments for improving understanding of the effects of different management strategies on complex tropical systems and, particularly, for more-sustainable management of oil palm agriculture.

#### **6.2 | Larger implications for restoration across the tropics**

The findings of this thesis have important implications for restoration efforts across the tropics. First, we demonstrated that the need for restoration is large, owing to disturbance being widespread across tropical landscapes. Our meta-analysis found that studies on the effects of

disturbance on spiders have occurred in 24 countries across the American, African, Asian, and Australasian tropics, and indicated that types of disturbance are varied and have impacts on several microhabitats. We found that this disturbance led to declines in spider biodiversity, particularly in tropical forest and savannah habitats, and mirrored disturbance effects on other taxonomic groups (Newbold et al., 2015). We further demonstrated the scale of disturbance in the tropics through our studies in oil palm systems (Chapters 2 - 4). The expansion of oil palm has affected more than 20 million hectares across the tropics (FAO, 2019), with impacts on structural complexity, biodiversity, and ecosystem processes (Drescher et al., 2016; Foster et al., 2011). As oil palm is continuing to expand, including in relatively undisturbed regions such as West Africa (Davis et al., 2020), the ecological effects of this crop will only grow, making studies that aim to improve the sustainability of palm oil production increasingly important. We have demonstrated that, within existing oil palm systems, added disturbance will occur as plantations are replanted, resulting in changes in environmental conditions and arthropod biodiversity that could affect functioning in replanted oil palm systems. However, it is likely that replanting will have less substantial effects on ecological conditions than initial plantation establishment, as the magnitude of disturbance is less severe.

Despite the pervasiveness of disturbance across the tropics, our studies – and previous ones that focus on restoring tropical systems (e.g. Barral et al., 2015; De Beenhouwer et al., 2013) – indicate that there is a lack of knowledge of how to restore human-modified tropical landscapes, and the context-dependent factors that make successful restoration more likely. For instance, in Chapter 1, we showed that although the number of studies on restoration is increasing exponentially, studies on restoration of tropical systems, and especially tropical agricultural systems, are occurring at far lower rates. This lack of knowledge is also highlighted in recent efforts to propose “best practices” for restoration, which inherently acknowledge the lack of understanding of how to practically restore degraded systems. For instance, Di Sacco et al. (2021) published “Ten golden rules for restoration” globally and, in Chapter 1, we proposed best practices for restoring tropical agricultural systems in particular, describing 8 actions that are especially promising for improving knowledge of “where”, “what”, and “how” restoration of tropical agriculture should occur, and “who” should be involved in, and benefit from, restoration of these landscapes.

Although there are general principles that can increase the potential for restoration to provide socioecological benefits, it is noteworthy that this thesis demonstrates that there is no one-size-

fits-all approach to restoration. In Chapters 3 – 4, when studying industrial oil palm plantations, we found that the effects of restoration varied across taxonomic groups, microhabitats, and the amount of time elapsed since disturbance (i.e. replanting) occurred. Similarly, in Chapter 5, our meta-analysis found large variation in the effects of restoration initiatives on spider abundance and species richness, with some studies indicating that restoration increased spider biodiversity, while other studies indicated that restoration did not affect or led to declines in spider biodiversity. Previous studies have similarly highlighted that the ecological effects of restoration are variable, and that there is no “silver bullet” solution that will result in guaranteed benefits to biodiversity and functioning (e.g. Holl & Brancalion, 2020; Holl et al., 2011; Stuble et al., 2017). Several studies have examined the drivers of successful restoration initiatives across the tropics, and have found that successful restoration is linked to increased time elapsed since restoration began (César et al., 2021; Crouzeilles et al., 2016, 2017), greater coverage of natural habitat in surrounding landscapes (César et al., 2021; Crouzeilles et al., 2016, 2017), lower intensity of disturbance causing degradation (Ballauff et al., 2020; Crouzeilles et al., 2016), higher annual precipitation (Crouzeilles et al., 2017), and economic and socio-political factors that are supportive of restoration efforts (Chazdon, Lindenmayer, et al., 2020; Mansourian et al., 2018; Rey Benayas & Bullock, 2012). Our findings, and those of others (e.g. Cole et al., 2016; Holl et al., 2017; Reid et al., 2015, 2016; Holl et al., 2020), have demonstrated that the approach to restoration can be a key influencer of restoration success. However, it is noteworthy that some studies (e.g. Holl et al., 2020; Li et al., 2018; de la Peña-Domene et al., 2013; Ram et al., 2021; Shoo et al., 2016) have found that active restoration provides more benefits to recovering systems, while other studies have found that passive approaches to restoration may be equally (Barral et al., 2015; Jones et al., 2018), or more (Crouzeilles et al., 2017), successful. The studies in this thesis do not indicate whether passive or active approaches to restoration in tropical systems provide greater ecological benefits, as we found that passively restored riparian buffers made of mature oil palms did not consistently benefit arthropods across the oil palm commercial life cycle (Chapter 3); that restoring riparian buffers passively and actively did not benefit arthropods in replanted oil palm plantations within two years (Chapter 4); and that passive and active approaches to restoration did not consistently benefit spiders across the tropics (Chapter 5).

Our studies also indicated that, when restoring productive systems, restoration should be timed to particularly propitious stages in the crop system in order to increase the chances that restoration will provide benefits to biodiversity, and to make implementation of restoration

management more tractable. For instance, in Chapter 3, we found that passively restoring riparian buffers at the time of oil palm replanting was an effective way to maintain habitat heterogeneity in replanted oil palm plantations, and helped preserve some pre-replanting environmental conditions and levels of arthropod biodiversity in replanted oil palm plantations. It is likely that other tropical crop systems will similarly have periods during which restoration management can have especially large benefits for environmental conditions, biodiversity, and ecosystem processes, or may be easier to implement. For example, coconut agriculture is expanding quickly across the tropics, and particularly in island communities (Meijaard, Abrams, et al., 2020), and there is likely to be an opportunity to enhance structural and ecological complexity in new coconut plantations when they are first established. This management may be particularly valuable, as coconut agriculture threatens more species per million tons of oil produced than any other dominant vegetable oil crop (Meijaard, Abrams, et al., 2020).

Improving knowledge of how to successfully restore tropical systems, including tropical agricultural systems, using tractable strategies will require additional large-scale experiments that test the effects of different restoration interventions. Experiments should be robust in design to avoid bias in findings (Christie et al., 2020), and replicated across space and time to ensure that findings are applicable across different ecological and socio-political contexts. In this thesis, we studied the effects of restoration strategies on oil palm ecosystems in the RERTA Project and wider BEFTA Programme research framework, and we considered how restoration affected tropical spiders by analysing data from individual studies that assessed the effects of restoration on spiders in different tropical landscapes. These studies were based on, demonstrate the value of, and show the additional need for, large-scale, long-term, robustly-designed restoration experiments that help to improve understanding of how restoration can benefit environmental conditions, biodiversity, and ecosystem processes.

### **6.3 | Managing for biodiversity in oil palm systems**

This thesis has particular implications for managing for biodiversity in oil palm systems. In particular, we showed that replanting of oil palm plantations and restoration of riparian buffers could potentially affect levels of arthropod biodiversity in the canopy, understory, and ground microhabitats (Chapters 2 – 4). Other studies have demonstrated that oil palm management affects arthropod biodiversity in other microhabitats, for instance, in the leaf-litter (Teuscher et al., 2016) and belowground in the soil (Ashton-Butt et al., 2018). We expect that the effects

of management on arthropod biodiversity will have knock-on impacts, as arthropods are important components of terrestrial food webs (Barnes et al., 2014) and contribute to diverse ecosystem functions including decomposition, herbivory, and seed dispersal (Eycott et al., 2019). Further, changes in arthropod biodiversity caused by management could affect oil palm yields as arthropods contribute to important ecosystem services in oil palm plantations including pollination and pest control (Li et al., 2019; Nurdiansyah et al., 2016). Managing for arthropod biodiversity could, therefore, increase productivity in oil palm plantations, providing win-win solutions for conservation and palm oil production (Luke, Advento, Aryawan, et al., 2020).

### **6.3.1 | Replanting of oil palm systems**

The long commercial life cycle (20 – 30 years) of oil palm makes it an ideal crop in which to manage for biodiversity (Luke, Advento, Aryawan, et al., 2020). Although considering the ecological effects of management across the entirety of the crop's commercial life cycle is important, we demonstrated that replanting of oil palm plantations is a key period during which management can have potentially large effects on biodiversity. We showed that replanting of oil palm plantations using recommended strategies (including retaining mature oil palm riparian buffers, planting a leguminous cover crop immediately after mature palms were felled, and using chopped-up mature palms as mulch in replanted landscapes) changes understory vegetation composition, canopy openness, and soil temperature, but does not affect understory vegetation height. These changes in environmental conditions were mirrored by shifts in arthropod order-level composition and spider species-level composition in the canopy, understory, and ground microhabitats; and spider abundance and species richness in the canopy and understory microhabitats. Encouragingly, in Chapters 2 and 4, we found no negative effects of replanting on total arthropod abundance in the canopy and understory microhabitats, or spider abundance and species richness in the canopy and ground microhabitats, indicating that replanting does not negatively affect all aspects of arthropod biodiversity in oil palm systems.

As oil palm is a dominant habitat in some regions (Ramdani & Hino, 2013), and many mature plantations have already been, or will soon be, replanted (Snaddon et al., 2013), our findings have important implications for ecological changes that will occur across the tropics. Whilst our findings, and those of others (Ashton-Butt et al., 2019; Kurz et al., 2016; Waters, 2018; Woodham et al., 2019), have indicated that replanting using recommended strategies will not catastrophically disrupt oil palm systems, the changes we detected in environmental conditions

and biodiversity following replanting could still indicate widespread loss of biodiversity and changes in ecosystem processes in oil palm landscapes. We, therefore, conclude that increased efforts should be made to implement management strategies at the time of oil palm replanting that help maintain pre-replanting environmental conditions, and levels of biodiversity and functioning, in replanted oil palm landscapes.

### **6.3.2 | Restoration of riparian buffers in oil palm systems**

In Chapters 3 and 4, we assessed whether ecological restoration was a form of management that could help support biodiversity in oil palm plantations when they are replanted. Specifically, we assessed the ecological effects of maintaining and restoring riparian buffers in replanted oil palm plantations. We considered both passive (Chapters 3 and 4) and active (Chapter 4) approaches to riparian buffer restoration. Passive riparian restoration consisted of leaving mature oil palms in place at the time of replanting; stopping the use of herbicides, pesticides, and fertilisers within buffer boundaries; and allowing succession of native vegetation to occur. Active riparian restoration involved planting six native tree species in place of, or amongst, mature palms at the time of replanting; stopping the use of herbicides, pesticides, and fertilisers within buffer boundaries; and allowing succession of native vegetation to occur. Although we tested the comparative ecological benefits of passive and active approaches to riparian restoration in Chapter 4, the RERTA Project is still in its early days, and therefore we cannot – at this point – argue with confidence whether actively or passively restoring riparian buffers is better for biodiversity in oil palm plantations. We expect to be able to provide clearer recommendations for when passive or active approaches should be used to restore riparian areas in oil palm upon collecting additional data over a longer time period. However, it is noteworthy that our findings in Chapter 3 and those of a previous study (Woodham et al., 2019) demonstrated that passively restored riparian buffers provide few benefits to oil palm ecosystems across the commercial life cycle, and we therefore suggest that passive approaches to riparian restoration will not be sufficient to provide a full suite of possible benefits to biodiversity and ecosystem processes in replanted oil palm plantations. It is, therefore, likely that more active approaches to riparian buffer management are needed (e.g. ‘*Mature enriched*’ and ‘*Enriched only*’ from the RERTA Project).

Our studies complement other research investigating the benefits of retaining forest margins around rivers during establishment of oil palm plantations, such as ongoing studies at the Stability of Altered Forest Ecosystems (SAFE) Project (Chellaiah & Yule, 2018a, 2018b,

2018c; Giam et al., 2015; Gray et al., 2017; Gray et al., 2016; Gray et al., 2014; Gray & Lewis, 2014; Gray et al., 2015; Gray et al., 2019; Luke, Dow, et al., 2017; Luke, Barclay, et al., 2017; Mitchell et al., 2018; Singh et al., 2015; Williamson et al., 2021). The SAFE Project is based in Sabah, Malaysia (Ewers et al., 2011), which is relatively near the plantations we sampled for this thesis, and therefore findings from our projects are likely comparable. Studies in the SAFE Project landscape have demonstrated that maintaining forested buffers in oil palm plantations can diversify microclimatic conditions (Williamson et al., 2021), help support the biodiversity of taxa including insects and birds (Gray et al., 2016; Gray et al., 2014; Gray et al., 2015; Gray et al., 2019; Knowlton et al., 2017; Luke, Dow, et al., 2017; Mitchell et al., 2018), and contribute to delivery of ecosystem services such as mitigating soil erosion and improving water quality (Chellaiah & Yule, 2018a; Luke, Barclay, et al., 2017). Further research is needed to determine the benefits of forested buffers in oil palm systems, relative to riparian buffers that are being passively and actively restored.

Previous research has indicated that many disturbed systems recover within relatively short timeframes (i.e. under 10 years), and that physical aspects of ecosystems recover along roughly the same timescale as biodiversity (Jones & Schmitz, 2009; Meli et al., 2017). Our studies indicated that riparian buffers being restored in oil palm plantations differed environmentally from surrounding cultivated areas. However, we found little evidence that these environmental changes corresponded to consistent benefits to arthropod biodiversity (Chapter 3), if any benefits at all (Chapter 4). Our findings are, therefore, at odds with other studies from the restoration literature. In Chapters 3 and 4, we suggested that this disparity in findings could be attributed to a longer time period being needed for riparian restoration to provide benefits to arthropods and overarching effects of oil palm replanting that prevented early effects of riparian restoration from being observed. Also, the disparity in findings may be caused by other local- and landscape-level factors, for instance, the effects of riparian restoration may have been outweighed by the continued use of chemicals in surrounding cultivated areas that are applied to promote crop growth, and the dominance of generalist arthropod species in oil palm systems that are relatively robust to environmental changes (Chey, 2006; Chung et al., 2000; Fayle, Edwards, et al., 2015). Further, we may not have found effects of riparian restoration owing to the plantations in which we sampled being > 30 km from the nearest forest. Previous studies have shown that proximity to forest, and percent forest in the surrounding landscape, are important predictors of successful restoration (César et al., 2021). It is additionally noteworthy that there were limitations to our study designs that may have prevented effects of restoration

from being observed. For instance, in Chapter 4, we only observed effects of the RERTA treatments across two rivers in SMARTRI plantations, and assessed effects of the RERTA treatments on arthropods primarily at the order-level. This limited replication and relatively coarse level of taxonomic resolution may have masked effects of the RERTA treatments on arthropod biodiversity. Identifying which, if any, of these factors were principally responsible for our findings was beyond the scope of this thesis and, therefore, additional studies are needed. Longer-term observations are needed to observe whether positive ecological effects of riparian restoration are forthcoming.

### **6.3.3 | Directions for future research on management of oil palm systems**

Our studies indicate several clear directions for future research on management of oil palm systems. First, we demonstrate that research is needed to identify management strategies that can help offset changes in environmental conditions and biodiversity that are caused by oil palm replanting. In this thesis, we assessed how replanting using a suite of recommended strategies affected oil palm ecosystems. Future studies should investigate the impacts of individual strategies, and work to identify strategies that successfully maintain pre-replanting ecological conditions in replanted oil palm landscapes. We made some headway on this endeavour through our studies on riparian buffers in Chapters 3 and 4. In addition to our studies on terrestrial arthropods in the canopy, understory, and ground microhabitats, the effects of replanting have so far been assessed for frogs (Kurz et al., 2016), soil invertebrates (Ashton-Butt et al., 2019), and several ecosystem functions and multifunctionality (Woodham et al., 2019). Future studies that investigate the effects of replanting on a wider range of taxonomic groups and ecosystem functions are needed, to provide a more wholistic understanding of how replanting affects oil palm ecosystems.

This thesis also indicates clear directions for future research on riparian restoration in oil palm systems. First, our studies indicate that relatively long periods of time (at least greater than two years) may be needed to identify effects of riparian restoration on arthropod biodiversity in replanted oil palm systems. Our studies, therefore, indicate that future research on restoring riparian buffers in oil palm plantations should take place over several years, at minimum. We note that there is currently no set end date for data collection in the RERTA Project, and therefore long-term observations of the effects of the RERTA riparian restoration treatments on oil palm ecosystems will occur. Additionally, although this thesis features several riparian restoration options, we certainly do not consider all possible strategies for restoring riparian

buffers. For instance, in the active restoration treatments in RERTA, we have planted six tree species at fixed distances either amongst (*'Mature enriched'*) or in place of (*'Enriched only'*) oil palms. Future research should test whether other tree species, planted at different densities, lead to more effective or faster benefits to oil palm ecosystems. Also, future research should investigate how the width of passively and actively restored riparian buffers affects their relative benefits to oil palm ecosystems, as previous studies have indicated that wider riparian reserves provide larger benefits to biodiversity (Gray et al., 2017; Mitchell et al., 2018). In addition, future research should assess whether the distance from riparian buffers to native habitat, and the percentage of native habitat in the surrounding landscape, affect the ability of riparian buffers to provide benefits to biodiversity. These factors have previously been shown to predict successful restoration in tropical landscapes (César et al., 2021), owing to native habitat being a valuable source of native species. Further, future research should assess the effects of passively and actively restoring buffers on a wider range of taxonomic groups, ecosystem functions, and socioeconomic conditions. The RERTA Project already plans to assess the effects of riparian restoration treatments on many of these response variables (Luke, Advento, Aryawan, et al., 2020). Collectively, this future research will enable better assessment of the cost-benefit trade-offs of the RERTA riparian restoration treatments across different socioecological contexts, ultimately allowing determination of which approaches should be considered best-practices for restoring riparian areas in oil palm plantations, and other tropical agricultural systems, across the tropics.

Finally, it is noteworthy that the plantations we sampled are representative of industrial oil palm plantations across Southeast Asia. However, factors such as soil conditions and rainfall vary within and between plantations, and these factors can affect how management impacts oil palm ecosystems (Allen et al., 2015; Berkelmann et al., 2018; Kotowska et al., 2016; Krashevskaya et al., 2015; Luke, Advento, Dow, et al., 2020). Therefore, future research should test how management, such as replanting and passive and active restoration of riparian buffers, affects oil palm systems that differ in their geography and climate from the plantations in which we sampled. Further, studies are urgently needed in smallholder plantations, which represent approximately 60% of oil palm plantations in Southeast Asia (Descals et al., 2020). In comparison to industrial oil palm plantations, there is substantially less knowledge of what management strategies are being used by smallholder farmers, and how these strategies affect levels of biodiversity and functioning in smallholder plantations (Reiss-Woolever et al., 2021). Additional studies across more socioecological contexts are therefore needed to demonstrate

the extent to which the findings of this thesis are applicable to oil palm systems across the tropics.

### **6.3.4 | Informing future management in oil palm systems**

It is critical that findings from future studies on oil palm management are communicated effectively to policymakers, sustainability certification organisations and, importantly, oil palm managers, to ensure their widespread uptake. For instance, we will communicate findings from this thesis to members of the palm oil industry (for instance, at industry conferences such as the International Congress on Oil Palm and the Environment, “ICOPE”; <https://icope-series.com/ICOPE/>) and the Roundtable on Sustainable Palm Oil (RSPO, 2018), which is the most widely recognised certifier of sustainable palm oil worldwide. We note that our arthropod findings are especially relevant to RSPO Principle 7.1, “Pests, diseases, weeds, and invasive introduced species are effectively managed using appropriate integrate pest management (IPM) techniques”, as many arthropods – such as spiders – contribute to pest management in oil palm systems (Hinsch & Turner, 2017; Michalko et al., 2019). As the replanting strategies we studied in Chapter 2 included using chopped-up mature palms as mulch and planting a cover crop to maintain soil health, our findings are relevant to RSPO Principle 7.3, “Waste is reduced, recycled, reused and disposed of in an environmentally and socially responsible manner” and RSPO Principle 7.4, “Practices maintain soil fertility at, or where possible improve soil fertility to, a level that ensures optimal and sustained yield”. Owing to the potential contributions of riparian buffers to preventing erosion, improving water quality, and mitigating greenhouse gas emissions (Luke, Slade, et al., 2019), future studies from the RERTA Project will be relevant to RSPO Principle 7.5, “Practices minimise and control erosion and degradation of soils”; Principle 7.8, “Practices maintain the quality and availability of surface and groundwater”; and Principle 7.10, “Plans to reduce pollution and emissions, including greenhouse gases (GHG) are developed, implemented and monitored and new developments are designed to minimise GHG emissions”. Finally, over time, the RERTA active restoration treatments (i.e. ‘*Mature enriched*’ and ‘*Enriched only*’) should become increasingly rainforest-like and, therefore, be considered high conservation value (HCV) or high carbon stock (HCS) areas. If this is the case, findings from the RERTA Project will also be relevant to RSPO Principle 7.12, “HCVs and HCS forests in the managed area are identified and protected or enhanced”.

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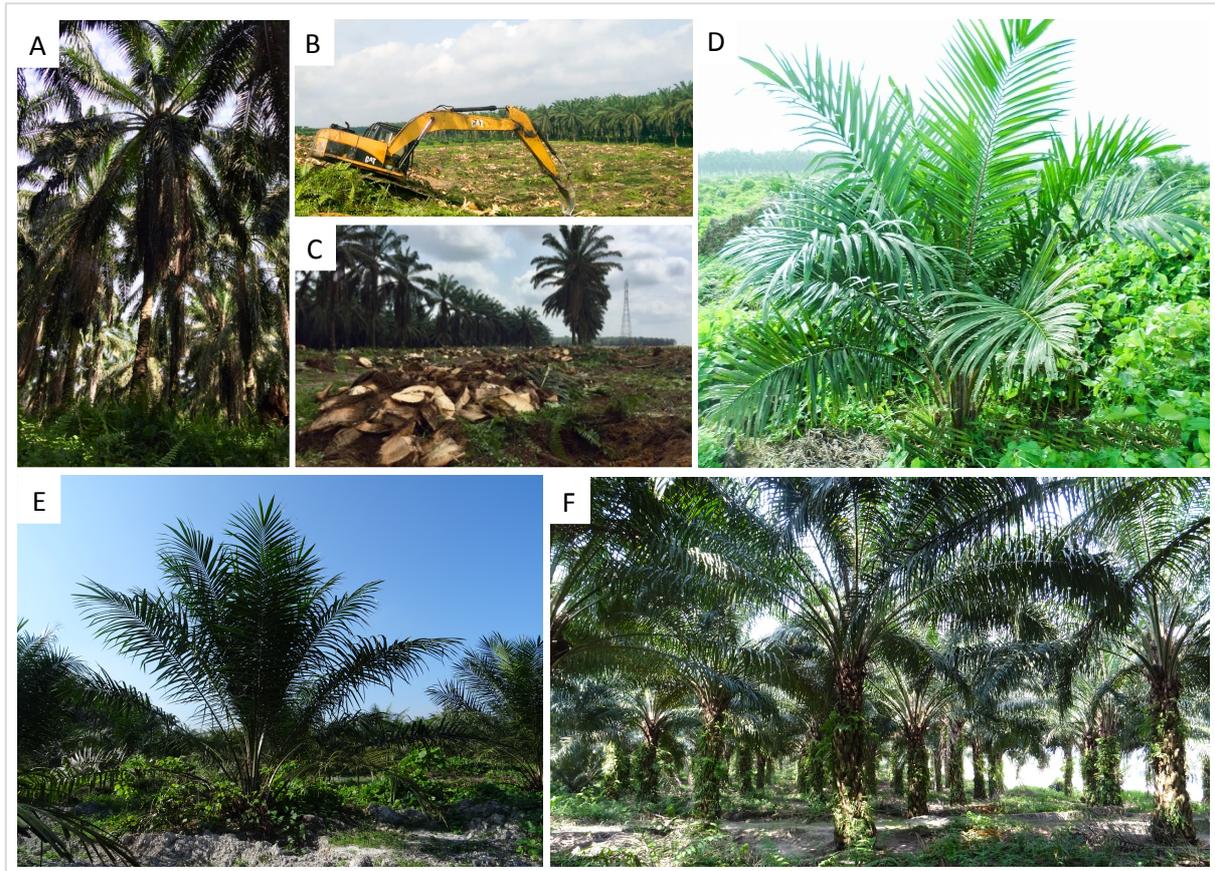
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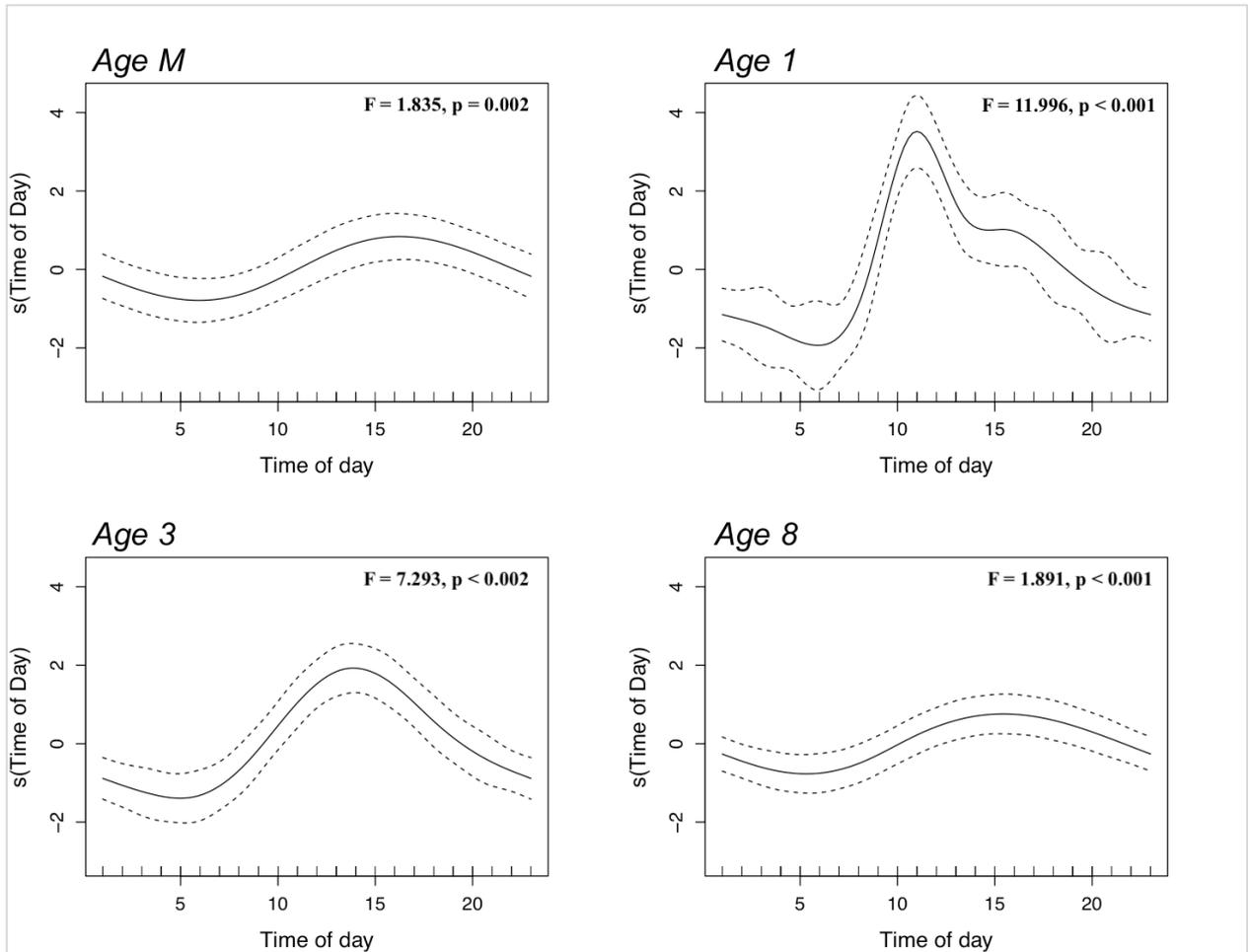
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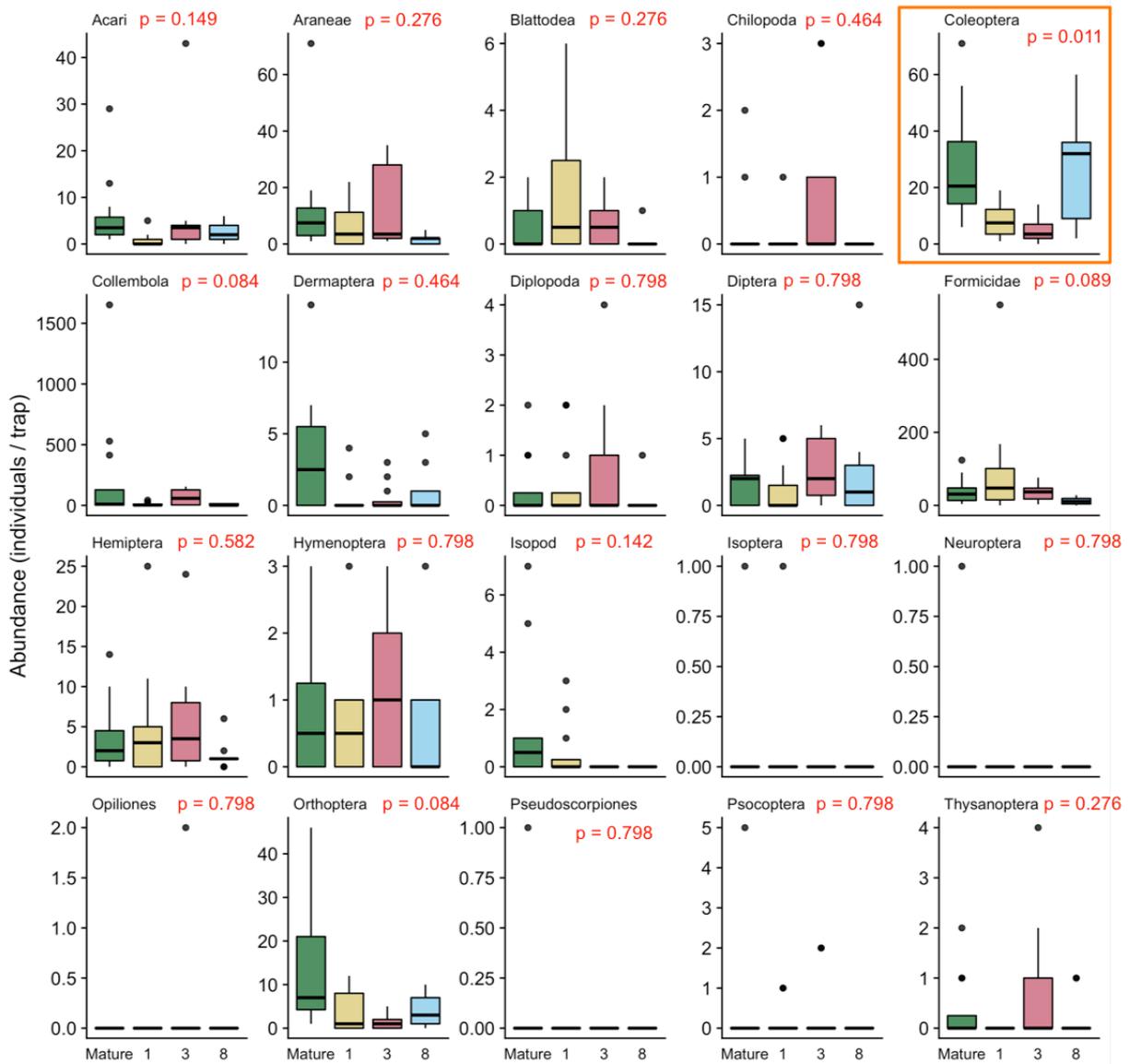
## Supplementary Materials – Chapter 2



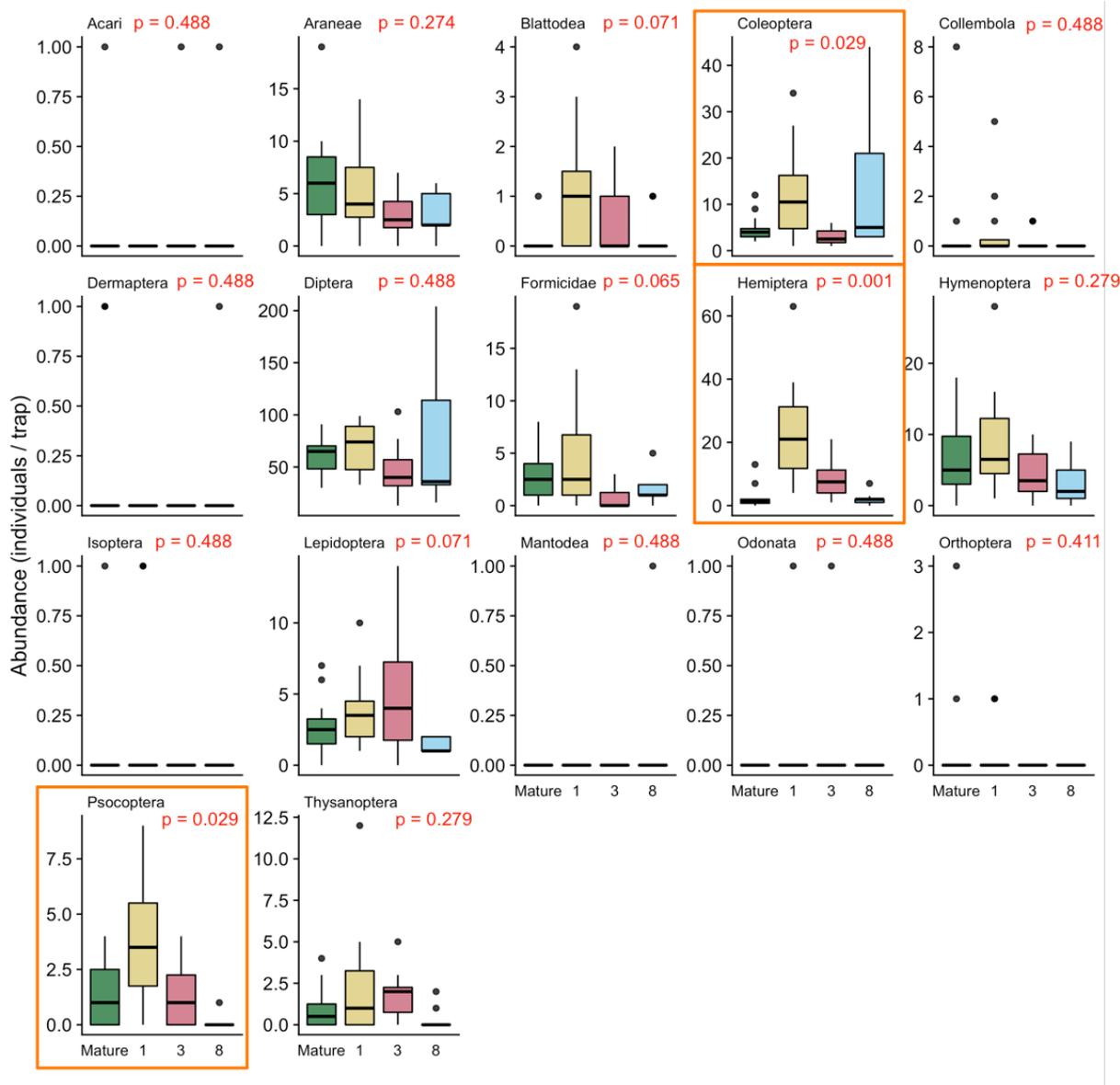
**Figure S2.1.** Photographs of oil palm at different stages of the replanting and regrowth process: Mature first-generation oil palms, scheduled for replanting (*Age M*) (A); a site recently cleared for planting second-generation palms using a large digger, with a retained mature oil palm riparian buffer in the background (B); mounds of recently cut palms that were chopped and left as mulch for newly planted palms (C); replanted 1-year-old palm, which is surrounded by a planted leguminous cover crop (*Age 1*) (D); replanted 3-year-old palms (*Age 3*) (E); and replanted 8-year-old palms (*Age 8*) (F). Photos taken by Michael Pashkevich, Anak Agung Ketut Aryawan, and Martina Faika Harianja.



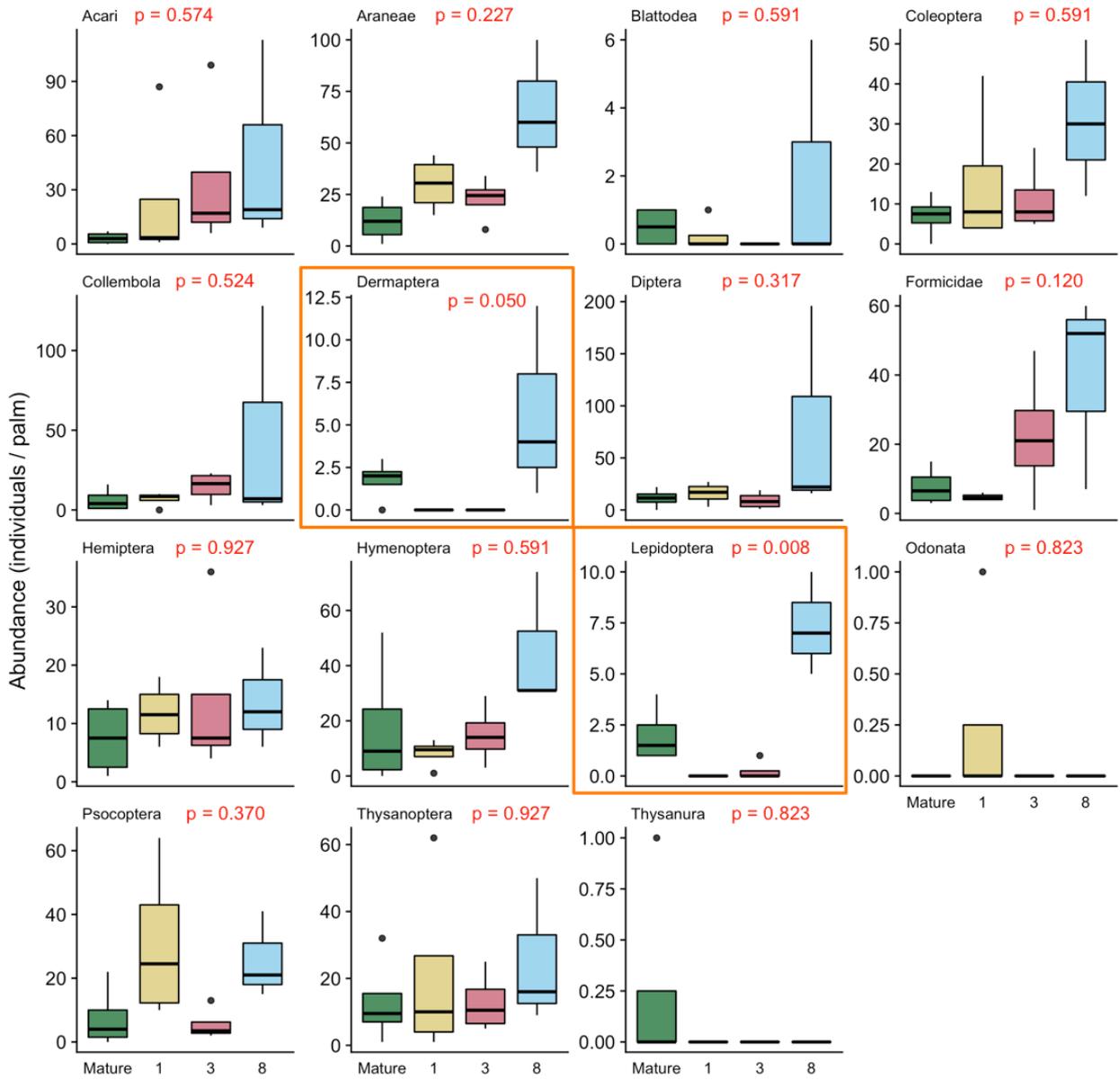
**Figure S2.2.** Plotted smoothing functions (time of day multiplied by covariate cohort) that were fitted in the generalised additive model used to analyse soil temperature. The smoothing functions were applied to the time of day at which soil temperature was recorded. Plots show how smoothers accounted for cross-day variability in temperature within each cohort. Dotted lines indicate 2 standard errors around the estimate of each smoothing function. *P*-values, and associated *F*-statistics, are given to indicate whether temperature varied significantly with the smoothing function applied to time of day within each cohort.



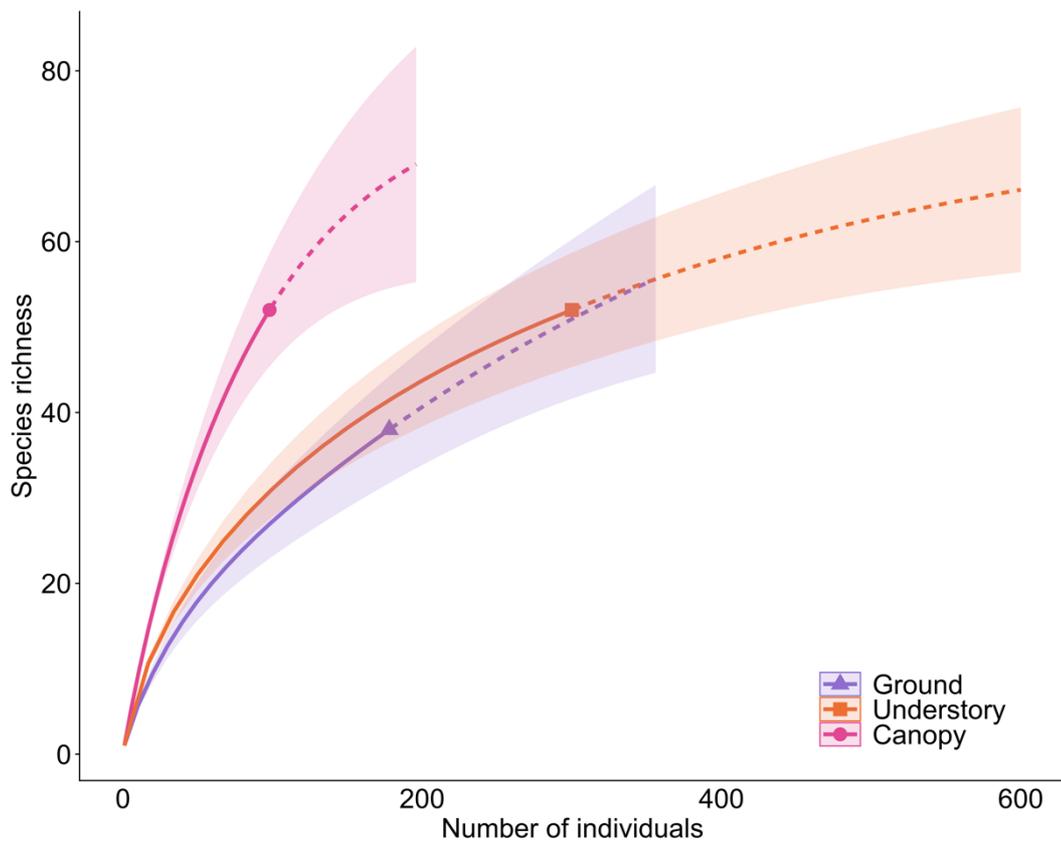
**Figure S2.3.** Boxplots of abundance per pitfall trap of *ground arthropods* across oil palm age cohorts (*Mature, Age 1, Age 3, Age 8*). Boxplots display median and interquartile ranges, and black circles indicate outliers. Orange boxes highlight orders with significant differences in abundance across studied cohorts ( $p < 0.05$ ), with  $p$ -values for all likelihood ratio tests given in orange.



**Figure S2.4.** Boxplots of abundance per sticky trap of *understory arthropods* across oil palm age cohorts (*Mature, Age 1, Age 3, Age 8*). Boxplots display median and interquartile ranges, and black circles indicate outliers. Orange boxes highlight orders with significant differences in abundance across studied cohorts ( $p < 0.05$ ), with  $p$ -values for all likelihood ratio tests given in orange.



**Figure S2.5.** Boxplots of abundance per palm of *canopy arthropods* across oil palm age cohorts (*Mature, Age 1, Age 3, Age 8*). Boxplots display median and interquartile ranges, and black circles indicate outliers. Orange boxes highlight orders with significant differences in abundance across studied cohorts ( $p < 0.05$ ), with  $p$ -values for all likelihood ratio tests given in orange.



**Figure S2.6.** Species accumulation curves for the observed spider communities in the ground, understory, and canopy microhabitats. We plot both interpolated (solid lines) and extrapolated (dotted lines) species richness. We extrapolated to double the number of observed individuals (Chao et al., 2014; Gotelli & Colwell, 2001).

**Table S2.1.** Information about estate management practices in the study sites. We sampled in fifteen sites across four age cohorts and four estates. Management information was obtained from surveys sent to estate managers. We focussed on eight management categories: application of fertilisers, pesticides, and herbicides; trapping of pests; cutting of vegetation; fruit harvesting; planting of beneficial plants; and allowance of livestock within the area. Estate management data were not available for *Age M* sites in Ujung Tanjung Estate.

Estate		Age M		Age 1		Age 3		Age 8
		Palapa	Ujung Tanjung	Libo	Palapa	Libo	Samsam	Palapa
<b>Fertilisers</b>	Application method	Manually and by machine	--	Manually and by machine	Manually	By machine	Manually and by machine	Manually
	Chemicals used	Palm oil mill effluent and organic mix	--	Macro and micro nutrients	Urea, potash, borate, phosphate, kieserite	Urea, potash, dolomite, phosphate, kieserite	Urea, potash, borate, phosphate, kieserite	Urea, potash, borate, phosphate, kieserite
	Applications per year	Eight	--	Two	Variant	Two	Two	Variant
<b>Pesticides</b>	Application method	Knapsack sprayer	--	Knapsack sprayer	Knapsack sprayer	Knapsack sprayer	Knapsack sprayer	Knapsack sprayer
	Chemicals used	Cypermethrin	--	Cypermethrin	Cypermethrin	Cypermethrin	Cypermethrin	Cypermethrin
	Applications per month	Two	--	Two	Two	Only applied during pest outbreaks	Only applied during pest outbreaks	Two
<b>Pest trapping</b>	Trapping method	Rhinoceros beetle pheromone trap	--	None	Rhinoceros beetle pheromone trap	Rhinoceros beetle pheromone trap	Rhinoceros beetle pheromone trap	Rhinoceros beetle pheromone trap
<b>Herbicides</b>	Application method	Knapsack sprayer	--	Knapsack sprayer	Knapsack sprayer	Knapsack sprayer	Knapsack sprayer	None
	Chemicals used	Glifosat, Ammonium glufosinate, Methyl metsulfuron	--	Glifosat, Ammonium glufosinate, Methyl metsulfuron	Ammonium glufosinate, Methyl metsulfuron	Glifosat	Glifosat, Ammonium glufosinate, Methyl metsulfuron	None
	Applications per year	Three	--	Three to four	Four	Three to four	Four	Not applicable
<b>Vegetation cutting</b>	Cutting method	Blade	--	Blade	Blade	None	Blade	Blade
	Cuttings per year	Three	--	Two	Four	Not applicable	Two	Four
<b>Harvesting</b>	Harvesting method	Tractor and crane grabber	--	Not applicable	Not applicable	Tractor and crane grabber	Tractor and crane grabber	Tractor and crane grabber
	Harvests per month	Four	--	None	None	Four	Four	Four
<b>Beneficial plants</b>	Species planted	<i>Turnera sp.</i> and <i>Antigonon sp.</i>	--	<i>Turnera sp.</i> and <i>Antigonon sp.</i>	<i>Turnera sp.</i> and <i>Antigonon sp.</i>	<i>Turnera sp.</i> and <i>Antigonon sp.</i>	<i>Turnera sp.</i> and <i>Antigonon sp.</i>	<i>Turnera sp.</i> and <i>Antigonon sp.</i>
<b>Livestock</b>	Present or absent	Absent	--	Absent	Absent	Absent	Absent	Absent

**Table S2.2.** List of spider morphospecies found in the *ground, understory, and canopy microhabitats*. Only adult spiders were identified to morphospecies. For each morphospecies, we indicate whether it was found in the ground, understory, or canopy microhabitat. Boxes that are highlighted in orange indicate that morphospecies abundance in that microhabitat varied significantly across the chronosequence, as determined by univariate analyses from our species-level community composition analyses.

Family	Morphospecies	Ground	Understory	Canopy
Anapidae	Anapidae sp. 1			X
	Anapidae sp. 2			X
Araneidae	Araneidae sp. 2		X	
	Araneidae sp. 3		X	
	Araneidae sp. 4		X	
	Araneidae sp. 6		X	
	Araneidae sp. 7		X	
	Araneidae sp. 8		X	
	Araneidae sp. 9		X	
	Araneidae sp. 10		X	
	Araneidae sp. 11		X	
	Araneidae sp. 12		X	
	Araneidae sp. 13			X
	Araneidae sp. 14		X	X
	Araneidae sp. 15		X	X
	Araneidae sp. 18			X
	Araneidae sp. 22		X	
	Araneidae sp. 23		X	
	Araneidae sp. 24		X	X
	Araneidae sp. 25		X	
	Araneidae sp. 26			X
	Gasteracantha sp. 1		X	
	Gasteracantha sp. 2		X	
	Gasteracantha sp. 3		X	
	Gasteracantha sp. 4		X	
	Gasteracantha sp. 5		X	
	Nephila pilipes		X	
Clubionidae	Clubionidae sp. 1		X	
Corinnidae	Corinnidae sp. 1		X	

**\*\* Continued on next page.**

Linyphiidae	Linyphiidae sp. 3			X
	Linyphiidae sp. 5			X
	Linyphiidae sp. 6	X		
	Linyphiidae sp. 10	X		
	Linyphiidae sp. 11			X
	Linyphiidae sp. 14			X
	Linyphiidae sp. 16			X
	Linyphiidae sp. 17	X		X
	Linyphiidae sp. 19	X		
	Liocranidae	Liocranidae sp. 1	X	
Lycosidae	Lycosidae sp. 1	X		
	Lycosidae sp. 2	X		
	Lycosidae sp. 4	X		
	Lycosidae sp. 6	X		
	Lycosidae sp. 7	X		
	Lycosidae sp. 8	X		
	Lycosidae sp. 9	X		
	Lycosidae sp. 13	X		
	Lycosidae sp. 17	X		
	Lycosidae sp. 18	X		
	Lycosidae sp. 19	X		
	Lycosidae sp. 20	X		
	Lycosidae sp. 21	X		
Lycosidae sp. 23	X			
Mysmenidae	Mysmenidae sp. 1			X
	Mysmenidae sp. 2			X
Oonopidae	Ischnothyreus sp. 1	X		
	Oonopidae sp. 3			X
	Oonopidae sp. 5			X
	Oonopidae sp. 6	X		X
	Oonopidae sp. 7	X		
	Oonopidae sp. 8			X
	Oonopidae sp. 10	X		X
	Oonopidae sp. 11			X
	Oonopidae sp. 13			X
	Oonopidae sp. 15			X
Oonopidae sp. 16	X			
Oonopidae sp. 18	X			
Oxyopidae	Oxyopidae sp. 1		X	
	Oxyopidae sp. 6	X		
Pholcidae	Pholcidae sp. 1			X

**\*\* Continued on next page.**

Salticidae	Salticidae sp. 2			X
	Salticidae sp. 6		X	
	Salticidae sp. 8	X		
	Salticidae sp. 11	X		
	Salticidae sp. 12	X		
	Salticidae sp. 14		X	
	Salticidae sp. 15		X	
	Salticidae sp. 16		X	
	Salticidae sp. 18		X	
Symphytognathidae	Symphytognathidae sp. 1			X
Tetragnathidae	Opadometa sp. 1		X	
	Opadometa sp. 2		X	
	Tetragnatha sp. 1		X	
	Tetragnathidae sp. 1		X	
	Tetragnathidae sp. 2		X	
	Tetragnathidae sp. 3		X	
	Tetragnathidae sp. 4		X	
	Tetragnathidae sp. 5			X
	Tetragnathidae sp. 6			X
Theridiidae	Argyroides sp. 1		X	
	Argyroides sp. 2		X	X
	Ariamnes sp. 1			X
	Ariamnes sp. 2			X
	Rhomphaea sp. 1			X
	Rhomphaea sp. 2			X
	Rhomphaea sp. 3			X
	Theridiidae sp. 4		X	
	Theridiidae sp. 5		X	
	Theridiidae sp. 6		X	
	Theridiidae sp. 8		X	X
	Theridiidae sp. 9			X
	Theridiidae sp. 10			X
	Theridiidae sp. 13			X
	Theridiidae sp. 15			X
	Theridiidae sp. 17	X		
	Theridiidae sp. 18			X
	Theridiidae sp. 21	X		
	Theridiidae sp. 23	X		
	Theridiidae sp. 25	X		
	Theridiidae sp. 26		X	X
	Theridiidae sp. 29			X
	Theridiidae sp. 31			X
	Theridiidae sp. 32			X
	Theridiidae sp. 35			X
	Theridiidae sp. 37	X		
	Theridiidae sp. 39	X		
	Theridiidae sp. 40	X		
	Theridiidae sp. 41			X
	Tylorida sp. 3		X	X
	Tylorida sp. 4		X	X

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Theridiosomatidae	Theridiosomatidae sp. 1			X
	Theridiosomatidae sp. 2		X	
Thomisidae	Amyciaea sp. 1			X
	Amyciaea sp. 2			X
Trachelidae	Trachelidae sp. 1	X		
Uloboridae	Uloboridae sp. 1		X	
	Uloboridae sp. 2		X	
	Uloboridae sp. 3			X
	Uloboridae sp. 4		X	
	Uloboridae sp. 5		X	
Zodariidae	Zodariidae sp. 4	X		

## Supplementary materials – Chapter 3

**Supplementary Text 3.1.** Additional details on modelling:

**Bayesian regression models (GLMMs).** We used GLMMs to determine an effect of *Cohort* and *Distance* on canopy openness, variation in openness, vegetation height, soil temperature, total arthropod abundance, spider abundance, and spider species richness. We ran all GLMMs for 50,000 iterations using four chains and a thinning rate of 2. We discarded the first 4000 iterations as warmup / burn-in samples, and controlled the behaviour of the NUTS algorithm to decrease the number of divergent transitions (*adapt\_delta* = 0.95 or, when necessary, 0.99). For our canopy openness analysis, we fitted *normal(0,1)* priors on model intercepts, *normal(0,5)* priors on fixed effects, and *gamma(0.01,0.01)* priors on beta-binomial phi parameters. For all other analyses, we fitted *normal(0,10)* priors on model intercepts, *normal(0,1)* priors on fixed effects, and *normal(0,1)* priors on the standard deviation of random effects. In addition to these, we fitted *normal(0,1)* priors on the standard deviation of splines in our soil temperature analysis, and *gamma(0.01,0.01)* priors on negative binomial shape parameters in our total arthropod abundance and spider abundance analyses.

We determined that mixing was good by inspecting MCMC trace plots and ensuring that *Rhat* values were <1.1, the ratio of effect sample size to total sample size was > 0.1, and no autocorrelation was present within the MCMC chains (Muth et al., 2018). No issues were detected. We validated models by verifying that no patterns were present when Pearson residuals were plotted against fitted values, included covariates, and random effect levels (to verify that no spatial autocorrelation remained). We then used posterior predictive checks to ensure that attributes of data that were simulated from each model accurately reflected the real dataset from which each model was generated (Gabry et al., 2019). Model validation and posterior predictive checks required *bayesplot* (Gabry et al., 2019) and *tidybayes* (Kay & Mastny, 2020).

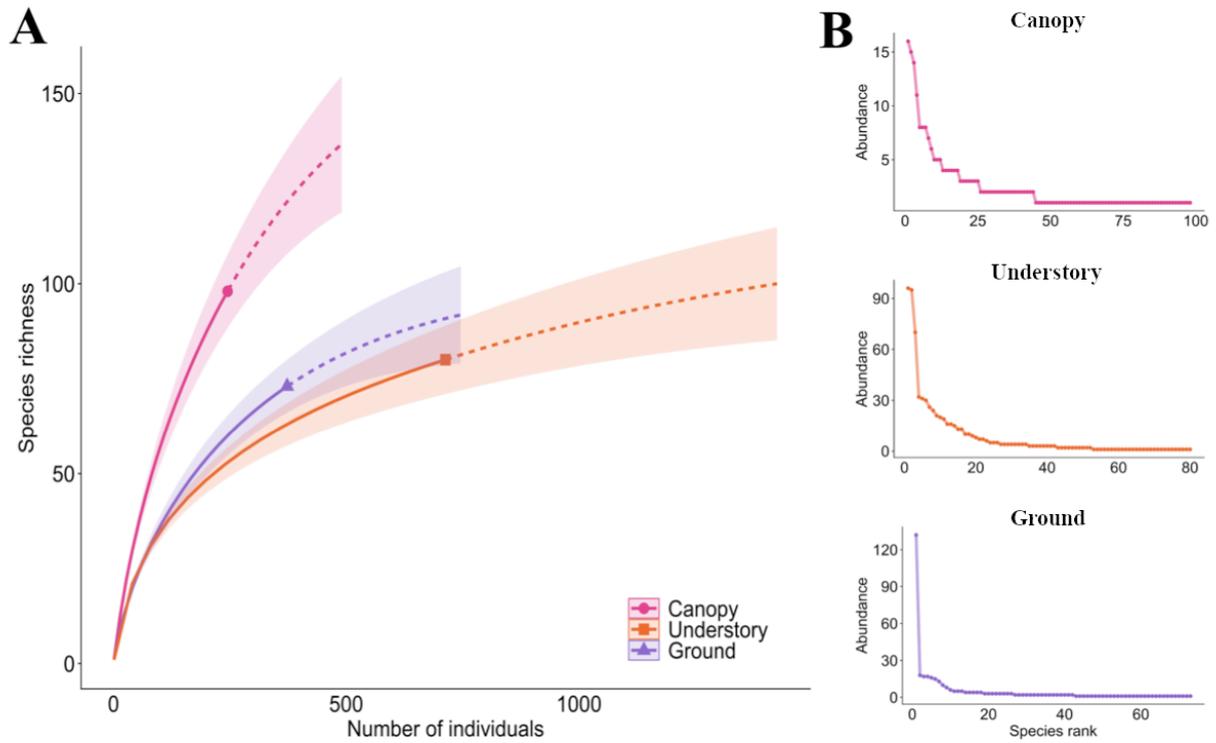
**Bayesian generalised linear latent variable model (GLLVM).** We used a GLLVM to determine an effect of *Cohort* and *Distance* on ground cover. We ran the model for 50,000 iterations using one chain (Hui & Blanchard, 2020) and a thinning rate of 10. We discarded the first 8000 iterations as warmup / burn-in samples. We fitted a normal prior with mean zero and

variance 1 on all column-specific intercepts, a normal prior with mean zero and variance 10 on the latent variable coefficients, and a half-Cauchy prior with mean zero and variance 5 on the standard deviation of the random effects normal distribution. We determined that mixing was good by inspecting MCMC trace plots. We validated our GLLVM by plotting Dunn-Smyth residuals against linear predictors, row indices, and column indices and ensuring no patterns were present. We also visually inspected Q-Q plots to ensure that a normal distribution was present.

**Multivariate generalised linear models (mGLMs).** We used mGLMs to determine an effect of *Cohort* and *Distance* on arthropod order-level composition and spider species-level composition. We validated models by verifying that no patterns were present when Dunn-Smyth residuals were plotted against fitted values and included covariates.



**Figure S3.1.** A photograph of a mature oil palm riparian buffer in a plantation that was recently cleared for replanting. In the plantation in which we sampled, mature first-generation oil palms are cleared for replanting using large diggers. The diggers do not enter mature palm buffers, and so these strips of mature oil palm along plantation rivers are left intact. Photo taken by Michael Pashkevich.



**Figure S3.2.** Species accumulation curves (A) and rank abundance curves (B) for the observed spider communities in the canopy, understory, and ground microhabitats. In A, we plot both interpolated (solid lines) and extrapolated (dotted lines) species richness. We extrapolated to double the number of observed individuals (Chao et al., 2014; Gotelli & Colwell, 2001).

**Table S3.1.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *canopy openness* model: *Canopy openness* ~ *Cohort\*Distance*. We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the log odds ratio scale and with a HPD interval probability of 0.95.

Comparison		Lower HPD	Upper HPD	Estimate	Comparison		Lower HPD	Upper HPD	Estimate		
Age M-Buffer	---	Age 1-Buffer	-3.335	0.774	-1.242	Age 8-Buffer	---	Age 8-Edge	-6.627	7.182	-0.036
Age M-Buffer	---	Age 3-Buffer	-3.375	0.483	-1.401	Age 8-Buffer	---	Age M-Core	-9.966	0.398	-4.269
Age M-Buffer	---	Age 8-Buffer	-0.548	8.962	3.759	<b>Age 8-Buffer</b>	---	<b>Age 1-Core</b>	<b>-21.424</b>	<b>-6.776</b>	<b>-13.281</b>
Age M-Buffer	---	Age M-Edge	-3.830	0.000	-1.857	<b>Age 8-Buffer</b>	---	<b>Age 3-Core</b>	<b>-13.963</b>	<b>-4.138</b>	<b>-8.505</b>
<b>Age M-Buffer</b>	---	<b>Age 1-Edge</b>	<b>-16.574</b>	<b>-4.884</b>	<b>-9.708</b>	Age 8-Buffer	---	Age 8-Core	-6.344	7.953	0.452
<b>Age M-Buffer</b>	---	<b>Age 3-Edge</b>	<b>-6.886</b>	<b>-2.797</b>	<b>-4.734</b>	<b>Age M-Edge</b>	---	<b>Age 1-Edge</b>	<b>-14.210</b>	<b>-3.300</b>	<b>-7.815</b>
Age M-Buffer	---	Age 8-Edge	-1.433	10.711	3.601	<b>Age M-Edge</b>	---	<b>Age 3-Edge</b>	<b>-4.508</b>	<b>-1.342</b>	<b>-2.858</b>
Age M-Buffer	---	Age M-Core	-2.825	1.747	-0.530	<b>Age M-Edge</b>	---	<b>Age 8-Edge</b>	<b>0.776</b>	<b>12.307</b>	<b>5.481</b>
<b>Age M-Buffer</b>	---	<b>Age 1-Core</b>	<b>-15.705</b>	<b>-4.716</b>	<b>-9.268</b>	Age M-Edge	---	Age M-Core	-0.616	3.390	1.319
<b>Age M-Buffer</b>	---	<b>Age 3-Core</b>	<b>-6.815</b>	<b>-2.729</b>	<b>-4.728</b>	<b>Age M-Edge</b>	---	<b>Age 1-Core</b>	<b>-13.511</b>	<b>-3.152</b>	<b>-7.365</b>
Age M-Buffer	---	Age 8-Core	-1.183	11.821	4.136	<b>Age M-Edge</b>	---	<b>Age 3-Core</b>	<b>-4.453</b>	<b>-1.350</b>	<b>-2.865</b>
Age 1-Buffer	---	Age 3-Buffer	-1.953	1.576	-0.166	<b>Age M-Edge</b>	---	<b>Age 8-Core</b>	<b>0.862</b>	<b>13.377</b>	<b>6.009</b>
<b>Age 1-Buffer</b>	---	<b>Age 8-Buffer</b>	<b>0.542</b>	<b>10.383</b>	<b>5.003</b>	<b>Age 1-Edge</b>	---	<b>Age 3-Edge</b>	<b>0.489</b>	<b>11.560</b>	<b>4.911</b>
Age 1-Buffer	---	Age M-Edge	-2.383	1.138	-0.623	<b>Age 1-Edge</b>	---	<b>Age 8-Edge</b>	<b>6.471</b>	<b>22.852</b>	<b>13.756</b>
<b>Age 1-Buffer</b>	---	<b>Age 1-Edge</b>	<b>-15.017</b>	<b>-3.924</b>	<b>-8.474</b>	<b>Age 1-Edge</b>	---	<b>Age M-Core</b>	<b>4.404</b>	<b>15.800</b>	<b>9.196</b>
<b>Age 1-Buffer</b>	---	<b>Age 3-Edge</b>	<b>-5.393</b>	<b>-1.714</b>	<b>-3.497</b>	Age 1-Edge	---	Age 1-Core	-7.567	8.619	0.417
<b>Age 1-Buffer</b>	---	<b>Age 8-Edge</b>	<b>0.031</b>	<b>11.814</b>	<b>4.848</b>	<b>Age 1-Edge</b>	---	<b>Age 3-Core</b>	<b>0.319</b>	<b>11.349</b>	<b>4.925</b>
Age 1-Buffer	---	Age M-Core	-1.436	2.994	0.693	<b>Age 1-Edge</b>	---	<b>Age 8-Core</b>	<b>6.615</b>	<b>23.808</b>	<b>14.264</b>
<b>Age 1-Buffer</b>	---	<b>Age 1-Core</b>	<b>-14.184</b>	<b>-3.780</b>	<b>-8.031</b>	<b>Age 3-Edge</b>	---	<b>Age 8-Edge</b>	<b>3.704</b>	<b>15.369</b>	<b>8.377</b>
<b>Age 1-Buffer</b>	---	<b>Age 3-Core</b>	<b>-5.352</b>	<b>-1.708</b>	<b>-3.494</b>	<b>Age 3-Edge</b>	---	<b>Age M-Core</b>	<b>2.315</b>	<b>6.416</b>	<b>4.199</b>
<b>Age 1-Buffer</b>	---	<b>Age 8-Core</b>	<b>0.179</b>	<b>12.864</b>	<b>5.375</b>	<b>Age 3-Edge</b>	---	<b>Age 1-Core</b>	<b>-10.655</b>	<b>-0.238</b>	<b>-4.479</b>
<b>Age 3-Buffer</b>	---	<b>Age 8-Buffer</b>	<b>0.707</b>	<b>10.434</b>	<b>5.175</b>	Age 3-Edge	---	Age 3-Core	-1.609	1.584	-0.007
Age 3-Buffer	---	Age M-Edge	-2.050	1.098	-0.458	<b>Age 3-Edge</b>	---	<b>Age 8-Core</b>	<b>3.775</b>	<b>16.322</b>	<b>8.899</b>
<b>Age 3-Buffer</b>	---	<b>Age 1-Edge</b>	<b>-14.835</b>	<b>-3.735</b>	<b>-8.268</b>	Age 8-Edge	---	Age M-Core	-11.253	0.977	-4.116
<b>Age 3-Buffer</b>	---	<b>Age 3-Edge</b>	<b>-5.014</b>	<b>-1.733</b>	<b>-3.326</b>	<b>Age 8-Edge</b>	---	<b>Age 1-Core</b>	<b>-22.206</b>	<b>-6.355</b>	<b>-13.274</b>
<b>Age 3-Buffer</b>	---	<b>Age 8-Edge</b>	<b>0.294</b>	<b>11.923</b>	<b>5.025</b>	<b>Age 8-Edge</b>	---	<b>Age 3-Core</b>	<b>-15.261</b>	<b>-3.620</b>	<b>-8.364</b>
Age 3-Buffer	---	Age M-Core	-1.078	3.051	0.861	Age 8-Edge	---	Age 8-Core	-8.440	9.466	0.480
<b>Age 3-Buffer</b>	---	<b>Age 1-Core</b>	<b>-13.992</b>	<b>-3.566</b>	<b>-7.829</b>	<b>Age M-Core</b>	---	<b>Age 1-Core</b>	<b>-14.924</b>	<b>-4.394</b>	<b>-8.787</b>
<b>Age 3-Buffer</b>	---	<b>Age 3-Core</b>	<b>-5.001</b>	<b>-1.746</b>	<b>-3.327</b>	<b>Age M-Core</b>	---	<b>Age 3-Core</b>	<b>-6.304</b>	<b>-2.278</b>	<b>-4.200</b>
<b>Age 3-Buffer</b>	---	<b>Age 8-Core</b>	<b>0.303</b>	<b>12.827</b>	<b>5.543</b>	Age M-Core	---	Age 8-Core	-0.685	12.032	4.643
<b>Age 8-Buffer</b>	---	<b>Age M-Edge</b>	<b>-10.987</b>	<b>-1.209</b>	<b>-5.631</b>	<b>Age 1-Core</b>	---	<b>Age 3-Core</b>	<b>0.305</b>	<b>10.589</b>	<b>4.482</b>
<b>Age 8-Buffer</b>	---	<b>Age 1-Edge</b>	<b>-22.067</b>	<b>-6.857</b>	<b>-13.723</b>	<b>Age 1-Core</b>	---	<b>Age 8-Core</b>	<b>6.507</b>	<b>23.111</b>	<b>13.806</b>
<b>Age 8-Buffer</b>	---	<b>Age 3-Edge</b>	<b>-13.897</b>	<b>-4.098</b>	<b>-8.535</b>	<b>Age 3-Core</b>	---	<b>Age 8-Core</b>	<b>3.695</b>	<b>16.219</b>	<b>8.878</b>

**Table S3.2.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *variation in canopy openness* model: *Variation in openness ~ Cohort\*Distance*. We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the response scale and with a HPD interval probability of 0.95.

Comparison		Lower HPD	Upper HPD	Estimate	Comparison		Lower HPD	Upper HPD	Estimate
Age M-Buffer	--- Age 1-Buffer	-0.533	0.831	0.146	Age 8-Buffer	--- Age 8-Edge	-0.512	1.129	0.318
Age M-Buffer	--- Age 3-Buffer	-0.960	0.298	-0.329	Age 8-Buffer	--- Age M-Core	-0.937	0.648	-0.145
Age M-Buffer	--- Age 8-Buffer	-0.229	1.132	0.456	<b>Age 8-Buffer</b>	--- <b>Age 1-Core</b>	<b>0.074</b>	<b>1.800</b>	<b>0.922</b>
Age M-Buffer	--- Age M-Edge	-0.620	0.604	-0.025	<b>Age 8-Buffer</b>	--- <b>Age 3-Core</b>	<b>-1.808</b>	<b>-0.185</b>	<b>-0.996</b>
<b>Age M-Buffer</b>	--- <b>Age 1-Edge</b>	<b>1.172</b>	<b>2.742</b>	<b>1.948</b>	Age 8-Buffer	--- Age 8-Core	-0.058	1.589	0.758
Age M-Buffer	--- Age 3-Edge	-1.367	0.073	-0.648	<b>Age M-Edge</b>	--- <b>Age 1-Edge</b>	<b>1.159</b>	<b>2.730</b>	<b>1.976</b>
Age M-Buffer	--- Age 8-Edge	-0.007	1.563	0.774	Age M-Edge	--- Age 3-Edge	-1.356	0.095	-0.624
Age M-Buffer	--- Age M-Core	-0.308	0.918	0.311	<b>Age M-Edge</b>	--- <b>Age 8-Edge</b>	<b>0.010</b>	<b>1.575</b>	<b>0.803</b>
<b>Age M-Buffer</b>	--- <b>Age 1-Core</b>	<b>0.601</b>	<b>2.167</b>	<b>1.382</b>	Age M-Edge	--- Age M-Core	-0.363	1.039	0.336
Age M-Buffer	--- Age 3-Core	-1.267	0.182	-0.542	<b>Age M-Edge</b>	--- <b>Age 1-Core</b>	<b>0.581</b>	<b>2.213</b>	<b>1.406</b>
<b>Age M-Buffer</b>	--- <b>Age 8-Core</b>	<b>0.428</b>	<b>2.000</b>	<b>1.213</b>	Age M-Edge	--- Age 3-Core	-1.271	0.234	-0.514
Age 1-Buffer	--- Age 3-Buffer	-1.253	0.294	-0.475	<b>Age M-Edge</b>	--- <b>Age 8-Core</b>	<b>0.408</b>	<b>2.039</b>	<b>1.240</b>
Age 1-Buffer	--- Age 8-Buffer	-0.515	1.115	0.310	<b>Age 1-Edge</b>	--- <b>Age 3-Edge</b>	<b>-3.429</b>	<b>-1.758</b>	<b>-2.599</b>
Age 1-Buffer	--- Age M-Edge	-0.966	0.609	-0.172	<b>Age 1-Edge</b>	--- <b>Age 8-Edge</b>	<b>-2.063</b>	<b>-0.286</b>	<b>-1.173</b>
<b>Age 1-Buffer</b>	--- <b>Age 1-Edge</b>	<b>0.942</b>	<b>2.623</b>	<b>1.802</b>	<b>Age 1-Edge</b>	--- <b>Age M-Core</b>	<b>-2.445</b>	<b>-0.808</b>	<b>-1.636</b>
<b>Age 1-Buffer</b>	--- <b>Age 3-Edge</b>	<b>-1.626</b>	<b>-0.012</b>	<b>-0.795</b>	Age 1-Edge	--- Age 1-Core	-1.435	0.325	-0.569
Age 1-Buffer	--- Age 8-Edge	-0.234	1.504	0.630	<b>Age 1-Edge</b>	--- <b>Age 3-Core</b>	<b>-3.327</b>	<b>-1.640</b>	<b>-2.491</b>
Age 1-Buffer	--- Age M-Core	-0.648	0.935	0.164	Age 1-Edge	--- Age 8-Core	-1.616	0.166	-0.737
<b>Age 1-Buffer</b>	--- <b>Age 1-Core</b>	<b>0.406</b>	<b>2.067</b>	<b>1.236</b>	<b>Age 3-Edge</b>	--- <b>Age 8-Edge</b>	<b>0.571</b>	<b>2.240</b>	<b>1.424</b>
Age 1-Buffer	--- Age 3-Core	-1.507	0.113	-0.687	<b>Age 3-Edge</b>	--- <b>Age M-Core</b>	<b>0.206</b>	<b>1.712</b>	<b>0.960</b>
<b>Age 1-Buffer</b>	--- <b>Age 8-Core</b>	<b>0.173</b>	<b>1.917</b>	<b>1.069</b>	<b>Age 3-Edge</b>	--- <b>Age 1-Core</b>	<b>1.200</b>	<b>2.860</b>	<b>2.030</b>
<b>Age 3-Buffer</b>	--- <b>Age 8-Buffer</b>	<b>0.024</b>	<b>1.552</b>	<b>0.785</b>	Age 3-Edge	--- Age 3-Core	-0.657	0.894	0.106
Age 3-Buffer	--- Age M-Edge	-0.425	1.054	0.303	<b>Age 3-Edge</b>	--- <b>Age 8-Core</b>	<b>1.020</b>	<b>2.687</b>	<b>1.862</b>
<b>Age 3-Buffer</b>	--- <b>Age 1-Edge</b>	<b>1.437</b>	<b>3.077</b>	<b>2.276</b>	Age 8-Edge	--- Age M-Core	-1.293	0.334	-0.465
Age 3-Buffer	--- Age 3-Edge	-1.045	0.414	-0.322	Age 8-Edge	--- Age 1-Core	-0.291	1.487	0.606
<b>Age 3-Buffer</b>	--- <b>Age 8-Edge</b>	<b>0.286</b>	<b>1.920</b>	<b>1.103</b>	<b>Age 8-Edge</b>	--- <b>Age 3-Core</b>	<b>-2.130</b>	<b>-0.465</b>	<b>-1.319</b>
Age 3-Buffer	--- Age M-Core	-0.111	1.371	0.640	Age 8-Edge	--- Age 8-Core	-0.449	1.322	0.438
<b>Age 3-Buffer</b>	--- <b>Age 1-Core</b>	<b>0.894</b>	<b>2.533</b>	<b>1.710</b>	<b>Age M-Core</b>	--- <b>Age 1-Core</b>	<b>0.276</b>	<b>1.841</b>	<b>1.069</b>
Age 3-Buffer	--- Age 3-Core	-0.948	0.519	-0.212	<b>Age M-Core</b>	--- <b>Age 3-Core</b>	<b>-1.568</b>	<b>-0.112</b>	<b>-0.853</b>
<b>Age 3-Buffer</b>	--- <b>Age 8-Core</b>	<b>0.734</b>	<b>2.373</b>	<b>1.543</b>	<b>Age M-Core</b>	--- <b>Age 8-Core</b>	<b>0.134</b>	<b>1.697</b>	<b>0.902</b>
Age 8-Buffer	--- Age M-Edge	-1.259	0.324	-0.482	<b>Age 1-Core</b>	--- <b>Age 3-Core</b>	<b>-2.735</b>	<b>-1.072</b>	<b>-1.920</b>
<b>Age 8-Buffer</b>	--- <b>Age 1-Edge</b>	<b>0.613</b>	<b>2.350</b>	<b>1.492</b>	Age 1-Core	--- Age 8-Core	-1.029	0.740	-0.168
<b>Age 8-Buffer</b>	--- <b>Age 3-Edge</b>	<b>-1.901</b>	<b>-0.294</b>	<b>-1.105</b>	<b>Age 3-Core</b>	--- <b>Age 8-Core</b>	<b>0.917</b>	<b>2.587</b>	<b>1.757</b>

**Table S3.3.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *vegetation height* model:  $Vegetation\ height \sim Distance + (1 | Site)$ . We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the response scale and with a HPD interval probability of 0.95.

Comparison			Lower HPD	Upper HPD	Estimate
Buffer	---	Edge	-0.047	0.408	0.179
<b>Buffer</b>	---	<b>Core</b>	<b>0.120</b>	<b>0.573</b>	<b>0.347</b>
Edge	---	Core	-0.059	0.399	0.168

**Table S3.4.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *soil temperature* model:  $Temperature \sim Cohort + Distance + s(Time, by = Cohort) + s(Time, by = Distance) + (1 | Site)$ . We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the response scale and with a HPD interval probability of 0.95.

Comparison		Lower HPD	Upper HPD	Estimate
Age M-Buffer	--- Age 1-Buffer	-1.370	0.381	-0.488
Age M-Buffer	--- Age 3-Buffer	-0.818	0.772	-0.021
Age M-Buffer	--- Age 8-Buffer	-0.453	1.144	0.367
<b>Age M-Buffer</b>	--- <b>Age M-Core</b>	<b>-0.458</b>	<b>-0.099</b>	<b>-0.277</b>
Age M-Buffer	--- Age 1-Core	-1.635	0.155	-0.762
Age M-Buffer	--- Age 3-Core	-1.128	0.505	-0.296
Age M-Buffer	--- Age 8-Core	-0.727	0.902	0.090
Age 1-Buffer	--- Age 3-Buffer	-0.510	1.425	0.466
Age 1-Buffer	--- Age 8-Buffer	-0.167	1.773	0.854
Age 1-Buffer	--- Age M-Core	-0.692	1.095	0.212
<b>Age 1-Buffer</b>	--- <b>Age 1-Core</b>	<b>-0.458</b>	<b>-0.099</b>	<b>-0.277</b>
Age 1-Buffer	--- Age 3-Core	-0.795	1.171	0.190
Age 1-Buffer	--- Age 8-Core	-0.423	1.544	0.578
Age 3-Buffer	--- Age 8-Buffer	-0.496	1.253	0.388
Age 3-Buffer	--- Age M-Core	-1.067	0.562	-0.257
Age 3-Buffer	--- Age 1-Core	-1.695	0.275	-0.744
<b>Age 3-Buffer</b>	--- <b>Age 3-Core</b>	<b>-0.458</b>	<b>-0.099</b>	<b>-0.277</b>
Age 3-Buffer	--- Age 8-Core	-0.805	0.988	0.111
Age 8-Buffer	--- Age M-Core	-1.467	0.163	-0.643
<b>Age 8-Buffer</b>	--- <b>Age 1-Core</b>	<b>-2.091</b>	<b>-0.119</b>	<b>-1.131</b>
Age 8-Buffer	--- Age 3-Core	-1.546	0.237	-0.664
<b>Age 8-Buffer</b>	--- <b>Age 8-Core</b>	<b>-0.458</b>	<b>-0.099</b>	<b>-0.277</b>
Age M-Core	--- Age 1-Core	-1.370	0.381	-0.488
Age M-Core	--- Age 3-Core	-0.818	0.772	-0.021
Age M-Core	--- Age 8-Core	-0.453	1.144	0.367
Age 1-Core	--- Age 3-Core	-0.510	1.425	0.466
Age 1-Core	--- Age 8-Core	-0.167	1.773	0.854
Age 3-Core	--- Age 8-Core	-0.496	1.253	0.388

**Table S3.5.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *understory arthropod abundance* model:  $Abundance \sim Cohort * Distance + (I | Site)$ . We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the log scale and with a HPD interval probability of 0.95.

Comparison		Lower HPD	Upper HPD	Estimate	Comparison		Lower HPD	Upper HPD	Estimate
Age M-Buffer	--- Age 1-Buffer	-0.542	0.936	0.188	Age 8-Buffer	--- Age 8-Edge	-0.642	0.277	-0.181
Age M-Buffer	--- Age 3-Buffer	-0.161	1.329	0.596	Age 8-Buffer	--- Age M-Core	-1.218	0.416	-0.408
Age M-Buffer	--- Age 8-Buffer	-0.578	1.009	0.203	Age 8-Buffer	--- Age 1-Core	-0.172	1.600	0.711
Age M-Buffer	--- Age M-Edge	-0.443	0.286	-0.080	Age 8-Buffer	--- Age 3-Core	-1.167	0.575	-0.277
Age M-Buffer	--- Age 1-Edge	<b>0.386</b>	<b>1.947</b>	<b>1.155</b>	Age 8-Buffer	--- Age 8-Core	-0.637	0.286	-0.187
Age M-Buffer	--- Age 3-Edge	-0.456	1.068	0.327	<b>Age M-Edge</b>	--- <b>Age 1-Edge</b>	<b>0.434</b>	<b>2.029</b>	<b>1.235</b>
Age M-Buffer	--- Age 8-Edge	-0.805	0.831	0.022	Age M-Edge	--- Age 3-Edge	-0.386	1.170	0.408
Age M-Buffer	--- Age M-Core	-0.572	0.161	-0.204	Age M-Edge	--- Age 8-Edge	-0.755	0.914	0.105
Age M-Buffer	--- Age 1-Core	<b>0.140</b>	<b>1.694</b>	<b>0.915</b>	Age M-Edge	--- Age M-Core	-0.508	0.264	-0.123
Age M-Buffer	--- Age 3-Core	-0.860	0.663	-0.072	<b>Age M-Edge</b>	--- <b>Age 1-Core</b>	<b>0.202</b>	<b>1.788</b>	<b>0.996</b>
Age M-Buffer	--- Age 8-Core	-0.798	0.833	0.017	Age M-Edge	--- Age 3-Core	-0.797	0.759	0.009
Age 1-Buffer	--- Age 3-Buffer	-0.426	1.198	0.406	Age M-Edge	--- Age 8-Core	-0.751	0.916	0.097
Age 1-Buffer	--- Age 8-Buffer	-0.860	0.871	0.015	<b>Age 1-Edge</b>	--- <b>Age 3-Edge</b>	<b>-1.695</b>	<b>-0.001</b>	<b>-0.829</b>
Age 1-Buffer	--- Age M-Edge	-1.042	0.496	-0.269	<b>Age 1-Edge</b>	--- <b>Age 8-Edge</b>	<b>-2.040</b>	<b>-0.239</b>	<b>-1.131</b>
Age 1-Buffer	--- Age 1-Edge	<b>0.515</b>	<b>1.401</b>	<b>0.968</b>	<b>Age 1-Edge</b>	--- <b>Age M-Core</b>	<b>-2.161</b>	<b>-0.564</b>	<b>-1.358</b>
Age 1-Buffer	--- Age 3-Edge	-0.686	0.952	0.139	Age 1-Edge	--- Age 1-Core	-0.697	0.245	-0.241
Age 1-Buffer	--- Age 8-Edge	-1.025	0.724	-0.164	<b>Age 1-Edge</b>	--- <b>Age 3-Core</b>	<b>-2.100</b>	<b>-0.408</b>	<b>-1.228</b>
Age 1-Buffer	--- Age M-Core	-1.147	0.387	-0.391	<b>Age 1-Edge</b>	--- <b>Age 8-Core</b>	<b>-2.053</b>	<b>-0.248</b>	<b>-1.137</b>
Age 1-Buffer	--- Age 1-Core	<b>0.296</b>	<b>1.148</b>	<b>0.729</b>	Age 3-Edge	--- Age 8-Edge	-1.194	0.589	-0.305
Age 1-Buffer	--- Age 3-Core	-1.101	0.536	-0.260	Age 3-Edge	--- Age M-Core	-1.315	0.252	-0.530
Age 1-Buffer	--- Age 8-Core	-1.053	0.701	-0.173	Age 3-Edge	--- Age 1-Core	-0.227	1.456	0.587
Age 3-Buffer	--- Age 8-Buffer	-1.259	0.468	-0.393	Age 3-Edge	--- Age 3-Core	-0.827	0.015	-0.399
Age 3-Buffer	--- Age M-Edge	-1.432	0.115	-0.675	Age 3-Edge	--- Age 8-Core	-1.199	0.575	-0.310
Age 3-Buffer	--- Age 1-Edge	-0.262	1.422	0.559	Age 8-Edge	--- Age M-Core	-1.037	0.634	-0.227
Age 3-Buffer	--- Age 3-Edge	-0.697	0.153	-0.270	Age 8-Edge	--- Age 1-Core	-0.018	1.779	0.893
Age 3-Buffer	--- Age 8-Edge	-1.447	0.316	-0.573	Age 8-Edge	--- Age 3-Core	-0.970	0.801	-0.096
Age 3-Buffer	--- Age M-Core	<b>-1.564</b>	<b>-0.017</b>	<b>-0.800</b>	Age 8-Edge	--- Age 8-Core	-0.487	0.456	-0.005
Age 3-Buffer	--- Age 1-Core	-0.517	1.157	0.319	<b>Age M-Core</b>	--- <b>Age 1-Core</b>	<b>0.338</b>	<b>1.916</b>	<b>1.121</b>
Age 3-Buffer	--- Age 3-Core	<b>-1.087</b>	<b>-0.243</b>	<b>-0.670</b>	Age M-Core	--- Age 3-Core	-0.653	0.900	0.131
Age 3-Buffer	--- Age 8-Core	-1.451	0.308	-0.579	Age M-Core	--- Age 8-Core	-0.610	1.048	0.220
Age 8-Buffer	--- Age M-Edge	-1.095	0.543	-0.285	<b>Age 1-Core</b>	--- <b>Age 3-Core</b>	<b>-1.839</b>	<b>-0.160</b>	<b>-0.988</b>
Age 8-Buffer	--- Age 1-Edge	<b>0.076</b>	<b>1.855</b>	<b>0.951</b>	<b>Age 1-Core</b>	--- <b>Age 8-Core</b>	<b>-1.817</b>	<b>-0.010</b>	<b>-0.897</b>
Age 8-Buffer	--- Age 3-Edge	-0.769	0.986	0.123	Age 3-Core	--- Age 8-Core	-0.796	0.976	0.091

**Table S3.6.** Results of post-hoc tests assessing differences in the optimal *understory arthropod order-level community composition* model:  $Composition \sim Cohort + (1 | Site)$ . We indicate significant pairwise comparisons in bold font: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ . The significance of cohort to the model, and associated likelihood ratio test statistic, are also provided.

Factor	LRT statistic	p-value
<i>f(Cohort)</i>	<b>224.0</b>	<b>&lt;0.001***</b>

Comparison	LRT statistic	p-value
Age M --- Age 1	109.64	<b>&lt;0.001***</b>
Age 1 --- Age 8	104.26	<b>&lt;0.001***</b>
Age 1 --- Age 3	75.56	<b>&lt;0.001***</b>
Age M --- Age 3	61.32	<b>0.006**</b>
Age 3 --- Age 8	53.92	<b>0.013*</b>
Age M --- Age 8	49.4	<b>0.013*</b>

**Table S3.7.** Results of post-hoc tests assessing differences in the optimal *ground arthropod order-level community composition* model:  $Composition \sim Cohort + (1 | Site)$ . We indicate significant pairwise comparisons in bold font: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ . The significance of cohort to the model, and associated likelihood ratio test statistic, are also provided.

Factor	LRT statistic	p-value
<i>f(Cohort)</i>	<b>228.1</b>	<b>0.008**</b>

Comparison		LRT statistic	p-value
Age M	--- Age 3	86.78	<b>0.007**</b>
Age 3	--- Age 8	81.73	<b>0.01**</b>
Age M	--- Age 1	77.34	<b>0.013*</b>
Age M	--- Age 8	66.78	<b>0.027*</b>
Age 1	--- Age 8	65.13	<b>0.027*</b>
Age 1	--- Age 3	63.54	<b>0.027*</b>

**Table S3.8.** List of spider morphospecies found in the *canopy*, *understory*, and *ground microhabitats*. Only adult spiders were identified to morphospecies. For each morphospecies, we indicate whether it was found in the canopy, understory, or ground microhabitat. Boxes that are highlighted in orange indicate that morphospecies abundance in that microhabitat varied significantly across the chronosequence, as determined by univariate analyses from our species-level community composition analyses.

Family	Morphospecies	Canopy	Understory	Ground
Anapidae	Anapidae sp. 1	X		
	Anapidae sp. 2	X		
Araneidae	Araneidae sp. 1		X	
	Araneidae sp. 2		X	
	Araneidae sp. 3		X	
	Araneidae sp. 4		X	
	Araneidae sp. 5		X	
	Araneidae sp. 6		X	
	Araneidae sp. 7		X	
	Araneidae sp. 8		X	
	Araneidae sp. 9		X	
	Araneidae sp. 10		X	
	Araneidae sp. 11	X	X	
	Araneidae sp. 12		X	
	Araneidae sp. 13	X	X	
	Araneidae sp. 14	X	X	
	Araneidae sp. 15	X	X	
	Araneidae sp. 16	X		
	Araneidae sp. 17	X		
	Araneidae sp. 18	X		
	Araneidae sp. 19	X		
	Araneidae sp. 20			X
	Araneidae sp. 21			X
	Araneidae sp. 22	X	X	
	Araneidae sp. 23	X	X	
	Araneidae sp. 24	X	X	
	Araneidae sp. 25			X
Araneidae sp. 26	X			
Gasteracantha sp. 1	X	X		
Gasteracantha sp. 2	X	X		
Gasteracantha sp. 3		X		
Gasteracantha sp. 4	X	X		
Gasteracantha sp. 5		X		
Nephila pilipes			X	
Clubionidae	Clubionidae sp. 1		X	
	Clubionidae sp. 2	X		
	Clubionidae sp. 3	X		

**\*\* Continued on next page**

Corinnidae	Corinnidae sp. 1		X
	Corinnidae sp. 2	X	
	Corinnidae sp. 3	X	
	Corinnidae sp. 4	X	
Ctenidae	Ctenidae sp. 1		X
Gnaphosidae	Gnaphosidae sp. 1		X
Linyphiidae	Linyphiidae sp. 1	X	
	Linyphiidae sp. 2		X
	Linyphiidae sp. 3	X	
	Linyphiidae sp. 4		X
	Linyphiidae sp. 5	X	
	Linyphiidae sp. 6		X
	Linyphiidae sp. 7		X
	Linyphiidae sp. 8		X
	Linyphiidae sp. 9		X
	Linyphiidae sp. 10		X
	Linyphiidae sp. 11	X	
	Linyphiidae sp. 12	X	
	Linyphiidae sp. 13	X	
	Linyphiidae sp. 14	X	X
	Linyphiidae sp. 15		X
	Linyphiidae sp. 16	X	
	Linyphiidae sp. 17	X	X
	Linyphiidae sp. 18		X
	Linyphiidae sp. 19	X	X
Liocranidae	Liocranidae sp. 1		X
	Liocranidae sp. 2		X
Lycosidae	Lycosidae sp. 1		X
	Lycosidae sp. 2		X
	Lycosidae sp. 3		X
	Lycosidae sp. 4		X
	Lycosidae sp. 5		X
	Lycosidae sp. 6		X
	Lycosidae sp. 7		X
	Lycosidae sp. 8		X
	Lycosidae sp. 9		X
	Lycosidae sp. 10		X
	Lycosidae sp. 11		X
	Lycosidae sp. 12		X
	Lycosidae sp. 13		X
	Lycosidae sp. 14		X
	Lycosidae sp. 15		X
	Lycosidae sp. 16		X
	Lycosidae sp. 17		X
	Lycosidae sp. 18		X
	Lycosidae sp. 19		X
	Lycosidae sp. 20		X
	Lycosidae sp. 21		X
	Lycosidae sp. 22		X
	Lycosidae sp. 23		X
	Lycosidae sp. 24		X

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Mysmenidae	Mysmenidae sp. 1	X	X	
	Mysmenidae sp. 2	X		
	Mysmenidae sp. 3	X		
Nesticidae	Nesticidae sp. 1	X		
Oonopidae	Oonopidae sp. 1	X		
	Oonopidae sp. 2	X		
	Oonopidae sp. 3	X		
	Oonopidae sp. 4	X		
	Oonopidae sp. 5	X		
	Oonopidae sp. 6	X		X
	Oonopidae sp. 7			X
	Oonopidae sp. 8	X		X
	Oonopidae sp. 9			X
	Oonopidae sp. 10	X		X
	Oonopidae sp. 11	X		
	Oonopidae sp. 12	X		
	Oonopidae sp. 13	X		
	Oonopidae sp. 14	X		X
	Oonopidae sp. 15	X		
	Oonopidae sp. 16	X		X
	Oonopidae sp. 17			X
	Oonopidae sp. 18			X
Ischnothyreus sp. 1			X	
Oxyopidae	Oxyopidae sp. 1		X	
	Oxyopidae sp. 2		X	
	Oxyopidae sp. 3		X	
	Oxyopidae sp. 4		X	
	Oxyopidae sp. 5		X	
	Oxyopidae sp. 6			X
Pholcidae	Pholcidae sp. 1		X	
Salticidae	Salticidae sp. 1	X	X	
	Salticidae sp. 2	X		
	Salticidae sp. 3	X		
	Salticidae sp. 4	X		
	Salticidae sp. 5	X		
	Salticidae sp. 6		X	
	Salticidae sp. 7	X		
	Salticidae sp. 8			X
	Salticidae sp. 9			X
	Salticidae sp. 10			X
	Salticidae sp. 11			X
	Salticidae sp. 12			X
	Salticidae sp. 13		X	
	Salticidae sp. 14		X	
	Salticidae sp. 15		X	
	Salticidae sp. 16		X	
	Salticidae sp. 17		X	
	Salticidae sp. 18		X	

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Symphytognathidae	Symphytognathidae sp. 1	X		
	Symphytognathidae sp. 2	X		
Tetragnathidae	Opadometa sp. 1	X	X	
	Opadometa sp. 2		X	
	Tetragnatha sp. 1	X	X	
	Tetragnathidae sp. 1	X	X	
	Tetragnathidae sp. 2		X	
	Tetragnathidae sp. 3		X	
	Tetragnathidae sp. 4		X	
	Tetragnathidae sp. 5	X		
	Tetragnathidae sp. 6	X		
	Tylorida sp. 1	X	X	
	Tylorida sp. 2		X	
	Tylorida sp. 3	X	X	
	Tylorida sp. 4	X	X	
	Theridiidae	Argyrodes sp. 1		X
Argyrodes sp. 2		X	X	
Ariamnes sp. 1		X		
Ariamnes sp. 2		X		
Rhomphaea sp. 1		X		
Rhomphaea sp. 2		X		
Rhomphaea sp. 3		X		
Theridiidae sp. 1			X	
Theridiidae sp. 2			X	
Theridiidae sp. 3			X	
Theridiidae sp. 4			X	
Theridiidae sp. 5		X	X	
Theridiidae sp. 6			X	
Theridiidae sp. 7			X	
Theridiidae sp. 8		X	X	
Theridiidae sp. 9		X		
Theridiidae sp. 10		X		
Theridiidae sp. 11		X		
Theridiidae sp. 12		X		
Theridiidae sp. 13		X		
Theridiidae sp. 14		X		
Theridiidae sp. 15		X		
Theridiidae sp. 16			X	
Theridiidae sp. 17		X		X
Theridiidae sp. 18		X		
Theridiidae sp. 19			X	
Theridiidae sp. 20		X		
Theridiidae sp. 21			X	
Theridiidae sp. 22			X	
Theridiidae sp. 23			X	
Theridiidae sp. 24			X	
Theridiidae sp. 25			X	
Theridiidae sp. 26	X	X		

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	Theridiidae sp. 27	X		
	Theridiidae sp. 28		X	
	Theridiidae sp. 29	X		
	Theridiidae sp. 30		X	
	Theridiidae sp. 31	X		
	Theridiidae sp. 32	X		
	Theridiidae sp. 33	X		
	Theridiidae sp. 34	X		
	Theridiidae sp. 35	X		
	Theridiidae sp. 36			X
	Theridiidae sp. 37			X
	Theridiidae sp. 38			X
	Theridiidae sp. 39			X
	Theridiidae sp. 40			X
	Theridiidae sp. 41	X		
Theridiosomatidae	Theridiosomatidae sp. 1	X		
	Theridiosomatidae sp. 2		X	
	Theridiosomatidae sp. 3		X	
Thomisidae	Amyciaea sp. 1	X		
	Amyciaea sp. 2	X		
	Thomisidae sp. 1		X	
	Thomisidae sp. 2	X		
	Thomisidae sp. 3	X		
Trachelidae	Trachelidae sp. 1			X
Uloboridae	Uloboridae sp. 1		X	
	Uloboridae sp. 2		X	
	Uloboridae sp. 3	X	X	
	Uloboridae sp. 4		X	
	Uloboridae sp. 5		X	
	Uloboridae sp. 6		X	
Unknown	Unknown sp. 1			X
Zodariidae	Zodariidae sp. 1			X
	Zodariidae sp. 2			X
	Zodariidae sp. 3			X
	Zodariidae sp. 4			X

**Table S3.9.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *understory spider abundance* model:  $Abundance \sim Cohort * Distance + (1 | Site)$ . We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the log scale and with a HPD interval probability of 0.95.

Comparison					Comparison						
		Lower HPD	Upper HPD	Estimate			Lower HPD	Upper HPD	Estimate		
Age M-Buffer	---	Age 1-Buffer	-0.542	0.936	0.188	Age 8-Buffer	---	Age 8-Edge	-0.642	0.277	-0.181
Age M-Buffer	---	Age 3-Buffer	-0.161	1.329	0.596	Age 8-Buffer	---	Age M-Core	-1.218	0.416	-0.408
Age M-Buffer	---	Age 8-Buffer	-0.578	1.009	0.203	Age 8-Buffer	---	Age 1-Core	-0.172	1.600	0.711
Age M-Buffer	---	Age M-Edge	-0.443	0.286	-0.080	Age 8-Buffer	---	Age 3-Core	-1.167	0.575	-0.277
<b>Age M-Buffer</b>	---	<b>Age 1-Edge</b>	<b>0.386</b>	<b>1.947</b>	<b>1.155</b>	Age 8-Buffer	---	Age 8-Core	-0.637	0.286	-0.187
Age M-Buffer	---	Age 3-Edge	-0.456	1.068	0.327	<b>Age M-Edge</b>	---	<b>Age 1-Edge</b>	<b>0.434</b>	<b>2.029</b>	<b>1.235</b>
Age M-Buffer	---	Age 8-Edge	-0.805	0.831	0.022	Age M-Edge	---	Age 3-Edge	-0.386	1.170	0.408
Age M-Buffer	---	Age M-Core	-0.572	0.161	-0.204	Age M-Edge	---	Age 8-Edge	-0.755	0.914	0.105
<b>Age M-Buffer</b>	---	<b>Age 1-Core</b>	<b>0.140</b>	<b>1.694</b>	<b>0.915</b>	Age M-Edge	---	Age M-Core	-0.508	0.264	-0.123
Age M-Buffer	---	Age 3-Core	-0.860	0.663	-0.072	<b>Age M-Edge</b>	---	<b>Age 1-Core</b>	<b>0.202</b>	<b>1.788</b>	<b>0.996</b>
Age M-Buffer	---	Age 8-Core	-0.798	0.833	0.017	Age M-Edge	---	Age 3-Core	-0.797	0.759	0.009
Age 1-Buffer	---	Age 3-Buffer	-0.426	1.198	0.406	Age M-Edge	---	Age 8-Core	-0.751	0.916	0.097
Age 1-Buffer	---	Age 8-Buffer	-0.860	0.871	0.015	<b>Age 1-Edge</b>	---	<b>Age 3-Edge</b>	<b>-1.695</b>	<b>-0.001</b>	<b>-0.829</b>
Age 1-Buffer	---	Age M-Edge	-1.042	0.496	-0.269	<b>Age 1-Edge</b>	---	<b>Age 8-Edge</b>	<b>-2.040</b>	<b>-0.239</b>	<b>-1.131</b>
<b>Age 1-Buffer</b>	---	<b>Age 1-Edge</b>	<b>0.515</b>	<b>1.401</b>	<b>0.968</b>	<b>Age 1-Edge</b>	---	<b>Age M-Core</b>	<b>-2.161</b>	<b>-0.564</b>	<b>-1.358</b>
Age 1-Buffer	---	Age 3-Edge	-0.686	0.952	0.139	Age 1-Edge	---	Age 1-Core	-0.697	0.245	-0.241
Age 1-Buffer	---	Age 8-Edge	-1.025	0.724	-0.164	<b>Age 1-Edge</b>	---	<b>Age 3-Core</b>	<b>-2.100</b>	<b>-0.408</b>	<b>-1.228</b>
Age 1-Buffer	---	Age M-Core	-1.147	0.387	-0.391	<b>Age 1-Edge</b>	---	<b>Age 8-Core</b>	<b>-2.053</b>	<b>-0.248</b>	<b>-1.137</b>
<b>Age 1-Buffer</b>	---	<b>Age 1-Core</b>	<b>0.296</b>	<b>1.148</b>	<b>0.729</b>	Age 3-Edge	---	Age 8-Edge	-1.194	0.589	-0.305
Age 1-Buffer	---	Age 3-Core	-1.101	0.536	-0.260	Age 3-Edge	---	Age M-Core	-1.315	0.252	-0.530
Age 1-Buffer	---	Age 8-Core	-1.053	0.701	-0.173	Age 3-Edge	---	Age 1-Core	-0.227	1.456	0.587
Age 3-Buffer	---	Age 8-Buffer	-1.259	0.468	-0.393	Age 3-Edge	---	Age 3-Core	-0.827	0.015	-0.399
Age 3-Buffer	---	Age M-Edge	-1.432	0.115	-0.675	Age 3-Edge	---	Age 8-Core	-1.199	0.575	-0.310
Age 3-Buffer	---	Age 1-Edge	-0.262	1.422	0.559	Age 8-Edge	---	Age M-Core	-1.037	0.634	-0.227
Age 3-Buffer	---	Age 3-Edge	-0.697	0.153	-0.270	Age 8-Edge	---	Age 1-Core	-0.018	1.779	0.893
Age 3-Buffer	---	Age 8-Edge	-1.447	0.316	-0.573	Age 8-Edge	---	Age 3-Core	-0.970	0.801	-0.096
<b>Age 3-Buffer</b>	---	<b>Age M-Core</b>	<b>-1.564</b>	<b>-0.017</b>	<b>-0.800</b>	Age 8-Edge	---	Age 8-Core	-0.487	0.456	-0.005
Age 3-Buffer	---	Age 1-Core	-0.517	1.157	0.319	<b>Age M-Core</b>	---	<b>Age 1-Core</b>	<b>0.338</b>	<b>1.916</b>	<b>1.121</b>
<b>Age 3-Buffer</b>	---	<b>Age 3-Core</b>	<b>-1.087</b>	<b>-0.243</b>	<b>-0.670</b>	Age M-Core	---	Age 3-Core	-0.653	0.900	0.131
Age 3-Buffer	---	Age 8-Core	-1.451	0.308	-0.579	Age M-Core	---	Age 8-Core	-0.610	1.048	0.220
Age 8-Buffer	---	Age M-Edge	-1.095	0.543	-0.285	<b>Age 1-Core</b>	---	<b>Age 3-Core</b>	<b>-1.839</b>	<b>-0.160</b>	<b>-0.988</b>
<b>Age 8-Buffer</b>	---	<b>Age 1-Edge</b>	<b>0.076</b>	<b>1.855</b>	<b>0.951</b>	<b>Age 1-Core</b>	---	<b>Age 8-Core</b>	<b>-1.817</b>	<b>-0.010</b>	<b>-0.897</b>
Age 8-Buffer	---	Age 3-Edge	-0.769	0.986	0.123	Age 3-Core	---	Age 8-Core	-0.796	0.976	0.091

**Table S3.10.** Pairwise comparisons of estimated marginal means between factor levels in the optimal *understory spider species richness* model:  $Richness \sim Cohort + (1 | Site)$ . We concluded that factor levels were meaningfully different if the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero (indicated in bold). Results are given on the log scale and with a HPD interval probability of 0.95.

Comparison			Lower HPD	Upper HPD	Estimate
<b>Age M</b>	---	<b>Age 1</b>	<b>0.336</b>	<b>1.185</b>	<b>0.760</b>
<b>Age M</b>	---	<b>Age 3</b>	<b>0.022</b>	<b>0.823</b>	<b>0.435</b>
Age M	---	Age 8	-0.236	0.605	0.186
Age 1	---	Age 3	-0.790	0.106	-0.326
<b>Age 1</b>	---	<b>Age 8</b>	<b>-1.044</b>	<b>-0.104</b>	<b>-0.576</b>
Age 3	---	Age 8	-0.699	0.196	-0.248

**Table S3.11.** Results of post-hoc tests assessing differences in the optimal *canopy spider species-level community composition* model:  $Composition \sim Cohort * Distance + (1 | Site)$ . No pairwise comparisons were significantly different from each other ( $p > 0.05$ ). The significance of *Cohort*, *Distance*, and the interaction of these factors to the model, and associated likelihood ratio test statistics, are also provided. We indicate significance in bold font: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ .

Factor	LRT statistic	p-value
<i>f(Cohort)</i>	<b>257.1</b>	<b>0.041*</b>
<i>f(Distance)</i>	<b>408.7</b>	<b>0.003**</b>
<i>f(Cohort*Distance)</i>	<b>70.3</b>	<b>0.002**</b>

Comparison	LRT statistic	p-value	Comparison	LRT statistic	p-value
Age 1-Core --- Age 8-Core	80.67	0.099	Age 1-Edge --- Age M-Core	39.160	0.843
Age 3-Edge --- Age 8-Core	72.53	0.216	Age 3-Buffer --- Age 1-Core	39.070	0.843
Age 1-Edge --- Age 8-Core	72.37	0.216	Age 1-Edge --- Age 1-Core	39.050	0.843
Age M-Buffer --- Age 8-Core	70.71	0.216	Age 1-Edge --- Age 3-Core	38.590	0.843
Age 8-Buffer --- Age 1-Edge	70.07	0.216	Age M-Edge --- Age 3-Edge	38.020	0.843
Age 8-Buffer --- Age 1-Core	69.08	0.216	Age M-Buffer --- Age M-Edge	37.860	0.843
Age 8-Buffer --- Age 3-Edge	69	0.216	Age M-Edge --- Age 1-Edge	37.670	0.843
Age 3-Buffer --- Age 8-Core	64.99	0.256	Age 8-Edge --- Age 3-Core	37.360	0.843
Age 3-Core --- Age 8-Core	63.92	0.262	Age M-Edge --- Age 8-Edge	37.340	0.843
Age 8-Buffer --- Age M-Edge	62.53	0.272	Age 1-Edge --- Age 3-Edge	37.060	0.843
Age M-Edge --- Age 8-Core	61.96	0.275	Age M-Buffer --- Age 8-Edge	35.420	0.843
Age 1-Buffer --- Age 8-Core	60.5	0.297	Age 3-Buffer --- Age 3-Edge	34.890	0.843
Age 8-Buffer --- Age 3-Core	59.29	0.313	Age M-Buffer --- Age M-Core	34.460	0.843
Age M-Core --- Age 8-Core	56.26	0.408	Age 3-Buffer --- Age 8-Edge	34.260	0.843
Age 3-Buffer --- Age 8-Buffer	56.1	0.408	Age 1-Buffer --- Age 8-Edge	34.090	0.843
Age 1-Buffer --- Age 8-Buffer	52.72	0.532	Age 3-Buffer --- Age 3-Core	33.850	0.843
Age 8-Buffer --- Age 8-Core	52.31	0.534	Age 1-Buffer --- Age 1-Core	33.520	0.843
Age 8-Edge --- Age 1-Core	51.41	0.534	Age 1-Buffer --- Age 1-Edge	33.510	0.843
Age 8-Buffer --- Age M-Core	50.06	0.557	Age M-Core --- Age 3-Core	32.640	0.843
Age M-Buffer --- Age 1-Core	47.81	0.672	Age 3-Buffer --- Age 1-Edge	30.740	0.843
Age 8-Edge --- Age 8-Core	47.39	0.682	Age 3-Buffer --- Age M-Core	30.600	0.843
Age 3-Edge --- Age 8-Edge	46.81	0.682	Age M-Buffer --- Age 3-Buffer	30.140	0.843
Age M-Buffer --- Age 3-Edge	45.36	0.726	Age M-Edge --- Age 3-Core	29.690	0.843
Age M-Buffer --- Age 1-Edge	45.03	0.726	Age 3-Edge --- Age 3-Core	29.550	0.843
Age M-Core --- Age 1-Core	44.72	0.726	Age 3-Buffer --- Age M-Edge	29.110	0.843
Age 1-Edge --- Age 8-Edge	44.15	0.731	Age 1-Buffer --- Age M-Core	27.830	0.843
Age 3-Edge --- Age M-Core	43.33	0.753	Age M-Buffer --- Age 1-Buffer	26.820	0.843
Age M-Buffer --- Age 3-Core	42.58	0.779	Age 8-Edge --- Age M-Core	26.580	0.843
Age M-Buffer --- Age 8-Buffer	41.72	0.805	Age 1-Buffer --- Age 3-Edge	25.530	0.843
Age 3-Edge --- Age 1-Core	40.69	0.822	Age 1-Buffer --- Age 3-Core	24.470	0.843
Age M-Edge --- Age 1-Core	40.45	0.822	Age 1-Buffer --- Age M-Edge	23.570	0.843
Age 1-Core --- Age 3-Core	39.63	0.843	Age 1-Buffer --- Age 3-Buffer	21.130	0.843
Age 8-Buffer --- Age 8-Edge	39.58	0.843	Age M-Edge --- Age M-Core	19.570	0.843

**Table S3.12.** Results of post-hoc tests assessing differences in the optimal *understory spider species-level community composition* model:  $Composition \sim Cohort * Distance + (1 | Site)$ . No pairwise comparisons were significantly different from each other ( $p > 0.05$ ). The significance of *Cohort*, *Distance*, and the interaction of these factors to the model, and associated likelihood ratio test statistics, are also provided. We indicate significance in bold font: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ .

Factor	LRT statistic	p-value
<i>f(Cohort)</i>	246.9	<0.001***
<i>f(Distance)</i>	532.1	<0.001***
<i>f(Cohort*Distance)</i>	166.4	<0.001***

Comparison	LRT statistic	p-value	Comparison	LRT statistic	p-value
Age M-Edge --- Age 3-Core	118.52	0.062	Age 8-Buffer --- Age 1-Edge	67.310	0.577
Age M-Edge --- Age 3-Edge	109.38	0.105	Age 1-Buffer --- Age 8-Core	66.470	0.578
Age M-Buffer --- Age 3-Core	107.9	0.108	Age 1-Buffer --- Age 1-Core	61.300	0.729
Age M-Edge --- Age 1-Edge	104.72	0.123	Age 3-Buffer --- Age 3-Edge	57.930	0.821
Age M-Core --- Age 3-Core	103.8	0.125	Age 1-Buffer --- Age 1-Edge	57.870	0.821
Age M-Edge --- Age 1-Core	102.77	0.125	Age 3-Buffer --- Age 8-Edge	57.250	0.824
Age 8-Edge --- Age 3-Core	100.32	0.139	Age 1-Buffer --- Age M-Core	56.840	0.827
Age 8-Buffer --- Age 3-Core	98.17	0.149	Age 3-Buffer --- Age 8-Buffer	55.090	0.844
Age 1-Buffer --- Age 3-Core	96.61	0.153	Age M-Buffer --- Age 8-Core	55.020	0.844
Age 3-Core --- Age 8-Core	95.53	0.157	Age 8-Edge --- Age M-Core	54.170	0.849
Age 3-Buffer --- Age M-Edge	94.42	0.159	Age 3-Buffer --- Age 1-Edge	54.110	0.849
Age 3-Edge --- Age M-Core	89.98	0.212	Age 1-Buffer --- Age 8-Edge	53.830	0.849
Age M-Buffer --- Age 1-Core	87.34	0.244	Age M-Buffer --- Age 8-Edge	53.120	0.849
Age M-Buffer --- Age 3-Edge	86.87	0.247	Age M-Edge --- Age 8-Core	50.340	0.873
Age M-Core --- Age 1-Core	85.23	0.261	Age 3-Edge --- Age 1-Core	50.210	0.873
Age M-Buffer --- Age 1-Edge	85.12	0.261	Age 1-Edge --- Age 3-Edge	49.420	0.875
Age 3-Edge --- Age 8-Edge	84.78	0.261	Age 1-Buffer --- Age 3-Buffer	47.480	0.907
Age 1-Edge --- Age M-Core	84.44	0.261	Age M-Buffer --- Age 1-Buffer	47.240	0.907
Age 3-Buffer --- Age 3-Core	84.01	0.261	Age M-Core --- Age 8-Core	46.520	0.907
Age 1-Core --- Age 3-Core	81.32	0.292	Age 3-Edge --- Age 3-Core	46.120	0.907
Age 1-Edge --- Age 3-Core	80.03	0.318	Age 3-Buffer --- Age 1-Core	45.240	0.907
Age 3-Buffer --- Age M-Core	78.86	0.339	Age M-Buffer --- Age 8-Buffer	44.970	0.907
Age M-Buffer --- Age 3-Buffer	74.54	0.442	Age M-Edge --- Age 8-Edge	43.910	0.907
Age 8-Buffer --- Age 3-Edge	73.43	0.465	Age 1-Buffer --- Age 8-Buffer	43.640	0.907
Age 3-Edge --- Age 8-Core	72.46	0.488	Age 8-Buffer --- Age M-Edge	42.470	0.907
Age 1-Edge --- Age 8-Edge	72.38	0.488	Age M-Buffer --- Age M-Edge	41.420	0.907
Age 1-Edge --- Age 8-Core	71.09	0.514	Age M-Edge --- Age M-Core	38.700	0.907
Age 1-Core --- Age 8-Core	71.06	0.514	Age 8-Buffer --- Age M-Core	38.540	0.907
Age 3-Buffer --- Age 8-Core	70.39	0.521	Age 8-Buffer --- Age 8-Edge	35.920	0.907
Age 1-Buffer --- Age M-Edge	68.37	0.577	Age M-Buffer --- Age M-Core	34.850	0.907
Age 1-Buffer --- Age 3-Edge	68.32	0.577	Age 8-Edge --- Age 8-Core	32.370	0.907
Age 8-Edge --- Age 1-Core	68.09	0.577	Age 8-Buffer --- Age 8-Core	30.250	0.907
Age 8-Buffer --- Age 1-Core	67.45	0.577	Age 1-Edge --- Age 1-Core	17.910	0.907

**Table S3.13.** Results of post-hoc tests assessing differences in the optimal *ground spider species-level community composition* model:  $Composition \sim Cohort * Distance + (1 | Site)$ . No pairwise comparisons were significantly different from each other ( $p > 0.05$ ). The significance of *Cohort*, *Distance*, and the interaction of these factors to the model, and associated likelihood ratio test statistics, are also provided. We indicate significance in bold font: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ .

Factor	LRT statistic	p-value
<i>f(Cohort)</i>	191.9	0.209
<b><i>f(Distance)</i></b>	<b>335.0</b>	<b>0.002**</b>
<b><i>f(Distance*Cohort)</i></b>	<b>79.5</b>	<b>0.002**</b>

Comparison		LRT statistic	p-value	Comparison		LRT statistic	p-value
Age M-Buffer --- Age 1-Edge	73.16	0.121	Age M-Buffer --- Age M-Core	35.520	0.904		
Age 1-Edge --- Age M-Core	71.88	0.127	Age 1-Edge --- Age 8-Core	34.990	0.904		
Age 3-Buffer --- Age M-Core	64.41	0.24	Age M-Buffer --- Age M-Edge	33.120	0.932		
Age 3-Edge --- Age M-Core	58.52	0.414	Age 8-Edge --- Age 1-Core	32.660	0.932		
Age M-Core --- Age 3-Core	56.73	0.469	Age 8-Buffer --- Age 1-Core	32.530	0.932		
Age 1-Edge --- Age 3-Edge	55.42	0.504	Age 1-Buffer --- Age 3-Buffer	31.900	0.932		
Age 1-Edge --- Age 3-Core	54.8	0.524	Age M-Edge --- Age M-Core	31.790	0.932		
Age 3-Buffer --- Age 1-Edge	54.54	0.524	Age 1-Buffer --- Age 3-Core	31.420	0.932		
Age 1-Buffer --- Age 1-Edge	52.53	0.591	Age 1-Buffer --- Age 8-Edge	30.930	0.932		
Age M-Edge --- Age 1-Edge	52.3	0.593	Age M-Buffer --- Age 8-Core	30.740	0.932		
Age M-Buffer --- Age 3-Buffer	50.31	0.664	Age 3-Edge --- Age 8-Edge	30.730	0.932		
Age 3-Buffer --- Age 1-Core	48.81	0.718	Age 1-Buffer --- Age 1-Core	29.850	0.932		
Age M-Buffer --- Age 1-Core	48.27	0.725	Age 3-Buffer --- Age 3-Core	29.820	0.932		
Age M-Core --- Age 1-Core	47.7	0.735	Age 1-Core --- Age 8-Core	29.340	0.932		
Age 8-Edge --- Age M-Core	47.7	0.735	Age 3-Core --- Age 8-Core	29.310	0.932		
Age 1-Core --- Age 3-Core	46.76	0.735	Age 1-Buffer --- Age 3-Edge	29.230	0.932		
Age M-Buffer --- Age 3-Core	46.65	0.735	Age 1-Buffer --- Age M-Edge	28.800	0.932		
Age 8-Buffer --- Age 1-Edge	44.77	0.787	Age 3-Buffer --- Age 3-Edge	28.720	0.932		
Age M-Edge --- Age 3-Core	44.34	0.797	Age M-Edge --- Age 8-Edge	28.700	0.932		
Age 3-Buffer --- Age M-Edge	44.33	0.797	Age 8-Buffer --- Age M-Edge	28.640	0.932		
Age 1-Buffer --- Age M-Core	43.76	0.797	Age 3-Buffer --- Age 8-Core	27.480	0.932		
Age 8-Buffer --- Age M-Core	43.43	0.797	Age 8-Buffer --- Age 3-Core	26.780	0.932		
Age M-Edge --- Age 3-Edge	42.83	0.797	Age 3-Edge --- Age 3-Core	26.340	0.932		
Age 1-Edge --- Age 1-Core	42.72	0.797	Age 3-Buffer --- Age 8-Buffer	25.120	0.932		
Age M-Buffer --- Age 8-Edge	42.51	0.797	Age M-Buffer --- Age 1-Buffer	24.780	0.932		
Age M-Core --- Age 8-Core	41.63	0.797	Age 8-Buffer --- Age 3-Edge	24.620	0.932		
Age M-Buffer --- Age 3-Edge	41.47	0.797	Age M-Edge --- Age 8-Core	24.410	0.932		
Age 3-Edge --- Age 1-Core	40.72	0.797	Age 1-Buffer --- Age 8-Buffer	22.040	0.932		
Age 3-Buffer --- Age 8-Edge	39.55	0.826	Age 8-Edge --- Age 8-Core	21.530	0.932		
Age 1-Edge --- Age 8-Edge	39.24	0.826	Age 3-Edge --- Age 8-Core	21.430	0.932		
Age M-Edge --- Age 1-Core	37.9	0.863	Age 1-Buffer --- Age 8-Core	20.580	0.932		
Age M-Buffer --- Age 8-Buffer	36.51	0.883	Age 8-Buffer --- Age 8-Edge	19.130	0.932		
Age 8-Edge --- Age 3-Core	35.66	0.904	Age 8-Buffer --- Age 8-Core	14.230	0.932		

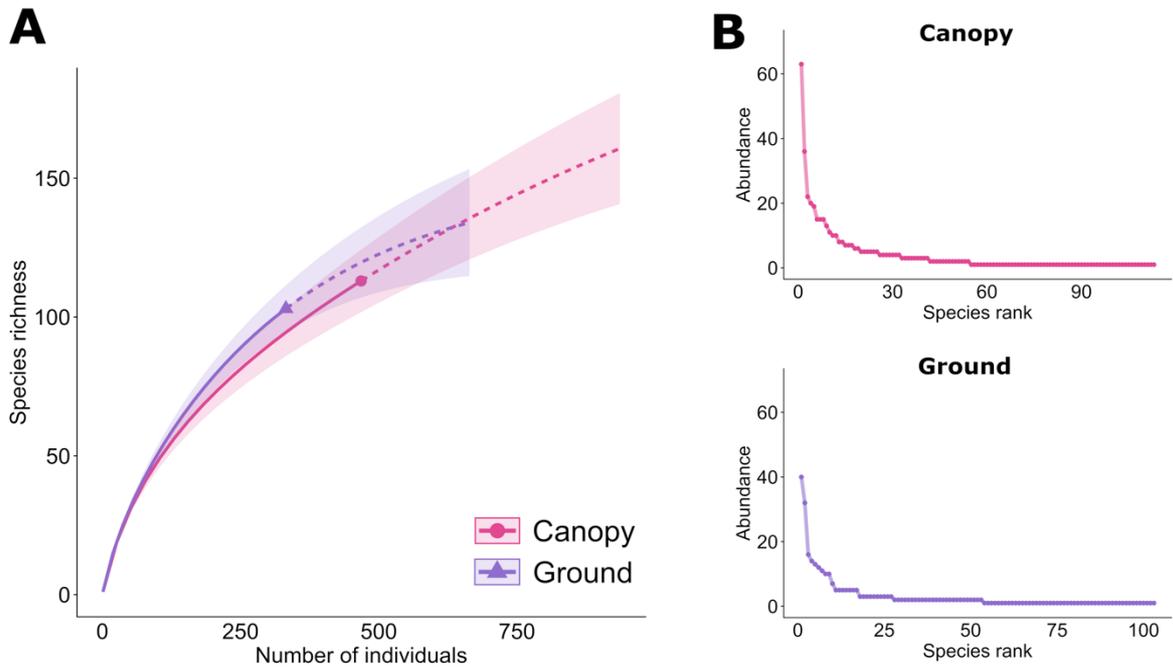
## Supplementary materials – Chapter 4

**Supplementary Text 4.1.** Additional details on modelling:

**Fitting Bayesian regression models (GLMMs).** We used GLMMs to assess the effects of *PrePost*, *Treatment*, and *Distance* on total arthropod abundance, spider abundance, and spider species richness. We ran GLMMs for 50,000 iterations using four chains and a thinning rate of 2, discarded the first 4000 iterations as warm-up / burn-in samples, and increased *adapt\_delta* to 0.99 as needed to decrease the number of divergent transitions. We fitted  $normal(0, 10)$  priors on model intercepts,  $normal(0, 1)$  priors on fixed effects,  $normal(0, 1)$  priors on standard deviation of random effects, and  $gamma(0.01, 0.01)$  priors on negative binomial shape parameters. When applicable, we fitted zero-inflated parameters with  $beta(1, 1)$  priors. Posterior predictive checks (see *Chapter 3 – Supplementary Text 3.1* for details of posterior predictive checks) indicated that data simulated from our spider analyses sometimes did not reflect the real datasets from which models were generated. We therefore re-fitted these models with the following adjustments on the priors:  $normal(0, 10)$  priors on fixed effects (spider abundance and species richness in the canopy),  $normal(0, 10)$  priors on standard deviation of random effects (spider abundance and species richness in the canopy), and  $gamma(1, 1)$  priors on negative binomial shape parameters (spider species richness in the canopy and ground). Posterior predictive checks from these re-fitted models showed no issues.

**Validating GLMMs and multivariate generalised linear models (mGLMs).** We validated our GLMMs and mGLMs, as described in *Chapter 3 – Supplementary Text 3.1*.





**Figure S4.2.** Species accumulation curves (A) and rank abundance curves (B) for the spider communities we sampled in the canopy and ground microhabitats. As we were unable to match males and females within a species, we considered each unique male and female as a separate species. In (A), we plotted both interpolated (solid lines) and extrapolated (dotted lines) species richness. We extrapolated to twice the number of observed individuals, as per Chao et al (2014) and Gotelli & Colwell (2001). For ground spiders in (A) and (B), we plotted spiders from all samples (i.e. not the subset of spiders featured in our sensitivity analyses).

**Table S4.1.** Models that we fitted to analyse changes in the abundance of arthropods in the canopy, understory, and ground microhabitats, and abundance and species richness of spiders in the canopy and ground microhabitats. After fitting and validating all models, we used LOO-IC to determine the optimal model of best fit.

<b>Models:</b>	
Response ~	PrePost*Treatment*Distance + (1   Triplet)
	PrePost*Treatment + Distance + (1   Triplet)
	PrePost*Distance + Treatment + (1   Triplet)
	Treatment*Distance + PrePost + (1   Triplet)
	PrePost + Treatment + Distance + (1   Triplet)
	PrePost*Treatment + (1 Triplet)
	PrePost + Treatment + (1 Triplet)
	PrePost*Distance + (1 Triplet)
	PrePost + Distance + (1 Triplet)
	Treatment*Distance + (1 Triplet)
	Treatment + Distance + (1 Triplet)
	PrePost + (1 Triplet)
	Treatment + (1 Triplet)
	Distance + (1 Triplet)
	1 + (1 Triplet)

**Table S4.2.** Effects of ‘*PrePost*’, ‘*Treatment*’, and ‘*Distance*’ on total arthropod abundance and arthropod order-level community composition (canopy, understory, and ground microhabitats); and spider abundance, species richness, and species-level community composition (canopy and ground microhabitats). We present the optimal model (determined using LOO-IC for total arthropod abundance, spider abundance, and spider species richness; and a backwards stepwise selection procedure for arthropod order-level composition and spider species-level composition) and Bayesian R<sup>2</sup> value and associated standard error for each model. We do not provide R<sup>2</sup> values for our community composition analyses, as this is not a feature supported by the package (*mvabund*) used for these analyses.

**Optimal model for each response:**

<b>Response</b>	<b>Optimal model</b>	<b>Bayesian R<sup>2</sup> ± Est. Err.</b>
<i>All arthropods abundance</i>		
Canopy	~ 1 + (1   Triplet)	19.9 ± 7.4%
Understory	~ <i>PrePost</i> + (1   Triplet)	41.7 ± 3.7%
Ground	~ <i>PrePost</i> + (1   Triplet)	25.2 ± 7.9%
<i>All arthropods composition</i>		
Canopy	~ <i>PrePost</i>	-
Understory	~ <i>PrePost*Treatment*Distance</i>	-
Ground	~ <i>PrePost</i>	-
<i>Spider abundance</i>		
Canopy	~ 1 + (1   Triplet)	20.8 ± 8.1%
Ground	~ 1 + (1   Triplet)	9.2 ± 6.1%
<i>Spider species richness</i>		
Canopy	~ 1 + (1   Triplet)	16.6 ± 7.8%
Ground	~ 1 + (1   Triplet)	4.2 ± 4.3%
<i>Spider composition</i>		
Canopy	~ <i>PrePost*Treatment*Distance</i>	-
Ground	~ <i>PrePost*Treatment*Distance</i>	-

**Table S4.3.** Spider morphospecies (adults only) that were found in the canopy and ground microhabitats. Morphospecies within a family do not always start at 1 (e.g. *Araneidae sp. 1*), as spiders were part of larger dataset.

Family	Morphospecies	Canopy	Ground
Anapidae	Anapidae sp. 2	X	
Araneidae	Araneidae sp. 3	X	
	Araneidae sp. 6	X	
	Araneidae sp. 8	X	
	Araneidae sp. 12	X	
	Araneidae sp. 13	X	
	Araneidae sp. 14	X	
	Araneidae sp. 15	X	
	Araneidae sp. 17	X	
	Araneidae sp. 22	X	
	Araneidae sp. 23	X	
	Araneidae sp. 27	X	
	Araneidae sp. 28	X	
	Araneidae sp. 29	X	
	Araneidae sp. 30	X	
	Araneidae sp. 31	X	
	Araneidae sp. 32	X	
	Araneidae sp. 33	X	
	Araneidae sp. 34	X	
	Gasteracantha sp. 1	X	
Barychelidae	Barychelidae sp. 1		X
Clubionidae	Clubionidae sp. 2	X	
	Clubionidae sp. 4	X	
Corinnidae	Corinnidae sp. 5		X
	Corinnidae sp. 6		X
	Corinnidae sp. 7		X
Ctenidae	Ctenidae sp. 1		X
Gnaphosidae	Gnaphosidae sp. 2	X	
	Gnaphosidae sp. 3	X	
	Gnaphosidae sp. 4	X	
Hersiliidae	Hersiliidae sp. 1	X	
Linyphiidae	Linyphiidae sp. 2		X
	Linyphiidae sp. 3	X	
	Linyphiidae sp. 4	X	X
	Linyphiidae sp. 6		X
	Linyphiidae sp. 8		X
	Linyphiidae sp. 9		X
	Linyphiidae sp. 10	X	X
	Linyphiidae sp. 11	X	X
	Linyphiidae sp. 12		X
	Linyphiidae sp. 13	X	
	Linyphiidae sp. 15		X
	Linyphiidae sp. 16	X	
	Linyphiidae sp. 17	X	
	Linyphiidae sp. 18	X	X

**\*\* Continued on next page**

	Linyphiidae sp. 19	X	X
	Linyphiidae sp. 20		X
	Linyphiidae sp. 21		X
	Linyphiidae sp. 22	X	X
	Linyphiidae sp. 23	X	X
	Linyphiidae sp. 24		X
	Linyphiidae sp. 25		X
	Linyphiidae sp. 26		X
	Linyphiidae sp. 27	X	
	Linyphiidae sp. 28	X	
	Linyphiidae sp. 29	X	
	Linyphiidae sp. 30		X
Liocranidae	Liocranidae sp. 1		X
	Liocranidae sp. 2		X
	Liocranidae sp. 3		X
Lycosidae	Lycosidae sp. 1		X
	Lycosidae sp. 2		X
	Lycosidae sp. 3		X
	Lycosidae sp. 4		X
	Lycosidae sp. 6		X
	Lycosidae sp. 7		X
	Lycosidae sp. 8		X
	Lycosidae sp. 9		X
	Lycosidae sp. 11		X
	Lycosidae sp. 12		X
	Lycosidae sp. 13		X
	Lycosidae sp. 14		X
	Lycosidae sp. 16		X
	Lycosidae sp. 17		X
	Lycosidae sp. 19		X
	Lycosidae sp. 21		X
	Lycosidae sp. 22		X
	Lycosidae sp. 23		X
	Lycosidae sp. 25		X
	Lycosidae sp. 26		X
	Lycosidae sp. 27		X
	Lycosidae sp. 28		X
Mimetidae	Mimetidae sp. 1	X	
Mysmenidae	Mysmenidae sp. 1	X	X
	Mysmenidae sp. 2	X	
	Mysmenidae sp. 4		X
Nesticidae	Nesticidae sp. 1		X
Oonopidae	Ischnothyreus sp. 2		X
	Oonopidae sp. 1	X	
	Oonopidae sp. 2	X	
	Oonopidae sp. 4	X	
	Oonopidae sp. 5	X	
	Oonopidae sp. 6	X	
	Oonopidae sp. 7	X	X

**\*\* Continued on next page**

	Oonopidae sp. 8	X	X
	Oonopidae sp. 9		X
	Oonopidae sp. 10	X	
	Oonopidae sp. 11	X	
	Oonopidae sp. 12	X	
	Oonopidae sp. 13	X	X
	Oonopidae sp. 16	X	X
	Oonopidae sp. 18		X
	Oonopidae sp. 19		X
	Oonopidae sp. 20		X
	Oonopidae sp. 21	X	X
	Oonopidae sp. 22	X	
Oxyopidae	Oxyopidae sp. 1	X	
	Oxyopidae sp. 2	X	
	Oxyopidae sp. 3		X
	Oxyopidae sp. 6		X
	Oxyopidae sp. 7		X
Salticidae	Salticidae sp. 1	X	
	Salticidae sp. 4	X	
	Salticidae sp. 8		X
	Salticidae sp. 9		X
	Salticidae sp. 15	X	
	Salticidae sp. 18	X	
	Salticidae sp. 19		X
	Salticidae sp. 20	X	
	Salticidae sp. 21	X	
	Salticidae sp. 22	X	
	Salticidae sp. 23	X	
	Salticidae sp. 24	X	
	Salticidae sp. 25	X	
	Salticidae sp. 26	X	
Scytodidae	Scytodidae sp. 1	X	X
	Scytodidae sp. 2	X	X
Sparassidae	Sparassidae sp. 1		X
Symphytognathidae	Symphytognathidae sp. 3		X
Tetrablemmidae	Tetrablemmidae sp. 1		X
	Tetrablemmidae sp. 2		X
Tetragnathidae	Opadometa sp. 1	X	
	Opadometa sp. 2	X	X
	Tetragnathidae sp. 1	X	
	Tetragnathidae sp. 4	X	
	Tetragnathidae sp. 5	X	
	Tylorida sp. 1	X	
	Tylorida sp. 3	X	
	Tylorida sp. 4	X	
Theraphosidae	Theraphosidae sp. 1		X
Theridiidae	Ariamnes sp. 2	X	
	Theridiidae sp. 2	X	
	Theridiidae sp. 8	X	
	Theridiidae sp. 9	X	

**\*\* Continued on next page**

	Theridiidae sp. 11	X	
	Theridiidae sp. 13	X	
	Theridiidae sp. 17	X	X
	Theridiidae sp. 21	X	X
	Theridiidae sp. 22		X
	Theridiidae sp. 23		X
	Theridiidae sp. 24		X
	Theridiidae sp. 26	X	
	Theridiidae sp. 27	X	
	Theridiidae sp. 28	X	
	Theridiidae sp. 29	X	X
	Theridiidae sp. 30	X	
	Theridiidae sp. 32	X	
	Theridiidae sp. 33	X	
	Theridiidae sp. 36		X
	Theridiidae sp. 38		X
	Theridiidae sp. 42		X
	Theridiidae sp. 43	X	X
	Theridiidae sp. 44		X
	Theridiidae sp. 45		X
	Theridiidae sp. 46		X
	Theridiidae sp. 47		X
	Theridiidae sp. 48		X
	Theridiidae sp. 49		X
	Theridiidae sp. 50	X	
	Theridiidae sp. 51	X	
	Theridiidae sp. 52	X	
	Theridiidae sp. 53	X	
	Theridiidae sp. 54	X	
	Theridiidae sp. 55	X	
	Rhomphaea sp. 1	X	
	Rhomphaea sp. 2	X	
	Rhomphaea sp. 4	X	
Theridiosomatidae	Theridiosomatidae sp. 4		X
Thomisidae	Amyciaea sp. 2	X	
	Thomisidae sp. 3	X	
	Thomisidae sp. 4		X
	Thomisidae sp. 5		X
	Thomisidae sp. 6		X
	Thomisidae sp. 7		X
	Thomisidae sp. 8	X	
	Thomisidae sp. 9	X	
	Thomisidae sp. 10	X	
Trachelidae	Trachelidae sp. 1		X
	Trachelidae sp. 2		X
Uloboridae	Uloboridae sp. 3	X	
	Uloboridae sp. 5	X	
	Uloboridae sp. 7	X	
Zodariidae	Zodariidae sp. 1		X
	Zodariidae sp. 4		X
	Zodariidae sp. 6		X
	Zodariidae sp. 7		X

## Supplementary materials – Chapter 5

**Supplementary Text 5.1.** List of the 91 studies that were included in our meta-analysis.

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**Table S5.1.** The 11 searches we ran in the ISI Web of Science Core Collection to find relevant studies. We ran the search on 4 March 2021. ‘TS’ is the Web of Science field tag for ‘Topic’, which focusses searches on relevant terms in the titles, abstracts, author keywords, and keywords plus (i.e. keywords generated automatically by Web of Science, based on the titles of studies) of studies. We excluded ‘TS = (monkey)’ from our searches to reduce the number of studies focussed on spider monkeys.

Term
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(rangeland) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(agri* OR cultiv*) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(graz* OR cattle OR rearing OR livestock) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(logg*) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(fire OR burn*) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(pesticid* OR chemical) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(fragmentat*) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(farm*) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(forest AND “land use” OR management) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(“land use”) NOT TS=(monkey)
TS=(spider OR araneae OR arachnid) AND TS=(tropic*) AND TS=(management) NOT TS=(monkey)

**Table S5.2.** Raw data extracted from the studies that focussed on *disturbance and spider abundance*, met our inclusion criteria, and from which sufficient data could be extracted for use in meta-analysis. We include the study name, sampling design score ('1' = samples not spatially or temporally independent or replicated; '2' = samples spatially and / or temporally independent or replicated), broad-level habitat type ('Forest', 'Savannah', 'Cropland', 'Other'), type of disturbance ('Conversion to cropland', 'Multiple disturbances', 'Conversion to pasture', 'Logging', 'Clearance of landscapes', 'Fire', 'Forest fragmentation', 'Intensification of agricultural management', 'Increased application of pesticides'), microhabitat type ('Aerial', 'Understory', 'Ground', 'Soil', 'Multiple microhabitats'), biome ('TSF' = temperate seasonal forest, 'TRF' = tropical rainforest, 'TSFS' = tropical seasonal forest/savannah, 'SD' = subtropical desert); the number of treatment-control comparisons within a study; and the *Hedges' D* and associated variance for each treatment-control comparison.

Study	Score	Habitat	Type of Disturbance	Microhabitat	Biome	Comparison	Hedges' D	Variance
Anjos et al. 2016	1	Other	Fire	Ground	TSF	1	-0.0619	0.1667
	1	Other	Fire	Ground	TSF	2	-0.4256	0.1704
Ashton-Butt et al. 2018	2	Cropland	Intensification of crop management	Soil	TRF	1	-0.2223	0.1677
Ashton-Butt et al. 2019	2	Cropland	Clearance of landscapes	Soil	TRF	1	-0.5107	0.2652
	2	Cropland	Clearance of landscapes	Soil	TRF	2	-0.3935	0.2200
	2	Cropland	Clearance of landscapes	Soil	TRF	3	-0.0311	0.2020
	2	Cropland	Clearance of landscapes	Soil	TRF	4	-0.0098	0.1909
Banks et al. 2007	2	Forest	Conversion to pasture	Ground	TRF	1	0.2301	0.3355
	2	Forest	Conversion to cropland	Ground	TRF	2	0.7198	0.3549
Baretta et al. 2007	1	Forest	Multiple disturbances	Soil	TSF	1	-1.9998	0.9999
	1	Forest	Multiple disturbances	Soil	TSF	2	-1.1141	0.7701
	1	Forest	Multiple disturbances	Soil	TSF	3	-2.8675	1.3519
Benítez-Malvido et al. 2014	2	Forest	Multiple disturbances	Understory	TRF	1	-0.6680	0.2112
	2	Forest	Multiple disturbances	Understory	TRF	2	-0.1306	0.2004
Benítez-Malvido et al. 2020	2	Forest	Forest fragmentation	Understory	TRF	1	0.1962	0.3349
Benito et al. 2005	2	Savannah	Clearance of landscapes	Ground	TSFS	1	-4.0758	0.1709
	2	Savannah	Conversion to pasture	Ground	TSFS	2	-3.5993	0.1455
	2	Savannah	Conversion to pasture	Ground	TSFS	3	-1.1508	0.0648
	2	Savannah	Conversion to pasture	Ground	TSFS	4	-3.1502	0.1245
Bommarco et al. 2011	1	Cropland	Increased application of pesticides	Understory	TSFS	1	-0.3331	0.2253
	1	Cropland	Increased application of pesticides	Understory	TSFS	2	-0.5115	0.2295
Brown et al. 2004	2	Other	Multiple disturbances	Soil	TRF	1	-0.1412	0.2864
	2	Other	Multiple disturbances	Soil	TRF	2	-0.2326	0.2517
Burghouts et al. 1992	2	Forest	Logging	Ground	TSFS	1	-0.0219	0.0667
Cabra-García et al. 2010	2	Forest	Multiple disturbances	Aerial	TSFS	1	0.0135	0.3333
	2	Forest	Conversion to pasture	Aerial	TSFS	2	-1.2589	0.3994
	2	Forest	Clearance of landscapes	Aerial	TSFS	3	-1.7499	0.4609
	2	Forest	Multiple disturbances	Aerial	TSFS	4	0.0066	0.3333
	2	Forest	Conversion to pasture	Aerial	TSFS	5	-1.1672	0.3901
	2	Forest	Clearance of landscapes	Aerial	TSFS	6	-1.5700	0.4360
	2	Forest	Multiple disturbances	Aerial	TSFS	7	-0.4275	0.3409
	2	Forest	Conversion to pasture	Aerial	TSFS	8	-1.5422	0.4324
	2	Forest	Multiple disturbances	Aerial	TSFS	9	-0.1582	0.3344
	2	Forest	Conversion to pasture	Aerial	TSFS	10	-1.2471	0.3981
	2	Forest	Multiple disturbances	Ground	TSFS	11	0.2155	0.3353
	2	Forest	Conversion to pasture	Ground	TSFS	12	-0.6693	0.3520
	2	Forest	Clearance of landscapes	Ground	TSFS	13	-1.0773	0.3817
	2	Forest	Multiple disturbances	Ground	TSFS	14	0.2284	0.3355
	2	Forest	Conversion to pasture	Ground	TSFS	15	-0.6858	0.3529
	2	Forest	Clearance of landscapes	Ground	TSFS	16	-1.2398	0.3974
	2	Forest	Multiple disturbances	Ground	TSFS	17	0.8651	0.2734
	2	Forest	Conversion to pasture	Ground	TSFS	18	0.4875	0.2574
	2	Forest	Clearance of landscapes	Ground	TSFS	19	0.3143	0.2531
	2	Forest	Multiple disturbances	Ground	TSFS	20	0.7439	0.2673
	2	Forest	Conversion to pasture	Ground	TSFS	21	0.3991	0.2550
	2	Forest	Clearance of landscapes	Ground	TSFS	22	0.1645	0.2508
	2	Forest	Multiple disturbances	Ground	TSFS	23	-0.8294	0.2172
	2	Forest	Multiple disturbances	Ground	TSFS	24	0.0000	0.0000

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Cabra-García et al. 2012	2	Forest	Conversion to cropland	Ground	TSF	1	-0.3153	0.1229
	2	Forest	Conversion to pasture	Ground	TSF	2	0.0255	0.1125
	2	Forest	Conversion to cropland	Ground	TSF	3	-0.1442	0.1432
	2	Forest	Conversion to pasture	Ground	TSF	4	0.0634	0.1340
	2	Forest	Conversion to cropland	Ground	TSF	5	-0.0210	0.1429
	2	Forest	Conversion to pasture	Ground	TSF	6	0.0823	0.1340
Calvi et al. 2010	2	Forest	Multiple disturbances	Ground	TSFS	1	-9.2608	2.3441
	2	Forest	Multiple disturbances	Ground	TSFS	2	2.2322	0.3246
Cassano et al. 2016	2	Cropland	Intensification of crop management	Multiple	TSFS	1	-0.4576	0.1710
Chen & Tso 2004	2	Forest	Logging	Multiple	TRF	1	-2.3996	1.7198
	2	Forest	Multiple disturbances	Multiple	TRF	2	-1.1272	1.1588
	2	Forest	Multiple disturbances	Multiple	TRF	3	-2.0582	1.5295
Chen et al. 2013	2	Other	Conversion to cropland	Understory	TSFS	1	-1.7958	0.2264
	2	Other	Conversion to cropland	Understory	TSFS	2	-0.3331	0.1127
Cunha Neto et al. 2012	2	Forest	Conversion to cropland	Ground	TSFS	1	-1.0996	0.2558
	2	Forest	Conversion to cropland	Ground	TSFS	2	-0.6284	0.2332
	2	Forest	Conversion to cropland	Ground	TSFS	3	-0.8257	0.2562
	2	Forest	Conversion to pasture	Ground	TSFS	4	-0.5504	0.2450
	2	Forest	Conversion to cropland	Ground	TSFS	5	-0.7589	0.2871
	2	Forest	Conversion to cropland	Ground	TSFS	6	-0.4638	0.2750
	2	Forest	Conversion to cropland	Ground	TSFS	7	-0.5785	0.2790
	2	Forest	Conversion to pasture	Ground	TSFS	8	-0.4166	0.2594
Da Silva 2017	2	Cropland	Increased application of pesticides	Understory	TSFS	1	-1.1241	0.5790
	2	Cropland	Increased application of pesticides	Understory	TSFS	2	-0.9090	0.5516
	2	Cropland	Increased application of pesticides	Understory	TSFS	3	-1.4237	0.6267
	2	Cropland	Increased application of pesticides	Understory	TSFS	4	-0.8573	0.5459
Darras et al. 2019	2	Cropland	Intensification of crop management	Soil	TSFS	1	0.1947	0.5024
	2	Cropland	Intensification of crop management	Soil	TSFS	2	0.0000	0.5000
	2	Cropland	Intensification of crop management	Soil	TSFS	3	0.2324	0.5034
Dawes-Gromadzki 2007	2	Savannah	Fire	Ground	TSFS	1	-1.8775	0.1067
Dominik et al., 2017	2	Cropland	Intensification of crop management	Ground	TSFS	1	0.3666	0.4067
	2	Cropland	Intensification of crop management	Understory	TSFS	2	-0.2672	0.4036
	2	Cropland	Intensification of crop management	Ground	TSFS	3	0.2152	0.5029
	2	Cropland	Intensification of crop management	Understory	TSFS	4	-0.1701	0.5018
	2	Cropland	Intensification of crop management	Ground	TSFS	5	-0.0312	0.4000
	2	Cropland	Intensification of crop management	Understory	TSFS	6	-0.2934	0.4043
Edwards et al. 2012	2	Forest	Logging	Ground	TSFS	1	-0.0324	0.1667
	2	Forest	Logging	Ground	TSFS	2	-0.0890	0.1668
	2	Forest	Logging	Understory	TSFS	3	0.0577	0.1667
	2	Forest	Logging	Understory	TSFS	4	-0.2301	0.1678
Floren & Deeleman-Reinhold 2005	2	Forest	Clearance of landscapes	Aerial	TSFS	1	-0.2593	0.1630
	2	Forest	Clearance of landscapes	Aerial	TSFS	2	-0.8006	0.1364
	2	Forest	Clearance of landscapes	Aerial	TSFS	3	-0.2254	0.1377
	2	Forest	Clearance of landscapes	Aerial	TSFS	4	-0.1728	0.1625
	2	Forest	Clearance of landscapes	Aerial	TSFS	5	-0.3170	0.1814
	2	Forest	Clearance of landscapes	Aerial	TSFS	6	-0.3381	0.1497
Franco et al. 2016	2	Savannah	Conversion to pasture	Soil	TSFS	1	0.1247	0.2227
	2	Savannah	Conversion to cropland	Soil	TSFS	2	0.0000	0.0000
	2	Forest	Conversion to pasture	Soil	TSFS	3	-0.9863	0.2492
	2	Forest	Conversion to cropland	Soil	TSFS	4	-1.4768	0.2828
	2	Forest	Conversion to pasture	Soil	TSFS	5	-0.9094	0.2452
	2	Forest	Conversion to cropland	Soil	TSFS	6	-0.9094	0.2452
Fredericksen & Fredericksen 2002	2	Forest	Multiple disturbances	Ground	TSFS	1	-0.0317	0.2500
Goehring et al. 2002	2	Forest	Forest fragmentation	Ground	TRF	1	0.0859	0.6673
	2	Forest	Conversion to cropland	Ground	TRF	2	0.6327	0.7000
Gonçalves-Souza et al. 2007	2	Forest	Multiple disturbances	Understory	TSFS	1	0.8623	0.4619
	2	Forest	Multiple disturbances	Multiple	TSFS	2	-0.3907	0.4508
	2	Forest	Multiple disturbances	Understory	TSFS	3	0.3074	0.4370
	2	Forest	Multiple disturbances	Multiple	TSFS	4	0.1421	0.4453
Gras et al. 2016	2	Cropland	Intensification of crop management	Aerial	TSFS	1	-0.1474	0.6685
	2	Cropland	Intensification of crop management	Aerial	TSFS	2	0.1774	0.6693
	2	Cropland	Intensification of crop management	Aerial	TSFS	3	0.8001	0.8974
	2	Cropland	Intensification of crop management	Aerial	TSFS	4	0.3916	0.8487
	2	Cropland	Intensification of crop management	Aerial	TSFS	5	0.7851	0.8950
Houston & Melzer 2018	2	Savannah	Clearance of landscapes	Ground	TSFS	1	-0.1942	0.2512
	2	Savannah	Clearance of landscapes	Understory	TSFS	2	-0.0846	0.2502
	2	Savannah	Conversion to pasture	Ground	TSFS	3	-0.6614	0.5273
	2	Savannah	Conversion to pasture	Ground	TSFS	4	-0.4107	0.5105
	2	Savannah	Conversion to pasture	Understory	TSFS	5	-0.2508	0.5039
	2	Savannah	Conversion to pasture	Understory	TSFS	6	-1.4740	0.6358
Jocqué et al. 2005	1	Forest	Multiple disturbances	Ground	TSFS	1	-0.1657	0.1489
	1	Forest	Multiple disturbances	Ground	TSFS	2	-0.6280	0.2879
	1	Forest	Multiple disturbances	Ground	TSFS	3	-0.1380	0.4452
	1	Forest	Multiple disturbances	Ground	TSFS	4	-0.6719	0.2681
Kapoor 2008	2	Forest	Multiple disturbances	Multiple	TSFS	1	-0.3381	0.5915
	2	Forest	Multiple disturbances	Multiple	TSFS	2	-1.2526	0.7974
	2	Forest	Multiple disturbances	Multiple	TSFS	3	0.5238	0.8608

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Lemessa et al. 2015	2	Cropland	Intensification of crop management	Ground	TSF	1	0.4346	0.1661
	2	Cropland	Intensification of crop management	Ground	TSF	2	0.1638	0.1581
Letourneau 1987	2	Cropland	Intensification of crop management	Ground	TSFS	1	0.0991	0.0556
	2	Cropland	Intensification of crop management	Ground	TSFS	2	0.0214	0.0556
	2	Cropland	Intensification of crop management	Understory	TSFS	3	-0.0662	0.0556
Lingbeek et al. 2017	2	Other	Multiple disturbances	Ground	SD	1	-0.2099	0.1676
	2	Other	Multiple disturbances	Ground	SD	2	-1.1909	0.1962
	2	Other	Multiple disturbances	Ground	SD	3	0.0603	0.1667
	2	Other	Multiple disturbances	Ground	SD	4	-1.9069	0.2424
	2	Other	Multiple disturbances	Ground	SD	5	0.1037	0.1669
	2	Other	Multiple disturbances	Ground	SD	6	-0.5925	0.1740
Lo-Man-Hung et al. 2008	2	Forest	Clearance of landscapes	Ground	TSFS	1	0.0017	0.0400
	2	Forest	Conversion to cropland	Ground	TSFS	2	0.1113	0.0401
Lo-Man-Hung et al. 2011	2	Forest	Multiple disturbances	Ground	TSFS	1	-0.0330	0.0792
	2	Forest	Multiple disturbances	Ground	TSFS	2	0.1882	0.0976
	2	Forest	Conversion to pasture	Ground	TSFS	3	-0.1282	0.0468
	2	Forest	Conversion to cropland	Ground	TSFS	4	-0.1580	0.0920
	2	Forest	Conversion to cropland	Ground	TSFS	5	-0.3852	0.2718
Loranger et al. 1998	2	Forest	Clearance of landscapes	Ground	TSFS	1	-0.1343	0.2005
	2	Forest	Clearance of landscapes	Ground	TSFS	2	-0.0571	0.2001
	2	Forest	Conversion to pasture	Ground	TSFS	3	-0.2579	0.2017
	2	Forest	Conversion to pasture	Ground	TSFS	4	-0.0452	0.2001
	2	Forest	Conversion to cropland	Ground	TSFS	5	-0.5354	0.2072
Méndez-Castro & Rao 2014	2	Forest	Conversion to cropland	Aerial	TSF	1	0.0208	0.0333
Maas et al. 2013	2	Cropland	Intensification of crop management	Multiple	TSFS	1	0.3045	0.1101
	2	Cropland	Intensification of crop management	Multiple	TSFS	2	0.0931	0.1178
	2	Cropland	Intensification of crop management	Multiple	TSFS	3	0.5816	0.1480
	2	Cropland	Intensification of crop management	Multiple	TSFS	4	0.3490	0.1519
	2	Cropland	Intensification of crop management	Multiple	TSFS	5	0.2722	0.1511
Marín et al. 2016	2	Forest	Conversion to cropland	Ground	TRF	1	1.3003	0.2137
	2	Forest	Conversion to cropland	Ground	TRF	2	1.9374	0.2496
	2	Forest	Conversion to cropland	Ground	TRF	3	-1.0120	0.2429
	2	Forest	Conversion to cropland	Ground	TRF	4	1.8456	0.2738
Marquini et al. 2002	1	Cropland	Increased application of pesticides	Understory	TSFS	1	-0.0200	0.0333
Martins et al. 2009	2	Cropland	Increased application of pesticides	Understory	TSFS	1	1.8836	0.7217
	2	Cropland	Increased application of pesticides	Understory	TSFS	2	2.2502	0.8165
	2	Cropland	Increased application of pesticides	Understory	TSFS	3	3.1430	1.1174
	2	Cropland	Increased application of pesticides	Understory	TSFS	4	2.4950	0.8891
	2	Cropland	Increased application of pesticides	Understory	TSFS	5	2.9769	1.0539
	2	Cropland	Increased application of pesticides	Understory	TSFS	6	2.1080	0.7777
	2	Cropland	Increased application of pesticides	Understory	TSFS	7	1.8957	0.7246
Mathieu et al. 2005	1	Forest	Multiple disturbances	Ground	TSFS	1	-0.1366	0.0493
	1	Forest	Conversion to cropland	Ground	TSFS	2	-0.2847	0.0351
	1	Forest	Conversion to pasture	Ground	TSFS	3	-0.0231	0.0253
	1	Forest	Clearance of landscapes	Ground	TSFS	4	-0.0534	0.0659
Neilly et al. 2020	2	Savannah	Conversion to pasture	Ground	TSFS	1	-0.0998	0.1669
	2	Savannah	Conversion to pasture	Ground	TSFS	2	0.0722	0.1668
	2	Savannah	Conversion to pasture	Ground	TSFS	3	0.0795	0.1668
	2	Savannah	Conversion to pasture	Ground	TSFS	4	-0.0179	0.3333
	2	Savannah	Conversion to pasture	Ground	TSFS	5	-0.0341	0.3334
	2	Savannah	Conversion to pasture	Ground	TSFS	6	0.1856	0.3348
Nogueira et al. 2006	2	Forest	Forest fragmentation	Multiple	TSF	1	-0.5938	0.2610
Nordberg & Schwarzkopf 2019	2	Savannah	Conversion to pasture	Multiple	TSFS	1	-0.4630	0.3423
	2	Savannah	Conversion to pasture	Multiple	TSFS	2	0.0441	0.3334
	2	Savannah	Conversion to pasture	Multiple	TSFS	3	-0.2708	0.3364
	2	Savannah	Conversion to pasture	Multiple	TSFS	4	-0.2986	0.3370
	2	Savannah	Conversion to pasture	Multiple	TSFS	5	0.2722	0.3364
	2	Savannah	Conversion to pasture	Multiple	TSFS	6	0.1884	0.3348
Nordberg et al. 2018	2	Savannah	Conversion to pasture	Multiple	TSFS	1	-0.1103	0.3338
	2	Savannah	Conversion to pasture	Multiple	TSFS	2	0.0000	0.3333
	2	Savannah	Conversion to pasture	Multiple	TSFS	3	0.0896	0.3337
Pauli et al. 2011	1	Forest	Conversion to cropland	Soil	TSFS	1	-0.0308	0.0667
	1	Forest	Conversion to cropland	Soil	TSFS	2	-0.0685	0.0667
	1	Forest	Conversion to cropland	Soil	TSFS	3	0.0314	0.0667
	1	Forest	Conversion to cropland	Soil	TSFS	4	0.0000	0.0667
	1	Forest	Conversion to pasture	Soil	TSFS	5	-0.1082	0.0668
Pellens & Garay 1999a	1	Forest	Conversion to cropland	Ground	TSFS	1	-0.8795	0.1687
	1	Forest	Conversion to cropland	Ground	TSFS	2	-0.8504	0.1678
	1	Forest	Conversion to cropland	Ground	TSFS	3	-0.0290	0.1539
	1	Forest	Conversion to cropland	Ground	TSFS	4	-0.1799	0.1545
	1	Forest	Conversion to cropland	Ground	TSFS	5	0.1125	0.1605
	1	Forest	Conversion to cropland	Ground	TSFS	6	-0.1350	0.1606
	1	Forest	Conversion to cropland	Ground	TSFS	7	0.1580	0.1543
	1	Forest	Conversion to cropland	Ground	TSFS	8	0.2221	0.1548
Pellens & Garay 1999b	2	Forest	Conversion to cropland	Ground	TSFS	1	0.2223	0.1548
	2	Forest	Conversion to cropland	Ground	TSFS	2	0.1323	0.1606

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Pinkus-Rendón et al. 2006	1	Forest	Conversion to cropland	Understory	TRF	1	0.5132	0.3443
	1	Forest	Conversion to cropland	Understory	TRF	2	0.3423	0.3382
	1	Forest	Conversion to cropland	Understory	TRF	3	0.9379	0.3700
	1	Forest	Conversion to cropland	Understory	TRF	4	0.7343	0.3558
Potapov et al. 2020	2	Forest	Conversion to cropland	Soil	TRF	1	-4.6814	1.8697
	2	Forest	Conversion to cropland	Soil	TRF	2	-1.5330	0.6469
	2	Forest	Conversion to cropland	Soil	TRF	3	-3.5405	1.2835
	2	Forest	Conversion to cropland	Ground	TRF	4	-1.0788	0.5727
	2	Forest	Conversion to cropland	Ground	TRF	5	-1.9887	0.7472
	2	Forest	Conversion to cropland	Ground	TRF	6	-1.5119	0.6429
	2	Forest	Conversion to cropland	Soil	TRF	7	-0.7816	0.5382
	2	Forest	Conversion to cropland	Soil	TRF	8	-0.3027	0.5057
	2	Forest	Conversion to cropland	Soil	TRF	9	-2.5348	0.9016
	2	Forest	Conversion to cropland	Ground	TRF	10	0.3380	0.5071
	2	Forest	Conversion to cropland	Ground	TRF	11	0.3196	0.5064
	2	Forest	Conversion to cropland	Ground	TRF	12	-0.5445	0.5185
Radford & Andersen 2012	2	Savannah	Fire	Understory	TSFS	1	-3.0174	1.0691
Ramos et al. (Unpublished)	2	Forest	Conversion to cropland	Aerial	TRF	1	-0.2231	0.5031
	2	Forest	Conversion to cropland	Aerial	TRF	2	-3.1175	1.1074
	2	Forest	Conversion to cropland	Aerial	TRF	3	-2.2238	0.8091
	2	Forest	Conversion to cropland	Aerial	TRF	4	-0.3045	0.5058
	2	Forest	Conversion to cropland	Aerial	TRF	5	-1.3883	0.6205
	2	Forest	Conversion to cropland	Aerial	TRF	6	-2.0990	0.7754
Rego et al. 2005	2	Forest	Forest fragmentation	Multiple	TRF	1	0.3586	0.2580
	2	Forest	Forest fragmentation	Multiple	TRF	2	-0.1919	0.2551
Rossi & Blanchart 2005	2	Forest	Logging	Soil	TRF	1	0.0183	0.3667
	2	Forest	Logging	Soil	TRF	2	-0.2500	0.3695
	2	Forest	Conversion to pasture	Soil	TRF	3	-0.7108	0.3896
	2	Forest	Conversion to pasture	Soil	TRF	4	-0.9556	0.4082
	2	Forest	Conversion to cropland	Soil	TRF	5	-1.0720	0.4189
Schoenly et al. 2003	2	Cropland	Increased application of pesticides	Understory	TSFS	1	-0.0674	0.6670
Sewlal & Hailey 2019	2	Forest	Conversion to cropland	Multiple	TSFS	1	-0.8530	0.3636
	2	Forest	Conversion to cropland	Multiple	TSFS	2	-0.1299	0.3340
Silva et al. 2012	1	Forest	Conversion to pasture	Aerial	TSFS	1	0.0768	0.1334
	1	Forest	Conversion to pasture	Aerial	TSFS	2	-0.0286	0.1333
	1	Forest	Conversion to pasture	Aerial	TSFS	3	-0.2451	0.1343
	1	Forest	Conversion to pasture	Aerial	TSFS	4	0.0239	0.1333
	1	Forest	Conversion to pasture	Aerial	TSFS	5	-0.0295	0.1333
	1	Forest	Conversion to pasture	Aerial	TSFS	6	0.0399	0.1334
Silva Moço et al. 2009	2	Forest	Conversion to cropland	Ground	TSFS	1	0.0137	0.1667
	2	Forest	Conversion to cropland	Ground	TSFS	2	0.0685	0.1668
	2	Forest	Conversion to cropland	Ground	TSFS	3	0.0163	0.1667
	2	Forest	Conversion to cropland	Ground	TSFS	4	0.1535	0.1672
	2	Forest	Conversion to cropland	Ground	TSFS	5	-0.2124	0.1676
	2	Forest	Conversion to cropland	Soil	TSFS	6	-0.0822	0.1668
	2	Forest	Conversion to cropland	Soil	TSFS	7	0.0064	0.1667
	2	Forest	Conversion to cropland	Soil	TSFS	8	0.0360	0.1667
	2	Forest	Conversion to cropland	Soil	TSFS	9	-0.2376	0.1678
	2	Forest	Conversion to cropland	Soil	TSFS	10	-0.0658	0.1668
Silveira et al. 2010	1	Forest	Fire	Ground	TSFS	1	-0.0087	0.0500
	1	Forest	Fire	Ground	TSFS	2	0.1082	0.0501
	1	Forest	Fire	Ground	TSFS	3	-0.0684	0.0500
	1	Forest	Fire	Ground	TSFS	4	-0.9965	0.0562
Spear 2016	2	Cropland	Intensification of crop management	Aerial	TRF	1	-1.4614	0.4223
	2	Cropland	Intensification of crop management	Understory	TRF	2	-0.4880	0.3433
	2	Cropland	Intensification of crop management	Ground	TRF	3	0.0171	0.3333
Teodoro et al. 2011	2	Forest	Conversion to cropland	Understory	TSFS	1	-0.4685	0.3425
	2	Forest	Conversion to cropland	Understory	TSFS	2	-0.6918	0.3533
	2	Forest	Conversion to pasture	Understory	TSFS	3	-0.6277	0.3498
	2	Forest	Conversion to cropland	Understory	TSFS	4	-0.1760	0.3346
Tsai et al. 2006	1	Forest	Logging	Multiple	TRF	1	0.0893	0.1335
	1	Forest	Multiple disturbances	Multiple	TRF	2	-0.0541	0.1334
	1	Forest	Multiple disturbances	Multiple	TRF	3	-0.3114	0.1349
Tsukamoto & Sabang 2005	1	Forest	Conversion to cropland	Ground	TRF	1	-0.2470	0.1679
Turner & Foster 2009	2	Forest	Logging	Understory	TRF	1	-0.0597	0.1000
	2	Forest	Logging	Aerial	TRF	2	0.0458	0.1000
	2	Forest	Logging	Ground	TRF	3	-0.1979	0.1005
	2	Forest	Conversion to cropland	Understory	TSFS	4	0.1077	0.1001
	2	Forest	Conversion to cropland	Aerial	TSFS	5	-0.0076	0.1000
	2	Forest	Conversion to cropland	Ground	TSFS	6	-0.9756	0.1119
Uehara-Prado et al. 2009	2	Forest	Multiple disturbances	Ground	TSF	1	-1.1236	0.3859
Vasconcelos et al. 2009	2	Savannah	Fire	Ground	TSFS	1	-0.6265	0.3497
Vorley 1985	1	Cropland	Increased application of pesticides	Understory	TSFS	1	-1.5451	0.6492
	1	Cropland	Increased application of pesticides	Understory	TSFS	2	-1.5331	0.6469
	1	Cropland	Increased application of pesticides	Understory	TSFS	3	-0.4581	0.5131
	1	Cropland	Increased application of pesticides	Understory	TSFS	4	-0.2818	0.5050

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Watt et al. 1997	1	Forest	Clearance of landscapes	Aerial	TSFS	1	-0.0700	0.2001
	1	Forest	Clearance of landscapes	Aerial	TSFS	2	-0.1731	0.2007
	1	Forest	Clearance of landscapes	Aerial	TSFS	3	-0.1472	0.1337
	1	Forest	Clearance of landscapes	Aerial	TSFS	4	-0.5785	0.1389
	1	Forest	Clearance of landscapes	Aerial	TSFS	5	-0.1649	0.1338
	1	Forest	Clearance of landscapes	Aerial	TSFS	6	-0.0944	0.1335
	1	Forest	Clearance of landscapes	Aerial	TSFS	7	-0.0906	0.0801
	1	Forest	Clearance of landscapes	Aerial	TSFS	8	-0.0132	0.0800
	1	Forest	Clearance of landscapes	Aerial	TSFS	9	-0.1433	0.0802
	1	Forest	Clearance of landscapes	Aerial	TSFS	10	-0.0413	0.0650
	1	Forest	Clearance of landscapes	Aerial	TSFS	11	0.0504	0.0800
	1	Forest	Clearance of landscapes	Aerial	TSFS	12	-0.1748	0.0803
	1	Forest	Clearance of landscapes	Aerial	TSFS	13	-0.1654	0.0803
	1	Forest	Clearance of landscapes	Aerial	TSFS	14	-0.2600	0.0807
Wong et al. 2016	1	Forest	Conversion to cropland	Ground	TSFS	1	-1.6987	0.4536
	1	Forest	Conversion to cropland	Ground	TSFS	2	-0.7787	0.3586
	1	Forest	Conversion to cropland	Ground	TSFS	3	-0.5750	0.3471
	1	Forest	Conversion to cropland	Ground	TSFS	4	-0.8259	0.3618
	1	Forest	Conversion to cropland	Ground	TSFS	5	-0.4609	0.3422
Yang & Chen 2009	1	Forest	Conversion to cropland	Ground	TSFS	6	-0.2135	0.3352
	1	Forest	Clearance of landscapes	Multiple	TSFS	1	0.2710	0.2018
	1	Forest	Clearance of landscapes	Multiple	TSFS	2	0.1575	0.2006
	1	Forest	Clearance of landscapes	Multiple	TSFS	3	-0.1545	0.2006
Yankelevich et al. 2006	1	Forest	Clearance of landscapes	Multiple	TSFS	4	0.1787	0.2008
	2	Forest	Logging	Soil	TSF	1	-0.5794	0.5210
	2	Forest	Logging	Soil	TSF	2	-0.7723	0.5373
	2	Forest	Logging	Soil	TSF	3	-0.8055	0.5406
	2	Forest	Logging	Ground	TSF	4	0.4316	0.5116
	2	Forest	Logging	Ground	TSF	5	0.3536	0.5078
	2	Forest	Logging	Ground	TSF	6	0.3118	0.5061
	2	Forest	Logging	Soil	TSF	7	0.1791	1.0040
Yanoviak et al. 2003	2	Forest	Logging	Ground	TSF	8	-0.9062	1.1027
	1	Forest	Multiple disturbances	Aerial	TRF	1	0.3040	0.1349
	1	Forest	Conversion to pasture	Aerial	TRF	2	0.3972	0.2706
	1	Forest	Multiple disturbances	Understory	TRF	3	-0.1180	0.1336
	1	Forest	Conversion to pasture	Understory	TRF	4	0.2763	0.2686
Zheng et al. 2015	2	Forest	Conversion to cropland	Aerial	TSFS	1	-0.7706	0.5371
	2	Forest	Conversion to cropland	Aerial	TSFS	2	-1.5058	0.6417
	2	Forest	Conversion to cropland	Aerial	TSFS	3	-1.5215	0.6447
	2	Forest	Conversion to cropland	Aerial	TSFS	4	-3.5076	1.2690
	2	Forest	Conversion to cropland	Aerial	TSFS	5	-0.8954	0.5501
	2	Forest	Conversion to cropland	Aerial	TSFS	6	-3.0412	1.0780

**Table S5.3.** Raw data extracted from the studies that focussed on *disturbance and spider species richness*, met our inclusion criteria, and from which sufficient data could be extracted for use in meta-analysis. We include the study name, sampling design score ('1' = samples not spatially or temporally independent or replicated; '2' = samples spatially and / or temporally independent or replicated), broad-level habitat type ('Forest', 'Savannah', 'Cropland', 'Other'), type of disturbance ('Conversion to cropland', 'Multiple disturbances', 'Conversion to pasture', 'Logging', 'Clearance of landscapes', 'Fire', 'Forest fragmentation', 'Intensification of agricultural management', 'Increased application of pesticides'), microhabitat type ('Aerial', 'Understory', 'Ground', 'Soil', 'Multiple microhabitats'), biome ('TSF' = temperate seasonal forest, 'TRF' = tropical rainforest, 'TSFS' = tropical seasonal forest/savannah, 'SD' = subtropical desert); the number of treatment-control comparisons within a study; and the *Hedges' D* and associated variance for each treatment-control comparison.

Study	Score	Habitat	Type of Disturbance	Microhabitat	Biome	Comparison	Hedges' D	Variance
Benítez-Malvido et al. 2020	2	Forest	Forest fragmentation	Understory	TRF	1	0.2034	0.3351
Cabra-García et al. 2010	2	Forest	Multiple disturbances	Aerial	TSFS	1	0.3572	0.3387
	2	Forest	Conversion to pasture	Aerial	TSFS	2	-0.8183	0.3612
	2	Forest	Clearance of landscapes	Aerial	TSFS	3	-0.8896	0.3663
	2	Forest	Multiple disturbances	Aerial	TSFS	4	0.2784	0.3366
	2	Forest	Conversion to pasture	Aerial	TSFS	5	-0.9049	0.3675
	2	Forest	Clearance of landscapes	Aerial	TSFS	6	-0.9706	0.3726
	2	Forest	Multiple disturbances	Aerial	TSFS	7	-0.4510	0.3418
	2	Forest	Conversion to pasture	Aerial	TSFS	8	-1.3125	0.4051
	2	Forest	Multiple disturbances	Aerial	TSFS	9	-0.1609	0.3344
	2	Forest	Conversion to pasture	Aerial	TSFS	10	-0.9862	0.3739
	2	Forest	Multiple disturbances	Ground	TSFS	11	0.0252	0.3334
	2	Forest	Conversion to pasture	Ground	TSFS	12	-0.8438	0.3630
	2	Forest	Clearance of landscapes	Ground	TSFS	13	-1.3925	0.4141
	2	Forest	Multiple disturbances	Ground	TSFS	14	-0.0125	0.3333
	2	Forest	Conversion to pasture	Ground	TSFS	15	-0.8899	0.3663
	2	Forest	Clearance of landscapes	Ground	TSFS	16	-1.4196	0.4173
	2	Forest	Multiple disturbances	Ground	TSFS	17	0.5645	0.2600
	2	Forest	Conversion to pasture	Ground	TSFS	18	0.6659	0.2639
	2	Forest	Clearance of landscapes	Ground	TSFS	19	0.4433	0.2561
	2	Forest	Multiple disturbances	Ground	TSFS	20	0.7596	0.2680
	2	Forest	Conversion to pasture	Ground	TSFS	21	0.7450	0.2673
	2	Forest	Clearance of landscapes	Ground	TSFS	22	0.5671	0.2600
	2	Forest	Multiple disturbances	Ground	TSFS	23	-1.0492	0.2275
	2	Forest	Multiple disturbances	Ground	TSFS	24	0.0000	0.0000
Cabra-García et al. 2012	2	Forest	Conversion to cropland	Ground	TSF	1	-0.4506	0.1244
	2	Forest	Conversion to pasture	Ground	TSF	2	-0.0821	0.1126
	2	Forest	Conversion to cropland	Ground	TSF	3	-0.4150	0.1459
	2	Forest	Conversion to pasture	Ground	TSF	4	-0.0634	0.1340
	2	Forest	Conversion to cropland	Ground	TSF	5	-0.2083	0.1436
	2	Forest	Conversion to pasture	Ground	TSF	6	0.0444	0.1340
Chen & Tso 2004	2	Forest	Logging	Multiple	TRF	1	-0.9806	1.1202
	2	Forest	Multiple disturbances	Multiple	TRF	2	-0.8165	1.0833
	2	Forest	Multiple disturbances	Multiple	TRF	3	-1.4725	1.2710
Chen et al. 2013	2	Other	Conversion to cropland	Understory	TSFS	1	-0.8472	0.1800
	2	Other	Conversion to cropland	Understory	TSFS	2	-0.3826	0.1131
Gonçalves-Souza et al. 2007	2	Forest	Multiple disturbances	Understory	TSFS	1	0.5243	0.4439
	2	Forest	Multiple disturbances	Multiple	TSFS	2	-0.6505	0.4621
	2	Forest	Multiple disturbances	Understory	TSFS	3	0.2269	0.4353
	2	Forest	Multiple disturbances	Multiple	TSFS	4	0.1276	0.4451
Jocqué et al. 2005	1	Forest	Multiple disturbances	Ground	TSFS	1	-0.1177	0.1486
	1	Forest	Multiple disturbances	Ground	TSFS	2	-0.5842	0.2864
	1	Forest	Multiple disturbances	Ground	TSFS	3	-0.1234	0.4451
	1	Forest	Multiple disturbances	Ground	TSFS	4	-0.6682	0.2679

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Kapoor 2008	2	Forest	Multiple disturbances	Multiple	TSFS	1	0.2395	0.5874
	2	Forest	Multiple disturbances	Multiple	TSFS	2	-0.3623	0.6776
	2	Forest	Multiple disturbances	Multiple	TSFS	3	0.2432	0.8392
Lemessa et al. 2015	2	Cropland	Intensification of crop management	Ground	TSF	1	0.1679	0.1629
	2	Cropland	Intensification of crop management	Ground	TSF	2	0.1146	0.1578
Lingbeek et al. 2017	2	Other	Multiple disturbances	Ground	SD	1	0.0000	0.1667
	2	Other	Multiple disturbances	Ground	SD	2	-0.5590	0.1732
	2	Other	Multiple disturbances	Ground	SD	3	0.0997	0.1669
	2	Other	Multiple disturbances	Ground	SD	4	-0.1679	0.1673
	2	Other	Multiple disturbances	Ground	SD	5	-0.2161	0.1676
	2	Other	Multiple disturbances	Ground	SD	6	-0.3555	0.1693
Lo-Man-Hung et al. 2008	2	Forest	Clearance of landscapes	Ground	TSFS	1	-0.0062	0.0400
	2	Forest	Conversion to cropland	Ground	TSFS	2	0.1748	0.0402
Lo-Man-Hung et al. 2011	2	Forest	Multiple disturbances	Ground	TSFS	1	-0.0857	0.0793
	2	Forest	Multiple disturbances	Ground	TSFS	2	0.2245	0.0977
	2	Forest	Conversion to pasture	Ground	TSFS	3	-0.1237	0.0468
	2	Forest	Conversion to cropland	Ground	TSFS	4	-0.1524	0.0920
	2	Forest	Conversion to cropland	Ground	TSFS	5	-0.3717	0.2717
Méndez-Castro & Rao 2014	2	Forest	Conversion to cropland	Aerial	TSF	1	0.0697	0.0334
Marín et al. 2016	2	Forest	Conversion to cropland	Ground	TRF	1	0.2004	0.1778
	2	Forest	Conversion to cropland	Ground	TRF	2	0.2189	0.1724
	2	Forest	Conversion to cropland	Ground	TRF	3	-0.3238	0.2187
	2	Forest	Conversion to cropland	Ground	TRF	4	0.0179	0.1964
Mathieu et al. 2005	1	Forest	Multiple disturbances	Ground	TSFS	1	-0.1455	0.0493
	1	Forest	Conversion to cropland	Ground	TSFS	2	-0.2369	0.0350
	1	Forest	Conversion to pasture	Ground	TSFS	3	-0.1537	0.0254
	1	Forest	Clearance of landscapes	Ground	TSFS	4	-0.0317	0.0659
Nogueira et al. 2006	2	Forest	Forest fragmentation	Multiple	TSF	1	0.0000	0.2500
Pinkus-Rendón et al. 2006	1	Forest	Conversion to cropland	Understory	TRF	1	-1.4808	0.4247
	1	Forest	Conversion to cropland	Understory	TRF	2	0.3137	0.3374
	1	Forest	Conversion to cropland	Understory	TRF	3	1.1917	0.3925
	1	Forest	Conversion to cropland	Understory	TRF	4	1.0614	0.3803
Potapov et al. 2020	2	Forest	Conversion to cropland	Soil	TRF	1	-1.1385	0.5810
	2	Forest	Conversion to cropland	Soil	TRF	2	-1.9004	0.7257
	2	Forest	Conversion to cropland	Soil	TRF	3	-2.6895	0.9521
	2	Forest	Conversion to cropland	Ground	TRF	4	-1.3323	0.6109
	2	Forest	Conversion to cropland	Ground	TRF	5	-1.6239	0.6648
	2	Forest	Conversion to cropland	Ground	TRF	6	-1.2520	0.5980
	2	Forest	Conversion to cropland	Soil	TRF	7	-0.7178	0.5322
	2	Forest	Conversion to cropland	Soil	TRF	8	-0.5241	0.5172
	2	Forest	Conversion to cropland	Soil	TRF	9	-2.4274	0.8683
	2	Forest	Conversion to cropland	Ground	TRF	10	0.3509	0.5077
	2	Forest	Conversion to cropland	Ground	TRF	11	0.2801	0.5049
	2	Forest	Conversion to cropland	Ground	TRF	12	-0.5862	0.5215
Ramos et al. (Unpublished)	2	Forest	Conversion to cropland	Aerial	TRF	1	0.0119	0.5000
	2	Forest	Conversion to cropland	Aerial	TRF	2	-4.0703	1.5354
	2	Forest	Conversion to cropland	Aerial	TRF	3	-1.7760	0.6971
	2	Forest	Conversion to cropland	Aerial	TRF	4	-0.2047	0.5026
	2	Forest	Conversion to cropland	Aerial	TRF	5	-0.8677	0.5471
	2	Forest	Conversion to cropland	Aerial	TRF	6	-1.4254	0.6270
Schoenly et al. 2003	2	Cropland	Increased application of pesticides	Understory	TSFS	1	0.0000	0.6667
Sewlal & Hailey 2019	2	Forest	Conversion to cropland	Multiple	TSFS	1	-0.4498	0.3418
	2	Forest	Conversion to cropland	Multiple	TSFS	2	-1.3505	0.4093
Spear 2016	2	Cropland	Intensification of crop management	Aerial	TRF	1	-0.6205	0.3494
	2	Cropland	Intensification of crop management	Understory	TRF	2	-0.9491	0.3709
	2	Cropland	Intensification of crop management	Ground	TRF	3	0.2014	0.3350
Teodoro et al. 2011	2	Forest	Conversion to cropland	Understory	TSFS	1	-0.3601	0.3387
	2	Forest	Conversion to cropland	Understory	TSFS	2	-0.7116	0.3544
	2	Forest	Conversion to pasture	Understory	TSFS	3	-0.4647	0.3423
	2	Forest	Conversion to cropland	Understory	TSFS	4	-0.1799	0.3347
Tsai et al. 2006	1	Forest	Logging	Multiple	TRF	1	0.1456	0.1337
	1	Forest	Multiple disturbances	Multiple	TRF	2	-0.1447	0.1337
	1	Forest	Multiple disturbances	Multiple	TRF	3	-0.4415	0.1366
Uehara-Prado et al. 2009	2	Forest	Multiple disturbances	Ground	TSF	1	1.1735	0.3907
Woinarski et al. 2002	1	Savannah	Conversion to pasture	Ground	TSFS	1	-0.0306	0.5001
	1	Savannah	Multiple disturbances	Ground	TSFS	2	-0.0012	0.5000
	1	Savannah	Conversion to pasture	Ground	TSFS	3	-0.2369	0.5035
	1	Savannah	Multiple disturbances	Ground	TSFS	4	-0.4659	0.5136
	1	Savannah	Conversion to pasture	Ground	TSFS	5	-0.7741	0.5374
	1	Savannah	Multiple disturbances	Ground	TSFS	6	-0.6168	0.5238
	1	Savannah	Conversion to pasture	Ground	TSFS	7	0.0731	0.5003
	1	Savannah	Multiple disturbances	Ground	TSFS	8	-0.5197	0.5169
Yanoviak et al. 2003	1	Forest	Multiple disturbances	Aerial	TRF	1	-0.6352	0.1401
	1	Forest	Conversion to pasture	Aerial	TRF	2	-0.4953	0.2728
	1	Forest	Multiple disturbances	Understory	TRF	3	-0.4773	0.1371
	1	Forest	Conversion to pasture	Understory	TRF	4	-0.2230	0.2679
Zheng et al. 2015	2	Forest	Conversion to cropland	Aerial	TSFS	1	-0.7218	0.5326
	2	Forest	Conversion to cropland	Aerial	TSFS	2	-2.8160	0.9956
	2	Forest	Conversion to cropland	Aerial	TSFS	3	-1.0261	0.5658
	2	Forest	Conversion to cropland	Aerial	TSFS	4	-2.8108	0.9938
	2	Forest	Conversion to cropland	Aerial	TSFS	5	-0.7414	0.5344
	2	Forest	Conversion to cropland	Aerial	TSFS	6	-3.3061	1.1832

**Table S5.4.** Raw data extracted from the studies that focussed on *restoration and spider abundance*, met our inclusion criteria, and from which sufficient data could be extracted for use in meta-analysis. We include the study name, sampling design score ('1' = samples not spatially or temporally independent or replicated; '2' = samples spatially and / or temporally independent or replicated), broad-level habitat type ('Savannah', 'Cropland'), approach to restoration ('Passive', 'Active'), microhabitat type ('Aerial', 'Understory', 'Ground', 'Soil', 'Multiple microhabitats'), biome ('TRF' = tropical rainforest, 'TSFS' = tropical seasonal forest/savannah); the number of treatment-control comparisons within a study; and the *Hedges'* *D* and associated variance for each treatment-control comparison.

Study	Score	Habitat	Approach to Restoration	Microhabitat	Biome	Comparison	Hedges' D	Variance
Ashraf et al. 2018	1	Cropland	Active	Ground	TSFS	1	0.0145	0.0048
	1	Cropland	Active	Ground	TSFS	2	0.0118	0.0048
	1	Cropland	Active	Ground	TSFS	3	0.0121	0.0048
	1	Cropland	Active	Ground	TSFS	4	0.0101	0.0048
	1	Cropland	Active	Ground	TSFS	5	0.0127	0.0048
	1	Cropland	Active	Ground	TSFS	6	0.0105	0.0048
	1	Cropland	Active	Ground	TSFS	7	0.0081	0.0048
	1	Cropland	Active	Ground	TSFS	8	0.0085	0.0048
	1	Cropland	Active	Ground	TSFS	9	0.0062	0.0048
	1	Cropland	Active	Ground	TSFS	10	0.0085	0.0048
Ashton-Butt et al. 2018	2	Cropland	Active	Soil	TRF	1	0.0197	0.1667
Brotodjojo et al. 2019	1	Cropland	Active	Understory	TSFS	1	0.3387	0.4057
	1	Cropland	Active	Understory	TSFS	2	0.2487	0.4031
Esquivel-Gómez et al. 2017	2	Cropland	Active	Multiple	TSFS	1	0.3956	0.2303
Forbes & Northfield 2017	2	Cropland	Active	Multiple	TSFS	1	0.1512	0.2006
Ghazali et al. 2016	2	Cropland	Active	Ground	TSFS	1	0.0481	0.0333
Hooks & Johnson 2006	1	Cropland	Active	Understory	TSFS	1	-0.2193	0.3353
	1	Cropland	Active	Understory	TSFS	2	-0.1350	0.3341
	1	Cropland	Active	Understory	TSFS	3	-0.9998	0.4500
	1	Cropland	Active	Understory	TSFS	4	-0.5238	0.4137
Horgan et al., 2017	1	Cropland	Active	Understory	TSFS	1	0.1441	0.2005
	1	Cropland	Active	Understory	TSFS	2	0.1242	0.2004
	1	Cropland	Active	Multiple	TSFS	3	-0.3234	0.2026
	1	Cropland	Active	Multiple	TSFS	4	0.1165	0.2003
	1	Cropland	Active	Understory	TSFS	5	0.0085	0.2000
	1	Cropland	Active	Understory	TSFS	6	-0.0477	0.2001
	1	Cropland	Active	Multiple	TSFS	7	-0.0462	0.2001
	1	Cropland	Active	Multiple	TSFS	8	-0.2954	0.2022
Horgan et al., 2019	1	Cropland	Active	Understory	TSFS	1	-0.0293	0.0417
	1	Cropland	Active	Understory	TSFS	2	-0.0003	0.0417
	1	Cropland	Active	Understory	TSFS	3	0.0138	0.0370
	1	Cropland	Active	Understory	TSFS	4	0.1708	0.0372
Houston & Melzer 2018	2	Savannah	Passive	Ground	TSFS	1	0.0686	0.5003
	2	Savannah	Passive	Ground	TSFS	2	0.2546	0.5041
	2	Savannah	Passive	Understory	TSFS	3	-0.6940	0.5301
	2	Savannah	Passive	Understory	TSFS	4	-2.2146	0.8065
Koji et al. 2007	1	Cropland	Active	Understory	TSFS	1	-0.0816	0.0801
	1	Cropland	Active	Understory	TSFS	2	0.1845	0.0803
Kyamanywa et al. 1993	1	Cropland	Active	Ground	TSFS	1	-1.0582	0.3800
	1	Cropland	Active	Ground	TSFS	2	-0.4783	0.3429
Midega et al. 2006	1	Cropland	Active	Understory	TSFS	1	0.2931	0.2527
	1	Cropland	Active	Understory	TSFS	2	0.9024	0.2754
Midega et al. 2008	1	Cropland	Active	Multiple	TSFS	1	0.6953	0.5302
	1	Cropland	Active	Multiple	TSFS	2	0.7678	0.5368
	1	Cropland	Active	Multiple	TSFS	3	1.3624	0.6160
	1	Cropland	Active	Multiple	TSFS	4	1.5514	0.6504

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Pashkevich, Luke, et al. (In Review)	2	Cropland	Passive	Ground	TRF	1	-0.2719	0.1682
	2	Cropland	Passive	Ground	TRF	2	-0.2274	0.1677
	2	Cropland	Passive	Ground	TRF	3	-0.5425	0.1728
	2	Cropland	Passive	Ground	TRF	4	0.0524	0.2223
	2	Cropland	Passive	Understory	TRF	5	-0.3883	0.5094
	2	Cropland	Passive	Understory	TRF	6	0.3956	0.5098
	2	Cropland	Passive	Understory	TRF	7	-1.0359	0.5671
	2	Cropland	Passive	Understory	TRF	8	-0.3670	0.6779
	2	Cropland	Passive	Aerial	TRF	9	0.2295	0.5033
	2	Cropland	Passive	Aerial	TRF	10	-1.7609	0.6938
	2	Cropland	Passive	Aerial	TRF	11	-0.2362	0.5035
	2	Cropland	Passive	Aerial	TRF	12	-0.7934	0.7191
Pashkevich et al. (Unpublished)	2	Cropland	Active	Ground	TRF	1	-0.3052	0.2529
	2	Cropland	Passive	Ground	TRF	2	-0.0662	0.2501
	2	Cropland	Active	Ground	TRF	3	-0.3807	0.2545
	2	Cropland	Active	Aerial	TRF	4	0.1471	0.2507
	2	Cropland	Passive	Aerial	TRF	5	-0.4242	0.2556
	2	Cropland	Active	Aerial	TRF	6	-0.0197	0.2500
Radford & Andersen 2012	2	Savannah	Passive	Understory	TSFS	1	-0.1172	0.1948
	2	Savannah	Passive	Understory	TSFS	2	-0.1351	0.4173
	2	Savannah	Passive	Understory	TSFS	3	0.0959	0.2340
	2	Savannah	Passive	Understory	TSFS	4	0.0014	0.2159
Spear 2016	2	Cropland	Active	Aerial	TRF	1	-0.7951	0.3597
	2	Cropland	Active	Understory	TRF	2	0.0568	0.3335
	2	Cropland	Active	Ground	TRF	3	-0.5366	0.3453

**Table S5.5.** Raw data extracted from the studies that focussed on *restoration and spider species richness*, met our inclusion criteria, and from which sufficient data could be extracted for use in meta-analysis. We include the study name, sampling design score ‘1’ = samples not spatially or temporally independent or replicated; ‘2’ = samples spatially and / or temporally independent or replicated), broad-level habitat type (‘Cropland’), approach to restoration (‘Passive’, ‘Active’), microhabitat type (‘Aerial’, ‘Understory’, ‘Ground’, ‘Multiple microhabitats’), biome (‘TRF’ = tropical rainforest, ‘TSFS’ = tropical seasonal forest/savannah); the number of treatment-control comparisons within a study; and the *Hedges’ D* and associated variance for each treatment-control comparison.

Study	Score	Habitat	Approach to Restoration	Microhabitat	Biome	Comparison	Hedges' D	Variance
Esquivel-Gómez et al. 2017	2	Cropland	Active	Multiple	TSFS	1	0.6450	0.2371
Horgan et al., 2017	1	Cropland	Active	Understory	TSFS	1	0.1909	0.2009
	1	Cropland	Active	Understory	TSFS	2	0.1171	0.2003
	1	Cropland	Active	Multiple	TSFS	3	-0.1216	0.2004
	1	Cropland	Active	Multiple	TSFS	4	0.0358	0.2000
	1	Cropland	Active	Understory	TSFS	5	0.0668	0.2001
	1	Cropland	Active	Understory	TSFS	6	-0.1862	0.2009
	1	Cropland	Active	Multiple	TSFS	7	-0.1541	0.2006
	1	Cropland	Active	Multiple	TSFS	8	-0.6978	0.2122
Horgan et al., 2019	1	Cropland	Active	Understory	TSFS	1	-0.0420	0.0417
	1	Cropland	Active	Understory	TSFS	2	-0.0185	0.0417
Pashkevich, Luke, et al. (In Review)	2	Cropland	Passive	Ground	TRF	1	-0.2363	0.1678
	2	Cropland	Passive	Ground	TRF	2	-0.0739	0.1668
	2	Cropland	Passive	Ground	TRF	3	-0.0154	0.1667
	2	Cropland	Passive	Ground	TRF	4	0.0373	0.2223
	2	Cropland	Passive	Understory	TRF	5	0.1820	0.5021
	2	Cropland	Passive	Understory	TRF	6	0.8099	0.5410
	2	Cropland	Passive	Understory	TRF	7	-1.0094	0.5637
	2	Cropland	Passive	Understory	TRF	8	0.0000	0.6667
	2	Cropland	Passive	Aerial	TRF	9	0.3115	0.5061
	2	Cropland	Passive	Aerial	TRF	10	-0.6689	0.5280
	2	Cropland	Passive	Aerial	TRF	11	-0.2024	0.5026
	2	Cropland	Passive	Aerial	TRF	12	-0.1796	0.6694
Pashkevich et al. (Unpublished)	2	Cropland	Active	Ground	TRF	1	-0.2706	0.2523
	2	Cropland	Passive	Ground	TRF	2	-0.2418	0.2518
	2	Cropland	Active	Ground	TRF	3	-0.3081	0.2530
	2	Cropland	Active	Aerial	TRF	4	0.0584	0.2501
	2	Cropland	Passive	Aerial	TRF	5	-0.3877	0.2547
	2	Cropland	Active	Aerial	TRF	6	0.0981	0.2503
Spear 2016	2	Cropland	Active	Aerial	TRF	1	-0.6593	0.3514
	2	Cropland	Active	Understory	TRF	2	0.0000	0.3333
	2	Cropland	Active	Ground	TRF	3	0.0000	0.3333

### Supplementary Equation 5.1.

*Hedges' D* and its variance were calculated as:

$$D = \frac{Y_1 - Y_2}{\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}} * \left(1 - \frac{3}{4(n_1 + n_2 - 2) - 1}\right)$$

$$\text{Variance (Hedges' D)} = \frac{n_1 + n_2}{n_1 n_2} + \frac{D^2}{2(n_1 + n_2)}$$

wherein,  $Y_1$  and  $Y_2$  are two means from treatment and control sites, respectively;  $n_1$  and  $n_2$  are the sample sizes associated with these means; and  $s_1$  and  $s_2$  are the standard deviations associated with these means.