PLANT INVASION OF TROPICAL RAINFOREST REMNANTS

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Abstract

Intact tropical rainforests are considered to be robust to exotic plant invasions. However, land-use change across the tropics is altering the structure and native species composition of rainforests, potentially making these landscapes vulnerable to invasion. I examined local and landscape-scale factors that affect exotic plant invasion in remnant forest sites surrounded by oil-palm plantations across Sabah, Malaysian Borneo, spanning gradients in landscape-scale fragmentation and local forest disturbance. Invasion (exotic richness and abundance) was higher when there was greater local forest disturbance and propagule pressure, the latter due to increased landscape fragmentation. Invasion and young native tree diversity were negatively related, indicating the potential for impacts on regeneration processes. At 21 forest sites within oil-palm plantations, exotic species richness declined from oil palm (mean=9.2 species/transect) to forest edge (7.8 species) to inside rainforest remnants (3.1 species in disturbed forest), and only one species, *Clidemia hirta*, invaded intact forest. Exotic communities inside forest remnants were functionally distinct from those found in oil-palm, (generally taller, woody and dispersed by vertebrates), providing evidence that trait-filtering is occurring. Herbivory in the most common invader, *C. hirta*, reduced the reproductive output of *C. hirta* plants and was found to be higher when co-occurring with a native confamiliars, suggesting host-sharing is occurring between *C. hirta* and related natives. Nonetheless, *C. hirta* plants experienced overall lower herbivory and more individuals were reproductively active, possibly placing *C. hirta* at a competitive advantage relative to native confamiliars. This research shows that rainforest remnants within highly fragmented landscapes experience low invasion if local forest disturbance is low, but that *C. hirta* is almost always present and so other exotic plant species with similar traits to *C. hirta* may readily invade these forests in future. Forest fragmentation is predicted to increase, but improving canopy cover may provide protection from exotic plant invasion.

We do not inherit the Earth from our Ancestors,
we borrow it from our Children.

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Amat, me, Robin, Susannah and Azlin during fieldwork (photo credit: Robin Hayward)

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Authors declaration

I declare that the work presented in this thesis is my own. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

This thesis involved collaboration with Dan S. Chapman (DSC), Lindsay F. Banin (LFB), Jane K. Hill (JKH), Mark Hughes (MH), Joseph Tangah (JT), Kok Loong Yeong (KLY), Susannah Fleiss (SF), Ahmad Jelling (AJ), Bernadus Bala Ola (BBO) and Azlin Bin Sailim (ABS).

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EHW, LFB, MH, JKH and DSC conceived the ideas. EHW, LFB, MH, SF, JT, JKH, CB, YKL, ABS, AJ and DSC designed methodology; EHW, SF, ABS and AJ collected the data; BBO and AJ led plant identification; EHW and DSC analysed the data; EHW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data collected for this study are available to download from the Environmental Information Data Centre: Waddell et al. (2020d) Vegetation and habitat data for fragmented and continuous forest sites in Sabah, Malaysian Borneo, 2017. NERC Environ Inf Data Cent. https://doi.org/10.5285/c67b06b7-c3f6-49a3-baf2-9fc3a72cb98a

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E.H.W., D.S.C., J.K.H., M.H. and L.F.B. conceived the ideas and E.H.W., D.S.C., J.K.H., M.H., J.T., A.B.S. and L.F.B. designed the methodology. E.H.W. and A.B.S. collected the data, E.H.W. and D.S.C. analysed the data and E.H.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Chapter 4

This study is currently in preparation for submission to *Biotropica* as:

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All papers are reproduced in full in this thesis, with minor formatting alterations. The text was written by myself with input from DSC, LFB, JKH and MH. The study methodology was designed with help from DSC, LFB, JKH, MH, JT, SF, YKL, ABS and AJ. Data was collected with help from SF, ABS and AJ, and JT and KLY provided logistical support for fieldwork. E.H.W. analysed the data with guidance from D.S.C. The study was supervised by DSC, LFB, JKH and MH.

Project rationale

Across the tropics, land-use change is fragmenting and degrading large areas of forest, altering the environmental conditions and the composition of native plant communities (Pütz et al. 2011; Haddad et al. 2015). These anthropogenic landscapes create new pathways for the introduction and invasion of exotic plant species (Hulme 2009; Seebens et al. 2015). Introduced exotic plants frequently colonise disturbed habitats within anthropogenic landscapes (e.g. agricultural plantations, roadsides and human settlements; Fee, Tui, Bin, & Hoy, 2017; Lugo & Gucinski, 2000; Rembold, Mangopo, Tjitrosoedirdjo, & Kreft, 2017; Teo, Tan, Corlett, Wong, & Lum, 2003) and may spread into remaining areas of native tropical rainforest. Remnant forests within these landscapes are often degraded due to the effects of fragmentation and previous disturbances such as commercial logging (Laurance et al. 2002; Ferraz et al. 2003; Pütz et al. 2011; Malhi et al. 2014; Arellano-Rivas et al. 2016), leaving them more susceptible to exotic plant invasions when compared with intact forests. These rainforest remnants are often retained within agricultural landscapes for conservation reasons to maintain native biodiversity and meet certification standards (Arroyo-RodrÍguez and Mandujano 2006; Yeong et al. 2016; Lucey et al. 2017; Scriven et al. 2017), and invading exotic plants may threaten these conservation set-asides by disrupting regeneration of native forest species. Despite their conservation value, very little is known about plant invasions in tropical forests when compared with temperate regions (Fine 2002; Pyšek et al. 2008), with only a handful of studies previously looking at the ecological processes driving plant invasion in tropical forests.

In this thesis, I summarise literature on the history of plant invasions and the processes that drive and mediate invasions, before discussing land-use change in the tropics and how human-driven disturbances have opened up landscapes and forests to potential exotic plant invasion. I then discuss the drivers of exotic plant invasions in tropical rainforests, by systematically searching and reviewing current literature, and identifying the knowledge gaps (Chapter 1). Through fieldwork, I collect new empirical data on the native and invading plant communities within a network of forest remnants within agricultural landscapes in Sabah, Malaysian Borneo. This mosaic of oil palm plantations and forest remnants in Sabah, provides an excellent study system to examine invasion across gradients of human disturbance in tropical landscapes. From the plant community data I determine which exotic species are successfully invading forest remnants from adjacent oil palm plantations, identify the local and landscape characteristics of forest sites that facilitate invasion (Chapter 2), and the traits associated with exotic species successfully invading forests (Chapter 3). Finally, I carry out an investigation into patterns of herbivory in the most common invasive species within these landscapes, *Clidemia hirta*, to determine why this species is such a successful invader of tropical rainforests (Chapter 4). Finally, I discuss the findings of this thesis in the context of current knowledge about tropical plant invasions, discussing both the wider implications of my results and further work needed to reduce exotic plant invasion within conservation planning of tropical landscapes.

As tropical forests are becoming increasingly fragmented and the emerging threat of exotic species has the potential to cause further degradation, there is an urgent need to understand the processes driving tropical plant invasions. Identifying key aspects of invasion in tropical rainforest remnants will assist conservation planning of plantations and management practices within forest remnants in the future, ensuring remaining areas of natural forest are managed to be as robust as possible to invasion and thereby preventing further environmental degradation.

Chapter 1

Old-growth rainforest in Danum Valley (photo credit: Robin Hayward)

General introduction

1.1 Abstract

As global transport links have increased, exotic species have spread to every part of the planet and are now recognised as a major driver of ecological change. However, there is a geographical bias in our understanding of invasion ecology with a lack of studies based in tropical regions. In this chapter, I review information on the driving factors of invasions, common invasion hypotheses, land-use in the tropics and oil palm cultivation in South-East Asia. I also conduct a systematic review of the literature on plant invasion within tropical rainforests and present the main aims of my thesis. Across biomes and taxa it is thought that an exotic species must overcome sequential ecological filters when invading new areas and these are influenced by four factors: propagule pressure; the abiotic conditions of invaded ecosystem; and biotic characteristics of both the invading species and invaded ecosystem. Intact tropical forests are often considered to be resistant to exotic plant invasion due to low propagule pressure and disturbance, and high diversity of the native community, meaning all niches are occupied. However, land-use change is increasing across the tropics opening up these landscapes to the introduction of exotic plant propagules that colonise new infrastructures, including roads and settlements. Fragmentation of the landscape and commercial logging cause remaining areas of rainforest to become degraded, changing the abiotic conditions and the biotic characteristics of the native forest. These altered conditions change the nature of competition within the native forest community and may open up ecological niches to the invasion and colonisation of exotic plants within forest remnants. However, from my systematic review I found that studies based in tropical rainforests are rare and as such there is currently no consensus over the role of biotic characteristics (of both the invaded ecosystem and invading species) and abiotic conditions (e.g. soil) on invasion. Furthermore, it is unclear how land-use change and disturbance at a landscape scale

influences the establishment of exotic species within forest remnants. It is vital to improve our understanding of how exotic plant invasion occur in such landscapes as rainforest remnants are often retained for conservation reasons, especially in landscapes dominated by agriculture and can be crucial in maintaining local biodiversity and ecosystem services.

1.2 Overview of plant invasions

For millennia, humans have been moving and trading goods across continents, with long-range trading starting as early 35,000 BCE (Before Common Era) and the first maritime trading network occurring by 1,500 BCE (Smith 2008; Manguin 2016). The industrial revolution and development of transport technology in the mid 18th Century saw an exponential increase in trade, connecting every corner of the globe by ships and trains, soon followed by aeroplanes in the early 1900s (Hulme 2009; Seebens et al. 2015). With these links, exotic species have spread into new regions, invading every country and ecosystem across the planet (Hulme 2009; Seebens et al. 2017). The introduction of exotic species into new areas by human actions is either deliberate (i.e. intentional introduction) or accidental (i.e. unintentional introduction; Lockwood, Hoopes, & Marchetti, 2013). In terrestrial ecosystems, human-mediated dispersal of exotic species is much more dynamic and diverse than natural dispersal, meaning that in some cases propagules can travel across continents in days or hours, spreading far from their native range (Lockwood et al., 2013). The most common route of intentional introduction of exotic plant species is through ornamental, horticultural or agroforestry plants (Reichard and White 2001; Dehnen-Schmutz et al. 2007; Lambdon et al. 2008), which spread from domestic and botanical gardens to colonise natural ecosystems in their introduced area (Hulme 2015). In Europe, the USA and Australia, almost two thirds of exotic plants are thought to have derived from intentional introduction, with many becoming invasive pests (Reichard and White 2001; Mack and Erneberg 2002; Virtue et al. 2004; Dehnen-Schmutz et al. 2007). In tropical countries, the method of introduction is not as clear as in temperate countries due to a lack of record and studies investigating this, but it is likely to be a combination of intentional and accidental introductions.

There are many routes for exotic propagules to be unintentionally introduced into a new area, for example when transporting goods (e.g. food, agricultural products, biofuel) the ballast of the ship is made up of gravel, stones and soil often containing plant material and seeds amongst it, which spread after being offloaded at ports (Mack et al. 2003). Small exotic plants or unwanted seeds can be mixed in with potted plants, soil or crop seeds shipped in the horticultural and ornamental plant trade (Lockwood et al. 2013). Seeds can also easily and readily be transported by vehicles (e.g. mud in tyres; Ansong & Pickering, 2013) as well as on humans themselves. In one study, researchers recorded nearly 25,000 seeds from 70 different species, including 19 exotic species, on 207 pieces of clothing (socks, trousers and shoes) from hikers in one Australian park (Mount and Pickering 2009), demonstrating the ease of unintentional transport of propagules into natural systems. Unlike intentional introductions of crop and ornamental plants that often have the date of introduction recorded, the date a new species arrived accidentally is usually unknown, meaning their invasion history is less clear (Mack 2003). This is especially true for many tropical regions, where there are fewer records of the date of establishment for invasive species when compared to Europe and North America (Bakar 2004; Seebens et al. 2020), which impedes our understanding of rate of spread in these landscape.

Box 1.1: Terminology used in thesis

There are many terms in invasion ecology that are used inter-changeably and can often cause confusion for non-specialist readers, i.e. exotic, non-native, alien and non-indigenous species. For congruence in this thesis I will use the same terms throughout which are largely taken from Richardson et al. (2000), Catford et al. (2009) and Lockwood, Hoopes, & Marchetti (2013).

Colonisation – survival of exotic propagules in a new area.

Exotic species – species that have been introduced by humans outside their native range (i.e. have not established naturally), and have established a naturalized breeding population, spreading to other areas. Also known as non-native, alien or non-indigenous species in some invasion ecology literature.

Establishment – a combination of colonisation and naturalisation.

Exotic occurrence – observation of exotic plants within an area, which could be a colonised, naturalised or invasive species.

Exotic propagules – seeds or other structures that can be dispersed and give rise to a new plant.

Impact – the effect an invasive species has on the ecology of the new area or an economic impact; based on human perception.

Introduction – arrival of exotic propagules into a new area.

Invasive species – exotic species that have a negative ecological or economic impact, or that spread aggressively.

Naturalisation – formation of a self-sustaining population of colonised exotic plants, able to survive and reproduce.

Propagule pressure – a composite measure of the number of exotic individuals introduced to a new area during one event and the number of these introduction events. If either the number of individuals or events increases, propagule pressure will increase.

Spread – self-sustaining population growing in abundance and expanding its geographical range within its introduced range.

Transportation – movement of exotic propagules from their native range to a new area by humans.

Once introduced and established within a new region, some exotic species become invasive, causing ecological and economic harm (Mooney 2005). Invasive species may alter the natural environment, displacing native species and reducing local and regional native biodiversity (Mooney 2005). These species can decrease the production of ecosystem goods by industries (e.g. agriculture, fisheries and forestry) and disrupt important ecosystem services (e.g. freshwater provisioning; carbon sequestration for climate regulation), leading to large economic losses (Pejchar and Mooney 2009). The total costs for these losses and to control the spread of invasive species (plants and animals) have been estimated at about US$120 billion per year in the United States (Pimentel et al. 2005) and US$33.5 billion in South-East Asia (Nghiem et al. 2013). In addition, in tropical regions large proportions of the human population are reliant on forest products and services for their livelihoods (Sodhi et al. 2010) and this must be valued properly to fully account for the impact of service losses due to invasive species.

To date, most research into the drivers of biological invasions has focused on the temperate biome, principally in North America and Europe which, historically, have had high incidences of invasive species being reported across temperate ecosystems (Fine 2002; Pyšek et al. 2008). In the tropics, intact continental forests are generally considered robust to invasion (Rejmánek 1996; Fine 2002; Denslow and DeWalt 2008). However, rapid globalization and increased connectedness in recent decades and the changing landscape in most tropical regions (e.g. large-scale agriculture, commercial logging; Malhi et al., 2014; Seebens et al., 2015; Sodhi et al., 2010; see sections 1.4: Land-use change in tropical landscapes) may have facilitated the spread of exotic species, and opened up these forests to be invaded. Newly connected tropical countries are considered to megadiverse (e.g. Indonesia, Malaysia, Thailand and Peru) and the invasion of exotic species may threaten endemic and rare species found in these countries (Seebens et al. 2015). However, the geographical bias in invasion studies (Pyšek et al. 2008) currently restricts our understanding of the patterns of global plant invasions because the processes driving invasion in tropical regions may differ from temperate regions due to differences in the environmental conditions and native communities.

1.3 Process of plant invasions

Invasion is theorised as a staged process, with the stages being divided by barriers, or ecological filters, that a species must pass through before progressing to the next stage (Figure 1.1; Box 1.1) – species that successfully overcome all of these barriers are ultimately defined as being invasive (Colautti and MacIsaac 2004). Human activities influence most stages of invasion but particularly at the start during transportation and introduction, and also in the spread of species once established (Catford et al. 2009). Each stage is influenced by the following four factors: propagule pressure, the abiotic conditions of the invaded ecosystem and biotic characteristics of both the invading species and invaded ecosystem (Pyšek and Richardson 2006). Usually, all factors must be accommodating for invasion to occur (Catford et al. 2009), although the influence of one or more factors may be stronger than the others in a given invasion scenario (Figs. 1.1 and 1.2). In addition, interactions amongst factors are present in most potential invasion pathways (Fig. 1.2) and invasion hypotheses (Table 1.1), and therefore mediate invasion successes (Catford et al. 2009). Identifying the most influential factors in a given invasion scenario helps us understand the mechanisms driving invasion and is crucial in the control of invasive species; something that is lacking in tropical regions. I now discuss each of these four factors and how they can contribute to facilitating plant invasions.

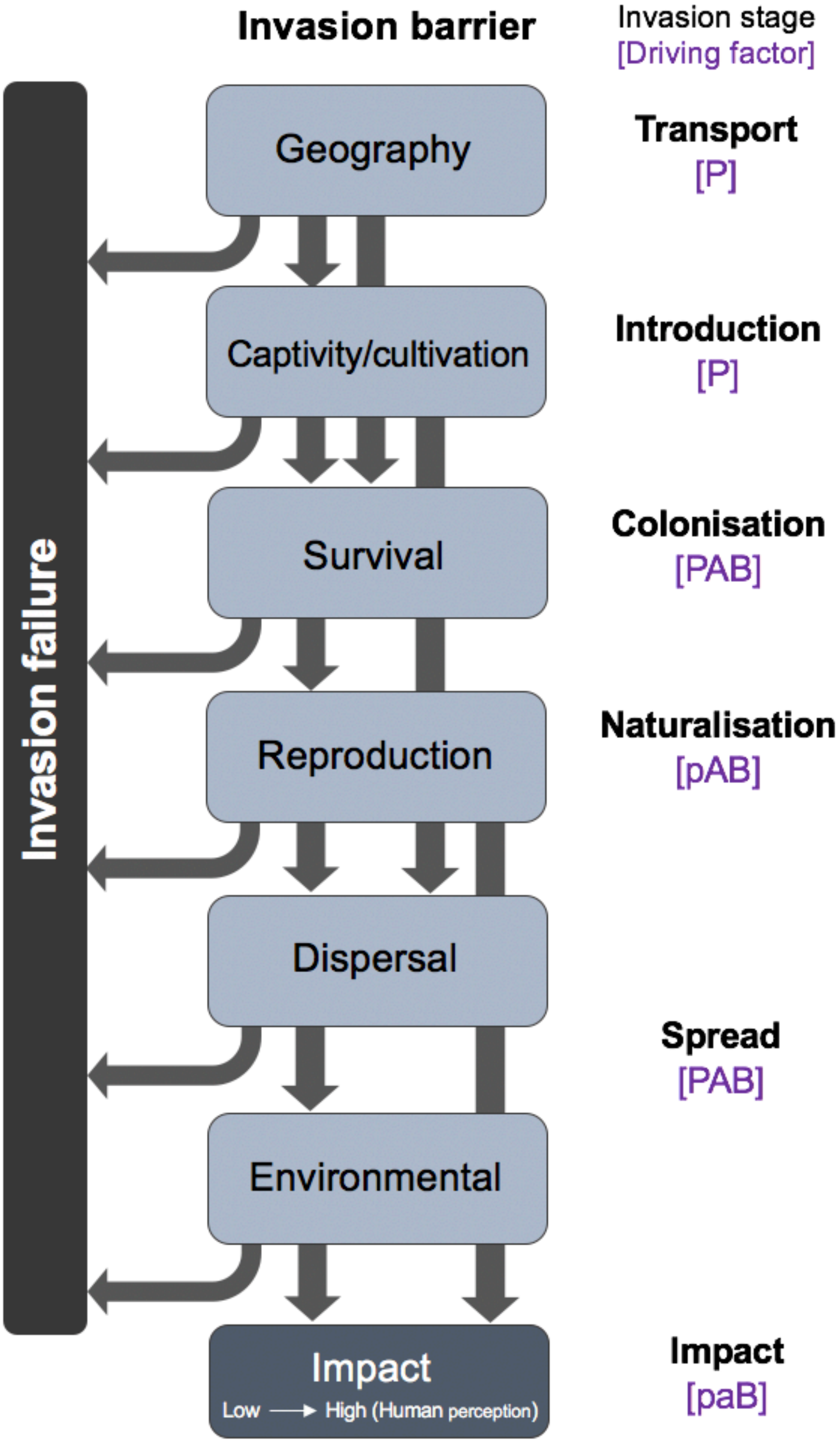


Figure 1.1: Schematic diagram of the stages of invasion including barriers to invasion and the driving factors. Figure is based on figures and information in Catford et al. (2009) and Lockwood et al., (2013). Driving factors: P = propagule pressure; A = abiotic conditions; B = biotic characteristics (capitals indicate the higher strength of the factor).

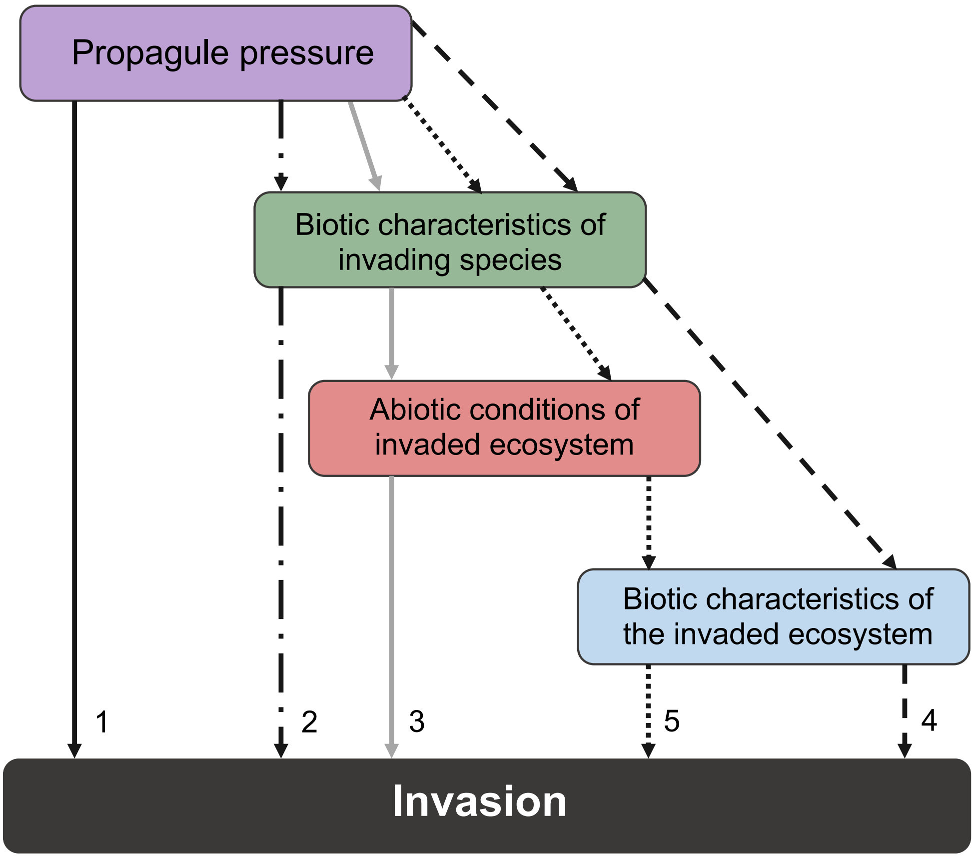


Figure 1.2: Potential invasion pathways involving combinations of propagule pressure, abiotic and biotic characteristics. The pathways increase in their complexity from 1 to 5. The drivers of invasion for each pathway include the factor plus interactions if present (e.g. Pathway 2 = Propagule pressure + Biotic characteristics of invading species + an interaction between these two factors).[Figure adapted from Fig. 2 in Catford et al., 2009].

Propagule pressure and interactions with other factors

In order for an exotic species to become invasive, there must be sufficient propagule pressure for the species to become introduced to new areas and to expand its geographical range (Eppstein and Molofsky 2007). Propagule pressure is particularly important in the stages that are influenced heavily by human activities (transportation, introduction and spread) due to the limitations of geographical barriers (Catford et al. 2009). If propagule pressure is high enough it can result in immediate invasion success as there are enough propagules to establish a large population in one generation

(Pathway 1 in Fig 1.2, see 'Propagule pressure hypothesis' in Table 1.1; Colautti, Grigorovich, & MacIsaac, 2006; Lockwood, Cassey, & Blackburn, 2005). However, usually other factors are also influential, in addition to interactions between factors. For example, invading exotic species with functional traits that result in higher reproductive fitness and more efficient dispersal (e.g. small seed mass, greater number of seeds per fruit, high germination rate and long-distance dispersal; Colautti et al., 2006; Pyšek & Richardson, 2006; Rejmánek & Richardson, 1996) will likely influence both natural and human-mediated dispersal of exotic species and rapidly spread into new areas, increasing local propagule pressure (Pathway 2 in Fig. 1.2). Propagule pressure can be influenced by the abiotic conditions in the invaded ecosystem (Richardson et al. 2000) with some habitats allowing for easier introduction of propagules. For example, there is often high abundance of exotic plants along the sides of rivers as these features act as dispersal corridors for exotic species that are dispersed by water (i.e. Pathway 3 in Fig. 2; Tickner, Angold, Gurnell, & Mountford, 2001). The biotic characteristics of the invaded ecosystem can also directly influence propagule pressure by the presence of suitable animal dispersers (Pathways 4 and 5 in Fig. 1.2; Cordeiro, Patrick, Munisi, & Gupta, 2004).

Abiotic conditions of invaded ecosystem

Once propagules of an exotic species have arrived at a new locale, the habitat must be suitable for that species to survive for invasion to be successful, or else the invading species will be filtered out at this stage (Weiher and Keddy 1995; Mitchell et al. 2006). Environmental filtering, in which abiotic barriers restrict which species establish is apparent in the colonisation of all plants not just exotic species (Weiher and Keddy 1995), and is usually driven by the life-history and functional traits of the invading species (Procheş et al. 2008) and whether they are competitive relative to the extant community or have the capacity to adapt. All forms of disturbance, both natural and anthropogenic, promote invasion of exotic species and native weeds through increased resource availability (Davis et al. 2000b; Blumenthal 2006; Theoharides and Dukes 2007). Increased resource availability (e.g. light, space, nutrients) facilitates germination and survival of exotic propagules because there is more physical space for colonisation to occur and reduced interspecific competition (Davis, Grime, Thompson, Davis, & Philip, 2000). The majority of exotic species tend to be ruderal species that are light-loving, which explains why open habitats, such as riparian areas, forest gaps, and grasslands, are generally more heavily invaded (Planty-Tabacchi et al. 1996; Ehrenfeld 1997), as well as roadsides and waste lands (Lugo and Gucinski 2000; Teo et al. 2003). In forest habitats, invasion is higher within canopy gaps and at the edges of forest remnants compared with the forest interior, driven by disturbance related edge effects (Honnay et al. 2002; Vilà and Ibáñez 2011; Dawson et al. 2015). Closed canopy forests can only be colonised by shade-tolerant species, which are not as common as light-loving exotic species but tend to be more invasive (Martin et al. 2009). This knowledge largely comes from temperate forests, raising the question of whether increasing edge effects in tropics will follow same invasion trajectory.

Biotic characteristics of invaded ecosystem

The biotic characteristics of the invaded community are important to invasion because an invading species has to be able to establish within the native biotic community, overcoming barriers of native competitors and the impact of natural enemies (e.g. herbivores and pathogens; Levine, Adler, & Yelenik, 2004). The Biotic Resistance Hypothesis (Levine et al., 2004; Table 1.1) states that in more diverse ecosystems, invading species experience strong competition from native species and/or the effects of native herbivores or pathogens that they have no defence against, and so fail to invade (Table 1.1; Keane & Crawley, 2002). However, the effect of biotic resistance may not necessarily prevent invasion but may regulate the spread and impact of exotic species by limiting their population growth once established (Levine et al. 2004). In megadiverse tropical forests, high species richness of native flora and pests (i.e. herbivores and pathogens) is thought to contribute to low invasion (Fine 2002; Denslow and DeWalt 2008) but empirical evidence supporting this theory is lacking (see section 1.5: Plant invasion of tropical rainforests).

Biotic characteristics of invading species

The set of traits often associated with highly invasive species include a ruderal life history, high genotypic and phenotypic plasticity, rapid growth, high and early fecundity and fertility (Colautti, Grigorovich, & MacIsaac, 2006; Nathan et al., 2008; Pyšek & Richardson, 2006; Rejmánek & Richardson, 1996). In addition, some invasive species have highly specialised functional traits that confer an advantage over both native species and other exotics, making them super competitors (Strayer 2012). The existence of these specialised functions increases a plant species' chances of successful invasion, especially in favourable conditions (Strayer 2012). For example, invasive species that have the ability to fix nitrogen can out-compete native pioneer species in nutrient-poor environments (Osunkoya et al. 2005), and polyploid species, a trait of most invasive plants in Singapore (Pandit et al. 2006), can adapt better to ecological extremes than native diploid species (Hagerup 1933). However, there is no set of traits universal to all invasive species, and these traits vary among species and ecosystems (Pyšek and Richardson 2008). Hence, an invading exotic species may have similar traits to native species, suggesting a pre-adaptation to local conditions (Lodge, Whitfeld, Roth, & Reich, 2018) or alternatively may have a different set of traits from those of the native community and therefore fill vacant ecological niches (i.e. 'Limiting similarity hypothesis'; Mathakutha et al., 2019). If being ecologically similar to natives is important for invasion success, then being more phylogenetically related to the native community may also be advantageous, due to phylogenetic conservatism of functional traits (Flynn et al. 2011).

Common invasion hypotheses

There are numerous hypotheses discussed in the invasion ecology literature that try to explain patterns of invasion at different temporal and spatial scales (Davis et al., 2000; Mitchell et al., 2006; Richardson & Pyšek, 2006). These invasion hypotheses often share similarities with one another, and Catford et al. (2009) made proposals to unify these hypotheses, highlighting patterns and commonalities. A summary of 13 common hypotheses is shown in Table 1.1 (adapted from Tables 2 and 3 in Catford et al., 2009). Of these hypotheses, most facilitate invasion but one hypothesis impedes invasion (BRH), and most have more than one influential factor (i.e. propagule pressure, abiotic conditions, biotic characteristics of the invading species and biotic characteristics of the invaded ecosystem, plus human interference). Invasion hypotheses are considered to be context dependent, therefore, it is important to explore the different hypotheses that may be influencing invasion within your study system (e.g. tropical rainforests).

The empirical support for different invasion hypotheses varies among taxa and habitats (Jeschke et al. 2012). A meta-analysis of six leading hypotheses (Biotic Resistance, Invasional Meltdown, Novel Weapons, Enemy Release Hypotheses, Island Susceptibility and Tens Rule) revealed those that included both aspects of the new environment (either abiotic conditions or biotic characteristics) and the biotic characteristics of the invading species (i.e. functional traits), yielded the most support (54-77% of studies). These included Invasional Meltdown, Novel Weapons and Enemy Release Hypotheses, which had relatively uniform support across taxa (plants, invertebrates and vertebrates) and habitats (terrestrial, freshwater and marine). On the other hand, there was little support for Biotic Resistance across all taxa and habitats, and even less so in vascular plants and terrestrial environments (Jeschke et al. 2012).

Table 1.1: Summary of 14 common hypotheses in invasion ecology including hypothesis definition, influential factors and support for the hypothesis within tropical forests. Adapted from Tables 2 and 3 in Catford et al. (2009). Influential factors: H = Human influence, P= Propagule pressure, A = Abiotic conditions, Bi = Biotic characteristics of invading species, Bc = Biotic characteristics of invaded ecosystem.

Hypothesis	**Definition**	**Influential factors**	**Key references (bold = in tropical rainforest)**
Biotic resistance	The native community resists successful invasion because native species are strong competitors and/or invading species have no defence against herbivores or pathogens.	Bc	**Bufford, Lurie, & Daehler, 2016**; Levine et al., 2004; Parker & Hay, 2005
Disturbance	Natural or human-led disturbance events increase available resources, disrupt succession and allow the opportunity for establishment of exotic species.	H, A, Bi	Colautti et al., 2006; Hood & Naiman, 2000; Sher & Hyatt, 1999
Empty niche	The invaded community is unsaturated and there are empty niches that exotic species can fill.	A, Bi	Hierro, Maron, & Callaway, 2005; MacArthur, 1970
Enemy release	An invading species benefits from escaping its natural enemies (herbivores, pathogens) that restricts population growth in its native range.	Bi, Bc	Colautti & MacIsaac, 2004; **Dawson, Burslem, & Hulme, 2009c; DeWalt, Denslow, & Ickes, 2004;** Joshi & Vrieling, 2005; Keane & Crawley, 2002; **Liu, Stiling, & Pemberton, 2007**

Evolution of Increased Competitive Ability	Similar to 'Enemy Release' (see above). An invading species that escapes its natural enemies can allocate resources from defence to growth and reproduction, which increases its competitive ability.	Bi, Bc	Callaway & Ridenour, 2004; Joshi & Vrieling, 2005
Global competition	Similar to 'Propagule pressure' (see below). The greater number of exotic species that are introduced into an area, the more likely it is that there will be an invasive species with super competitor traits.	H, P, Bi	Alpert, 2006; Colautti et al., 2006
Habitat filtering	An invading species is able to overcome environmental barriers and is therefore adapted to the current abiotic conditions of the new ecosystem. Colonised exotic species are more functionally similar.	A, Bi	Procheş et al., 2008; Weiher & Keddy, 1995
Ideal weed	Invading species has super competitor characteristics (functional traits) which allows it to outcompete native species and invade.	H, P, Bi	Elton, 1958; Rejmánek & Richardson, 1996
Invasion meltdown	Invading species are more likely to successfully invade if there are already invasive species established in the invading system.	A, Bi, Bc	Mack, 2003; Simberloff & Von Holle, 1999
Limiting similarity	Invading species and native species are functional distinct from one another, therefore there are empty niches for exotic species to fill.	Bc	Macarthur & Levins, 1967; Mathakutha et al., 2019
Naturalisation	Successful invasions are due a combination of to human activities, high propagule pressure, suitable environmental conditions and ideal interactions with the community in the invaded community.	H, P, A, Bi, Bc	Lonsdale, 1999; Pyšek & Richardson, 2006; Richardson & Pyšek, 2006
Novel weapons	The invading species has a novel trait that is not present in the recipient community, which gives them a competitive advantage over natives.	Bi, Bc	Callaway & Ridenour, 2004; Hierro et al., 2005
Propagule pressure	Successful invasion increases when there are large numbers of propagules per introduction event and a high frequency of introductions, due to high genetic diversity, seed swamping, continual supplementation, and higher probability of introduction to favourable environment.	H, P, Bi	Colautti et al., 2006; Lockwood et al., 2005; Lonsdale, 1999; Pyšek & Richardson, 2006; Richardson & Pyšek, 2006

Specialist-generalist	Invasion success is highest when the invading species is a generalist but pests (herbivores, pathogens) in the invaded community are highly specialist and invaders escape predation.	Bc	Callaway & Ridenour, 2004

The resilience of intact tropical forests to invasion is considered to be high due to low propagule pressure and disturbance levels, and high diversity of the native community leading to competitive exclusion (i.e. no empty niches) and/or reduced establishment and spread from the impact of high pest diversity (i.e. Biotic Resistance Hypothesis; see reviews Denslow & DeWalt, 2008; Fine, 2002; Rejmánek, 1996). Specifically, it is theorised that the native community of tropical forests has such high functional diversity that there are no available ecological niches and that native species competitively exclude exotics from establishment (Denslow & DeWalt, 2008). Furthermore, high pest load (i.e. herbivore and pathogen diversity and abundance) within these forests is also thought to control invading exotic populations (Levine et al. 2004; Denslow and DeWalt 2008). There is some evidence that when invasion of tropical forests does occur it may be due to release from natural enemies, as seen in the highly invasive shrub *Clidemia hirta* in Hawaii ('Enemy Release Hypothesis; DeWalt, Denslow, & Ickes, 2004). However, land-use change in the tropics has increased considerably since these reviews were published and new information on the drivers of tropical invasion have been revealed in more recent studies (see section 1.5: Plant invasion of tropical forests).

1.4 Land-use change in tropical landscapes

In the tropics, land-use change is a major driver of ecological change, and has led to landscape fragmentation, the loss of biodiversity, spreading of fire, increasing of CO_2 and climate change and the spread of invasive plants (Malhi et al. 2014). It is now estimated that only 20% of the remaining tropical forest area is considered to be intact ‘old-growth’ forest, with the average annual forest loss across the tropics three times higher in the period 2011–2013 than it was in 2001–2003 (Potapov et al. 2017). Large-scale deforestation and forest degradation in the tropics is predominantly driven by expansion of agriculture (Kissinger et al. 2012; Haddad et al. 2015) and commercial logging practices (Malhi et al. 2014; Curtis et al. 2018), resulting in highly fragmented tropical forests amongst an anthropogenic matrix in some regions (Gaveau et al., 2014; Pütz et al., 2014; Sodhi, Koh, Brook, & Ng, 2004). Fragmentation and disturbance alter the abiotic conditions and biotic characters of the forest remnants (Broadbent et al. 2008; Laurance et al. 2011; Lôbo et al. 2011), and can leave them vulnerable to the invasion of exotic plants that are introduced to these landscapes via newly built roads (Hulme 2009).

Impact of land-use change on native forests

Fragmentation and commercial logging alter the structure of remaining rainforest due to timber removal and disturbance-related tree mortality (Laurance et al. 2002; Malhi et al. 2014; Gibbs and Salmon 2015). The reduction in canopy cover increases light in the forest understorey, which affects the abiotic conditions of remnant forest patches, when compared with more intact forest (Laurance et al. 2002). In addition, environmental gradients from forest edge to interior have been recorded for temperature, humidity, wind-speeds and soil erosion, with most changes detected within 100 m of the forest edge, termed ‘edge effects’ (Jose et al. 1996; Laurance et al. 1998, 2002; Broadbent et al. 2008). The magnitude of these edge effects is determined by the shape and area of remnant forest patches (Didham & Lawton, 1999; Hill & Curran, 2003), with irregular-shaped or elongated remnants having more edge habitat than more regular-shaped remnants (i.e. square or circular; Bennett & Saunders, 2010). Changes to abiotic conditions driven by edge effects alter the forest structure, increasing the presence of lianas and mortality of adult trees (Ferreira and Laurance 1997; Laurance et al. 1998). Increased tree mortality alters canopy-gap dynamics and further elevates light levels at edges, which decreases the abundance of understorey plant species adapted for shaded, moist forest interiors, lowering interspecific competitiveness and opening up niches to the colonisation of non-forest specialist species at edges (Benitez-Malvido 1998). Hence, it is expected that there will be high invasion (i.e. more exotic species and/or higher abundance) at anthropogenetic forest edges.

Fragmentation and selective logging drives species losses and thus alters the community composition of native plants, animals and soil microbes and disrupts native species interactions (Laurance et al. 2006, 2011; Arellano-Rivas et al. 2016). Within selectively logged and isolated (from larger tracts of forest) forest remnants, reduced regeneration of native old-growth tree species can occur through decreased pollination and dispersal, which can shift the tree species composition to earlier successional states with lower community-average wood density (Laurance et al. 2006; Lôbo et al. 2011; Pütz et al. 2011; Gibbs and Salmon 2015; Qie et al. 2017). Changes to abiotic conditions and the biotic native community are greater in small, isolated remnants and accumulate over time (Ferraz et al., 2003; Gonzalez, 2000; Haddad et al., 2015; Hill & Curran, 2003). For example, these small, isolated remnants tend to have fewer mother trees and specialised pollinator and seed dispersers remaining due to small areas, and there is reduced movement of these animal dispersers and pollinators between tracts of forest (Arroyo-RodrÍguez et al. 2009; Chazdon et al. 2009).

Fragmentation of tropical forests is predicted to increase, due to cyclical deforestation processes (i.e. deforestation and degradation making new areas of forest more accessible and susceptible to further degradation; Nowosad and Stepinski 2019), which will result in more isolated and smaller forest remnants (Taubert et al. 2018). However, even small remnant areas of forest are crucial for maintaining local and regional biodiversity and ecosystem services within modified tropical landscapes (Fleiss et al., 2020; Hill et al., 2011; Koh, 2008; Matos et al., 2020; Ricketts, 2004; Stride et al., 2018; Volenec & Dobson, 2020). Therefore, it is vital to expand our knowledge of processes that may cause further degradation and reduce the conservation value of these forests, including the invasion of exotic species.

1.5 Plant invasion of tropical rainforests

Intact tropical forests are often considered to be resistant to exotic plant invasion; however, it is unclear if the low number of reported invasions is simply due to a lack of studies carried out in tropical forests (Fine 2002; Peh 2010; Seebens et al. 2020). Furthermore, evidence from other biomes has demonstrated that disturbance associated with land-use change increases plant invasions, therefore, the spread of exotic plants is likely to increase within degraded tropical landscapes given recent rates of deforestation (Hulme 2009; Seebens et al. 2015). I conducted a systematic search of the literature to summarise the current knowledge of the drivers of exotic plant invasion within tropical rainforests (i.e. propagule pressure, abiotic conditions and biotic characteristics of both the invading species and invaded ecosystem, as well as the role of human-driven disturbances), in order to identify research gaps to be addressed in this thesis and future work. Following systematic review protocols (see Pullin & Stewart 2006; details in Appendix 1: Text 1.1) my search of the published literature retained studies that were either observational or field experiments and that focused on the drivers of exotic plant invasion within tropical rainforests, which yielded 30 studies

(Table 1.2). Exotic plant invasion was quantified as either the presence of exotic species, exotic species richness, exotic abundance, biomass, basal area, cover, growth rates, survival, reproductive output and/or photosynthetic performance.

These 30 papers were distributed across the tropics (Fig. 1.3); however none of the three main tropical regions could be considered to be well studied and areas with more extensive tracts of intact forest are less studied (i.e. Amazon and the Congo Basins). This lack of studies could be due to resilience to invasion within intact tropical rainforest; however, given that these regions are increasingly fragmented due to land-use change (Taubert et al. 2018), and this is a relatively recent change, it is likely there is a lack of attention given to exotic species within these regions. There were just eleven studies that focused on surveying whole community of exotic species (i.e. multiple exotic species from different plant groups) compared to studies on a single exotic species (*n*=12) or targeted group of species (e.g. one genus or exotic trees; *n*=7). This small number of multi-species studies makes it difficult to draw robust conclusions on the drivers of exotic plant invasion within rainforest habitats, showing the current paucity of data available to understand invasion drivers in tropical rainforests. I now briefly summarise commonalities in the findings of these eleven studies.

Variables conveying greater propagule pressure were studied in only three studies (Tables 1.2 and 1.3; Figs. 1.4 and 1.5) despite the importance of this factor in all invasion pathways (Fig. 1.2; Eppstein & Molofsky, 2007). Two studies found that increased propagule pressure promoted invasion, measured by the distance from forest edge (significantly more invasion inside the forest closer to the forest edge, after controlling for abiotic conditions altered by edge effects; Dawson et al., 2015) and the abundance of exotic species found outside the forest (Dawson et al. 2011). The third study found no significant effect of the distance between the forest edge and the nearest source population outside the forest (Dawson et al. 2009b), suggesting that the abundance of exotics outside tropical rainforests may be more influential than distance from source population to forest edge. However, there are too few studies to confirm this.

A measure of disturbance, either human-driven i.e. from edge effects or logging, or natural from cyclones, was assessed in all eleven community-level studies and in all studies, disturbance increased invasion (Table 1.2 and Figs. 1.4 and 1.5). I found that increased canopy openness, which incorporates a measure of both the abiotic conditions (i.e. light levels) and previous disturbance (i.e. logging or cyclone damage), almost always increases invasion inside tropical rainforests (Teo et al. 2003; Baret et al. 2008; Dawson et al. 2015; Döbert et al. 2017a). These findings are expected based on the 'Disturbance' hypothesis (Davis et al. 2000b; Theoharides and Dukes 2007). Generally, measures of human disturbance differed across studies (e.g. increased land-use change, edge effects, remnant size and local forest structural change due to logging) but in all cases, human disturbance was positively related to invasion (Wiser et al. 2002; Dawson et al. 2015; Döbert et al. 2017a; Rembold et al. 2017; Galindon et al. 2018). However, it is unclear whether landscape-levels of disturbance (e.g. degree of fragmentation) promote invasion in tropical rainforests, as only one study investigated this and no significant effect was found (i.e. forest loss due to logging and density of roads in the surrounding landscape; Döbert et al., 2017). Nevertheless, there seems to be consensus that locally disturbed rainforests with more open canopies (i.e. high light levels) are more susceptible to invasion by exotic plants.

Table 1.2: Summary of 30 studies investigating exotic plant invasion of tropical rainforests. All studies were observational field studies with the exception of two that also had a field experiment element (denoted by *) and two that were solely field experiments (denoted by **).

Region	Citation	Country	Response variable	Study focus	Plant group
Africa	Adhiambo et al. (2019)	Kenya	Abundance	Single species	Tree
	Baret et al. (2008)*	Reunion	Abundance & germination of most common species	Multi-species	Multiple
	Brown and Gurevitch (2004)	Madagascar	Percentage of plants that were exotic	Target species	Trees & shrubs
	Brown et al. (2009)	Madagascar	Percentage of plants that were exotic	Target species	Woody species
	Cordeiro et al. (2004)*	Tanzania	Dispersal & germination of seeds	Single species	Tree
	Dawson et al. (2009)	Tanzania	Presence in forest	Multi-species	Multiple
	Dawson et al. (2009)	Tanzania	Presence in forest	Target species	Woody species
	Dawson et al. (2011)	Tanzania	Abundance & Weed Risk Assessment Score	Multi-species	Multiple
	Dawson et al. (2015)	Tanzania	Species richness & abundance (adults, saplings & seedlings)	Multi-species	Multiple
	Edward et al. (2009)	Tanzania	Stem density & basal area	Single species	Tree
North America	Barbosa et al. (2017)	USA (Hawaii)	Canopy cover	Single species	Tree
	DeWalt et al. (2004)**	Costa Rica & USA (Hawaii)	Herbivory rates, growth and survival	Single species	Shrub
	Ibanez et al. (2019)	USA (Hawaii and American Samoa)	Species richness & cover	Target species	Trees
Oceania	Dyer et al. (2018)	Fiji	Abundance	Single species	Palm tree
	Murphy et al. (2008)	Australia	Species richness	Multi-species	Multiple

	Tng et al. (2016)	Australia	Basal area & seedling density	Single species	Tree
	Wiser et al. (2002)	Tonga	Species richness & cover (Ancient & modern introductions)	Multi-species	Multiple
South Asia	Joshi et al. (2009)	India (Western Ghats)	Abundance	Target species	Shrubs
South-East Asia	Dillis et al. (2018)	Indonesia	Reproductive output	Single species	Tree
	Döbert et al. (2017)	Malaysia (Borneo)	Species richness, biomass, LAI	Multi-species	Multiple
	Fujinuma and Harrison (2012a)	Malaysia (Peninsular)	Abundance	Single species	Shrub
	Galindon et al. (2018)	Philippines	Species richness	Multi-species	Multiple
	Le et al. (2018)	Malaysia (Peninsular)	Density	Single species	Shrub
	Le et al. (2019)**	Brunei	Photosynthetic performance	Target species	Tree
	Neo et al. (2017)	Singapore	Species richness	Multi-species	Multiple
	Nghiem et al. (2015)**	Singapore	Growth and survival rates	Target species	Trees
	Peters (2001)	Malaysia (Peninsular)	Abundance & growth rate	Single species	Shrub
	Rembold et al. (2017)	Indonesia	Species richness & abundance	Multi-species	Multiple
	Teo et al. (2003)	Singapore	Species richness	Multi-species	Multiple
	Yeo et al. (2014)	Singapore	Abundance of seedlings	Single species	Palm tree

Table 1.3: Summary of 11 published studies investigating the invasion of multiple exotic plant species within tropical rainforests, including all significant and non-significant results tested in each study.

Citation	**Country**	**Method**	**Response(s)**	**Significantly higher invasion:**	**Non-significant effects:**
Baret et al. (2008)	Reunion	Observational	Abundance	In canopy gaps caused by cyclones vs. forest understorey	
Dawson et al. (2015)	Tanzania	Observational	Richness & abundance (Adults, saplings & seedlings)	In secondary forest vs semi-natural forest. Closer to forest edge for adults, saplings and seedlings. This effect was strongest in secondary forests. Of saplings and seedlings in more open canopy.	
Dawson et al. (2011)	Tanzania	Observational	Abundance	In disturbed forests by bird dispersed exotic species By species that were planted in higher numbers outside the forest (propagule pressure)	Between SLA, seed mass, foliar nutrient concentration index (N, P, K, Mg and Ca) or residence time and invasion in either disturbed or intact forests
Dawson et al. (2009)	Tanzania	Observational	Invasion success (i.e. presence at different stages)	Forest establishment by bird or primate dispersed exotic species Forest establishment by exotic species with greater seed mass (mg)	Between propagule pressure (e.g. minimum distance between species in botanical gardens and forest edge), residence time (i.e. year of first planting in botanical gardens), climate in native range (i.e. midpoint of native latitudinal range), vegetative reproduction, growth rate, shade tolerance, number of seeds per fruit and breeding system on invasion of forests
Döbert et al. (2017)	Malaysia (Borneo)	Observational	Richness & biomass	With greater local logging intensity (i.e. forest canopy loss)	Between landscape-scale logging intensity (i.e. landscape forest canopy loss), distance to nearest main road, density of minor

				With soil compaction index (i.e. PCA component with high bulk density and low moisture) With lower biomass of seedlings from dominant tree family (Dipterocarpaceae)	roads, elevation or soil fertility index (i.e. PCA component with high total N and available P) and invasion
Galindon et al. (2018)	Philippines	Observational	Richness	In small sized remnant forests	
Murphy et al. (2008)	Australia	Observational & field experiment	Richness	After cyclone across all disturbance levels With increasing removal of leaf litter and debris Significantly positive correlation between exotic and native species richness	
Neo et al. (2017)	Singapore	Observational	Richness		Between total soil N or available soil K and P and invasion
Rembold et al. (2017)	Indonesia	Observational	Richness & abundance	With increasing land-use change (i.e. from primary rainforest remnant, agroforestry, rubber plantation and oil palm plantation)	
Teo et al. (2003)	Singapore	Observational	Richness	With decreasing canopy cover With increasing soil pH With decreasing soil C and N	Between native species richness, soil Ca and available K on invasion
Wiser et al. (2002)	Tonga	Observational	Richness & cover (Ancient & modern exotics)	Of modern exotic (richness & cover) in abandoned plantation Of ancient exotic (cover) in smaller forest remnants Of modern exotic (cover) in forest remnants with lower soil total N Of modern exotic (cover) in forest remnants with lower soil available P	Between native species richness (as a measure of disturbance) and canopy cover on invasion

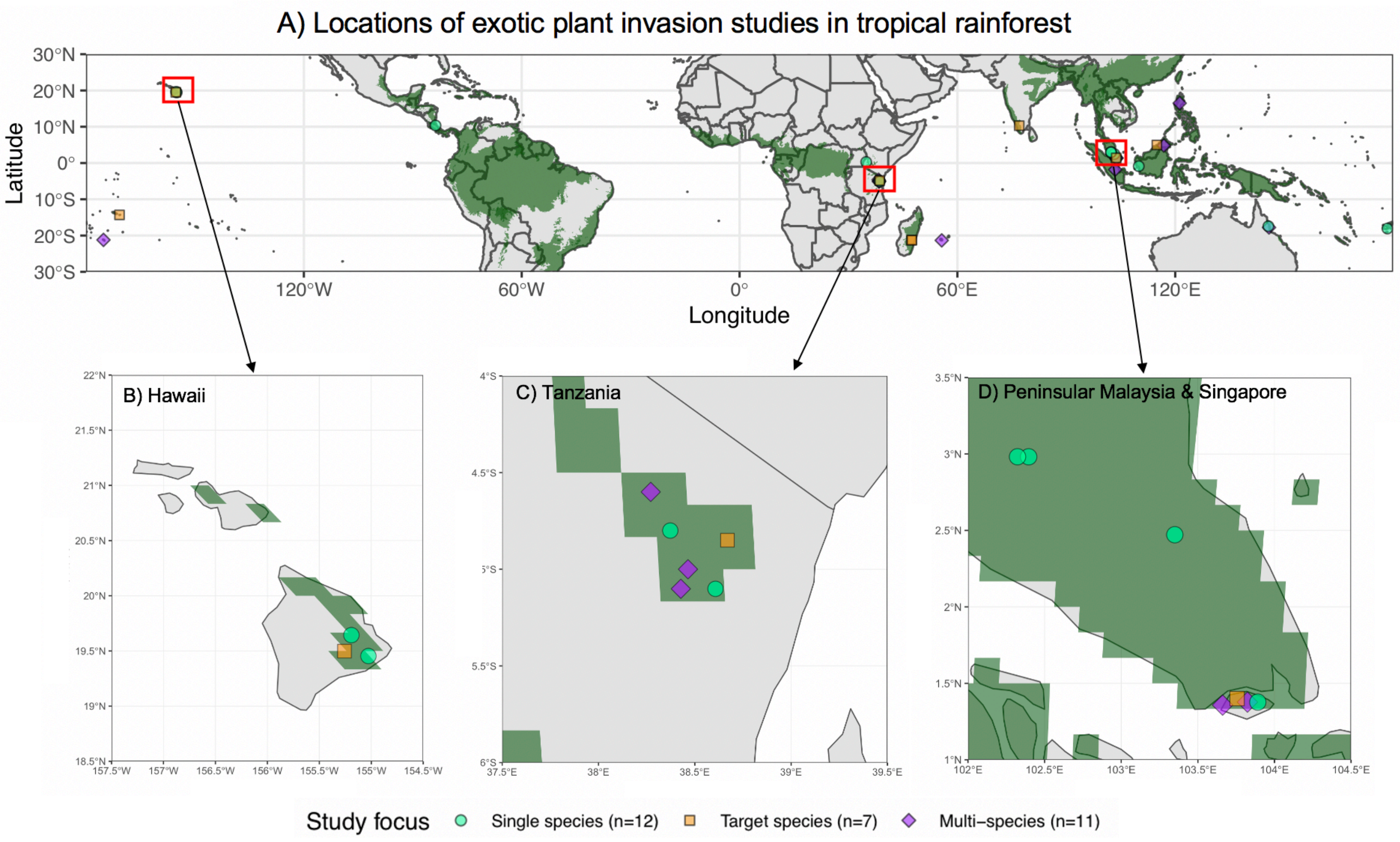
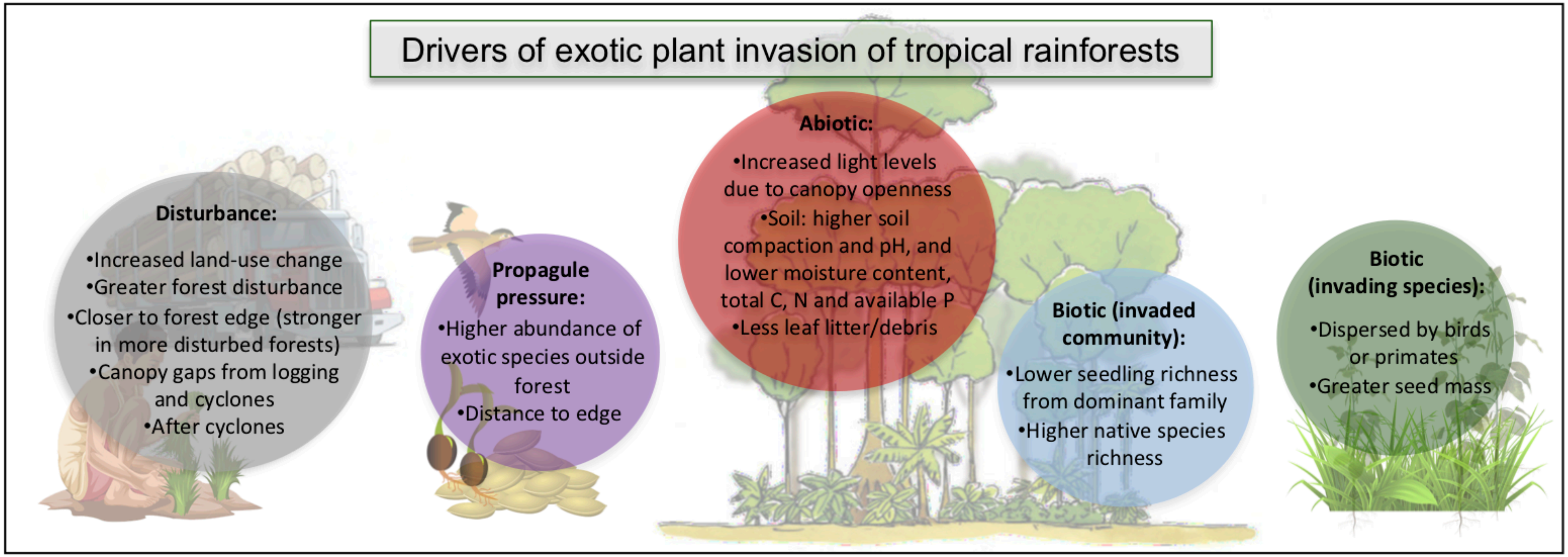


Figure 1.3: A) Map of study location of 30 exotic plant invasion studies based in tropical rainforests, split by study focus and zoomed in on regions with multiple studies: B) Hawaii, C) Tanzania and D) Peninsular Malaysia and Singapore. The green shading shows the distribution of tropical humid forests (Hansen et al., 2008; available: https://glad.geog.umd.edu/projects/gfm/humidtropics/data.html). Target species = targeted group of species, e.g. one exotic genus or all trees; multi-species = multiple exotic species from different plant groups (e.g. shrubs, forbs, trees).



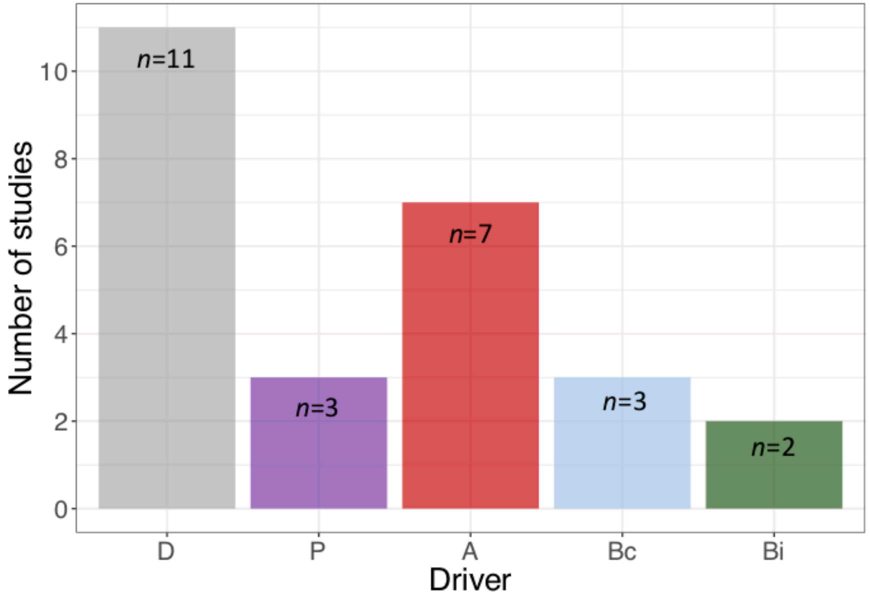


Figure 1.5 (top): Summary of the significant drivers of exotic plant invasion in tropical rainforests from the 11 studies that focused on multiple exotic species based on a systematic search of the literature. See Table 1.2 for full study details including non-significant terms. Drivers grouped by the four factors introduced in Fig. 1.1 plus the additional role of disturbance.

Figure 1.4 (left): Number of studies for each of the drivers of exotic plant invasion in tropical rainforests from the 11 studies that focused on multiple exotic species. D = Disturbance, P = Propagule pressure, A = Abiotic, Bc = Biotic characteristics of the invaded community and Bi = Biotic characteristics of the invading species. Some studies tested the effects of multiple drivers, see Table 1.2 for full details.

By contrast, there was limited support for the Biotic Resistance Hypothesis, with conflicting conclusions (i.e. negative correlation; Döbert et al., 2017; positive correlation; Murphy et al., 2008 and no correlation; Teo et al., 2003) despite the notion that high native diversity is why intact forests are apparently robust to invasion. In addition, I found no study that had examined the effect of either native functional or phylogenetic diversity on exotic plant invasion at the community level. Thus, high taxonomic native species diversity itself may not impede exotic species establishment, but instead high functional diversity could result in biotic resistance (Denslow and DeWalt 2008) because this maybe be more closely related to niche saturation. There was also no consensus in the role of soil nutrients and pH on invasion, with both significant and non-significant results for the same variable across five studies (Table 1.3), which may reflect different individual nutrient requirements of exotic species or co-variation with other terms. Finally, only two studies assessed the role of functional traits of invading species and these studies revealed that the plant communities found within tropical forests were more likely to comprise of species that are dispersed by vertebrates and have a larger seed mass (Dawson et al. 2009b, 2011), with other measured traits being non-significant (see Table 1.2). However, these two studies were from the same location (i.e. same exotic community), and therefore, it is unclear if these traits are important for invasion of tropical forests in other regions.

This literature review revealed significant gaps in our understanding of the drivers of plant invasion in tropical rainforests, with most driving factors addressed by only a few studies and no study considering the relative importance of all factors known to be drivers of plant invasion. Thus, this limits our capacity to draw general and robust conclusions on the drivers of plant invasion within tropical rainforests. In particular, few studies investigated the biotic characteristics of the invading exotic community or of the invaded native ecosystem, despite theory that biotic resistance impedes invasion in tropical forests and the role species traits have on overcoming the barriers of invasion. I found that local disturbance was a well-established driver unlike the role of landscape-level disturbances which was understudied despite its likely role in the invasion of these landscapes. Hence, I identify that there are clear knowledge gaps in our understanding of the role of: (i) landscape-level disturbances, (ii) the biotic characteristics of the invaded native community (e.g. biotic resistance by high native diversity) and (iii) the functional and life-history traits of the invading exotic species on invasion within tropical rainforests.

1.6 Oil palm cultivation in South-East Asia

The field studies in this thesis focus on the oil palm-forest landscape in Sabah, Malaysian Borneo, where conversion to oil palm is the main land-use change driver. The African oil palm (*Elaeis guineensis* Jacq) is the highest yielding, cheapest and most widely used commercial vegetable oil crop in the world (Basiron 2007; USDA 2019). The expansion of oil palm in South-East Asia in recent decades, has resulted in this industry contributing significantly to the economy in Malaysia and Indonesia, where oil palm production is the highest in the world (Cramb and McCarthy 2016). The area used for oil palm cultivation trebled across Malaysia and Indonesia in the period 1990-2012 to 7.2 million ha (~3.2% of the total land area), with this expansion resulting in the deforestation of native tropical forest (often logged prior to conversion; Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011) in over half of new plantings (i.e. 55-59% expanded area; Koh & Wilcove, 2008). These land-use changes have also led to the tropical forests in South-East Asia being considered the most globally threatened, with levels of deforestation (Achard et al. 2002; Sodhi et al. 2004) and logging intensity

(Lewis et al. 2015) amongst the highest in the world. In 1973 'old-growth' forest covered 76% of Borneo, by 2016 that had decreased to 50% (Gaveau, 2017). This rate is projected to increase further across South-East Asia with up to 98% of original forest cover being lost in the Philippines and some islands of Indonesia by 2022 (UNEP 2007).

Figure 1.6: Oil palm plantation in the South-East of Sabah, showing the different stages of oil palm tree growth from first planting (back right) to mature trees (foreground). Embedded rainforest remnants can be seen on the horizon.

As the demand for palm oil has increased across the globe, knowledge of the environmental impact of oil palm cultivation on tropical forests and biodiversity has become widespread. This led to the establishment of the multi- stakeholder membership organisation, Roundtable on Sustainable Palm Oil (RSPO; www.rspo.org) in 2004, which aims to minimised both environmental and social impacts of palm oil (RSPO 2018). Members of the RSPO are required to maintain areas of 'High Conservation Value' (HCV; www.hcvnetwork.org) in order to adhere to the RSPO's principles and criteria for sustainability. These HCVs are kept for six reasons, including to conserve rare or threaten native biodiversity or habitats, to increase landscape connectivity, to prevent soil erosion, protect resources for community needs and maintain areas of cultural value (Senior et al. 2015). Although, in practice, some forest remnants that were considered unsuitable for oil palm cultivation prior to 2004, because they are on steep slopes, areas that regularly flood or unsuitable soil, are now managed retrospectively as HCVs (Senior *et al.*, 2015).

Open and disturbed areas within oil palm plantations, such as roadsides, provide suitable conditions for the establishment of populations of exotic plant species (Fee et al. 2017; Rembold et al. 2017; see Table 1.4 for a list of exotic weeds in Malaysia). There are several exotic species that are considered to be invasive withing plantations including *Clidemia hirta, Chromolaena odorata* and *Mimosa pudica* (Table 1.4; CABI, 2019; Fee et al., 2017; Witt, 2017) and millions of US dollars are spent attempting to control them within agricultural lands across South-East Asia (Nghiem et al. 2013). Remnant areas of rainforest embedded within agricultural landscapes (HCVs) may be particularly vulnerable to invasion by exotic species established within oil palm planted areas (Rembold et al. 2017). However, plant invasions within South-East Asia are particularly poorly studied (e.g. no studies on plants between 2006-2008; Peh 2010), with just five studies found that looked at the invasion of the full exotic community within South-East Asian tropical rainforests (systematic review findings in section 1.5). Therefore, it is important to improve our understanding of exotic plant invasions within these landscapes, which may impact both palm oil production and regeneration of remaining areas of natural rainforest (HCVs). Especially within RSPO-certified plantations that have to effectively manage weeds and invasive introduced species as part of their criterion (RSPO 2018). Furthermore, the invasion of degraded areas of forest within agricultural landscapes may act as a stepping stone to colonise larger tracts of more intact forests that are protected by the government outside these plantations, and may therefore threaten regional biodiversity.

Table 1.4: List of common exotic plant species found in Malaysia, including those recorded in Sabah, Malaysian Borneo. Sources are [1] CABI (2020); [2] ISSG (2020); [3] (Döbert et al. 2017a); [4] (Bakar 2004); [5] Pallewatta et al. (2003). * denotes species recorded in Sabah. † denotes inclusion of species in '100 of the World's Worst Invasive Alien Species' by ISSG (2020).

Latin name	**Growth form**	**Family**	**Source**
*Acacia auriculiformis**	Tree	Fabaceae	1
*Acacia confusa**	Tree	Fabaceae	1, 2
*Acacia mangium**	Tree	Fabaceae	1, 2
Acacia mearnsii†	Tree	Fabaceae	1, 2
*Adenanthera pavonina**	Tree	Fabaceae	1, 2
*Ageratum conyzoides**	Herb	Asteraceae	1, 2, 3
*Albizia saman**	Tree	Fabaceae	1
Amaranthus spinosus	Herb	Amaranthaceae	1
Asystasia gangetica	Herb	Acanthaceae	2, 5
*Axonopus compressus**	Grass	Poaceae	1, 3
*Calopogonium mucunoides**	Herbaceous climber	Fabaceae	1, 3
*Centrosema pubescens**	Herbaceous climber	Fabaceae	3
*Chromolaena odorata**†	Shrub	Asteraceae	1, 2, 3, 5
*Cinnamomum burmanni**	Tree	Lauraceae	1
*Cleome rutidosperma**	Herb	Cleomaceae	1
*Clidemia hirta**†	Shrub	Melastomataceae	1, 2, 3
*Clitoria ternatea**	Herbaceous climber	Fabaceae	1
Crassocephalum crepidioides	Herb	Asteraceae	1
*Cyperus kyllingia**	Sedge	Cyperaceae	3
*Cyperus luzulae**	Sedge	Cyperaceae	3
*Eichhornia crassipes**†	Aquatic herb	Pontederiaceae	1, 2, 5
*Eleusine indica**	Grass	Poaceae	1, 5
*Erechtites valerianifolius**	Herb	Asteraceae	1
*Fimbristylis dura**	Sedge	Cyperaceae	3
*Gliricidia sepium**	Tree	Fabaceae	1
*Hyptis brevipes**	Herb	Lamiaceae	1
*Hyptis capitata**	Herb	Lamiaceae	1, 3
*Hyptis suaveolens**	Herb	Lamiaceae	1
Lantana camara†	Shrub	Verbenaceae	1
*Leucaena leucocephala**†	Tree	Fabaceae	1, 2

*Ludwigia hyssopifolia**	Aquatic herb	Onagraceae	1
*Mangifera indica**	Tree	Anacardiaceae	1
Mikania micrantha†	Herbaceous climber	Asteraceae	1, 2, 5
*Mimosa diplotricha**	Shrub	Fabaceae	1, 2, 3, 5
Mimosa pigra†	Shrub	Fabaceae	1, 2, 5
*Mimosa pudica**	Shrub	Fabaceae	1, 2, 3
*Murdannia nudiflorum**	Herb	Commelinaceae	1
*Paspalum conjugatum**	Grass	Poaceae	1
Passiflora foetida	Herbaceous climber	Passofloraceae	1
*Phyllanthus amarus**	Herb	Phyllanthaceae	3
*Pinus caribaea**	Tree	Pinaceae	1
Piper aduncum	Shrub	Piperaceae	1, 2
*Pithecellobium dulce**	Tree	Fabaceae	1
*Polygala paniculate**	Herb	Polygalaceae	3
Psidium cattleianum†	Shrub	Myrtaceae	1, 2
*Ricinus communis**	Shrub	Euphorbiaceae	1
*Scleria levis**	Sedge	Cyperaceae	3
*Spathodea campanulata**†	Tree	Bignoniaceae	1, 2
Sphagneticola trilobata†	Herb	Asteraceae	1, 2
*Tephrosia candida**	Tree	Fabaceae	1
Varronia curassavica	Shrub	Boraginaceae	5
*Zingiber montanum**	Herb	Zingiberaceae	1

1.7 Thesis aims and objectives

The overall aim of my thesis is to investigate plant invasions of rainforest remnants within human-modified tropical landscapes dominated by oil palm. Studies examining invasion of tropical rainforests are rare, and my thesis is the first to examine a range of environmental and ecological factors leading to invasion of forest remnants embedded within an oil palm dominated tropical landscape in Sabah, Malaysian Borneo.

My objectives are:

1. To determine how local and landscape factors influence exotic plant invasion and native community diversity along a gradient of landscape fragmentation and local forest disturbance (Chapter 2).

2. To determine whether there is environmental trait filtering of exotic species' functional traits during colonisation from oil palm into forest remnants (Chapter 3).
3. To determine the ecological factors that influence herbivory in the most common exotic plant in the study system, *Clidemia hirta*, and whether this may help to explain the success of this highly invasive tropical species (Chapter 4).

I addressed the thesis objectives by collecting data through surveys within a fragmented and disturbed tropical rainforest study system in Sabah (Chapters 2-4). Oil palm plantations are widespread in Sabah, making up ~20% of the land area (Reynolds et al. 2011) and remnant areas of rainforests embedded within these plantations are retained as HCVs (RSPO, 2018). These remnant rainforests of varying size provide an excellent study system to investigate the impact of land-use change on the invasion of tropical rainforests, as well as the effect of logging disturbance which occurred prior to conversion to oil palm. By bringing together this information, I will determine the how exotic plant invasions are occurring within human-modified tropical landscapes, providing information that will aid the conservation of these threatened forest remnants.

Thesis chapter hypotheses:

Chapter 2: Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants

The aim of this chapter is to investigate factors influencing invasion of exotic plant species within disturbed forest remnants in commercial oil palm dominated landscapes in Sabah, including landscape-level fragmentation, local forest disturbance, soil characteristics and the diversity of the native community. Using structural equation modelling, I test the following hypotheses:

H1) Invasion will be positively correlated with landscape fragmentation, local forest disturbance and propagule pressure.

H2) The native plant community will respond negatively to land-use change (i.e. greater landscape fragmentation and local forest disturbance).

H3) Invasion will be negatively correlated with native plant community diversity.

Chapter 3: Trait filtering during exotic plant invasion of tropical rainforest remnants along a disturbance gradient

In this chapter I investigate evidence for environmental trait-based filtering during the invasion of tropical rainforest remnants from highly disturbed, human-modified oil palm habitats. The aim of this chapter is to examine why certain species invade rainforest remnants from the oil palm areas whereas others do not, identifying the functional traits determining invasion success. I test the following hypotheses:

H1) Habitat disturbance and light levels decrease from oil palm areas into intact forest, and so I expect exotic species richness and occurrence to decrease accordingly.

H2) The exotic community inside the forest will have traits that indicate effective dispersal and allow propagules to readily spread from oil palm source populations into forest remnants (i.e. long-distance dispersal and small, light seeds).

H3) The exotic community inside the forest will have traits that promote the establishment of persisting populations in a forest environment (i.e. able to compete with native understorey community).

Chapter 4: Canopy cover and proximity to native confamiliars affect herbivory of an invasive shrub in Bornean rainforests.

In this chapter, I examine the ecological factors that influence herbivory on the commonest exotic species in the study sites, *Clidemia hirta* plants, which may explain its establishment success within its introduced range of Sabah. The success of *C. hirta* invasion in Hawaii has been associated with release from natural enemies, however Hawaii has no native members of the same family (Melastomataceae), whilst native confamiliar species do occur in Sabah. Therefore the impact of herbivores and pathogens on *C. hirta* may be greater in Sabah where the probability of host-switching by native insects may be greater. I test the following hypotheses:

H1) Herbivory is higher in native Melastomataceae shrubs than in exotic *C. hirta* plants.

H2) Herbivory is higher in exotic *C. hirta* when it is in close proximity to native Melastomes that have high herbivory damage.

H3) Herbivory is influenced by variation in light levels due to forest disturbance and changes to canopy cover.

H4) Herbivory reduces the reproductive output of *C. hirta* plants.

Chapter 2

Oil palm landscape with embedded rainforest remnants

Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants

2.1 Abstract

Intact tropical rainforests are considered robust to plant invasions. However, land-use change alters the structure and species composition of native forest, opening up tropical landscapes to invasion. Yet, the relative roles of key drivers on tropical forest invasions remain little investigated. We examine factors affecting plant invasion of rainforest remnants in oil-palm dominated landscapes in Sabah, Malaysian Borneo. We hypothesized that invasion is greater in highly fragmented landscapes, and in disturbed forests with lower native plant diversity (cf. old-growth rainforests). Native and exotic plants were surveyed in 47 plots at 17 forest sites, spanning gradients in landscape-scale fragmentation and local forest disturbance. Using partial least squares path-modelling, we examined correlations between invasion, fragmentation, forest disturbance, propagule pressure, soil characteristics and native plant community. We recorded 7004 individuals from 329 genera in total, including eight exotic species (0-51% of individuals/plot, median=1.4%) representing shrubs, forbs, graminoids and climbers. The best model (R^2=0.343) revealed that invasion was correlated with disturbance and propagule pressure (high prevalence of exotic species in plantation matrix), the latter being driven by greater fragmentation of the landscape. Our models revealed a significant negative correlation between invasion and native tree seedlings and sapling community diversity . Increasing landscape fragmentation promotes exotic plant invasion in remnant tropical forests, especially if local disturbance is high. The association between exotic species invasion and young native tree community may have impacts for regeneration given that fragmentation is predicted to increase and so plant invasion may become more prevalent.

Keywords: *agricultural landscapes; forest degradation; fragmentation; non-native species; oil palm; structural equation modelling*

2.2 Introduction

Exotic species invasion is recognised as a major agent of environmental change across all ecosystems (Sala et al., 2005). Invasion is considered to be a function of four factors: propagule pressure, the abiotic characteristics of the invaded system, and the biotic characteristics of both the invaded system and invading species, all of which can be altered by human activity (Pyšek and Richardson 2006). In a given invasion scenario these factors contribute to varying degrees, and it is crucial to identify the relative role of each in driving invasion in a particular ecosystem (Catford et al. 2009). Many temperate forests are highly invaded by exotic plants due to historic land-use change causing substantial forest cover loss and resulting in highly fragmented and disturbed landscapes (McNeely 1995; Williams 2003; Haddad et al. 2015). Conversely, intact, lowland, humid tropical forests are usually considered to be robust to plant invasions due to low propagule pressure, low forest disturbance and because exotic species typically do not thrive in the strongly shaded conditions within undisturbed forests (Fine 2002; Denslow and DeWalt 2008). In addition, it has been hypothesised that the typically high native diversity in tropical rainforests means there are fewer empty niches, providing biotic resistance to invading exotic plants (Fine 2002; Denslow and DeWalt 2008). However, land-use change is impacting large tracts of forest across the tropics (Haddad et al., 2015; Pütz et al., 2014; Qie et al., 2017), opening up these landscapes to exotic propagules and further disturbance in the remaining patches of forest (Hulme 2009). Forest degradation alters the availability of light and other resources, changing the nature of inter-specific competition (Denslow and DeWalt 2008; Carson and Schnitzer 2011), and potentially exposes these forest patches to invasion of exotic plants. Yet, despite this, little is known about plant invasions within human-modified tropical landscapes (Kueffer et al. 2013), including remnant forests which are crucial for maintaining local and regional native biodiversity.

Large-scale deforestation in the tropics is predominantly driven by expansion of agriculture, and these agricultural areas have high levels of disturbance and abiotic conditions which differ from those of intact tropical forests (Malhi et al. 2014; Curtis et al. 2018). Abiotic conditions in tropical agricultural areas (e.g. high light levels, high temperature, low humidity, altered soil nutrients and pH) promote establishment of ruderal exotic plant species that are transported and introduced by humans via extensive networks of roads (Fee et al., 2017; Padmanaba & Sheil, 2014; Von der Lippe & Kowarik, 2007; With, 2002), resulting in exotic-rich weed-covered banks along disturbed roadsides (Fee et al., 2017). These highly disturbed agricultural areas provide an on-going source of propagules and may promote invasion of natural forest remnants embedded within these landscapes. From the few studies of plant invasions within humid tropical forests, the presence of exotic species correlates with variables that are associated with propagule pressure, including distance from source population and to forest edge (Edward et al. 2009; Dawson et al. 2015). If propagule pressure is high enough, seed swamping of new environments can result in successful exotic establishment, regardless of whether the conditions of the invaded system are ideal for that species (see Propagule pressure hypothesis; Colautti, Grigorovich, & MacIsaac, 2006; Lockwood, Cassey, & Blackburn, 2005). Nonetheless, abiotic and biotic factors also contribute to the invasion process.

Disturbance has been foundational in the formulation of several invasion hypotheses (e.g. Disturbance, Habitat filtering, Empty niche and Increased Resource Availiabilty hypotheses; see Catford et al. 2009 for invasion hypothesis overview), therefore invasion is expected to be higher in the most disturbed tropical rainforests. Commercial selective logging and the impact of fragmentation (e.g. via edge effects) alter the structure of remaining rainforest due to timber removal and disturbance-related tree mortality (Laurance et al. 2002; Malhi et al. 2014; Gibbs and Salmon 2015). The reduction in canopy cover increases light in the forest understorey, which affects the abiotic conditions of remnant forest patches, when compared with continuous, undisturbed forest (Laurance et al. 2002). Gradients from forest edge to interior have been recorded for temperature, humidity, wind intensity and soil erosion, with the most extreme differentiation seen at forest edges, known as edge effects (Laurance et al. 2002). In disturbed tropical forests, more exotic plants have been recorded at forest edges, driven by a combination of increased propagule pressure and increased canopy openness and soil disturbance associated with forest edge conditions and anthropogenic influence (Peters 2001a; Harper et al. 2005; Edward et al. 2009; Dawson et al. 2015; Döbert et al. 2017a). However, these studies only looked at a few forest sites, only one studied a gradient of disturbance (Döbert et al. 2017a) and none have considered gradients in landscape fragmentation.

In addition to forest structural changes caused by logging and fragmentation, changes to species community composition also occur due to disruption of native species interactions (Laurance et al. 2011; Arellano-Rivas et al. 2016). For example, removal of large timber trees and isolation from larger tracts of forest reduce the regeneration of native old-growth tree species through reduced fruiting and dispersal events, shifting tree species composition to earlier successional states with lower community-average wood density (Laurance et al. 2006; Lôbo et al. 2011; Pütz et al. 2011; Gibbs and Salmon 2015; Qie et al. 2017). The negative impacts of fragmentation on native species communities are greater in small, isolated fragments and accumulate over time (Gonzalez 2000; Ferraz et al. 2003; Hill and Curran 2003; Haddad et al. 2015), with the understorey tree community strongly affected due to adult trees producing fewer viable seeds (i.e. extinction debt; Stride et al. 2018). Therefore, forest remnants may be particularly vulnerable to invasions due to reduced biotic resistance arising from the loss of native forest species. However, evidence for biotic resistance to exotic plant invasion in tropical rainforests is limited (Fine 2002; Levine et al. 2004; Denslow and DeWalt 2008), with no consensus currently (Teo et al. 2003; Brown et al. 2006). Thus it is still unclear whether biotic interactions between native and exotic species (i.e. biotic resistance from the native community as well as suppression of native growth by invading exotic species) play a significant role in mediating invasion of tropical forests.

South-East Asia has the highest rates of deforestation (Achard et al. 2002; Sodhi et al. 2004) and logging (primarily trees from Dipterocarpaceae; Lewis et al. 2015; Brearley et al. 2016) in the world (Bryan et al., 2013; Gaveau, Salim, & Arjasakusuma, 2017; Hansen et al., 2008), due in particular to the expansion of oil palm (*Elaeis guineensis* Jacq.) cultivation in Malaysia and Indonesia in recent decades. This expansion of agriculture results in a highly fragmented forest landscape made up of commercial oil palm plantations with uncultivated, often heavily logged forest remnants (Reynolds et al. 2011). These remnant forests are therefore usually highly degraded and contain reduced assemblages of both plants and animals, compared with old-growth continuous forest, particularly if very little core forest area remains within the remnants (Lucey et al. 2017). However, these forest remnants can be important for conserving biodiversity and ecosystem services and for connecting forest patches within oil palm dominated regions, even if they are highly degraded (Yeong, Reynolds and Hill, 2016; Lucey et al., 2017; Scriven et al., 2017; Fleiss et al., 2020).

In this study, we examine the relative influence of fragmentation, forest disturbance, propagule pressure, soil characteristics and native community composition on exotic plant invasions of forest remnants within oil palm-dominated landscapes in Sabah, Malaysian Borneo. Studies examining invasion of tropical forests are rare, and this study is the first to examine a range of environmental and ecological factors leading to invasion of forest remnants embedded within an oil palm landscape. We use partial least squares path modelling (PLS-PM) to test the expectation that invasion is positively correlated with landscape-scale fragmentation, local forest disturbance and propagule pressure, and negatively correlated with native community diversity, whilst accounting for soil characteristics. We also expect the native community to respond negatively to land-use change.

2.3 Methods

Study sites

Between July and October 2017, we sampled 47 plots within 17 sites distributed widely across the state of Sabah, Malaysian Borneo (Fig. 2.1a). Sites were selected to span a wide gradient of fragmentation and disturbance, including isolated, heavily logged, small forest remnants (<15 ha) that were fully surrounded by oil palm, as well as larger, heavily logged forest remnants (>100 ha) that were connected at the plantation boundary to larger tracts of government protected forest (Table S2.1). Forest sites in oil-palm dominated landscapes (*n*=13 sites), which have between 1 and 64% natural forest cover remaining within a 2km radius buffer surrounding study plots (see section below; characterising fragmentation; Table S2.1), were compared with four sites within an extensive tract of intact 'continuous' logged and unlogged protected forest (>1 million ha; Fig. 2.1a). These continuous forest sites provided baseline data for comparison of forest remnants within an oil palm landscape and also represented variation in levels of forest disturbance in the region, including both fully protected unlogged forest (*n*=2) and commercially logged sites (*n*=1 site in once-logged forest; *n*=1 site in twice-logged forest). Thus, our choice of sites spanned a gradient in the degree to which the landscape surrounding our sites was fragmented as well as the intensity to which the forest areas were previously commercially selectively logged.

Sites within oil palm plantations were conservation set-asides, and the majority were managed as sites with 'High Conservation Values' (HCVs, Senior et al., 2015), which the plantations retain and manage as part of the Roundtable on Sustainable Palm Oil (RSPO) certification process for sustainable palm oil (RSPO, 2018). These sites were selectively logged to varying degrees in the 1990s prior to oil palm cultivation (see details below on disturbance quantification) and were generally unsuitable for planting oil palm (i.e. too steep or too rocky). Study sites were at least 1 km apart to avoid spatial autocorrelation. The maximum distance between sites is c. 192km with elevation range from 42-267 m above sea level, hence we do not expect the climate to vary greatly between sites.

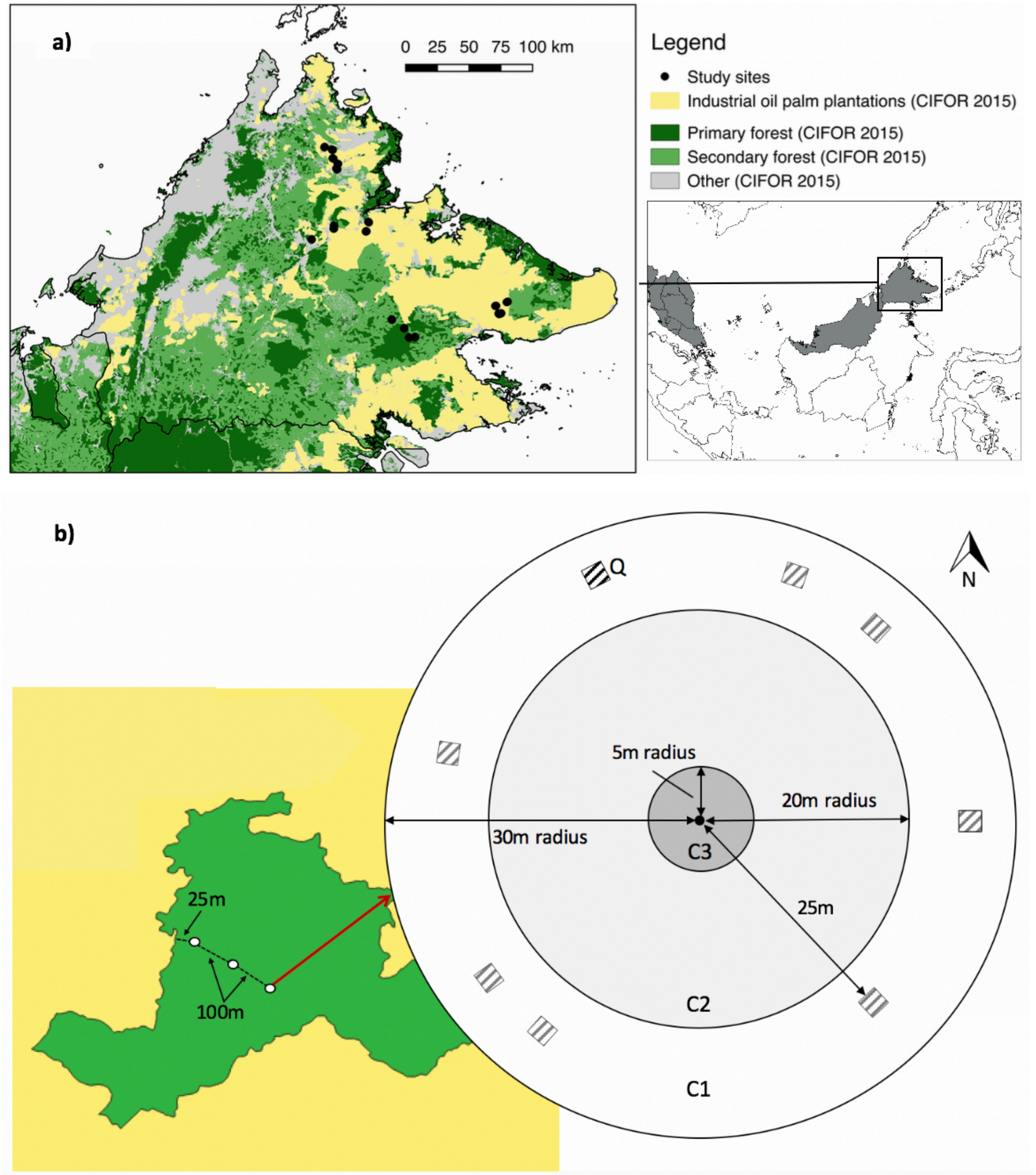


Figure 2.1: a) Map of study locations, forest cover and industrial oil palm plantations within Sabah, on the island of Borneo (inset). b) Schematic diagram of experimental plot design within fragmented and continuous forest sites. Distance of plots from forest edge and between plots are shown along with the radiuses of each plot and subplot, and location of quadrats. Measurements are as follows: C1 = trees ≥25 cm DBH; C2 = trees 10-25 cm DBH; C3 = tree saplings 2-10 cm DBH and Q = tree seedlings (<2 cm DBH) and other ground vegetation (including shrubs, forbs and grasses). See text for full details on floristics surveys. CIFOR forest cover dataset available at Gaveau, Salim and Arjasakusuma (2017).

Plot-level surveys of native and exotic plants

We surveyed plants in two or three circular plots (30 m radius; 0.28 ha) per site, depending on forest extent at each site, with only two in the smallest remnants (<12.5 ha; *n sites*=4). We used a four-level nested approach to sample plants within different size classes (Fig 2.1b). The diameter-at-breast height (DBH) was recorded for all large trees ≥25 cm DBH within the 0.28ha plot (Fig 2.1b; C1), all small trees 10-25 cm DBH within a sub-plot of 20m radius (Fig 2.1b; C2), and all tree saplings 2-10 cm DBH within a sub-plot of 5m radius (Fig 2.1b; C3). Tree seedlings and other ground vegetation (forbs, shrubs, climbers, ferns and graminoids, from herein referred to simply as ground vegetation) were surveyed in eight 1x1 m quadrats (Fig. 2.1b; Q) located 25 m from the plot centre along eight randomly chosen bearings. Within each of these quadrats, we recorded all plants (tree seedlings, shrubs, climbers, forbs, graminoids and ferns) rooted inside the quadrat, and ≤2 cm DBH. We considered an individual as a plant with a distinct root system; for adult trees, tree saplings and tree seedlings individuals were straightforward to distinguish. All ground vegetation, including clonal species (e.g. graminoids and climbers) that can appear as distinct individuals above ground yet connected below ground, was manually removed from the soil to determine number of individuals for each morpho-genus, with unknown individuals taken as vouchers for identification. Adult trees and saplings were identified to genus in the field by an experienced local botanist (co-author AJ). Voucher specimens and photographs of plants in the quadrats were used to identify individuals by a botanist at Danum Valley Field Centre (co-author BBO) and the herbarium at the Forest Research Centre, Sepilok. Exotic species were identified based on lists and guides of Sabah's known exotic plants prepared prior to fieldwork (Chapter 1: Table 1.4; Bakar, 2004; CABI, 2019; Döbert et al., 2017a; ISSG, 2020; Pallewatta et al., 2003) and confirmed by botanists from vouchers. The observed number of exotic species and number of exotic stems per plot were used as measurements of invasion within a plot. All analyses were carried out at plot-level, and at the level of genus, due to the challenges of reliably identifying native plants to species level in diverse tropical forests. Exotic plants were identified to the species level.

Quantifying the native community

We computed two measures of native community alpha diversity; observed genus richness and Faith's phylogenetic diversity (PD; Faith, 1992). Faith's PD is the total sum of phylogenetic branch lengths between species – we chose this measure because it is intended to capture the evolutionary signal in functional traits and as such is associated with functional diversity and can be a valuable predictor of ecosystem-level responses (Flynn et al. 2011). These diversity metrics were calculated per plot (*n*=47) for the total dataset and separately for trees, saplings, seedlings and the ground vegetation. Individuals that could not be identified to genus (*n*=17; <1% of all stems) were removed from the dataset prior to phylogenetic analyses. A phylogeny was created using Phylomatic v.3 (Webb and Donoghue, 2005; available at http://phylodiversity.net/phylomatic/ [accessed 4 May 2018]) and a pruned version of the Angiosperm Phylogeny Groups APGIII maximally resolved supertree of angiosperms (R20120829). Two genera could not be included in the phylogeny, as they were not part of the original supertree, leaving 303 genera for inclusion. The phylogeny was rooted and branch lengths were based on node ages (most recent common ancestor) of Wikstrom, Savolainen and Chase (2001) and estimated using the 'BladJ' algorithm in Phylocom (Webb et al. 2008). From the resulting phylogeny, phylogenetic diversity (PD; the sum of the total branch lengths measured in millions of years; Faith, 1992) was calculated using the ‘picante’ package (Kembel et al. 2010) in R Studio 2.14 (R Core Team 2019).

Characterising fragmentation, disturbance, propagule pressure and soil

We measured forest fragmentation in the surrounding landscape by quantifying the area of forest and non-forest habitat (m^2) within a 2 km radius buffer surrounding each plot. This buffer is a proxy for the dispersal potential of native forest species (i.e. more forest in the buffer would likely indicate a higher presence of mother trees as well as pollinators and animal dispersers). This buffer included forested areas not connected to forest remnants where plots were carried out, as well as connected forest within which the plots were embedded. Quantification of buffer habitat was carried out using drone images provided by plantation managers taken during May-November 2016, after which we assume no or negligible change to forested area within plantations had occurred before fieldwork took place (July-October 2017), due to protections in place. Plots in ‘continuous’ sites were almost entirely forest, but the tract of continuous forest nonetheless contains some small settlements (i.e. field research centre) and so there were small areas of non-forest (<0.5%) in buffer zones around these plots. Within the 2km buffer, the amount of forest edge in the landscape was also calculated using the ‘rgeos’ and ‘raster’ packages (Hijmans and van Etten 2012; Bivand and Rundel 2013), and was equal to the number of raster grid cells (5x5 m) the forest edge passed through. A unitless index of edge density was calculated for each plot as the area of edge cells divided by the area of forest cells. This edge density index was a proxy for the amount of edge habitat in the landscape that would likely be highly degraded based on edge effects. The time since fragmentation was calculated from the year of first planting of oil palm (between 1991 and 2009) as provided by estate managers.

At all sites, we derived two proxy variables for local forest community structure and recovery since disturbance (primarily the result of previous commercial selective logging, except at the two unlogged 'continuous' sites). These two variables were: (i) the number of large stems (>25 cm DBH) belonging to the tree family Dipterocarpaceae, which comprises ~22% of tree species and 61% of biomass in the region (Slik et al. 2003; Saner et al. 2012), and provides a useful comparison between disturbed remnants and unlogged 'continuous' forest; and (ii) average plot-level wood density for trees >10cm DBH was calculated, because wood density can be an indicator of successional status in forest species (Slik et al. 2008; Feeley et al. 2011; Qie et al. 2017). Wood density was calculated for each genus using the 'BIOMASS' package in R (Réjou-Méchain et al. 2017), based on the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009).

As a direct proxy of propagule pressure, exotic plant species richness and abundance were measured along two 100m transects located within the oil palm matrix at each site. The first transect was along the roadside of a major unpaved plantation road (lorries and car traffic) and the second at the oil palm-forest edge, either along an unpaved minor road (mostly motorbike traffic) or oil palm terrace track (pedestrians). Along both 100m transects, the presence/absence of 18 exotic species were recorded in each 1m section and 1m either side of the transect line (i.e. 2m^2 sections). Exotic species richness was computed as the total number of exotic species (out of 18) recorded across these two transects. Exotic species abundance was the total number of 1m transect sections (n=100 per transect) that species were present in, and total abundance of all exotics was computed across the two transects (i.e. out of 18 species x 200 sections = 3600).

To measure soil available phosphorus and pH the topsoil was sampled in each plot (20 cm core; n=5 per plot: one at the plot centre and four 15 m from centre in each of the cardinal directions). After drying (at 50°C) soil samples were thoroughly mixed and sub-sampled for analyses at plot level (n=47). Soil chemistry was analysed at the Forest Research Centre, Sepilok, Sabah. Available phosphorus was extracted using water and measured using the molybdenum-blue method and read at 880nm on a spectrophotometer (following Anderson & Ingram, 1994). Soil pH was measured with a combination glass-calomel electrode in a 1:2.5 ratio of soil to deionised water.

Data analysis

We analysed the relative importance of different factors in invasion using partial least squares path modelling (PLS-PM; see Table 2.1 for a summary of variables and Appendix 2: Text S2.1 for full details on PLS-PM method and variable selection) using the 'plspm' R package (Sanchez and Trinchera 2012; see Waddell and Chapman 2020 for the R code). PLS-PM is a variance-based structural equation modelling method, which fits multiple regressions using measured and latent variables connected in a pathway reflecting ecological theory (Sanchez, 2013). Latent variables are those which cannot be observed or directly measured but are of conceptual interest and are indicated by their associated measured variables, which comprise at least two highly correlated measured variables. Some measured variables were transformed (Table 2.1) to improve normality, in accordance with modelling assumptions (Appendix 2: Text S2.1). All measured variables were centred and scaled (mean of 0 and variance of 1) prior to input into the PLS-PMs to assist with model convergence and interpretation.

Table 2.1: Measured variables included in the structural equation models. Including details of each variable, transformations used to prepare data for analysis and which latent variables are indicated by each measured variable. Abbreviations are: log10 = base 10 logarithm, ln + 1 = natural log + 1 and sqrt = square root. Measured variables which were multiplied by minus one, to ensure the latent variable reflected the processes we labelled them with, are indicated by *-1.

Latent variable	**Measured variable**	**Details**	**Transformation**
Fragmentation	Area of non-forest	m^2 within 2km buffer	untransformed
	Edge density	the amount of forest edge/forest area within 2km buffer	untransformed
	Age	years since fragmentation	ln +1
Disturbance	Number of large dipterocarps	number of large stems (>25 cm DBH) per plot	(sqrt)*-1
	Wood density	average wood density of adult trees (>10 cm DBH) per plot	(log10)*-1
Soil characteristics	Soil pH	average pH of five 20 cm soil cores	log10
	Available phosphorus (P)	average available P of five 20 cm soil cores	log10
Propagule pressure	Exotic richness outside	number of exotic species along two transects, in oil palm matrix	untransformed
	Exotic abundance outside	abundance of exotic species along two transects, in oil palm matrix	untransformed
Native community	Native genera richness	observed genera count per plot	untransformed
	Native abundance	observed number of individuals per plot	untransformed
	Native phylogenetic diversity	Faith's phylogenetic diversity per plot	untransformed
Invasion	Exotic genera richness	number of exotic genera per plot	ln +1
	Exotic abundance	number of exotic stems per plot	ln +1

All models were developed starting from the full specification in Fig. 2.2 and removing non-significant terms in a stepwise manner until all retained links were statistically significant ($P < 0.05$; Sanchez, 2013). Two-sided P-values for standardised path coefficients (i.e. the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable) were estimated by 10,000 bootstrap estimations. In ‘plspm’, site identity cannot be included as a random effect, so site effects were accommodated by taking bootstrap samples at the level of site, i.e. bootstrap samples were made by randomly selecting sites and all their constituent plots, with replacement.

We first fitted the model on the full dataset, i.e. where native community diversity comprised recorded native plants of all size classes. We then fitted separate PLS-PMs for native adult trees, tree saplings, tree seedlings and ground vegetation to test whether different subsets of the native community were more strongly correlated with invasion. As we do not know the directionality of the relationship between native community diversity and invasion, we tested all models in both directions for this relationship. In all cases, models were assessed for validity and reliability in both the measurement and structural model (see Appendix 2: Text 2.1 for details on PLS-PM model evaluation).

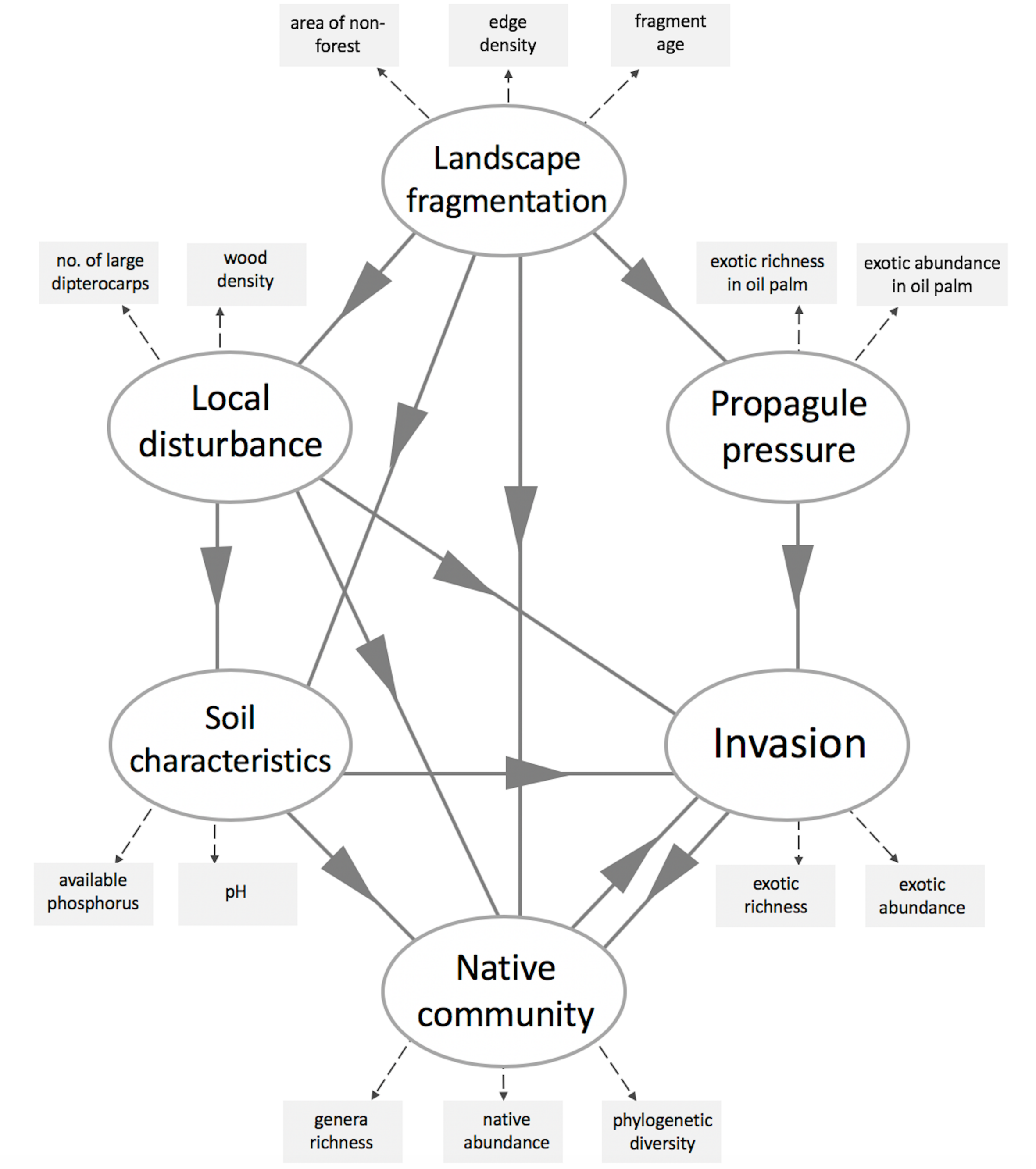


Figure 2.2: Hypothetical partial least squares path model showing the relationships between fragmentation, disturbance, propagule pressure, soil characteristics and native plant diversity on invasion within of lowland tropical forests. Latent variables are shown in ovals and the measured variables in rectangles. Measurement model is represented by the dashed lines and the structural model is represented by the solid lines. Models were tested in both directions for the relationship between native community and invasion indicated by the double arrows. Full details on these variables are in Table 2.1 and within the text.

2.4 Results

In the 47 plots we surveyed a total of 6,999 individuals (Tables S2.2) from 329 genera, including eight exotic species, ranging from 0-7 species (median = 1) and 0-51% of stems (median = 1.4%) per plot. Exotic species included shrubs, forbs, graminoids and climbers (there were no exotic trees). The most abundant exotic was a common tropical exotic shrub, *Clidemia hirta* (Melastomataceae), which made up 73.8% of all exotic stems (Table S2.3). The second most common exotic was also a shrub, *Chromolaena odorata* (11% of exotic stems), and the other six species were either forbs, climbers or a graminoid (1-4% of exotic stems).

Overall, native richness ranged from 18-69 genera/plot (median 45) with plots in the 13 oil palm remnant sites having lower richness (median of 42 genera/plot; range 18-69) compared with continuous sites (median of 46.5 genera/plot; range 39-57). In continuous sites the most common native genus amongst adult trees was Shorea (Dipterocarpaceae), for saplings Mallotus (Euphorbiaceae), for seedlings Shorea (Dipterocarpaceae) and for ground vegetation Selaginella (Selaginellaceae). By contrast in the oil palm remnant sites, the most common native genera were Ficus (Moraceae), Hopea (Dipterocarpaceae), Glochidion (Phyllanthaceae) and Selaginella (Selaginellaceae) for the same size classes, respectively.

The final PLS-PMs (Figs 2.3, 2.4, S2.1 and S2.2) explained 34% of the variation in invasion, 74% of variation in propagule pressure, between 26-53% of native community diversity and 55% of soil characteristics (all of which are latent variables informed by 2-3 measured variables). There was strong evidence in support of our final PLS-PMs in terms of the reliability and validity of the measurement model and an adequate fit of the structural model (see Appendix 2: Text S2.1, Tables S2.4-2.6 for model evaluation).

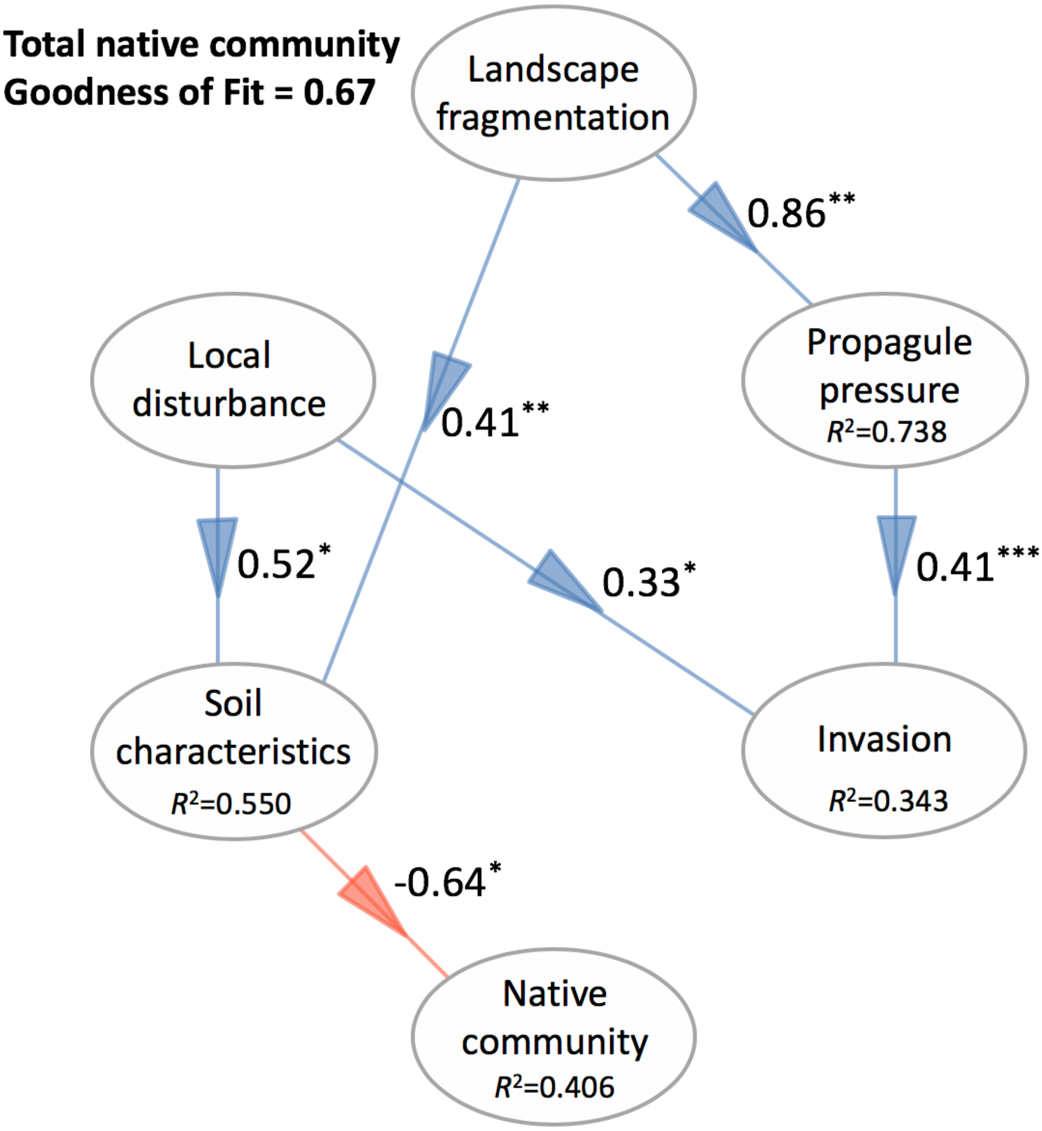


Figure 2.3: Fitted partial least squares path model showing the relationships between fragmentation, disturbance, propagule pressure, soil characteristics and native plant diversity on invasion within of lowland tropical forests. The model was simplified from the specification in Fig. 2.2 by removing non-significant effects. The goodness-of-fit index for the model and R^2 values for the endogenous latent variables are displayed. Standardised path coefficients and P-values were estimated by 10,000 bootstrap estimations. Standardised path coefficients are shown next to arrows, red indicates a negative correlation and blue a positive correlation. They denote the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable. P-values: * = P<0.05; ** = P<0.01 and *** = P<0.001.

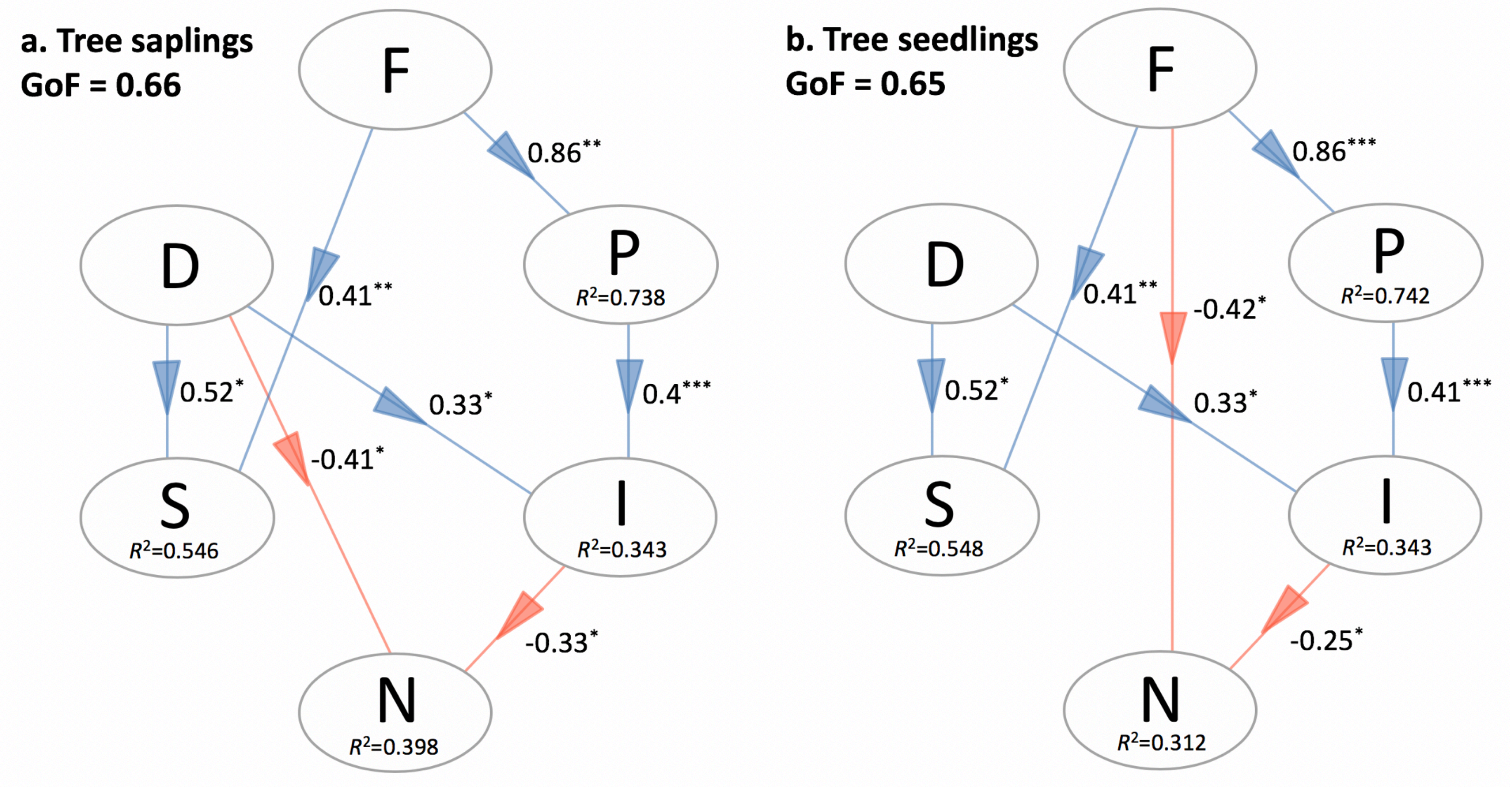


Figure 2.4: Partial least squares path model showing the relationships between fragmentation, disturbance, propagule pressure, soil characteristics and invasion on a) native tree sapling and b) native seedling diversity. The model was simplified from the specification in Fig. 2.2 by removing non-significant effects. The goodness-of-fit index (GoF) for each model and R^2 values for the endogenous latent variables are displayed. Standardised path coefficients and P-values were estimated by 10,000 bootstrap estimations. Standardised path coefficients are shown next to arrows, red indicates a negative correlation and blue a positive correlation. They denote the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable. P-values based on 10,000 bootstrap estimations: * = P<0.05; ** = P<0.01; *** = P<0.001. Abbreviations: F = Fragmentation, D = Disturbance, P = Propagule pressure, S = Soil characteristics, N = Native community and I = Invasion.

Drivers of invasion

After removal of non-significant terms, the best model with the full native community (i.e. combining data for native adult trees, saplings, seedlings and ground vegetation; Fig. 2.3), found a strong direct positive correlation between propagule pressure and invasion ($P<0.001$), with a strong indirect positive correlation of fragmentation ($P<0.01$) on invasion via increased propagule pressure. Forest disturbance also had a direct positive correlation with invasion ($P<0.05$), but there was no significant effect of total native community diversity or soil characteristics ($P>0.05$) on invasion.

Models accounting separately for native adult trees, saplings, seedlings and ground vegetation communities did not support a role of native community diversity on invasion (native ⟶ invasion; Fig. S2.1 and Table S2.7). However, when the direction of the biotic relationship in the model was reversed, i.e. invasion ⟶ native, we found significant negative effects of invasion on native tree sapling and tree seedling communities (Fig. 2.4; tree saplings: standardised path coefficients = -0.348, $P = 0.012$, $R^2 = 0.4$; tree seedlings: standardised path coefficients = -0.28, $P<0.01$, $R^2 = 0.299$). In these models, there was no significant effect of invasion on the total native community, adult trees or ground vegetation (Fig. S2.2).

Responses of the native community to land-use change

The exotic and native communities (both total and subsets) responded differently to disturbance and fragmentation (Figs 2.3, 2.4, S2.1 and S2.2). The total native community was indirectly correlated negatively with both fragmentation and disturbance, via their positive influence on soil characteristics (i.e. higher native diversity and abundance when there was low soil pH and available soil phosphorus; Fig. 2.3 and Table S2.7). Instead, invasion was positively correlated with these land-use change variables, as we hypothesised. In the native subsets (Figs 2.4, S2.1 and S2.2, and Table S2.7), adult tree and tree sapling communities were directly negatively correlated with disturbance, tree seedling community was directly negatively correlated with fragmentation, and the ground vegetation community (forbs, shrubs, climbers, ferns and graminoids) was indirectly negatively correlated with both fragmentation and disturbance, via interactions with soil characteristics. Hence, all the native community subsets (adult trees, tree saplings, tree seedlings and ground vegetation) were negatively associated with disturbance and fragmentation.

2.5 Discussion

Our study found that a higher degree of landscape fragmentation leads to higher invasion of exotic plant species in forest remnants, due to a greater source population of exotic plants found in the anthropogenic (i.e. plantation) areas of these landscapes. In contrast, we found little effect of soil characteristics and the native community on exotic invasion, but a negative influence of exotic invasion on the native tree sapling and seedling communities.

Fragmentation drives propagule pressure to increase invasion

Landscape fragmentation (i.e. lower forest cover, more edge habitat and a longer history of forest clearance) promotes higher invasion of the oil palm matrix (planted areas and roads), which increases the likelihood of remnant forests being invaded by exotics due to increased propagule pressure. We expected that greater numbers of exotic species would have established in the oil palm matrix because of enhanced transport of propagules (Ansong and Pickering 2013) and the higher availability of resources brought about through disturbance, which would promote colonisation by exotic species (Fee et al., 2017). Small, isolated forest remnants that are completely surrounded by oil palm, or other agricultural areas (c.f. those contiguous with larger tracts of forest) may therefore have more exotic propagules arriving from all directions, facilitating the invasion process. Although exotic invasions have not yet been thoroughly examined in fragmented tropical rainforests, similar patterns to those in this study have been reported in many natural habitats within fragmented landscapes, with invasion highest in small, isolated remnants (Vilà and Ibáñez 2011). We conclude that propagule pressure, driven by fragmentation, is the main factor influencing invasion of exotics in our study (based on total effect sizes in Table S2.7), however, invasion is generally low unless there is high local disturbance of the forest.

Increased invasion in disturbed forests

We found that invasion is more likely in forests with high levels of previous disturbance, represented by those with fewer large dipterocarp trees and lower average wood density, indicative of forest regressing to an early successional state. The strong positive relationship between disturbance and invasion is likely to indicate increased resource availability (e.g. light and space) associated with commercial selective logging, providing opportunities for invading exotics to colonize. The correlation between invasion and increased resource availability following disturbance is found across many habitats and disturbance regimes (natural and anthropogenic), and underpins several invasion hypotheses (Davis et al. 2000a; Hood and Naiman 2000; Colautti et al. 2006). In tropical forests, increased light levels following selective logging can also lead to increases in native pioneer species and native weeds (Catford et al. 2009; Lockwood et al. 2013) and these environmental factors are likely to be instrumental in driving the invasion of exotic species observed in our data. Therefore, fragmentation and disturbance may operate synergistically; land-use change may bring exotic species propagules into the oil palm matrix, but these exotic species will only establish in the remnant forests if local conditions are suitable and disturbance promotes these conditions.

Little evidence for biotic interactions

We found no signal of biotic resistance to invasion from the native community in our results when the models specified an effect of the native community on invasion, which is in line with wider meta-analysis of terrestrial plant invasions (Jeschke et al. 2012). However, when the models specified an effect of invasion on the native community, we found significant negative correlations between invasion and native tree sapling and seedling communities. This may indicate either the impact of a dominant exotic inhibiting native recruitment or be driven by indirect effects of land-use change on these cohorts of native trees (i.e. indirect effect of the disturbance latent variable on saplings via invasion and similarly fragmentation on seedlings).

These findings may be explained by young native trees and exotic shrubs (~85% of exotic stems) having higher niche overlap than other components of the native community (i.e. adult trees and ground vegetation) because they have a similar woody habit and occupy the same lower understorey environment. Exotic species may have disrupted the recruitment of current tree saplings and seedlings, which would have been young saplings or seeds when exotic species first invaded these forests post-fragmentation (8 – 26 years before sampling), by outcompeting them for resources. The dominant exotic recorded in this study, *Clidemia hirta* (74% of exotic individuals), exhibits functional traits associated with high competitive ability (e.g. high seed number, fast growth rate, early age of reproduction, asexual reproduction, fruits produced year round and very large seed bank), allowing for rapid population growth (Rejmánek and Richardson 1996; Singhakumara et al. 2000; Daehler 2003), making it a highly invasive species and a pest throughout most of its introduced range (Wester and Wood 1977; Gerlach 1993). Similar patterns have been observed in temperate forests with dominant invasive species disrupting native seedling growth (Gorchov and Trisel 2003; Stinson et al. 2006), and in selectively logged Malaysian tropical rainforests, Döbert et al. (2017) found fewer Dipterocarpaceae seedlings where exotic biomass was higher. Therefore, high niche overlap may lead to strong competition between young trees and exotic shrubs for resources such as light. In addition, *C. hirta* and *Chromolaena odorata* (the second most common exotic invasive species recorded) both have allelopathic effects, which have been shown to significantly reduce native seed germination and growth during laboratory studies (Hu and Zhang 2013; Ismaini 2015).

Our results are correlational and do not track changes in the native community over time, so inferring biotic interactions is problematic. Nevertheless, our results indicate that invasion of exotic plants is more closely associated with the lack of young native trees than other components of the native plant community (e.g. ground vegetation and adult trees) in these forests, and patterns are likely driven by *Clidemia hirta*. However, in order to determine the mechanisms driving observed biotic relationships in our data, as well as the true directionality of observed relationships, long-term manipulative field experiments would be required.

Native and exotic plants respond differently to disturbance and fragmentation

Our results suggest that different components of human land-use change correlate, at varying strengths, with different subsets of the native community (adult trees, tree saplings, tree seedlings and ground vegetation). The strong direct correlation between disturbance and native adult tree diversity could potentially be driven by the disturbance variables included in the models being derived from the adult tree community (i.e. number of large dipterocarp trees remaining and mean adult tree wood density per plot). However, as this relationship is also found with sapling diversity, a true relationship between habitat disturbance and both tree communities seems plausible. This may be due to logging decreasing diversity by the physical removal of specific species via timber extraction (i.e. dipterocarps), affecting both timber trees (adult trees) and collateral damage to other trees surrounding the extracted tree, both over- and understorey (Malhi et al. 2014). In addition, altered abiotic conditions brought about by logging practices (e.g. increased light, temperature, soil erosion) result in tree mortality and reduced fruiting in adult trees which in turn reduce recruitment (Gibbs and Salmon 2015), decreasing the richness of old-growth forest species in fragments.

The association between fragmentation and tree seedling diversity (and to a lesser extent the marginally significant correlation with tree saplings) in our data means there are fewer seedlings in areas with less forest in the landscape, more edge habitat and in older plantations. This could reflect an extinction debt driven by pollination and dispersal limitations in highly fragmented landscapes (Ghazoul and McLeish 2001), which would have clear implications for the future regeneration of these forests (Haddad et al. 2015). Stride et al (2018) found similar results in other fragmented forest sites in our study region, with seedling richness 30% lower in forest remnants than in undisturbed old-growth forest.

The weak negative correlation between ground vegetation community composition and both fragmentation and disturbance (SI Table S7), may be due to this component of the plant community also containing light-loving native weedy species (e.g. grasses and forest edge shrubs), which act much the same as exotics in that they proliferate with disturbance (Catford et al. 2009; Lockwood et al. 2013). These native weeds could therefore dilute the relationship between native ground vegetation typical of old-growth forest and the effects of land-use change in our models. Changes in the native plant community associated with disturbance, as well as the invasion of exotic species, are likely to impact important ecosystem services in these forests, such as biodiversity, functional stability and carbon storage.

2.6 Conclusions and conservation implications

Exotic species are an understudied component of fragmented tropical landscapes, despite being an emerging threat to the natural regeneration of native tree communities within remnant forests. Indeed, three of the eight exotic species we found (*Clidemia hirta*, *Chromolaena odorata* and *Mikania micrantha*) are considered amongst the world's worst 100 invasive species due to their ability to modify the ecosystems they invade (Lowe et al. 2000), with *C. hirta* in particular, considered a pest across much of its introduced range (Wester and Wood 1977; Gerlach 1993; Peters 2001a; Teo et al. 2003). Our study shows for the first time that fragmentation and local disturbance increase the invasion of exotic species in rainforest remnants within anthropogenic landscapes. Therefore, we suggest that better management to control exotic populations within oil palm plantations (e.g. along roadsides and in oil palm planted areas), along with active regeneration of forest remnants to improve overall forest quality and canopy cover is important to reduce exotic invasions. In a natural resource management context, the way in which invasive species move through a landscape should be considered in the design of multi-functional landscapes, to ensure that these species do not undermine the conservation of forest remnants. This would involve consideration of maintaining large interior and closed canopy forests and reducing edge effects and propagule transport within the landscape. Vulnerable recovering forests in particular should be protected.

Our results highlight the consequences of fragmentation and logging on the invasion of remnant forests but also the impact on the native plant community. These findings are of critical importance given that around 80% of tropical forests are currently fragmented and/or anthropogenically modified (Potapov et al. 2017). Fragmentation is predicted to increase, with increases in the number of isolated forest remnants as well as decreases in their average size (Taubert et al. 2018) as a result of cyclical deforestation processes (i.e. deforestation and degradation making new areas of forest more accessible and susceptible to further degradation; Nowosad and Stepinski 2019). Therefore, invasion of forest remnants is likely to increase in future due to continuing deforestation, leading to changes in plant community composition and altered patterns of native regeneration, thereby potentially impacting local and regional biodiversity. Given, that maintaining regeneration of remnant forests is necessary for the sustainability of human dominated tropical landscapes, including RSPO-certified oil palm plantations (Senior et al. 2015), it is vital that the impacts of invading exotic species within these forests are properly evaluated and included in future studies.

2.7 Author contributions and acknowledgements

EHW, LFB, MH, JKH and DSC conceived the ideas. EHW, LFB, MH, SF, JT, JKH, CB, YKL, ABS, AJ and DSC designed methodology; EHW, SF, ABS and AJ collected the data; BBO and AJ led plant identification; EHW and DSC analysed the data; EHW led the writing of

the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data collected for this study are available to download from the Environmental Information Data Centre (Waddell et al. 2020d).

Chapter 3

Mikania micrantha growing on oil palm tree

Trait filtering during exotic plant invasion of tropical rainforest remnants along a disturbance gradient

3.1 Abstract

Human-modified tropical landscapes are often invaded by exotic plant species, but relatively few species are able to colonise remnant areas of rainforest embedded within such landscapes. The functional traits of successful invaders of natural versus anthropogenic habitats are poorly known, especially in tropical regions, and identifying such traits provides insight into the mechanisms that drive invasion. Here, we examine the invasion of tropical rainforest remnants along a disturbance gradient, within a human-modified agricultural landscape, and determine whether exotic species that invade these forests are selected according to particular traits. We surveyed the occurrence of 18 exotic species along 100m transects in four habitats - oil palm road, forest-oil palm edges, and disturbed and intact forest within rainforest remnants - at 21 sites across Sabah, Malaysian Borneo. We collated data on four functional traits relevant to the barriers plants encounter when colonising new environments (e.g. dispersal and persistence) and tested whether trait filtering occurs during invasion of rainforest remnants. Exotic species richness declined significantly from oil palm (mean 9.2 species per transect) to forest edge (7.8 species) to inside rainforest remnants (3.1 species in disturbed forest), and only one species, *Clidemia hirta*, invaded intact forest. Exotic communities within rainforest remnants had long-distance (vertebrate) dispersal, were woodier and had taller maximum heights, compared to those found in oil palm. For each trait, the community-weighted mean for the forest edge community was intermediate between oil palm and disturbed forest, suggesting trait filtering during the invasion of rainforest remnants. Our study provides strong evidence that trait filtering occurs during invasion from human-modified agricultural habitats into previously disturbed forests via the forest edge. Successful invasion of rainforest remnants requires relatively long-distance dispersal, in particular by vertebrates, as well as traits that are more similar to those of native forest species (i.e. tall and woody), making these exotic species more able to compete and persist in that environment. Our results show that disturbed tropical rainforests with open canopies are susceptible to invasion and highlight the traits of exotic species which can invade rainforest habitats, and which may pose a threat to regenerating tropical rainforests.

Keywords: *agricultural landscapes*, *Clidemia hirta, community composition, competition, functional traits, non-native species, oil palm, tropical rainforests*

3.2 Introduction

Understanding the processes driving plant invasion within different ecosystems has been a long-standing goal of ecological science (Elton 1958; Lodge 1993). As human population and land-use change increases, it is vital to understand these processes in human-modified landscapes. Successful invasion of any habitat requires species to overcome sequential ecological barriers separating different stages of invasion: introduction, establishment, spread and impact (Levine et al. 2004). Life-history and functional traits of invading species are influential at each stage of invasion and play an important role in key invasion hypotheses (Catford, Jansson, & Nilsson, 2009). As such, identifying the traits of successful invaders provides insight into which mechanisms are driving invasion and can facilitate predictions of whether an invading species will be successful in a particular habitat.

There is no set of traits universal to all invading species and across all invaded habitats, as ecological barriers faced by exotic species vary between ecosystems (Pyšek and Richardson 2008). However, exotic species will readily spread into new areas if they have traits associated with efficient dispersal (e.g. many seeds produced regularly, small seed mass, long-distance dispersal; Colautti, Grigorovich, & MacIsaac, 2006; Nathan et al., 2008; Pyšek & Richardson, 2006; Rejmánek & Richardson, 1996). Once introduced, invading species will only establish persisting populations if they are adapted to the environmental conditions of the invaded habitat and can compete successfully with the native species community, and those that are not adapted will be filtered out (Weiher and Keddy, 1995; Procheş *et al.*, 2008). The traits which facilitate invasion in one habitat may not confer the same outcome in another due to differences in environmental conditions (Sher and Hyatt 1999). In disturbed habitats, the increase in resource availability promotes invasion (Davis et al. 2000b; Blumenthal 2006) as the majority of invasive species are light-loving ruderal species (i.e. r-strategists; Pyšek & Richardson, 2008; Rejmánek & Richardson, 1996). Therefore, many exotic species are unlikely to invade undisturbed environments where resource availability (i.e. light and space) is low, including closed-canopy forest ecosystems. In both temperate and tropical forests, only those exotic species that have some degree of shade tolerance and traits that allow them to compete with the native flora will establish, which could for example include high relative growth rate, large above-ground biomass, high maximum height and high photosynthetic rates (Weiher et al. 1999; Koike 2001; Pyšek and Richardson 2008; van Kleunen et al. 2010; Bufford et al. 2016). Thus, exotic species that are invasive in highly disturbed anthropogenic habitats may not necessarily be able to colonise adjacent less-disturbed, closed-canopy natural habitats.

The spread of exotic species into natural tropical forest habitats from invaded anthropogenic areas is not frequently considered in the invasion ecology literature as tropical forests have been considered to be robust to plant invasions thus far (Fine

2002). However, deforestation across the tropics, due to recent expansion of large-scale agricultural practices, has resulted in exotic plant species being frequently introduced by humans via newly-created transport networks (Levine and D'Antonio 2003; Hulme 2009; Seebens et al. 2015). These heavily invaded agricultural areas may act as sources of exotic propagules that disperse into areas of native forest retained within these landscapes as conservation set-asides (Waddell et al., 2020a). However, traits that result in successful invasion of open agricultural areas are likely to differ from those that result in successful invasion of natural forest habitats. In this study we investigate, for the first time, the spread of exotic plants along a gradient of disturbance from highly invaded, anthropogenic habitats (oil palm plantations) into native tropical rainforest remnants that are recovering from disturbance, and test whether there is selection for particular traits across the disturbance gradient.

The abiotic conditions and biotic communities of native rainforest remnants are very different to agricultural areas (Laurance et al. 2002), and so the anthropogenic habitat edge is likely to act as a strong ecological barrier to invasion. However, within tropical forest remnants themselves, the forest structure and community can be highly heterogeneous due to a combination of edge effects and intensity of previous disturbance (e.g. logging; Broadbent et al., 2008; Laurance et al., 2011; Lôbo, Leão, Melo, Santos, & Tabarelli, 2011). These disturbances result in physical gaps in the canopy, which increase light levels and thus facilitate the establishment of introduced exotic propagules (Döbert, Webber, Sugau, Dickinson, & Didham, 2017a; Peters, 2001; Teo, Tan, Corlett, Wong, & Lum, 2003; Waddell et al., 2020a). Many exotic species are not well adapted to closed-canopy, intact forests, however, and habitat filtering may mean that only a few shade-tolerant species present in the landscape can establish and persist in these environments (Koike 2001; Martin and Marks 2006; Dawson et al. 2009b).

In many parts of South-East Asia, land-use change has resulted in a highly fragmented landscape with disturbed rainforest remnants surrounded by predominately oil palm plantations, particularly in Malaysia and Indonesia (Gaveau et al., 2014). These landscapes provide a useful system to study exotic species that have established populations in the oil palm matrix and examine how they disperse and colonise within remnant forests (i.e. conservation set-asides). The understorey of oil palm plantations are known to be dominated by exotic plant species (Fee et al. 2017; Rembold et al. 2017), therefore the threat of invasion into areas of remaining forest is high due to this constant source of propagules. It is important to determine the vulnerability of rainforest remnants to invasion because they have been shown to be crucial for maintaining local and regional biodiversity (Hill et al. 2011), ecosystem services (Ricketts 2004; Koh 2008) and carbon storage (Fleiss et al. 2020) within sustainable agricultural tropical landscapes. Therefore, disentangling the mechanisms that drive invasion in disturbed forests will help in the management of human-modified tropical landscapes, as well as advance our knowledge of plant invasion processes within tropical forests.

In order to investigate the processes driving plant invasion of tropical rainforest remnants, we compare species and trait compositions of exotic species found along a gradient of disturbance within a human-modified agricultural landscape in Sabah, Malaysian Borneo. Disturbance and light levels decrease along this gradient from oil-palm agricultural areas to closed canopy, intact forest, and so we expect exotic species richness and occurrence to decrease accordingly. We then specifically examine functional traits that address the barriers exotic plants encountered during the colonisation of new environments (i.e. invasion), including dispersal (dispersal syndrome and seed mass) and persistence (potential competitive ability: maximum plant height, longevity: stem density and seed production: seed mass; Weiher et al., 1999). Based on previous studies, we expect the exotic community inside the forest to have traits that indicate efficient dispersal and allow propagules to readily spread from oil palm source populations into rainforest remnants (i.e. long-distance dispersal and small, light seeds), as well as traits that promote the establishment of persisting populations (higher maximum height, woody habit) and populations may either benefit from efficient dispersal of smaller seeds or resource provision of larger seeds.

3.3 Methods

Study sites and transect surveys

Exotic plant communities were studied over two field seasons (July – October 2017 and February – April 2019) in six large-scale oil palm plantations in Sabah, Malaysian Borneo, which had remaining areas of native forest embedded within them (Fig. 3.1). These forest conservation set-asides (hereafter termed 'rainforest remnants') had usually been left unplanted because they were unsuitable for oil palm cultivation (e.g. too steep or rocky) and had been commercially logged (with varying intensity, e.g. due to differences in topography), prior to plantation development, probably between ~1991-2009 (Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011). Most of these rainforest remnants are currently managed retrospectively as sites of 'High Conservation Value' (HCV; Senior *et al.*, 2015), and therefore should not have experienced significant ongoing direct human disturbance as indicated by the certification process for sustainability developed in 2005 by the Roundtable on Sustainable Palm Oil (RSPO, 2018). Across the six plantations, exotic species were surveyed at 21 sites, in areas of oil palm abutting rainforest remnants. The majority of these rainforest remnants (*n*=15 sites) were fully surrounded by oil palm, with six sites connected to a larger area of forest reserve outside the plantation boundary. Even though these sites were connected to other forest patches, these six sites were predominately surrounded by oil palm and had experienced the same disturbance histories as the other sites (see Table S3.1 for individual site details). Sites were at least 1 km apart to avoid spatial autocorrelation. At each study site, 100m transects were surveyed in up to four different habitats (Fig. 3.1c), to capture variation in exotic species occurrences dispersing from oil palm planted areas to forest-oil palm edges and then into disturbed logged forest (hereafter 'disturbed forest') and intact logged forest (hereafter 'intact forest'). The four habitats differed in terms of light levels and past and current disturbance (Table S3.2 and Fig. S3.1). Oil palm transects (*n*=21) were located along the roadsides of major unpaved plantation roads. Forest-oil palm edge transects (*n*=21) were either along small unpaved roads (motorbike traffic only) or along oil palm terraces abutting forest. Disturbed forest transects (*n*=20) were located on average 53 m from the closest forest-oil palm edge, along old logging skid trails, abandoned oil palm terraces or unpaved roads (no longer in use). They were in highly degraded forest habitat that varied in terms of canopy openness and understorey ground cover. Intact forest transects (*n*=16) were on average 90 m from the closest edge and were considered to be structurally intact (i.e. closed-canopy forest), which was usually on steep slopes with a generally sparse ground cover. Due to previous disturbance (i.e. logging and clearing) and most remnants being small (<100 ha; Table S3.1) the majority of these forests are likely to have extensive edge effects that extend throughout the rainforest remnant (Lucey et al., 2017).

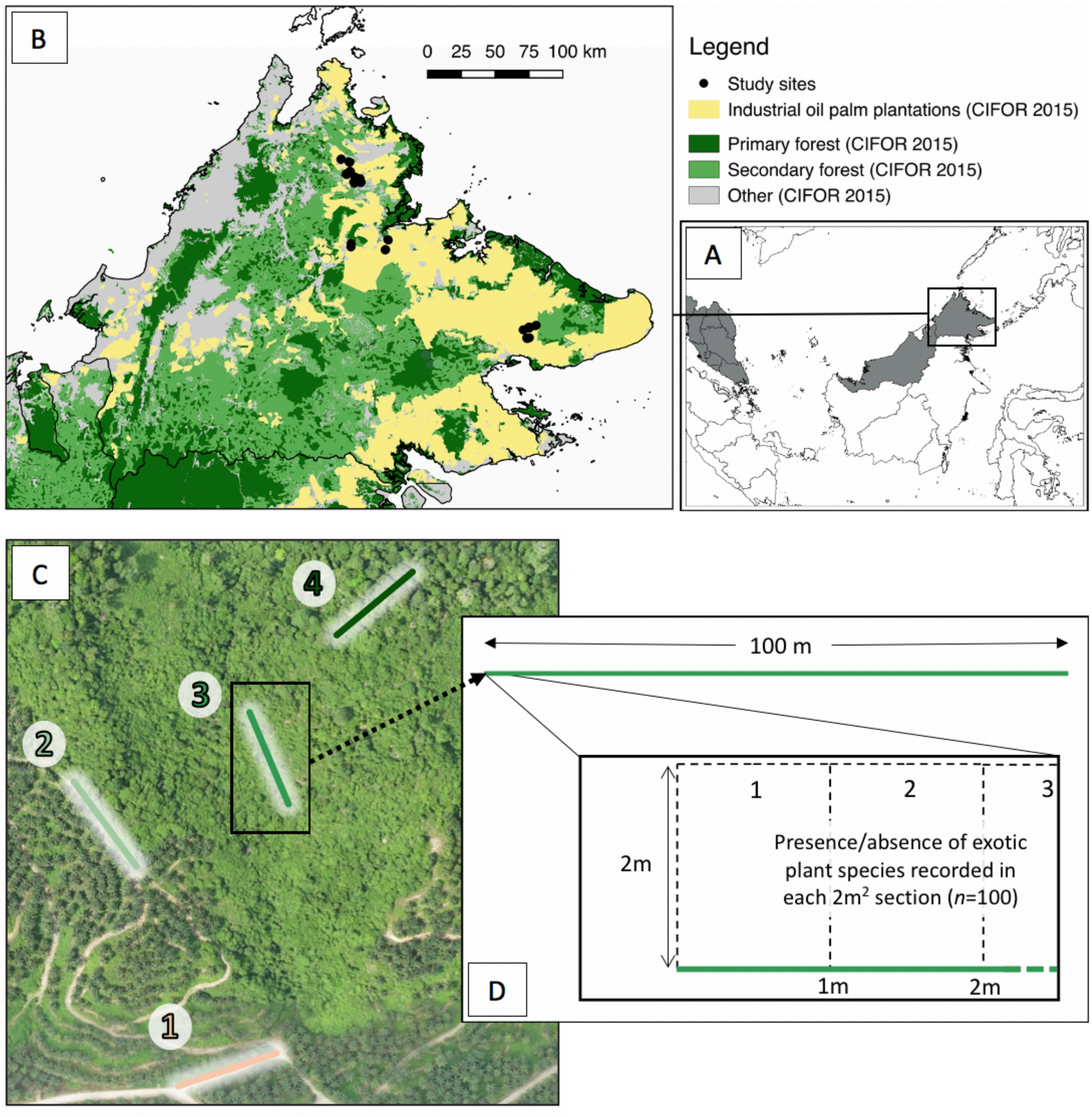

Figure 3.1: Study location on Borneo (A), within the Malaysian state of Sabah (B), showing the 21 study site locations (black circles), and areas of primary and logged forest and industrial oil palm plantations (Gaveau, Salim, & Arjasakusuma, 2017). (C) Drone image of site F2, showing transect locations (i.e. four habitats). 1 = oil palm, 2 = forest-oil palm edge, 3 = disturbed forest, and 4 = intact forest. Oil palm = major plantation roadside; Forest-oil palm edge = minor plantation road or terrace where oil palm meets forest; Disturbed forest = skid trail, old road or abandoned terrace; Intact forest = closed canopy forest. (D) Transect sampling. Transects were 100m x 2m with presence/ absence recorded for each exotic species (n=18) in each 1 m ($2m^2$) section along the transect.

Access inside the forest was not possible at one of the 21 sites because it was too steep, and there was no forest site that was deemed to be 'intact' in five very small (<12.5 ha) and highly disturbed rainforest remnants. In oil palm planted areas, active weed management, including herbicide spraying and vegetation cutting, occurred predominantly around the base of oil palm trees. We do not expect these localised management practices to lead to major changes in species composition within the surveyed parts of the oil palm habitat, because our oil palm transects were carried out away from the bases of oil palm trees, in areas which were not sprayed or cleared recently.

Along each 100m transect, the presence/absence of exotic plant species was recorded within every 1m section and 1m either side of the transect (i.e. 2m^2 sections; Fig. 3.1d). The presence of exotic species in each 1 m section of the transect was our measure of occurrence (i.e. range = 0-100 per species per transect). Pilot transects during the first field season were used to identify exotic species known to be present in Sabah, based on species list produced from literature and online resources (Chapter 1: Table 1.4; Bakar, 2004; CABI, 2019; Döbert et al., 2017a; ISSG, 2020; Pallewatta et al., 2003), and any additional suspected exotic species encountered in the field (over both field seasons), were identified and their exotic status in Sabah confirmed with the help of local botanists (Danum Valley Research Centre and Sandakan Herbarium). We did not include a leguminous cover crop (*Calopogonium mucunoides*) that was intentionally planted in the oil palm areas, exotic graminoids due to identification challenges, nor any morphospecies that could not be identified to species. This left 18 exotic species, which we believe to be representative of the exotic plant community found within these landscapes.

In order to determine variation in the canopy structure and light levels between and within the four habitats, canopy cover was recorded every 20 m (five points in total per transect, with the mean of four measurements facing each cardinal direction per point) using a concave spherical densiometer (www.forestry-suppliers.com). To examine the complexity of the forest structure, the number of large native trees (> 20cm diameter at breast height (DBH)) along the transect was recorded every 10m, five metres either side of the transect and not including oil palm trees. Mean canopy cover (%) and total number of large native trees were used as measures of forest openness and canopy complexity at the transect level.

Functional traits of exotic community

Trait data for the 18 study species were obtained from online databases (predominately species datasheets in the Invasive Species Compendium (CABI 2019) and Kew Seed Database (Royal Botanic Gardens Kew 2019) but see Table S3.3 for additional sources) for traits that address potential barriers to colonisation (Table 3.1). Functional traits were selected for inclusion in the analysis if there were data on at least 75% of the study species (Table 3.1). This resulted in four species-level traits for analysis: plant maximum height (indication of potential competitive ability), plant woodiness (proxy for stem density), seed dry mass and dispersal syndrome (including both primary and secondary dispersal modes; see Table S3.3 for species-level trait expressions). Average functional trait values per species were calculated for seed dry mass when multiple data points were available. Dispersal syndromes were classified into a binary code for adaptation to long-distance (i.e. wind, water, and vertebrate) or short-distance (e.g. gravity/unspecified, vegetative propagation, ballistic or invertebrate) dispersal. Additionally, binary traits for presence/absence of vertebrate dispersal and wind dispersal were retained for analysis, to determine which long-distance dispersal mode was the most prevalent in the exotic forest community (we excluded the consideration of water dispersal due to lack of rivers in our study sites). Note that these binary dispersal traits are non-exclusive, e.g. *Chromolaena odorata* is dispersed by both wind and vertebrates.

Table 3.1: List of plant functional traits linked to invasion success of rainforest remnants. Data were compiled predominately from each species datasheet in the Invasive species compendium by the Centre for Agriculture and Bioscience International (CABI; www.cabi.org/isc/) and Kew Seed Database (data.kew.org/sid/), see Table S1 for additional sources and individual species trait expressions. The number of species for which data are available (out of the 18 species surveyed) are in parentheses. '*Predicted relationship*' refers to the expected filtering during invasion from oil palm to forest edge and into disturbed forest and then intact forest, based on previous studies: (Rejmánek and Richardson 1996; Weiher et al. 1999; Pyšek and Richardson 2008; van Kleunen et al. 2010; Dawson et al. 2011).

Trait	**Data type**	**Mechanism**	**Predicted relationship**
Plant woodiness/ stem density (n=18)	Binary (woody or non-woody)	Longevity	Increased woodiness
Plant maximum height (n=18)	Continuous	Potential competitive ability (e.g. for light)	Increased height
Seed dry mass (n=16)	Continuous	Reproductive fitness (i.e. seed production and dispersal distance) and establishment success	Smaller seed mass (dispersal), or large (establishment)
Dispersal syndrome (n=18)			
Long-distance	Binary (long-distance or short-distance)	Reproductive fitness	Increase in long distance dispersal
Vertebrate dispersed	Binary (vertebrate dispersed or not)	Reproductive fitness, plant-animal interactions	Increase in vertebrate dispersal
Wind dispersed	Binary (wind dispersed or not)	Reproductive fitness	Decrease in wind dispersal

Community weighted mean trait values (CWM; weighted by species occurrence) were calculated per transect using the 'FD' package (Laliberté et al. 2014) in R 3.4.2 (R Core Team, 2019). For binary traits (plant woodiness, long distance dispersal, vertebrate dispersal, wind dispersal), we calculated the proportion and number of 'occurrences' (presences in 1m transect sections) with and without the trait. Prior to CWM calculations, plant maximum height and seed dry mass were $\log_{10}$ transformed to improve normality, as well as model convergence (see statistical analyses below). Co-variance and phylogenetic relationships amongst traits were tested and it was concluded that these would have little impact on CWM (see Appendix 3: Text S3.1).

Statistical analyses

Exotic species community composition

We tested for differences in the occurrences of each study species in the four habitats using Bayesian Generalised Linear Mixed Models (GLMMs; i.e. 18 models), using the 'blme' R package (Dorie and Dorie 2015). Unlike traditional GLMMs, Bayesian GLMMs can accommodate complete separation in a logistic regression (i.e. an explanatory variable that completely separates the response variable into all zeros or ones) by allowing priors on the fixed effect terms (Bolker 2015). This was the case for occurrence data in our study, where some species were never recorded inside rainforest remnants. In our models, we used highly uninformative Gaussian priors for all fixed effects, with means of 0 and variances of 9 and no covariance between them. For each model, the response variable combined the frequencies of presence/absence of the species in each 1 m transect section (ranging 0–100), the fixed effects were habitat (four levels: oil palm, edge, disturbed forest and intact forest) and canopy cover (as both linear and non-linear quadratic terms to account for nonlinear individual species responses to light). Site and transect-level random effects were included to account for pseudo-replication. Species with very low total occurrence across all transects (<50 occurrences across all 78 transects) were not analysed. For each model, we tested whether geographical distance among transects was influencing our findings using Moran's I autocorrelation tests but found no evidence for geographic structuring in residuals of any of the models (see Appendix 3: Text S3.1).

To compare compositional similarity of exotic species across the four habitats we conducted an ordination using nonmetric multidimensional scaling (NMDS) on a Bray-Curtis dissimilarity matrix (Magurran, 2013). Ordinations were conducted on transect-level data, based upon the total occurrence of species per transect (i.e. total number of 1m sections where the species was recorded present, range = 0-100/transect) using the 'vegan' package (Oksanen et al. 2007; Dorie and Dorie 2015). We assessed the marginal effect of habitat and structure (canopy cover and number of large trees) on community composition using a PERMANOVA (Permutational Multivariate Analysis of Variance), with 999 permutations to calculate significance.

Functional trait variation across habitats

To test for differences in each of the four functional traits among the four habitats, Bayesian GLMMs were fitted with fixed effects of habitat and canopy cover, and random effects of site and transect. Six separate models were run for the following response variables: CWMs of $\log_{10}$ plant maximum height and seed dry mass (with Gaussian error distributions), and binomial proportion that were woody, long-distance dispersed, vertebrate dispersed and wind dispersed (with binomial errors). Pairwise comparisons between habitats were carried out with a Tukey post hoc test using the 'emmeans' package (Lenth and Lenth 2018). For each model the residuals were tested for geographic structuring and no evidence was found for any trait model (see Appendix 3: Text S3.1).

Finally, robustness of the results was evaluated by re-fitting the models without the dominant invasive species, *Clidemia hirta*, to determine whether relationships were maintained across the remaining exotic plant community.

3.4 Results

Exotic species community composition

Oil palm plantations and forest-oil palm edges were highly invaded with similar exotic species richness and occurrence (Fig. 3.2 and Table S3.4; plantation mean richness = 9.2 species/transect (SE ± 0.58), mean occurrence = 12.94/transect (SE ± 3.76); edge richness = 7.8 species/transect (SE ± 0.69), occurrence = 12.73/transect (SE ± 3.14) respectively), although the species compositions on each transect differed significantly between the two habitats, as well as between sites within habitat (Fig. 3.3). Species richness and occurrence then decreased markedly in disturbed forests, where a subset of the exotic community present in the oil palm and forest edge habitats was found (Fig. 3.2 and Table S3.4; mean richness = 3.1/transect (SE ± 0.64); mean occurrence = 3.66/transect (SE ± 0.88)), and only one species (*Clidemia hirta*) was found in intact forest, where it was found at low levels of occurrence (mean = 0.91/transect (SE ± 0.21)).

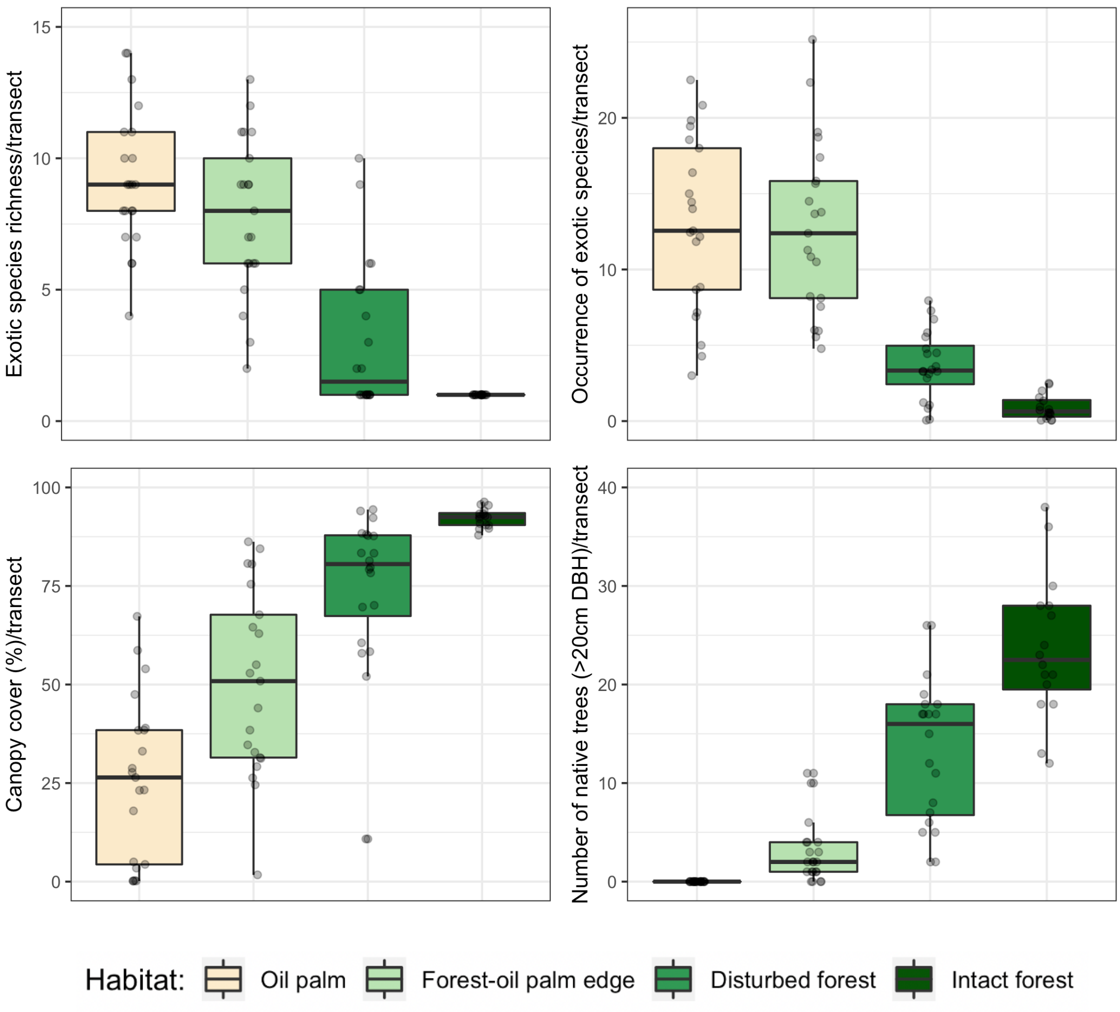

Figure 3.2: Exotic plant species richness and occurrence, and local habitat variables in four habitats in Sabah, Malaysian Borneo. Oil palm = major plantation roadside; Forest-oil palm edge = minor plantation road or terrace where oil palm meets forest; Disturbed forest = skid trail, old road or abandoned terrace; Intact forest = closed canopy forest. See main text and Table S3.2 for full habitat descriptions.

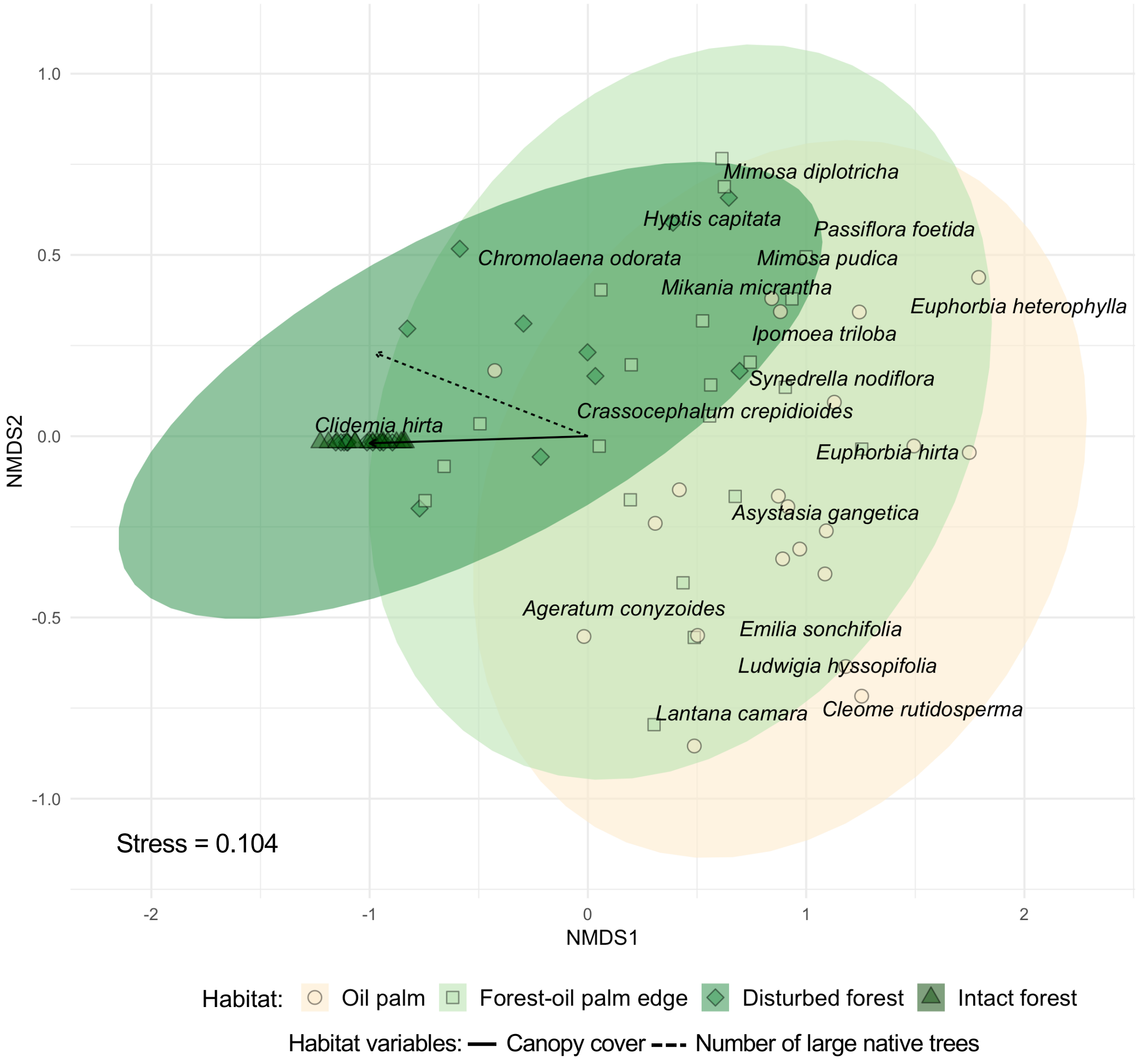

Figure 3.3: Non-metric multidimensional scaling (NMDS) of species composition based on Bray Curtis index for oil palm, forest edge, disturbed forest and intact forest. Each symbol represents one transect and species names are in italics. Habitat is the same as described in Fig. 3.1. Results of Permutational Multivariate Analysis of Variance, with 999 permutations were: number of large trees, *P*=0.350; habitat, *P*=0.001; canopy cover *P*=0.001. For visualisation, random x-axis jitter has been added to the intact forest points, which were composed of a single species and so had no variation in NMDS scores.

Whilst 18 exotic species were recorded overall, no single transect contained all 18 species (oil palm: 4-14 species per transect, Forest-oil palm edge: 2-13 species, disturbed forest: 1-10 species; Fig. 3.2). The tropical shrub *Clidemia hirta* made up ~33% of all occurrences (Table S3.4). Some species had very low occurrence and appeared on only a few transects (e.g. *Lantana camara* and *Crassocephalum crepidioides*; Table S3.4), whereas some species were very common (i.e. *Asystasia gangetica* and *Ageratum conyzoides*; Table S3.4 and Fig. S3.2). Of the six most abundant species, some decreased in occurrence from oil palm into disturbed forest (e.g. *A. conyzoides, A. gangetica* and *Mimosa pudica*; Table S3.4 and Fig. S3.2) whereas some species became more common at forest edges than in plantations and decreased again in forest habitats (e.g. *Clidemia hirta*, *Chromolaena odorata* and *Hyptis capitata*; Table S3.4 and Fig. S3.2).

As expected, canopy cover and number of large native trees both increased from oil palm to intact forest (Fig. 3.2 and Table S3.5). Bayesian GLMMs for the 16 species with sufficient occurrence data to analyse, showed that the occurrence of five species (including two of the most abundant; *Clidemia hirta* and *Chromolaena odorata*) were significantly associated with canopy cover, both with linear and quadratic terms (Table S3.6 and Fig. S3.3). Thus, some species were more common at intermediate light levels (e.g. *A. conyzoides, Clidemia hirta* and *Chromolaena odorata*) and others require full light (e.g. *Euphorbia hirta*). Habitat remained significant for most species (n=11) after controlling for the effect of canopy cover (Table S3.6), suggesting some additional environmental, spatial or biotic factors were also important for affecting the occurrences of these exotic species.

Differences between species composition based on Bray Curtis distance measures showed that habitat separated on NMDS ordination plots, with oil palm plantation and intact forest the most different, and edge transects intermediate (Fig. 3.3). Both habitat and canopy cover significantly affected species composition and helped to drive the observed separation in community composition (Fig 3.3; PERMANOVA; habitat, R^2=0.1, P<0.001; canopy cover, R^2=0.06, P<0.001). The additional effect of distance to forest edge was tested for forest transects only, as a proxy for propagule pressure, and was found to have no significant effect on the occurrence of any species (see Appendix 3: Text S3.1). This confirms the role of local environmental conditions in driving observed species compositions.

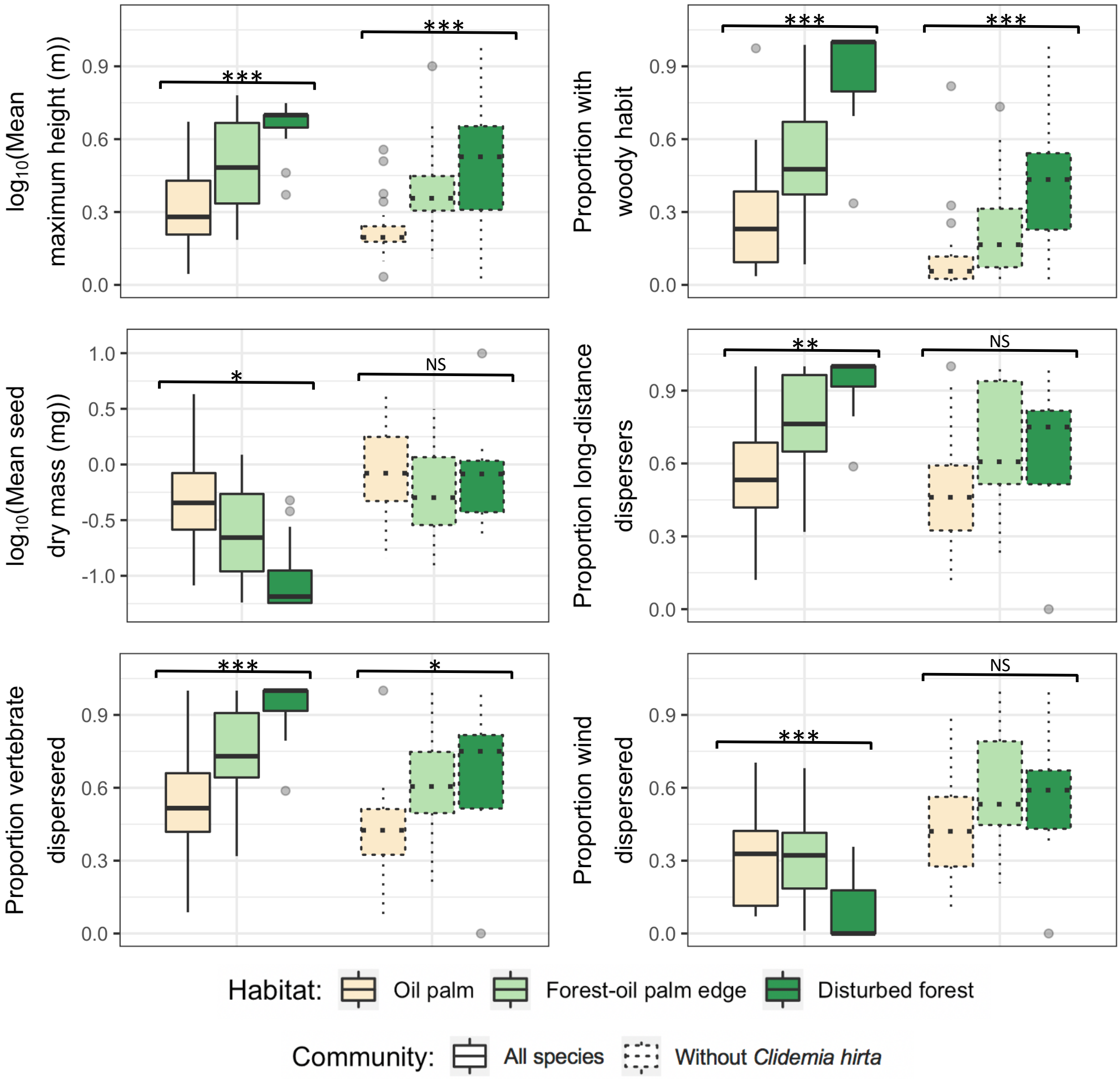

Figure 3.4: Trends in six functional traits of exotic species (n=18) across three habitats from oil palm plantation into rainforest remnants with all species included (block outline) and dominant invasive *Clidemia hirta* excluded (dotted outline). *P*-values are from ANOVA, after controlling for canopy cover, on Bayesian Generalized Linear Mixed Models (*** = P<0.001; ** = P<0.01; * = P<0.05; NS = non-significant). Pairwise comparisons between habitats detailed in SI Table S8.

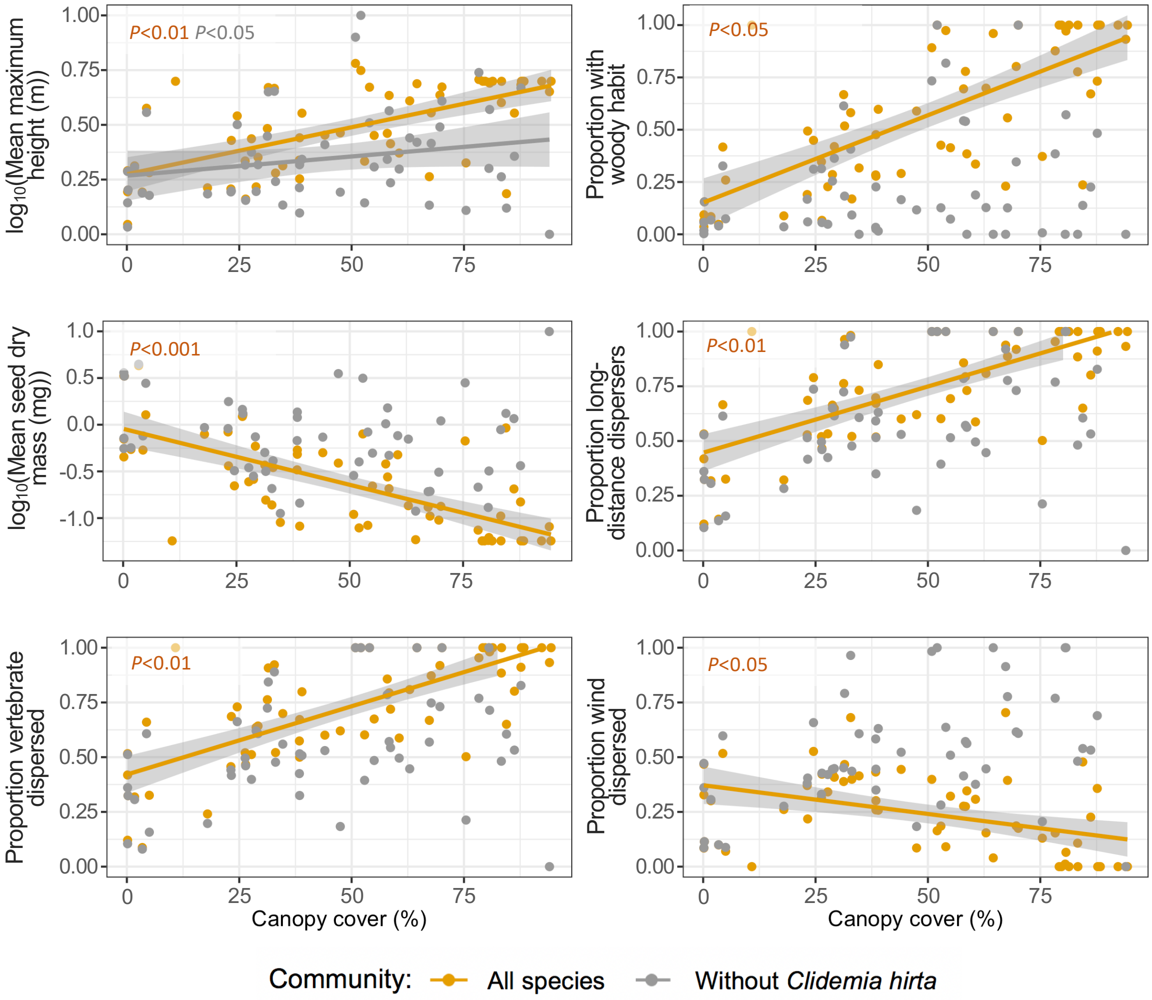

Figure 3.5: Trends in six functional traits of exotic species (n=18) in relation to canopy cover, with all exotic species included (orange) and with dominant invasive *Clidemia hirta* excluded (grey). Regression lines are on the raw data of those significant relationships from the results of Bayesian Generalized Linear Mixed Models, after controlling for habitat. *P*-values are the significant results of ANOVA tests.

Functional trait filtering

The exotic community showed clear trends in mean functional trait values along the disturbance gradient, despite there being different exotic source communities in the oil palm across sites (Fig. 3.4, Tables S3.4 and S3.5). Plant height and woodiness increased, and seed dry mass decreased from oil palm into intact forest. Additionally, exotic species adapted for long-distance dispersal (i.e. vertebrate or wind dispersed) were more common inside rainforest remnants. All traits were significantly related to habitat as well as to canopy cover (Figs. 3.4 and 3.5, and Table S3.7).

To test the robustness of the trait results, we removed the dominant exotic species, *Clidemia hirta*, from the analyses, but found this did not substantively change the main findings. The remaining exotic community (*n*=17 species) exhibited increased height, woodiness and vertebrate dispersal from plantation to disturbed forest (Fig. 3.4, Tables S3.7). Whilst the direction of effect was the same, the effect of canopy cover became non-significant when *C. hirta* was removed (Fig. 3.5), apart from woodiness which remained significant. As with the species composition analyses, distance to forest edge had no significant effect on the mean functional trait value of forest communities for any trait (see Appendix 3: Text S3.1).

3.5 Discussion

Our results revealed for the first time that exotic plant communities inside rainforest remnants, retained for conservation, were not random subsets of the species established in the oil palm. Although most species were found in low numbers inside rainforest remnants, with the exception of *C. hirta*, clear trends in traits that are important in colonisation processes were seen along the disturbance gradient from oil palm to inside rainforest remnants. Species with traits which are advantageous for persistence within oil palm planted areas (i.e. herbaceous species with local dispersal, e.g. *A. gangetica*) start to decrease in abundance at the forest edge, and exotic communities are rather more dominated by vertebrate dispersed shrubs inside the disturbed areas of rainforest remnants. This shift suggests locally dispersed herbaceous species that dominate outside rainforest remnants, cannot disperse readily into the forest and/or are not sufficiently well adapted to forest environmental conditions to compete with the native community.

Our study also supported previous findings that closed canopy rainforest have low levels of invasion (Teo et al. 2003; Dawson et al. 2015; Döbert et al. 2017a), and provided the first evidence of this result in conservation set-asides embedded within oil palm plantations. Despite most remnants being small in size (<100 ha; *n sites* = 15) and the intact forests being on average less than 100 m from a heavily invaded anthropogenic matrix (Appendix 3: Text S3.1 and Table S3.5) only one exotic species was found. However, we found that the most disturbed areas of these rainforest remnants are much more susceptible to invasion predominately due to disturbance history and a more open canopy, and not because they were on average closer to the forest edge and therefore sources of propagules. The number of exotic species and their occurrence decreased along the disturbance gradient (from oil palm to intact forest), which is likely partly attributed to the reduction in resource availability (e.g. light), as well as other factors that vary between habitat.

The most common species we recorded, *Clidemia hirta,* is known to be found only in open areas in its native range but can invade closed canopy forest throughout its introduced range (DeWalt, Denslow, & Ickes, 2004), and was the only species found in closed canopy forest in this study. Indeed, we noted that *C. hirta* was smaller in the very shaded parts of these forests, which may indicate growth restriction in shaded, closed canopy areas. However, we report for the first time that this species is significantly more abundant in a forest edge habitat, which we believe is due to *C. hirta* favouring intermediate light levels as supported by the relationship with canopy cover.

Dispersal into rainforest remnants

We found that rainforest remnants are more likely to be invaded by exotic species with longer-range dispersal syndromes, presumably because they are better able to disperse seed inside rainforest remnants without the requirement of human assistance. Other studies have shown landscape-scale habitat heterogeneity reduces the spread of short-distance dispersed invasive species but has little impact on species that disperse long-distances (Marco et al. 2011). This may explain our finding that long-distance dispersal (i.e. vertebrate, wind and water) promotes invasion in our highly heterogeneous anthropogenic landscape.

We found species that are vertebrate-dispersed (internally and externally, and both primary or secondary dispersal modes) are more likely to invade forests than those dispersed solely by wind or without long distance dispersal adaptations. In these landscapes it is likely that small birds and bats are effective dispersers of species with fleshy fruit (e.g. *C. hirta*), having been identified as the main dispersers of exotic woody species in tropical rainforests (Rejmánek 1996), as well as preferentially foraging in and adjacent to areas of recovering tropical rainforest canopy gaps (Schupp et al. 1989). Secondary dispersal by terrestrial mammals is also likely to occur for those species with different primary dispersal mechanisms (e.g. the wind dispersed *Chromolaena odorata*). It is likely that bearded pigs (*Sus barbatus*), observed residing inside most rainforest remnants and foraging in the oil palm matrix, are picking up propagules in their fur and dispersing them inside the forest (CABI, 2019; Fujinuma & Harrison, 2012; Peters, 2001). Although, there is significantly reduced mammal (Bernard, Baking, Giordano, Wearn, & Ahmad, 2014), and bird (Scriven et al., *in review*) richness inside these rainforest remnants, and within surrounding oil palm planted areas (Edwards et al. 2014), our results suggest that there are sufficient vertebrates present in these landscapes to disperse exotic plant seeds into rainforest remnants. Our most dominant exotic plant species, *C. hirta*, is most likely dispersed by generalist bird species, which make up a larger percentage of the bird community in these conservation set-asides compared with primary forests (41% c.f. 29%; Scriven et al., unpublished data).

In this study, we considered only natural dispersal agents as there should be no significant on-going disturbances in these rainforest remnants. However, previous disturbance may have facilitated early propagule arrival into these forests on the machinery used during timber extraction; this has been observed as a mechanism in the introduction of invasive grasses in tropical dry forests (Veldman and Putz 2010), as well as the role of domestic vehicles across a range of habitats (Ansong and Pickering 2013). In addition, forest set-asides may experience low levels of human disturbance, and so propagules may be dispersed by people moving through the forest, by transporting seeds attached to clothing (Mount and Pickering 2009).

Persistence within forest environments

The shift to exotic species with greater maximum heights inside rainforest remnants indicates that the ability to compete for light is an important marker of success in the forest environment (Weiher et al. 1999). Other invasive exotic species have been found to be taller when compared with non-invasive exotic species (Gallagher et al. 2015). In addition, the increased woodiness (i.e. stem density) of the exotic forest community is indicative of increased longevity and so species that survive longer (i.e. perennial shrubs) are more likely to persist within the disturbed areas of these rainforest remnants than herbaceous annuals. The ability to survive and successfully compete with native forest species is necessary for persistence within new environments

(Weiher et al. 1999) and there is likely greater niche overlap and therefore competition between young native trees and exotic shrubs, than small herbaceous exotic species.

The positive relationship between canopy cover and woodiness in our results (and same trend with maximum height) suggests that light is driving some of the observed patterns of trait filtering. In the more shaded forest, shrubby exotic species may be more likely to successfully compete for light with native species. Dominant herbaceous species found in the oil palm, and at the forest-oil palm edge, with the capacity for long-distance dispersal (e.g. *Ageratum conyzoides*) by contrast are unable to establish and persist in large numbers inside the forest. The inclusion of data on leaf functional traits could provide additional insight on the trait filtering mechanisms occurring during colonisation, especially the relationship with light, because they provide information on another dimension of resource acquisition and allocation. Specific leaf area (SLA) is also well-correlated with growth rates (Lambers and Poorter 1992) and high SLA is often attributed to invasive species (Hamilton et al. 2005; Grotkopp and Rejmánek 2007). Although foliar data were lacking for our species, this would be a useful focus of future work to help ascertain whole-plant trade-offs.

Habitat and other influential factors

Our finding that trait patterns and differences in species occurrences are significantly explained by habitat may derive from differences in land-use history that impact environmental conditions other than light. For example, along the disturbance gradient there is likely to be a change in the soil conditions, with high compaction in the most disturbed areas (those outside forest and on skid trails or roads inside rainforest remnants), which is known to promote exotic plant establishment in logged tropical rainforests (Döbert et al. 2017a). In addition, increased soil compaction can have a negative impact on native species regeneration (Hattori et al. 2013) and thus reduce competition between exotic and native species. Soil pH and nutrients are known to influence exotic plant richness in tropical rainforests (Teo et al. 2003), however, a previous study in these rainforest remnants found characteristics of the soil (specifically pH and available P) to be less important for invasion than other drivers (Waddell et al., 2020a). Outside the rainforest remnants, soil characteristics are likely to be more influential on the exotic plant community due to the addition of fertilisers (that add N, P and K to the soil) and presence of leguminous cover crops which increase N availability (Huenneke et al. 1990).

The role of exotic species traits is likely to be one of several processes driving invasion within this landscape, and it is probable that other factors are also at play. Species-specific biotic interactions that vary among habitats may also be influential, as exotic species are known to both lose and gain biotic interactions when invading new areas (e.g. presence of available pollinators (Sargent and Ackerly 2008), soil microbes (Reinhart and Callaway 2006), damage from herbivory and pathogens (DeWalt, Denslow, & Ickes, 2004)). Therefore, specific interactions with abiotic and biotic factors not recorded in this study may contribute to individual species invasion success alongside the variables we analysed.

In addition, invasion is a dynamic process and therefore species persisting in oil palm plantations may still be expanding their populations into rainforest remnants (resulting in a time lag on colonisation) as has been recorded in temperate rainforest remnants (Essl et al. 2012). Invasion time lags are thought to be shorter in tropical regions than in temperate regions, and shorter for exotic herbaceous species than woody species (Daehler 2009). However, invasions within tropical rainforests are poorly understood and therefore lag times may still be occurring in these forests, especially in the newer plantations. For example, *Lantana camara* is a prolific invader across the tropics (Lowe et al. 2000) but it was present only in very low numbers in this study, and only outside the forest, despite being frequently grown as an ornamental in settlements, suggesting invasion lag effects. Additional studies which track compositional changes over time would help to elucidate the relative influence of these different factors.

Conservation implications and management suggestions

Our results suggest exotic plant invasion might not be an imminent threat to native rainforest remnants if they have low levels of previous disturbance and high canopy cover. However, rainforest remnants within agricultural areas are often small and highly degraded due to disturbance from logging and extensive edge effects (Reynolds et al. 2011; Haddad et al. 2015; Lucey et al. 2017), as well as being isolated from larger tracts of primary forest. These disturbances are known to alter the native plant community to include a higher proportion of pioneer and non-forest specialists (Laurance et al. 2006; Pütz et al. 2011) and isolation can reduce pollination and dispersal of native trees (Ghazoul and McLeish 2001), both of which negatively impacts the natural regeneration of forest species (Haddad et al. 2015) and may result in the intact parts of these forests becoming degraded over time. In these circumstances, exotic species may be able to spread through the forest into new gaps, using the disturbed areas of these forests (i.e. old skid trails and roads) as ‘stepping stones’ to invade deeper into the forest core.

Although we believe the 18 species we recorded in this study to be a good representation of the exotic plant community in these landscapes, we recognise that other species may be present in other parts of these landscapes, especially in the oil palm. In addition, native non-forest generalists that proliferate with disturbance and increased light availability (e.g. *Callicarpa, Melastoma, Uncaria*) were also observed in the rainforest remnants but were not recorded during this study. This native 'weedy' community may follow the same trait patterns observed in the exotic community, because native understorey tropical plants are known to become less functionally diverse inside primary rainforest when compared with repeatedly logged rainforest (Döbert et al. 2017b). Our results provide useful information about which exotic plant species and their associated traits, are invading these forests, including species that are known to suppress the regeneration of native species through competition and allelopathic effects (e.g. *Clidemia hirta* and *Chromolaena odorata;* Ambika, 1980; Ishmaini and Lesstari, 2015; Nakamura & Nemoto, 1993).

To help reduce invasion and thus minimise any potential negative impacts on native rainforest regeneration, as well as improving overall habitat quality for forest biodiversity, we recommend active forest restoration within canopy gaps in conservation set-asides, which may combine enrichment planting and weed removal. This would be especially beneficial in highly disturbed sites which lack closed canopy forest, in order to decrease light levels in the understorey and reduce colonisation by most exotic species. In addition, we suggest targeted removal of exotic species with the traits highlighted in this study from the source population in oil palm areas to stop or slow the spread into rainforest remnants, especially in new plantings where exotic populations may not yet have established. Likewise, we caution against planting of exotic species for ornamental reasons, for example, the ornamental species, *Lantana camara*, which has the traits that would, according to our results, make it a successful invader of remnant forests (i.e. it is a vertebrate dispersed shrub). Furthermore, as the anthropogenic forest-oil palm edge is the avenue for invasion in these forests, as seen in other tropical rainforests (Dawson et al. 2015), decreasing the edge to area ratio in rainforest remnants is likely to help minimise invasion, as well as reducing edge effects on native forest species richness and structure, which are known to be greater in irregular shaped fragments (Didham and Lawton 1999; Bennett and Saunders 2010). These suggested measures could be incorporated into certification procedures and documentation (e.g. RSPO) to help ensure that exotic species do not become a threat to the conservation status and long-term sustainability of these important remnants.

3.6 Conclusions

Our study is the first to show strong evidence for trait-filtering of exotic species as the environment changes from anthropogenic habitats into remnant areas of recovering native tropical rainforests along a disturbance gradient. Successful invasion of rainforest remnants requires species to have both adaptation for long-distance dispersal, in particular vertebrate dispersal, and traits that facilitate competition with native forest species (i.e. tall and woody), but there must also be a level of disturbance (i.e. canopy openness). Our results highlight both the type of forest susceptible to invasion (i.e. previously disturbed with an open canopy) and the type of exotic species that can invade remnant areas of native forest within increasingly anthropogenic tropical landscapes (Potapov et al. 2017). These rainforest remnants maintain biodiversity within agricultural tropical landscapes, and our findings provide a first view of which exotic species invade the understorey of these conservation set-asides. Although, it is not yet clear whether these exotics affect long-term regeneration of native forest communities, a precautionary approach is to introduce management practices that facilitate native seedling regeneration and increase canopy cover, to decrease the occurrence of most exotic species and reduce potential impact**.**

3.7 Author contributions and acknowledgements

E.H.W., D.S.C., J.K.H., M.H. and L.F.B. conceived the ideas and E.H.W., D.S.C., J.K.H., M.H., J.T., A.B.S. and L.F.B. designed the methodology. E.H.W. and A.B.S. collected the data, E.H.W. and D.S.C. analysed the data and E.H.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data collected for this study are available to download from the Environmental Information Data Centre (Waddell et al. 2020b).

Chapter 4

Clidemia hirta growing next to a rock in closed canopy forest

Canopy cover and proximity to native confamiliars affects herbivory of an invasive shrub in Bornean rainforests

4.1 Abstract

Tropical rainforest remnants may be invaded by exotic plants from surrounding anthropogenic areas, especially if these species have a competitive advantage over neighbouring native species. One such advantage is escaping herbivory pressure when exotics are outside their native range. The invasive shrub *Clidemia hirta* is the most widespread invasive plant in remaining areas of tropical forest in Sabah, Malaysian Borneo. Escape from herbivores may contribute to their success in this region, as seen in Hawaii, part of its introduced range. However, unlike in Hawaii, there are related native species in Borneo (Melastomataceae) and therefore shared natural enemies could reduce benefits of escape from herbivores. Here, we investigate whether herbivory in *Clidemia hirta* is affected by the presence of confamiliar native plants in 21 rainforest remnants within oil palm landscapes in Sabah. We recorded two measures of herbivory (occurrence per plant and intensity per leaf) in *C. hirta* and related native *Melastoma* spp. plants along 100m transects at forest remnant edges and within forest remnants (on average ~53 m from edges). We examined the effects of proximity to native confamiliars and their herbivory damage, habitat (comparing transects in forest edge vs forest interior) and local canopy cover on herbivory in *C. hirta*, as well as the impact of herbivory on reproduction. Overall, *C. hirta* had lower herbivory (median occurrence=79% of leaves per plant; median intensity=6% of leaf area) than natives (93% and 20% respectively). Herbivory increased with proximity to native *Melastoma* plants with high herbivory damage and in locations with greater canopy cover. We found evidence that herbivory negatively impacted reproductive output in *C. hirta*. The association between herbivory rates in *C. hirta* and *Melastoma* may suggest host-sharing by specialist herbivores is occurring. The lower herbivory rates detected in more open canopy locations may make highly disturbed forest remnants in these landscapes more susceptible to invasion by *C. hirta*. Invasive species, such as *C. hirta,* may be less successful invaders in regions with native confamiliars that harbour populations of natural enemies, providing a 'biological control' service for exotic plant species by impacting fitness.

Keywords: *biological control*; *Clidemia hirta; enemy release; host-sharing; invasive species; phytophagous herbivores; Sabah, Malaysian Borneo; tropical rainforests*

4.2 Introduction

Widespread deforestation, fragmentation and forest degradation across the tropics has opened up landscapes to the potential for invading exotic plant species (Haddad et al. 2015; Lewis et al. 2015), first into anthropogenic areas (e.g. pastures and plantations) then, to a degree, into remnant rainforests (Chapter 2; Rembold et al. 2017; Waddell et al. 2020a). The abiotic conditions and native biotic communities in forest remnants are altered by the effects of logging and fragmentation (Broadbent et al. 2008; Laurance et al. 2011; Lôbo et al. 2011); increased light levels and reduced biotic resistance result in these forests being more susceptible to exotic plant invasion (Chapter 2; Dawson et al. 2015; Döbert et al. 2017a; Waddell et al. 2020a). When exotic species invade new ecosystems they both gain and lose biotic interactions. New interactions may have either positive (i.e. pollination and dispersal promoting reproduction and spread) or negative influences (i.e. herbivory reducing fitness) on whether an invading species successfully establishes and persists within its introduced ecosystem (Catford et al. 2009).

The interaction between plants and their natural enemies (insects, mammals and pathogens) is an important ecological process that reduces individual competitive ability, plant growth and reproduction, and increases mortality (Marquis 1984; Eichhorn et al. 2010). Plants and herbivores have evolved together resulting in specialised plant defences (Coley & Aide, 1991) and host-specific enemies (Gaston, 1993; Hodkinson & Casson, 1991; Marquis, 1991). As such, exotic plant species invading new areas may escape enemies from their native ranges and have lower enemy pressure in the new location ('Enemy Release Hypothesis'; Keane and Crawley, 2002), resulting in lower productivity losses and potentially gaining a competitive advantage and increased population growth in comparison to extant natives. Plants released from herbivory may shift resource allocation from defence to growth and reproduction, giving the invading species a further competitive advantage ('Evolution of Increased Competitive Ability Hypothesis'; Blossey and Notzold, 1995). The strength of the enemy release effect in invasion may be strongly influenced by the degree of phylogenetic relatedness between the invading species and the native community in the invaded ecosystem, because related species are more likely to share specialist herbivores due to phylogenetic conservatism of insect host choice (Lockwood *et al.*, 2001; Dawson, Burslem and Hulme, 2009). Therefore, an invading exotic species with related native species present in the invaded habitat, will likely suffer higher herbivory pressure from specialist herbivores already adapted to that family or genus. Conversely, introduced exotic species with no native relatives may become highly invasive as release from herbivory could allow them to invest more resources into growth and reproduction, compared with native neighbours (DeWalt et al. 2004). In global-scale meta-analyses, these closely related hypotheses have had mixed support (Liu and Stiling 2006; Jeschke et al. 2012; Felker-Quinn et al. 2013; Meijer et al. 2016) which suggests that release from enemies may be context dependent, differing between species, habitats and biomes (Shea and Chesson 2002; Jeschke et al. 2012). Nonetheless, the few studies conducted in the tropics support the hypothesis that some exotic species gain competitive advantages by escaping their enemies, which suggests that these processes could be particularly important in this biome (DeWalt, Denslow and Ickes, 2004; Liu, Stiling and Pemberton, 2007; Dawson, Burslem and Hulme, 2009).

In highly diverse tropical forests (Turner, 2001), the same woody families are widespread across the tropics (Gentry 1988), therefore an invading tropical woody exotic species within these common families, is likely to encounter native confamiliars. This high diversity is partly driven by herbivory due to distance and density dependent mortality (i.e. the Janzen-Connell hypothesis; Janzen 1970; Connell 1971) in which adult trees and shrubs act as reservoirs or cues for enemies to attack nearby conspecific saplings and seedlings (<10 m; Hubbell 1986; Condit et al. 1992, 1994; Folgarait et al. 1995). Thus, the distance to and density of related plants is important factor in the herbivory levels of native species, and likely of exotic species too. In addition to high diversity, plants in tropical forests experience greater herbivory than in temperate forests (Coley & Barone, 1996; Marquis & Braker, 1994) due in part to host clade specialist insect herbivores (Hodkinson and Casson 1991; Marquis 1991; Gaston 1993; Ødegaard et al. 2005; Weiblen et al. 2006), that cause more damage than generalist insect species (Barone, 1998). Therefore, invading exotic plant species in tropical forests have the potential to be exposed to high levels of herbivory, although it is likely dependent on the presence of related natives and specialist herbivores. The geographic scale at which this interaction between presence of related native species and enemy release is important, and is currently not known because the few studies that have considered the role of herbivory in tropical invasions have not tested this (Dawson et al., 2009b; DeWalt et al., 2004; Norghauer, Martin, Mycroft, James, & Thomas, 2011; Peters, 2005).

In addition to enemy release, anthropogenic disturbance may indirectly influence levels of herbivory of exotic plants in tropical forests, as abiotic conditions and biotic interactions are altered due to fragmentation and degradation (i.e. reduced diversity of plants and animals in small isolated remnants; Haddad et al. 2015), which can impact long-term community dynamics (Coley & Barone, 1996). Across biomes, the influence of light on herbivory is species-specific to both host plants and herbivores, and may either increase or reduce the damage caused by natural enemies (Whitham 1991). In tropical regions, there is evidence that herbivory is greater in high light environments for native tree saplings (Folgarait et al. 1995) but no difference was detected between open and closed canopy habitats for the invasive shrub *Clidemia hirta* in its introduced and natives ranges (Hawaii and Costa Rica respectively; DeWalt, Denslow and Ickes, 2004). Richness and abundance of herbivores are known to increase with recent logging disturbance and canopy openness in tropical forests (Basset et al. 2001; Ewers et al. 2015). However, this is thought to be driven by greater leaf production by native seedlings in more open canopies and not as a result of the environmental conditions associated with canopy cover (Basset et al. 2001). In fragmented tropical landscapes, herbivory rates have been shown to be highest in the largest, more intact forest remnants (Ruiz-Guerra et al. 2010). Thus, the relationship between the degree of disturbance and altered light levels, and herbivory in tropical forests is complex, and may differ between native and exotic species as well as under different disturbance regimes. Forest remnants within fragmented landscapes have less canopy cover when compared to old growth forest, and also have altered species community composition and other abiotic conditions (e.g. soil nutrients), which may impact herbivory dynamics. However, there are a lack of studies examining herbivory within disturbed tropical rainforest remnants and none that consider the role of herbivory on invading exotic species.

In this study, we examine the ecological factors that influence herbivory on the invasive tropical shrub *Clidemia hirta* (Melastomataceae) within Sabah, Malaysian Borneo, and which may contribute to its establishment success within its introduced range. Firstly, we investigate whether herbivory in *C. hirta* is lower compared to native Melastomataceae (*Melastoma* spp.) shrubs that occupy a similar ecological niche. We then test whether herbivory rates on *C. hirta* are influenced by proximity to related native *Melastoma* plants and the extent of herbivory on them. Secondly, we investigate whether herbivory varies with abiotic conditions (light levels from variation in canopy cover) and the level of disturbance (forest edges adjacent to agricultural plantations vs. forest remnant interiors). Finally, we tested whether herbivory reduces the reproductive output of *C. hirta* plants. Due to *C. hirta's* ability to invade and modify tropical forest interiors (Chapter 3; DeWalt et al. 2004; Waddell et al. 2020b), it is important to improve understanding of biotic interactions in its introduced range, especially in forests vulnerable to biotic degradation. Further knowledge of interactions that directly impact its survival, growth and reproductive output, will assist efforts to control its populations and spread across the tropical landscapes.

4.3 Methods

Study species

The highly invasive tropical shrub *Clidemia hirta* (L.) D. Don (Melastomataceae) is native to Central and South America (Mexico to Paraguay, and the Caribbean) but is invasive across tropical Africa, Asia and Pacific Islands (CABI, 2020), including being the only widespread species invading closed canopy forests in Sabah (Chapter 3; Waddell et al. 2020b). The success of *C. hirta* in its introduced range in Hawaii is thought to be in part due to escape from natural enemies (DeWalt et al. 2004). However, Hawaii has no native members of the Melastomataceae family, therefore host-sharing may be less likely (DeWalt et al. 2004); similar levels of herbivory were found in native Venezuelan populations and invasive Peninsular Malaysian populations (where there are native Melastomataceae), suggesting enemy release may not occur in Malaysia (Peters 2005). Species belonging to the *Melastoma* genus are non-forest specialist shrubs that occupy similar habitats to *C. hirta* (i.e. road-sides, open-structure forest). There are 41 species within the *Melastoma* genus found in Borneo (Wong 2016) and identification can be difficult due to very similar morphologies and hybridizations (Wu et al. 2019); however the majority of plants encountered in the lowlands of Sabah are *Melastoma malabathricum,* the most widespread and common species in Borneo (Wong 2016).

Study sites

We carried out surveys of herbivory on *C. hirta* and native *Melastoma* spp. plants in 21 forest remnant sites within oil palm plantations in Sabah, Malaysian Borneo (Fig 4.1a-b). Forest remnant sites were conservation set-asides (hereafter ‘forest remnants’), mostly sites specified as those containing High Conservation Values (HCVs, Senior *et al.*, 2015), as part of the certification process for sustainability (Roundtable on Sustainable Palm Oil (RSPO), 2018). Forest remnants were originally retained because they were unsuitable for oil palm cultivation (e.g. too steep or rocky) and had been commercially logged (with varying intensity), prior to plantation development, probably between ~1991-2009 (Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011). In each site, 100m transects were established in two forest habitats, one at the forest-plantation edge (hereafter 'forest edge') and one in the forest remnant interior (on average 53m from nearest forest edge; hereafter 'forest interior'; Fig. 4.1c). The forest interior transect was located in regenerating forest following clearance, either along logging skid trails, old roads or abandoned oil palm terraces (see Table S4.1 for site and transect details). These two forest habitats were chosen in order to survey different levels of disturbance as well as wide variation in canopy openness that might influence plant densities and herbivores communities. Closed canopy intact forest was not surveyed due to the rarity of *C. hirta* in this habitat (Chapter 3; Waddell et al. 2020b). The two forest habitats differed in terms of light levels and species present, including density of *C. hirta* plants (Chapter 3; Waddell et al. 2020b). In total, we obtained data for 41 transects (one forest interior transect was too steep for survey). Within each transect, up to ten *C. hirta* plants were surveyed for herbivory (selected as the nearest individual to each 10 m mark along the transect). For each *C. hirta* plant surveyed, the nearest native *Melastoma* individual (< 10 m), if present, was also surveyed for herbivory. Only plants >30cm height were selected, as these plants typically had at least four fully developed leaves for examining herbivory (median = 22 leaves per plant; Table S4.2), in line with the leaf sampling strategy (see below).

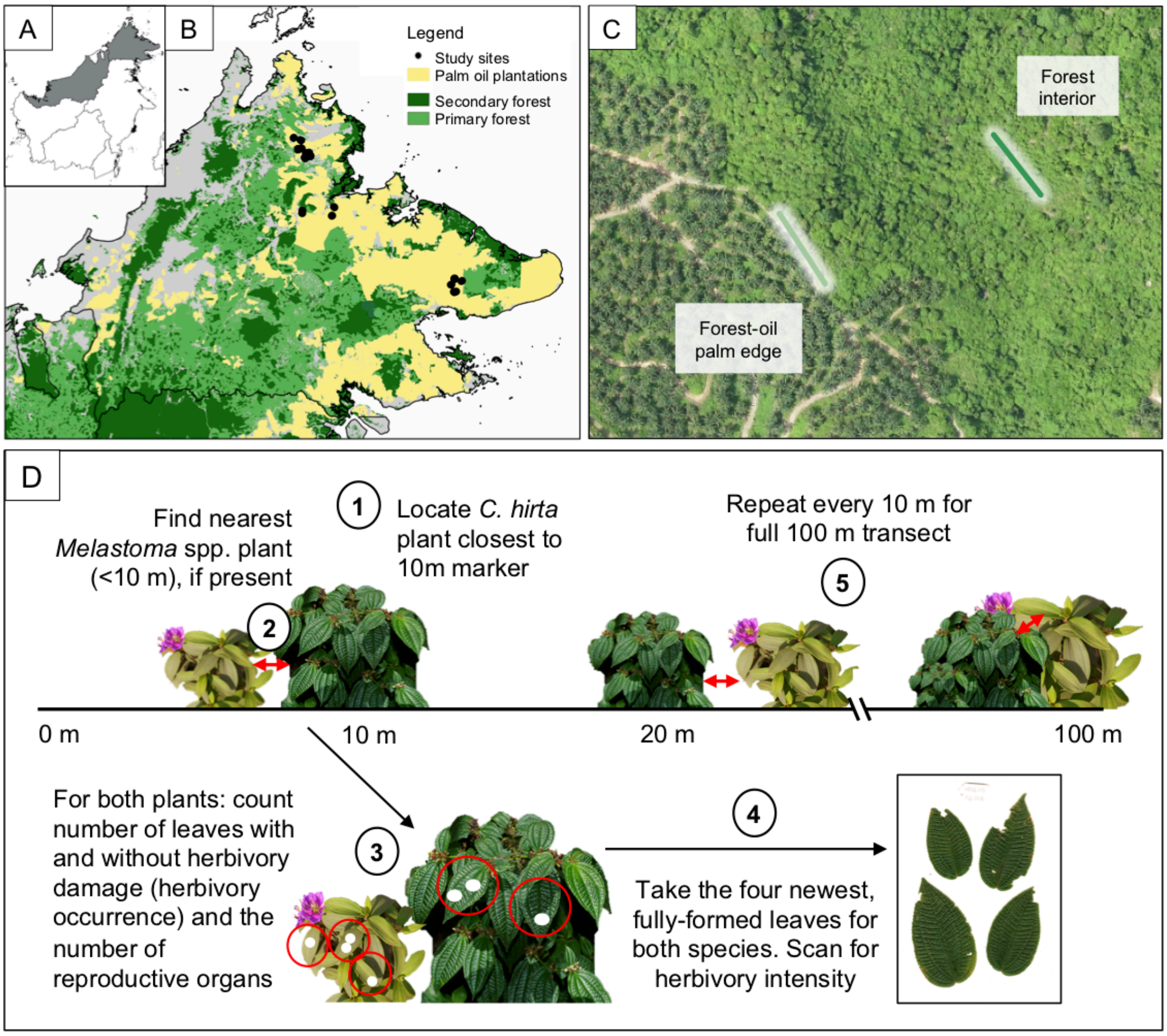

Figure 4.1: Map of the island of Borneo (a) showing the study locations, forest cover and industrial oil palm plantations within Sabah (b). Drone image of forest remnant site embedded within oil palm plantation showing the locations of the transects (c). Schematic diagram of sampling design (d). See text for full details on herbivory sampling. CIFOR forest cover dataset available at Gaveau, Salim and Arjasakusuma (2017).

Herbivory measurements

In this paper, we use the term ‘herbivory’ to refer to any type of leaf damage including insects (e.g. galls, tissue removal by chewing and leaf scarring), mammals and pathogens, reflecting the difficulty in distinguishing causes of leaf damage (Coley and Barone 1996). For each individual plant, both *C. hirta* and *Melastoma*, we recorded two measures of herbivory in order to capture different sources of variation that may occur as a result of herbivore feeding behaviour; herbivory occurrence and intensity (Fig. 4.1d). Herbivory occurrence was recorded by counting the total number of leaves and those that were damaged by herbivory to derive a proportion of damaged leaves per plant. To measure herbivory intensity, the first four fully expanded leaves closest to the shoot apical meristems were sampled. New leaves were chosen to minimise effects of leaf age on accumulated herbivory over time. Both sides of the leaves were scanned into high resolution colour images within six hours (to avoid leaf degradation) using an Epson Perfection V39 Scanner. Herbivory intensity for each leaf was graded by eye from scanned images to the nearest 10%, with the lowest category of <10% further divided into 0%, 0-2%, 2-5% and 5-10%, due to the relatively high proportion of leaves within this category. The middle value for each category was used as the herbivory intensity score in analyses (e.g. 0, 1, 3.5, 7.5, 15 etc) and treated as a continuous variable for analysis at leaf-level (see 'Statistical analyses' section). To test whether leaf herbivory was correlated with reduced reproductive fitness, the numbers of reproductive organs (buds, flowers, immature fruits and ripe fruits) per plant were recorded, if present.

Variables influencing herbivory

Three main explanatory variables were recorded to examine factors that may influence herbivory damage in *C. hirta*. These were distance to the nearest native *Melastoma* plants and their herbivory rate, habitat (forest edge vs. forest interior) and local canopy cover. We also measured two other variables that we believed may be influential on herbivory but that were not foci within our hypotheses, namely plant size and local density of *C. hirta* (see below).

To test whether proximity to native *Melastoma* plants affects herbivory of *C. hirta*, and especially if native plants have high herbivory damage, we calculated a composite variable to capture these two variables simultaneously. This composite variable (hereafter 'proximity index'; *P* in formula) uses a distance decay function (Moilanen and Nieminen 2002) to capture variation in the distance between *C. hirta* and the nearest native *Melastoma* plant (*d* in formula) and herbivory damage on that *Melastoma* plant (*h* in formula). The following formula was used to calculate the proximity index:

$$P = h * \exp\left(-{}^{d}/_{x}\right)$$

In preliminary models, the proximity index was optimised for parameters *h* (*Melastoma* herbivory occurrence vs. intensity) and distance decay parameter (*x* in formula, ranging 1-10), which we found to be *x*=2 and *h*=native herbivory intensity for exotic herbivory occurrence, and *x*=5 and *h*=native herbivory intensity for exotic herbivory intensity (see Appendix 4: Text S4.1 and Table S4.3).

The disturbance level was captured by the two habitats, either highly disturbed forest edge or previously disturbed forest interior. Percentage canopy cover was recorded every 20 m along the transect (five points per transect, with the mean of four measurements facing each cardinal direction per point; recorded by the same observer each time) using a concave spherical densiometer (www.forestry-suppliers.com). As an indicator of the light levels experienced by each surveyed plant, we used the nearest canopy cover measurement or the average of the two closest if the plant was equally spaced between two densiometer measurements.

We recorded the total number of leaves as a measure of plant size. We recorded the presence of *C. hirta* in each 1m section (and 1m either side of the transect line; total sample area 2m^2), along the length of the 100 m transect, and defined the 'local density of *C. hirta*' as the number of plants within 5m either side of each focal *C. hirta* plant (presence out of 10 sections).

Statistical analyses

We modelled herbivory occurrence and herbivory intensity separately, as we found these two herbivory measurements to be only weakly positively correlated (Spearman rank correlation coefficient = 0.28, $P<0.001$; SI Fig S4.1), and therefore may measure different components of variation in herbivory. We used Generalised Linear Mixed Models (GLMMs) using the 'lme4' R package (Bates et al. 2015). For 'herbivory occurrence' all models had a binomial error distribution with the frequency of damaged and undamaged leaves as the response variable. For 'herbivory intensity' all models had a Gaussian error distribution and natural log +1 transformed herbivory intensity (category of percentage damage) as the response variable. While the fixed effects of models varied according to the question being addressed (detailed below), the random effect structure stayed the same for all models (individual plant nested within transect nested within site). To improve model convergence across all models, continuous fixed effects were scaled to unit variance and centred on zero. For each model, all possible combinations of terms in the maximal model were compared using the '*dredge*' function in the 'MuMIn' R package (Bartoń 2013) and the best model selected based on minimising the Akaike Information Criterion (AIC_c). The variance explained by the best model (conditional R^2) and each of the fixed effect terms within (marginal R^2) were estimated for each model using the 'rsquared.GLMM' function in 'MuMIn' (Nakagawa et al. 2017). The variance explained by each fixed effect included in the top model was estimated separately by removing effects one by one and calculating the difference in the marginal R^2 value.

In order to test whether herbivory damage is lower in exotic *C. hirta* than in related native plants, herbivory was compared between species. GLMMs were fitted for herbivory occurrence and herbivory intensity separately, with fixed effects of species and an interaction with habitat (forest edge or forest interior) to test whether inter-specific differences in herbivory varied with disturbance level.

To test the effects of proximity to herbivory on natives (i.e. proximity index), habitat and local canopy cover on herbivory in *C. hirta*, whilst controlling for plant size and local density of *C. hirta*, models were fitted for only those *C. hirta* plants that were co-occurring with a *Melastoma* individual (i.e. within 10 m; n=196). Fixed effects included 'proximity index', habitat and local canopy cover (%), as well as plant size (total number of leaves per plant) and local density of *C. hirta* (0-10 of $2m^2$ sections *C. hirta* was present surrounding focal *C. hirta*). To test whether these variables may influence herbivory differently under different levels of disturbance (i.e. forest edge vs forest interior), an interaction with habitat was included for all fixed effects. These two models were re-fitted using our full dataset which included all *C. hirta* plants recorded (n=366), with fixed effects the same excluding 'proximity index', to test the effect of habitat and local canopy cover on herbivory in *C. hirta*, using a larger dataset.

To examine the effect of herbivory on the reproductive output of *C. hirta*, a GLMM was fitted with the total number of reproductive organs per plant (buds, flowers, immature fruit and ripe fruit) as the response variable with a Poisson error distribution and fixed effects of herbivory occurrence, herbivory intensity, habitat, local canopy cover, plant size and local density of *C. hirta*. We also tested for interacting effects between all fixed effect terms and habitat, in order to examine whether these variables influence reproductive output differently under different disturbance levels.

4.4 Results

Differences between habitats

Canopy cover varied significantly between the two habitats (median cover on edge transect = 49%, interior = 83%; Fig 4.2; Table S4.2; *P*<0.01) and within habitats (range of <1-94% on edge transects and 8-96% inside forest remnants; Fig 4.2), showing that despite the higher median value some forest interiors had very open canopies. On average there was little difference in plant size between habitats for *C. hirta* (median = 22 leaves per plant at the edge cf. 24 leaves inside the forest; Table S4.3; *P*=0.16) or native *Melastoma* (20 cf. 17 leaves per plant respectively). Likewise, there was little difference in the local density of *C. hirta* at forest edges (median 8 plants surrounding focal *C. hirta* plant) than on interior transects (6 plants; Table S4.3; *P*=0.49). Additional measurements of Specific Leaf Area (area of fresh leaf/dry mass; SLA) in *C. hirta* (see Appendix 4: Text S4.2 for full methods and results), revealed a highly significant increase from edge to forest interior, meaning *C. hirta* leaves were significantly thinner inside the forest.

Differences in herbivory rates between C. hirta and related natives

Herbivory was significantly lower in exotic *C. hirta* than in native *Melastoma* for both herbivory occurrence (15% lower in *C. hirta* plants compared with *Melastoma* plants; Tables 4.1 and Fig. 4.2; *P*<0.001) and herbivory intensity (15.9% lower per leaf for *C. hirta* compared with *Melastoma*; *P*<0.001). Despite differences between forest edge and forest interiors in terms of past and current disturbances, we found no significant effect of habitat (edge/interior) on herbivory rates for either exotic or native species.

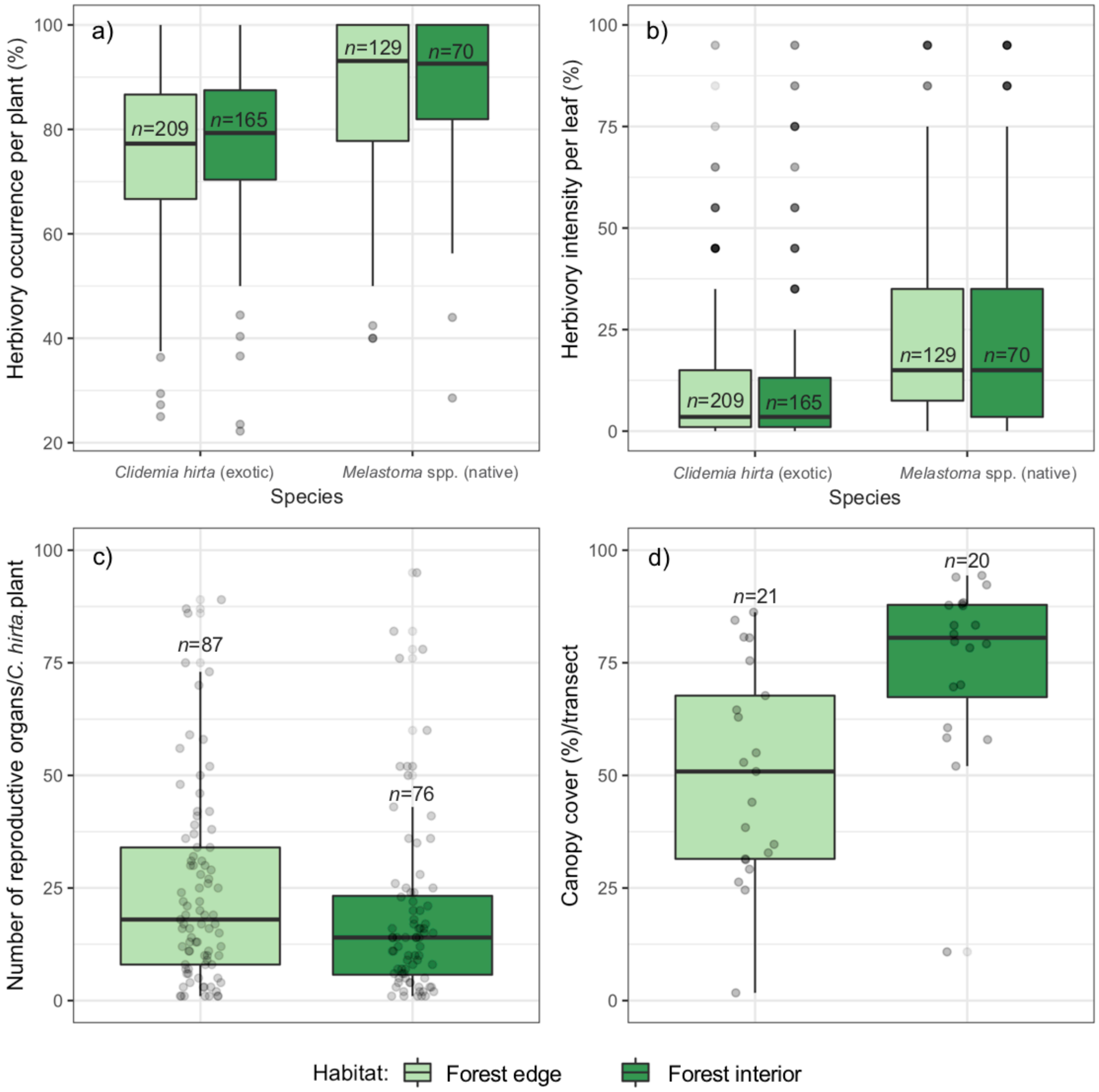

Figure 4.2: Herbivory rates in exotic *Clidemia hirta* and native *Melastoma* spp. plants at forest-oil palm edge and in disturbed forest of forest set asides within oil palm plantations, in Sabah, Malaysian Borneo. a) Difference in herbivory occurrence between species ('herbivory occurrence' = percentage of leaves per plant that are damaged by herbivory). b) Difference in herbivory intensity between species ('Herbivory intensity' = percentage of leaf area that is damaged by herbivory). c) Difference in the number of reproductive organs found per reproductively active *C. hirta* plants between forest edge and forest interior. d) Difference in canopy cover between forest edge and forest interior. Canopy cover was significant different at $P<0.01$ between habitats (GLMM, canopy cover was $\log_{10}$ transformed to improve model normality).

Table 4.1: Summary of Generalised Linear Mixed Models investigating drivers and impacts of herbivory in exotic shrub *Clidemia hirta*, in Sabah, Malaysian Borneo. Model numbers correspond to our three hypotheses (see aims) and full model descriptions are outlines in 'Statistical analyses' in the methods, including all fixed effects tests. 'Herbivory occurrence' = percentage of leaves per plant that are damaged by herbivory and 'Herbivory intensity' = percentage of leaf area that is damaged by herbivory. R^2_m = Marginal R^2, which indicates the R^2 for all fixed effects included in the model, R^2_c = Conditional R^2, which indicates the R^2 of the full model (Fixed effects + random effects). Fixed effects in top model is based on 'dredge' output. Interactions between fixed effects are denoted by an 'x'. ns = non-significant. R^2 = the R^2 for each individual fixed effect.

Model	**Response variable**	**R^2_m**	**R^2_c**	**Fixed effects in top model**	**Estimate**	***P***	**R^2**
1. Comparison between species	*Herbivory occurrence*	0.056	0.085	Species (*C. hirta*)	1.036	**<0.001**	**0.056**
	Herbivory intensity	0.158	0.554	Species (*C. hirta*)	0.988	**<0.001**	**0.158**
2. Influence of proximity to native plants (proximity index), disturbance and canopy cover	*Herbivory occurrence*	0.013	0.026	Canopy cover	0.126	0.082	0.005
				Proximity index	0.173	**0.011**	**0.008**
	Herbivory intensity	0.026	0.381	Proximity index	0.167	**0.002**	**0.026**
2. Influence of habitat and canopy cover (full dataset)	*Herbivory occurrence*	0.009	0.031	Habitat (*Forest*)	0.022	0.870	0.000
				Plant size	0.011	0.837	0.001
				Canopy cover	0.127	**0.031**	**0.004**
				Habitat x plant size	-0.199	**0.016**	**0.004**
	Herbivory intensity	0	0.414	-	-	-	-
3. Effect of herbivory on reproductive output in *C. hirta*	*Number of reproductive organs*	0.284	0.284	Plant size	1.644	**<0.001**	**0.231**
				C. hirta density	0.825	**0.002**	**0.055**
				Herbivory intensity	-0.768	**0.018**	**0.007**
				Habitat (*Forest*)	0.483	0.192	0.001
				Habitat x density	-0.488	0.189	0.01
				Habitat x herb. intensity	0.819	0.054	0.021

Influence of native species on exotic herbivory

For both measures of herbivory (occurrence and intensity), we found higher damage on *C. hirta* plants closer to related native plants with high levels of herbivory (Fig. 4.3a and Table 4.1; *P*<0.001). Solving the proximity index equation shows that the rate of herbivory damage in native *Melastoma* is more influential in driving herbivory in *C. hirta* than the distance between the plants. For example, there was no difference in expected herbivory occurrence in *C. hirta* between 0-10m distance when using the lowest native herbivory damage recorded (1% herbivory intensity), but there was an expected 13% increase in herbivory occurrence in *C. hirta* between 0 and 10m when using the highest recorded native herbivory damage (92.5%).

Influence of disturbance and light on exotic herbivory

Herbivory occurrence in *C. hirta* was significantly higher at locations with higher canopy cover (Fig. 4.3b and Table 4.1; *P*<0.05), suggesting that light levels are influential in determining rates of herbivory, although canopy cover explains less variance than proximity to natives in our models (Table 4.1). While we found no direct influence of habitat on herbivory, there was a significant interaction between plant size and habitat (Table 4.1; *P*<0.05) which revealed that the occurrence of herbivory was lower on larger *C. hirta* plants, but only for transects located within the forest remnants. We found no evidence of density-dependent herbivory occurring on *C. hirta* across models (i.e. there was no significant effect of local *C. hirta* density on either herbivory measurement; Table 4.1). Overall, we found considerable unexplained variation around the significant relationships between herbivory in *C. hirta* and the tested drivers, as shown in the scatterplots (Figs 4.3a-b), and the low R^2 terms for fixed effects in our models (R^2 ranging 0.004-0.231; Table 4.1), suggesting there are other factors influencing herbivory in *C. hirta* that we did not record.

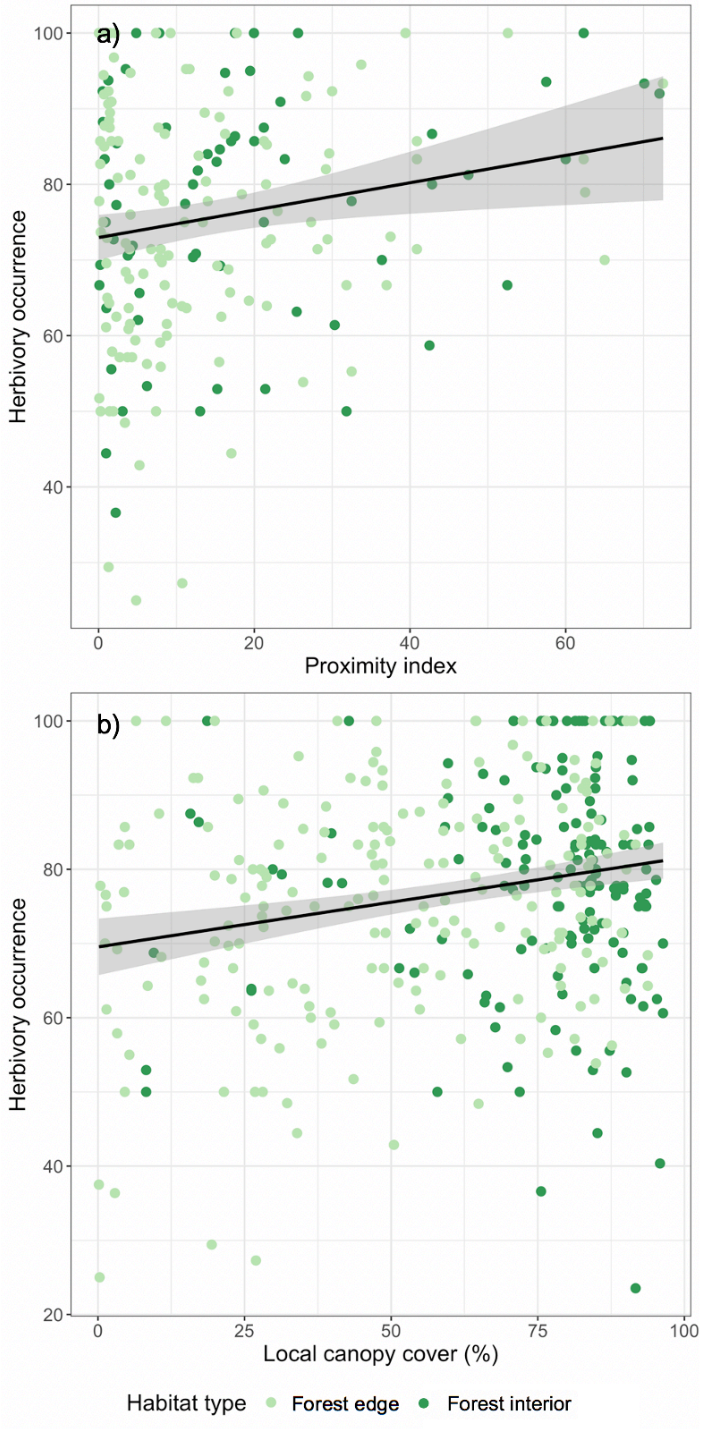

Figure 4.3: Relationship between herbivory occurrence in exotic *Clidemia hirta* plants and a) local canopy cover (*n*=366) and b) index of proximity to native *Melastoma* spp (*n*=196). 'Proximity index' = composite variable based on distance decay, combining distance to nearest native plant and herbivory intensity recorded on that plant (see methods for full details). Data is raw data and does not control for other variables.

Effect of herbivory on reproduction

We found a significant negative effect of herbivory intensity on the number of reproductive organs produced by *C. hirta* (Table 4.1; $P<0.05$). In addition, there was increased reproductive output on larger plants (Table 4.1; $P<0.001$) and when there was a higher local density of *C. hirta* ($P<0.01$). There was no effect of habitat or local canopy cover on reproductive output. Overall, reproductive output was significantly higher for exotic *C. hirta* with 44.5% of *C. hirta* individuals being reproductively active compared to 7.1% of native *Melastoma* spp individuals (Table S4.3; $P<0.001$), and of those reproductively active plants *C. hirta* had significantly more organs per plant (median of 15) compared to *Melastoma* plants (3 organs; Table S4.3; $P<0.001$).

4.5 Discussion

This study has shown for the first time that herbivory damage in invading exotic *C. hirta* shrubs is affected by proximity to damaged related native plants, suggesting that host-sharing of specialist herbivores may be happening and therefore potentially impacting *C. hirta* performance within its range in Sabah. We found no difference in herbivory damage between highly disturbed forest edge habitats and less disturbed forest interior habitats, but we did find greater herbivory in areas with higher canopy cover, showing *C. hirta* plants in more intact forests experience increased herbivory damage. Greater herbivory was negatively correlated with the reproductive output of *C. hirta* plants, as measured by the number of reproductive organs present, suggesting that damage by herbivores may be having a negative impact on the fitness of *C. hirta*. However, overall we found *C. hirta* plants experienced lower herbivory and a higher percentage of individuals were reproductively active compared with native *Melastoma* plants, which may place *C. hirta* at a competitive advantage over confamiliar native species.

Host-sharing between exotics and natives

Escape from natural enemies has allowed *C. hirta* to aggressively invade the native forests of Hawaii, where there are no native species belonging to the same family, Melastomataceae (DeWalt et al. 2004). Our finding of a positive association between herbivory damage in *C. hirta* and proximity to native related species, may mean there are shared herbivores that are adapted to feeding on Melastomes despite *C. hirta* not being native to Borneo. This is in agreement with other studies that found evidence of phylogenetic conservatism of herbivores in tropical plant species (Ødegaard et al. 2005; Weiblen et al. 2006), including in exotic species (Dawson, Burslem and Hulme, 2009). In this study, herbivores and pathogens were not explicitly observed but evidence of the same family of moth (tussock moths, Lymantriidae; Georg Hantke *pers. comm.*) was observed on leaves of both exotic and native species (Fig S4.2a-b) as well as similar patterns of disease (Figs S4.2c-e). The significance of the proximity index indicates that specialist herbivores are driving patterns in herbivory that we observe, but further investigation to identify the role of specific herbivores and pathogens would further elucidate our findings and confirm whether they belong to specialist or generalist groups.

The overall levels of herbivory intensity (i.e. percentage leaf area removed) we recorded in *C. hirta* were higher than those recorded in Hawaii where no native Melastomataceae are present (median 6.1% of leaf area removed in Sabah cf 0.9% in Hawaii; DeWalt, Denslow and Ickes, 2004). However, the levels of herbivory damage we recorded were comparable to *C. hirta's* native range of Costa Rica (4.4%; DeWalt, Denslow and Ickes, 2004) and introduced range in Tanzania where native confamiliar species are also present (4.68%; Dawson, Burslem and Hulme, 2009). Our measurements of herbivory intensity were lower than those levels recorded by Peters (2005) in introduced Peninsular Malaysia (~13%) and native Venezuela (~12.5-14%) despite being measured in comparable ways (i.e. percentage leaf area removed). These comparisons with other studies suggest herbivory is always higher where confamiliars are present within the native flora, giving strength to the argument that host-sharing is occurring in our sites. Despite our finding that *C. hirta* had much lower herbivory damage than natives (6.1% cf 20% herbivory intensity per leaf), there is not the same evidence for enemy release in Sabah that has been recorded in Hawaii. Herbivory intensity is apparently not high enough to exclude *C. hirta* from these forests, but it may be enough to regulate populations, preventing *C. hirta* from gaining the competitive advantage it has in Hawaii to become aggressively invasive. This is a form of biotic resistance called biotic containment (Levine et al. 2004), in which natural enemies help contain populations by lowering growth and reproduction and thus spread.

Role of light in herbivory damage

Our result that the occurrence of herbivory was higher in locations with higher canopy cover is in contrast to DeWalt et al. (2004) who found no difference in herbivory levels in *C. hirta* between fully open and partially close canopy in native (Costa Rica) and introduced ranges (Hawaii). The association between herbivory and canopy cover we found could suggest that either a physiological adaptation of *C. hirta* to low light conditions was occurring that also increases the likelihood of herbivory, or that herbivores and/or pathogens have a habitat preference to particular light levels.

Adaptations by plants to lower light conditions may make them more susceptible to herbivory damage. For example, Specific Leaf Area (SLA) is known to increase with declining light levels, especially in the understorey of tropical rainforests where light is a limiting factor (Poorter 1999; Steinger et al. 2003). Higher SLA indicates a thinner leaf (often correlated with lower leaf toughness) which may make plants more susceptible to herbivory. Studies on tropical trees have found both support for (Coley, 1988; Coley, 1983) and against (Poorter, Van de Plassche, Willems, & Boot, 2004) a positive relationship between herbivory and SLA. Indeed, SLA data collected for *C. hirta* plants (*n*=294) in the same forest remnant sites showed strong increasing trends over a gradient from oil palm plantation to intact forest, and with increasing canopy cover (Fig S4.3). Having higher SLA inside the forest with closed canopies may maximise carbon gain at low light levels, but leave plants susceptible to increased herbivory damage due to larger, thinner leaves that are easier to damage. Conversely *C. hirta* plants in more open areas may have thicker leaves to withstand higher temperatures and to avoid water loss (a limiting factor in open areas with higher temperatures), which also may help in their defence against herbivores (Blumenthal et al. 2020). Although, we did not measure SLA on the same plants we measured herbivory, and so do not know if there is an association between SLA and herbivory at an individual level, the strong trend with SLA recorded in the same transects suggests it may be influential and requires further investigation.

The increase in herbivory with canopy cover may also result from herbivores in human-modified landscapes having a preference for more closed canopy habitats, where the abiotic conditions may be more favourable (e.g. cooler temperatures and higher humidity) when compared to drier open habitats. However, an experimental field study in tropical Guyana, the converse was found that the richness and abundance of herbivores increased in recently created canopy gaps within tropical forests (averaging 74% canopy cover; Basset et al. 2001). The richness and abundance of tropical herbivores is strongly predicted by plant species diversity (Novotny et al. 2006; Basset et al. 2012), and disturbance from logging and fragmentation reduces native plant community composition in remaining areas of tropical forest (Chapter 2; Laurance et al. 2002, 2011; Arellano-Rivas et al. 2016) and promotes plant invasion (Chaper 2; Teo et al. 2003; Döbert et al. 2017b; Rembold et al. 2017; Waddell et al. 2020a). Within our sites, the diversity and abundance of native tree communities (adults, sapling and seedlings) inside forest remnants declined with increasing land-use change (i.e. fragmentation and logging; Chapter 2; Waddell et al. 2020a) and the average exotic plant richness and abundance increased with disturbance (Chapter 3; Waddell et al. 2020b). Thus, if the plant community varies between our forest remnant sites depending on local and landscape-level disturbance, the herbivore community is likely to vary as well, with individual species responses to disturbance.

Role of plant defences

Herbivory is a complex ecological process that involves many stochastic variables that can be difficult to measure in observational studies especially in highly diverse tropical rainforest. The low variation explained by each significant fixed effect in our models (Table 1), reveals that other unaccounted factors are contributing to variation in herbivory in *C. hirta*, including at the environmental (e.g. nutrients in soil) and taxonomic level (e.g. plant defences and herbivore and host richness). Leaf traits that reflect plant defences are known to influence herbivory, including leaf toughness and presence of trichomes (i.e. hairs) and concentrations of leaf nutrients and chemical defences (e.g. tannins; Coley and Barone, 1996). Both *C. hirta* and *Melastoma* have trichomes and are of similar thicknesses (Shiels, Ennis, & Shiels, 2014; Turner & Tan, 1991), therefore both these defences are unlikely to explain additional variation in our data. Low leaf Nitrogen levels are unattractive to herbivores (Kursar and Coley 1991) and leaf nutrient concentrations are driven by concentrates found in the soil. In tropical dry forests, the addition of fertilisers (N and Phosphorus) has been found to increase leaf nutrient concentrations and promote herbivory damage, but effects vary between species (Campo and Dirzo 2003). In oil palm planted areas, the addition of both fertiliser (that add N, P and Potassium to the soil) and leguminous cover crops that increase N availability (Huenneke et al. 1990) may increase leaf nutrient concentrations at the forest edge, but not inside the forest as these forest remnants were almost always above oil palm areas on steep outcrops. However, as we found no significant difference between forest edge and inside the forest it is unlikely that the addition of fertiliser and cover crop as a significant effect on our observed patterns.

Impact of herbivory on the invasiveness of Clidemia hirta

The negative association we found between herbivory intensity and number of reproductive organs suggests that damage by herbivores may reduce *C. hirta* fitness. Lower seed production from reduced reproductive output could affect both local population growth and dispersal, reducing spread rates and local dominance of *C. hirta*. Herbivory is known to reduce fitness as plants move resources away from reproduction to defence (Eichhorn et al., 2010; Marquis, 1984). However, *C. hirta* is widespread in these landscapes including inside continuous ‘old-growth’ rainforests (with ~92% mean canopy cover; Chapter 2; Waddell et al. 2020a). Thus, *C. hirta* is seemingly a successful invader of intact tropical rainforests in Sabah despite increased herbivory pressure with canopy cover and reduced reproductive output. Nevertheless, whilst *C.*

hirta is widespread in tropical South-East Asia (Chapter 2; Peters, 2001; Waddell et al., 2020a) and considered to be an invasive pest (Fee et al. 2017), this herbivory pressure may be enough to limit populations. Thus, populations of *C. hirta* in Sabah, and other parts of its introduced range with native confamiliars, may not be as invasive and damaging to native biodiversity as seen in Hawaii (Smith, 1985; CABI, 2020), although further investigation into herbivory and invasiveness across its introduced range is required to conclude this. Our results suggest herbivory may negatively affect reproduction and thus the long-term spread of *C. hirta*. However, our data is from one time point and a thorough investigation into the impact of herbivory on growth rates and reproductive output using field exclusion experiments such as in DeWalt et al. (2004) is required in order to draw robust conclusions on the effect of herbivory on *C. hirta* persistence in Sabah. In addition, these results highlight that other exotic species that have no native confamiliars may pose the highest risk to these habitats, especially those species with the traits known to increase colonisation within tropical forest remnants (Chapter 3; Waddell et al., 2020b; Dawson et al., 2009).

4.6 Conclusion

Clidemia hirta is one of the most prevalent exotic invaders of tropical forests, including the rainforest remnants embedded in oil palm landscapes in South-East Asia. Our study is the first to show increased herbivory on invasive *Clidemia hirta* shrubs when co-occurring with native confamiliars plants, suggesting host-sharing by specialist herbivores is occurring and that escape from enemies does not occur in Borneo as it does in other parts of its introduced range (i.e. Hawaii). Our finding that herbivory rates in *C. hirta* were comparable to its native range and that herbivory reduces *C. hirta*'s reproductive output, highlights that herbivory damage may reduce fitness of *C. hirta* plants. However, the lower herbivory rate in *C. hirta* compared with native *Melastoma* and much higher overall reproductive output, may put *C. hirta* at a competitive advantage to natives that occupying similar niches (i.e. woody ruderal, vertebrate dispersed shrubs). Our finding that there is reduced herbivory in more open tropical forests may result in the spread and colonisation of *C. hirta* in the most degraded forest remnants. These forest remnants are crucial for maintaining biodiversity within human-modified tropical landscapes (e.g. oil palm plantation). By increasing the canopy cover of native forest trees, the overall habitat quality will improve to reduce the number of exotic species invading (Chapter 3; Waddell et al., 2020b) and it may also limit the spread of *C. hirta* by lowering reproductive outputs and therefore fitness, due to increased herbivore activity in closed canopy forests. Although, capturing complex plant-herbivore interactions in observational studies is challenging, this study provides the first investigation into herbivory damage in invasive *C. hirta* in its introduced range of Sabah, Malaysian Borneo. Our results reveal drivers of herbivory in this highly invasive tropical shrub, points to future work in improving our understanding of *C. hirta* as a successful invader in tropical forests and helps towards controlling its spread.

4.7 Author contributions

EHW, LFB, MH, JKH and DSC conceived the ideas. EHW, LFB, MH, SF, JT, JKH, CB, YKL, ABS, AJ and DSC designed methodology; EHW, SF, ABS and AJ collected the data; BBO and AJ led plant identification; EHW and DSC analysed the data; EHW led the writing of the manuscript.

Chapter 5

View across oil palm plantation at sunset with rainforest remnants on the horizon

General discussion

5.1 Abstract

Studies on the exotic plant invasion of tropical rainforests are rare, especially in fragmented human-modified landscapes, despite the increasing prevalence of such landscapes across the tropics. The results presented in this thesis have increased our understanding of plant invasion within tropical rainforests, in particular rainforest embedded within oil-palm dominated landscapes. My findings include: (i) establishing which factors make a rainforest remnant more invasible, (ii) the characteristics of exotic species that successfully colonise these forests, and (iii) the ecological factors that influence herbivory in the most common exotic species in my study landscape, *Clidemia hirta*. I found that invasion of forest remnants in fragmented landscapes can be low despite being surrounded by a heavily invaded oil-palm matrix, but only if local forest disturbance remains low and canopy structure remains relatively intact. This forest disturbance, caused primarily by commercial selective logging prior to plantation establishment, alters the native forest community and forest structure (i.e. wood density, number of large dipterocarp trees and canopy cover), which changes the abiotic conditions. Light levels drive patterns in individual exotic species occurrence, with most preferring high light environments, a few species preferring intermediate light levels and only one species able to persist in low-light conditions within forests (*C. hirta*). Within these forest remnants there may also be a level of biotic resistance by the native community. This is evidenced by a negative relationship between invasion and young native tree diversity (i.e. genera richness, number of stems and phylogenetic diversity), as well as evidence that herbivory (due to host-sharing with confamiliar native species) reduces reproductive output of *C. hirta* plants. *C. hirta* is the most common species recorded in the study and only invader of intact closed canopy rainforests, within both small remnants and continuous 'old-growth' forest. However, other exotic species with

similar traits to *C. hirta* (i.e. vertebrate dispersed shrubs) may pose a threat to these forest remnants in the future, especially if these species have a degree of shade tolerance and can persist in intact areas of forests, as does *C. hirta*. To help ensure these forests are robust to invasion, active management to increase canopy cover would reduce exotic species richness and occurrence as well as increasing herbivory pressure on *C. hirta*, which may reduce its spread by decreasing fitness. In addition, active planting of native tree seedlings may help to reduce invasion and will improve native diversity within forest, increasing their conservation value and providing co-benefits.

5.2 Summary of thesis findings

This thesis has investigated the invasion of rainforest remnants by exotic plant species within human-modified tropical landscapes. I had three objectives: (i) to identify which local and landscape factors make rainforest remnants more susceptible to exotic plant invasion, (ii) to investigate the characteristics of exotic species that successfully colonise these forests, and (iii) determine the ecological factors that influence herbivory in the most common exotic plant, *Clidemia hirta*, and whether these factors help to explain the success of this highly invasive tropical species. Here I review the key findings from each Chapter in the context of current knowledge about tropical plant invasions, discussing both the wider implications of my results and further work needed to reduce exotic plant invasion within conservation planning of tropical landscapes.

Chapter 2: Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants

In this chapter, I investigated the factors influencing invasion by exotic plant species of rainforest remnants that span a gradient in local and landscape disturbance. Invasion was found to be correlated with local forest disturbance and propagule pressure (high richness and occurrence of exotic species in the surrounding plantation matrix), the latter being driven by greater fragmentation of forest in the landscape. Thus, increasing forest fragmentation promotes exotic plant invasion in remnant tropical forests, especially if local disturbance is high. I also found a significant negative correlation between invasion and native tree seedlings and sapling community diversity, and that the native tree community responded negatively to land-use change. These results suggest that the association between exotic species invasion and young native tree community may have impacts for native regeneration. This is especially important given that fragmentation is predicted to increase and so exotic plant invasion may become more problematic in the future.

Chapter 3: Trait filtering during exotic plant invasion of tropical rainforest remnants along a disturbance gradient

In this chapter, I investigated environmental trait-based filtering during the invasion of tropical rainforest remnants from highly-disturbed, human-modified agricultural habitats. Exotic species richness and occurrence declined significantly from oil palm to forest edge to inside the disturbed areas of rainforest remnants, and only one species, *Clidemia hirta*, invaded intact forest. However, I found that the species invading rainforest remnants were not a random subset of the species found in the oil palm matrix. Instead, successful invasion of rainforest remnants required relatively long-distance dispersal, in particular by vertebrates, as well as traits that are more similar to those of native forest species (i.e. tall and woody), presumably making these exotic species better equipped to compete and persist in the forest environment. For each trait, the community-weighted mean for the forest edge community was found to be intermediate between oil palm and disturbed forest, which provides strong evidence that trait-filtering occurs during invasion of rainforest remnants. In addition, my results show that disturbed tropical rainforests with open canopies are more susceptible to invasion than those with more intact canopies and highlight the traits of exotic species which can invade rainforest habitats. Together, this progresses our ability to use traits to identify species that might pose a threat in regenerating forests and environments most at risk.

Chapter 4: Canopy cover and proximity to native confamiliars affects herbivory of an invasive shrub in Bornean rainforests

In this chapter I examined the ecological factors that influence herbivory of *Clidemia hirta* plants, which is hypothesised to influence its establishment success within its introduced range. I found that *C. hirta* plants had lower herbivory than native comfamiliars, but that herbivory levels were comparable to those in *C. hirta's* native range and higher than in introduced populations in Hawaii, where the high abundance of *C. hirta* has been attributed to escape from enemies. Herbivory increased with proximity to native *Melastoma* plants with high herbivory damage, suggesting that host-sharing by specialist herbivores has occurred. I also found that herbivory was higher in areas with a more closed canopy, and that *C. hirta* plants with higher herbivory damage tended to have reduced reproductive output. These results show that lower herbivory pressure in open canopy forest may make disturbed forest remnants in these landscapes more susceptible to invasion by *C. hirta*. They also suggest that highly invasive species, such as *C. hirta,* may be less successful invaders in regions with native confamiliars that harbour populations of natural enemies, providing a 'biological control' service for exotic plant species by impacting their productivity.

5.3 How invasible are tropical rainforests: updating the concept of a robust ecosystem?

The current theory that intact tropical forests are generally resilient to plant invasion made by review papers (Rejmánek 1996; Fine 2002; Denslow and DeWalt 2008) was supported for the intact forest sites investigated in this thesis (Chapter 2), as was the claim that all tropical forests likely contain at least one exotic species (Usher 1991). Since these previous review papers established the idea that invasion is low in tropical forests, there has been an increase in the globalisation and connectivity of tropical regions (Seebens et al. 2018) as well as a rise in deforestation and degradation of remaining tropical forests (Potapov et al. 2017; Curtis et al. 2018). Thus, potentially there has also been an increase in exotic plant invasions. However, my systematic investigation into current literature (section 1.6. in Chapter 1) showed that there remains a severe lack of studies into the role of land-use change on invasion of tropical rainforests (Wiser et al. 2002; Rembold et al. 2017) and none that looked specifically at fragmentation.

Within intact 'old-growth' rainforests, such as Danum Valley Conservation Area, there is very low invasion underneath full canopy (Chapter 2), despite several exotic species having established populations within nearby settlements (i.e. Danum Valley Field Centre) and along roadsides. However, these 'old-growth' rainforests do experience some level of invasion by *Clidemia hirta*, mostly along narrow trails and in small canopy gaps up to at least 1.5 km from source populations of exotic propagules at the field centre and main road (Fig. 5.1). Within once-and twice-logged forest connected to large tracts of intact forest, the level of invasion was found to be higher than intact forest (i.e. more individuals) but it was still only *C. hirta* that was found inside these forests. This suggests that more degraded areas of rainforest are more susceptible to invasion (i.e. due to disturbance related to selective logging) and that *C. hirta* is the most aggressive invader of tropical rainforests in Sabah.

Figure 5.1: *Clidemia hirta* within intact 'old-growth' rainforest in the Danum Valley Conservation Area, approximately 1.5 km from the main road and field centre.

In Chapter 2, rainforest remnants embedded within agricultural landscapes were found to have much higher rates of invasion (i.e. number of exotic species and their occurrence) compared to more intact sites within a continuous tract of forest (Fig. 5.2). Land-use change is driving this pattern of invasion, with greater landscape fragmentation (i.e. less forest cover and more edge habitat within the landscape and a longer history of forest clearance) increasing invasion of forest remnants through increased propagule pressure (i.e. number of exotic species and their occurrence in the surrounding oil palm planted areas). Areas of forests embedded in landscapes with fewer remaining forest areas with relatively more edge habitat in the landscape (i.e. within 2km radius buffer surrounding survey plots) are therefore, more invasible by exotic species. Roads and plantation traffic likely bring in the majority of exotic propagules into these agricultural landscapes, where populations establish in oil palm planted areas and roadsides, and some exotic species then spread into remnant forests. Fragmented landscapes are becoming increasingly common across the tropics (Taubert et al. 2018), and therefore the spread of existing and new exotic species is likely to continue into these newly opened up and fragmented landscapes. In addition, the number of exotic species and their occurrence was found to increase gradually from intact closed canopy forest within these remnants (1 species) to disturbed forest (mean 3.1 species) to the forest edge (7.8 species) and into oil palm (9.2 species); this further supports the conclusion that increasing disturbance from land-use change in tropical rainforest landscapes promotes exotic plant invasion. Rembold et al. (2017) found a similar result that oil palm and rubber plantations were more invaded than both agroforestry and remaining areas of natural forest within human-modified landscapes. Plantations necessitate settlements and extensive networks of roads, and these provide the ideal habitat for many exotic plant species to invade (e.g. high light and disturbance; Blumenthal, 2006; Davis, Grime, & Thompson, 2000; Theoharides & Dukes, 2007) and these established populations increase the volume of exotic propagules in the environment, increasing propagule pressure. However, there can be relatively low invasion of forest remnants within these fragmented landscapes if local forest disturbance is low and hence there is high canopy cover.

Figure 5.2: Tropical rainforests in Sabah. A – native tree seedlings in the understorey of intact ‘old-growth’ forest in Danum Valley (remnant number F1; Table S2.1). B – Heavily invaded roadside in Sabahmas oil palm plantation adjacent to a rainforest remnant on the right (remnant F3). C – Invaded understorey in rainforest remnant (F3; 57 ha), predominately by exotic *Chromolaena odorata* and native weed *Urena lobata*. D – Large remaining native tree within small rainforest remnant (remnant F13 ~10 ha). Photo credit for D: Azlin Bin Sailim.

By surveying along a gradient of local forest disturbance (i.e. unlogged, once- and twice-logged and heavily-logged forest) and using a path-modelling approach, I found that invasion is likely to be low if the remnant forest remains intact in terms of forest structure (i.e. more adult trees belonging to Dipterocarpaceae and higher wood density; Chapter 2). Furthermore, higher local canopy cover is associated with lower abundance and diversity of exotic species (Chapter 3), and this is likely driven by the lower understory light levels within more intact forests. In line with most exotic species, the majority of exotic species recorded in this study prefer high or intermediate light levels (Chapter 3) and only *Clidemia hirta* appears to be sufficiently shade tolerant to invade deep into closed canopy forest. Therefore, most exotic species that are introduced into these plantations thrive only in the open, disturbed habitats and are filtered out by unsuitable abiotic conditions (i.e. low light) inside forest remnants with intact canopies. Less disturbed forests at a later successional state (i.e. higher wood density), with high canopy cover and many large dipterocarps remaining (>20cm DBH) are more robust to invasion because there is less light reaching the forest floor preventing exotic propagule establishment. These forests are more structurally complex, likely due to less intense commercial logging history. My finding that logged tropical forests are more invasible corroborates those of another study, also conducted in rainforests in Sabah (Döbert et al. 2017a). My results provide critical empirical data to confirm theoretical ideas that landscape fragmentation and subsequent forest degradation increases invasion in tropical forest landscapes (Rejmánek 1996).

Within forest remnants there may also be a level of biotic containment (a type of biotic resistance; see Levine et al. 2004) in which native diversity helps control the spread of exotic species, thereby containing these populations. This biotic containment is seen in both the negative relationship between invasion and young native tree diversity (i.e. genus richness, number of stems and phylogenetic diversity; Chapter 2) and herbivory lowering fitness in *Clidemia hirta* (Chapter 4). Higher invasion when young native tree diversity is lower (Chapter 2), may be because there are available niches to fill (Empty Niche Hypothesis). In addition, there is likely to be greater niche overlap between young native trees and the exotics species that do invade these remnants (i.e. vertebrate dispersed shrubs; Chapter 3), than the exotic forbs which are prevalent in the oil palm but that fail to colonise the forest interiors (such as *Ageratum conyzoides* and *Asystasia gangetica*). Therefore, exotic species more similar to the native understorey community, and adapted to the environment, are more successful invaders. These findings improve our understanding of the mechanisms driving successful invasion of these forest remnants and they also help to identify current and future problematic species capable of establishing within these landscapes (see discussion in section 5.4). Although *C. hirta* is widespread across Sabah, herbivory (associated with proximity to native related plants) was found to reduce reproductive output, which supports the idea of biotic containment (Levine et al. 2004). The native pest diversity in these forests may be sufficient to contain this species and so reduce its spread and invasiveness in Sabah. However, my finding of reduced herbivory in open forests (Chapter 4) suggests disturbance may lessen the impact of pests on this species and promote its spread within disturbed habitats.

These findings on what makes tropical forests invasible in Sabah have added to our understanding of the drivers of invasion of multiple exotic species in tropical rainforests (i.e. exotic community-level factors; Chapters 2 and 3; Fig. 5.3) as well as widening our knowledge of the understudied yet highly invasive species, *Clidemia hirta*, within South-East Asian tropical rainforests. Specifically, I have examined the role of local and landscape disturbances (i.e. impact of logging and forest fragmentation), abiotic conditions (i.e. soil conditions and canopy cover), biotic characteristics of the invaded community (i.e. native community diversity and herbivory pressure), and the biotic characteristics of the invading species (i.e. functional and life-history traits). These findings may be applicable to other tropical regions (e.g. Central and South America and Central Africa) and different types of tropical forest (e.g. dry or seasonally dry forests) but additional comparable studies are needed. For example, differences in native flora, including the dominance of Dipterocarpaceae in South-East Asia (Gentry 1988), could drive differences in both the response of forests to disturbances and level of biotic resistance/containment to exotic plant invasions. There are also differences in forest structure between the regions that may affect canopy structure, light availability and therefore invasibility. For example, the forests in South-East Asia are comparatively taller and have higher biomass that those found in the Neotropics and Central Africa (Banin et al. 2012; Sullivan et al. 2017). Additionally, dry tropical forests are generally more fragmented and disturbed than tropical moist forests (Rejmánek 1996), and therefore, may be more readily invaded. Future studies comparing regions and forest types would help elucidate similarities and differences in the drivers of invasion with all types of tropical forests.

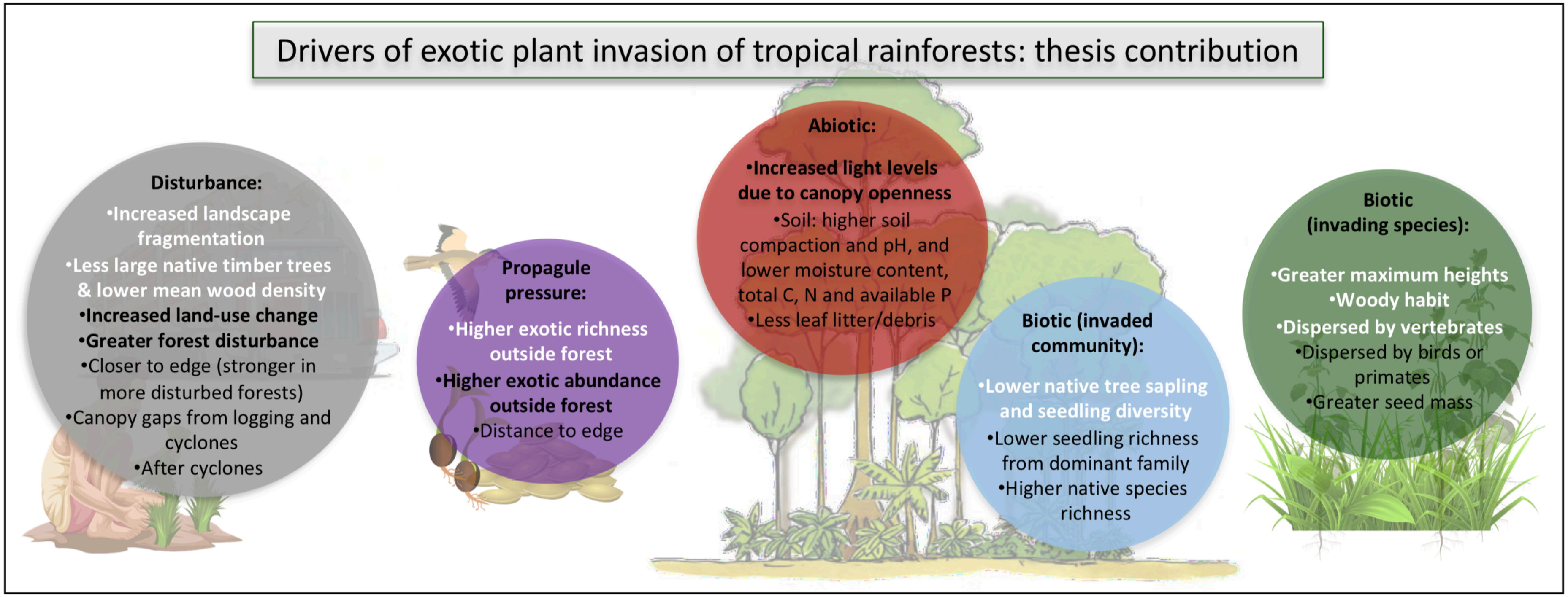

Figure 5.3: Summary of the drivers of exotic plant invasion in tropical rainforests from 11 published studies with multiple exotic species (Fig. 1.4) plus the results from this thesis. New results from this thesis are in white and previously investigated variables that were supported by my results are in bold.

5.4 Is *Clidemia hirta* the only threat to closed-canopy tropical rainforests?

My finding that *Clidemia hirta* is the only exotic species to invade closed-canopy rainforest in Sabah (both rainforest remnants embedded within oil-palm plantations and more continuous logged and unlogged forests) is expected as *C. hirta* is considered one of the only tropical exotic plant species capable of invading the understorey of undisturbed tropical forest (DeWalt et al., 2004; Döbert et al., 2017a; Peters, 2001). Across much of its introduced range, *C. hirta* is considered an extremely invasive species, including Pacific Islands, India, South-East Asia, Eastern Africa and Australia (Wester and Wood 1977; Rejmánek 1996; Strahm 1999; DeWalt et al. 2004; Dawson et al. 2011; CABI 2019), but despite this, *C. hirta* is understudied compared to specific temperate exotic species (Kueffer et al., 2013). *C. hirta* has been most well-studied in Hawaii, where its success at invading native forests has been attributed to escape from natural enemies, whilst in its native Costa Rican forests enemies restricted its population to disturbed, open areas (DeWalt et al. 2004). My finding that *C. hirta* experiences comparable herbivory rates in Sabah as found in its native range, and much lower than in Hawaii (Chapter 4), suggests that release from enemies is not occurring to the same level in Sabah as it does in Hawaii. Furthermore, the negative relationship between herbivory and reproductive output suggests that populations of *C. hirta* in these forest remnants may be contained due to herbivory pressures. However, overall *C. hirta* has lower herbivory and higher reproductive output in Sabah than native confamiliar *Melastoma*, that occupy a similar niche to *C. hirta* (weedy shrub). Thus, despite herbivory reducing fitness in *C. hirta* it may still gain a competitive advantage over other exotic species, native confamiliars and potentially native young trees. Multi-species field experiments tracking herbivory, growth and mortality rates, along with reproductive output, would help determine the impact herbivory has on fitness and survival, and whether *C. hirta* does out-compete these other species.

Clidemia hirta has the traits that I identified as being important for invasion of forest remnants – being woody, tall, and vertebrate dispersed (Chapter 3), but my finding that the exotic community still had these traits when *C. hirta* was excluded from analyses, shows that there are other exotic species, with similar traits to *C.hirta* present in these forests. So why are these species currently not as widespread as *C. hirta*? And could these species be a future threat to intact forests in Sabah? The other species present within these forests, albeit in much lower numbers and only in disturbed forest, that have these same traits include, *Chromolaena odorata, Mimosa pudica* and *Mimosa diplotrich*a. These species are highly invasive in much of their introduced range including tropical Australia, India, Africa, South-East Asia and Pacific islands (Gautier 1992; Padmanaba et al. 2017; CABI 2019), and *C. odorata* and *M. pudica* are considered amongst the world's top invasive species (including plants, animals and micro-organisms; Lowe et al. 2000). One reason they appear not to have been so successful in the landscapes I have studied may be because of differences in their modes of dispersal. These three species are primarily dispersed by wind or water, and are only secondarily dispersed by vertebrates externally if seeds get stuck in the fur of passing mammals. In plantations, dispersal by wind and water may be restricted due to native trees reducing wind flow into forest interiors and a lack of water bodies, and reduced terrestrial mammal diversity in these landscapes may restrict secondary dispersal (Bernard et al. 2014; Edwards et al. 2014). Conversely, *C. hirta*'s success may be partly driven by internal vertebrate dispersal, likely by ingestion of fruits by generalist birds, as there are more birds in highly-fragmented oil-palm dominated tropical landscapes than terrestrial mammals (Edwards et al. 2014).

In addition to these species (*C. odorata, M. pudica* and *M. diplotricha*), the Neotropical shrub *Lantana camara*, is dispersed by vertebrates in a similar way to *C. hirta*, and is also present within oil palm planted areas but in very low numbers in just a few sites (Chapter 3). This species is highly invasive across much of the tropics (CABI 2019), and is also considered one of the world's worst invasive species (Lowe et al. 2000), so the reason it is not more widespread in the Sabah or found inside these forest remnants is unclear. One explanation may be that *L. camara* does not have the same level of shade tolerance that *C. hirta* has as documented by DeWalt et al. (2004) in Hawaii. In addition, my finding that the Specific Leaf Area of *C. hirta* leaves increases from oil palm into intact forest, may be evidence that *C. hirta* is able to adapt to varying light conditions found within human-modified landscapes, and this adaptability may drive its success over other exotic species. Furthermore, time lags in invasion may explain why these species have not yet invaded these forests to the same levels as *C. hirta*, with their populations still expanding (Essl et al. 2012). Invasion time lags are thought to be shorter in tropical regions than in temperate regions, and shorter for exotic herbaceous species than woody species (Daehler 2009). However, data on the introduction date of tropical exotic species are scarce, especially for unintentional introductions with most only having an approximate date (Seebens et al. 2020).

In order to minimise future invasion by a highly aggressive exotic invader, a risk assessment of potential future invasive species could be undertaken for any species found within agricultural areas. Risk assessments for tropical weeds have already been developed (Daehler et al. 2004; Chong et al. 2011) based on a well-established protocol from Australia and New Zealand, called the Australian Weed Risk Assessment (Pheloung et al. 1999), that either 'reject' weeds or 'accept' non-weeds of concern. These assessments are made up of around 49 yes/no questions on the invasion history, ecology and biogeography of the invading species, along with life-history and functional traits, including life-span, dispersal mode and shade tolerance (Pheloung et al. 1999; Daehler et al. 2004). The WRA score is the sum of these answers with each question being awarded between -3 and 5 points (most -1 to 1) depending on the answer, and those with >6 points are rejected and deemed to be a risk as a potential invasive species. Common exotic shrubs present in Malaysia (i.e. those included in Table 1.1; with the exception of *Varronia curassavica* that has not been assessed) are considered to be high risk weeds based on prior risk assessments (Table 5.1). Some of these exotic species have unknown distributions in Sabah, such as *M. pigra, P. aduncum, P. cattleianum* and *V. curassavica*, but as they are considered invasive in other regions of their introduced range, they may eventually become invasive in Sabah if they spread undetected. In addition, the distribution of *Miconia calvescens* is unknown in much of South-East Asia but it is considered to be one of the world's worst invasive species, especially of fragmentated tropical rainforest, and has been highlighted as potentially being as invasive as its confamiliar, *C. hirta* (CABI 2020). Thus, these eleven highlighted species and other widespread tropical invasive shrubs should be considered as a potential threat to forest remnants in Sabah and also other degraded forests across the tropics.

Table 5.1: List of exotic shrubs that are or potentially may become invasive in tropical rainforests of Sabah, Malaysian Borneo and their weed risk assessment scores. All species are originally from the Neotropics with the exception of _R. communis_ that is from North-Eastern Africa. Dispersal mode and shade tolerance from weed risk assessments (WRA). Dispersal mode is covered by questions 7.04 to 7.07 and shade tolerance in question 4.09. Sources for WRA scores in footnotes. * = recorded in oil palm plantations and ** = recorded inside rainforest remnants in Sabah during this study. † denotes inclusion of species in ‘100 of the World's Worst Invasive Alien Species’ by ISSG (2020).

Species name	**Family**	**Dispersal mode**	**Shade tolerance**	**WRA scores**
†_Chromolaena odorata**_	Asteraceae	Wind	Yes – seedlings only	28[a]
†_Clidemia hirta**_	Melastomataceae	Vertebrate internal	Yes	27[a] , 28[c]
†_Lantana camara*_	Verbenaceae	Vertebrate internal	Yes	32[a],21[b],20[c]
†_Miconia calvescens_	Melastomataceae	Vertebrate internal	Yes	14[a,b]
Mimosa diplotricha**	Fabaceae	Water/ vertebrate external	No evidence	24[a,b]
†_Mimosa pigra_	Fabaceae	Water/ vertebrate external	No	25[a,b]
Mimosa pudica**	Fabaceae	Water/ vertebrate external	Yes	18[a],23[c]
Piper aduncum	Piperaceae	Vertebrate internal	No	18[a,b]
†_Psidium cattleianum_	Myrtaceae	Vertebrate internal	Yes	18[a,b]
Ricinus communis	Euphorbiaceae	Ballistic	No	21[a,b]
Varronia curassavica	Boraginaceae	Vertebrate internal	No[1]	n/a

a = Pacific Island Ecosystems at Risk (2020) [available = www.hear.org/pier/index.html]
b = Daehler and Denslow (2020) [available = www.botany.hawaii.edu/faculty/daehler/wra/]
c = Dawson et al. (2009).
1 = USDA (2013) Weed risk assessment for _Cordia curassavica_ (Jacq.) Roem. & Schult. (Boraginaceae) – Black sage [available at https://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/wra/Cordia_ curassavica_WRA.pdf] (accessed 22 October 2020).

5.5 Future work and conservation of fragmented tropical landscapes – ensuring rainforest remnants are robust to invasion.

In tropical agricultural landscapes, remnant forests are crucial for conservation of native biodiversity and ecosystem services (Fleiss et al., 2020; Hill et al., 2011; Koh, 2008; Matos et al., 2020; Ricketts, 2004; Stride et al., 2018; Volenec & Dobson, 2020). However, very few studies have examined exotic species in such landscapes (Chapter 1:

section 1.5; Döbert et al. 2017; Rembold et al. 2017). The results of my thesis have added to our understanding of the drivers of invasion within these landscapes and in tropical forests as a whole (Fig. 5.3). Specifically, the empirical evidence that greater forest fragmentation encourages invasions within agricultural areas and helps increase the spread of propagules into forest remnants, and that forests which have altered abiotic conditions and native biotic communities due to the impact of logging are more susceptible to invasion by exotics. However, my study has also raised several questions that could be answered in future research. An important question still to answer is whether or not these exotic species are detrimental for forest regeneration, as has been shown for other tropical forests (Wester and Wood 1977; Ramaswami and Sukumar 2014; Chiou et al. 2016). If there is a detrimental impact on native species, which exotic species are driving this and what is the extent of their impact? My finding of an association between higher invasion and reduced native tree sapling and seedling diversity in these forest remnants, could suggest a negative impact of exotic species on the native community (Chapter 2). A similar negative relationship was also observed between between dipterocarp seedlings and exotic biomass by Döbert et al. (2017) in a different region of Sabah. Manipulative field experiments measuring growth and survival rates of both exotic and native species would be required to determine the direction of the relationship I found – whether the presence of exotic species reduces native tree sapling and seedling diversity over time, or if the establishment of exotic species is lower where young native tree diversity is higher (i.e. native biotic resistance to invasion).

It is vital to protect remaining forests from further degradation due to exotic plant invasions in order to conserve biodiversity, supporting RSPO guidelines (RSPO, 2018). Although it is unlikely that all exotic plants can be excluded or eliminated from forests within Sabah, the results of this study demonstrate there should be effective ways to minimise the level of invasion. My findings have yielded practical suggestions for reducing invasion risk within these forest remnants, which may also be relevant to other rainforest remnants in other tropical landscapes. Increasing canopy cover (e.g. to >87.5% as found in intact forest; Chapter 3) would help to exclude all exotic species with the exception of *C. hirta* and also increase herbivory pressure for *C. hirta*, which could suppress its productivity and thus reduce its spread in these forests. Active restoration of these forests by planting native tree seedlings or removal/thinning of climbers, pioneers and exotics, could increase canopy cover and native diversity (and therefore increase biotic resistance/containment) over time (Adjers et al. 1995; Swinfield et al. 2016; Wheeler et al. 2016; Freitas et al. 2019). However, restoration of tropical forests has varying success. Active planting of native tree seedlings can quickly increase canopy cover (Freitas et al. 2019) and above ground carbon, but is slower to increase overall diversity (Wheeler et al. 2016). Planting is also more successful when maintained for several years (Adjers et al. 1995), which can increase costs, and overall, seedling planting is a more expensive restoration method than restoration via removal of pioneers and exotic species (Swinfield et al. 2016) and natural regeneration. The use of herbicide is commonly used and an effective method to control invasive species across biomes (Kettenring and Adams 2011); however, the use of pesticides in forest remnants within RSPO-certified plantations would be against the RSPO guidelines and may also have a detrimental impact on native species (RSPO, 2018). Targeted removal of exotic plants in oil palm planted areas for those exotic species with traits associated with successful invasion of forests, could decrease spread into forest remnants by reducing propagule pressure in the landscape. This includes species that are known to be present in these landscapes, *Clidemia hirta, Chromolaena odorata, Mimosa pudica,* *Mimosa diplotricha* and *Lantana camara*, and also any new exotic species that may be introduced to oil palm landscapes in the future (Table 5.1).

5.6 Conclusions

I found that invasion of tropical rainforest remnants in Sabah by exotic plants depends on interactions between propagule pressure, landscape fragmentation, local forest disturbance, traits of the invading species and biotic characteristics of the invaded community. All tropical rainforests in Sabah, including intact 'old-growth' forest, are likely to have at least one exotic plant species, and this is also probably true for rainforests in other regions of the tropics. Forest remnants within human-modified landscapes are more invasible but invasion can remain relatively low if local forest disturbance is minimal. However, if local forest disturbance is high, invasion rates are very likely to increase due to altered abiotic conditions, disrupted native communities and biotic interactions. *Clidemia hirta* is the most common exotic species of disturbed and intact rainforest within Sabah, and probably across much of its introduced range. However, other exotic species with similar traits to *C. hirta* may become important invasive species in Sabah, especially if they have a degree of shade tolerance at some point in their life cycle. Management of these forest remnants is unlikely to fully exclude exotic plant species, but to reduce overall invasion levels and fitness of *C. hirta* will require restoration of high levels of canopy cover and complex forest structure within these forests.

Appendix 1: Supporting Information for Chapter 1

Text S1.1: Systematic search methods

A systematic search of studies focusing on plant invasions within tropical rainforests was carried out in March 2020 following the protocol in Pullin & Stewart 2006. Peer-reviewed journals were searched on ISI Web of Science using the following key word combinations: (*tropic* AND (*forest* OR wood* OR jungle) NEAR/5 AND (invas* OR non-native OR non-indigenous OR exotic*) NEAR/5 (plant* OR flora* OR tree* OR herb* OR shrub* OR understorey* OR communit* OR divers* OR richness*)). Our search criteria included studies that were observational or field experiments that focused on the drivers of exotic plant invasion within tropical rainforests. Studies I excluded were lab and common garden studies, those based in tropical dry (i.e. seasonally dry, monsoon, deciduous or semi-deciduous forests) and those that tested monitoring methods, assessed the impact of exotic plants or tested the effectiveness of control methods. I also excluded those that did not have explicit data on the effect of at least one driver on a measurable variable of exotic plant invasion (i.e. exotic plant invasion was quantified as either the presence of exotic species, exotic species richness, exotic abundance, biomass, basal area, cover, growth rates, survival, reproductive output and/or photosynthetic performance), including species that qualitatively mention exotic invasion occurrence. If a study did not state the specific forest type, I used the Köppen-Geiger climate classification to confirm the study location was in the tropical rainforest climatic zone (Kottek et al. 2006).

The database results yielded 1208 papers, and after excluding irrelevant titles 538 papers remained. The abstracts of these 538 were read and 92 papers that met the above criteria were kept for further assessment. The full text was then read for these 92 and those that met our full criteria kept for inclusion in the review. Only studies with full text in English language were included. A total of 30 publications investigating drivers of exotic plant invasion within tropical rainforests met our criteria. Details of each study were recorded, including: location of the fieldwork (country, study site name, latitude and longitude), type of study (i.e. observational or field experiment), response variable (e.g. exotic species richness, exotic abundance, exotic biomass, exotic cover, exotic functional traits and exotic herbivory rates), study focus (i.e. single species, specific group or full community), plant form group (i.e. forb, graminoid, climber, shrub, tree or multiple), exotic species studied and finally, all the measured explanatory driver variables and the directional effect of each driver has on invasion (four possible levels for each driver per study: positive, negative or no significant effect, or variable not included). Literature was managed and read within Mendeley, and information was extracted and recorded on a Microsoft Excel spreadsheet.

Appendix 2: Supporting Information for Chapter 2

Text S2.1: Partial least square path modelling methodology and model evaluation

Structural equation modelling (SEM) allows a conceptual framework to be developed to test causality through multiple regressions of latent variables modelled in a pathway which reflects ecological theory (Grace and Pugesek 1997). Partial least square path modelling (PLS-PM) is a variance-based SEM technique for testing and estimating causality amongst latent variables. PLS-PM differs from the traditional covariance-based SEM techniques in many ways (see Esposito Vinzi *et al.*, 2010), including the ability to use smaller datasets and include both formative and reflective latent variables. Latent variables (also called unobserved variables, constructs or factors) are those of conceptual interest in the model, which cannot be observed or directly measured. Instead, latent variables are indicated by their associated measured variables (also called observed or manifest variables or indicators), which are at least two highly correlated observable/measurable variables. The relationships between the latent variables is known as the structural model, and this combined with the outer measurement model is known as the path diagram. Within path diagrams latent variables are represented by an ellipsis, measured variables by a rectangle and straight arrows represent the relationships between variables, and directionality. Exogenous latent variables act only as predictors for other latent variables (i.e. Fragmentation and Disturbance latent variables in this study), and endogenous latent variables are dependent variables (i.e. Soil characteristics, Native community and Invasion in this study).

We measured the degree of 'Fragmentation' as the amount of forest and forest edge to area ratio ('edge density') within the surrounding landscape and time since the forest was converted to oil palm. This incorporates increased edge effects (e.g. amount of poorer quality edge habitat), the dispersal potential for native species (e.g. amount of forest nearby, (Haddad et al. 2015)) and time for the plant community to respond to the effects of fragmenting the landscape. The abundance and richness of exotic species found in the oil palm planted areas represent the exotic population in the surrounding landscape and were used as a measure of 'Propagule pressure'. The number of large dipterocarps and mean wood density of adult trees are measures of local forest community structure and recovery since disturbance (e.g. logging (ITTO, 1997) and current succession stage (Slik et al. 2008; Feeley et al. 2011; Qie et al. 2017)). For 'Soil characteristics', pH and available phosphorus were included as both are known to influence exotic species occurrence (Davis et al. 2000a; Teo et al. 2003). Our latent variables were characterised as the following (main text Fig. 2.2): greater 'Fragmentation' represents landscapes with less forest, higher edge-to-forest area ratio, which was fragmented longer ago; greater "'Propagule pressure' represents sites with higher exotic species richness and abundance within oil palm planted areas; greater 'Disturbance' represents plots with fewer large dipterocarp trees and lower mean wood density across adult trees; higher values of the 'Soil characteristics' latent variable represent plots with higher pH and higher levels of available P; greater 'Native community' represents high genera richness, stem density (i.e. abundance) and phylogenetic diversity; and greater 'Invasion' represents high exotic genera richness and abundance.

Model assessment of PLS-PM is a two-step process, firstly the reliability and validity of the measurement model is assessed by evaluating all measured variables meet the commonly suggested criteria (Chin 1998; Sanchez 2013). The convergent validity (or unidimensionality) of the measurement model means that each indicator loads significantly on the latent variables they were intended to represent, this is checked by having an average variance extracted (AVE) score which is above 0.50. The measured variables are considered reliability if they have standardised loadings above 0.70 (all measured variables were considered reliable in all models with the exception of 'native abundance' for the total native community and ground vegetation community models). Internal consistency is considered satisfactory if the Cronbach's alpha and composite reliability (or Dillon-Goldstein's rho) are over 0.70 for each latent variable. The discriminant validity assesses whether measured variables load more strongly with a different latent variable than they were intended to represent, this is done by firstly checking the cross-loading of indicators (i.e. loadings should be highest on the associated latent variable). Secondly, the square root of each latent variable's AVE has to be greater than its correlation with each of the remaining latent variables (Fornell and Larcker 1981). Our measurement model meets the criteria outlined above (Tables S2.3-5) which gives strong evidence for the reliability and validity (both convergent and discriminant) of the latent variables.

The second step in model evaluation is the assessment of the structural model, this is checked by firstly looking at the coefficient of determination (R^2) of endogenous latent variables, which is the amount of variance in the endogenous variable explained by its exogenous latent variables. Values of $R<0.30$, $0.30<R<0.60$ and $R>0.60$ (although some consider: $R<0.20$, $0.20<R<0.50$ and $R>0.50$) are considered weak, moderate and substantial respectively (Sanchez 2013). The Goodness of Fit index (GoF), this is calculated from the geometric mean of the average communality index and the average R^2 value. There is no threshold for GoF but high values are considered better (Sanchez 2013). The GoF indices from our results ranged from 0.62 to 0.68 across all models (Figs 2.3, 2.4, S2.1 and S2.2), with the total community have a GoF of 0.67.

Table S2.1: Summary of the 17 study sites in Sabah, Malaysian Borneo where floristic surveys were carried out to determine the relative influence of fragmentation, propagule pressure, disturbance, soil and native community on invasion. Abbreviations are: DVCA = Danum Valley Conservation Area and OP = oil palm. Average % area that is forest in buffer = average percentage of 2km radius buffer that is forest area across plots, Average edge = average amount of forest edge within 2 km buffer, Average age = Average number of years since fragmentation, based on year on first planting of oil palm surrounding current forest area (accessed from Wilmar Ltd maps). Exotic richness and abundance in oil palm = number of species and abundance of exotic plants across two 100m transects within oil palm matrix.

Site	District	Matrix around site	Logging history	Average % area that is forest in buffer	Average edge	Average age	Exotic richness in oil palm	Exotic abundance in oil palm
F1	DVCA	-	Pristine	99.6	1130	0	0	0
F2	Lahad Datu	OP	Heavily logged	10.3	7293	20	12	529
F3	Lahad Datu	OP	Heavily logged	10	8936	24	15	500
F4	DVCA	-	Pristine	99.8	621	0	0	0
F5	Beluran	OP	Heavily logged	9.6	9444	27	11	518
F6	Beluran	OP	Heavily logged	0.9	5577	25.3	12	777
F7	Beluran	OP	Heavily logged	6	12,751	26	10	496
F8	Beluran	OP	Heavily logged	34	16,047	22	10	198
F10	Sugut	Forest & OP	Heavily logged	62.9	17,907	9	6	105
F11	Sugut	Forest & OP	Heavily logged	62.2	14,085	9	12	529
F12	Sugut	Forest & OP	Heavily logged	27	15,736	14	9	361
F13	Sugut	OP	Heavily logged	6.3	11,989	15	11	487
F14	Sugut	OP	Heavily logged	55	19,101	18	9	405
F15	Lahad Datu	OP	Heavily logged	5	9884	22	13	467
F16	Lahad Datu	Forest & OP	Heavily logged	46.3	4152	13.3	14	694
F17	DVCA	-	Once logged	100	0	0	0	0
F18	DVCA	-	Twice logged	100	0	0	0	0

Table S2.2: Summary of the 47 plots in Sabah, Malaysian Borneo where floristic surveys were carried out to determine drivers of invasion. Column names left to right are: Site number (see Table S2.1 for details on each site); plot number; number of large dipterocarp individuals (>25 cm DBH); mean wood density for trees >10 cm DBH; mean soil pH; mean soil available phosphorus; species richness for: exotics, adult trees (>10cm DBH), tree saplings (2-10 cm DBH), tree seedlings (<2 cm DBH) and ground vegetation; and abundance of: exotics, adult trees, tree saplings, tree seedlings and ground vegetation.

Site no.	**Plot no.**	*No. of dipter.*	*Mean wood density*	*Soil pH*	*Soil available P*	**Richness**					**Abundance**				
						Exotics	*Adult trees*	*Saplings*	*Seedlings*	*Ground veg.*	*Exotics*	*Adult trees*	*Saplings*	*Seedlings*	*Ground veg.*
1	1	6	0.55	4.19	0.47	0	13	17	16	13	0	23	25	42	51
1	2	9	0.55	4.18	0.56	0	23	15	25	7	0	37	32	64	17
1	3	21	0.54	4.11	0.52	1	20	16	17	18	2	69	32	56	72
2	1	0	0.46	5.86	1.08	1	4	7	5	5	2	28	17	8	39
2	2	0	0.48	5.84	0.69	7	8	6	7	13	83	19	10	8	44
2	3	10	0.56	5.82	0.56	1	21	12	7	1	1	50	28	7	2
3	1	0	0.42	6.45	1.32	6	9	4	4	10	44	77	11	19	208
3	2	1	0.42	6.39	3.43	5	5	4	9	6	18	41	16	18	57
3	3	2	0.42	6.47	3.14	1	9	3	4	5	2	46	5	7	15
4	1	10	0.56	4.89	1.1	0	31	10	15	13	0	60	15	45	53
4	2	11	0.56	4.7	0.9	1	27	11	14	5	1	49	16	31	10
4	3	5	0.55	4.35	0.5	1	22	9	14	6	1	54	16	49	35
5	1	44	0.51	4.32	0.69	0	15	14	17	8	0	90	18	108	13
5	2	13	0.49	4.32	0.78	1	16	11	7	13	4	77	15	55	24
5	3	33	0.55	4.68	0.67	1	19	11	10	11	7	58	20	21	40
6	1	9	0.54	4.9	1.1	1	21	9	8	6	6	50	11	12	8
6	2	1	0.45	4.78	1.02	1	13	6	3	12	9	38	11	5	25
7	1	36	0.59	4.16	0.69	1	34	15	7	16	2	87	23	12	21
7	2	27	0.54	4.23	0.72	1	24	10	12	11	1	75	29	16	27

8	1	13	0.57	6.01	0.93	0	31	12	11	14	0	75	19	23	23
8	2	14	0.59	5.14	2.11	1	24	14	8	13	1	63	27	15	92
8	3	7	0.55	5.15	3.16	0	20	11	6	11	0	53	16	11	55
10	1	20	0.60	4.16	0.57	0	30	12	11	9	0	80	27	20	49
10	2	17	0.53	4.42	0.47	0	23	14	11	13	0	50	15	14	21
10	3	15	0.58	4.31	0.59	1	39	15	16	8	2	80	25	20	20
11	1	12	0.52	4.54	0.78	1	30	13	10	13	32	59	13	13	24
11	2	20	0.52	4.38	0.63	1	34	17	13	18	22	76	20	16	41
11	3	5	0.53	4.19	0.63	1	38	11	13	19	13	68	18	32	43
12	1	5	0.49	4.86	0.65	0	27	12	5	14	0	56	16	11	34
12	2	9	0.52	4.68	0.35	0	36	8	9	17	0	69	16	11	32
12	3	22	0.54	4.52	0.91	0	32	9	13	11	0	80	11	16	17
13	1	32	0.56	4.29	1.24	1	33	13	13	5	18	91	22	17	36
13	2	25	0.57	4.42	0.53	1	30	11	11	7	9	69	22	21	19
14	1	15	0.52	4.33	0.31	1	28	7	7	8	7	90	8	10	14
14	2	19	0.56	4.42	0.47	1	32	7	4	6	15	81	12	4	17
14	3	8	0.52	4.63	0.65	1	24	12	5	12	32	52	19	7	51
15	1	1	0.43	6.52	3.7	2	5	8	3	10	3	43	10	4	69
15	2	5	0.48	6.63	1.58	1	13	8	9	4	7	52	18	13	33
16	1	27	0.60	5.35	0.83	0	29	11	6	2	0	75	19	8	3
16	2	16	0.57	5.47	0.39	3	26	9	7	10	10	52	14	9	16
16	3	19	0.58	5.25	0.47	2	26	9	4	5	2	57	14	4	5
17	1	23	0.54	4.36	0.46	1	23	7	12	10	13	53	13	39	20
17	2	23	0.57	4.25	0.4	0	24	12	8	13	0	65	19	21	135
17	3	28	0.56	4.33	0.38	1	29	13	8	12	2	69	18	27	118
18	1	24	0.53	4.12	0.56	0	35	14	11	6	0	86	32	17	33
18	2	10	0.47	4.27	0.58	1	20	10	10	17	2	48	21	18	37
18	3	13	0.50	4.1	0.85	0	25	19	21	9	0	77	29	28	16

Table S2.3: List of eight exotic species surveyed in 13 forest fragments and four continuous sites in Sabah, Malaysian Borneo. Plots = the total number of the 47 plots that that species was present in; Sites = the total number of the 17 sites that that species was present in; and Individuals = the total number of individuals of that species across all 17 sites.

Species	Family	Growth form	Plots	Sites	Individuals
Clidemia hirta	Melastomataceae	Shrub	29	14	276
Chromolaena odorata	Asteraceae	Shrub	3	3	42
Hyptis capitata	Lamiaceae	Forb	3	2	16
Asystasia gangetica	Acanthaceae	Creeping forb	3	2	14
Paspalum conjugatum	Poaceae	Graminoid	7	5	10
Ageratum conyzoides	Asteraceae	Forb	1	1	6
Calopogonium mucunoides	Fabaceae	Climber	2	2	5
Mikania micrantha	Asteraceae	Climber	3	2	4

Table S2.4: Partial least squares path modelling model evaluation for the total native community. Model evaluation statistics represent validity and reliability of the measurement model if Dillon-Goldstein's rho and Cronbach's alpha are >0.7 and Average variance extracted is >0.5.

Model evaluation statistic	**Latent variable**					
	Fragmentation	Disturbance	Soil characteristics	Propagule pressure	Native community	Invasion
Average variance extracted	0.839	0.861	0.816	0.956	0.987	0.897
Dillon-Goldstein's rho	0.940	0.926	0.900	0.978	0.994	0.946
Cronbach's alpha	0.904	0.839	0.778	0.954	0.987	0.885

Table S2.5: Correlations between latent variables in the total native community model and square-root of each latent variables' AVE. Correlations between latent variables should be lower than the square-root of AVE for each latent variable, which are in parenthesis.

Latent variable	Fragmentation	Disturbance	Soil characteristics	Propagule pressure	Native community	Invasion
Fragmentation	(0.915)					
Disturbance	0.26	(0.928)				
Soil characteristics	0.544	0.629	(0.903)			
Propagule pressure	0.859	0.272	0.493	(0.978)		
Native community	-0.375	-0.620	-0.647	-0.38	(0.993)	
Invasion	0.344	0.437	0.313	0.494	-0.404	(0.947)

Table S2.6: Loadings and cross-loadings of all measured variables in the total native community model showing how well they associate with their latent variable. The loadings of measured variables should load higher on their associated latent (indicated by bold) than any other latent variable. Latent variable abbreviations: Frag. = Fragmentation, Dist. = Disturbance, Soil = Soil characteristics, Native = Native community and Prop = Propagule pressure.

Measured variable	**Latent variable**	**Cross-loadings**					
		Frag.	Dist.	Soil	Native	Prop.	Invasion
Area of non-forest	Frag.	**0.982**	0.303	0.554	-0.417	0.859	0.354
Edge density	Frag.	**0.822**	0.222	0.428	-0.329	0.536	0.246
Age	Frag.	**0.937**	0.19	0.502	-0.288	0.907	0.331
Number of large dipterocarps	Dist.	0.165	**0.928**	0.605	-0.543	0.202	0.386
Wood density	Dist.	0.318	**0.928**	0.562	-0.608	0.303	0.425
Soil pH	Soil	0.518	0.613	**0.927**	-0.678	0.536	0.38
Available phosphorus	Soil	0.461	0.514	**0.879**	-0.449	0.333	0.161
Native genera richness	Native	-0.387	-0.619	-0.648	**0.994**	-0.374	-0.389
Native phylogenetic diversity	Native	-0.357	-0.614	-0.617	**0.993**	-0.382	-0.414
Exotic richness outside	Prop.	0.876	0.308	0.585	-0.38	**0.979**	0.478
Exotic abundance outside	Prop.	0.803	0.222	0.373	-0.364	**0.977**	0.488
Exotic genera richness	Invasion	0.301	0.345	0.179	-0.26	0.481	**0.94**
Exotic abundance	Invasion	0.347	0.475	0.401	-0.491	0.457	**0.954**

Table S2.7: Total effects of fragmentation, disturbance, soil characteristics and native community on invasions within fragmented lowland tropical rainforests. Direct effects are the standardised path coefficients (displayed in Figs 2.3, 2.4, S2.1 and S2.2). Indirect effects are the influence of one latent variable on another by taking an indirect path, they are obtained by multiplying the path coefficients in the indirect pathway. Total effect is the sum of the direct and indirect effects. The strongest effect on invasion is highlighted in bold for each community, and the strongest effect on native community is highlighted with an underscore. Abbreviations: Frag = Fragmentation, Dist = Disturbance, Prop = Propagule pressure, Soil = Soil characteristics, Native = Native community and Invas. = Invasion.

Path	**total**			**adult trees**			**saplings**			**seedlings**			**understorey**		
	direct	indirect	total	direct	indirect	total	direct	indirect	total	direct	indirect	total	direct	indirect	total
Frag. → Soil	0.408	0	0.408	0.408	0	0.408	0.407	0	0.407	0.408	0	0.408	0.408	0	0.408
Frag. → Native	0	-0.26	-0.26	0	0	0	0	0	0	-0.509	0	-0.509	0	-0.129	-0.129
Frag. → Prop.	0.893	0	0.893	0.859	0	0.859	0.859	0	0.859	0.861	0	0.861	0.859	0	0.859
Frag. → Invas.	0	0.329	0.329	0	0.348	0.348	0	0.348	0.348	0	0.349	0.349	0	0.348	0.348
Dist. → Soil	0.523	0	0.523	0.521	0	0.521	0.52	0	0.52	0.521	0	0.521	0.523	0	0.523
Dist. → Native	0	-0.33	-0.33	-0.724	0	-0.724	-0.558	0	-0.558	0	0	0	0	-0.166	-0.166
Dist. → Invas.	0.344	0	0.344	0.327	0	0.327	0.327	0	0.327	0.327	0	0.327	0.327	0	0.327
Prop. → Invas.	0.369	0	**0.37**	0.405	0	**0.405**	0.405	0	**0.405**	0.405	0	**0.405**	0.405	0	**0.405**
Soil → Native	-0.6	0	-0.64	0	0	0	0	0	0	0	0	0	-0.317	0	-0.317
Frag. → Soil	0.408	0	0.408	0.408	0	0.408	0.407	0	0.407	0.408	0	0.408	0.408	0	0.408
Frag. → Native	0	-0.26	-0.26	0	0	0	0	-0.114	-0.114	-0.422	-0.087	-0.508	0	-0.129	-0.129
Frag. → Prop.	0.859	0	0.859	0.859	0	0.859	0.859	0	0.859	0.861	0	0.861	0.859	0	0.859
Frag. → Invas.	0	0.348	0.348	0	0.348	0.348	0	0.347	0.347	0	0.348	0.349	0	0.348	0.348
Dist. → Soil	0.523	0	0.523	0.521	0	0.521	0.52	0	0.52	0.521	0	0.521	0.523	0	0.523
Dist. → Native	0	-0.33	-0.33	-0.724	0	-0.724	-0.413	-0.108	-0.521	0	-0.081	-0.081	0	-0.166	-0.166
Dist. → Invas.	0.327	0	0.327	0.327	0	0.327	0.328	0	0.328	0.327	0	0.327	0.327	0	0.327
Prop. → Invas.	0.405	0	**0.405**	0.405	0	**0.405**	0.404	0	**0.404**	0.405	0	**0.405**	0.405	0	**0.405**
Soil → Native	-0.64	0	-0.64	0	0	0	0	0	0	0	0	0	-0.317	0	-0.317
Prop → Native	0	0	0	0	0	0	0	-0.133	-0.133	0	-0.101	-0.101	0	0	0
Invas. → Native	0	0	0	0	0	0	-0.329	0	-0.329	-0.249	0	-0.248	0	0	0

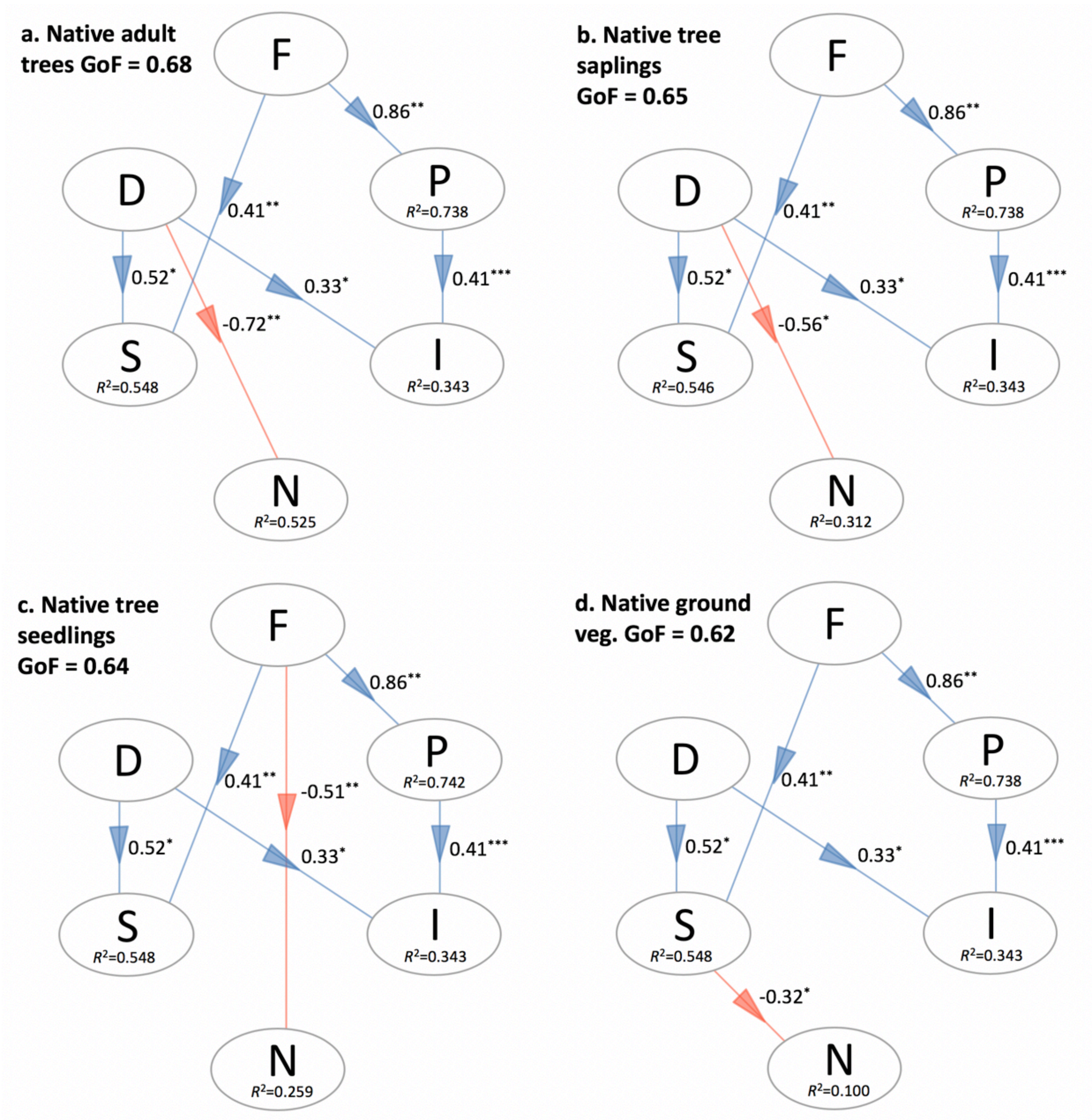

Fig. S2.1 Partial least squares path model showing the relationships between landscape-scale fragmentation (F), local forest disturbance (D), propagule pressure (P), soil characteristics (S) and native plant diversity (N) on invasion (I) for four different native floristic communities. The model was simplified from the specification in Fig. 2.2 by removing non-significant effects. The goodness-of-fit index (GoF) for each model and R^2 values for the endogenous latent variables are displayed. Standardised path coefficients and *P*-values were estimated by 10,000 bootstrap estimations. Standardised path coefficients are shown next to arrows, red indicates a negative correlation and blue a positive correlation. They denote the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable. *P*-values based on 10,000 bootstrap estimations: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. Abbreviations: F = Fragmentation, D = Disturbance, P = Propagule pressure, S = Soil characteristics, N = Native community and I = Invasion.

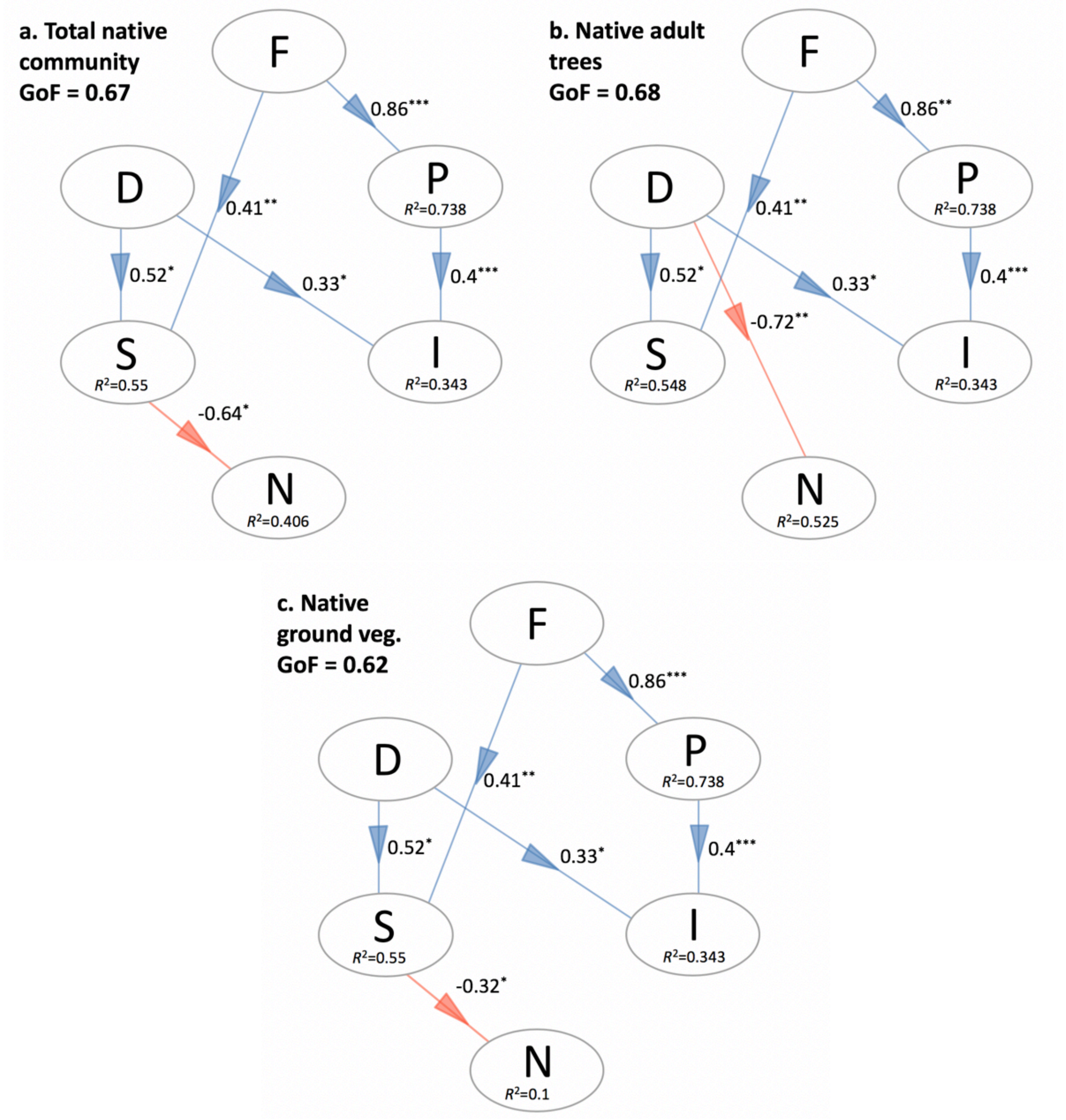

Fig. S2.2 Partial least squares path model showing the relationships between landscape-scale fragmentation (F), local forest disturbance (D), propagule pressure (P), soil characteristics (S) and invasion (I) on native plant diversity (N) for three different native floristic communities. The model was simplified from the specification in Fig. 2.2 by removing non-significant effects. The goodness-of-fit index (GoF) for each model and R^2 values for the endogenous latent variables are displayed. Standardised path coefficients and *P*-values were estimated by 10,000 bootstrap estimations. Standardised path coefficients are shown next to arrows, red indicates a negative correlation and blue a positive correlation. They denote the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable. *P*-values based on 10,000 bootstrap estimations: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. Abbreviations: F = Fragmentation, D = Disturbance, P = Propagule pressure, S = Soil characteristics, N = Native community and I = Invasion.

Appendix 3: Supporting Information for Chapter 3

Text S3.1: Additional analyses

Trait co-variance – Co-variance amongst traits was investigated and five correlations were detected, including plant woodiness and seed dry mass, plant maximum height and long-distance dispersal, vertebrate and wind dispersed, and long-distance dispersal with both vertebrate and wind dispersed (Fig. S3.4). We recorded five correlations but none between the three most significant traits (woodiness, plant maximum height and vertebrate dispersed), therefore this result is unlikely to impact our main conclusions of trait filtering.

Trait phylogenetic relationships – To quantify whether the distribution of our selected traits is affected or not by the phylogenetic relationships between our species, we calculated Moran's I autocorrelation coefficient in R Studio 3.4.2 (R Core Team, 2019) using the function 'Moran.I' within package "ape' (Paradis et al. 2004; Paradis 2019), using the raw trait data and a phylogeny of our exotic species. The phylogeny was created using Phylomatic v.3 (Webb and Donoghue, 2005; available at phylodiversity.net/phylomatic/ [accessed 24 Nov 2019]) and a pruned version of the Angiosperm Phylogeny Groups APGIII maximally resolved supertree of angiosperms (R20120829; Group, 2009). One species could not be included in the phylogeny, *Cleome rutidosperma*, as it was not part of the original supertree. The phylogeny was rooted and branch lengths were based on node ages (most recent common ancestor) of Wikstrom, Savolainen and Chase (2001) and estimated using the 'BladJ' algorithm in Phylocom (Webb et al. 2008) in R Studio using the function 'rbladj' within package "brranching' (Chamberlain, 2019).

We did not find a strong phylogenetic signal apart from a weak positive correlation in wind dispersed species (*P*=0.047), however, we expect this signal to have little impact on community trait values (CWM) and model outputs.

Geographic structuring in models – To quantify whether the spatial arrangement of the transects had an effect on the composition of exotic species and thus impacted our findings, we calculated Moran's I autocorrelation coefficient using the function 'Moran.I' within package 'ape' (Paradis et al. 2004; Paradis 2019) on the geographic coordinates of the transects (Table S3.5) and model residuals. This was run for the individual species models and for each functional trait.

Across all models we found no evidence of geographic structuring in the model residuals (*P*>0.05), and thus we conclude that the spatial arrangement of our transects did not influence our findings.

Influence of distance from edge – To test whether distance to the nearest forest edge had a significant influence on species' occurrences and community weighted functional trait means, we re-ran our models of individual species and each functional trait for a subset of the data that included forest transects only. Distance to edge was calculated as the average distance from each transects start and end locations to the closest forest edge and was calculated in GeoViewer (available: www.extensis.com/geoviewer) using high-resolution drone images of plantations. Distance to edge was scaled and model priors were adjusted for each model to accommodate for the additional fixed effect and the reduction of levels of habitat.

For those species found inside the forest at more than one site, we found no significant effect of distance to edge on the occurrence of any species. We also found no significant effect of distance to edge on any of our six functional trait models. Therefore, we conclude that there is no evidence that distance to edge changes our conclusions of species occurrence and functional trait models.

In addition, we tested the effect of distance to edge on total exotic occurrence by fitting Generalised Linear Mixed Models (GLMMs) using the 'lme4' R package (Bates et al. 2015), with a poisson error distribution, the total exotic occurrence per transect as the response variable, fixed effects of distance to edge, habitat (two levels: disturbed forest and Intact forest) and canopy cover (both linear and quadratic) and random effects of transect and site. This model was then run with total species richness per transect as the response variable, and the same error distribution, fixed and random effects. The top models for each GLMM were selected out of all possible combinations of the fixed effects (using the '*dredge*' function in the 'MuMIn' R package (Bartoń 2013)), and for both GLMMs distance to edge was not included in the top model. Therefore, we conclude that there was no significant effect of distance to edge on either total exotic occurrence or species richness for the forest transects.

Table S3.1: Summary of 21 sites where the occurrence of 18 exotic species were recorded across four habitats in Sabah, Malaysian Borneo. Size of forest remnant = hectares of rainforest within Wilmar plantation boundary, to the nearest 1 ha (unless very small; <20ha). Size data were collected from plantation maps provided by plantation managers during the first field season (July-Oct. 2017). Disturbed forest transect location = details on the location and therefore disturbance history of each 'disturbed forest' transect, information provided by plantation managers. Site description = whether the forest remnant was discrete and fully surrounded by oil palm (n=15 sites) or connected to a forest reserve out with the plantation boundary (n=6; denoted by a superscript †). See Reynolds, Payne, Sinun, Mosigil, & Walsh (2011) for forest reserve classifications.

Site	Plantation name	Size of forest remnant (ha)	Disturbed forest transect location	Site description
F2	Sabahmas	89	Skid trail	Discrete forest remnant
F3	Sabahmas	57	Terrace/skid trail	Discrete forest remnant
F5	Reka Halus	52	Skid trail	Discrete forest remnant
F6	Reka Halus	12.5	Skid trail	Discrete forest remnant
F7	Kiabau	8.8	Skid trail	Discrete forest remnant
F8	Kiabau	25	Road/ skid trail	Discrete forest remnant
F11†	Sekar Imej	1375	Skid trail	Connected to forest remnant: commercial forest reserve (Class II)
F12	Sapi Sugut	82	Road/skid trail	Discrete forest remnant (part of larger discrete forest remnant (~200 ha) but split by main plantation road)
F13	Sri Kamusan	10	Skid trail	Discrete forest remnant
F14†	Sri Kamusan	525	Skid trail	Connected to forest remnant: commercial forest reserve (Class II)
F15	Sabahmas	3.25	Skid trail	Discrete forest remnant
F16†	Sabahmas	506	Road	Connected to forest remnant: wildlife forest reserve (Class VII)
F19	Sri Kamusan	15	Skid trail	Discrete forest remnant

F20[†]	Sri Kamusan	525	Skid trail	Connected to forest remnant: commercial forest reserve (Class II)
F21	Sri Kamusan	35	Road/ skid trail	Discrete forest remnant
F22	Sekar Imej	17.7	Road/skid trail	Discrete forest remnant (separated from forest remnant where F11 was located by small amount of oil palm)
F23[†]	Sapi Sugut	377	Road/skid trail	Connected to forest remnant: commercial forest reserve (Class II)
F24	Kiabau	9	n/a	Discrete forest remnant
F25	Sabahmas	13.2	Skid trail	Discrete forest remnant (separated from forest remnant where F16 and F26 were located by small amount of oil palm)
F26[†]	Sabahmas	506	Road	Connected to forest remnant: wildlife forest reserve (Class VII)
F27	Sabahmas	10.2	Terrace/skid trail	Discrete forest remnant

Table S3.2: Four habitats within oil-palm dominated landscapes, in Sabah, Malaysian Borneo, where exotic species occurrences were recorded along 100m transects. All information was gathered from observations during fieldwork and conversations with plantation staff, including plantations managers and RSPO (Roundtable on Sustainable Palm Oil) officers. n = number of transects carried out in each location.

Habitat	**Location**	**Description**	**Canopy openness**	**Past disturbance**	**Current disturbance**
Oil palm (n=21)	Roadside of nearest major plantation road	Weedy bank with both exotic and native weed species (small shrubs, herbs, graminoids and climbers)	Always open on one side due to road but degree of cover dependent on age of adjacent oil palm	Area selectively commercially logged prior to deforestation for conversion to oil palm. Some sites replanted after full lifecycle of oil palm	Continuous plantation traffic from lorries, cars and motorbikes. Sporadic herbicide spraying and mechanical digging
Forest-oil palm edge (n=21)	Forest edge, either along small road or oil palm terrace	Forest edge habitat with exotic and native weedy species found throughout oil palm areas, but also native forest species, including trees	Partially open on one side, dependent on whether along small road or terrace (and therefore on age of oil palm)	Forested area selectively commercially logged prior to conversion to oil palm	Not managed by plantation (i.e. no herbicide spraying). Some light traffic from motorbikes and presence of plantation workers
Disturbed forest (n=20)	Maturing gap within rainforest remnant: either a skid trail, old road (not in use) or abandoned terrace. Usually close to forest edge (mean distance to edge = 53m)	Open forest habitat with fewer forest native tree species and varying levels of understorey	Partially closed canopy	Selectively logged forest that had been previously cleared	Not managed by plantation. Evidence of illegal hunting in some sites (e.g. snares and makeshift huts). Several sites have pig activity (groups and nests)
Intact forest (n=16)	Inside rainforest remnant, usually on steep slope (mean distance to edge = 90m)	Closed forest habitat with forest native tree species and generally a sparse understorey	Closed canopy	Selectively logged	Not managed by plantation. Evidence of illegal hunting and pigs in some sites.

Table S3.3: List of traits for 18 exotic plant species surveyed in Sabah, Malaysian Borneo. Data were compiled for each species from species datasheets in the Invasive Species Compendium (available a www.cabi.org/isc/), unless specified by a superscript letter (references in footnote), for all traits apart from 'Seed dry mass' data, which were sourced for all species from the Royal Botanic Gardens Kew Seed Information Database (available at: data.kew.org/sid/). Dispersal syndrome abbreviations from left to right are as follows: Vertebrate internal, vertebrate external, wind, water, vegetative propagation, invertebrate, ballistic and gravity/unspecified.

Species name	**Species description**	**Seed dry mass (g/1000 seeds)**	**Plant max. height (m)**	**Woody**	**Long distance dispersal syndrome**				**Short distance dispersal syndrome**			
					Vert. inter.	*Vert. exter.*	*Wind*	*Water*	*Veg. prop.*	*Invert.*	*Bal.*	*Grav./ unsp.*
A. gangetica	Perennial creeper (erect, decumbent, or clambering)	9.95	1	0	0	0	0	0	1	0	1	0
A. conyzoides	Annual forb (erect and branching)	0.13	2[a]	0	0	1	1	1	0	0	0	0
C. odorata	Perennial shrub (erect or lianescent and much branched)	0.4	10	1	0	1	1	0	0	0	0	0
M. micrantha	Perennial vine (twining and much-branching)	0.09	6[b]	0	0	1	1	1	1	0	0	0
C. rutidosperma	Annual forb (erect or spreading and branched)	2.525	1	0	0	0	0	0	0	1	0	0
M. pudica	Perennial shrub (low growing and much branched)	5.3	1	1	0	1	0	1	0	0	0	0
M. diplotricha	Perennial shrub (low growing or climbing and much branched)	NA	3[c]	1	0	1	0	1	0	0	0	0
H. capitata	Perennial forb (erect and branching)	0.284	2.5[d]	0[e]	0	0	0	0	0	0	0	1

C. hirta	Perennial shrub (erect and much branched)	0.057	5	1	1	1	0	0	0	0	0	0
L. hyssopifolia	Annual forb (erect aquatic or semi-aquatic)	0.14	3	0	0	0	0	0	0	0	0	1
E. heterophylla	Annual forb (erect)	6	2	0	0	0	0	0	0	0	1[f]	0
I. triloba	Annual vine (twining)	12.6	3	0	0	0	0	0	0	0	0	1
S. nodiflora	Annual forb (erect)	0.675	0.8	0	0	1	1	0	0	0	0	0
E. sonchifolia	Annual forb (erect)	NA	0.7	0	0	0	1	0	0	0	0	0
E. hirta	Annual forb (semi-erect and creeping)	0.077	0.5	0	0	0	0	0	0	1[g]	0	1
P. foetida	Annual or perennial vine (twining and much branched)	9	5	0	1	0	0	0	0	0	0	0
L. camara	Perennial shrub (erect and much branched)	11	5	1	1	0	0	0	0	0	0	0
C. crepidioides	Annual forb (erect and sparingly branched)	0.23	1	0	0	0	1	0	0	0	0	0

a = *A.* conyzoides datasheet on Global invasive Species Database (available at: issg.org/database/welcome/)
b= (Day et al. 2016)
c= FAO Invasive Pest Fact Sheet for *M. diplotricha* (available at: www.fao.org/forestry/13377-0977cb34791475aa6a7a360640f09778.pdf)
d= Queensland Government Weeds of Australia Fact Sheet (available at: keyserver.lucidcentral.org/weeds/data/media/Html/hyptis_capitata.htm)
e= (Keller and Armbruster 1989)
f= FAO Weed species fact sheet (available at: www.fao.org/agriculture/crops/thematic-sitemap/theme/biodiversity/weeds/listweeds/eup-het/en/)
g= Plant use for *E. hirta* (available at: uses.plantnet-project.org/en/Euphorbia_hirta_(PROTA))

Table S3.4: Mean occurrence of 18 exotic species recorded in four habitats across 21 sites in Sabah, Malaysian Borneo. 'Mean exotic species richness/transect' = average number of species found per transect within each habitat. 'Mean occurrence of exotic species/transect' = average occurrence of 18 exotic species per transect within each habitat. SE = standard error of the mean. Number of transects per habitat is shown in parenthesis. See main text and Table S3.2 for descriptions of habitat.

Species	**Oil palm (n=21)**	**Forest-oil palm edge (n=21)**	**Disturbed forest (n=20)**	**Intact forest (n=16)**
	Mean (± S.E.)/ transect	*Mean (± S.E.)/ transect*	*Mean (± S.E.)/ transect*	*Mean (± S.E.)/ transect*
Asteraceae				
Ageratum conyzoides	**35.86 (± 8.08)**	**28.29 (± 5.63)**	2.5 (± 1.35)	0
Chromolaena odorata	9.33 (± 4.76)	28 (± 6.53)	**5 (± 1.88)**	0
Crassocephalum crepidioides	0.33 (± 0.24)	0.48 (± 0.48)	0	0
Emilia sonchifolia	9.24 (± 3.64)	2.67 (± 1.13)	0	0
Mikania micrantha	14.76 (± 4.78)	17.33 (± 4.11)	1.75 (± 0.68)	0
Synedrella nodiflora	4.86 (± 2.65)	6.48 (± 4.55)	0.35 (± 0.3)	0
Acanthaceae				
Asystasia gangetica	**48.05 (± 6.7)**	**35.38 (± 8.26)**	**3.3 (± 1.74)**	0
Cleomaceae				
Cleome rutidosperma	12.48 (± 5.4)	0.38 (± 0.38)	0.5 (± 0.5)	0
Convolvulaceae				
Ipomoea triloba	11.43 (± 5.03)	2.14 (± 1.58)	0.25 (± 0.25)	0
Euphorbiaceae				
Euphorbia heterophylla	3.05 (± 2.16)	1.19 (± 0.67)	0	0
Euphorbia hirta	13.29 (± 4.09)	9.81 (± 3.89)	0	0
Fabaceae				
Mimosa diplotricha	2.67 (± 2.4)	2.19 (± 1.24)	0.15 (± 0.15)	0
Mimosa pudica	6.95 (± 2.77)	8.57 (± 4.39)	2.6 (± 1.33)	0
Lamiaceae				

Hyptis capitata	3.86 (± 3.34)	7 (± 2.51)	2.65 (± 1.42)	0
Melastomataceae				
Clidemia hirta	**38.9 (± 7.59)**	**67.05 (± 6.2)**	**46.7 (± 6.25)**	**16.31 (± 3.72)**
Onagraceae				
Ludwigia hyssopifolia	16.57 (± 3.31)	10.24 (± 3.77)	0	0
Passifloraceae				
Passiflora foetida	1.24 (± 0.62)	1.62 (± 0.96)	0.05 (± 0.05)	0
Verbenaceae				
Lantana camara	0.14 (± 0.11)	0.29 (± 0.29)	0	0
Mean exotic species richness/transect:	9.2 (± 0.58)	7.8 (± 0.69)	3.1 (± 0.64)	1 (± 0)
Mean occurrence of exotic species/transect:	12.94 (± 3.76)	12.73 (± 3.14)	3.66 (± 0.88)	0.91 (± 0.21)

Table S3.5: Summary of 78 transects where the occurrence of 18 exotic species were recorded in Sabah, Malaysian Borneo. Sites were fully surrounded by oil palm planted areas with the exception of six that were connected to a forest reserve outside plantation boundary (those sites are denoted by a superscript †). 'Start coordinates' taken at 0m for each transect with a Garmin GPS and 'End coordinates' taken at 100m. 'Distance to edge' was calculated as the average distance from the start and end coordinates to the forest edge. 'Species richness' = number of species found per transect. 'Mean occurrence' = average occurrence of 18 exotic species per transect. See main text and Table S3.2 for descriptions of habitat and main text for the methods to measure 'Canopy cover' and 'Number of large trees'.

Site	Habitat	Start coordinates		End coordinates		Distance to edge	Canopy cover	Number of large trees	Species richness	Mean occurrence
		Lat	Long	Lat	Long					
F2	Oil palm	5.13615	118.443383	5.13583333	118.44245		0.16	0	9	12.44
	Forest-oil palm edge	5.13811667	118.4419	5.13865	118.441317		44.05	1	10	17.39
	Disturbed forest	5.13838333	118.441983	5.13916667	118.441683	41	87.68	11	6	3.11
	Intact forest	5.14005	118.444633	5.14078333	118.444467	249	92.04	13	1	0.56
F3	Oil palm	5.1335	118.429133	5.13345	118.42825		3.44	0	12	14
	Forest-oil palm edge	5.13378333	118.427933	5.13445	118.428267		26.32	2	11	13.78
	Disturbed forest	5.13443333	118.42725	5.13435	118.42815	44	83.31	15	5	6.72
	Intact forest	5.13786667	118.425817	5.13868333	118.42565	35	90.38	18	1	0.56
F5	Oil palm	5.78901667	117.4963	5.78983333	117.496067		17.94	0	10	16.39
	Forest-oil palm edge	5.79855	117.502467	5.79795	117.502017		75.46	4	6	12.39
	Disturbed forest	5.7978	117.50203	5.7978	117.50121	48	88.09	21	1	0.83
	Intact forest	5.79838	117.50026	5.79841	117.49948	239	92.77	38	1	2
F6	Oil palm	5.72976667	117.481267	5.72898333	117.4809		0.16	0	11	20.83
	Forest-oil palm edge	5.73313333	117.484017	5.73246667	117.483483		1.72	0	11	22.33
	Disturbed forest	5.7306	117.48655	5.73126667	117.486117	70	94.02	17	2	3.28
F7	Oil palm	5.75605	117.250283	5.75545	117.25075		4.37	0	10	19.44
	Forest-oil palm edge	5.75035	117.255	5.75078333	117.2545		86.22	2	6	8.11
	Disturbed forest	5.75043333	117.254133	5.74985	117.254817	35	94.38	19	1	1.22
	Intact forest	5.75058333	117.254083	5.75005	117.2545	24	94.12	27	1	1.33

F8	Oil palm	5.76846667	117.24965	5.76755	117.249633		26.42	0	7	5
	Forest-oil palm edge	5.77058333	117.255567	5.771	117.255133		52.89	1	8	6
	Disturbed forest	5.76936667	117.254533	5.76878333	117.255183	75	10.82	2	1	0.06
	Intact forest	5.77043333	117.254683	5.76995	117.254083	80	92.56	12	1	0.06
F11†	Oil palm	6.31223333	117.249433	6.31176667	117.250117		27.72	0	11	18.56
	Forest-oil palm edge	6.31848333	117.241883	6.31836667	117.24335		31.46	2	9	10.83
	Disturbed forest	6.31746667	117.243267	6.31743333	117.242533	46	87.78	17	1	1.06
	Intact forest	6.31725	117.24255	6.31788333	117.241883	65	93.29	21	1	0.33
F12	Oil palm	6.25246667	117.25965	6.25208333	117.260467		33.08	0	8	11.83
	Forest-oil palm edge	6.25771667	117.248617	6.25786667	117.247833		50.86	3	5	8.22
	Disturbed forest	6.25575	117.249117	6.25591667	117.249867	93	81.38	5	1	3.28
	Intact forest	6.2556	117.2497	6.25546667	117.250383	111	95.68	24	1	0.94
F13	Oil palm	6.211	117.288983	6.21123333	117.288117		67.29	0	8	12.56
	Forest-oil palm edge	6.2168	117.283683	6.21631667	117.283667		55.02	1	9	14.5
	Disturbed forest	6.2163	117.282967	6.21643333	117.282183	72	88.35	17	1	4.5
	Intact forest	6.2166	117.282617	6.21656667	117.281767	84	90.85	36	1	0.72
F14†	Oil palm	6.19525	117.264417	6.19445	117.26455		38.95	0	8	8.83
	Forest-oil palm edge	6.17726667	117.275617	6.17665	117.275833		34.69	1	6	13.67
	Disturbed forest	6.17701667	117.2761	6.17628333	117.2761	23	79.72	18	1	3.28
	Intact forest	6.17643333	117.276533	6.17628333	117.2772	98	87.88	23	1	0.44
F15	Oil palm	5.18818333	118.409533	5.18728333	118.409517		0.16	0	8	6.89
	Forest-oil palm edge	5.19465	118.405967	5.19441667	118.406767		84.45	10	12	19.06
	Disturbed forest	5.19426667	118.405617	5.1938	118.404917	26	57.93	5	9	5.83
F16†	Oil palm	5.21596667	118.4804	5.21598333	118.48125		28.76	0	13	19.83
	Forest-oil palm edge	5.22075	118.487017	5.22076667	118.486167		31.26	4	9	18.72
	Disturbed forest	5.22096667	118.487267	5.22143333	118.487983	83	70.1	17	3	4.44
	Intact forest	5.22123333	118.48745	5.22173333	118.488117	115	93.29	22	1	1.56

F19	Oil palm	6.21601667	117.31695	6.2163	117.316183		53.98	0	4	4.28
	Forest-oil palm edge	6.21711667	117.31105	6.2168	117.3103		64.54	4	3	5.56
	Disturbed forest	6.21718333	117.3087	6.21661667	117.308117	14	79.2	18	1	5.56
	Intact forest	6.21706667	117.3088	6.2174	117.3096	14	89.44	20	1	2.5
F20†	Oil palm	6.20621667	117.322083	6.2054	117.322117		47.48	0	7	7.17
	Forest-oil palm edge	6.20045	117.319733	6.20063333	117.31915		67.71	0	7	11.28
	Disturbed forest	6.19773333	117.318317	6.1971	117.31785	61	83.36	26	1	2.83
	Intact forest	6.19781667	117.3182	6.19716667	117.317683	58	89.6	30	1	0.78
F21	Oil palm	6.19606667	117.278317	6.19615	117.27915		58.66	0	6	14.44
	Forest-oil palm edge	6.19776667	117.27505	6.19745	117.274367		80.71	6	4	5.94
	Disturbed forest	6.19801667	117.274967	6.1988	117.27455	58	52.06	2	2	3.39
	Intact forest	6.19783333	117.2748	6.19836667	117.27415	63	92.46	28	1	2.44
F22	Oil palm	6.31161667	117.259317	6.31146667	117.260017		23.25	0	6	8.67
	Forest-oil palm edge	6.31318333	117.259517	6.31245	117.259517		80.55	11	2	4.78
	Disturbed forest	6.31281667	117.259817	6.31315	117.260533	28	92.3	26	1	0.11
	Intact forest	6.31281667	117.261217	6.31228333	117.260583	73	96.31	28	1	0.06
F23†	Oil palm	6.25438333	117.2395	6.25358333	117.239533		38.38	0	9	18
	Forest-oil palm edge	6.25753333	117.234167	6.25711667	117.234817		32.82	3	7	15.67
	Disturbed forest	6.25776667	117.236483	6.25791667	117.23735	55	58.35	7	4	7.28
F24	Oil palm	5.75841667	117.2628	5.75845	117.2637		23.14	0	14	22.5
	Forest-oil palm edge	5.75365	117.263333	5.75428333	117.263167		24.55	1	11	15.83
F25	Oil palm	5.20901667	118.448017	5.20883333	118.4472		0.26	0	9	12.17
	Forest-oil palm edge	5.21106667	118.4474	5.21178333	118.447567		38.43	2	9	10.5
	Disturbed forest	5.21171667	118.44695	5.21105	118.4467	65	69.65	12	6	4.78
	Intact forest	5.21108333	118.447067	5.2109	118.446267	71	90.48	18	1	0.06
F26†	Oil palm	5.21085	118.462633	5.21115	118.463483		38.43	0	9	3
	Forest-oil palm edge	5.21395	118.464483	5.21343333	118.464017		62.92	0	6	7.56

	Disturbed forest	5.21426667	118.4644	5.21481667	118.4638	78	60.58	6	10	7.94
	Intact forest	5.21435	118.464483	5.2151	118.464817	75	95.48	21	1	0.17
F27	Oil palm	5.14388333	118.411367	5.14431667	118.412117		5	0	14	15
	Forest-oil palm edge	5.14705	118.4135	5.14661667	118.412783		29.18	0	13	25.17
	Disturbed forest	5.14735	118.413033	5.14748333	118.412267	47	78.32	8	5	3.61

Table S3.6: Results of Bayesian Generalised Linear Mixed Model testing the effect of habitat and canopy cover on the occurrence of 18 exotic species in Sabah, Malaysia. Direction of relationship, for canopy cover: negative = decreased occurrence of species with increasing canopy cover, positive = increased occurrence of species with increasing canopy cover; for canopy cover^2 ; negative = highest occurrence at intermediate canopy cover, positive = lowest occurrence at intermediate canopy cover.

Species	Null model testing:							
	Habitat		Canopy cover			Canopy cover^2		
	Chi-Sq	*p*	direction	Chi-Sq	*p*	direction	Chi-Sq	*p*
A. gangetica	21.087	**<0.001**	-	0.199	0.66	-	0.37	0.54
A. conyzoides	22.233	**<0.001**	+	6.6	**0.01**	-	8.2	**0.004**
C. odorata	15.474	**0.001**	+	6.26	**0.01**	-	14.1	**<0.001**
M. micrantha	15.23	**0.002**	-	0.006	0.94	-	1.96	0.16
C. rutidosperma	16.913	**<0.001**	-	1.86	0.17	-	0.11	0.74
M. pudica	4.4	0.22	+	0.085	0.77	-	0.79	0.37
M. diplotricha	9.59	**0.022**	+	15.01	**<0.001**	-	18.66	**<0.001**
H. capitata	8.45	**0.038**	+	0.22	0.63	-	1.54	0.21
C. hirta	20.234	**<0.001**	+	17.53	**<0.001**	-	9.04	**0.002**
L. hyssopifolia	19.19	**<0.001**	+	1.81	0.18	-	2.4	0.12
E. heterophylla	9.16	**0.027**	-	2.68	0.1	+	4.45	**0.035**
I. triloba	4.99	0.17	-	0.74	0.39	-	0.83	0.36
S. nodiflora	7.72	0.052	+	1.09	0.3	-	0.26	0.6
E. sonchifolia	11.295	**0.01**	+	2.89	0.09	-	1.92	0.16
E. hirta	0.39	0.94	-	4.39	**0.04**	-	6.1	**0.01**
P. foetida	0.66	0.88	-	1.18	0.28	-	1.34	0.25

Table S3.7: Results of Bayesian Generalised Linear Mixed Model testing differences in community weighed mean of six functional traits in 18 exotic species across four habitats and with canopy cover, in Sabah, Malaysia. SE = Standard error of the mean. Df = degrees of freedom. Df was calculated using Kenward-Roger method. *P* value adjustment was carried out using a Tukey method for comparing a family of 4 estimates. Traits and *P* values in bold indicate those which remain significant when *Clidemia hirta* has been removed from analyses.

Trait	**Variable**	**All species**				**Without *Clidemia hirta***			
		df	Direction of effect	Likelihood-ratio test	*p*	*df*	Direction of effect	Likelihood-ratio test	*p*
Plant woodiness	*Habitat*	3	+	33.57	**<0.001**	2	+	18.91	**<0.001**
	Canopy cover	1	+	8.53	**0.003**	1	-	4.12	**0.042**
Plant maximum height (m)	*Habitat*	3	+	22.12	**<0.001**	2	+	14.98	**<0.001**
	Canopy cover	1	+	4.23	**0.04**	1	-	2.68	0.1
Seed dry mass (g/1000 seeds)	*Habitat*	3	-	8.95	**0.03**	2	-	2.91	0.23
	Canopy cover	1	-	16.12	**<0.001**	1	-	0.86	0.35
Long distance dispersal	*Habitat*	3	+	15.69	**0.001**	2	+	4.05	0.13
	Canopy cover	1	+	7.7	**0.005**	1	+	0.85	0.36
Vertebrate dispersed	*Habitat*	3	+	23.1	**<0.001**	2	+	9.1	**0.01**
	Canopy cover	1	+	7.22	**0.007**	1	+	0.22	0.64
Wind dispersed	*Habitat*	3	-	31	**<0.001**	2	+	3.64	0.16
	Canopy cover	1	-	4.57	**0.03**	1	+	3.03	0.08

Table S3.8: Differences in pairwise comparisons of six functional traits from 18 exotic species across four habitats, after accounting for the effect of canopy cover, in Sabah, Malaysia. Models were run with and without the dominant species *Clidemia hirta* included. *SE* = Standard error of the mean. *Df* = degrees of freedom. Df in binomials models Test statistic = *t* ratio for Gaussian models (i.e. continuous data) and *z* ratio for binomial models (i.e. binary data). Significant *P* are in bold.

Trait	**Pairwise comparison**	All species					Without *Clidemia hirta*				
		Estimate	*SE*	*df*	Test statistic	*p*	Estimate	*SE*	*df*	Test statistic	*p*
Plant woodiness	*OP – Edge*	-0.72	0.40	-	-1.79	0.27	-1.74	0.47	-	-3.66	**<0.001**
	OP – Disturbed	-2.71	0.60	-	-4.53	**<0.001**	-3.44	0.74	-	-4.67	**<0.001**
	OP – Intact	-5.50	1.33	-	-4.13	**<0.001**	-	-	-	-	-
	Edge – Disturbed	-1.99	0.47	-	-4.19	**<0.001**	-1.7	0.59	-	-2.87	**0.011**
	Edge – Intact	-4.78	1.28	-	-3.73	**0.001**	-	-	-	-	-
	Dist. – Intact	-2.80	1.28	-	-2.19	0.126	-	-	-	-	-
Plant maximum height (m)	*OP – Edge*	-0.14	0.04	57.6	-3.54	**0.004**	-0.21	0.06	31.90	-3.35	**0.004**
	OP – Disturbed	-0.26	0.05	63.1	-5.16	**<0.001**	-0.42	0.10	42.90	-4.35	**<0.001**
	OP – Intact	-0.27	0.06	63.2	-4.42	**<0.001**	-	-	-	-	-
	Edge – Disturbed	-0.12	0.04	57.4	-3.1	**0.017**	-0.21	0.08	39.30	-2.64	0.06
	Edge – Intact	-0.13	0.05	59.2	-2.72	**0.04**	-	-	-	-	-
	Dist. – Intact	-0.01	0.04	55.4	-0.25	0.99	-	-	-	-	-
Seed dry mass (g/1000 seeds)	*OP – Edge*	0.14	0.10	56.90	1.38	0.518	0.18	0.16	33.40	1.13	0.500
	OP – Disturbed	0.37	0.13	61.50	2.86	**0.029**	-0.07	0.22	46.70	-0.32	0.945
	OP – Intact	0.43	0.16	61.40	2.73	**0.040**	-	-	-	-	-
	Edge – Disturbed	0.23	0.10	56.60	2.30	0.111	-0.25	0.18	43.10	-1.35	0.378
	Edge – Intact	0.29	0.12	58.00	2.36	0.097	-	-	-	-	-

	Dist. – Intact	0.06	0.10	54.90	0.57	0.941	-	-	-	-	-
Long distance dispersal	*OP – Edge*	-0.68	0.45	-	-1.50	0.440	-0.85	0.41	-	-2.08	0.094
	OP – Disturbed	-1.80	0.67	-	-2.68	**0.037**	-0.94	0.65	-	-1.44	0.319
	OP – Intact	-4.38	1.46	-	-3.00	**0.015**	-	-	-	-	-
	Edge – Disturbed	-1.13	0.54	-	-2.09	0.158	-0.09	0.54	-	-0.16	0.986
	Edge – Intact	-3.70	1.41	-	-2.62	**0.043**	-	-	-	-	-
	Dist. – Intact	-2.58	1.41	-	-1.83	0.259	-	-	-	-	-
Vertebrate dispersed	*OP – Edge*	-0.79	0.38	-	-2.08	0.158	-0.61	0.24	-	-2.50	**0.007**
	OP – Disturbed	-2.15	0.58	-	-3.71	**0.001**	-1.01	0.41	-	-2.46	**0.02**
	OP – Intact	-4.77	1.39	-	-3.44	**0.003**	-	-	-	-	-
	Edge – Disturbed	-1.36	0.46	-	-2.95	**0.017**	-0.40	0.34	-	-1.18	0.55
	Edge – Intact	-3.97	1.34	-	-2.96	**0.017**	-	-	-	-	-
	Dist. – Intact	-2.62	1.34	-	-1.95	0.21	-	-	-	-	-
Wind dispersed	*OP – Edge*	-0.50	0.39	-	-1.27	0.582	-0.68	0.37	-	-1.86	0.150
	OP – Disturbed	0.87	0.54	-	1.60	0.377	-0.30	0.58	-	-0.52	0.863
	OP – Intact	4.45	1.40	-	3.19	**0.008**	-	-	-	-	-
	Edge – Disturbed	1.37	0.45	-	3.07	**0.012**	0.38	0.48	-	0.80	0.702
	Edge – Intact	4.95	1.37	-	3.62	**0.002**	-	-	-	-	-
	Dist. – Intact	3.58	1.36	-	2.63	**0.042**	-	-	-	-	-

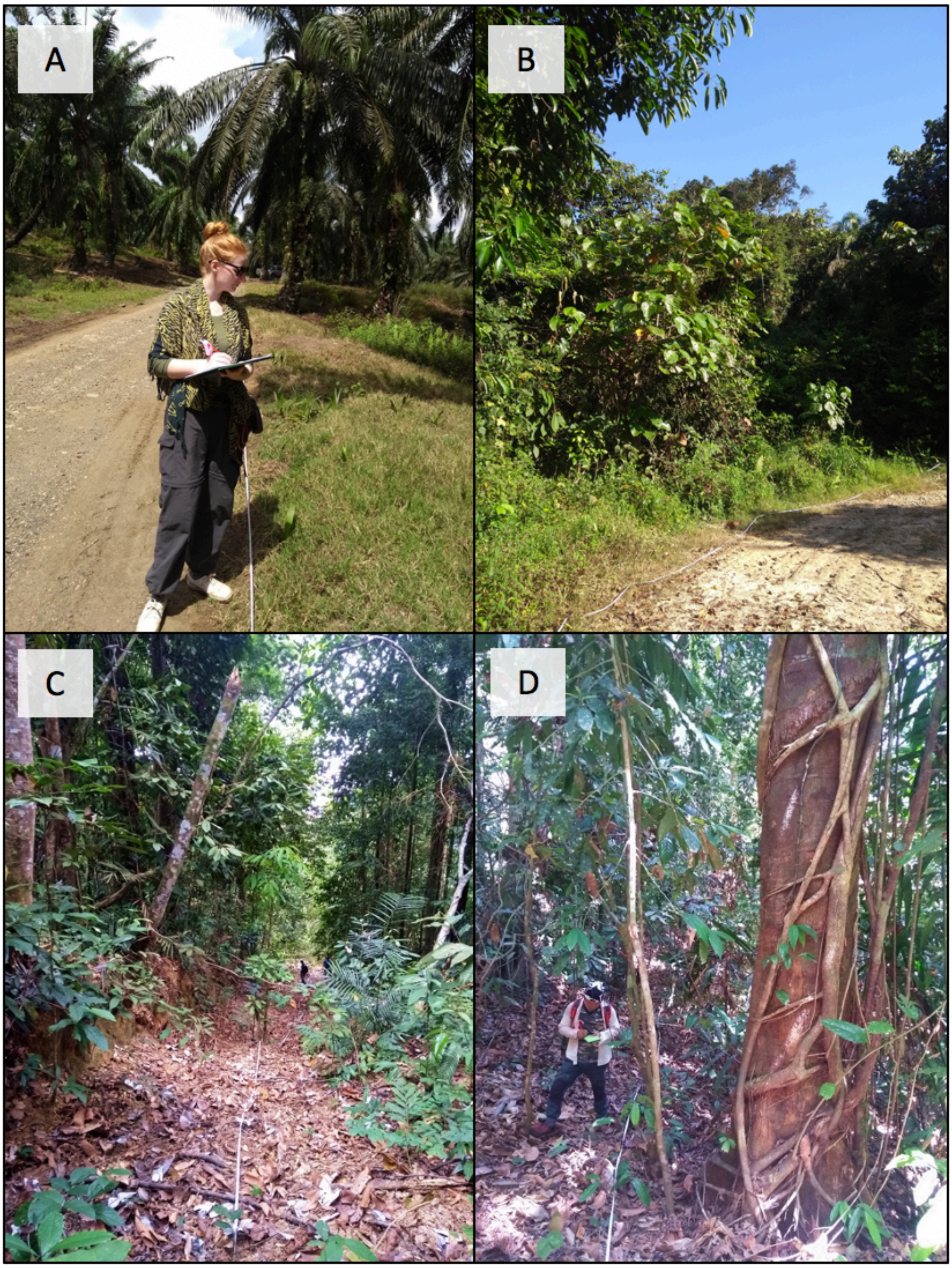

Figure S3.1: Photographs showing the four habitats: A = oil palm, B = forest-oil palm edge, C = disturbed forest and D = intact forest.

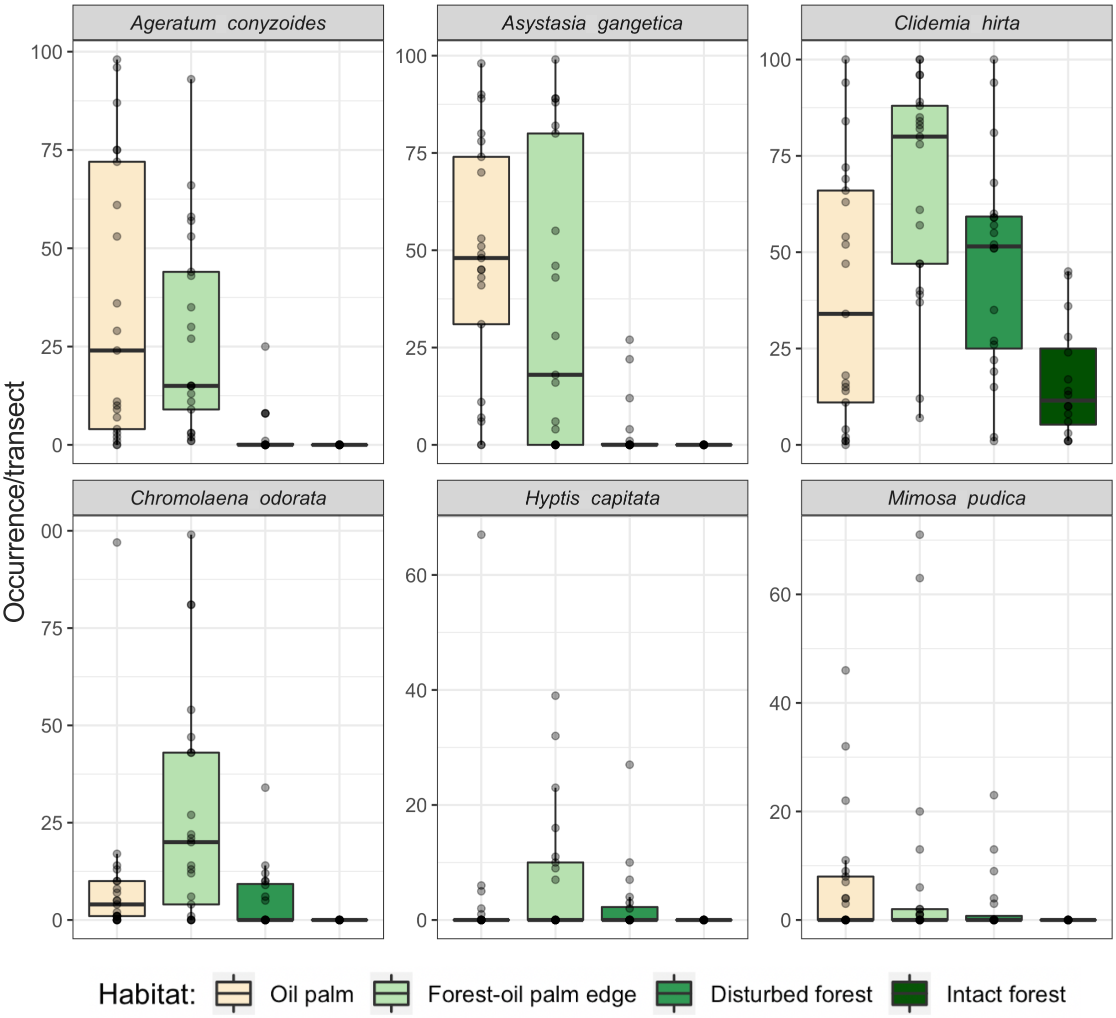

Figure S3.2: Occurrence of the six most common exotic species recorded across four habitats within oil palm dominated landscapes in Sabah, Malaysian Borneo. Occurrence = the proportion of 1 m sections a species was recorded present along each 100 m transect.

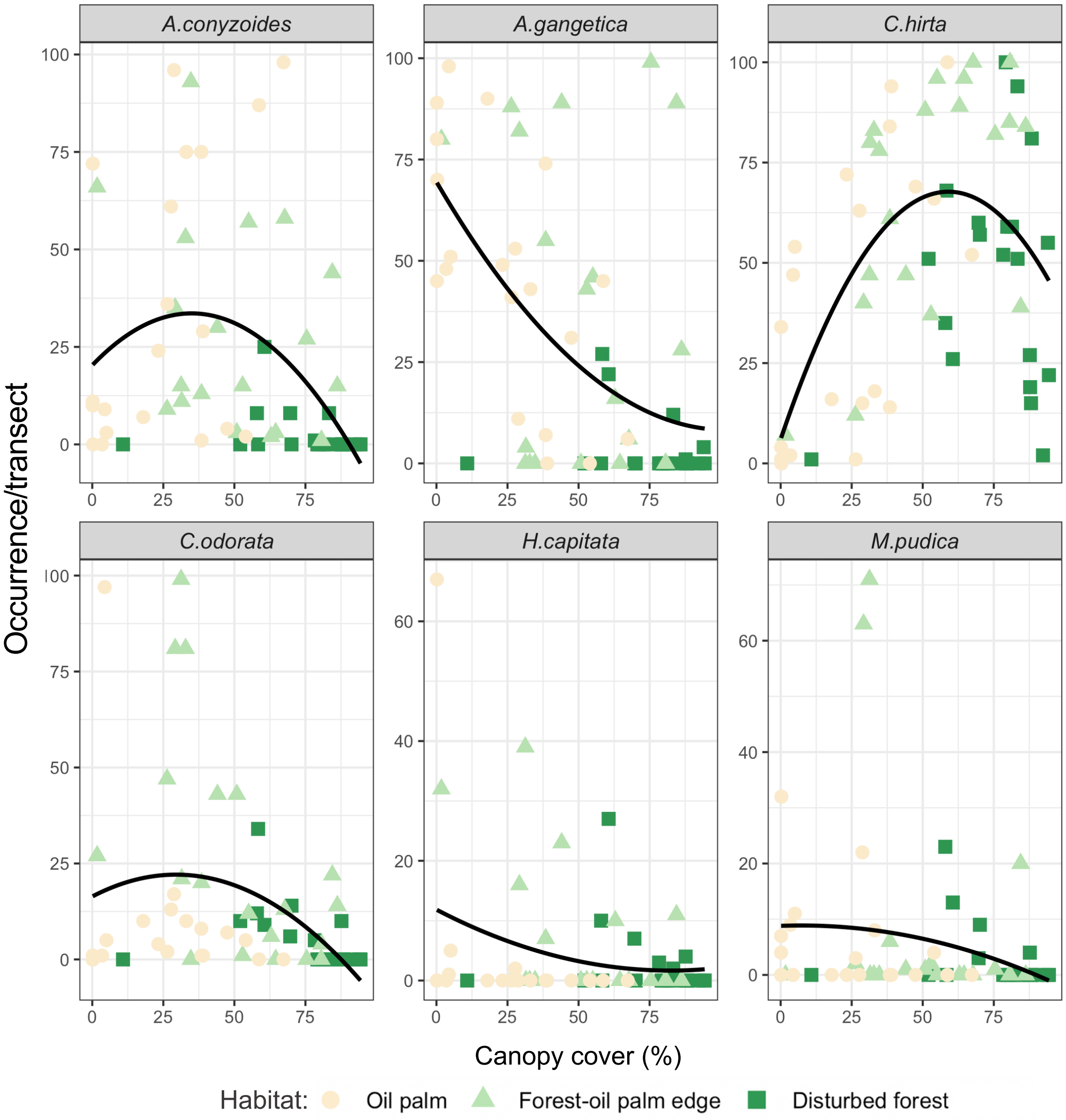

Figure S3.3: Relationship between canopy cover and the six most common exotic species recorded across three habitats within oil palm dominated landscapes in Sabah, Malaysian Borneo. Occurrence = the proportion of 1 m sections a species was recorded present along each 100 m transect. Regression lines were fitted to linear models for each species with the following formula = occurrence ~ canopy cover + $(\text{canopy cover})^2$.

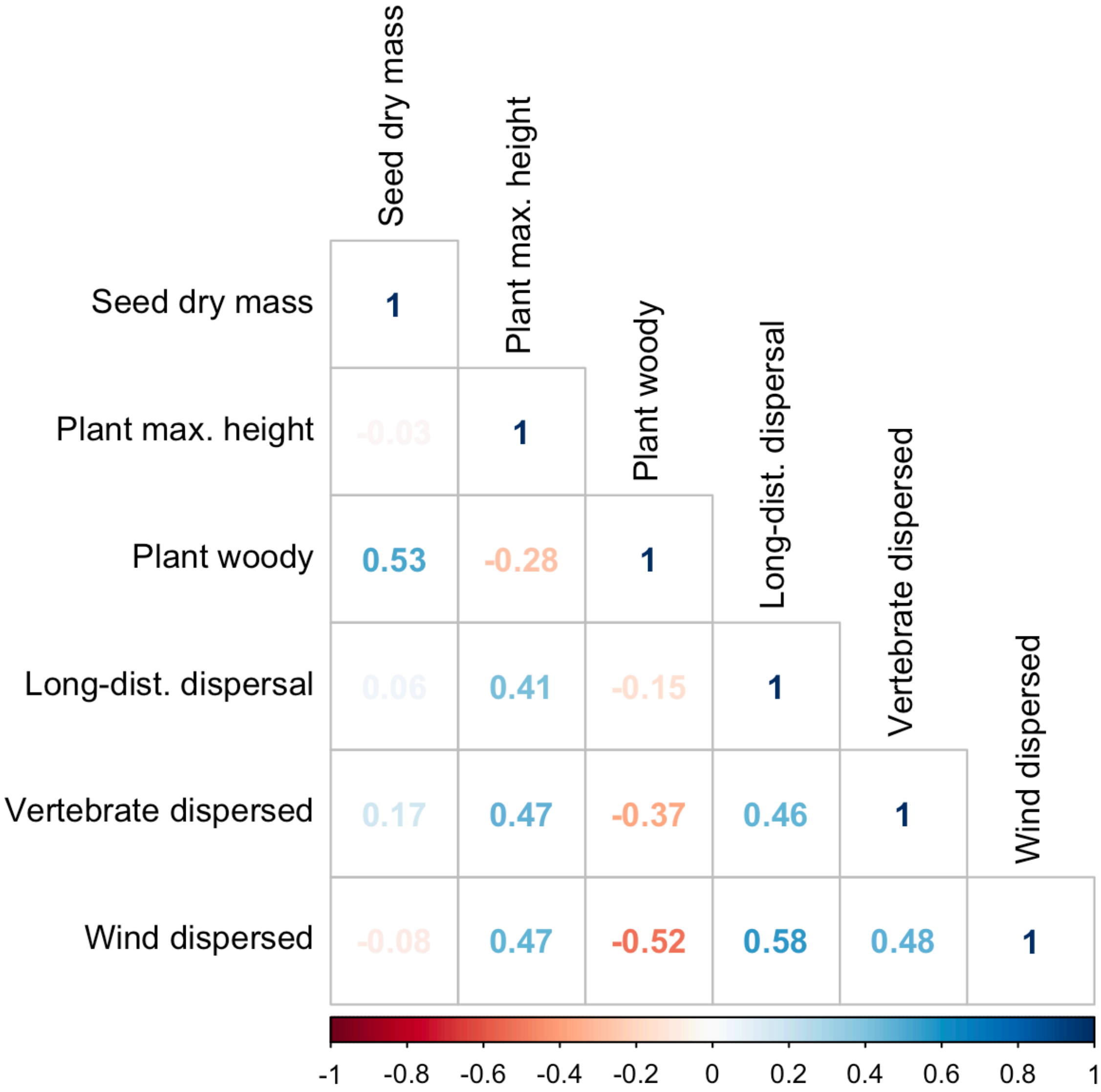

Figure S3.4: Correlations between six functional traits of exotic species (n=18) recorded across transects in oil palm dominated landscapes in Sabah, Malaysian Borneo. Data are raw trait data for each species. The two continuous traits, seed dry mass and plant maximum plant, were both $\log_{10}$ transformed to improve normality.

Appendix 4: Supporting Information for Chapter 4

Table S4.1: Summary of 21 sites where herbivory rates in exotic shrubs *Clidemia hirta* were recorded in two habitats in Sabah, Malaysian Borneo. Size of forest remnant = hectares of forest within Wilmar plantation boundary, to the nearest 1 ha (unless very small; <20ha). Size data was collected from plantation maps provided by plantation managers during the first field season (July-Oct. 2017). Disturbed forest transect location = details on the location and therefore disturbance history of each 'disturbed forest' transect, information provided by plantation managers. Forest remnants were either discrete and fully surrounded by oil palm (n=15) or connected to a forest reserve out with the plantation boundary (n=6; denoted by a †).

Site	Plantation name	Size of forest remnant (ha)	Transect location	Habitat	Start coordinates		End coordinates		Distance to edge	Canopy cover
					Lat	Long	Lat	Long		
F2	Sabahmas	89	Minor road	Forest-oil palm edge	5.13811667	118.4419	5.13865	118.441317	-	44.05
			Skid trail	Disturbed forest	5.13838333	118.441983	5.13916667	118.441683	41	87.68
F3	Sabahmas	57	Terrace	Forest-oil palm edge	5.13378333	118.427933	5.13445	118.428267	-	26.32
			Terrace/skid trail	Disturbed forest	5.13443333	118.42725	5.13435	118.42815	44	83.31
F5	Reka Halus	52	Terrace	Forest-oil palm edge	5.79855	117.502467	5.79795	117.502017	-	75.46
			Skid trail	Disturbed forest	5.7978	117.50203	5.7978	117.50121	48	88.09
F6	Reka Halus	12.5	Minor road	Forest-oil palm edge	5.73313333	117.484017	5.73246667	117.483483	-	1.72
			Skid trail	Disturbed forest	5.7306	117.48655	5.73126667	117.486117	70	94.02
F7	Kiabau	8.8	Terrace	Forest-oil palm edge	5.75035	117.255	5.75078333	117.2545	-	86.22
			Skid trail	Disturbed forest	5.75043333	117.254133	5.74985	117.254817	35	94.38
F8	Kiabau	25	Minor road	Forest-oil palm edge	5.77058333	117.255567	5.771	117.255133	-	52.89
			Road/skid trail	Disturbed forest	5.76936667	117.254533	5.76878333	117.255183	75	10.82
F11†	Sekar Imej	1375	Minor road	Forest-oil palm edge	6.31848333	117.241883	6.31836667	117.24335	-	31.46
			Skid trail	Disturbed forest	6.31746667	117.243267	6.31743333	117.242533	46	87.78
F12	Sapi Sugut	82	Minor road	Forest-oil palm edge	6.25771667	117.248617	6.25786667	117.247833	-	50.86

			Road/skid trail	Disturbed forest	6.25575	117.249117	6.25591667	117.249867	93	81.38
F13	Sri Kamusan	10	Minor road	Forest-oil palm edge	6.2168	117.283683	6.21631667	117.283667	-	55.02
			Skid trail	Disturbed forest	6.2163	117.282967	6.21643333	117.282183	72	88.35
F14†	Sri Kamusan	525	Minor road	Forest-oil palm edge	6.17726667	117.275617	6.17665	117.275833	-	34.69
			Skid trail	Disturbed forest	6.17701667	117.2761	6.17628333	117.2761	23	79.72
F15	Sabahmas	3.25	Minor road	Forest-oil palm edge	5.19465	118.405967	5.19441667	118.406767	-	84.45
			Skid trail	Disturbed forest	5.19426667	118.405617	5.1938	118.404917	26	57.93
F16	Sabahmas	506	Terrace	Forest-oil palm edge	5.22075	118.487017	5.22076667	118.486167	-	31.26
			Road	Disturbed forest	5.22096667	118.487267	5.22143333	118.487983	83	70.1
F19	Sri Kamusan	15	Minor road	Forest-oil palm edge	6.21711667	117.31105	6.2168	117.3103	-	64.54
			Skid trail	Disturbed forest	6.21718333	117.3087	6.21661667	117.308117	14	79.2
F20†	Sri Kamusan	525	Terrace	Forest-oil palm edge	6.20045	117.319733	6.20063333	117.31915	-	67.71
			Skid trail	Disturbed forest	6.19773333	117.318317	6.1971	117.31785	61	83.36
F21	Sri Kamusan	35	Minor road	Forest-oil palm edge	6.19776667	117.27505	6.19745	117.274367	-	80.71
			Road/skid trail	Disturbed forest	6.19801667	117.274967	6.1988	117.27455	58	52.06
F22	Sekar Imej	17.7	Terrace	Forest-oil palm edge	6.31318333	117.259517	6.31245	117.259517	-	80.55
			Road/skid trail	Disturbed forest	6.31281667	117.259817	6.31315	117.260533	28	92.3
F23†	Sapi Sugut	377	Minor road	Forest-oil palm edge	6.25753333	117.234167	6.25711667	117.234817	-	32.82
			Road/skid trail	Disturbed forest	6.25776667	117.236483	6.25791667	117.23735	55	58.35
F24	Kiabau	9	Minor road	Forest-oil palm edge	5.75365	117.263333	5.75428333	117.263167	-	24.55
F25	Sabahmas	13.2	Minor road	Forest-oil palm edge	5.21106667	118.4474	5.21178333	118.447567	-	38.43
			Skid trail	Disturbed forest	5.21171667	118.44695	5.21105	118.4467	65	69.65
F26†	Sabahmas	506	Terrace	Forest-oil palm edge	5.21395	118.464483	5.21343333	118.464017	-	62.92
			Road	Disturbed forest	5.21426667	118.4644	5.21481667	118.4638	78	60.58
F27	Sabahmas	10.2	Minor road	Forest-oil palm edge	5.14705	118.4135	5.14661667	118.412783	-	29.18
			Terrace/skid trail	Disturbed forest	5.14735	118.413033	5.14748333	118.412267	47	78.32

Table S4.2: Summary of herbivore damage on exotic *Clidemia hirta* and native *Melastoma* spp. shrubs in two habitat types, in Sabah, Malaysian Borneo. Forest-oil palm edge = minor plantation road or oil palm terrace where oil palm planted area meets forest remnant; Disturbed forest = abandoned skid trail, road or terrace inside forest. Reproductive organs = buds, flowers, immature fruit and ripe fruit. * denotes variables that were tested with a GLMM looking at the differences in *C. hirta* between habitats (local density was natural log +1 transformed with Gaussian error distribution; plant size had a poisson error distribution). ** denotes variables that were tested with a GLMM looking at the differences between species (plants either reproductively active or not had a binomial error distribution; number of reproductive organs per reproductively active individual had a poisson error distribution). All models had random effects of transect number nested within site.

	Exotic *Clidemia hirta*			Native *Melastoma* spp.		
	Total	Forest-oil palm edge	Forest interior	Total	Forest-oil palm edge	Forest interior
Average number of individuals surveyed per transect (out of 10)	8.9	9.8	8	4.8	6.1	3.4
Median local density of *C. hirta* (out of 10)*	8	8	6	-	-	-
Median plant size (total number of leaves per plant)*	22	22	24	19	20	17
Median herbivory damage per plant	78%	77%	79%	93%	93%	93%
Median herbivory damage per leaf	6.1%	5.8%	6.3%	20%	20%	20%
Percentage of plants that were reproductively active**	44.5%	42.2%	47.5%	7.1%	8.5%	4.5%
Median reproductive organs per reproductively active plant**	15	18	14	3	3	3

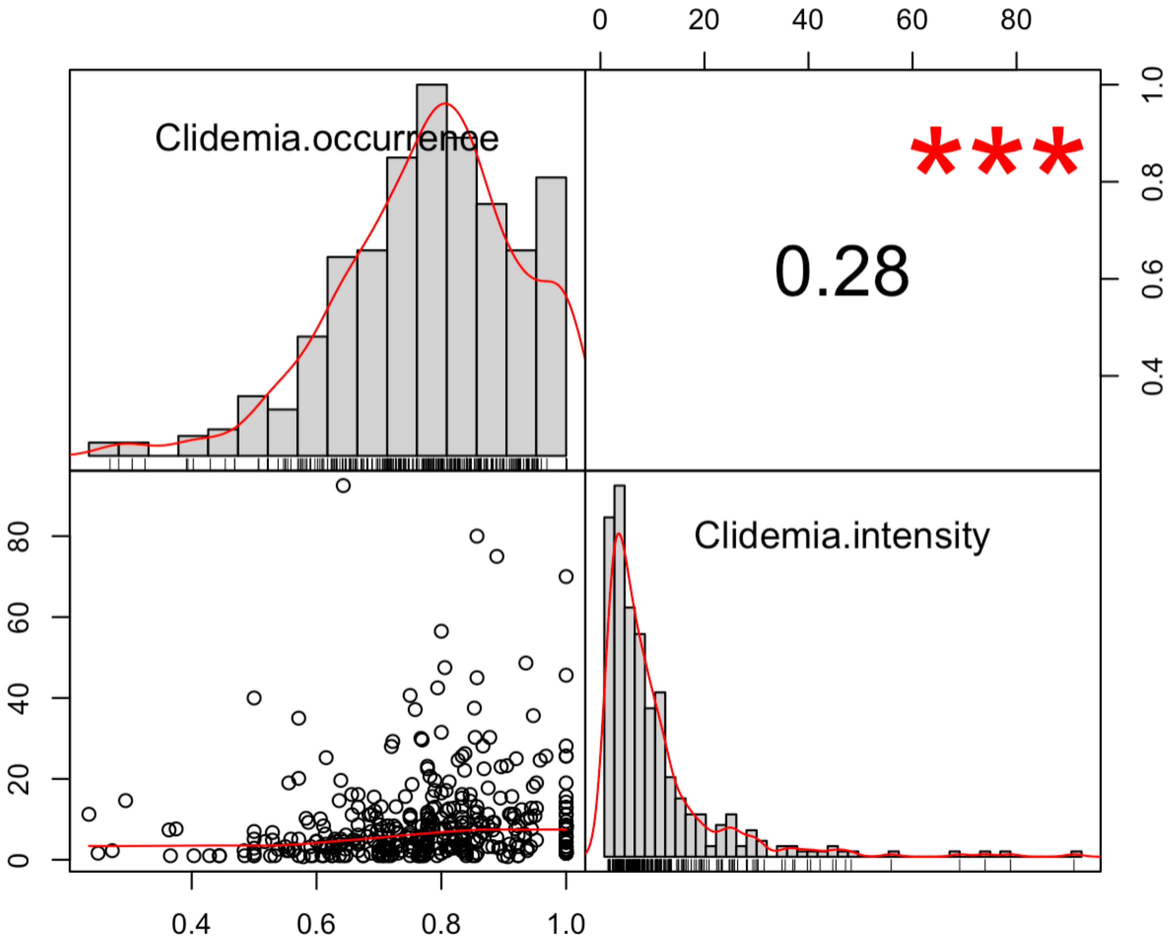

Figure S4.1: Spearman rank correlation between herbivory occurrence per plant and herbivory intensity per leaf recorded in exotic *Clidemia hirta* plants across transects in oil palm dominated landscapes in Sabah, Malaysian Borneo. Data are raw trait data for each species.

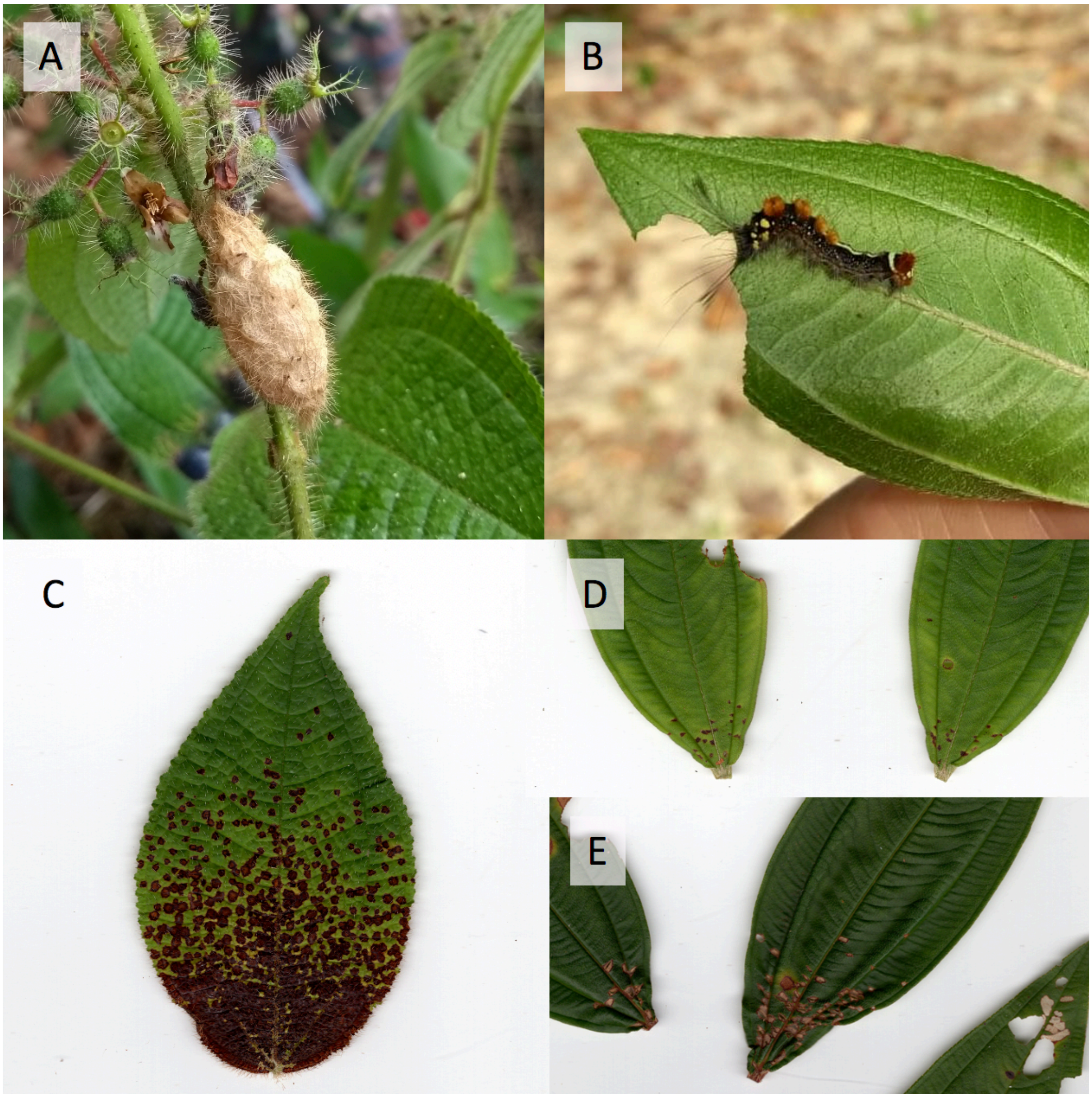

Figure S4.2: Photographers of A) Tussock moth cocoon on *Clidemia hirta* plant, B) Tussock moth caterpillar feeding on *Melastoma* spp. plant, C) disease on *Clidemia hirta* plant and D-E) disease on *Melastoma* spp. plant, in oil palm dominated landscapes in Sabah, Malaysian Borneo. Identification by Georg Hantke, a curatorial preparator at National Museums of Scotland.

Text S4.1: Testing parameters for composite variable

To test the best fit for parameters *h* and *x* for the ‘proximity index’, two GLMMs were fitted, with herbivory occurrence and herbivory intensity as the response variables and ‘proximity index’ as the only fixed effect (random effects remained the same). Each model was run 20 times whilst varying both *h* (native herbivory occurrence or native herbivory intensity) and *x* (1-10 m). We selected the combination that was the best fit (i.e. lowest *P*-value and highest AIC), which we found to be *x*=2 and *h*=native herbivory intensity for exotic herbivory occurrence, and *x*=5 and *h*=native herbivory intensity for exotic herbivory intensity (Table S4.3).

Table S4.3: Testing the best fit for two parameters *h* and *x* for ‘proximity index’ composite variable. *x* = distance decay parameter (ranging 1-10) and *h* = herbivory rate in native *Melastoma* spp. plants, either herbivory intensity per leaf or herbivory occurrence per plant. Model equation = herbivory occurrence in *C. hirta* (number of damaged leaves & number of undamaged leaves) or herbivory intensity in *C. hirta* (category of leaf area removed) ~Proximity index + (1|Site/Transect.number/ Clidemia.hirta.individual.code). Models were run using ‘glmer’ function with a binomial error distribution. Best fit for both response variables in bold.

	h = herbivory intensity				*h* = herbivory occurrence			
C. hirta **herbivory occurrence**	*x*	AIC	logLik	*p-value*	*x*	AIC	logLik	*P*
	1	1007.7	-498.8	0.0102	1	1011.6	-500.8	0.103
	2	**1007**	**-498.5**	**0.00685**	2	1011	-500.5	0.0708
	3	1007.5	-498.8	0.0091	3	1011	-500.5	0.068
	4	1008.1	-499.1	0.0128	4	1011	-500.5	0.0697
	5	1008.6	-499.3	0.0173	5	1011.1	-500.5	0.0724
	6	1009.1	-499.5	0.0221	6	1011.1	-500.6	0.0756
	7	1009.4	-499.7	0.027	7	1011.2	-500.6	0.079
	8	1009.7	-499.8	0.032	8	1011.3	-500.6	0.0827
	9	1009.9	-500	0.0367	9	1011.3	-500.7	0.0863
	10	1010.1	-500.1	0.0412	10	1011.4	-500.7	0.0904
C. hirta **herbivory intensity**	*h* = herbivory intensity				*h* = herbivory occurrence			
	x	AIC	LRT	*p-value*	*x*	AIC	LRT	*P*
	1	2148.4	6.99	0.0082	1	2148.4	1.846	0.174
	2	2148.4	8.326	0.0039	2	2148.4	1.862	0.172
	3	2148.4	8.923	0.00282	3	2148.4	1.707	0.191
	4	2148.4	9.1574	0.00247	4	2148.4	1.529	0.216
	5	**2148.4**	**9.216**	**0.00239**	5	2148.4	1.36	0.244
	6	2148.4	9.191	0.00243	6	2148.4	1.21	0.272
	7	2148.4	9.1288	0.0025	7	2148.4	1.076	0.3
	8	2148.4	9.052	0.0026	8	2148.4	0.958	0.33
	9	2148.4	8.971	0.00274	9	2148.4	0.855	0.36
	10	2148.4	8.891	0.00287	10	2148.4	0.764	0.38

Text S4.2: Specific Leaf Area in *Clidemia hirta*

Methods – In order to investigate variation in Specific Leaf Area (SLA; area of one side of a fresh leaf, divided by its oven-dry mass) between different habitat types, we measured SLA in oil palm (major plantation road), forest-oil palm edge, disturbed forest (interior forest transects herbivory was recorded) and intact forest (closed canopy forest) at each of the 21 sites. In each habitat type, we collected four leaves from five *C. hirta* individuals, if available (minimum three leaves from two individuals), spaced along length of transect were collected, following standard protocols (Pérez-Harguindeguy *et al.*, 2013). Leaf area (cm^2) was calculated using Leafscan app (Carlos Anderson, 2017). Leaves were then dried in a convection oven at a temperature of 60°C until a constant weight, before weighing with a Kern precision scale with 0.001g accuracy. The scales were calibrated, following the product instructions, every 10 samples.

Differences in SLA and raw leaf area between the four habitats were tested at the individual plant-level (average of four leaves) using two separate GLMMs, one with SLA as the response variable and one with leaf area, both with a Gaussian error distribution. The only fixed effect was habitat (four levels: oil palm, forest-oil palm edge, forest disturbed and intact forest) and both models had random effects of transect nested in site. Pairwise comparisons between habitats were carried out with a Tukey post hoc test. The relationship between both mean SLA and mean raw leaf area and canopy cover was tested at the transect-level (average of up to 10 plants) using two separate GLMMs, one with SLA as the response variable and one with leaf area, both with a Gaussian error distribution. The only fixed effect was mean canopy cover (average of five measurements spaced across transect) and a random effect of site. SLA was $\log_{10}$ transformed prior to input into all models to improve normality and model convergence.

Results – The effect of habitat on SLA was highly significant (Fig. S4.3; *P* < 0.001), and pairwise comparisons showed this significance occurred between all habitat pairings for SLA and for no pairwise comparison of average leaf area.

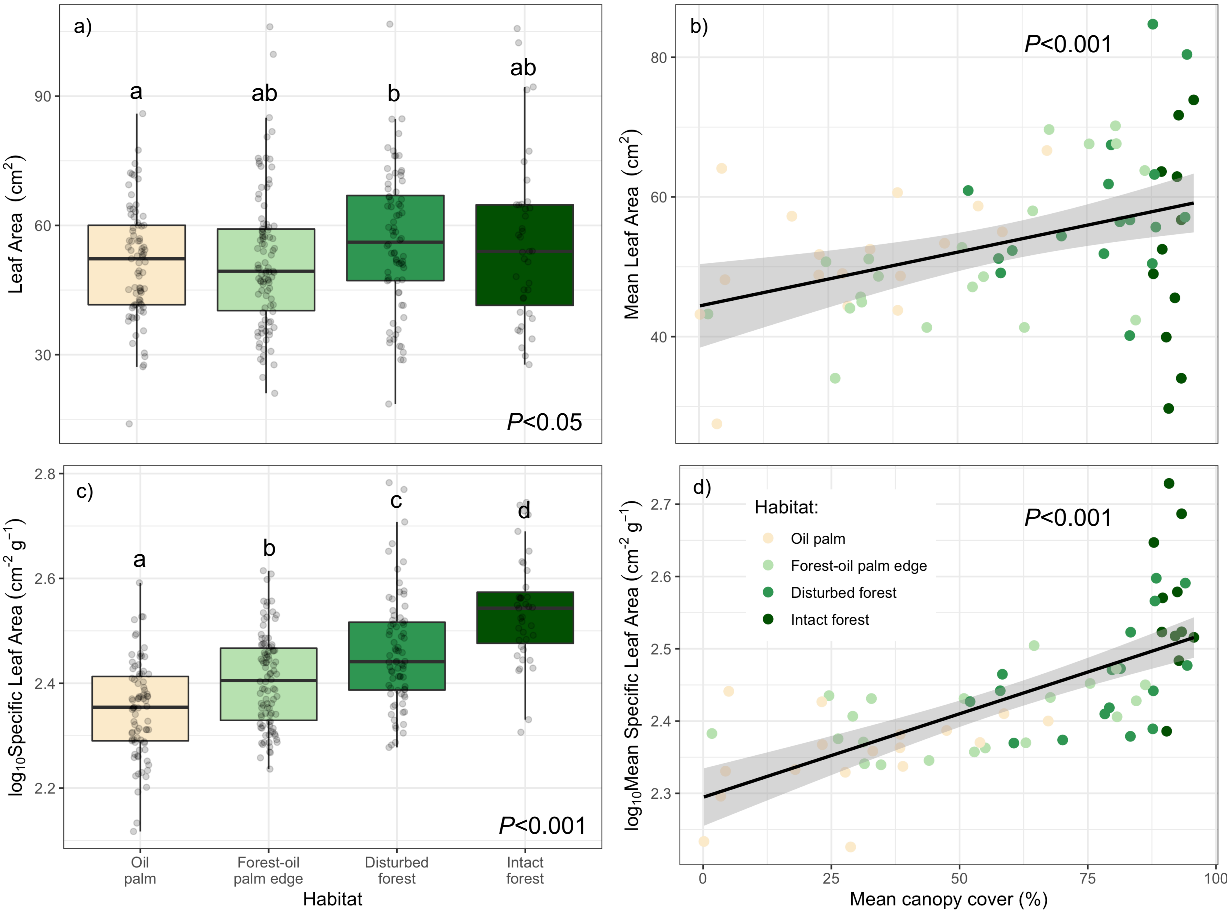

Figure S4.3: Relationship between leaf area in *Clidemia hirta* across four habitats (a) and with mean canopy cover (b), and relationship between Specific Leaf Area (SLA) in *Clidemia hirta* across four habitats (c) and with mean canopy cover (d). Oil palm = roadside of major plantation road; Forest-oil palm edge = minor plantation road or oil palm terrace where oil palm planted areas meets forest remnant; Disturbed forest = abandoned skid trail, road or terrace inside forest ; Intact forest = closed canopy forest. *P*-values based on ANOVA with Satterthwaite's method of degrees of freedom on GLMM output for all models. Letters indicate significant pairwise differences between habitats based on a Tukey post hoc test.

Text S4.3: Drivers of herbivory in native *Melastoma*

Methods – In order to examine the influence of abiotic and biotic factors on herbivory rates in native Melastoma species we used Generalised Linear Mixed Models (GLMMs) using the 'lme4' R package (Bates et al. 2015). As with exotic *C. hirta* data, we modelled herbivory occurrence and herbivory intensity separately, giving us two models. For herbivory occurrence models had a binomial error distribution with the frequency of damaged and undamaged leaves as the response variable. For herbivory intensity all models had a Gaussian error distribution and herbivory intensity (category of percentage damage) as the response variable. Both models had random effects of individual plant nested within transect nested within site. Fixed effects for both models included local canopy cover, plant size and local density of *C. hirta*, all effects had an interaction with habitat included in the model.

To improve model convergence, continuous fixed effects were scaled to unit variance and centred on zero, and herbivory intensity was $\log_{10}$ transformed. For both models, all possible combinations of the fixed effects were investigated using the '*dredge*' function in the 'MuMIn' R package (Bartoń 2013) and the top model selected.

Results – We found there was increased herbivory occurrence in native *Melastoma* in shaded environments (i.e. higher local canopy cover; $P<0.01$). There was also a strong interaction between habitat and local canopy cover (Fig. S4.4), with more herbivory occurrence observed in the open areas inside disturbed forest remnants and conversely, also more herbivory occurrence in closed canopy areas of the forest-oil edge ($P<0.001$). The model with herbivory intensity as the response had no significant terms.

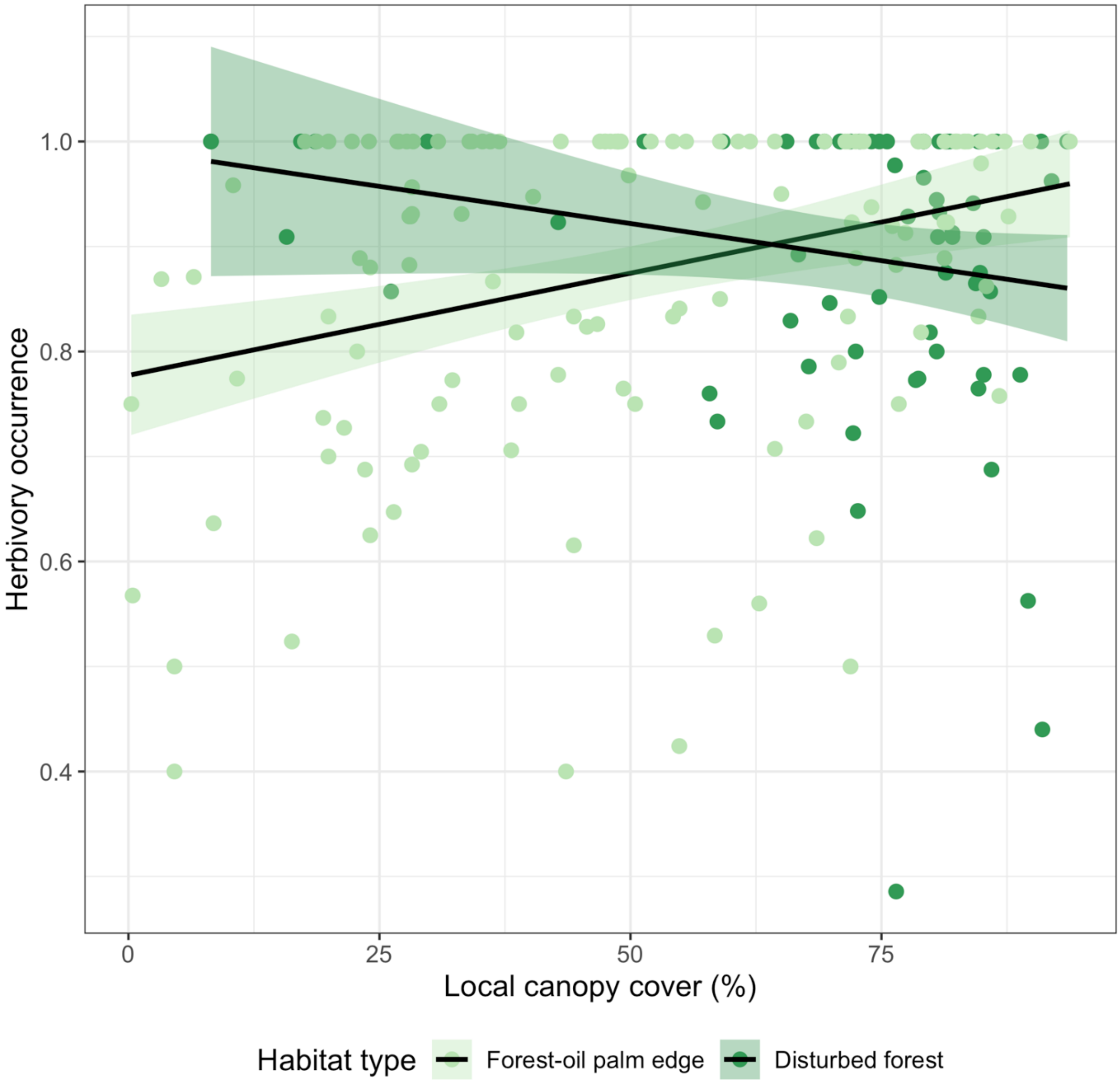

Figure S4.4: Relationship between herbivory in native *Melastoma* spp. and local canopy cover at forest-oil palm edge and in disturbed forest habitats of forest set asides within oil palm plantations, in Sabah, Malaysian Borneo. Herbivory per native plant=portion of damaged leaves per *Melastoma* spp. plant.

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