The
University
Of
Sheffield.

Maintenance and conservation of Dipterocarp diversity in tropical forests

---

Mohammad Nazrin B Abdul Malik

A thesis submitted in partial fulfilment of the degree of

Doctor of Philosophy

Faculty of Science

Department of Animal and Plant Sciences

November 2019

Thesis abstract

Many theories and hypotheses have been developed to explain the maintenance of diversity in plant communities, particularly in hyperdiverse tropical forests. Maintenance of the composition and diversity of tropical forests is vital, especially species of high commercial value. I focus on the high value dipterocarp timber species of Malaysia and Borneo as these have been extensive logged owing to increased demands from global timber trade. In this thesis, I explore the drivers of diversity of this group, as well as the determinants of global abundance, conservation and timber value.

The most widely supported hypothesis for explaining tropical diversity is the Janzen Connell hypothesis. I experimentally tested the key elements of this, namely density and distance dependence, in two dipterocarp species. The results showed that different species exhibited different density and distance dependence effects. To further test the strength of this hypothesis, I conducted a meta-analysis combining multiple studies across tropical and temperate study sites, and with many species tested. It revealed significant support for the Janzen-Connell predictions in terms of distance and density dependence.

Using a phylogenetic comparative approach, I highlight how environmental adaptation affects dipterocarp distribution, and the relationships of plant traits with ecological factors and conservation status. This analysis showed that environmental and ecological factors are related to plant traits and highlights the need for dipterocarp conservation priorities. Habitat destruction and population trend are highly associated with dipterocarp conservation status. I show that timber price value are strongly related to wood density traits that determine the commercial wood type. The results showed that increasing timber prices do not affect dipterocarp conservation status.

Overall this thesis provides new evidence of the mechanisms of species diversity maintenance particularly dipterocarp species from density and distance dependence perspectives. This thesis also highlights the importance of dipterocarp species adaptations in ecological and environmental perspectives, with perspectives on dipterocarp conservation and how this relates to commercial exploitation.

Acknowledgements

Foremost, I would like to express my gratitude to my supervisors Robert Freckleton and David Edwards for their help and support throughout my PhD period. Rob has guided and helped me a lot throughout my study since day one especially with his vast knowledge in ecology and statistical analysis. It allowed me to deeply understand the projects and things that were new to me. Dave helped me a lot in providing feedbacks and his fieldwork skills that made me a better field biologist. It has been wonderful learning experience for me in University of Sheffield.

I am grateful to Ain and Adrian, who have provided me moral and emotional support in my life. Ain assisted me a lot during my fieldwork in Danum Valley, Borneo. I'm also grateful to my other family members, Abah, Mama, Syafiq, Siti, Baba, Mama Ju, Anisa and Hakim that have supported me along the way.

I am also indebted to Rob's lab group and Mynas in providing me fun and productive workplace during my study. Special thanks to Felix, who has helped me during data analysis stage. I would like to thank university staff, Angela Doncaster and Allison Blake for being helpful in financial and admin paperwork for my PhD study. I thank Royal Society research assistants in Danum Valley Field Centre particularly Ahmad for their help during my fieldwork.

Finally, a special gratitude to Universiti Putra Malaysia and Malaysia Ministry of Higher Education for helping and providing funding for my PhD study. Thank you for everyone involved in my PhD journey.

TABLE OF CONTENTS

Chapter 1

Thesis Introduction

Tropical forests are generally known as the richest and most hyper-diverse ecosystem in the world. They are exceptional both in terms of biodiversity and forest structure (Whitmore, 1990; Brown *et al.*, 2013). Tropical rainforests play a vital role in timber production, biological conservation, carbon sequestration and global climate regulation(Bonan, 2008; Beer *et al.*, 2010). Tropical rainforests are considered as the most productive of all terrestrial ecosystems, and they are important in driving climate and soil conservation properties (Blaser et al., 2011). Only occupying 6% of Earth's land surface, tropical forests ecosystem generate habitat for more than 50% all known species and provide economic forest products and ecosystem services globally (Fearnside and Laurance, 2004; Gardner *et al.*, 2009; Achard *et al.*, 2014; Kormann *et al.*, 2018).

Tropical forests have long been recognised for its high species richness, yet the actual number of species in tropical rainforest still remains unknown. Slik et al. (2015) estimated that there are at least 40 000 tropical tree species, but possibility more than 53 000 throughout the globe. More than 50% of known fauna species can be found in tropical forest ecosystems (Zakaria *et al.*, 2016). At a global scale, latitudinal diversity gradients can be observed as biodiversity increases from poles to tropical regions (Ghazoul and Sheil, 2010). In addition, species richness in tropical forests varies among the regions with Neotropics possessing more species compared with Asian and African tropical regions (Primack and Corlett, 2005).

1.1 Maintenance of tropical forest species diversity

Understanding and explaining the mechanisms that maintain plant species diversity and prevent competitive exclusion in plant communities, especially in tropical forests, remains a big debating point among the ecologists. How high number of species manage to coexist in small spatial scales is one of the central questions in community ecology. For instance, tropical forests can support more than 280 plant species in a single hectare of forest plot particularly in Amazonian and Asian forests (Valencia, Balslev and Paz Y Miño C, 1994; De Oliveira and Mori, 1999; Zakaria *et al.*, 2016).

Many theories and hypotheses have been developed to explain the mechanisms that maintain the species diversity. These include niche resource partitioning, the Janzen-Connell hypothesis, Intermediate disturbance hypothesis (IDH) and neutral theory, amongst others (Janzen, 1970; Connell, 1971, 1978; Schoener, 1974a; Hubbell, 2001). In his review, Chesson (2000) stated that species coexistence involves two different processes: equalizing mechanisms by reduce average fitness differences between species; and stabilizing mechanisms increase negative intraspecific interactions relative to negative interspecific interactions.

The Janzen Connell hypothesis was proposed 48 years ago and is the most well-known and widely tested hypothesis for species coexistence in tropics (Janzen, 1970; Connell, 1971).This hypothesis suggests that specialist natural enemies such as pathogens, seed predators and insect herbivores maintain high species diversity by reducing the survival of the conspecific seed/seedlings when close to the conspecific adult trees (distance-dependence), and when they occur in high densities (density dependent). The net effect is to favour the survival of rare species over common ones, thus enhancing species diversity. This negative feedback can be categorised as stabilizing mechanism as stated in Chesson (2000). However, several studies such as meta-analysis by (Hyatt *et al.*, 2003) and Burkey (1994) found no support for Janzen Connell predictions. On the other hand, recent literature tested the Janzen-Connell predictions and found evidence on distance/density dependence in regulating species coexistence in plant communities (Terborgh, 2012; Comita *et al.*, 2014; Zhu *et al.*, 2015). Thus, further testing is needed to assess the Janzen-Connell effects in plant communities and species-specific response.

South-East Asian tropical lowland forests are dominated by trees from Dipterocarpaceae family, highly valued timber in global market. Dipterocarps is well known species for timber harvesting and a variety of non-timber forest products, which major contributor in Asian countries economy(Kleine and Heuveldop, 1993; Jomo, Chang and Khoo, 2004; Ashton, 2012).Such important roles of dipterocarps in tropical forest, it raises the needs of understand dipterocarps in ecological perspectives for better and sustainable management. To date, the predictions of the Janzen Connell mechanism have been tested in only a handful of dipterocarps species, and how they co-exist in plant communities is largely unknown (Curran and Webb, 2000; Massey *et al.*, 2006; Sun *et al.*, 2007; Takeuchi and Nakashizuka, 2007a; Bagchi, Press and Scholes, 2010). There is growing need for further testing of this prediction to establish knowledge of the processes determining dipterocarp species diversity.

1.2 Dipterocarps

The name Dipterocarpaceae is derived from Greek meaning (di= two, pteron= wing, karpos= fruit), leading to two-winged fruit (Latinized form: Dipterocarpus). It comprises 17 genera *(Anisoptera, Cotylelobium, Dipterocarpus, Dryobalanops, Hopea, Neobalanocarpus, Parashorea, Shorea, Marquesia, Monotes, Pseudomonotes, Pakaraimaea, Stemonoporus, Vateriopsis, Vateria, Vatica*, and *Upuna*) and about 695 species (Christenhusz & Byng 2016). The Dipterocarpaceae are large canopy or emergent trees with a pantropical distribution from northern South America to the Malay Archipelago. The tallest flowering trees in the tropics is a dipterocarp, *Shorea faguetiana*, with height of 88.3 metres in Tawau Hills National Park, Sabah, Malaysia (Ghazoul, 2016). Even with pantropical distribution, majority of species from this particular family dominated throughout South East Asian lowland forests. The greatest dipterocarps diversity occurs in Borneo(Ashton, 1982).

Dipterocarps involved in supra-annual mast flowering events particularly among canopy species(Ashton, Givnish and Appanah, 1988a). Dipterocarps is described as long-lived tree species, insect-pollinated and have strong habitat associations(Momose et al. 1998; Ashton & Kettle 2012; Kettle 2012).Dipterocarps also been associated with ectomychorrizal fungi as these fungi can affect the plant diversity pattern in various ecosystem(McGuire, 2008; Bachelot *et al.*, 2017).

1.3 Maintenance and conservation of dipterocarp species diversity

Timber harvesting and illegal logging on these high commercial values and excellent qualities of dipterocarp timber and non-timber forest products (NTFP) are the major drivers of tropical forest exploitations. Dipterocarp forest cover across South East Asia has declined by about 32 million hectares from 1990 to 2010 (Achard *et al.*, 2014). Lowland dipterocarp forests have been logged extensively in recent years (Achard et al. 2002.; Curran et al. 1999; Keenan et al. 2015). Because dipterocarp are highly habitat specific, forest clearance has greatly impacted on dipterocarp species diversity through forest fragmentation, forest fire and invasive species (Gardner *et al.*, 2009; Ghazoul and Sheil, 2010). For instance, establishment of invasive species such as bamboo at logging sites greatly suppressed dipterocarp seedling regeneration in Harapan Forest, Sumatra (de Kok *et al.*, 2015). Furthermore, forestry management guidelines for harvesting practice in dipterocarp forest take little account of the maintenance and conservation of dipterocarp species diversity (Kleine and Heuveldop, 1993; Ashton, 2012).

Forest degradation in dipterocarp forest is affecting dipterocarp conservation status. Based on the IUCN Red List of Threatened Species (IUCN, 2017), most dipterocarp species are listed as endangered and critically endangered owing to loss of extensive areas of forest. In total, about 115 dipterocarp species listed as endangered, 224 species as critically endangered and 2 species as extinct in the wild. Clearly this highly value and threatened groups is urgently requiring better management in terms of maintenance and conservation of populations.

Reduced Impact Logging (RIL) guidelines have been developed to minimise forest damage from timber harvesting. However it still remain unclear whether such practices can promote forest recovery, specifically preserving and conserving species diversity (Holmes *et al.*, 2002; Peña-Claros *et al.*, 2008; Putz *et al.*, 2008). Better understanding of dipterocarp species adaptation and life history strategies from ecological and environmental perspectives will provide information that can be used to develop sustainable and effective forest management.

Thesis overview

The overall objective of this thesis is to assess and provide knowledge regarding the maintenance and conservation of tropical forest diversity particularly the Dipterocarpaceae family, which dominates Southeast Asian Forest. I present four data chapters in this thesis to address my objectives and final chapter as general discussion of my findings.

In the Chapter 2, I used an experimental approach on two native dipterocarp species to identify the strength of Janzen Connell hypothesis (density and distance dependence), the most widely tested hypothesis in species diversity maintenance. To test density and distance dependent effects on species, I manipulated density, distance and species combinations in the experimental plots, and censused the naturally occurring seedlings plots as control plots. The plots were revisited after 12 months after planting. This experiment was conducted in Danum Valley Conservation Area, Sabah, Borneo which holds the greatest of dipterocarp diversity.

A large number of published Janzen-Connell studies have been published globally particularly from the Neotropics (Augspurger and Kitajima, 1992; Forget, 1993; C. a. Chapman and Chapman, 1996; Bell, Freckleton and Lewis, 2006; Swamy and Terborgh, 2010). Meta-analysis is a powerful tool that allows ecologists to synthesize and compare results from all studies that tested specific hypothesis (Harrison, 2011; Koricheva, Gurevitch and Mengersen, 2013). From published studies, broad questions have been addressed on how Janzen Connell effects vary with a range of factors. To synthesise these questions, in Chapter 3 I used meta-analysis to quantify the weight of evidence for distance and density dependence in tropical and temperate forest. I compared the magnitude of effect among different groups (i.e. variation in life history stages) as well as across the globe.

In hyperdiverse Southeast Asian forests, high dipterocarp species diversity occurs particularly in Thailand, Peninsular Malaysia, Sumatra Indonesia and Borneo Islands(Ashton 1982; Ashton 1988; Appanah 1993). The question of what drives the abundance of this group across the area in which it occurs is not well understood. Through analysing trait variances in a range of species, Chapter 4 assesses the ecological factors and traits underpinning dipterocarp diversity and distribution. This was carried out using phylogenetic comparative methods (PCM) to analyse environmental adaptations of dipterocarp species in tropical forest, and to test for evidence that evolutionary conservation might limit the species distribution. Several studies noted that PCM could be useful tools to examine phylogenetic signal, ecological and environmental drivers of trait variances in such contexts (Harvey and Pagel, 1991; Cooper, Freckleton and Jetz, 2011).

Dipterocarp life-history and woody traits may influence the wood type that determine timber price value in global market (Preston, Cornwell and DeNoyer, 2006; Chave *et al.*, 2009; Poorter *et al.*, 2010). Furthermore, increases in wood demand and timber price are the major causes of deforestation and forest degradation from logging that could threatened the high commercial value dipterocarp species conservation status(Dudley, Jeanrenaud and Sullivan, 2014; Pirard, Dal Secco and Warman, 2016). In Chapter 5, by using same phylogenetic comparative method as in Chapter 4, I assess the relationship of dipterocarp plants traits relationship with timber price value and test whether increasing timber price value affects dipterocarp conservation status.

Finally, in Chapter 6 I summarise the key findings in the thesis and further developments of maintenance and conservation of dipterocarp species in the future.

Chapter 2

Distance and density dependence in two native Bornean dipterocarp species

Abstract

The Janzen Connell hypothesis proposes that density and distance-dependent mortality generated by specialist natural enemies prevent competitive dominance. This mechanism has been proposed to explain the unusual diversity of tropical forests. Most literature on Janzen Connell mechanisms come from South/Central America, but there are only a few studies in South East Asian forests, which are characterised by a high proportion of mast-seeding species. The role of distance and density-dependence in mast fruiting species is still poorly understood. In a South East Asian system dominated by mast fruiting species we hypothesized that seedling density of dipterocarps (the predominant group of emergent trees) would decrease with distance, seedlings growth would increase, and herbivory would decrease with the distance, according to the predictions of the Janzen-Connell hypothesis. Experiments were conducted to determine the strength of the Janzen Connell mechanism by manipulating the density and identity of tree species (*Parashorea malaanonan* and *Shorea johorensis*) as a function of the distance from parent trees. Survival of conspecific seedlings is reduced near adult trees and at high densities of *Parashorea malaanonan*. High densities of seedlings decreased the growth of conspecific seedlings. Herbivory rates decreased with distance in low density areas. This study indicates that dipterocarp species experienced weak Janzen-Connell effects of distance and density-dependence at the growth stage studied. Future studies might focus on earlier life-history stages such as seeds and small seedlings, as well as studying mortality during mast-seeding events.

2.1 Introduction

Tropical rainforests are generally known as the most diverse ecosystem on Earth in terms of community structure and plant species diversity (Chazdon, 2003; Gardner *et al.*, 2009; Edwards *et al.*, 2014; Steege *et al.*, 2015). For many years, it has been a great challenge for ecologists to understand the process that maintain diversity in plant communities, and this is especially true in tropical forests which are megadiverse (Dalling, Hubbell and Silvera, 1998; Chesson, 2000; Terborgh, 2012; Bagchi *et al.*, 2014; Steege *et al.*, 2015). Therefore, there are various theories or hypotheses that attempt to explain the process that maintaining the tropical forest diversity (Schoener 1974;Janzen 1970;Connell 1971; Connell 1978; Hubbell 2001).

The question of explaining diversity has long been a problem for ecologists, because the number of species appears to greatly exceed the number of limiting resources (Hutchinson, 1961). Under such circumstances the competitive exclusion principle predicts that the superior species will drive other species to extinction (Hardin, 1960; Levin, 1970). Niche partitioning is a potential mechanism that explains high diversity (Schoener, 1974b). This theory suggests that competing species utilise environmental resources in different ways in order to help them to coexist by preventing competitive exclusion. However in hyper diverse systems it is somewhat difficult to image that there are sufficient distinct niches to support all species: the role of niche partitioning in maintaining overall level tropical forest diversity still remains debatable and is unlikely to be the only mechanism in maintaining plant diversity (Wright, 2002; Barot, 2004; Brown *et al.*, 2013).

To understand the mechanisms by which species diversity is maintained it is useful to recognise the roles of two different processes: equalizing mechanisms which decreasing average fitness differences between species; and stabilizing mechanisms which focus on reducing interspecific competition relative to intraspecific (Chesson, 2000; Wright, 2002). Chesson (2000) proposed that stabilizing mechanisms are essential in promoting long term and stable coexistence and this has been supported by theoretical work. There are a large number of studies that have been conducted to identify stabilizing mechanisms, and many of these have focused on resource niche partitioning (Schoener, 1974b; Press, Brown and Barker, 1997; Kobe, 1999; Brown *et al.*, 2013).

Currently the leading theory for explaining tropical forest diversity is the Janzen Connell hypothesis (Janzen 1970; Connell 1971). The Janzen-Connell hypothesis suggests that specialized natural enemies (pathogens, seed predators and herbivores) play a vital role in maintaining diversity of tropical plant species through a density-dependent mechanism. This works by reducing the survival of seeds and seedlings near conspecific adults where seed density is the highest. According to this hypothesis, host-specific natural enemies aggregate on high densities of seeds or seedlings of their hosts, increasing the mortality of these. Because these natural enemies are specialists (host-specific), the density-dependent nature of this mortality will help to prevent competitive exclusion. This is because locally abundant species will experience higher mortality than rare ones, thus allowing the rarer species to survive and coexist. As the population level rare species will tend to increase and common species become rarer. This density-dependence means that this outcome meets the criterion being a stabilizing mechanism that can promote the maintenance of diversity (Chesson, 2000).

Although the Janzen-Connell hypothesis is a stabilizing mechanism for maintaining diversity at the community level, it is based on processes operating at local spatial scales. At the scale of a parent tree, the effect is to reduce recruitment of conspecifics to very low level where the initial density of seeds density was highest (Stevenson, Link and Ramírez, 2005; Freckleton and Lewis, 2006; Massey *et al.*, 2006; Bagchi *et al.*, 2010). Usually this is close to conspecific adults, so that local density-dependence results in distance-dependent survival (Traveset, 1990a; Dalling, Hubbell and Silvera, 1998; Fukue *et al.*, 2007; Swamy and Terborgh, 2010). Distance-dependence and distance-dependence are therefore inversely related to each other with distance-dependence being an 'emergent property' of the Janzen-Connell hypothesis (Takeuchi and Nakashizuka, 2007b; Augspurger *et al.*, 2010; Swamy and Terborgh, 2010).

Based on field experiments there is growing evidence that natural enemies play a role in generating density and distance-dependent mortality (Wright 2002; Brook & Bradshaw 2006; Bagchi et al. 2010; Johnson et al. 2012). There is good evidence that survival of seed increases with distance from the parent tree while high densities of seed or seedlings increase mortality (Terborgh *et al.*, 1993; Norghauer *et al.*, 2006; Matthesius, Chapman and Kelly, 2011). Numerous studies have found that tropical species in forest plots are show density- or distance-dependence (Peres and Baider, 1997; Massey *et al.*, 2006; Norghauer *et al.*, 2006; Swamy and Terborgh, 2010).

Density and distance dependent effects have been observed to be stronger at the seedling stage compared to seed stage (Traveset, 1990b; Hyatt *et al.*, 2003; Comita *et al.*, 2014). In terms of the enemies that generate these effects, experimental studies on pathogens (Bagchi et al. 2010; Mangan et al. 2010), insect herbivores and both (Bagchi *et al.*, 2014) suggest that a suite of natural enemies could be responsible for generating density- and distance-dependence. Recent studies found that natural enemies such as insect and pathogen (fungi) exhibit high specialization in generating density and distance dependence in certain species (Sedio and Ostling, 2013; Fricke, Tewksbury and Rogers, 2014). In terms of phylogenetic distance, Bagchi, Press & Scholes (2010) demonstrated that seedling survival for closely related species that share natural enemies with a focal species is reduced when close to adults of the focal species but increased with phylogenetic dissimilarity from focal species.

Despite an accumulation of evidence, there are some limitations and gaps in the literature, however. The predominance of studies on Janzen Connell effects come from the Neotropical realm, particularly in Central and South America (Dalling et al. 1998; Forget 1992; Roberts & Heithaus 1986; Peres & Baider 1997; Swamy & Terborgh 2010; Stevenson et al. 2005; Augspurger & Kitajima 1992; Sanchez & Martinez 2010). By comparison there is a relative dearth in Africa (Hart, 1995; C. A. Chapman and Chapman, 1996; Matthesius, Chapman and Kelly, 2011), and Asia (Bagchi et al. 2010; Massey et al. 2006; Takeuchi & Nakashizuka 2007). Moreover, most of studies has been focused on single species approaches to identify density-dependent or distance-dependent in hyperdiverse forests (Coates-Estrada and Estrada, 1988; Burkey, 1994; Cintra and Horna, 1997; Norghauer *et al.*, 2006; Augspurger *et al.*, 2010). In testing

Janzen Connell effects, experimental manipulation is required to untangle distance and density effects explicitly since distance and density dependence are correlated with each other (Freckleton and Lewis, 2006).

One difference between forests on different continents concerns the prevailing reproductive cycles. In Southeast Asian forests, the dominant Dipterocarp species are usually involved in community wide mast fruiting events (Peter S Ashton, 1988; S. Appanah, 1993). It might be hypothesised that systems that undergo mast-fruiting may not experience strong density and distance-dependent predation because of predator satiation (Webb and Peart, 1999; Curran and Webb, 2000). This is because all species produce large numbers of seeds simultaneously, and there will be insufficient predators to generate significant mortality.

Several studies have found that predator satiation, especially in Dipterocarps, negatively affects the Janzen Connell mechanism (Peter S Ashton, 1988; Curran and Webb, 2000; Paoli, Curran and Zak, 2006). Several characteristics of Dipterocarp seeds and seedlings such as large size, poor chemical defence, and being energy rich make them attractive food for wild pigs, *Sus barbatus* (Peter S Ashton, 1988; Curran and Webb, 2000), and weevil beetles, family: Curculionidae (Lyal and Curran, 2000; Bagchi *et al.*, 2011). Pigs and weevils can be categorised as generalist natural enemies. From the perspective of maintaining diversity, generalist natural enemies have low diversity-enhancing effect compared with specialists (L. M. Curran and Leighton, 2000; Gilbert, 2005; Freckleton and Lewis, 2006). Theory suggests that generalist natural enemies should not generate Janzen Connell mechanisms

(Freckleton and Lewis, 2006). However some recent work has shown that limited amounts of generalism can nevertheless still yield diversity enhancement (Sedio and Ostling, 2013). Furthermore, variation in growth characteristics (especially during seedling stage) in Dipterocarps also influence the strength of Janzen Connell effects (Itoh *et al.*, 1995; Brown, Press and Bebber, 1999). Bagchi et al (2010) have shown evidence for distance-dependence in dipterocarps, however overall there is little understanding of the role of Janzen-Connell mechanisms in hyperdiverse forests with mast-seeding.

Here I address the issue of understanding Janzen Connell effects in a system dominated by Mast Seeding by examining the effect of distance and density on two Bornean dipterocarp species, *Parashorea malaanonan* and *Shorea johorensis*. I used experimental approach by manipulating the density and type of tree species (*Parashorea malaanonan* and *Shorea johorensis*) as a function of the distance from parent trees. The present study was conducted to test experimentally the strength of Janzen- Connell hypothesis in these two native dipterocarp species, specifically addressing the following hypotheses: 1) the survival of conspecific seedlings will decrease with close proximity to parent trees (distance-dependence) and within high density of conspecific seedlings (density-dependence) compared to heterospecific seedlings; 2) high density of conspecific seedlings will decrease the growth of conspecific seedlings; 3) Herbivory rates in conspecific seedling will decrease with distance from parent trees; and 4) Leaf herbivory in new leaves decrease with distance from parent trees.

2.2 Materials and methods

STUDY SYSTEM

This study was conducted at the Danum Valley Field Centre, Sabah, East Malaysia (4° 58’ N, 117°48’ E) which is located at eastern border of Danum Valley Conservation Area (DVCA). This forest is situated approximately 70km inland from town of Lahad Datu, Sabah. Danum Valley Conservation Area (Class 1 forest reserve) is 43 800 ha of primary lowland dipterocarp forest with relatively little human disturbance (Marsh & Greer 1992). The mean minimum and maximum temperature at the field centre is 22.6 °C and 31.2 °C respectively, while mean annual rainfall is around 2881 mm (Walsh *et al.*, 2011).

The Dipterocarpaceae is a family of hardwood, and is typically the most dominant family in the tropical forest in South East Asia (Peter S Ashton, 1988). Although this family is generally found in South East Asia, India, Sri Lanka, Philipines, Madagascar, Africa and Papua New Guinea (Peter S Ashton, 1988; S. Appanah, 1993; Ådjers *et al.*, 1995), Borneo is known as the region with highest diversity of Dipterocarpaceae (Ashton 1982). To date, there are approximately 16 genera with 695 identified species (Maarten J M Christenhusz and Byng, 2016). *Shorea, Dipterocarpus, Hopea, Parashorea, Neobalanocarpus, Dryobalanops* and *Vatica* are most common genera that are found in lowland Bornean forest (Ashton 1982). Dipterocarp timber is a vital economic resource of many South East Asian Countries (Appanah and Turnbull, 1998). Dipterocarps fruits are large and winged but usually dispersed over shorter distance (≤ 60-80m) in closed canopy forest (Whitmore, 1984; Smits, 1994)). Dipterocarpacaea generally exhibit community wide mast fruiting events (Peter S Ashton, 1988; L.

M. Curran and Leighton, 2000). Mast fruiting events of Dipterocarpacae usually occur during El Nino years (Peter S Ashton, 1988; Bebber, Brown and Speight, 2004). Most dipterocarp seedlings aggregated close to the adult tree and can survive in the understorey for a few years after germinating (Peter S Ashton, 1988). All dipterocarps species are generally dependent on ectomycorrhizal associations (Brearley, 2012).

Parashorea malaanonan is one of the native dipterocarp species in the DVCA (18.6 stems/ha) (Stoll and Newbery, 2005). *Parashorea malaanonan* is classified as White Seraya Light Hardwood and known as a fast-growing dipterocarp species in Borneo (Bagchi et al., 2010). Seedlings of *Parashorea malaanonan* are common in DVCA, since this species fruits more often than other dipterocarp trees (Bagchi, 2006). In DVCA, most *Parashorea malaanaonan* seeds fall beneath the parent tree canopy, resulting in a population that is highly spatial clustered (Ashton 1998, Bagchi et al. 2010). With winged seeds*,* *Parashorea malaanonan* seed dispersal has been previously reported as having a maximum of 30m with average density of 2.9 seeds m^{-2} (Bagchi 2006).

Shorea johorensis is native dipterocarp species, fast-growing and big emergent trees that can usually be found in Danum Valley Conservation Area, with 24.6 stems/ha (Brown and Whitmore, 1992; Stoll and Newbery, 2005). It belongs to Light Red Meranti group, excellent timber qualities and frequently used in plywood and veneer (Ådjers *et al.*, 1995). *Shorea johorensis* commonly occurs in Peninsular Malaysia, Borneo and Sumatra (Ashton 1998) .Most of the winged seed from large emergent *Shorea johorensis* trees usually fall a few tens of metre from the parents (Peter S Ashton, 1988; Brown, 1996). *Shorea johorensis* is listed in IUCN Red List as ‘Critically Endangered’ (Ashton 1998).

In this study, *Parashorea malaanonnan* and *Shorea johorensis* were chosen because both of this species are relatively common as dipterocarp adults in DVCA, involved in community-wide mast fruiting events and seedlings for these two dipterocarp species are easy to locate and are often intermingled (Peter S Ashton, 1988; Stoll and Newbery, 2005).

FIELD EXPERIMENT

Parent trees of *Parashorea malaanonan* and *Shorea johorensis* were located by searching along a 2 km network of trails adjacent to the field centre. These two species were distinguished in the field based on their key characteristics (Soepadmo, Saw and Chung, 2004).

Parashorea malaanonan – large tree to 60m tall, to 2 m diameter, dense dome-shaped crown. Bark dark, eventually blackish purple, fissured, thinly flaky. Young parts sparsely greyish brown pubescent, glabrescent except on bud , inflorescence and nut. Twigs terete, with amplexicaul stipule scars. Leaf buds lanceolate-falcate , to 6 x 2 mm. Stipules hastate, to 15 x 6 mm. Leaves thinly coriaceous, with visible corrugations between lateral veins, greyish silvery lepidote below; blade broadly elliptic-ovate, 9-15 x 3.5- 7.5 cm, base unequal, obtuse to broadly cuneate, margin wavy distally, apex acuminate, acumen, acumen to 1 cm long ; midrib prominent and glabrous below; lateral veins 9 -14 pairs, prominent below; intercostal venation slender, sinuate; petiole 1.2 – 2 cm long, somewhat geniculate, glabrescent (see Figure S3 in Appendix A for *Parashorea malaanonan* leaves).

Shorea johorensis – large emergent tree, to 50 m tall, to 1.6 m diameter; crown large, hemispherical; bole tall, straight, symmetrical; buttresses to 3 m tall, stout, prominent. Bark tawny- grey to fawn, overall appearing smooth, shallowly densely cracked and thinly oblong flaky. Twig, inflorescence, leaf bud, parts of perianth exposed in bud , stipules, bracteole, ovary, nut, petiole, venation below, and midrib above shortly evenly persistently greyish buff pubescent; young leaf caducously. Twigs 2 – 3 mm diameter apically, somewhat ribbed and compressed at first, much branched; stipule scars to 2 mm long, pale, falcate, descending. Leaf buds ovoid, compressed, 6-8 x 2-3 mm. Stipules lanceolate, to 35 x 7 mm, caducous. Leaves chartaceous, drying tawny-grey below; blade ovate, 9-14 x 4.5 -7.5 cm, base obtuse to subcordate, apex with slender and tapering acumen to 0.7 cm long; midrib evident, more or less flat, above, slender but prominent below; lateral veins 10 -12 pairs, slender but prominent below, arched towards their ends, the basal 3 – 6 pairs usually with paired scale-like domatia; intercostal venation densely scalariform, very slender; petiole 1.5 – 2cm long (see Figure S3 in Appendix A for *Shorea johorensis* leaves).

At each parent tree (diameter at breast height > 30 cm), one transect was set up from 2m - 30m away from parent tree (see Figure S1 in Appendix A). I checked that there were no adult trees within a distance of 30m of each parent tree. Twelve 1 m x 1 m plots (1m^2) were established along each transect, consisting of four experimental plots each at 2, 15 and 30 m from the parent tree, respectively (following Bagchi et al., 2010). Each plot was randomly assigned to one of four treatments: (1) low density of seedlings (Four seedlings m^{-2}), (2) high density of seedlings (Twelve seedlings m^{-2}), (3) mixed species with low density of seedlings and (4) mixed species with high density of seedlings (see Figure S2 in Appendix A). Ten replicates were included for each set of treatments (i.e. 240 quadrats were established in total for both species).

Seedlings of *Parashorea malaanonan* and *Shorea johorensis* (see Figure S3 in Appendix A) were obtained from the Innoprise - FACE Foundation Rainforest Rehabilitation Project (INFAPRO) nursery, near Danum Valley Field Centre. Currently, this nursery has stocks of 28 native dipterocarps species and 6 other indigenous species. All the dipterocarps seedlings in this nursery are collected from recent mast fruiting events. Germinated seeds of the two-study species were planted in polybags on July 2014 and kept in the nursery: thus, the seedlings used in this study were 2 years old.

Within the experimental plots, existing plants were removed and leaf litter on the ground was left. Seedlings were planted using a planting bar. This is used to prepare holes for seedlings planting. Planting bars provide suitable holes for small seedlings particularly in small plots and prevent excessive disturbance to the forest soil. In total across all treatments 96 seedlings were planted in twelve plots (four plots for each distance) adjacent to each parent tree.

In addition to the four 1m x 1m plots at each parent tree, three 1 m x 1 m plots (one each at 2, 15 and 30m) were established as controls in which all naturally occurring seedlings were monitored. During sampling, all plants within the plot were tagged, mapped, measured and identified to species. All plots were re-measured in June 2017.

MEASUREMENTS

Seedlings

All planted and naturally occurring seedlings were tagged with numbered aluminium labels and identified to species (or to the lowest taxonomic level possible) with the help of a plant botanist. The heights of all seedlings were measured by using a one metre ruler. Stem diameters were measured just below the cotyledon scar using a digital vernier caliper (Haase, 2008). For each seedling, all leaves surviving from the first census and new leaves produced during the interval were recorded.

In order to estimate measure of rate of herbivory, five leaves were selected from each seedling and numbered with unique number written on the underside of leaves with water based permanent marker during the first census (July 2016). Visual estimates were employed in this study where herbivory damage is estimated with eye as the percentage of leaf surface area removed (Stotz *et al.*, 2000). All seedlings were re-measured in June 2017. The number of marked leaves missing, and herbivory of new leaves also were recorded. In each plot, a spherical densitometer was used to determine canopy openness and light availability to seedlings (Lemmon 1956).

STATISTICAL ANALYSES

The survival and growth data were analysed separately for both focal species. To test for effects of distance and density treatment on survival of conspecific seedling, seedling data were analysed by using generalized linear models (GLMs) with a quasi-binomial distribution and logit link function. The quasi-binomial distribution was used to account for a small amount of dispersion. In order to analyse the effects of distance and density on growth and herbivory of planted seedlings, general linear model was used in order to determine whether the growth increment and herbivory correlates with the density or distance from the nearest to the conspecific adult trees of *P. malaanonan* and *S. johorensis*. Growth increment and herbivory were assessed in response to the fixed factors density, distance and their interaction. All statistical analyses were conducted in the statistical software environment R version 3.2.3 (R Core Team 2015).

2.3 Results

I tagged 1920 planted seedlings in the first census which consist of 960 of *P. malaanonan* and 960 of *S. johorensis*. In terms of natural occurring seedlings, 129 of *P. malaanonan* and 38 heterospecifics seedlings were identified surrounding adult trees of *P. malaanonan*, while surrounding adult trees of *S. johorensis,* 80 of *S. johorensis* and 53 of heterospecifics seedlings were identified. All heterospecifics seedlings were identified to species.

EFFECTS OF DISTANCE AND DENSITY ON SURVIVAL OF SEEDLINGS

There was a significant effect of distance from *P. malaanonan* adult trees on survival of the seedlings ($F_{1,\,169}$ = 9.544, P = 0.002). Survival of conspecific and heterospecific seedlings were highest at the far distance (30m) while lowest at the near distance (2m) (Fig. 1a). At near distance (2m), conspecific seedlings suffer higher mortality compared to heterospecific seedlings in both high- and low-density treatment. No significant effect of density treatment was observed on survival ($F_{1,\,167}$ = 2.279, P = 0.133).

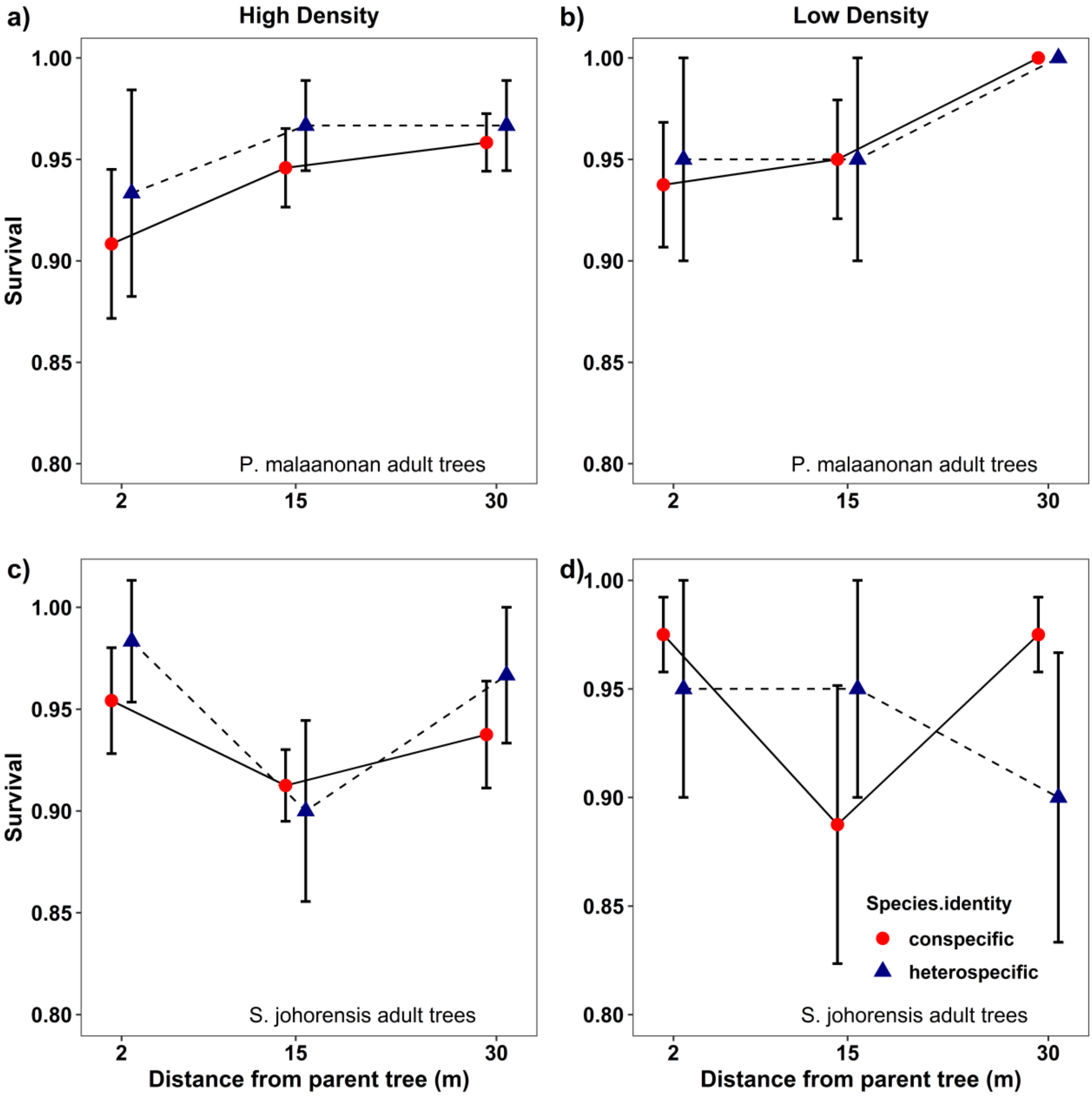


Figure 1*:* Seedling survival at for conspecific and heterospecific seedlings as a function of distance from *P. malaanonan* adult trees at high (a) and low (b) and distance from *S. johorensis* adult trees at high (c) and low (d) in distance-density experiment. Error bars represent standard error of the mean after transforming to the proportion scale.

Around *S. johorensis* adult trees, there was no significant trend in survival with distance for either species ($F_{1, 169}$ = 0.389, P = 0.534). Furthermore, no significant effects of density on seedlings survival was identified for either conspecific or heterospecific seedlings ($F_{1, 167}$ = 0.019, P = 0.891).

Table 1: F-statistics for generalized linear model to investigate the effect of distance and density treatment on survival of seedlings at *Parashorea malaanonan* and *Shorea johorensis* adult trees.

	Parashorea malaanonan			*Shorea johorensis*		
	df	Resid df	F (p-value)	df	Resid df	F(p-value)
Tree	9	170	4.691 (1.518e -05)***	9	170	0.899(0.528)
Distance	1	169	9.544 (0.002)**	1	169	0.389(0.534)
Species identity	1	168	1.254 (0.264)	1	168	0.027(0.869)
Density	1	167	2.279 (0.133)	1	167	0.019(0.891)
Distance*Species identity	1	166	0.006 (0.939)	1	166	0.001(0.972)
Distance * Density	1	165	1.585 (0.210)	1	165	0.005(0.944)
Species. Identity * Density	1	164	0.089 (0.766)	1	164	0.170(0.681)

Note: Values in the bracket is p-value
*Significant level at p < .05,
**Significant level at p< .01

EFFECTS OF DISTANCE AND DENSITY ON GROWTH OF SEEDLINGS

Height increment

There was a significant effect of density on height increments of both conspecific seedlings, *P. malaanonan* (Fig 2a,2b; $F_{1, 96}$ = 4.679, P = 0.033) and *S. johorensis* (Fig. 2c;2d; $F_{1, 96}$ = 4.970, P = 0.028). However, no significant effect of distance was observed on height increment for either conspecific seedlings for *P. malaanonan* ($F_{1, 96}$ = 0.032, P = 0.860) and *S. johorensis* ($F_{1, 96}$ = 0.904, P = 0.344).

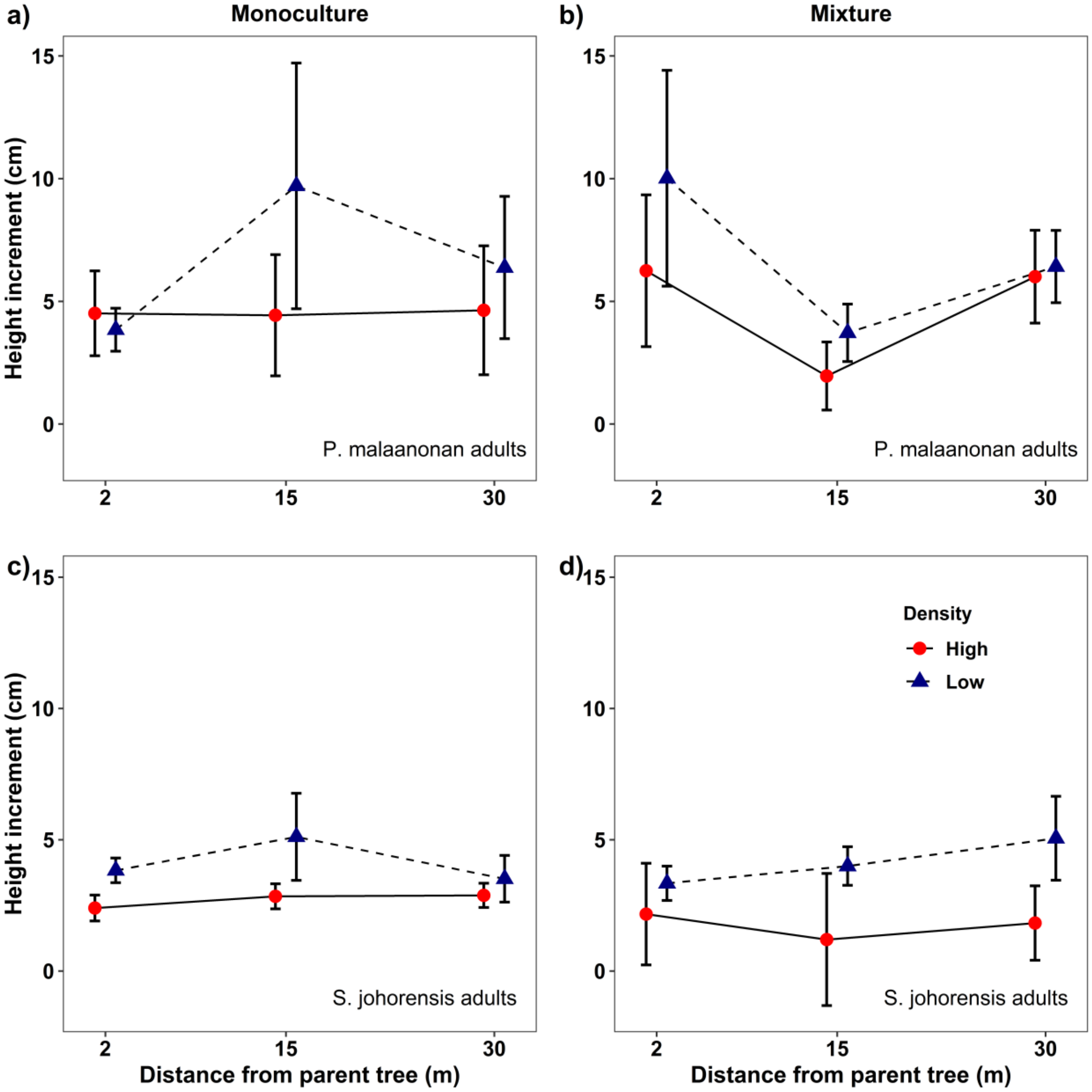


Figure 2: Effects of distance and density on height increment of conspecific seedlings from adult *P. malaanonnan* (a, b) and *S. johorensis* (c, d) trees with monoculture(a,c) or mixture (b,d) planting treatment.. Error bars represent standard error of the mean.

Diameter increment

There was a significant effect of mixture and monoculture planting treatment on diameter increment of conspecific seedlings around trees of *P. malaanonan* (Fig. 3a, 3b; $F_{1, 103}$ = 5.438, P = 0.022). A significant interaction was observed between the density treatment and the mixed and monoculture planting treatments ($F_{1, 103}$ = 3.988, P = 0.048).

Surrounding *S. johorensis* adult trees, there was highly significant effect of distance on diameter increment of conspecific seedlings (Fig. 3c; 3d: $F_{1, 102}$ =7.013, P = 0.009). Furthermore, a significant effect of density treatment was also observed on diameter increment of conspecific seedlings ($F_{1, 102}$ = 10.724, P = 0.001). There was a significant interaction between distance and density treatment ($F_{1, 102}$ = 4.304, P = 0.041): there was a positive effect of distance at low density, but not at high density.

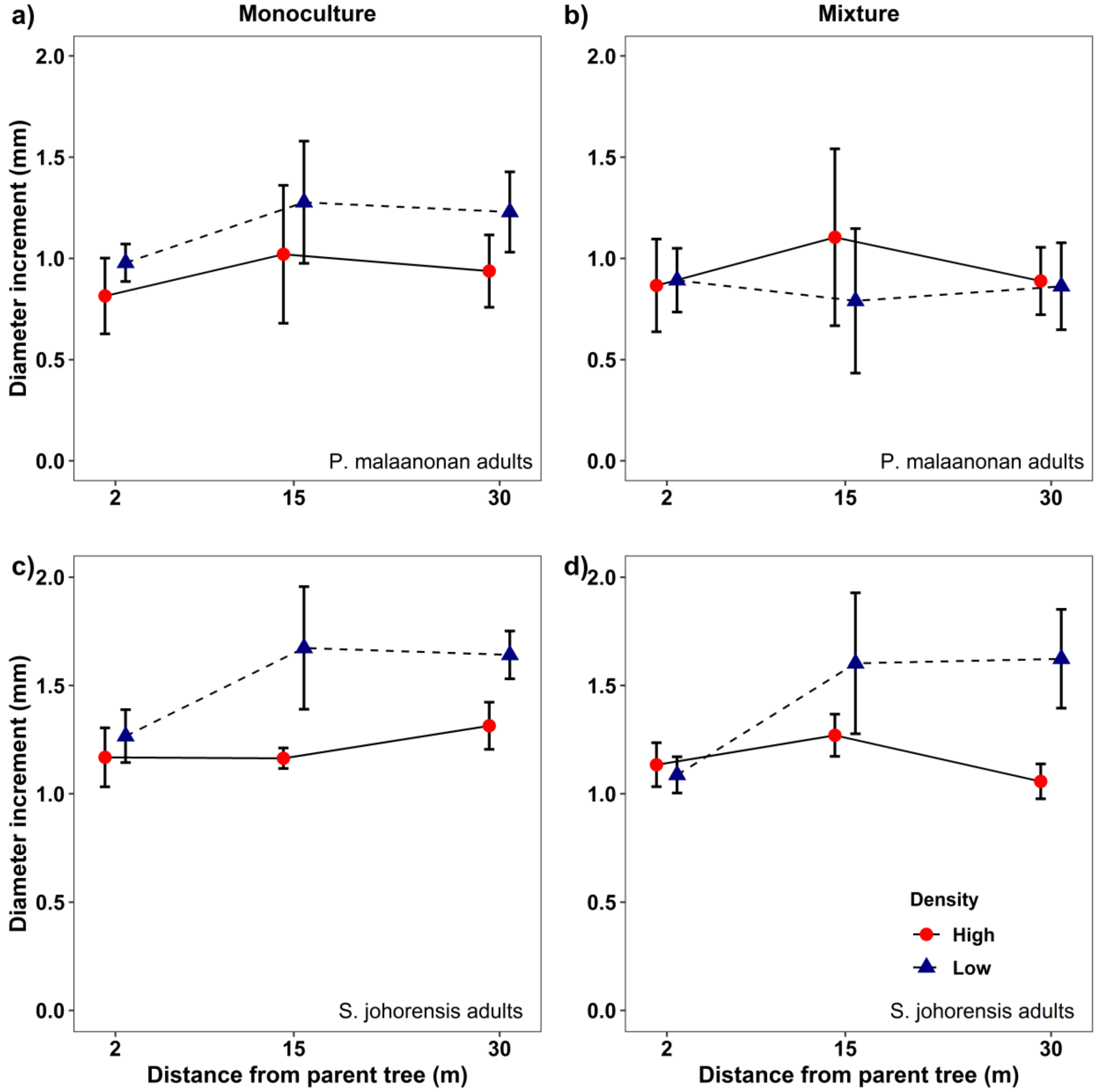


Figure 3: Effects of distance and density on diameter increment of conspecific seedlings from adult *P. malaanonnan* (a, b) and *S. johorensis* (c, d) trees with monoculture(a,c) or mixture (b,d) planting treatment.. Error bars represent standard error of the mean

Number of leaves

I found no significant effect of distance and density treatment on number of leaves of conspecific seedlings around both *P. malaanonan* and *S. johorensis* adult trees (Table 2).

Table 2: F-statistics results for general linear model analysis on effect of distance and density on growth increment for conspecific seedlings at *Parashorea malaanonan* and *Shorea johorensis* adult trees.

	Parashorea malaanonan		*Shorea johorensis*	
	df	*F*	df	*F*
Log Height				
Tree	9	2.831(0.005) **	9	2.916 (0.004) **
Distance	1	0.031(0.860)	1	0.904 (0.344)
Density	1	4.679(0.033) *	1	4.970 (0.028) *
Mix.mono	1	0.188(0.665)	1	0.685 (0.409)
Distance*Density	1	0.156(0.694)	1	0.334 (0.565)
Distance*Mix.mono	1	0.025 (0.875)	1	0.690 (0.408)
Density*Mix.mono	1	0.220 (0.640)	1	0.525 (0.471)
Log Diameter				
Tree	9	2.833(0.005) **	9	1.976 (0.049) *
Distance	1	0.145 (0.705)	1	7.013 (0.009) **
Density	1	1.519 (0.221)	1	10.724 (0.001) **
Mix.mono	1	5.438 (0.022) *	1	1.688 (0.197)
Distance*Density	1	0.163 (0.688)	1	4.304 (0.041) *
Distance*Mix.mono	1	0.559 (0.456)	1	0.216 (0.643)
Density*Mix.mono	1	3.988 (0.048) *	1	0.159 (0.691)
Log Number of leaves				
Tree	9	1.563 (0.136)	9	8.429 (2.542e-09)
Distance	1	0.791 (0.376)	1	0.050 (0.824)
Density	1	0.271 (0.604)	1	1.354 0.247)
Mix.mono	1	2.547(0.114)	1	0.259 (0.611)
Distance*Density	1	0.005 (0.947)	1	0.035 (0.852)
Distance*Mix.mono	1	0.023(0.880)	1	3.172 (0.078)
Density*Mix.mono	1	1.501(0.223)	1	0.843 (0.361)

Note: Values in the bracket is p-value
*Significant level at p < .05,
**Significant level at p< .01

EFFECTS OF DISTANCE FROM PARENTS AND DENSITY ON HERBIVORY OF SEEDLINGS

In the low-density treatment, herbivory rates of *P. malaanonan* seedlings and *S. johorensis* decreased with distance from adult *P. malaanonan* trees (Fig. 4) ($F_{1, 103}$ = 5.675, P = 0.019). A significant interaction was observed between distance and density variables ($F_{1, 103}$ = 9.165, P = 0.003), with a negative effect of distance in the low density, but not the high-density treatment (Fig. 4a;4b).

Around *S.johorensis* adult trees, there was a significant effect of distance on herbivory rate on *S .johorensis* seedlings ($F_{1, 102}$ = 6.363, P = 0.013). Herbivory rates of *S. johorensis* seedlings was negatively affected by seedling density ($F_{1, 102}$ = 7.969, P = 0.006). Furthermore, mixture and monoculture planting treatment also had a highly significant effect on herbivory rates in *S. johorensis seedlings* (Fig 4c; 4d, $F_{1, 102}$ = 9.038, P = 0.003).

Table 3: F-statistics results for general linear model analysis on effect of distance and density on herbivory rates of conspecific seedlings at *Parashorea malaanonan* and *Shorea johorensis* adult trees.

	Parashorea malaanonan		*Shorea johorensis*	
	df	*F*	df	*F*
Tree	9	2.542 (0.011) *	9	2.275 (0.023) *
Distance	1	5.675 (0.019) *	1	6.363 (0.013) *
Density	1	0.759 (0.386)	1	7.969 (0.006) **
Mix.mono	1	1.293 (0.258)	1	9.038 (0.003) **
Distance*Density	1	9.165 (0.003) **	1	1.762 (0.187)
Distance*Mix.mono	1	1.759 (0.188)	1	1.031 (0.312)
Density*Mix.mono	1	0.025 (0.875)	1	1.012 (0.317)

Note: Values in the bracket is p-value
*Significant level at $p < .05$,
**Significant level at $p< .01$

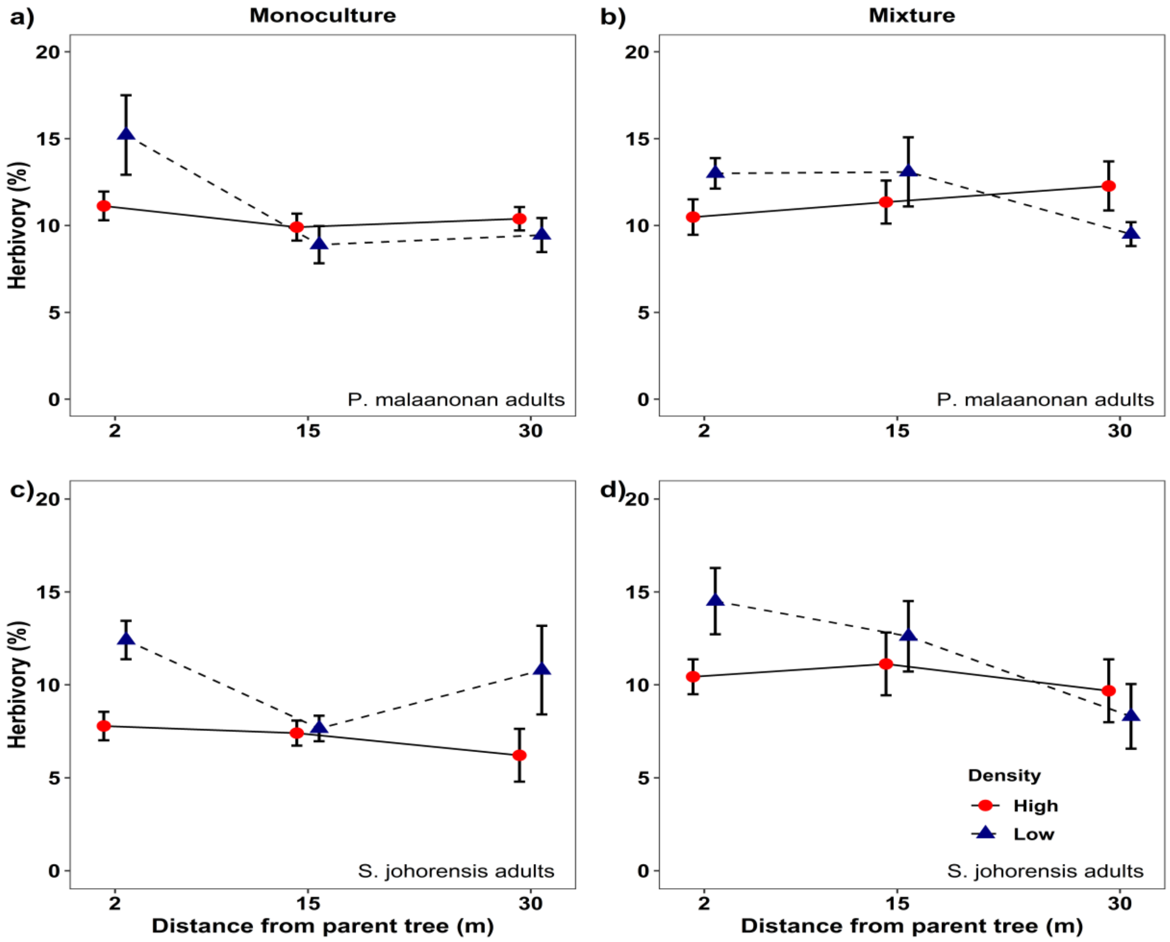


Figure 4: Effects of distance and density on herbivory rates of conspecific seedlings from adult *P. malaanonnan* (a, b) and *S. johorensis* (c, d) trees with monoculture(a,c) or mixture (b,d) planting treatment.. Error bars represent standard error of the mean

EFFECTS OF DISTANCE FROM PARENTS AND DENSITY ON HERBIVORY OF NEW LEAVES

There was no significant effect of distance and density on recruitment of new leaves in *P. malaanonan* and *S. johorensis* seedlings. We also found no significant effects of distance and density on leaf herbivory in *P. malaanonan* seedlings. However, there was a significant positive effect of distance on herbivory of new leaves in *S. johorensis* seedlings ($F_{1,\ 108} = 5.990$, P = 0.016). Effects of distance on herbivory varies significantly between density treatment. Thus, there was a significant interaction between distance and density ($F_{1,\ 108} = 4.547$, P = 0.035).

Table 4: F-statistics results for general linear model analysis on effect of distance and density on leaf recruitment and herbivory damage of conspecific seedlings at *Parashorea malaanonan* and *Shorea johorensis* adult trees.

	Parashorea malaanonan		*Shorea johorensis*	
	df	*F*	df	*F*
Log Number of new leaves				
Tree	9	1.185(0.314)	9	1.230 (0.285)
Distance	1	0.004 (0.947)	1	0.345 (0.558)
Density	1	1.945 (0.166)	1	1.478 (0.227)
Mix.mono	1	1.877 (0.174)	1	0.083 (0.774)
Distance*Density	1	0.366 (0.547)	1	2.633 (0.108)
Distance*Mix.mono	1	0.001 (0.976)	1	0.011 (0.916)
Density*Mix.mono	1	0.433 (0.512)	1	0.113 (0.738)
Herbivory of new leaves				
Tree	9	4.713 (3.572e-05)	9	3.282 (0.073)
Distance	1	0.243 (0.624)	1	5.990 (0.016) *
Density	1	2.177 (0.143)	1	1.949 (0.166)
Mix.mono	1	0.379 (0.539)	1	0.229 (0.633)
Distance*Density	1	0.290 (0.591)	1	4.547 (0.035) *
Distance*Mix.mono	1	2.122 (0.149)	1	0.031 (0.860)
Density*Mix.mono	1	3.932 (0.050)	1	1.334 (0.251)

Note: Values in the bracket is p-value
*Significant level at p < .05

EFFECT OF DISTANCE AND DENSITY ON CHLOROPHYLL CONTENT OF SEEDLINGS

There was no significant effect of distance and density on chlorophyll content of *P. malaanonan* seedlings (Table 5). Similarly,no significant effect of distance and density was observed on chlorophyll content of *S. johorensis* seedlings. There was a significant interaction between the distance and monoculture and mixture planting treatment (Fig. 5; $F_{1,\ 102}$ = 7.530, P = 0.007).

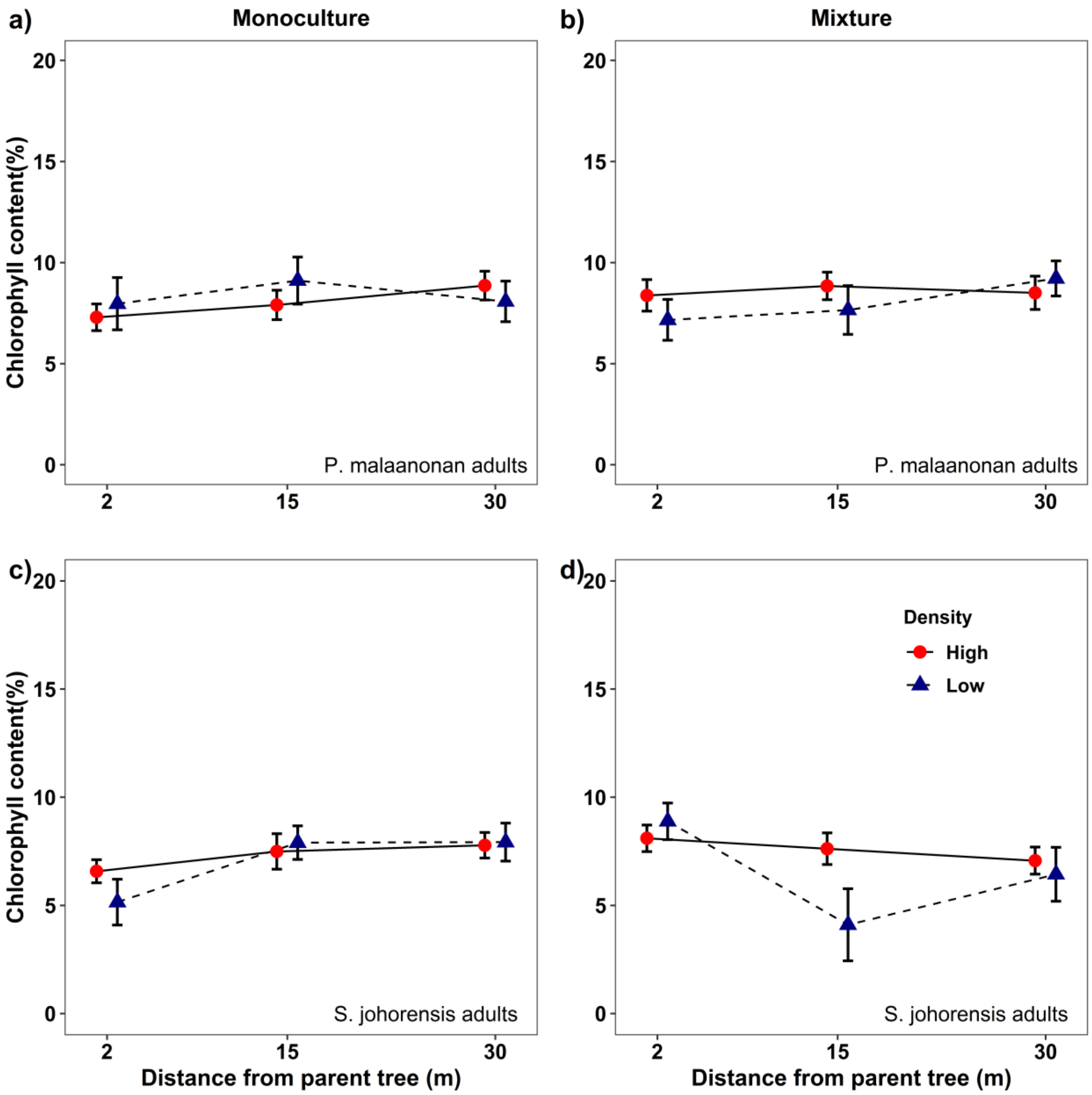


Figure 5: Effects of distance and density on chlorophyll content of conspecific seedlings from adult *P. malaanonnan* (a, b) and *S. johorensis* (c, d) trees with monoculture(a,c) or mixture (b,d) planting treatment.. Error bars represent standard error of the mean

Table 5: F-statistics results for general linear model analysis on effect of distance and density on chlorophyll content of conspecific seedlings at *Parashorea malaanonan* and *Shorea johorensis* adult trees.

	Parashorea malaanonan		*Shorea johorensis*	
	df	*F*	*df*	*F*
Tree	9	2.158 (0.031) *	9	1.335 (0.228)
Distance	1	3.338 (0.071)	1	0.063 (0.803)
Density	1	0.081 (0.777)	1	2.026 (0.158)
Mix.mono	1	2.546 (0.114)	1	2.614 (0.109)
Distance*Density	1	0.418 (0.520)	1	0.308 (0.580)
Distance * Mix.mono	1	0.482 (0.489)	1	7.530 (0.007) **
Density * Mix.mono	1	0.112 (0.739)	1	0.978 (0.325)

Note: Values in the bracket is p-value
*Significant level at p < .05,
**Significant level at p< .01

EFFECT OF DISTANCE ON SURVIVAL OF NATURAL SEEDLINGS

I found no significant effect of distance on survival of natural conspecific seedlings around either *P. malaanonan* or *S. johorensis* adult trees (Table 6).

Table 6: F-statistic for generalized linear model to investigate the effect of distance on survival of seedlings at *Parashorea malaanonan* and *Shorea johorensis* adult trees.

	Parashorea malaanonan		*Shorea johorensis*	
	df	*F*	df	*F*
Tree	9	0.897 (0.541)	9	0.593 (0.792)
Distance	1	0.079 (0.781)	1	0.679 (0.417)
Density	1	0.257 (0.616)	1	0.087 (0.771)
Species identity	1	0.294 (0.592)	1	1.143 (0.294)
Distance*Density	1	0.037 (0.850)	1	1.856 (0.184)
Distance * Species identity	1	0.630 (0.434)	1	1.010 (0.323)
Density * species identity	1	1.446 (0.239)	1	0.304 (0.586)

Note: Values in the bracket is p-value
*Significant level at p < .05

2.4 Discussion

Understanding distance and density-dependence in plant communities, and its effects on every plant species in the community, is essential for understanding species diversity maintenance in tropical forests (Schupp and Jordano, 2011; X. Liu *et al.*, 2012). My study revealed that different species exhibited contrasting effects of distance and density-dependence, compared with the predictions of the Janzen Connell hypothesis. The study showed that survival was reduced for seedlings located near the adult trees (distance dependence) for *P. malaanonan* indicating distance dependence occurs but density dependence was not detected in *P. malaanonan* seedlings. Furthermore, distance and density dependence were not detected in *S. johorensis* seedlings. I found that in both species, high densities of conspecific seedlings decreased the growth of conspecific seedlings . Herbivory rates in conspecific seedlings of both species decreased with distance. In addition, my study demonstrated that leaf herbivory for new leaves varies with the distance from the focal adult tree. These outcomes were observed in the seedling stands that were created experimentally. However, I did not observe the same outcomes in naturally occurring seedlings. In these, I failed to detect any evidence for distance or density-dependence.

EFFECT OF DISTANCE AND DENSITY ON SURVIVAL

In this study, my results exhibited that effect of distance on survival was stronger for conspecific seedlings than heterospecific seedlings around *P. malaanonan* adult trees while no density effect on conspecific seedlings. This finding is consistent with the distance dependence prediction which predicts survival of conspecific seedling is reduced when they are close to parent trees and favour the survival of heterospecifics (Janzen 1970, Connell 1971). To promote species coexistence, conspecific seedling must affect more than heterospecific in the process maintaining diversity (Hille Ris Lambers et al. 2002). This finding is supported by Bagchi, Press, et al. (2010) who found that survival of naturally occurring *P. malaanonan* seedlings suffered greater reductions near conspecific adult trees than heterospecifics.

However, I found contrasting results for conspecific seedlings around *S. johorensis* parent trees. In this case the survival of conspecific seedlings are unaffected by either distance or density. Possible explanations for the different result could include the natural enemies that negatively affect distance and density dependence relationship. Janzen (1970) and Connell (1971) emphasized that natural enemies must be host specific to generate distance and density dependence to favour heterospecifics. Generalist natural enemies attack wide variety of hosts that could influence the survival of conspecific seedlings at *S. johorensis* adult trees: if the enemies of *S.johorensis* are generalist, then this would weaken density and distance dependence. Another possibility is that density-dependence may occur at earlier life-history stages (see below).

Several studies have found that the strength of distance and density-dependent effects could be different between species due to distinct life-history strategies, how the species utilized resources for defence mechanism versus rapid growth or reversing trade-offs capabilities between susceptibility to predation, pathogens and herbivores versus competitive ability of species to thrive (Janzen 1970; Connell 1971; Coley & Barone 1996; Carson et al. 2008, Comita et al. 2014). Hence, the strength of Janzen-Connell effects is expected to vary depending on the species being tested, even at single study site. For instance, a study by Blundell & Peart (1998) in Gunung Palung National Park, West Kalimantan , Indonesian Borneo found that two of four Shorea dipterocarp species, *Shorea pinanga* and *Shorea hopeifolia* had significant distance-dependence while no distance-dependent effects observed in *Shorea parvifolia* and *Shorea longisperma.*

EFFECT OF DISTANCE AND DENSITY ON GROWTH

I observed that the negative effect of density on height increment in both *P. malaanonan* seedlings and *S. johorensis* seedlings was stronger in high density treatments compared to low densities. A study by Linkevicius et al (2014) demonstrated that high competition can lead to negative effects on height increment which can be observed in high density treatment plots. This suggest that when seedlings occur in high densities, intraspecific resource competition can affect the growth of the seedling, resulting in negative density dependent processes. These findings were in line with my expectation was that high density will inhibit growth of conspecific seedlings.

My results demonstrated that diameter increment for *S.johorensis* seedlings are highly affected with distance and density. Stoll & Newbery (2005) found that conspecifics seedlings and small trees may slow their growth when close to the adult conspecific trees in dipterocarps species. It is possible that adult trees may take phosphorus from conspecific seedlings that occur near to them via the root system. Several studies determined that ectomycorrhizal fungi found in the root system would increase phosphorus uptake from nearby nutrient sources and transfer to their host plants by extending roots ability (Perez-Moreno & Read 2000; Tibbett & Sanders 2002; Brearley 2012).

EFFECT OF DISTANCE AND DENSITY ON HERBIVORY

Results from this experiment revealed that there is effect of distance and density on herbivory rate in conspecific seedlings. Distance dependent process was observed on herbivory rates in the conspecific seedlings, but not density dependent process as herbivory rates in low density plots are higher than high density plots. It is possible because leaf herbivores are satiated with high densities of seedlings (Aide, 1992; Crawley and Long, 1995).

DENSITY DEPENDENCE AT DIFFERENT LIFE HISTORY STAGES

Janzen–Connell effects are thought to be most prevalent at early life stages, when individual seeds are more susceptible to natural enemy attack, especially seed predator and pathogens, and limited dipterocarp seed dispersal capabilities where most of seeds falls beneath the canopy and highly clumped (Daniel H Janzen, 1971; L. M. Curran and Leighton, 2000; Maycock et al., 2005; Ghazoul, 2016). In their original work, Janzen (1970) suggested that effects should be strong at both plant life stages, seed and seedling stages, in contrast to Connell (1971) who observed distance and density dependent effects at the seedling, but not at the seed stage. In this study, I failed to detect density dependence on these two species at seedling stage.

There are probably few factors that contributed to these results First, this probably due to very limited density range used in this study with only twelve seedlings in the high-density 1m^2 plots. Impacts of density are more likely to be detected with a larger range of density manipulations. For instance, Watkinson &

Harper (1978) demonstrated that negatively density-dependent relationship was observed in above a density of 100 flowering plant per 0.25 m^2. Secondly, density dependence was not detected in seedlings probably because of seedling age that I used in this study. Different life stages such as seed-seedling transition and young seedlings would probably experience stronger density dependent since it is more vulnerable to natural enemy attack such as pathogens. Several studies found that strong density-dependent effects in young seedlings and seed-seedling transitions in tropical species(Silva Matos, Freckleton and Watkinson, 1999; Bell, Freckleton and Lewis, 2006).

SPECIALIZED VERSUS GENERALIST HERBIVORES

Janzen-Connell hypothesis suggests that natural enemies such as insect herbivores must be host specific. Host specificity are required to drive Janzen-Connell mechanism in plant communities(Clark and Clark, 1984; Ali and Agrawal, 2012). Dyer et al (2007) demonstrated that insect herbivores are more specialized in the tropics. However, recent studies found that tropical insect herbivores are more general in their host preferences(Novotny and Basset, 2005; Weiblen *et al.*, 2006; Gilbert and Webb, 2007).

EXPERIMENTAL VERSUS OBSERVATIONAL RESULTS

I found no distance dependence effect on observational results in naturally occurring seedlings compared to our experimental study. This might be due to densities of natural seedlings in the start of my observational study were quite a bit lower than those in experimental plots where we found only three conspecific seedlings in one plot near the adult trees. However, it is perhaps not so surprising that there is little effect of distance or density where much of the density/distance dependence may already have happened in earlier stage.

I might get different results if I used different densities range in this study, especially if higher densities were employed. Mast fruiting dipterocarp species usually produce extremely large numbers of seeds beneath the parent tree, and this will affect the distance/density dependence effect in dipterocarp species. Several studies found that positive density/distance dependence was observed in dipterocarp species mediated by predator satiation(Curran and Webb, 2000; Lyal and Curran, 2000).

2.5 Conclusion

Overall, I found evidence on distance dependent effect in *P. malaanonan* seedlings when close to parent trees while no density dependence observed in *P. malaanonan* seedlings. For *S. johorensis*, no distance and density dependence were observed in conspecific seedlings. Distance and density dependent effects vary for both species tested in this study. Future studies should consider early life history stages (i.e. seed stage, seed-seedling transition and young seedlings) and whole-life cycle studies to detect distance and density dependence and their role in maintaining tropical forest diversity. When the times of individuals exposed to natural enemies increase, impacts of distance and density dependent effects are more likely to increase. Thus, longer studies duration should be more likely to detect significant effects of distance and density on survival in seedling stage compared to shorter studies.

Chapter 3

A meta- analysis of Janzen Connell effects on seed and seedling mortality

Abstract

48 years ago, the Janzen Connell hypothesis suggested that specialist natural enemies like pathogen, predators and herbivores caused mortality by reducing conspecific offspring survival when close to conspecific adults(distance dependence), and when the offspring occurs in high densities (density dependence) in order to prevent competitive dominance thus allowing species diversity to enhance. A large number of empirical tests have been carried out to test this hypothesis globally and the strength of Janzen- Connell mechanisms were varying across the studies depending on several factors such as latitude, precipitation and life stages. Thus, I conducted a meta-analysis by searching all the literature that tested this hypothesis and calculated the effect sizes of the studies to test the weight of evidence of Janzen- Connell predictions. I found significant evidence that Janzen-Connell mechanisms act as one of the processes for diversity maintenance in plant communities. Wide variation was observed across all the studies. Distance and density dependence are not related to latitude, precipitation and study duration. There was significant support that Janzen-Connell mechanism varied among the regions. Moreover, the negative effect of distance was higher in seedlings compared to seed stage while effect of density was greater in seed stage compared to seedling stage. Overall, my meta-analysis found general support for Janzen-Connell predictions. Additional studies are required and should focus on overall plant communities rather than handful species in order to provide better understanding of how Janzen- Connell mechanisms shaping the diversity maintenance pattern.

3.1 Introduction

In community ecology, understanding and explaining how large numbers of species manage to co-exist at small spatial scales with limiting resources remains a fundamental problem, especially in tropical forests (Hutchinson, 1961; Wright, 2002; Garzon-Lopez *et al.*, 2015; Bachelot *et al.*, 2017; Schemske and Mittelbach, 2017). Tropical forests are generally recognised as the most diverse terrestrial ecosystem on Earth and a vital testing ground for theories of species coexistence (Gardner *et al.*, 2009; Bagchi, Press and Scholes, 2010). In coexistence theory, species coexistence results from an interaction between two forces: equalising mechanisms which reduce fitness differences between species, and stabilizing mechanisms which increase intraspecific competition relative to interspecific competition (Chesson, 2000).

Currently, the Janzen Connell hypothesis is used extensively to explain the process that maintain tropical forest diversity (Janzen 1970, Connell 1971). This hypothesis proposes that density and distance-dependent mortality generated by specialist natural enemies that prevent competitive dominance through differential mortality of common and rare species(Janzen, 1970; Connell, 1971). It predicts that plants fail to recruit new offspring in areas of locally high density of conspecifics because specialist natural enemies such as seed predators, pathogens and insect herbivores will reduce survival of seeds/seedlings when they are close to conspecific adults (distance dependence) or in areas of high density seeds/seedlings (density dependence) (Augspurger and Kitajima, 1992; Notman, Gorchov and Cornejo, 1996; Bell, Freckleton and Lewis, 2006; Bagchi, Press and Scholes, 2010; Swamy and Terborgh, 2010). As a consequence of the Janzen-Connell effect, common species tend to suffer greater mortality, while rarer species have an advantage and tend to increase. Thus, this mechanism will facilitate coexistence among plant species and diversity is enhanced (Chesson, 2000; Freckleton and Lewis, 2006; Sedio and Ostling, 2013).

There is a large body of empirical work in support of the Janzen-Connell hypothesis, with numerous studies focused on survival and growth of seed/seedlings as a function of distance from adult trees, or high versus low densities of conspecifics (Augspurger and Kitajima, 1992; Hart, 1995; Notman, Gorchov and Cornejo, 1996; Freckleton and Lewis, 2006; Terborgh, 2012). Several studies have highlighted the importance of distance and density dependent mechanisms as drivers of mortality in forest ecosystem (Bell, Freckleton and Lewis, 2006; Augspurger *et al.*, 2010; Mangan *et al.*, 2010; Swamy and Terborgh, 2010).

Despite many published studies on Janzen-Connell effects in tropical forest, most of them come from Neotropics, mostly in South and Central America (Augspurger and Kitajima, 1992; Forget, 1993; C. A. Chapman and Chapman, 1996; Bell, Freckleton and Lewis, 2006; Swamy and Terborgh, 2010) with a few exceptions in South East Asia (Massey *et al.*, 2006; Bagchi, Press and Scholes, 2010) and Africa (Hart, 1995).This is supported by a review paper by Carson et al (2008) that found most literature on Janzen-Connell effects are dominated by lowland tropical forest of Barro Colorado Island (BCI) and areas in central Panama. There is an obvious question of the degree to which the results of this one study site are likely to be representative of tropical forests globally.

Such questions are not easily addressed using experimental approaches. Instead, for answering broad questions of this sort, meta-analysis is an effective tool since it provides quantitative methods for synthesizing and comparing multiple empirical studies that tested common hypotheses compared (Arnqvist and Wooster, 1995; Gurevitch and Hedges, 1999). Meta-analysis uses quantitative summaries that assess the magnitude of effect for tested hypothesis across all published studies and comparison of magnitude of effect among different groups (i.e. region, ecological factors). In this case, meta-analysis could be used to test the strength of Janzen-Connell effect since this hypothesis has been tested multiple times globally.

To date, only two meta-analyses have been carried out to test the weight of evidence from studies testing the Janzen-Connell hypothesis. A meta-analysis by Hyatt et al (2003) exhibited that there is no general support for distance dependence in tropical and temperate forests from 40 published studies and concluded that further testing was unnecessary. Conversely, Comita et al (2014) noted that there was significant evidence for distance and density dependent predictions of Janzen Connell effects from 63 published studies in tropical and temperate forests. Results of the meta-analysis of Comita et al. (2014) may have differed from Hyatt et al. (2003) owing to the broader search for articles (i.e. all journal indexed by Web of Knowledge) in Comita et al. compared to Hyatt et al. (2003), which was a search restricted to 10 major ecological journals. The larger sample sizes in the meta-analysis by Comita et al. (2014) are likely to increase the chances of detecting significant effects in testing Janzen-Connell predictions. There are several factors that these previous meta-analyses did not include, however. The relative roles of different natural enemies (e.g. insects versus pathogens or specialist versus generalist) that influenced Janzen-Connell effects was not tested in these meta-analyses. Natural enemies are responsible as agents that generate distance and density dependent processes. In their original work, Janzen (1970) and Connell (1971) emphasized that natural enemies must be host-specific to drive mortality of conspecifics offspring in order to favour heterospecifics. This will provide turnover in species composition which generalist natural enemies would fail to generate (Freckleton and Lewis, 2006).

The strength of Janzen-Connell predictions on distance and density dependent effects could vary depending on several factors. First, there is a study highlighted that there were variation in Janzen-Connell effects from latitude (Hille Ris LamBers, Clark & Beckage 2002). Furthermore, Janzen (1970) and Connell (1971) suggested that distance and density dependence are stronger in tropics compared to temperate forests because of host-specificity of natural enemies. In his paper, Janzen (1970) suggested that host specificity of seed predators, herbivores and pathogens is greater in the tropics than temperate zone. In review paper by Schemske et al. (2009), biotic interaction are often more important in tropical than temperate regions. This is supported by studies that found a greater proportion of the temperate herbivore is composed of generalist (Harpe 1977, Howe and Westley 1988) and that insect herbivores are more specialized in the tropic regions (Dyer et al. 2007) . However, a study by Novotny et al. (2006) found that there were no differences in host specificity of insect herbivores in tropical and temperate communities.

Furthermore, irrespective of latitude, the strength of distance and density-dependence may also be weaker in seasonal and drier habitat due to lower pest pressure (Givnish 1999). For example, Swinfield et al. (2012) showed that the effectiveness of pathogens as agents of density-dependence might depend on patterns of rainfall. Even comparing similar regions, biogeographic variation may influence the Janzen Connell effects. For example, dipterocarps species in Southeast Asian Forest exhibit community-wide mast fruiting and some studies stated that mast fruiting species may be unlikely to immediately experience strong density and distance-dependence(Janzen, 1970; Peter S Ashton, 1988; L. M. Curran and Leighton, 2000; Bagchi *et al.*, 2011). However, despite such predictions, previous meta-analyses have not examined global variation in the strength of the Janzen-Connell mechanism.

In this study, I conducted a thorough literature search to identify peer reviewed studies that tested the Janzen-Connell hypothesis on seed/seedling survival. My main objective is to use meta-analysis as a tool to determine weight of evidence for Janzen-Connell hypothesis. In my meta-analysis, I test the following hypotheses 1) Are distance and density dependent mortality stronger in tropics than temperate regions?, 2) Do wetter forests experience stronger Janzen-Connell effects compared to drier ones? 3) Do Janzen-Connell effects are varying among regions? 4) Are distance and density-dependence stronger in the seedling stage compared to the seed stage? and 5) What are the relative roles of natural enemies and host specificity (specialist versus generalist) in influencing distance and density dependent mortality?

3.2 Materials and methods

LITERATURE SEARCH

To identify tests of density and distance-dependence consistent with the Janzen-Connell hypothesis in tropical regions, I compiled data from thorough literature search using Google Scholar (https://scholar.google.co.uk) and Web of Science (https://apps.webofknowledge.com) in September 2017. Using the Google Scholar citation search engine, I performed searches by using keyword “plant density experimental manipulation ‘Janzen Connell’ “to capture experimental density dependence studies (yielded 768 results) and “distance experimental manipulation ‘Janzen Connell’ “for experimental distance dependence studies (yielded 619 results). Using the Web of Science search service, I performed searches by searching keyword topics: “Janzen-Connell hypothesis” (yielded 247 results), “conspecific density dependence” (392 results) and “conspecific distance dependence” (yielded 119 results). Outputs from both combined searches from Google Scholar and Web of Science led to a large number of articles that were then examined for inclusion criteria for this meta-analysis. I compiled all the results from the literature searches and removed all the duplicates. Furthermore, I also searched the lists of studies that had been included in meta-analysis of Comita et al., (2014) and Hyatt et al.(2003) to avoid any missing articles in my literature search.

In this meta-analysis, each article was examined to meet these inclusion criteria: (i) quantitative and written in English, (ii) studies conducted in tropical and temperate regions; (iii) experimental studies that manipulated conspecific density or distance from conspecific adult tree; or experiment with habitat treatment (i.e 'far' treatment: seeds placed in forest edge or canopy gap) (iv) study species were native plant and conducted in their natural habitat; (v) plants must can access by full range of natural enemies and (vi) studies that mentioned factors that caused seed/seedling mortality.

DATA ANALYSIS

All selected studies were categorized into the following groups: author, year, date of experiment conducted, study site details (biome, region, latitude, longitude and annual precipitation), focal species (species and family), life history stage (seeds/seedlings), duration of experiments, prediction tested (distance/density) and natural enemies. To categorise the geographical zone, I categorized all study sites as tropical or temperate. If site was reported as being sub-tropical, I categorised the site as tropical if within +23.5/-23.5 latitude from equator. In studies reporting multiple experiments that involved different species, different life history stage or different prediction tests, these were considered as separate tests within the same study. For studies of distance-dependence, I counted the total number of survivors and total number of deaths near to and far from conspecific adult trees in the all the selected studies. For any study that tested using multiple distances , I only compared results from the nearest and furthest from the conspecific adult tree. For studies of density-dependence, I counted the total number of survivors and total number of deaths at the highest and lowest density of conspecific density treatment. I used free software program Plot Digitizer (http://plotdigitizer.sourceforge.net) to extract data presented in graph from the studies . A list of all selected studies that were used in the meta- analysis for each distance and density dependence test are provided in Appendix B1.

Table 1: Definition of variables used the meta-analysis study

Data	Definition
Author	name of the authors in the study
Year	published year
Date	date of the experiments conducted
Biome	terrestrial habitat types that plants and animals live in it (i.e temperate forest, deciduous forest, mixed forest, subtropical forest and tropical forest
Study site	location of the experiment conducted (i.e. forest names, district/county and country)
Region	continents where the experiments conducted (i.e. America, Asia ,Africa and Europe)
Latitude	geographic coordinate of the study site that specifies the north–south position of a point on the Earth's surface, with an angle which ranges from 0° at the Equator to 90° (North or South) at the poles.
Longitude	geographic coordinate of the study site that specifies the east–west position of a point on the Earth's surface, with an angle east or west from the Prime Meridian, ranging from 0° at the Prime Meridian to +180° eastward and −180° westward
Zone	geographical zone where the study conducted (i.e. tropical and temperate)
Annual precipitation	amount of product of the condensation of atmospheric water vapour (rain) that falls under gravity in a year (units= millimetres (mm))
Species	organisms or individuals tested in the experiment (taxonomic rank)
Family	family of species tested in the experiment (taxonomic rank)
Life stage	plant life cycle forms tested in the study (i.e. seed and seedling)
Duration	amount of time experiment conducted (days)
Prediction tested	Distance dependence(near/far) and density dependence (high/low)
Natural enemies	Organisms/agents (i.e fungi, vertebrates, insect herbivores and others) that kill, decrease the reproductive potential of, or otherwise reduce the numbers of individual tested in the study.
Type of natural enemies	Generalist (natural enemy with wide variety diet) or specialist(natural enemy with a very restricted diet) that caused the seed/seedling mortality

All statistical analyses were conducted in the statistical software R 3.3.3 (R Core Team 2017) and the ‘metafor’ package version 1.9-9 was used to run the analysis (Comita *et al.*, 2014). In order to compare results across experiments, function escalc in ‘metafor’ package was used to calculate the estimated sampling variances and log odds ratio. Odd ratios can be defined as a measure of strength of effect in an outcome resulting from a treatment exposure and are widely used in the medical meta-analysis (Szumilas, 2010). In my study, I used odds ratios as ratio of odds of seed/seedling survival when near the adult tree/high density to the odds of seed/seedling survival when far from adult tree/low density. Then, I used a random effects model to determine whether the log odds ratio were significantly less than zero, which would imply that the survival is lower in near versus far treatment or in high versus low density treatment. In addition, I ran separate model to test whether these factors influenced the log odds ratio: i) latitude, ii) precipitation, iii) region / biome of the study site, iv) taxonomic group (family/species), v) life-history stage, vi) duration of experiment, and vii) natural enemies.

I used Cochran’s Q statistic (a measure of between-study variation) to detect heterogeneity of effects sizes (Hedges and Olkin 1985, Gurevitch and Hedges 1993). The P-value of the test indicates whether the variation among effect sizes is greater than would be expected especially in the categorical test (i.e tropical vs temperate, seed vs seedling).

3.3 Results

GEOGRAPHIC DISTRIBUTION

All studies were examined to ensure they meet all my criteria. Following this, I found a total of 103 articles, yielding 260 experiments that test distance (188 experiments) and density dependence (72 experiments). The majority of the experiments were conducted in tropical regions (169 experiments) compared with fewer in temperate zones (91 experiments; Fig. 1). All the experiments covered a wide extent of taxonomic and phylogenetic diversity, consist of experiments on 185 species and 65 families.

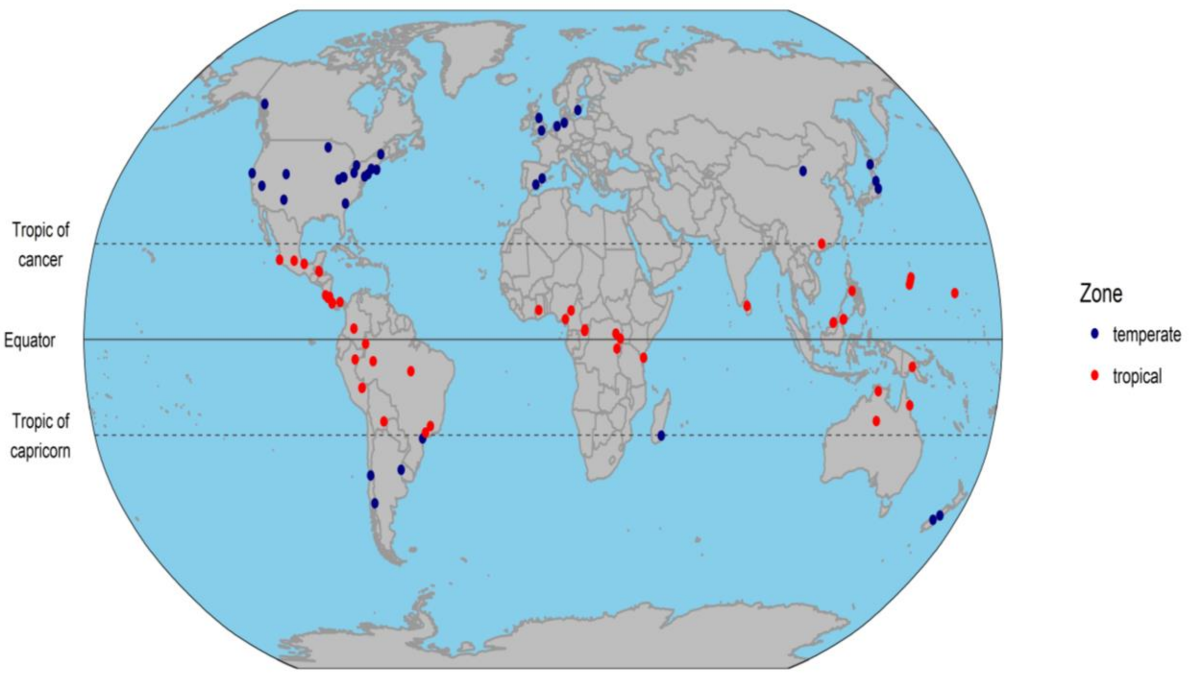


Figure 1: Distance and density dependence (Janzen Connell hypothesis) studies across tropical and temperate forest in global

DENSITY AND DISTANCE EFFECTS

When I ran overall model in the analysis, I used Z statistics to find statistical significance in order to accept or reject Janzen Connell hypothesis and found a significant negative effect of distance and density on survival (Z = -4.963, P <0.0001). In the model, estimated log odds ratio of seeds and seedlings located close to conspecifics or high density compared to those far from conspecifics or at low density was -0.55 (CI: -0.76 to -0.33). For test for heterogeneity to detect variation in treatment effects from all the studies, I observed a wide variability in effect sizes among the studies in overall model (QE = 9441.86, d.f = 259, P < 0.0001). For studies on effect of distance, I found a significant negative effect of distance on seeds and seedlings survival (log OR = -0.49 ± 0.14 (SE), Z = -3.45, P =0.006), while similar pattern were also observed in studies that testing effects of density on seeds and seedlings (log OR = -0.61 ± 0.14 (SE), Z = -4.34, P < 0.001). No significant difference were observed between density and distance tests in terms of their effect size (Q_M = 0.466, df = 1, P = 0.49).

EFFECTS OF LATITUDINAL AND PRECIPITATION GRADIENTS ON SEEDS AND SEEDLINGS SURVIVAL

In terms of absolute latitude factor, I found no significant effect on effect size (Q_M = 1.46, df = 1, *P* = 0.226; Fig. 2). Furthermore, there was no significant difference between studies located in the temperate versus studies in the tropics zone (Q_M = 0.284, df = 1, *P* = 0.59). In this study, I compared studies within a single region (studies from America and Asia) and I found no significant difference between tropical and temperate studies in the Americas (Q_M = 3.058, d.f. = 1, P = 0.08) even in Asia region (Q_M = 0.0871, df = 1, P = 0.768). No significant effect were observed in terms of overall precipitation on effect size (Q_M = 0.223, df = 1, P =

0.64, Fig. 3a). No significant difference between studies located in the tropics versus studies from temperate zone when compared in overall precipitation (Q_M = 0.71, df = 3, P = 0.871).

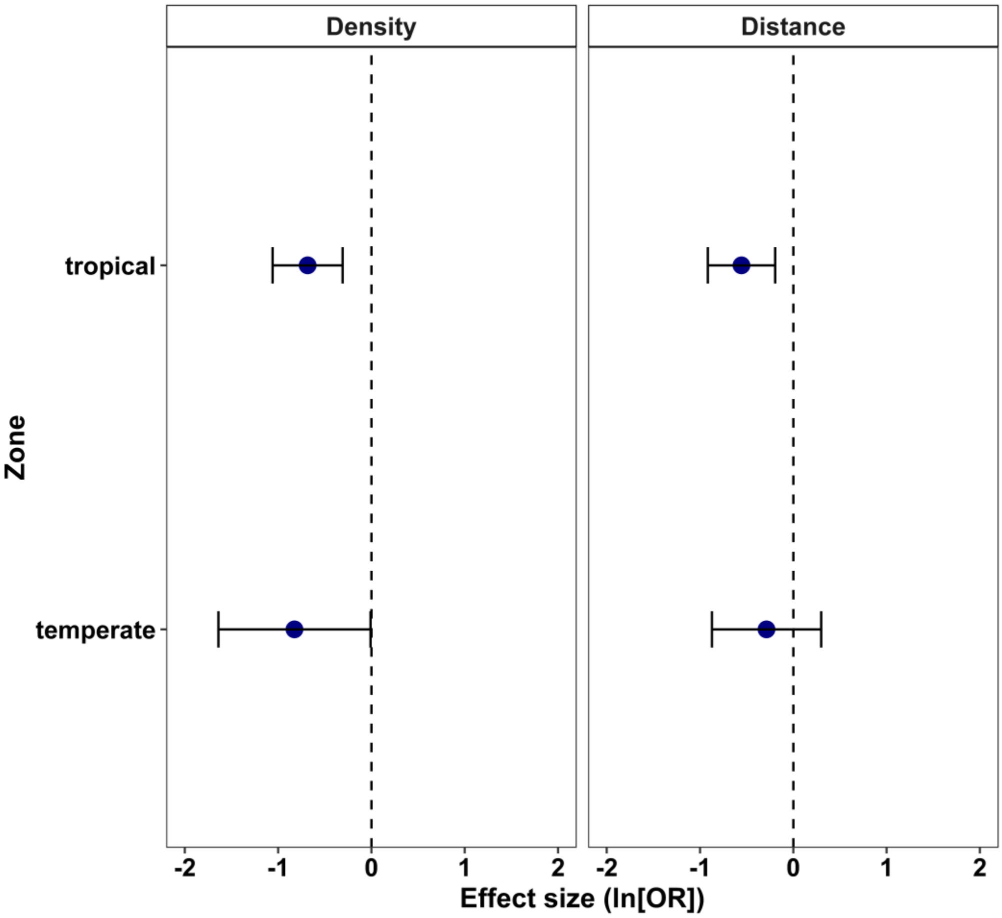


Figure 2: Effect size (log odds ratio) on effect of latitude on survival seeds and seedlings in the meta-analysis of experimental test of distance and density dependence. Effect sizes are indicated by points and error bars are estimated 95% confidence intervals.

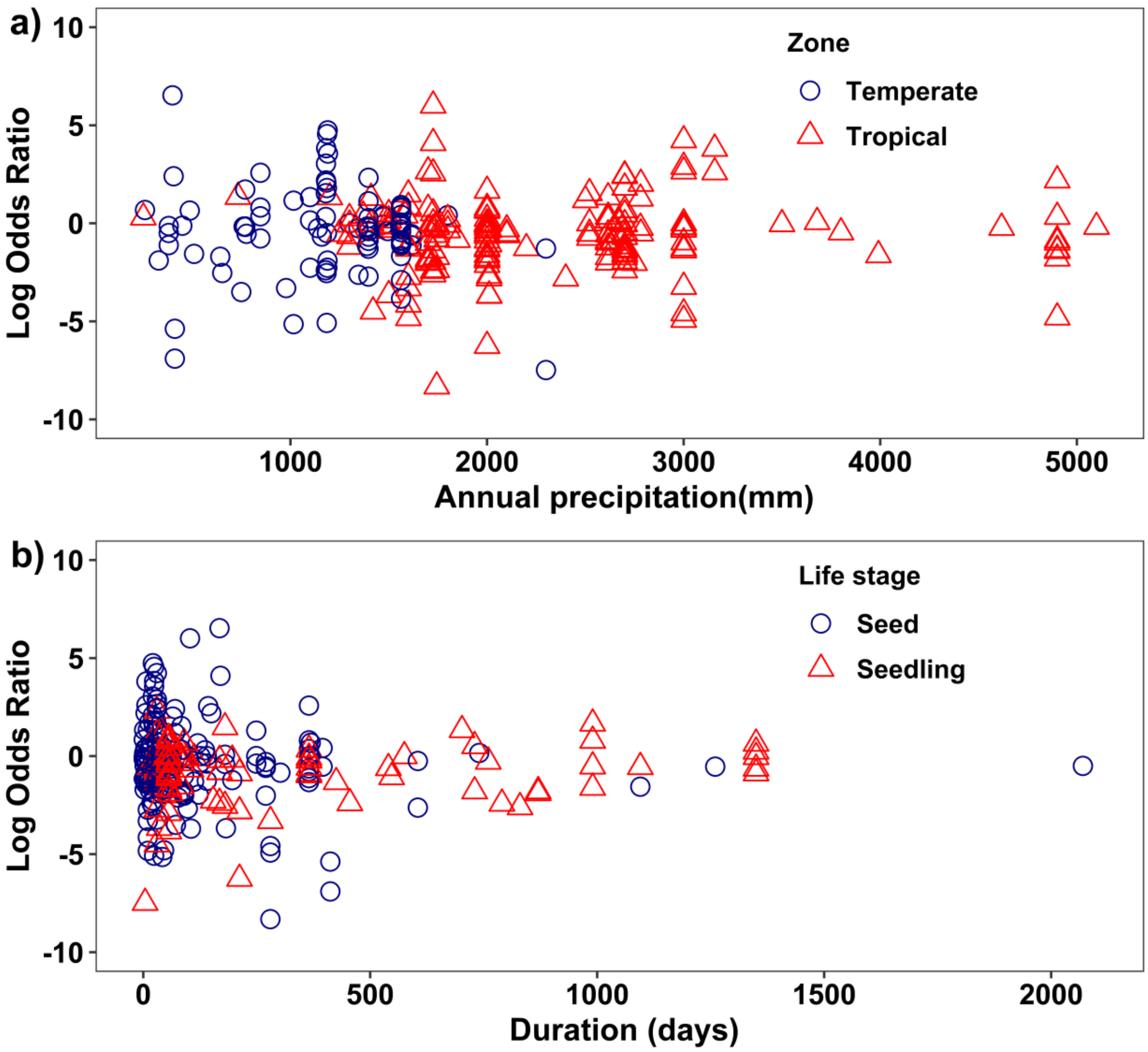


Figure 3: a) The effects of log annual precipitation on the log odds ratio of survival seeds and seedlings in the meta-analysis of experimental test of distance and density. b) The effects of duration of study on the log odds ratio of survival seeds and seedlings in the meta-analysis of experimental test of distance and density dependence.

EFFECTS OF STUDY DURATION ON THE SURVIVAL OF SEEDS AND SEEDLINGS SURVIVAL

There was no significant effect of study duration on effect size o(Q_M = 0.824, d.f. = 1, P = 0.36,). However, I found a significant difference between study duration and life stage on effect sizes (Q_M = 9.05, d.f. = 3, P = 0.03, Fig. 3b).

VARIATION AMONG GEOGRAPHIC REGIONS

When I ran overall model with all four regions included, I found a significant difference between geographic regions in terms of effect sizes (Q_M = 10.169, df = 3, *P* = 0.017). Among regions, Europe region exhibited significantly lower odds ratio than other three regions (Europe; log OR = - 1.75 ± 0.53, Asia; log OR = - 0.84 ± 0.21, America; log OR = - 0.40 ± 0.14, and Africa; log OR = - 0.03 ± 0.37). There was a significant interaction between geographic regions and zone on effect sizes (Q_M = 13.32, d.f. = 5, P = 0.021; Fig. 4).In temperate regions, Europe continent exhibited stronger negative effect on distance and density dependence compared to Asia and America (America: log OR = -0.07 ± 0.26; Asia: log OR = -0.77 ± 0.38; Europe: log OR = -1.80 ± 0.60 Q_M = 13.03, d.f. = 3,P = 0.005; Fig 4). Meanwhile in tropical regions, Asia continent suffered highest distance and density- dependent mortality whilst Africa continent experienced lowest distance and density dependent mortality (America: log OR = -0.59 ± 0.16; Asia: log OR = -0.88 ± 0.25; Africa: log OR = -0.03 ± 0.34; Q_M = 25.91, d.f. = 3,P < 0.001; Fig 4).Nevertheless, there were only few tests have been conducted in Europe, with 10 experimental tests (distance = 6 studies; density = 4 studies) and Africa, with 25 experimental tests, (distance = 18 studies; density = 7 studies).

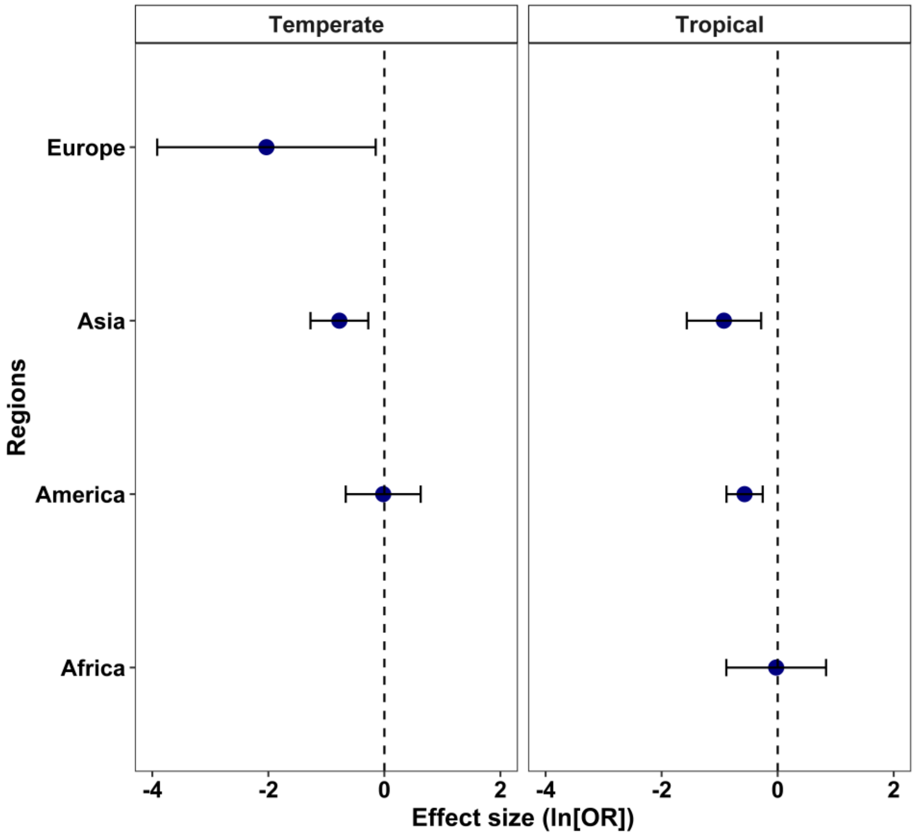


Figure 4: Variation in geographic regions on the log odds ratio of survival seeds and seedlings in the meta-analysis of experimental tests of distance and density dependence. Effect sizes are indicated by points and error bars are estimated 95% confidence intervals.

VARIATION AMONG LIFE HISTORY STAGE (SEED VERSUS SEEDLING)

There was a significant difference in effect sizes between life-history stages (Q_M = 6.33, d.f. = 1, P = 0.012; Fig. 5). Seedlings exhibited a significantly lower odds ratio with log OR = -0.89 ± 0.17, compared to seeds with log OR =-0.33 ± 0.14., This result indicated that at seedling stage, individuals experienced stronger negative effects of conspecific density and proximity. I ran separate model to investigate whether seeds and seedlings responded differently to distance and density treatments and there was a significant interaction (Q_M = 14.26, d.f. = 3, P = 0.0026), with seedlings exhibiting significantly stronger negative effects to distance compared to seeds (seedlings: log OR = -1.12 ± 0.23; seeds: log OR =

-0.15 ± 0.17; Q_M = 23.72, d.f. = 2,P <0.0001).In contrast, seeds showed more negative response to density compared to seedlings (seeds: log OR = -0.74 ± 0.19; seedlings: log OR = -0.45 ± 0.2; Q_M = 19.47, d.f. = 2, P < 0.0001).

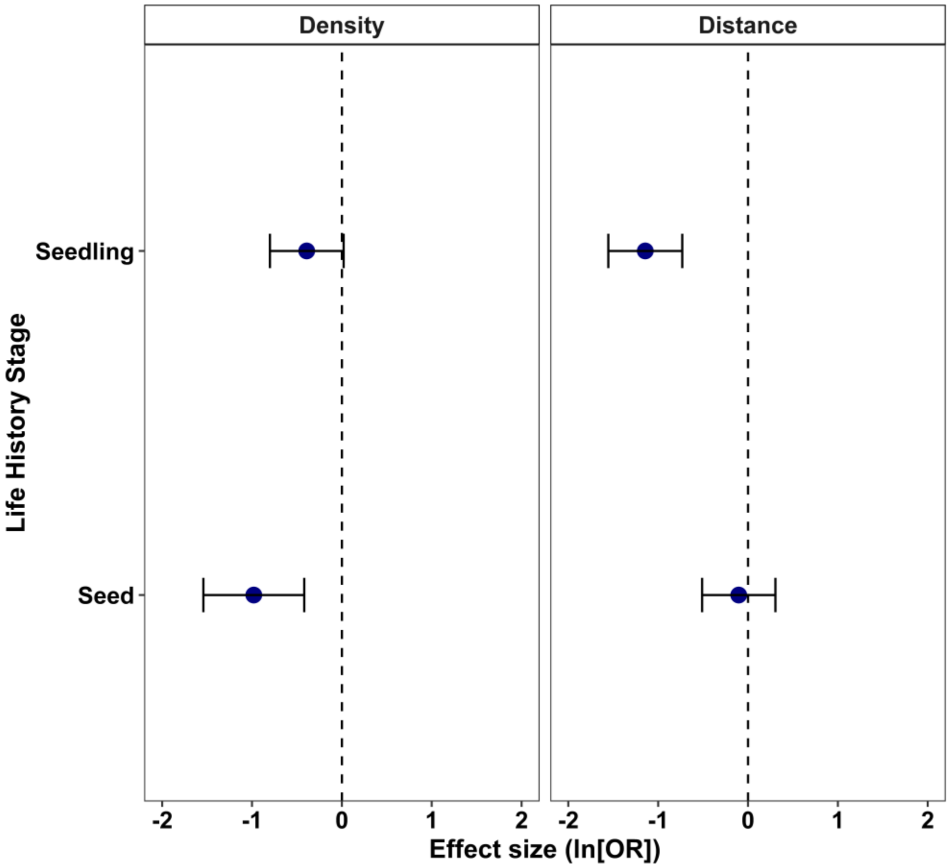


Figure 5: The effects of different life history stage tested in all studies on the log odds ratio of survival seeds and seedlings in the meta-analysis of experimental test of distance and density dependence. Effect sizes are indicated by points and error bars are estimated 95% confidence interval.

VARIATION OF NATURAL ENEMIES (SPECIALIST VERSUS GENERALIST)

I found no significant difference between the effect sizes resulting from different types of natural enemies (Q_M= 0.474, d.f. = 1, P = 0.49; Fig. 6). Specialist natural enemies showed significantly lower odds ratio than generalist (specialist: log OR= -0.72 ± 0.25; generalist: log OR = -0.53 ± 0.12), demonstrating that there was greater negative effects on survival of conspecific density and distance from parent tree caused by specialist natural enemies than generalist. There was no significant difference of natural enemies between tropical and temperate studies (Q_M= 1.31, d.f. = 3, P = 0.73) and no relationship was detected between natural enemies and prediction tested such as density and distance (Q_M = 3.01, d.f. = 3, P = 0.39)

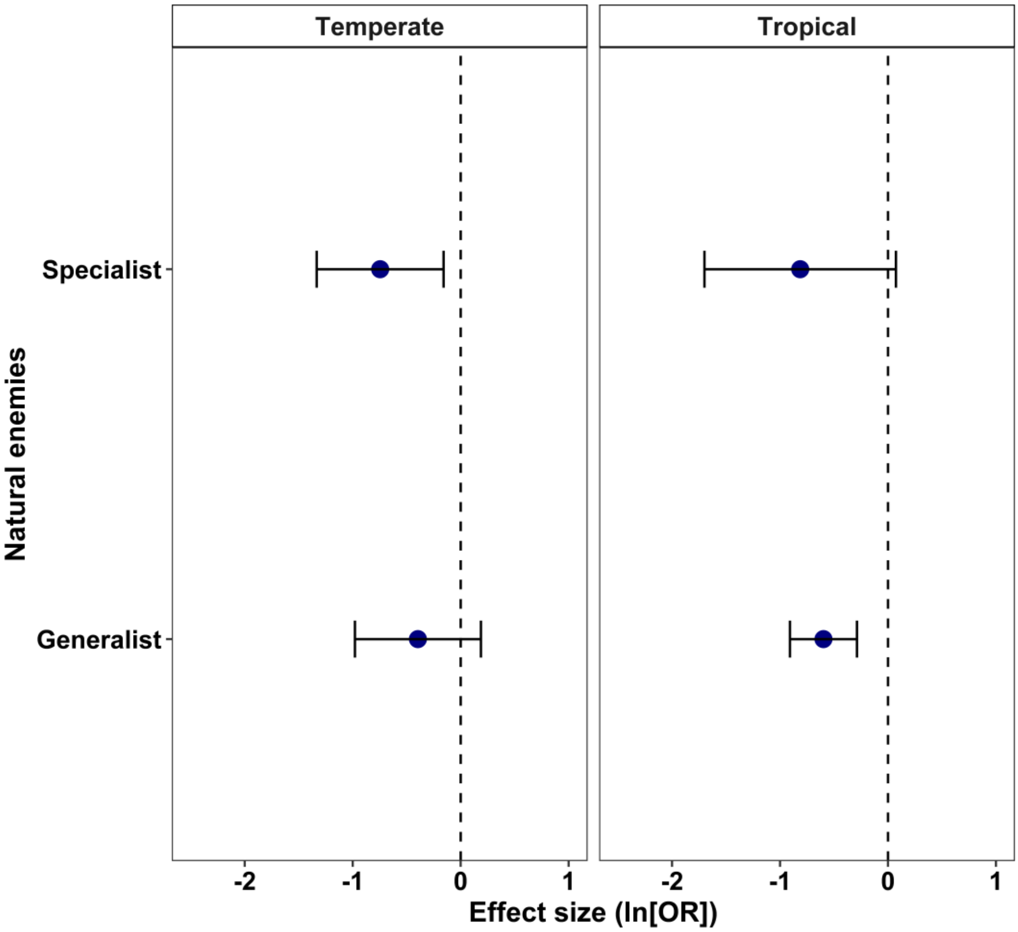


Figure 6: The effects of natural enemies in all studies on the log odds ratio of survival seeds and seedlings in the meta-analysis of experimental tests of distance and density dependence.

3.4 Discussion

My findings provide significant evidence for Janzen–Connell predictions in terms distance and density dependence. In summary, I found that the probability of mortality was higher at high densities or close to conspecific adult plants compared to area with low densities and far from conspecific adults. Moreover, the strength of density and distance dependence varies across studies. This suggests that density and distance dependent effects varies widely in plant communities depending on study site or species tested in the study. Furthermore, this large variation across all the studies could be due to methodological differences when setting up the experiment tests. For instance, differences in effect sizes among the studies could be due to manipulative variable such as minimum and maximum densities or distance that been applied in all the experiment tests. Despite of that , I found significant negative effect of distance- and density dependence on seeds and seedlings caused by natural enemies , consistent with Janzen–Connell predictions of the when pooling all the studies together.

HYPOTHESIS 1 : ARE DISTANCE AND DENSITY DEPENDENT MORTALITY STRONGER IN TROPICS THAN TEMPERATE REGIONS?

Several studies proposed that biotic interactions (i.e distance and density-dependent effects) are more intense at lower latitude (Coley & Aide 1991, Cornell, Sobel & Roy 2009) and supported with evidence (Roslin et al. 2017). In their original paper, Janzen (1970) and Connell (1971) suggested that the strength of distance and density dependence would be higher in the tropics compared to temperate. Nevertheless, I found no significant relationship between the strength of distance- or density- dependent survival and absolute latitude in my meta-analysis. This suggests that in both tropical and temperate plant communities, density and distance dependence may be a vital role in shaping survival patterns during seeds and seedlings stage. This finding is supported by previous meta-analyses, and recent syntheses that found density and distance dependent mortality are not stronger or more specialized towards the tropic regions (Comita et al. 2014, Hyatt et al. 2003, Kozlov, Lanta, Zverev & Zvera 2015, Poore et al. 2012).

Furthermore, a comparative studies by Hille Ris Lambers et al. (2002) found that density dependent mortality is not related to latitude when comparing 10 studies within 8 forest communities and some studies found density dependent mortality is prevalent in temperate forest as in tropical forest (Streng, Glitzenstein and Harcombe, 1989; Packer and Clay, 2000; Jones *et al.*, 2006) . However, only handful of species being tested at each single site in all the studies since most of the experimental studies in this meta-analysis used common species that usually required large number of seeds and seedling for experimental distance and density manipulation with specific number of replications. Plant life history traits such as shade tolerance could exhibit the differences in strength of distance and density dependence depending on species being tested (Kobe and Vriesendorp, 2011; Wu *et al.*, 2016; Zhu *et al.*, 2018).

Even so I did not find any differences in temperate and tropical studies on density and distance dependence, the causes that contributed to this such result are not being assess in this study. This would beg the question of why temperate forests are not as diverse as tropical forests across the globe in terms of latitudinal diversity gradient . Thus, many scientists have suggested that climatic factors could be one of the reason why there is high diversity in tropical forest compared to low diversity in temperate forest (Pianka, 1966; Moreira *et al.*, 2015; Schemske and Mittelbach, 2017).

On the other hand, phylogenetic niche conservatism could be another potential explanation to latitudinal diversity gradient. For instance, a study by (Wiens *et al.*, 2006) found that hyper diversity in tropical forest could due to ancient origin of tree species which colonized the tropics years ago and temperate regions are more being colonized recently. Therefore, my study suggests that the strength of distance and density dependence can be vary in the tropics and temperate regions.

HYPOTHESIS 2 : DO WETTER FORESTS EXPERIENCE STRONGER JANZEN CONNELL EFFECTS COMPARED TO DRIER FOREST?

I found no evidence that suggests annual precipitation affecting the strength of distance and density-dependence from natural enemies. This suggest that natural enemies attack are not always correlated with total annual rainfall since pathogens and insect herbivore attack could be more severe during dry season (Leigh et al. 2004).For instance, Coley & Barone (1996) found that tree species in dry forest suffers greater herbivory rates compared to species in wet forest implying that insects herbivore activity is higher during high temperature and low precipitation In wetter forest, plant tends to invest more in their physical and chemical defence from natural enemies which resulting to low herbivory rates (Coley and Barone, 1996; Molina-Montenegro, Badano and Cavieres, 2006).Based on my findings, the strength of distance and density dependence do not differ between dry and wet forest.

HYPOTHESIS 3 : VARIATION AMONG BIOGEOPRAPHIC AREAS

My findings found a significant evidence for relationship between the strength of Janzen Connell predictions among regions. This indicate that the strength of distance and density-dependent mortality varies among the continents. Based on my results, Europe regions experienced stronger Janzen Connell effects compared to others in temperate regions. However, I could not make strong assumptions about this result due to small number of studies from Europe continent. I hypothesized that Asia region would experience weaker distance and density dependent effect due to community wide masting fruiting events. This event are thought to cause seed predator to satiate which could result to positive density dependence(Janzen, 1971) .

Contrarily, I found Asia regions exhibit stronger distance and density dependence effects compared to other regions in tropical regions even most of studies in this meta-analysis comes from Neotropics. For instance, several studies found negative distance and density dependent effects in most dipterocarp species which involved in mast fruiting events (Blundell and Peart, 1998; Nakagawa *et al.*, 2005; Takeuchi and Nakashizuka, 2007a; Bagchi *et al.*, 2011). In this meta-analysis, only handful studies come from Europe, temperate America and Africa regions. Thus, additional studies from various regions are required in the future to fully assess this Janzen Connell patterns across the global.

HYPOTHESIS 4 : SEEDS VERSUS SEEDLING

In this meta-analysis, I found significantly stronger density and distance dependent mortality effects at the seedling stage compared to seed stage when pooling all the distance and density studies as I hypothesized before. This finding is supported with an observational study in North Queensland, Australia by Connell (1971) who noticed that distance and density dependence are more likely to have significant impact during seedling and sapling stages, but not at seed stage. However, when I separate the density and distance analysis, I found negative effects of density was stronger at seed stage compared to seedling stage while negative effects of distance are higher at seedling stage than seed stage. This interesting finding suggesting that distance and density dependent mortality effects on plant life stages are differ across the density and distance experimental studies.

As tree mortality rates could vary from year to year, higher mortality rates generally occur in earlier plant life stages (Clark and Clark, 1984; Connell, Green and Feb, 2000) For instance, several studies found that negative density dependent mortality are more prevalent in seed stage and seed to seedling transition stage compared to seedling stage (Harms *et al.*, 2000; Metz, 2007; Metz, Sousa and Valencia, 2010). Although all the seed experiments in this meta-analysis study are being assessed by seed removal and post-dispersal predation, I did find the evidence that density dependence still occur even in post-dispersal since pre-dispersal seed predation rates could be high and density-dependent, with seed predators that are generally attracted to high density of seeds and fruits on individual adult plants (Janzen, 1971; Kelly and Sullivan, 1997; L. M. Curran and Leighton, 2000; Comita *et al.*, 2014). Related to the results that I found, it may also reflect variation in the behaviour or type of natural enemies and host specificity that attack seedlings versus seeds. Small mammals seed predators and pathogens are more likely to contribute to Janzen Connell effects and could cause higher mortality at seed stage compared to seedling stage(Paine and Beck, 2007)

HYPOTHESIS 5 : SPECIALIST VERSUS GENERALIST NATURAL ENEMIES

Janzen (1970) and Connell (1971) proposed that specialist natural enemies such as pathogens, seed predators and insect herbivores act as agent in density and distance dependent mortality in preventing competitive exclusion to maintain species diversity. In this meta-analysis, I found no evidence in host-specificity that influence density and distance dependent mortality. However, specialist natural enemies exhibited lower odd ratio than generalist in the results suggesting that specialist natural enemies cause more negative effects on survival of conspecific density and distance from adult trees than generalist natural enemies. In simulation study, Sedio & Ostling (2013) demonstrated that Janzen Connell mechanism is sensitive to host specificity of natural enemies. No relationship was observed between natural enemies in tropical and temperate regions. I also found no relationship between prediction tested (density and distance) and natural enemies.

This result could be underestimate since all the experimental studies involved the plant that were accessible to the full range of natural enemies in natural habitat. Future meta-analysis studies for glasshouse and laboratory experiments on host-specificity natural enemies from distance and density dependence perspectives could provide more insight to what extent host-specificity natural enemies influence distance and density survival. Furthermore, analyses of host-specificity natural enemies in the future should consider phylogenetic relationship to the host plants and closely related plant species.

3.5 Conclusion

Overall, I found significant negative effects of distance and density on seeds and seedlings survival in plant communities globally in this meta-analysis indicating that Janzen-Connell mechanism is likely to be one of the mechanisms of diversity maintenance. There was no relationship between latitude and distance/density dependence consistent with previous meta-analysis by Comita et al. (2014).However, all the studies only tested handful of species at single site, my conclusion may not represent impacts of Janzen Connell mechanism in overall plant communities. Thus, meta-analysis on observational density and distance dependence studies on community level may provide better understanding on roles of Janzen Connell effects in plant communities. Based on the wide variation in effect sizes, every species exhibited different results in density and distance dependent mortality. Nevertheless, Janzen-Connell mechanism could contribute to maintenance of diversity in plant communities if some species or competitively dominant species are negatively affected, leaving rare species to survive(Carson *et al.*, 2008).

Chapter 4

An analysis of species trait variances in Dipterocarpaceae family

Abstract

The role of evolution of traits in shaping diversity in tropical forests remains poorly understood. Through analyses of traits variance as a function of evolutionary history and environmental variables could reveal how the pattern of species distribution. Furthermore, strength of phylogenetic signal in conservation status could provide insight on mechanisms that lead to phylogenetic conservatism in evolutionary time. The objectives of this study are to assess whether dipterocarp species traits are phylogenetically conserved through phylogenetic signal, indicating phylogenetic niche conservatism (PNC),to determine the drivers of dipterocarp species distribution, to examine relationship between morphological traits with habitat factors and assess correlation between conservation status and phylogeny. Here, I compiled a dataset of dipterocarp species plant traits from Dipterocarpaceae. Overall, I found significant evidence of phylogenetic conservatism of plant traits in dipterocarp species, with moderate phylogenetic signal. My findings showed elevational gradient data are involved in shaping dipterocarp species distribution across the global. Morphological traits such as height and diameter show phylogenetically dependent relationship with the habitat soil types. Shade tolerance traits are related to survival. Conservation status are related to phylogeny and has significant impact on population trend. This study emphasized that phylogenetic analysis are important and powerful tool in order to highlight importance of phylogenetic history of dipterocarp species traits and conservation priorities in dipterocarp biodiversity.

4.1 Introduction

Tropical forests have long been acknowledged as one of the most mega diverse terrestrial ecosystems in the world (Poore, 1991; Chesson, 2000). Co-occurrence of many species within the same community has led to the vast floristic richness in tropical forests (Whitmore, 1984; Poore, 1991). Much work has been undertaken by ecologists in an attempt to understand and explain this variation (see Chapter 2 and Chapter 3). To date, a great deal of this effort has been expended in trying to understand the ecological factors that drive diversity. Hypotheses such as the Janzen-Connell mechanism (Janzen, 1970; Connell, 1971) and the neutral theory (Hubbell, 2001) offer different perspectives on the factors that drive diversity. Although there is growing support for the Janzen-Connell mechanism (Swamy and Terborgh, 2010; Comita *et al.*, 2014; Zhu *et al.*, 2015; Du *et al.*, 2017), what both the theories have in common is that they are basically ecological in nature (Hubbell 2001). Thus, they do not consider the role of evolution or of traits in shaping distributions or diversity within tropical forests.

Across a pantropical distribution, species adapt to contrasting environments through the evolution of functional traits, and variation in these with environmental conditions is a fundamental feature of biological diversity (Ackerly, 2004). Pavoine et al. (2011) highlighted the need to assess the relationship between evolutionary processes, species traits variances and species interaction with the environment in order to fully understand the factors that drive variation in traits across different environments. Thus, in addition to understanding ecological diversity in terms of the numbers of species, there is also a need to document and explain diversity in species traits.

The need to understand evolutionary basis for trait variation has become more important given recent rapid anthropogenic changes in the global environment (Smith and Bernatchez, 2008; Hoffmann and Sgró, 2011). Specifically there are major concerns that evolution is often slow, with species tending to retain similar traits for long periods, and how this will potentially accelerate intense human impacts in this millennial age (Wiens *et al.*, 2010). A study by Chapin et al. (1993) highlighted that rapid evolution of traits on environmental stress may provide short-lived species to develop into stress-resistant plant. Furthermore, current alarming biodiversity trends could be resulted from slow evolution due to rapid changes in global environment (Turner *et al.*, 2012)

A key concept in understanding large-scale pattens in trait variation is phylogenetic niche conservatism (PNC; Harvey & Pagel 1991). As defined, for example, in Wiens & Graham (2005), this is the tendency of closely related species with common evolutionary history to share similar niche or ecological (i.e. morphology, physiology and life history) traits. There are multiple mechanisms and drivers of PNC. Essentially it results from physiological and ecological constraints on species that limit them to a restricted set of ecological or environmental niches (Harvey & Pagel 1991; Wiens & Graham 2005; Cooper et al. 2011). PNC is termed ‘phylogenetic conservatism’ because species inherit their niches from their ancestors rather than through *de novo* evolution. Consequently whole taxa can be limited to a similar subset of environments (Harvey and Pagel, 1991; Wiens and Graham, 2005; Cooper, Freckleton and Jetz, 2011). In the face of ongoing threats, this means that extinction is likely to be non-randomly distributed with respect to phylogeny and thus it is important to characterise PNC.

A suite of tests for PNC exist which revolve around measuring phylogenetic signal in key traits (Blomberg, Garland and Ives, 2003; Cooper, Freckleton and Jetz, 2011; Pavoine and Bonsall, 2011). These tests are based on Phylogenetic comparative methods (PCMs) which have been developed to measure phylogenetic signal in trait variance and associated environmental factors (Harvey and Pagel, 1991; Freckleton, Harvey and Pagel, 2002; Blomberg, Garland and Ives, 2003; Fritz and Purvis, 2010a; Cooper, Thomas and FitzJohn, 2016). These approaches measure phylogenetic niche conservatism by measuring how trait variation is associated with phylogeny (Kreier and Schneider, 2006; Cooper, Freckleton and Jetz, 2011; H. Liu *et al.*, 2012; Liu *et al.*, 2016). These approaches thus directly address the prediction of PNC that closely related species should share similar traits than distantly related ones.

Although testing for phylogenetic signal seems like a logical approach to investigate PNC, there are potential pitfalls and several studies have pointed that these methods can be limited and are dependent on the assumptions made, as well as the existence of possible statistical biases (Freckleton, 2009; Cooper, Freckleton and Jetz, 2011; Losos, 2011; Blomberg *et al.*, 2012; Cooper, Thomas and FitzJohn, 2016). It is important to recognise at the outset that when modelling comparative data, several different processes could yield the same outcome in the phylogenetic dispersion of traits (Revell et al. 2008). In modelling PNC, it is very important to specify the process by which it is believed PNC may evolve, as well as to clearly specify ‘null’ alternatives. This is because both phylogenetic signals, and the lack of it, could conceivably both be the consequence or not of PNC depending on the process (Cooper et al. 2011).

There are also potential statistical issues that affect such analyses. First, most analyses assume traits evolve according to a Brownian motion model (i.e. trait variance increases as linear function of time). This is a commonly used process used to model the outcome that closely related species share similar traits through inheritance from their ancestors, not because of independent evolution (Felsenstein, 1985a; Harvey and Pagel, 1991). Alternatives such as the Ornstein-Uhlenbeck (OU) model of trait evolution have been proposed (Hansen 1997). The OU model assumes that niche of a group of species is constrained, and that stabilizing selection prevents species moving too far from a niche optimum, resulting in weaker phylogenetic dependence than predicted by the Brownian model (Hansen, 1997). However, this model presents statistical difficulties, not least because of confounding with measurement error (Cooper et al. 2016). This again emphasises the need for careful specification of the underlying model, along with robust statistical testing.

In terms of tropical diversity, Borneo has been recognized as one of the greatest hotspots of plant species richness among the world's tropical rainforests (De Bruyn *et al.*, 2014). In South-East Asia, tropical lowland rainforests are dominated by large canopy trees from the dipterocarp family, with this group comprising over 50% of canopy trees (Ashton, Peter S., Givnish, T.J. , Appanah, 1988; Peter S Ashton, 1988). Owing to economic growth, these dipterocarp forests have been degraded by logging, shifting cultivation, conversion into other land uses such as rubber and oil palm plantations (Palmer, 2001; Jomo, Chang and Khoo, 2004; Sodhi *et al.*, 2004; Kummer and Turner, 2009).

In this study, I studied the Dipterocarpaceae family, which globally comprises 695 species within 16 genera. Dipterocarp species are highly regarded in terms of their timber market value, which has been a major economic contributor to South-East Asian countries (Appanah and Turnbull, 1998). The distribution of the dipterocarps is mainly limited to tropical and sub-tropical regions in which mean annual rainfall exceeds 1000mm. The three dipterocarp subfamilies occurs in specific regions: Dipterocarpoideae in Asia, Pakaraimoidae in South America and Monotoideae in Africa (Ghazoul, 2016).

There is evidence of environmental constraints on dipterocarp distributions. A large number of species occur below 1000m altitude. For instance, high dipterocarp species richness is observed in lowland rainforest with elevation up to 300m in Peninsular Malaysia, Thailand, Sumatera and Borneo (Ashton, 1982; Ashton, Givnish and Appanah, 1988b; Ghazoul, 2016). Soil type is one of the factors that appears to have contributed to this distribution pattern: the richest dipterocarp communities occur on the yellow sandy humult soil regions compared to homogenous clay soil regions (Russo *et al.*, 2005; Katabuchi *et al.*, 2012; Ghazoul, 2016). An important question is whether niche conservatism operates in limiting dipterocarp species adaptations to these environmental factors, and whether any such evolutionary conservation might limit species distributions.

Based on testing for the existence and strength of PNC we investigated how plant traits vary among Dipterocarps. My objectives were: (1) measure the phylogenetic signal in the plant traits of all known dipterocarp species in order to assess the degree to which PNC shapes trait distributions; (2) analyse how different ecological adaptations were associated with species distribution; (3) assess to which extent the morphological traits and species performance correlated with habitat and soil type in order to understand how traits are shaped by environmental factors; and (4) analyse the correlation between conservation status and phylogeny in the Dipterocarpaceae family to determine whether PNC contributes to extinction threats.

4.2 Materials and methods

Study group

Approximately 695 species and 16 genera have been described that belong to the Dipterocarpaceae (Maarten J.M. Christenhusz and Byng, 2016). The family has a pantropical distribution and is divided into three subfamilies, Dipterocarpoideae, Monotoideae and Pakaraimoideae. In Dipterocarpoideaa subfamily there are two tribes divided morphologically. The tribe Shoreae consists of five genera: *Shorea*, *Hopea, Neobalanocarpus, Dryobalanops and Parashorea*. The tribe Dipterocarpeae consists of eight genera: *Dipterocarpus, Anisoptera, Upuna, Cotylebium, Vatica, Vateria, Vateriopsis* and *Stemonoporus*(Ashton, 1982). The subfamily Monotoideae, consists of genus *Monotes* that distributed across Africa and Madagascar, *Marquesia* is indigenous to Africa and genus *Pseudomonotes* is endemic to Colombian Amazon(Ashton, 1982; Peter S Ashton, 1988; Ghazoul, 2016). Subfamily Pakaraimoideae consists only of a single species*, Pakaraimea dipterocarpaceae* which occurs in the

Guyana Highland, Venezuela (Maguire and Ashton, 1980). The source of nomenclature for the dipterocarp species used in this study was according to Symington (1974),Maguire et al. (1977), Ashton (1977,1982,1988), Kostermans (1978,1981,1982,1983,1992) and Londono et al. (1995).

Based on phylogenetic study by Ducousso et al. (2004),it noted that Asian dipterocarps share a common ancestor with the Sarcolaenaceae, a plant family that endemic to Madagascar. They are sub-canopy, canopy, or emergent trees with many species exceeding 50m in height (Peter S Ashton 1988; Ghazoul 2016). As noted above, the distribution of the family encompasses tropical and subtropical countries where the mean annual rainfall generally exceeds 1000mm. These include the South-East Asian countries, China, India, Sri Lanka, Guyana highlands, Colombia, Seychelles, Madagascar, Africa and Papua New Guinea (Ashton et al. 1988b; S. Appanah 1993; Ghazoul 2016).According to Ashton (1982), Borneo is the area with greatest diversity of Dipterocarpaceae.

Characteristically, the Dipterocarpaceae are involved in mast fruiting events, with synchronous intermittent (often >7 years) production of large seed crops (Janzen, 1974; S Appanah, 1993; Kelly and Sork, 2002). The predation satiation hypothesis is the best supported explanation for masting events, especially in dipterocarp species (Sork, 1993; Kelly and Sullivan, 1997; L M Curran and Leighton, 2000; Lyal and Curran, 2000). It predicts that plant occurs in high densities, to reduce the number of seed losses to the predators (Molles, 2002). In terms of pollination, this reproductive strategy is believed to maybe have evolved to attract more pollinators through immigration of pollinators, since pollination efficiency hypothesis suggests that mast fruiting events increase pollination success (Sakai, 2002). Moreover, several studies have found that dipterocarps are also pollinated by various insects during general flowering, with most dipterocarps in lowland forests being pollinated by bees, with beetles also playing a role (Momose *et al.*, 1998), and occasionally birds (Momose *et al.*, 1998; Sakai, 2002).

Dipterocarps are associated with ectomycorrhizal fungi (Brearley, 2012). Ectomycorrhizal colonisation in dipterocarp trees improves nutrient and water uptake (Brearley *et al.*, 2003; Paoli, Curran and Zak, 2006). However, they are characteristic of primary rainforest, but are much less frequent in logged forests. This is because ectomycorrhizal fungi are generally sensitive to disturbance such as logging and forest fire due to the changes of the soil environment (Jones, Durall and Cairney, 2003; Brearley, 2012).

Data collection

I compiled plant traits data for 544 dipterocarp species from a range of resources (Table 1). These included: (i) a literature search in Google Scholar with search terms ‘Dipterocarpaceae’ yielding 13,400 results; (ii) key monographs by Symington (1974) and Ghazoul (2016); and (iii) internet plant databases (IUCN Red List, PlantUse.net). Data that we collected for each species are:

1. Taxonomy (sub-family, tribe, genus, section and sub-section).
2. Habitat – forest habitat that inhabit by dipterocarp plants (i.e. lowland forest, upper hill dipterocarp forest and montane forest)
3. Geographic distribution: altitudinal data, estimated Extent of Occurrence and Area of Occupancy.

4. Quantitative traits: I recorded plant height, diameter at breast height (DBH), growth rate, leaf length, mean seed weight per kilo, fruit length, fruit width, wing length, dispersal, survival and wood density.
5. Qualitative traits: I recorded soil type, shade tolerance, chromosome number, flowering frequency, anthesis time, flower size, flower reward, flower colour, pollinator agents, number of wings, seed dispersal agent, wood type,
6. Threat and imperilment: I recorded conservation status (using IUCN red list status) and population trend (IUCN 2018).

Table 1: List of plant traits of dipterocarp species that have been used in this study

Traits	Definition	Units	Description of classes
Lower elevation limit	Low distance above sea level of species occurrence	m	Quantitative value
Upper elevation limit	High distance above sea level of species occurrence	m	Quantitative value
Endemism	Species that being unique to specific location		Qualitative (Widespread = 0, Endemic= 1)
Estimated Extent of Occurrence	“area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy”, (IUCN 2001)	km^2	Quantitative value
Estimated Area of Occupancy	“area within its 'extent of occurrence' which is occupied by a taxon, excluding cases of vagrancy”, (IUCN 2001)	km^2	Quantitative value
Habitat Soil type	Soil type that inhabited by plant (Voroney, 2007)		Qualitative (Soil type= Clay, Sandy, Loam, and Limestone Inhabiting? Yes= 1, No=0)

Height	Distance from ground level to the level top of the tree	m	Quantitative value
Diameter at breast height (DBH)	Measurement of tree stem at the height of 1.30 m	cm	Quantitative value
Growth rate	Girth increment per year	cm/per year	Quantitative value
Shade tolerance	Ability to tolerate low light level		Qualitative (Shade tolerant= 0, Intermediate= 1, Light demander= 2)
Leaf length	Length of the leaf in vascular plants from lamina tip to the petioles along lamina midrib (Cho *et al.*, 2007)	cm	Quantitative value
Flower size	Diameter of flower	mm	Qualitative (Small(<10mm) = 0, Medium(10—20mm) = 1, Large(>20mm) = 2)
Flower reward	Secretion or structure of the labellum that can be consumed or gathered by pollinators (Singer & Koehler 2004)		Qualitative (Type= Nectar, Pollen and Corolla, Produced? Yes= 1, No= 0)
Survival	Tree mortality	%	Quantitative value
Flowering frequency	Regularity of flowering in vascular plant		Qualitative (General= 0, Regular= 1)
Anthesis (Day)	Flowering period of plant (0600-1800)		Qualitative (Yes= 1, No= 0)
Anthesis (Night)	Flowering period of plant (1800-0600)		Qualitative (Yes=1, No=0)

Chromosome number	Number of DNA molecule that carry genetic information of plant (Battaglia, 1955)		Qualitative (Chromosome no x=7,10,11 and Polyploidy, Yes=1, No=0)
Outcrossing rate	Rates of crossing between different breeds	%	Quantitative value
Fruit length	Length of nut	mm	Quantitative value
Fruit width	Width of nut	mm	Quantitative value
Seed weight	Seed mass	seed per kilo	Quantitative value
Functional wing	Wings that involved in seed dispersal		Qualitative (Wing no= 0,2,3 and 5, Has? Yes= 1, No=0)
Functional wing length	Measurement of length of wings involved in dispersal	mm	Quantitative value
Wing loading	Fruit mass divided by wing surface area(Green, 1980)	cm^2/g	Quantitative value
Wood type	Hardwood type classification		Qualitative (Light Hardwood=0, Medium Hardwood= 1, Heavy Hardwood= 2)

Wood densities	“Measurement of the ratio of oven-dry mass of wood divided mass of water displaced by its green volume “ (Chave, no date)	g/cm^3	Quantitative value
Red List status	Species conservation status through criteria such as population size, rate of decline and geographic distribution as listed in IUCN Red List Categories (IUCN 2017)		Qualitative (Data Deficient= 0, Least Concern= 1, Near Threatened= 2, Vulnerable= 3, Endangered=4, Critically Endangered=5, Extinct in The Wild= 6)

Phylogenetic tree

By using the R package ‘S. PhyloMaker’, I constructed a phylogenetic tree by grafting dipterocarp genera and species included in this study onto a backbone phylogenetic hypothesis (Qian and Jin, 2016). I used PhytoPhylo mega-phylogeny as the backbone of this mega tree developed by Qian & Jin (2016), an updated and expanded version of Zanne et al.’s species-level phylogeny (Zanne *et al.*, 2014). Zanne et al ‘s phylogeny comprises about 30 771 seed plants and was time-calibrated for all branches using seven gene regions available in GenBank as well as fossil data .Moreover, PhytoPhylo includes all families of extant seed plants (Qian and Zhang, 2014) with five times more genera and over 55 times more species than the newest angiosperm supertrees (i.e., R20120829)(Qian and Jin, 2016).

On the other hand, genera and species that were not found or missing in the PhytoPhylo mega-phylogeny, S. PhyloMaker organized the data in three different approaches : (1) by adding genera or species as polytomies within their families (Scenario One); (2) by randomly adding genera or species within their families or genera (Scenario Two); and (3) by adding genera or species to their families or genera with the same approach used in the online software Phylomatic and BLADJ (Branch Length Adjuster) (Scenario Three). Using these three approaches, three phylogenies were generated at each level of resolution such as family, genus and species (see Appendix C2).

Phylogenetic Niche Conservatism

As noted above, following Cooper et al. (2011) it is important to define Phylogenetic Niche Conservatism as multiple definitions are possible. Here I take the view that Phylogenetic Niche Conservatism occurs when closely related species are similar through having inherited their niches from ancestors; conversely it is absent when species traits are evolutionarily labile and there is no relationship between traits and phylogeny.

To achieve my first objective, I calculated phylogenetic signal for environmental factors and each plant traits in my study to determine phylogenetically conserved traits. I used Pagel's λ to identify phylogenetic dependence based on prediction of Brownian model of trait evolution(Pagel, 1999; Freckleton, Harvey and Pagel, 2002). This parameter varies between zero and one: λ= 0 suggests that there is no phylogenetic signal, and λ=1 suggests that perfect phylogenetic dependence under Brownian motion model. I estimated λ values for each trait by using pgls function from R package caper (Orne 2013). The λ statistic was also used to control for phylogenetic signals in the linear models (Freckleton et al. 2002).

For my second objective, I assessed the drivers of geographic distribution of dipterocarp species by using elevational gradient data and soil type as predictor variables while geographic extent and extent of occurrence as response variable in the linear model. With respect of my third objective, I determined the relationship of between morphological traits (i.e. height, DBH) and species performance (i.e. growth ,survival) as response variable with habitat soil type and shade tolerance traits as predictor variable . Lastly, I used conservation status as response variables and population trends, habitat destruction as predictor variables in the linear model to assess correlation between conservation status and phylogeny in the Dipterocarpaceae family to demonstrate whether PNC contributes to extinction threats. All linear models were fitted by using pgls function in caper package in R software.

4.3 Results

I compiled 544 dipterocarp species with plant traits data from a range of resources in datasets and ran the models to determine whether traits are correlate with phylogeny using a measure of phylogenetic signals (See below).

Phylogenetic signal in single traits

Lower and upper elevation limit showed phylogenetic dependence, with values of λ 0.675 and 0.468 respectively ($P < 0.001$ for tests of $\lambda = 0$, Table 1), indicating some conservatism in altitudinal preferences. The geographic range of distribution in dipterocarp species showed weak phylogenetic dependence with λ value of 0.048 ($P < 0.05$ for $\lambda = 1$; Table 1). However, no phylogenetic signal was observed in estimated area of occupancy (P ns for $\lambda = 0$; ns for $\lambda = 1$). Only limestone soil type showed phylogenetic independence in the analyses (P ns for $\lambda = 0$; <0.001 for $\lambda = 1$).

Of the morphological traits, plant height, diameter at breast height (DBH), flower size, flower reward and shade tolerance showed phylogenetic dependence with λ values ranging from 0.41 to 0.831 (all $P < 0.001$ for tests of $\lambda = 0$; Table 1). Leaf length and flower reward nectar traits were significantly conserved in dipterocarp species with λ value of 0.216 and 0.221 respectively ($P < 0.05$ in $\lambda =$

0; Table 1). Survival showed phylogenetic independence (P ns for λ= 0; <0.001 for λ = 1). Flowering frequency in dipterocarp species showed phylogenetic dependence with λ of 0.687 (P < 0.001 in λ= 0; Table 1). For all genetic traits, there was phylogenetic dependence in dipterocarp species with all λ value of 1 except for outcrossing rate (P < 0.001 in λ= 0; Table 1).

In terms of seed traits, fruit length and wingless seed exhibited phylogenetic dependence with λ value of 0.500 and 0.505 respectively (P < 0.001 in λ= 0; Table 1). Seed weight showed phylogenetic signal with high λ value of 0.996 (P < 0.001 in λ= 0; Table 1). Functional wing length and fruit width had λ of 0.167 and 0.383 (P, 0.05 for λ= 0) In addition, timber type and wood densities showed phylogenetic dependence with λ value of 0.841 and 0.442 respectively (all P < 0.001 in λ= 0; Table 1).

Table 9: Pagel's lambda value based on dipterocarp phylogenetic tree in a model for single trait only

Trait (y)	n	y ~ 1		
		λ	$P_{(\lambda=0)}$	$P_{(\lambda=1)}$
Elevation				
Lower elevation limit (m)	523	0.675	***	***
Upper elevation limit (m)	523	0.468	***	***
Geographic distribution				
Widespread/Endemic	541	0.216	***	***
Estimated Extent of Occurrence	172	0.048	*	***
Estimated Area of Occupancy	11	0.000	ns	ns
Habitat Soil type				
Soil type (Clay)	310	0.196	*	***
Soil type (Sandy)	310	0.263	**	***
Soil type(Loam)	310	0.456	***	***
Soil type (Limestone)	310	0.000	ns	***
Morphological traits				
Height	387	0.547	***	***
Diameter at breast height	353	0.410	***	***
Growth rate	30	0.437	ns	ns
Shade tolerance	241	0.732	***	***
Leaf length (cm)	381	0.216	*	***
Flower size (mm)	392	0.831	***	***
Flower reward (Nectar)	323	0.221	*	***
Flower reward (Pollen)	323	0.122	***	***
Flower reward (Corolla)	323	0.047	**	***
Survival (%)	51	0.000	ns	***
Flowering event				
Flowering frequency	543	0.687	***	***
Anthesis (Day)	142	0	ns	***

Anthesis (Night)	142	1	***	ns
Genetic traits				
Chromosome no. (x=7)	544	1	***	ns
Chromosome no.(x=10)	544	1	***	ns
Chromosome no.(x=11)	544	1	***	ns
Polyploidy	544	1	***	ns
Outcrossing rate	19	0	ns	***
Seed traits				
Fruit length (mm)	282	0.500	***	***
Fruit width (mm)	239	0.383	**	***
Seed weight (seed per kilo)	65	0.996	***	ns
Wingless seed	543	0.505	***	***
Functional wing=2	543	1	***	ns
Functional wing= 3	543	1	***	ns
Functional wing= 5	543	1	***	ns
Functional wing length	111	0.167	**	***
Wing loading	25	0.000	ns	*
Timber type and density				
Wood type	484	0.841	***	***
Wood densities	238	0.442	***	***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant

Drivers of geographic distribution

The upper elevation limit showed statistically significant association with species distribution with weak phylogenetic dependence (λ= 0.227, P < 0.001 in λ= 0; Table 2; Fig.1). In all models for distribution versus elevational gradient, there were weak phylogenetic signal with λ values ranging from 0.202 to 0.227 (P < 0.001 for both λ= 0 and λ= 1; Table 2). Upper elevation limit exhibited significant relationship with estimated extent of species occurrence but showed no phylogenetic dependence (P ns for λ= 0; Table 2).

Table 2: F and λ values for phylogenetic linear models testing the relationships between a)species distribution and elevational gradient; b) extent of occurrence and elevational gradient

	n	Elevational gradient (F^P)		λ	P(λ=0)	P(λ=1)
		Lower limit (lwr)	Upper limit (upr)			
(a) Geographic extent						
Distribution~ lwr	519	0.073^{ns}		0.207	***	***
Distribution~ upr	519		6.423*	0.227	***	***
Distribution ~ lwr + upr	518	0.080^{ns}	10.268**	0.202	***	***
(b) Extent of Occurrence (EOO)						
EOO ~ lwr	171	0.001^{ns}		0.048	*	***
EOO ~ upr	171		9.516**	0.048	ns	***
EOO ~ lwr + upr	170	0.001^{ns}	11.529***	0.044	ns	***

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

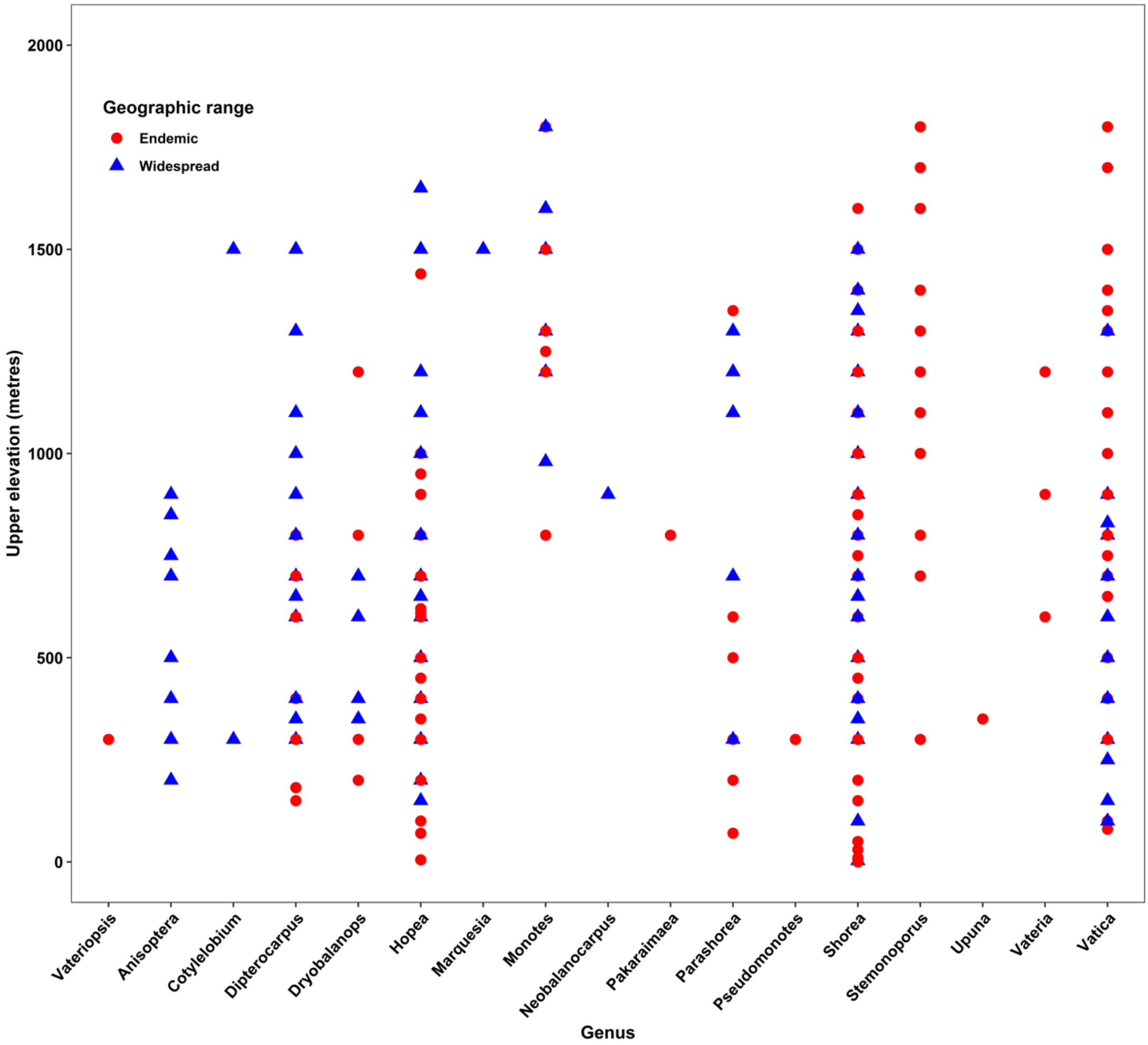


Figure 1*:* Relationship of upper elevation limit of each dipterocarp genera between geographic range

Of the variables measuring soil types, only the presence of limestone showed statistically significant with species distribution (Table 3), with weak phylogenetic signal ($\lambda = 0.275$, $P < 0.001$ in $\lambda = 0$; Table 3).There was a significant relationship between limestone soil type and estimated extent of occurrence (Table 3), but none of all these soil types showed phylogenetic dependence (all P ns for $\lambda = 0$; Table 3).

Table 3: F and λ values for phylogenetic linear models testing the relationships between a)species distribution and habitat soil types; b) extent of occurrence and habitat soil types

	n	Soil type (F^P)				λ	P (λ=0)	P (λ=1)
		Clay(c)	Sandy(s)	Loam(l)	Limestone(ls)			
(a) Geographic Extent								
Distribution~ Clay	307	3.130^{ns}				0.300	***	***
Distribution~ Sandy	307		1.005^{ns}			0.278	***	***
Distribution~ Loam	307			1.220^{ns}		0.282	***	***
Distribution~ Limestone	307				5.104*	0.275	***	***
Distribution~ c+ s + l + ls	304	3.112^{ns}	0.059^{ns}	0.883^{ns}	4.375*	0.288	***	***
(b) Extent of Occurrence (EOO)								
EOO~ Clay	110	0.195^{ns}				0.000	ns	***
EOO ~ Sandy	110		0.016^{ns}			0.000	ns	***
EOO ~ Loam	110			0.403^{ns}		0.000	ns	***
EOO ~ Limestone	110				20.221***	0.052	ns	***
EOO ~ c + s + l + ls	107	0.304^{ns}	0.006^{ns}	0.591^{ns}	21.003***	0.066	ns	***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant

Morphological traits and habitat factors

Given the large number of tests in the study, the chances of type 1 error are quite high when I carried out the analyses. Based on my results, Clay soil type showed a significant relationship with tree height, however there was no association of height with other soil types or shade tolerance (Table 4a), with significant phylogenetic dependence ($\lambda = 0.533$, $P < 0.001$; Table 4a). Meanwhile, habitat soil type such as clay and sandy exhibited significant association with tree diameter (Table 4b), and mild phylogenetic dependence with λ values of 0.450 and 0.427 respectively ($P < 0.001$ in $\lambda = 0$; Table 4).

In all the models of growth versus soil types and shade tolerance, there were no significant relationships (Table 4c). Furthermore, no phylogenetic signals were observed in all growth versus soil types and shade tolerance models, with λ values not distinguishable from either 0 or 1. When survival were model against soil types and shade tolerance, only shade tolerance traits showed a statistically significant association with survival (Table 4d; Fig.2). However, none of the models showed phylogenetic dependence (all P ns for λ= 0; Table 4d).

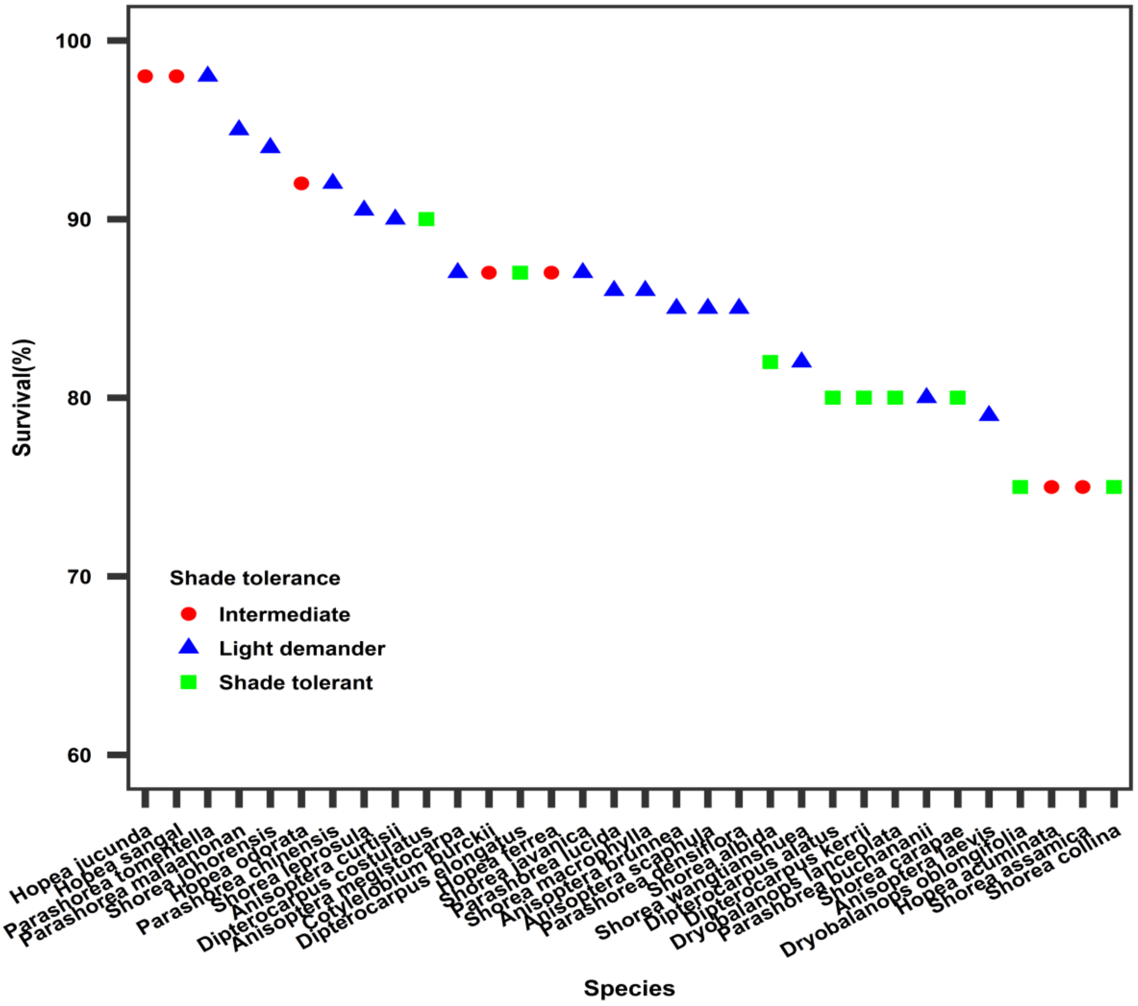


Figure 2: Survival rate of 32 dipterocarp species based on their shade tolerance trait

Table 4: F and λ values for phylogenetic linear model testing the relationship between morphological traits on soil types and shade tolerance

	n	F^P value	λ	P(λ=0)	P(λ=1)
(a) Height					
Clay	289	6.697**	0.533	***	***
Sandy	289	2.938^{ns}	0.516	***	***
Loam	289	0.120^{ns}	0.543	***	***
Limestone	289	0.024^{ns}	0.542	***	***
Shade Tolerance	171	0.416^{ns}	0.582	***	***
(b) Diameter at breast height (DBH)					
Clay	273	5.072*	0.450	***	***
Sandy	273	4.566*	0.427	***	***
Loam	273	0.833^{ns}	0.473	***	***
Limestone	273	0.627^{ns}	0.470	***	***
Shade Tolerance	162	0.136^{ns}	0.504	***	***
(c) Growth					
Clay	20	0.146^{ns}	0.392	ns	ns
Sandy	20	0.715^{ns}	0.264	ns	ns
Loam	20	0.001^{ns}	0.433	ns	ns
Limestone	20	3.046^{ns}	0.858	ns	ns
Shade Tolerance	21	0.108^{ns}	0.490	ns	ns
(d) Survival					
Clay	37	1.855^{ns}	0.000	ns	***
Sandy	37	0.727^{ns}	0.000	ns	***
Loam	37	1.018^{ns}	0.000	ns	***
Limestone	37	0.028^{ns}	0.000	ns	***
Shade tolerance	31	5.314*	0.000	ns	**

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

Conservation status and phylogeny

Species population trend exhibited a significant relationship with conservation status (Table 5), with strong evidence for phylogenetic dependence (λ= 0.536, P < 0.001 in λ= 0; Table 5). Furthermore, habitat destruction and percentage of habitat declined also showed significant association with conservation status but was not related to phylogeny (both P ns for λ= 0; Table 5).

Table 5: F and λ values for phylogenetic linear models testing the relationship between conservation status on population trend and habitat destruction

	n	F^P value	λ	P(λ=0)	P(λ=1)
Red List status					
Population trend	397	75.287***	0.536	***	***
Habitat destruction	397	34.812***	0.401	ns	***
Percentage of habitat decline	397	8.984**	0.000	ns	***

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

4.4 Discussion

Phylogenetic niche conservatism in dipterocarp species traits

My results revealed that there were significant phylogenetic signals in most of the plants traits we measured in dipterocarp species. Most of the plant traits were phylogenetically conserved indicating evidence of Phylogenetic Conservatism in these traits. Phylogenetic niche conservatism in Dipterocarpaceae might be associated with a suite of different evolutionary processes with implications for my understanding of biogeography and the future impacts of climate change, (Wiens and Graham, 2005).

The phylogenetic associations of dipterocarps have been difficult to uncover. Reasons include hybridization between species and interspecific heterogeneity in molecular and morphological traits (Peter S Ashton, 1988; Dayanandan *et al.*, 1999; Gamage *et al.*, 2006). For instance, Ashton (2014) noted that most of Philippine endemic dipterocarps are sister to Bornean dipterocarp species (i.e.*Hopea acuminata and Hopea sangal)*. In *Shorea* genus, interspecific hybridization is known in aseasonal rain forest in Malaysia and Indo-Burma(Ashton, 1982; Ishiyama *et al.*, 2008; Kamiya *et al.*, 2011). Clearly the evolutionary history of this group is complex. The existence of phylogenetic signal in a suite of traits indicates that, despite this complexity, some conservatism in traits exists. The obvious question is therefore whether this conservatism impacts on distributions or on population status in terms of conservation or population trends.

Environmental adaptations and species distribution

I found evidence that upper the elevation limits of dipterocarp species are related to distribution (widespread species have wider limits), but my data exhibited weak phylogenetic signal suggesting that PNC is weak (Hansen, 1997; Donoghue, 2008): the relationship between distribution and elevation showed no evidence for phylogenetic signal, thus although there is a relationship between these two variables, there is no evidence for a residual imprint of phylogeny. Many dipterocarp species are restricted to lowland forest, and species richness gradually decreases at around 400m above sea level. For instance, dipterocarp species in Sumatra such as *Shorea pauciflora, Shorea macroptera, Shorea singkawang* and *Anisoptera megistocarpa* are strictly limited to elevations up to 200m (Ghazoul, 2016). To date, there is little information on how elevational gradient influenced plant endemism (Kessler, 2002). My results showed that the upper elevation limit species extent of occurrence but doesn’t related to phylogeny. This suggests that the limits on extent of occurrence affect all species and do not affect different clades differentially.

My analyses demonstrated that the soil types inhabited by species are related to phylogeny suggesting that dipterocarp clades have undergone evolutionary adaptation to edaphic types. This is supported by work from Ashton (2014) who found that the occurrence of dipterocarps in Borneo is related to particular soil types. Tropical forest soils are heterogenous and the most common soil types in tropical forests are ultisols and oxisols which are highly weathered clay soils with low nutrient content and pH value(Shamshuddin and Fauziah, 2010; Ghazoul, 2016). A study by Potts et al. (2002) found that most of common soils that widely distributed in Borneo are ultisols; humult ultisols (poor in nutrient with raw hummus layer) and udult ultisols (fertile with lack of organic layer). However, in our study only limestone soil type showed significant relationship with distribution and species extent of occurrence. This result may be due to lack of soil type information in our data. Limestone soil type (alfisols) are rich in nutrients but these soils are less common soil type found in Borneo (Potts *et al.*, 2002; Ghazoul, 2016).

Morphological traits, habitats and life history strategies

My results suggest that habitat soil types exhibited significant relationships with tree height and diameter, particularly in clay and sandy soil types, and that there was moderate phylogenetic signal. This suggests evidence of phylogenetic conservatism in these morphological traits with their habitat soil types. Soil plays a significant role in shaping dipterocarp forest communities and plant growth (Paoli, Curran and Zak, 2006). Many tropical species especially dipterocarp grow in highly weathered clay soils which are acidic and have low nutrient content (Chazdon, 2003; Palmiotto *et al.*, 2004; Paoli, Curran and Zak, 2006; Peay *et al.*, 2010). However, the presence of humus content and ectomycorrhizal fungi association in dipterocarp species contributed to tree height and diameter growth by enhancing and retaining the nutrient uptake (Brearley *et al.*, 2003; Ducousso *et al.*, 2004; Baillie *et al.*, 2006; Paoli, Curran and Zak, 2006; Tedersoo *et al.*, 2007). Hence, my results supported that soil types particularly clay play a role in shaping plant growth development.

My data showed that survival was associated with shade tolerance traits, but there was no imprint of phylogeny. Shade tolerant species show high survival, potentially for many years. For instance, a long-term study by Delissio et al (2002) found that between 38 and 61 % of seedlings of four shade-tolerant dipterocarps, (*Cotylebium melanoxylon, Dipterocarpus globosus, Dryobalanops beccarii and Shorea beccariana*) survived over a decade in the understory. However, shade tolerant dipterocarp species unable to capitalize available light in canopy gap as light demanding and intermediate species. My results emphasized that the plant life history strategies traits influence the survival of the species.

Conservation status of dipterocarp

Timber exploitations of high commercial value dipterocarps is major driver of dipterocarp’s population decline in tropical forest. Furthermore, some dipterocarps like *Dipterocarpus lamellatus* and *Shorea blumutensis* occurs in small population size and limited geographic distribution could heavily affected by habitat loss and risk to extinct (Yeong, Reynolds and Hill, 2016). My findings revealed that population trend influenced the conservation status in dipterocarp species. This pattern was related to phylogeny, with the results showing moderate phylogenetic signal. This is supported by various studies that found extinction risk are correlated with phylogeny (Purvis *et al.*, 2005; Sjöström and Gross, 2006; Willis *et al.*, 2008; Fritz and Purvis, 2010b). As highlighted in previous studies, understanding evolutionary history in deciding conservation priorities could maximize conservation of biodiversity (Faith, 1992; Faith, Reid and Hunter, 2004; Redding and Mooers, 2006). In my analysis, habitat destruction (i.e. logging, urbanization and agricultural plantation) and loss of extensive habitat are a major factor that affected the conservation status of dipterocarps. Moreover, due to high value in global timber trade ,dipterocarp timbers with the high wood density that yield high prices faces threats in habitat destruction and timber exploitation (see Chapter 5). A study by Maycock *et al.* (2012) carried out in Sabah showed that how impact of habitat loss affected conservation status in dipterocarp, with projected percentage of habitat loss 21 % for *Shorea micans* to 99.5 % for *Dipterocarpus lamellatus*. 32 of the 33 dipterocarp species analysed in their study would have been classified as ‘Threatened’ under IUCN Red List criteria. My findings highlighted the conservation priorities of dipterocarp in the future in order for sustainable forest.

4.5 Conclusion

In summary, I found substantial evidence of phylogenetic conservatism of plant traits in dipterocarp species, with moderate phylogenetic signal in our results. Our findings showed elevational gradient are involved in shaping dipterocarp species distribution across the range of the group. Morphological traits such as height and diameter show phylogenetically dependent relationship with the habitat soil types. This study highlighted the significance of plant traits analysis and revealed the association plant traits and environmental factors in global. However, taxonomy of dipterocarps remains challenging at some levels. One limitation in this study is there was no complete phylogeny for all 544 dipterocarp species. Notwithstanding, phylogenetic analysis seems to be powerful tool in order to highlight conservation priorities in dipterocarp biodiversity since phylogenies provide an additional measure of biodiversity that complements species richness. Considering evolutionary distinctiveness should play a role in prioritizing species for conservation.

Chapter 5

Dipterocarp timber value: phylogenetic perspectives

Abstract

Dipterocarp timbers are highly valued and important sources for global timber trade in 21st century. Knowledge of plant traits and conservation status and how these influence the economic value particularly timber price value is essential in promoting sustainable timber resources. Here, I compiled a dataset of dipterocarp species plant traits from Dipterocarpaceae family and timber price value. In this study, I found significant relationship between particular plant traits such as genetic traits and wood type with timber price value. Furthermore, wood densities are highly correlated with timber price value. Timber price value do not affect the dipterocarp conservation status. As a conclusion, wood type and wood densities are the plant traits that are highly related to timber price value. High wood density and durable wood seems to have large impact on timber price value with high price. Timber price value do not driven by how rare the dipterocarp species is.

5.1 Introduction

South East Asian tropical forests are rich in natural resources with high commercial value, such as timber and non-timber forest products (NTFPs) (Barreto *et al.*, 1998; De Beer and McDermott, 2002; Pariona, Fredericksen and Licona, 2003; Ghazoul, 2016). This region produces large of tropical hardwood resources such as global timber, veneer and plywood for a range wood industries (Berry *et al.*, 2010). Countries including Malaysia, Indonesia and Thailand have dominated the global tropical timber trade by up to 80 percent (Peluso, Vandergeest and Potter, 1995). The Dipterocarpaceae is one of the plant families that provide good timber, plywood and NTFPs such as resin, dammar, balsam and essential oils (P S Ashton, 1988; Ghazoul, 2016). Dipterocarp timber species from are widely distributed in Asian tropical dipterocarp forests, and have been of major importance in global timber trade in the 20th and 21st centuries (Ashton, Givnish and Appanah, 1988b; Appanah and Turnbull, 1998; Chaudhary *et al.*, 2016; Sasaki *et al.*, 2016; Roopsind *et al.*, 2018).

Malaysia and Indonesia are two South East Asian countries generating the most dipterocarp timber, especially from Borneo which possesses the highest diversity and abundance of dipterocarps (Maycock *et al.*, 2012). The timber economy has historically contributed a major source of income in these countries. For instance, Indonesian timber exports generated about USD 6 billion through annual export revenue, of which 60% came from Kalimantan, Borneo; in Malaysia, timber and wood products contributed about USD 6.8 billion of national income in 2010 (Ghazoul 2016; PEMANDU 2010). In Thailand, about USD 805 million of national income comes from timber and wood products (USDA 2013).

Increasing demands on timber supply have caused large areas of lowland dipterocarp forest to be extensively logged in recent decades, leading to concerns about conservation status (Sohngen, Mendelsohn and Sedjo, 1999; Fisher, David P. Edwards, *et al.*, 2011). A wide range of forest management practices have been carried out in Asian dipterocarp forests in order to promote sustainable timber and forest resources. Reduced Impact Logging (RIL), selective logging, and selective management systems (e.g. involving shorter cutting cycles of 30 years, and lower diameter limits) have been introduced for forest management in Asian tropical forest to assist in managing dipterocarp forests following timber harvesting (Thang 1987, FAO 2010). Timber harvesting can impact soil nutrient status and increase soil compaction, hence reducing the survival rates of the remaining trees (Palmer, 2001; Magrach *et al.*, 2016).

Logging and conversion to other land uses seems to have on dipterocarp genetic diversity in tropical forest(Lee *et al.*, 2000; Tange *et al.*, 2000). A study by Palmer et al. (1998) highlighted the importance of timber tree genetics in shaping global timber price value. By assessing the relationship between genetic traits and timber value, it will provide useful information for forest managers to sustain high quality timber resources. Dipterocarp plant traits that relate to survival, growth rate and shade tolerance are particularly important in producing high timber qualities and enhanced financial values (Slik, 2006; Nock *et al.*, 2009). For instance, shade tolerance traits and slow growth are usually associated with high survival in closed forest(King *et al.*, 2005, 2006), but shade tolerant dipterocarp species cannot survive in high light conditions in large canopy gaps following intensive logging (Okuda et al. 2003; Nussbaum et al 1995). Shade tolerance trees tend to produce high wood density compared to light demanding trees (King *et al.*, 2005; Nock *et al.*, 2009). Because wood density and timber value are positively correlated, several studies have found that wood density is associated with plant functional traits, particularly shade tolerance traits and a vital factor in determining wood properties or wood type as well as timber value (Brown, 1949; Chave *et al.*, 2009; Nock *et al.*, 2009). This highlight the needs to assess relationships between wood density, life history traits and timber value. An improved understanding of plant traits is essential in sustainable timber resources and global timber value.

Exploitation of South East Asian tropical forest mainly results from the high demand for dipteropcarps in the timber market, and its high commercial value (Fisher et al. 2011; Hawthorne et al. 2011). High rates of exploitation would be likely to affect dipterocarp conservation status, especially because most dipterocarp species occur in South East Asian tropical forest (Ashton 1988; Appanah & Turnbull 1998). For instance, conservation assessment using the projection method suggested that 32 of 33 dipterocarps would be categorised as 'Threatened' according IUCN Red List status (Maycock et al (2012)). Analyses of the relationship between conservation status and timber price value could reveal how exploitation driven by high timber value might affect conservation status.

Phylogeny has provided many fundamental insights in biological studies (Gamage *et al.*, 2006; Sjöström and Gross, 2006; Qian and Zhang, 2014). Phylogeny has been used widely in helping to answer questions in ecology and evolutionary, patterns in community, and environmental variability in studies across multiple species (Felsenstein, 1985b; Ackerly, 2004; Wiens *et al.*, 2010;

Cooper, Freckleton and Jetz, 2011; H. Liu *et al.*, 2012). However, to my knowledge there is no phylogenetic comparative analysis between species traits vary with economic value. Addition of phylogenetic information could provide a vital way to assess how traits variance influence timber price value as well as promoting sustainable high-quality timber. For instance, closely related species that share similar traits might also tend to have similar timber price value (Chiew Thang, 1987; Tnah *et al.*, 2012). Including phylogeny together with trait data and prices should allow us to build a complete picture of the biotic factors driving timber values.

In this study, I used a phylogeny of the Dipterocarpaceae to assess the relationship between plant traits and timber values for dipterocarp species. My specific objectives were: (1) test whether variation in plant life traits influences dipterocarp timber market value; (2) assess the relationship between dipterocarp timber value and wood density; (3) analyse correlations between timber value and morphological and life history strategies traits; (4) test whether there are impacts of timber price on conservation status.

5.2 Materials and methods

Study group and phylogenetic tree

In this study, I used data from the Dipterocarpaceae. This family of large trees primarily occurs in tropical lowland rainforests, and comprises 17 genera with 695 known species (Maarten J.M. Christenhusz and Byng, 2016). As noted above, Dipterocarp timber trade is the one of the major economic contributors to South East Asian countries (Sohngen, Mendelsohn and Sedjo, 1999). I used a phylogenetic tree for the Dipterocarpaceae family that I built in Chapter 4 (see Chapter 4 for details).

Plant traits and Timber price values

I compiled plant trait data for 544 dipterocarp species from a range of resources. These included: (i) a literature search in Google Scholar with search terms 'Dipterocarpaceae' yielding 13 400 results; (ii) key monographs by Symington (1974) and Ghazoul (2016); and (iii) internet plant databases (IUCN Red List, PlantUse.net) (see details in Chapter 4). For timber price value, I collected data from International Tropical Timber Organization(ITTO) website (https://www.itto.int), and Malaysian Timber Industry Board (MTIB) timber price database (June 2018: http://www.mtib.gov.my). In this study, I used logs and sawn timber price value (i.e GMS, Scantlings and Strips) to assess the relationship with wood density. According to ITTO and MTIB, timber logs is the unprocessed raw timber tree trunk without branches with minimum diameter of 15.24 centimetres and minimum length of 1.2 metres. General Market Specification (GMS) sawn timber is wood product made from logs that have been sawed or second sawing with minimum two side of surfaced logs had been sawed according general timber market specification. Scantlings is wood product from logs that have been sawed with specific size; width (1 - 4 inches) x length (1.5 – 6 feet or up). Lastly, strips is the sawn timber with smaller size specification (i. e. 1 x 1 inch). In this study , I used United States Dollar (USD) as unit of currency throughout.

Phylogenetic analysis

I used Pagel's λ to test for phylogenetic dependence based on a Brownian model of trait variation (Pagel 1999; Freckleton et al. (2002)). This parameter varies between zero and one: λ= 0 suggests that there is no phylogenetic dependence, and λ=1 suggests that perfect phylogenetic dependence, as predicted by a Brownian model.

The λ statistic was used to control for phylogenetic non-independence in the residuals of linear models (e.g. following Freckleton et al. 2002). I used these models for testing relationships between plant traits, wood density and conservation status with timber value, and for building models for association between morphological traits and wood density. I estimated λ values in models of each trait correlated with timber price by using the pgls function from the R package caper (Orme et al. 2013).

To achieve my first objectives, linear models were fitted by using species' timber values as the response variable, whilst species' elevation, distribution, habitat soil type morphological traits, genetic traits, seed traits and wood type were entered as predictors. To address the second objective, I used wood density as the predictor variable, and timber and sawn timber price values as response variables in the models. For the third objective, I constructed linear models to test relationship between morphological and life history strategies traits as predictors with wood density as response variable. In order to test how timber price value might affected conservation status, I fitted linear models with conservation status using IUCN Red List classifications, population trend, habitat destruction, and% habitat decline as responses, whilst timber value was entered as the predictor variable. Linear models were fitted using the pgls function in the R package (Orme et al. 2013).

5.3 Results

Plant traits on global timber price value

I found no significant relationship between elevation, geographic distribution, habitat soil type, height or DBH with global timber price value (Table 1). The growth rate of dipterocarp species showed a weak significant association with timber price value, with no phylogenetic dependence (P ns for λ= 0; Table 1). Dipterocarp flowering frequency revealed weak significant association with timber price value with strong phylogenetic dependence (λ= 0.839, P< 0.001 for λ =0; Table 1).

In terms of genetic traits in dipterocarp species, there were significant associations between all chromosome number and timber price value, with strong phylogenetic dependence (λ= 0.833, all P< 0.001 for λ =0; Table 1). Polyploidy also showed statistically significant relationship with timber price (λ= 0.887, P< 0.001 for λ =0; Table 1).

Of the seed traits, seed weight showed a weak significant relationship with timber price, and strong phylogenetic dependence (λ= 0.982, P< 0.001 for λ =0; Table 1). From seed's functional wing traits, wingless seed showed strong significant association with timber price, and strong phylogenetic dependence (λ= 0.892, P< 0.001 for λ =0; Table 1). Wood type showed strong significant relationship with timber price, strong phylogenetic dependence ($\lambda = 0.932$, $P < 0.001$ for $\lambda = 0$; Table 1; Fig. 1).

Table 1: Model coefficient, F and λ values for phylogenetic linear model testing the relationship between timber price value and plant traits

Traits	n	Model coefficient (Estimate ± SE)	F^P value	λ	P $_{(λ= 0)}$	P $_{(λ = 1)}$
(a) Timber (logs/ton)						
Elevation						
Lower elevation limit (m)	320	0.02 ± 0.04	0.151^{ns}	0.852	***	***
Upper elevation limit (m)	320	1.12e-03 ± 2.04e-02	0.003^{ns}	0.852	***	***
Geographic distribution						
Widespread/Endemic	226	-19.63 ± 13.22	2.206^{ns}	0.857	***	***
Estimated Extent of Occurrence	93	-8.34e-06 ± 7.23e06	1.333^{ns}	0.778	***	***
Habitat Soil type						
Soil type (Clay)	173	-23.88 ± 14.06	2.883^{ns}	0.880	***	***
Soil type (Sandy)	173	7.73 ± 13.70	0.318^{ns}	0.875	***	***
Soil type (Loam)	173	-36.26 ± 37.04	0.959^{ns}	0.871	***	***
Soil type (Limestone)	173	-28.58 ± 33.67	0.720^{ns}	0.873	***	***
Morphological traits						
Height	194	0.48 ± 0.68	0.505^{ns}	0.827	***	***
Diameter at breast height	195	0.04 ± 0.16	0.070^{ns}	0.830	***	***
Growth rate	16	-51.38 ± 22.48	5.226*	0.000	ns	*
Shade tolerance	101	-12.49 ± 10.59	1.391^{ns}	0.878	***	***
Leaf length (cm)	204	-1.24 ± 1.21	1.049^{ns}	0.842	***	***
Flowering event						
Flowering frequency	227	-59.42 ± 23.84	6.212*	0.839	***	***

Genetic traits						
Chromosome no. (x=7)	227	127.38 ± 32.15	15.702***	0.833	***	***
Chromosome no.(x=10)	227	-152.99 ± 36.94	17.152***	0.833	***	***
Chromosome no.(x=11)	227	-127.38 ± 32.15	15.702***	0.833	***	***
Polyploidy	227	-180.78 ± 40.61	19.814***	0.887	***	***
Seed traits						
Seed weight (seed per kilo)	39	0.02 ± 0.01	5.424*	0.982	***	**
Wingless seed	227	703.67 ± 68.40	105.830***	0.892	***	***
Functional wing=2	227	-25.32 ± 48.34	0.274^{ns}	0.854	***	***
Functional wing= 5	227	-74.18 ± 31.95	5.392*	0.868	***	***
Functional wing length	69	-0.35 ± 0.65	0.287^{ns}	0.973	***	***
Timber type						
Wood type	227	117.92 ± 9.43	156.330***	0.932	***	***

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

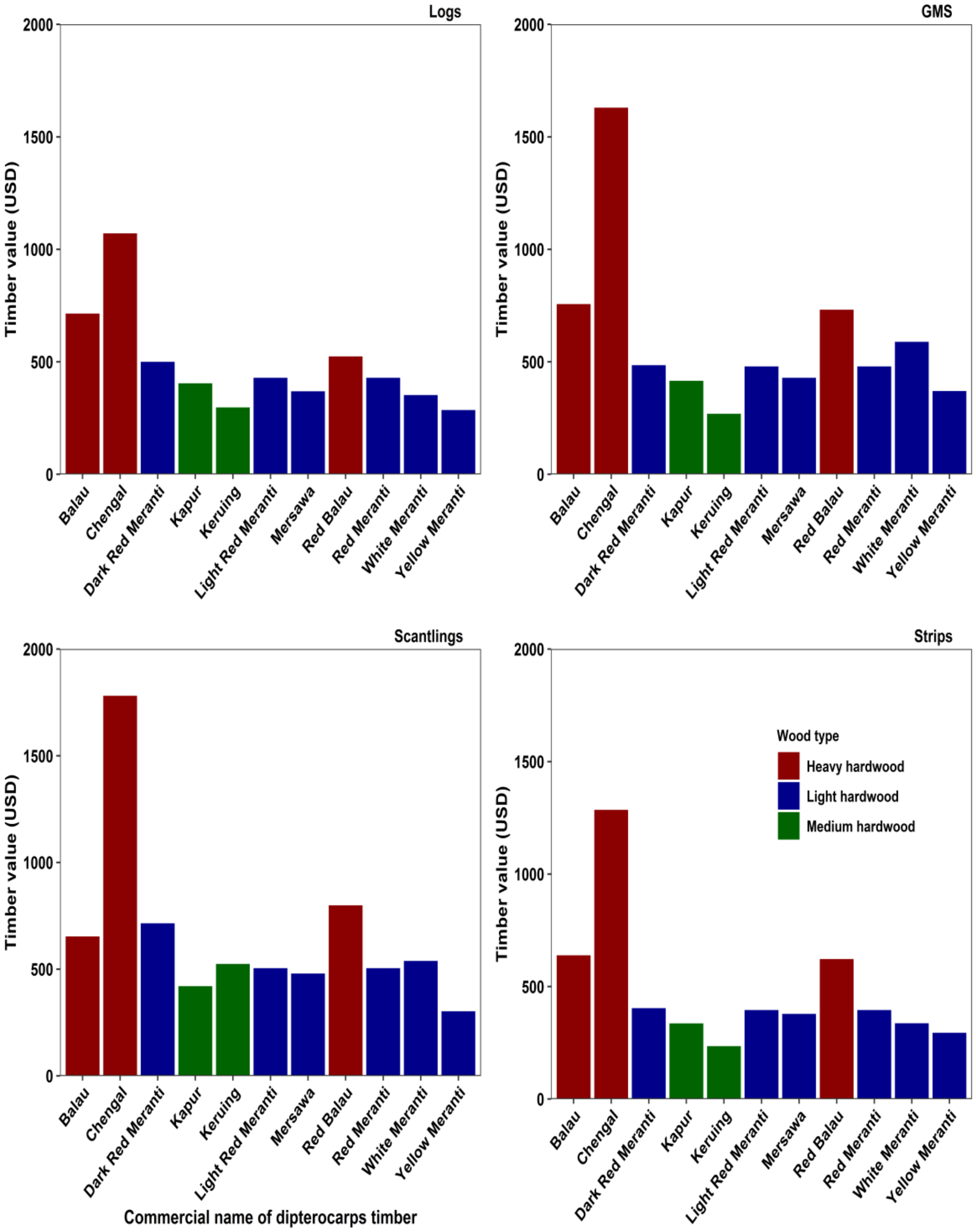


Figure 1: Timber price value for dipterocarp commercial names (Heavy hardwood= Chengal, Balau and Red Balau; Medium hardwood= Keruing, and Kapur; Light Hardwood= Dark Red Meranti,Light Red Meranti Red Meranti, Yellow Meranti and White Meranti)

Wood density and timber price value

Wood density showed a statistically significant association with timber price for GMS, and strong phylogenetic dependence (λ= 0.973, P< 0.001 for λ =0; Table 2; Fig 2a). Timber logs, strips and scantlings sawn timber, showed significantly related to wood density, and phylogenetic dependence with λ value ranging from 0.810 to 0.943 (all P< 0.001 for λ =0; Table 2, Fig. 2 b, c, d).

Table 2: Model coefficient, F and λ values for phylogenetic linear model testing the relationship of timber price value and wood densities (values are log-transformed)

	n	Model coefficient (Estimate ± SE)	F^P value	λ	P(λ=0)	P(λ=1)
(a) Timber (logs/ton)						
Wood density	136	0.630 ± 0.11	32.778***	0.900	***	***
(b) GMS (sawn timber/m^3)						
Wood density	136	0.536 ± 0.10	31.421***	0.973	***	***
(c) Strips (sawn timber/m^3)						
Wood density	136	0.667 ± 0.11	36.222***	0.943	***	***
(d) Scantlings (sawn timber/m^3)						
Wood density	136	0.465 ± 0.12	15.744***	0.810	**	***

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

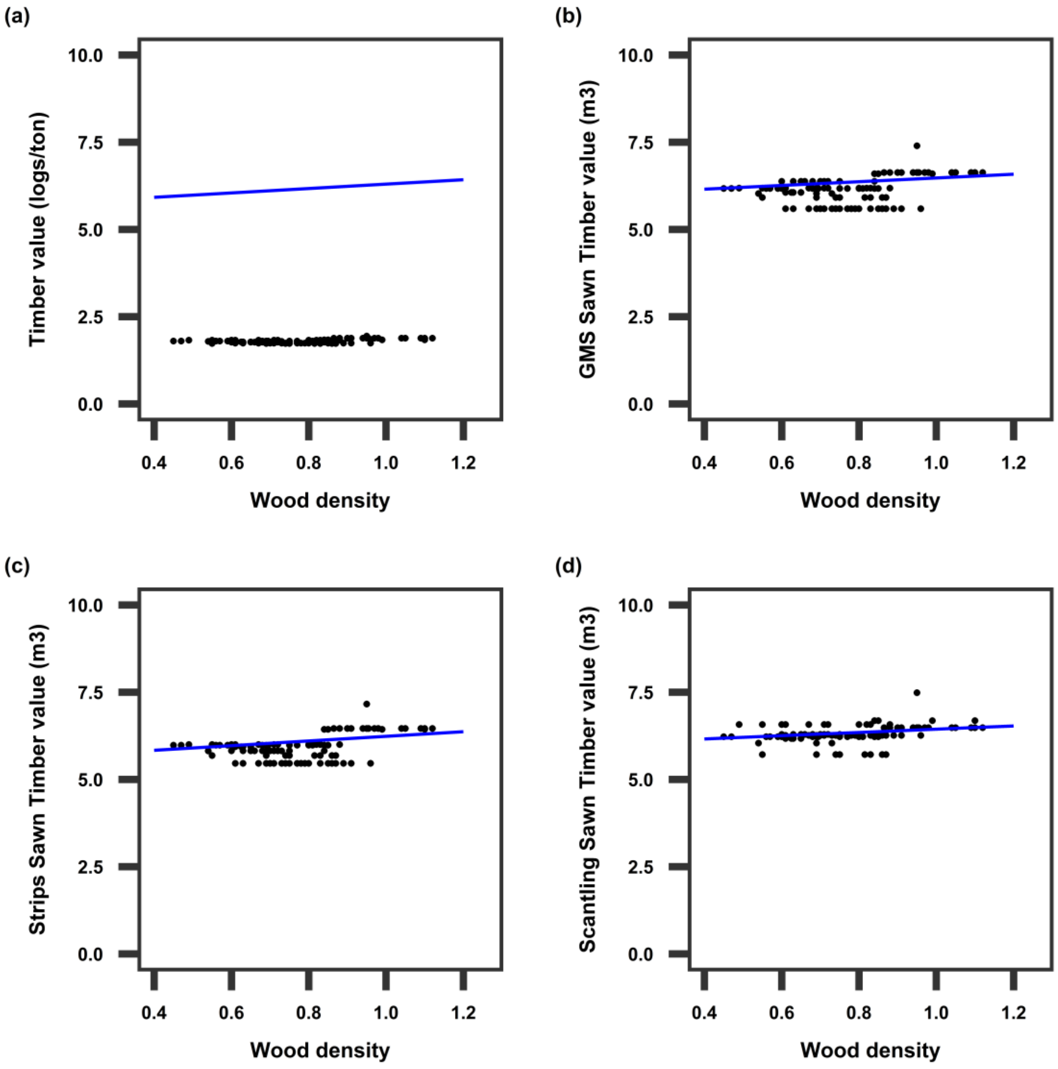


Figure 2: Timber price value for timber logs and sawn timbers based on their wood densities

Relationship between wood density and morphological & life history traits

I found no significant relationship between wood densities with height, diameter, growth rate and survival. However, there were phylogenetic dependence observed in the height and diameter models with λ value 0.419 and 0.451 respectively (all $P< 0.001$ for $λ =0$; Table 3). Shade tolerance traits was significantly associated with wood density, with moderate phylogenetic dependence ($λ= 0.574$, $P< 0.001$ for $λ =0$; Table 3). Strong association was observed in phylogenetic model between wood density and wood type, but with weak phylogenetic dependence (λ= 0.412, P< 0.001 for λ =0; Table 3).

Table 3: Model coefficient, F and λ values for phylogenetic linear models of wood density on morphological traits and life history traits

	n	Model coefficient (Estimate ± SE)	F^P value	λ	P(λ=0)	P(λ=1)
(a) Wood density						
Height	221	-0.0010 ± 0.0007	3.852^{ns}	0.419	***	***
Diameter at breast height	224	-0.0003 ± 0.0001	3.126^{ns}	0.451	***	***
Growth rate	23	-0.0014 ± 0.0026	0.278^{ns}	0.000	ns	***
Survival	40	-0.0039 ± 0.0021	3.324^{ns}	0.000	ns	***
Shade tolerance	124	-0.0590 ± 0.0205	8.087**	0.574	***	***
Wood type	236	0.0970 ± 0.0120	70.390***	0.412	**	***

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

Timber price and conservation status

I found no significant associations between timber price and conservation status of dipterocarp plant species as well as population trend, habitat destruction and percentage of habitat decline. Nevertheless, phylogenetic dependence was observed in all models with λ value ranging from 0.854 to 0.867 (all P< 0.001 for λ =0; Table 4; Fig 3).

Table 4: Model coefficient, F and λ values for phylogenetic linear models of timber price value on conservation status

	n	Model coefficient (Estimate ± SE)	F^P value	λ	P(λ=0)	P(λ=1)
a) Timber (logs/ton)						
Red List status	169	-1.313 ± 7.996	0.027^{ns}	0.867	***	***
Population trend	227	2.908 ± 16.421	0.031^{ns}	0.854	***	***
Habitat destruction	227	-2.023 ± 14.968	0.018^{ns}	0.854	***	***
Percentage of habitat decline	227	5.318 ± 5.380	0.977^{ns}	0.856	***	***

* P < 0.05; ** P < 0.01; *** P < 0.001; ns not significant

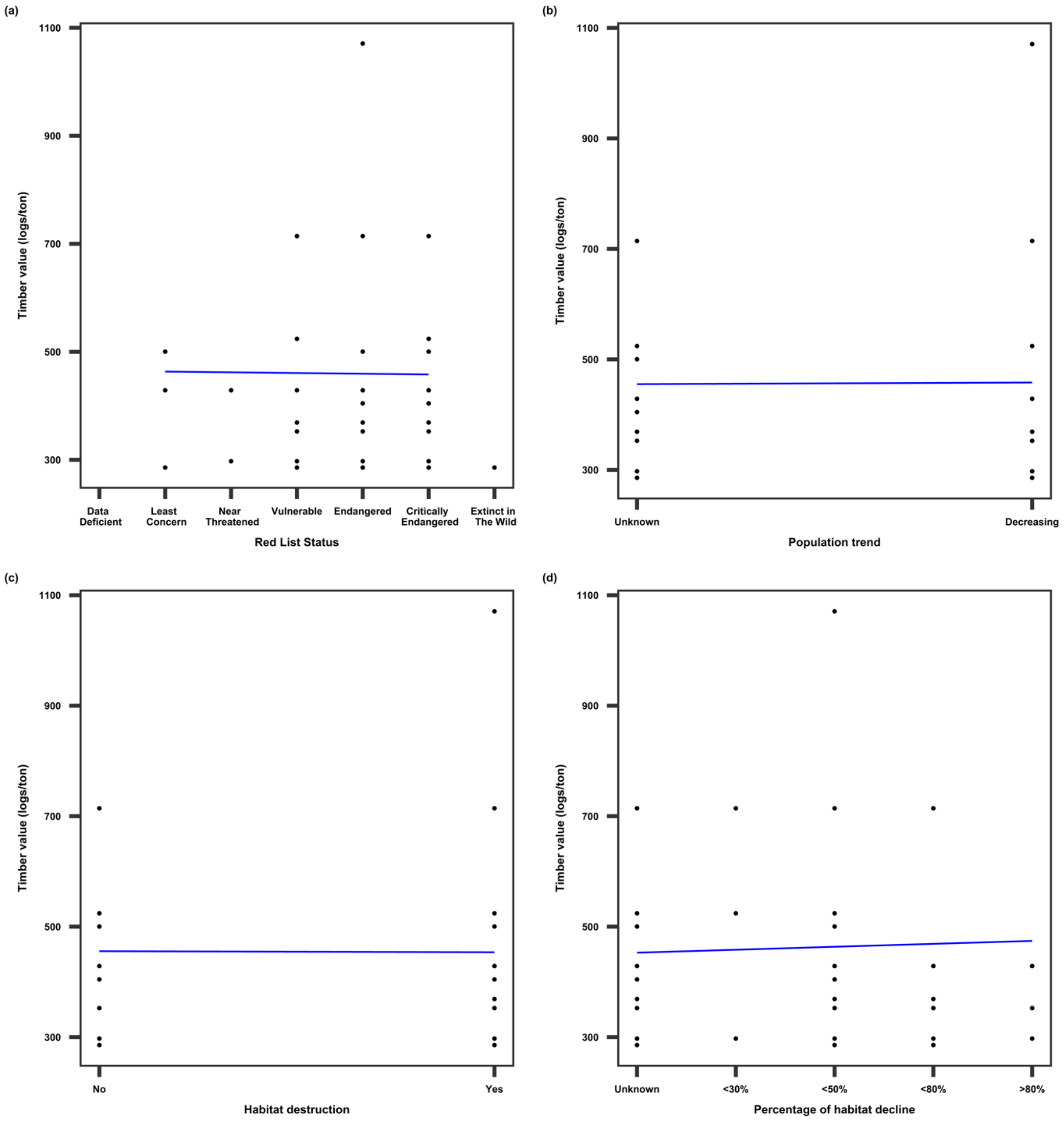


Figure 6: Timber value for logs/ton association with a) IUCN Red List status; b) Population trend; c) Habitat destruction; d) Percentage of habitat decline

5.4 Discussion

Overall, I found significant relationship between particular plant traits such as genetic traits and wood type with timber price value. Wood densities are highly correlated with timber price value. Surprisingly, I do not find any evidence that timber price value would affect the conservation status. Thus, my findings suggesting that biotic factors could act as vital component in driving timber price value.

Plant traits and global timber price value

I found no relationship between environmental variable such as elevational gradient, geographic distribution and habitat soil types with timber price value. This suggests that dipterocarp species environmental adaptation do not affect timber price value..

Flower size traits showed significant relationship with timber price value for dipterocarp species. This result could be due to flower characteristics that exhibited from high value dipterocarp species. For example, small-flowered species such as *Neobalanocarpus* hemii (Chengal) has the highest timber price value in Malaysia timber market (Tnah *et al.*, 2012). I found weak evidence of a correlation of flowering frequency with timber price. Dipterocarps species like *Shorea* spp. are usually involved in general flowering events but there are many species in Sumatra and Borneo from *Dipterocarpus* (Keruing) and *Dryobalanops* (Kapur), including *Neobalanocarpus hemii* in Peninsular Malaysia that flower annually or biennial (Krisnapillay and Tompsett 1998). In terms of seed traits, I detected low evidence on seed mass and five functional wing dipterocarp species effects on timber price value, whilst wingless seed showed stronger associations with timber price. This might be because wingless species tend to have high timber price value in Asian dipterocarp timber-based classification system by foresters.

I found little evidence of dipterocarp growth rates traits with timber price value. Fast growing dipterocarp species (i.e. *Parashorea* spp., *Anisoptera* spp. and some *Shorea* spp.) usually been logged frequently due to increasing demand in timber market(Yeong, Reynolds and Hill, 2016). Unfortunately, I do not have sufficient power in my analysis to make strong conclusions about the influence of growth rates on timber price because I have growth rate data on only 16 of 228 species with timber price value. Although, morphological traits such as height and diameter, survival, shade tolerance traits are major factors in influencing plant growth for the next cutting cycle for logging (Ådjers et al. 1995; Kuusipalo et al. 1996), in my analysis I found no evidence on morphological traits (i.e. Height, diameter), survival and shade tolerance traits on timber price value.

Based on my findings, the general lack of obvious correlations between plant’s traits particularly in seed and morphological traits with timber value probably reflects the generalised nature of the uses for which dipterocarp timber is used: there are usually many species within similar characteristics and typically the precise identity of a species’ timber is not important. This contrasts with many high value timber species (e.g. Mahogany, Rosewood, Teak), which have species-specific characteristics and uses. This is also evident in species’ timber values: notably in Figure 2, many species have similar values, with the overall range being rather narrow.

Wood densities impact on timber price value

In my study, I found significant relationship between wood density for timber logs and sawn timbers with timber price value with strong phylogenetic dependence. This result linked to the fact that higher wood density has higher timber price value. For example, Chengal (Neobalanocarpus) and Shorea subsection like Balau (Shorea) and Red Balau (Rubroshorea) have wood density range from 800 to 1160 kg/m^3 that been classified as heavy hardwood by foresters with high timber values in the market (Lopez 1981; Lopez 1983). *Neobalanocarpus hemii* is heavy hardwood species that occurs in Peninsular Malaysia, it is highly valued (see Fig. 2) and well-known timber where Malaysia is the only exporter of *Neobalanocarpus hemii* sawn timbers (Lopez 1983).

In a heavy hardwood timber report in Malaysia on PROSEA database, export of sawn Neobalanocarpus timbers was 8000m^{3,} with value about USD 2.1 million, meanwhile the export of Balau logs was 90 000 m^3 and its sawn timber 292 000 m^3, with a total value of USD 93 million, and the export of Red Balau logs was 12 500 m^3 and of sawn timber 750 m^3, value of US$ 1.5 million. Most of Asian dipterocarps are being classified by forester based on their wood density, wood type and commercial value and exclude species with little or no commercial value (Symington 1941, Ashton 1985). Furthermore, from engineering perspectives strong and durable wood exhibited high price of timber value .Wood density is correlated to the mechanical properties of wood in that as density increases, the strength of wood increases (Blakenhorn 2001). My findings highlighted that wood density are an indicator in determining timber price value.

Wood density on morphological traits and life history strategies traits

King et al. (2005) revealed that tree growth is expected to be associated with wood density since volume of wood produced with given unit of biomass is inversely proportional to its density. However, I found no evidence when modelling wood density with morphological traits such as height, DBH, survival and growth rate. This might be due to lack of growth rate data in our analysis.

Verburg et al. (2003) noted that wood density can provide vital information of life histories strategies traits of tree species. Recent studies have shown that there is relationship between wood density and the successional stage a species occupies (Chen *et al.*, 2017; Charles *et al.*, 2018). In my study, I found significant evidence on shade tolerance traits with wood density. My finding supported the suggestion that light demanding species has low wood density because it promotes rapid height development in high light condition by producing low density of wood (King *et al.*, 2006). Meanwhile, several studies found that shade-tolerant tree species tend to grow slowly and invest in dense, strong and damage-resistant wood that in turn lowers their mortality rates (Putz et al., 1983; Muller-Landau, 2004; van Gelder et al., 2006).

Timber value, conservation status and population trends

In terms of conservation status, I found no evidence on conservation status, population trend and habitat destruction of timber price value. This may be due timber price value are highly depending on wood type and density, but these are not species-specific. Thus, common species will suffice equally as well as rare ones if the timber characteristics fit the desire usage. Deforestation such as intensive logging, conversion to other land uses and agricultural expansion (oil palm and rubber plantations) are more likely to affect the conservation status of dipterocarps but not the value of timbers (Palmer, 2001; Jomo, Chang and Khoo, 2004; Forrest *et al.*, 2015; Ghazoul, 2016).

5.5 Conclusion

My study found that plant traits such as wood density and wood type are associated with timber price value. Overall, based on my findings I conclude that timber price values are mostly being driven by wood density and wood type. High wood density and durable wood seems to have large impact on timber price value with high price. Logging practices like Reduced Impact Logging (RIL) are known to be effective in reducing logging impacts and can preserve the timber hardwood species qualities for the next cutting cycle. Proper management planning is required in order to promote sustainable high-quality timber resources in the future.

Chapter 6

General discussion

6.1 General discussion

The experimental work presented in this thesis provides support that Janzen Connell hypothesis is a possibly a mechanism that maintains tropical forest diversity. Results from Chapter 2 and 3 suggest that distance and density dependence could be the potential explanation for species maintenance more widely, however the effects varies among species. Chapter 4 highlights how environmental adaptation affects species distribution and stresses the need for conservation priorities for dipterocarp species. In Chapter 5,the results suggest that wood densities are highly related to timber price value and do not affect dipterocarp conservation status. This suggests that timber price value does not drive species rarity.

6.2 Density and distance dependence

Mechanisms identified to date that promote biodiversity can be categorized in two major ways that are not necessarily exclusive. Although equalizing forces reduce fitness differences among species, stabilizing forces increase mortality with increasing population densities within a single species (Chesson 2000). The Janzen-Connell (JC) hypothesis (Janzen 1970, Connell 1971) refers to such stabilizing forces and states that seed and juvenile (i.e., seedling and sapling) survival rates decrease with increasing effects of accumulating host species–specific antagonists at lower distance to or at higher density of conspecific plants. As a consequence, dominant species are prevented from outcompeting less-dominant ones, thus promoting juvenile plant diversity (Terborgh 2012, Bever et al. 2015). The Janzen-Connell hypothesis is the widely known hypothesis for explaining species diversity maintenance, through distance and density dependence (Janzen 1970; Connell 1971). In Chapter 3, I used a meta-analysis approach and found significant support on Janzen-Connell mechanisms, revealing that most studied plant species undergo density and distance dependent effects in tropical systems, with even evidence found in temperate forest. This finding also suggest that Janzen Connells effects have been underestimated as drivers of plant diversity in temperate ecosystems. For instance, Peterman (2008) found that Janzen Connell effects are strong and widespread to maintain the diversity at the study site. Moreover, results in Chapter 3 supported by a large number of studies that have been undertaken, show significant support that density and distance dependent effects in mortality of seed/seedlings (Packer and Clay, 2000; Bell, Freckleton and Lewis, 2006; Norghauer *et al.*, 2006; Mangan *et al.*, 2010; Swamy and Terborgh, 2010) and previous meta-analysis(Comita *et al.*, 2014).

In Chapter 2, I used two native dipterocarp species and the experimental results revealed that different dipterocarp species exhibited different distance and density dependent effects in seedling stage with only distance dependence observed in *P. malaanonan* seedlings and no density dependence observed in those two species. Several studies showed that positive density dependent effects were observed in dipterocarp seeds(Sun *et al.*, 2007; Takeuchi and Nakashizuka, 2007b; Tokumoto *et al.*, 2009),whilst negative density dependent effects were observed on seedlings (Bagchi *et al.*, 2011; Oshima, Tokumoto and Nakagawa, 2015). Packer and Clay (2000) found seedling survival of *Prunus serotina* to display more distance than density dependence. These findings have been confirmed by Li et al. (2009) on seedlings of *Ormosia semicastrata* and by Xu et al. (2015) on seedlings of *Engelhardia fenzelii*. Moreover, predator satiation is more likely to cause positive density dependence in dipterocarp seed especially during mast year(Curran and Webb, 2000). Different in species-specific response to distance and density dependent effects make it difficult to draw inference.

My findings in Chapter 2 and Chapter 3 support the idea of Janzen Connell effects contributes to species diversity maintenance in tropical forests and possibly one of the mechanisms that explaining tropical forest diversity. Various studies did supported that Janzen Connell effects plays vital role in species coexistence in distance and density dependent manner(Silva Matos, Freckleton and Watkinson, 1999; Massey *et al.*, 2006; Swamy and Terborgh, 2010; Terborgh, 2012; Comita *et al.*, 2014). However, there are a few things need to take account in future work when addressing the role of Janzen Connell effects for species diversity maintenance. For instance , in the forest understory, tree seedlings are not only subjected to Janzen-Connell effects but may also compete for resources, which makes a causal interpretation of density-dependent Janzen-Connell effects even more difficult (Terborgh 2012). In addition, in a recent study LaManna et al. (2017) proposed that the strength of conspecific negative density-dependence increases from temperate to tropical forests as a result of more intense biotic interactions, Comita (2017) pointed out the possibility that stronger effects of abiotic factors at temperate latitudes might mask existing negative density dependence derived by biotic interactions (herbivory and competition).

Moreover, observational studies of density dependence typically include a much larger proportion of species in the community and may better reflect the strength of distance- and density dependent mortality at a site since the multispecies approaches should be more likely to reflect general trends than single species approaches.. A meta-analysis of community level observational studies would help shed light on the variation in density and distance dependence among regions, including any relationship with latitude. Furthermore, future experiments should consider early life history stage such seed stage, seed-seedling transition and early seedling stage to examine to what extent Janzen Connells effect in promoting and maintaining the diversity in tropical forests through life history stages.

6.4 Maintenance and conservation of dipterocarp

Southeast Asian tropical forest are dominated by dipterocarp species and occupied the most forest canopies(Maycock *et al.*, 2012). High commercial value of dipterocarps and their high density are the major reasons for exploitation of Southeast Asian tropical forests (Ghazoul, 2016). Sustainable forest management (SFM) has been developed to ensure the forest is managed to benefit in ecological, economic and socio-cultural terms (Prabhu, R., Colfer, C.J.P. & Dudley 1999). One of criteria and indicators in SFM is maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystem being highlighted in this thesis particularly in dipterocarp forest. Understanding mechanism that maintains tropical tree diversity can ensuring its high dipterocarp species richness and sustainable forest resources as highlighted in Chapter 2 and Chapter 3.

Evolution and diversity are the result from the interactions between plants and their environments and the consequences of these interactions over long periods of time. Plants continually adapt to their environments, and the diversity of environments that exists promotes plant diversity adapted to them. Thus, the role of evolution or of traits in shaping distributions or diversity within tropical forests should be explore for better understanding. Species adapt to contrasting environments through the evolution of functional traits, and variation in these with environmental conditions is a fundamental feature of biological diversity (Ackerly, 2004). Pavoine et al. (2011) highlighted the need to assess the relationship between evolutionary processes, species traits variances and species interaction with the environment in order to fully understand the factors that drive variation in traits across different environments. Phylogenetic analysis is powerful tools in order to assess the evolution of traits in shaping diversity in tropical forests.

By using phylogenetic analysis for dipterocarp species in Chapter 4, the results showed that elevational gradients shape dipterocarp species distributions across forests with most species occuring below 1000 metres. High dipterocarp species richness has been observed at elevations up to 300 metres (Ashton, 1982, 2012; Ghazoul, 2016). The Dipterocarpaceae achieve their greatest species richness and canopy dominance in lowland forest and aseasonal wet climates (Appanah and Turnbull, 1998). Exploitation of lowland dipterocarp forest for timber and conversion into other land uses cause conservation status of dipterocarp to deteriorate at an alarming rate, with most dipterocarp genera currently assigned Critically Endangered status (IUCN 2018)(see Chapter 4). Extensive illegal logging being driven by demands in timber economies has greatly impacted tropical forests even in protected areas(Palmer, 2001; Singh, 2014; Maryudi, 2016). A study by de Kok et al. (2015) found that invasive species such as bamboo easily establish in the post-logging area especially under canopy, and this has negative impacts on dipterocarp seedling regeneration in logged forest.

Analysis of plant traits that I used in this thesis offers a window to assess the diversity of dipterocarp plant communities globally , as well as how environmental factors will impact on dipterocarp species, and hence on highlighting the needs of conservation in dipterocarp species. In Chapter 4, my findings highlighted that habitat destruction and population trend are highly associated with conservation status of dipterocarp species. Thus, indicating that many species are at risk due to high rates of deforestation and exploitation of dipterocarp forest. There are many practices have been carried out for dipterocarp forest management such as liberation thinning, shelterwood system, enrichment planting, selective logging and Reduce Impact logging (RIL). Enrichment planting has been a tool in dipterocarp forest management, and several dipterocarp species have been successfully planted into natural forests (Appanah and Weinland 1993, 1996). Forest managers and policy maker should implement the ecological knowledge in managements and forest conservation practices for better results in order for sustainable forest resources without minimal or no damage to the forest .

With domination of Southeast Asian countries by tropical timber trade and increases in demand for products such as palm oil, dipterocarp forest have been extensively logged and converted to other land uses such as agroforestry, oil palm, rubber plantation (Hansen *et al.*, 2013; Achard *et al.*, 2014; Gaveau *et al.*, 2014; Carlson *et al.*, 2017). Increasing in timber price value and growing demand of wood supply could affect dipterocarp conservation status (Sohngen, Mendelsohn and Sedjo, 1999; Werner, 1999). However, I do not found significant evidence of timber price value on conservation status in Chapter 5. This suggests that timber price value is not driven by species rarity, but is more strongly related to wood density (Slik, 2006; Chave *et al.*, 2009).Wood density is thought to be the most important factor determining the timber price value of dipterocarps in the global market (Rana *et al.*, 2009), and species identity seems to be less important.

6.4 Conclusion

The results from this thesis suggest that Janzen Connell hypothesis could be the possible explanation of species diversity maintenance based on the meta-analysis (Chapter 3), even with different species-specific density and distance dependent effects observed in the experimental chapter on dipterocarp species (Chapter 2). In his review, Carson et al. (2008) pointed out Janzen Connell mechanism could contribute to diversity maintenance in plant communities, even only some of species within plant communities impacted by density- distance dependence, particularly the competitively dominant species by preventing competitive exclusion. Future studies should focus on natural enemies and host-specificity since these are the key components of Janzen-Connell mechanism, whereby specialist natural enemies are more likely to drive density/distance dependent effects compared to generalist. Studying through the seed stage, seed- to seedling transition should be carried out to determine to what degree Janzen Connell effects affect survival at all stages. This thesis also provide evidence of the factors determining the distribution and conservation status of high commercial value dipterocarp species from environmental, ecological and conservation perspectives (Chapter 4 and Chapter 5). With better understanding of factors threatening high valued dipterocarp species in terms of ecology and plant traits, forest manager and policy makers will be better informed for future sustainable management practices.

Literature cited

Achard, F. *et al.* (2014) ‘Determination of tropical deforestation rates and related carbon losses from 1990 to 2010’, *Global Change Biology*, 20(8), pp. 2540–2554. doi: 10.1111/gcb.12605.

Achard, F. *et al.* (no date) ‘Determination of deforestation rates of the world’s humid tropical forests’, *science.sciencemag.org*. Available at: http://science.sciencemag.org/content/297/5583/999.short (Accessed: 14 January 2019).

Ackerly, D. D. (2004) ‘Adaptation, Niche Conservatism, and Convergence: Comparative Studies of Leaf Evolution in the California Chaparral’, *The American Naturalist*, 163(5), pp. 654–671. doi: 10.1086/383062.

Ådjers, G. *et al.* (1995) ‘Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction and maintenance method of planting line on selected Shorea species’, *Forest Ecology and Management*, 73(1–3), pp. 259–270. doi: 10.1016/0378-1127(94)03488-I.

Aide, T. M. (1992) ‘Dry Season Leaf Production: An Escape from Herbivory’, *Biotropica*, 24(4), p. 532. doi: 10.2307/2389016.

Ali, J. G. and Agrawal, A. A. (2012) ‘Specialist versus generalist insect herbivores and plant defense’, *Trends in Plant Science*, 17(5), pp. 293–302. doi: 10.1016/j.tplants.2012.02.006.

Appanah, S. (1993) ‘Mass flowering of dipterocarp forests in the aseasonal tropics’, *Journal of Biosciences*, 18(4), pp. 457–474. doi: 10.1007/BF02703079.

Appanah, S (1993) ‘Mass flowering of dipterocarp forests in the aseasonal tropics’, *J. Biosci*, 18(4), pp. 457–474. Available at: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.525.8300&rep=rep1&type=pdf (Accessed: 23 May 2018).

Appanah, S. and Turnbull, J. M. (1998) *A review of dipterocarps: taxonomy, ecology and silviculture*, *Cifor*. doi: 10.2307/2844700.

Arnqvist, G. and Wooster, D. (1995) ‘Meta-analysis: synthesizing research findings in ecology and evolution', *Trends in Ecology & Evolution*, 10(6), pp. 236–240. doi: 10.1016/S0169-5347(00)89073-4.

Ashton, Peter S., Givnish, T.J. , Appanah, S. (1988) 'Staggered Flowering in the Dipterocarpaceae : New Insights Into Floral Induction and the Evolution of Mast Fruiting in the Aseasonal Tropics Author (s): P . S . Ashton , T . J . Givnish , S . Appanah Published by : The University of Chicago Press for Th', 132(1), pp. 44–66.

Ashton, P. (1982) *Dipterocarpaceae.* Available at: https://www.cabdirect.org/cabdirect/abstract/19820681886 (Accessed: 23 May 2018).

Ashton, P S (1988) 'Dipterocarp biology as a window to the understanding of tropical forest structure. Ann Rev Ecol Syst 19:347-370F877', *Biotropica*, 19(1), pp. 347–370. doi: 10.2307/23273027.

Ashton, Peter S (1988) 'Dipterocarp Biology as a Window to the Understanding of Tropical Forest Structure Author (s): Peter S . Ashton Source : Annual Review of Ecology and Systematics , Vol . 19 , (1988), pp . 347-370 Published by : Annual Reviews Stable URL : http://www.js', 19, pp. 347–370.

Ashton, P. S. (2012) 'Dipterocarp biology as a window to the understanding of tropical forest structure. Ann Rev Ecol Syst 19:347-370F877', *biotropica*, 19(1988), p. doi: 10.2307/23273027.

Ashton, P. S., Givnish, T. J. and Appanah, S. (1988a) 'Staggered Flowering in the Dipterocarpaceae: New Insights Into Floral Induction and the Evolution of Mast Fruiting in the Aseasonal Tropics', *The American Naturalist*. University of Chicago Press, 132(1), pp. 44–66. doi: 10.1086/284837.

Ashton, P. S., Givnish, T. J. and Appanah, S. (1988b) 'Staggered Flowering in the Dipterocarpaceae: New Insights Into Floral Induction and the Evolution of Mast Fruiting in the Aseasonal Tropics', *The American Naturalist*, 132(1), pp. 44–66. doi: 10.1086/284837.

Augspurger, C. K. *et al.* (2010) 'Pathogen mortality of tropical tree seedlings : studies of the effects of dispersal distance , experimental seedling density , and light conditions’, *Oecologia*, 61(2), pp. 211–217.

Augspurger, C. K. and Kitajima, K. (1992) ‘Experimental Studies of Seedling Recruitment from Contrasting Seed Distributions Author (s): Carol K . Augspurger and Kaoru Kitajima Published by : Wiley Stable URL : http://www.jstor.org/stable/1940675 REFERENCES Linked references are available on JSTO’, 73(4), pp. 1270–1284.

Bachelot, B. *et al.* (2017) ‘Arbuscular mycorrhizal fungal diversity and natural enemies promote coexistence of tropical tree species’, *Ecology*, 98(3), pp. 712–720. doi: 10.1002/ecy.1683.

Bagchi, R. *et al.* (2010) ‘Testing the Janzen-Connell mechanism: Pathogens cause overcompensating density dependence in a tropical tree’, *Ecology Letters*, 13(10), pp. 1262–1269. doi: 10.1111/j.1461-0248.2010.01520.x.

Bagchi, R. *et al.* (2011) ‘Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest’, *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1582), pp. 3246–55. doi: 10.1098/rstb.2011.0034.

Bagchi, R. *et al.* (2014) ‘Pathogens and insect herbivores drive rainforest plant diversity and composition.’, *Nature*. Nature Publishing Group, 506(7486), pp. 85–8. doi: 10.1038/nature12911.

Bagchi, R., Press, M. C. and Scholes, J. D. (2010) ‘Evolutionary history and distance dependence control survival of dipterocarp seedlings’, *Ecology Letters*, 13(1), pp. 51–59. doi: 10.1111/j.1461-0248.2009.01397.x.

Baillie, I. C. *et al.* (2006) ‘Spatial associations of humus, nutrients and soils in mixed dipterocarp forest at Lambir, Sarawak, Malaysian Borneo’, *Journal of Tropical Ecology*, 22(5), pp. 543–553. doi: 10.1017/S026646740600352X.

Barot (2004) ‘Mechanisms promoting plant coexistence: Can all the proposed processes be reconciled?’, *Oikos*, 106(1), pp. 185–192. doi: 10.1111/j.0030-1299.2004.13038.x.

Barreto, P. *et al.* (1998) ‘Costs and benefits of forest management for timber production in eastern Amazonia’, *Forest Ecology and Management*, 108(1–2), pp. 9–26. doi:

10.1016/S0378-1127(97)00251-X.

Battaglia, E. (1955) ‘Chromosome Morphology and Terminology’, *Caryologia*, 8(1), pp. 179–187. doi: 10.1080/00087114.1955.10797556.

Bebber, D. P., Brown, N. P. and Speight, M. R. (2004) ‘Dipterocarp seedling population dynamics in Bornean primary lowland forest during the 1997-8 El Niño-Southern Oscillation’, *Journal of Tropical Ecology*. University of Sheffield Library, 20(01), pp. 11–19. doi: 10.1017/S0266467404006133.

Beer, C. *et al.* (2010) ‘Terrestrial Gross Carbon Dioxide Uptake : Global Distribution and Covariation with Climate Terrestrial Gross Carbon Dioxide Covariation with Climate Uptake : Global Distribution and’, *Science*, pp. 4–9. Available at: http://science.sciencemag.org/content/early/2010/07/05/science.1184984.short (Accessed: 14 January 2019).

De Beer, J. H. and McDermott, M. J. (2002) ‘The Economic Value of Non-Timber Forest Products in Southeast Asia’, *International Union for Conservation of Nature and Natural Resources, Rue Mauverney 28 Gland CH-1196 Switzerland. 197*. Netherlands Committee for IUCN, p. 2002. doi: 10.1109/TNS.2004.834827.

Bell, T., Freckleton, R. P. and Lewis, O. T. (2006) ‘Plant pathogens drive density-dependent seedling mortality in a tropical tree’, *Ecology Letters*, 9(5), pp. 569–574. doi: 10.1111/j.1461-0248.2006.00905.x.

Berry, N. J. *et al.* (2010) ‘The high value of logged tropical forests: Lessons from northern Borneo’, *Biodiversity and Conservation*, 19(4), pp. 985–997. doi: 10.1007/s10531-010-9779-z.

Blomberg, S. P. *et al.* (2012) ‘Independent contrasts and PGLS regression estimators are equivalent’, *Systematic Biology*. Oxford University Press, pp. 382–391. doi: 10.1093/sysbio/syr118.

Blomberg, S. P., Garland, T. and Ives, A. R. (2003) ‘Testing for phylogenetic signal in comparative data: Behavioral traits are more labile’, *Evolution*, 57(4), pp. 717–745. doi: 10.1111/j.0014-3820.2003.tb00285.x.

Blundell, A. G. and Peart, D. R. (1998) ‘Distance-dependence in herbivory and foliar condition for juvenile Shorea trees in Bornean dipterocarp rain forest’, *Oecologia*, 117(1–2), pp. 151–160. doi: 10.1007/s004420050643.

Bonan, G. B. (2008) ‘Forests and climate change: Forcings, feedbacks, and the climate benefits of forests’, *Science*. American Association for the Advancement of Science, pp. 1444–1449. doi: 10.1126/science.1155121.

Brearley, F. Q. *et al.* (2003) ‘NUTRIENTS OBTAINED FROM LEAF LI TTER CAN IMPROVE THE GROWTH OF DIPTEROCARP SEEDLINGS Nutrisi Yang Diperoleh Dari Serasah Daun Meningkatkan Pertumbuhan Semai Dipterocarpaceae Ringkasan Pendahuluan’, *Area*, pp. 101–110. doi: 10.1046/j.0028-646x.2003.00851.x.

Brearley, F. Q. (2012) ‘Ectomycorrhizal Associations of the Dipterocarpaceae’, *Biotropica*, 44(5), pp. 637–648. doi: 10.1111/j.1744-7429.2012.00862.x.

Brook, B. W. and Bradshaw, C. J. A. (2006) ‘Strength of evidence for density dependence in abundance time series of 1198 species’, *Ecology*, 87(6), pp. 1445–1451. doi: 10.1890/0012-9658(2006)87[1445:SOEFDD]2.0.CO;2.

Brown, C. *et al.* (2013) ‘Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity.’, *Proceedings. Biological sciences / The Royal Society*, 280(1764), p. 20130502. doi: 10.1098/rspb.2013.0502.

Brown, H. P. (1949) *Textbook Of Wood Technology Vol I : Brown,H.P. : Free Download & Streaming : Internet Archive*, *Publisher McGraw Hill Book Company Inc.* Available at: https://www.cabdirect.org/cabdirect/abstract/19810669130 (Accessed: 20 November 2018).

Brown, N. (1996) ‘A gradient of seedling growth from the centre of a tropical rain forest canopy gap’, *Forest Ecology and Management*, 82(1–3), pp. 239–244. doi: 10.1016/0378-1127(95)03679-2.

Brown, N. D. and Whitmore, T. C. (1992) ‘Do Dipterocarp Seedlings Really Partition Tropical Rain Forest Gaps?’, *Philosophical Transactions: Biological Sciences*, 335(1275), pp. 369–378. doi: 10.1098/rstb.1992.0028.

Brown, N., Press, M. and Bebber, D. (1999) ‘Growth and survivorship of dipterocarp seedlings: differences in shade persistence create a special case of dispersal limitation’, *Philos Trans R Soc Lond B Biol Sci*, 354(1391), pp. 1847–1855. doi: 10.1098/rstb.1999.0526.

De Bruyn, M. *et al.* (2014) ‘Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity’, *Systematic Biology*. Oxford University Press, 63(6), pp. 879–901. doi: 10.1093/sysbio/syu047.

Burkey, T. V (1994) ‘Tropical Tree Species Diversity: a Test of the Janzen-Connel Model’, *Oecologia*, 97(April 1993), pp. 533–540.

Cagnacci, F. *et al.* (2010) ‘Preface’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), pp. 2155–2155. doi: 10.1098/rstb.2010.0098.

Carlson, K. M. *et al.* (2017) ‘Effect of oil palm sustainability certification on deforestation and fire in Indonesia’, *Proceedings of the National Academy of Sciences*, p. 201704728. doi: 10.1073/pnas.1704728114.

Carson, W. P. *et al.* (2008) ‘Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique’, in *Tropical forest community ecology*, pp. 210–241.

Chapin, F. S., Autumn, K. and Pugnaire, F. (1993) ‘Evolution of Suites of Traits in Response to Environmental Stress’, *The American Naturalist*, 142, pp. S78–S92. doi: 10.1086/285524.

Chapman, C. a. and Chapman, L. J. (1996) ‘Exotic tree plantations and the regeneration of natural forests in Kibale National Park, Uganda’, *Biological Conservation*, 76(3), pp. 253–257. doi: 10.1016/0006-3207(95)00124-7.

Chapman, C. A. and Chapman, L. J. (1996) ‘Frugivory and the Fate of Dispersed and Non-Dispersed Seeds of Six African Tree Species Authors (s): Colin A . Chapman and Lauren J . Chapman Published by : Cambridge University Press Stable URL : http://www.jstor.org/stable/2560303 Accessed : 29-03-201’, *Journal of Tropical Ecology*, 12(4), pp. 491–504. doi: 10.1017/S0266467404001403.

Charles, L. S. *et al.* (2018) ‘Species wood density and the location of planted seedlings drive early-stage seedling survival during tropical forest restoration’, *Journal of Applied Ecology*. Edited by M. Cadotte. John Wiley & Sons, Ltd (10.1111), 55(2), pp. 1009–1018. doi: 10.1111/1365-2664.13031.

Chaudhary, A. *et al.* (2016) ‘Impact of forest management on species richness: global meta-analysis and economic trade-offs’, *Scientific Reports*, 6, p. 23954. doi: 10.1038/srep23954.

Chave, J. *et al.* (2009) ‘Towards a worldwide wood economics spectrum’, *Ecology Letters*. Wiley/Blackwell (10.1111), 12(4), pp. 351–366. doi: 10.1111/j.1461-0248.2009.01285.x.

Chave, J. (no date) *Sixth Framework Programme (2002-2006) MEASURING WOOD DENSITY FOR TROPICAL FOREST TREES A FIELD MANUAL Measuring wood density for tropical forest trees field manual PAN-AMAZONIA project*. Available at: http://www.rainfor.org/upload/ManualsEnglish/wood_density_english[1].pdf (Accessed: 23 October 2018).

Chazdon, R. L. (2003) ‘Tropical forest recovery: legacies of human impact and natural disturbances’, *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1–2), pp. 51–71. doi: 10.1078/1433-8319-00042.

Chen, L. *et al.* (2017) ‘Tree growth traits and social status affect the wood density of pioneer species in secondary subtropical forest’, *Ecology and Evolution*. John Wiley & Sons, Ltd, 7(14), pp. 5366–5377. doi: 10.1002/ece3.3110.

Chesson, P. (2000) ‘Mechanisms of Maintenance of Species Diversity’, *Annual Review of Ecology and Systematics*, 31(2000), pp. 343–358.

Chiew Thang, H. (1987) ‘Forest management systems for tropical high forest, with special reference to peninsular Malaysia’, *Forest Ecology and Management*. Elsevier, 21(1–2), pp. 3–20. doi: 10.1016/0378-1127(87)90069-7.

Cho, Y. Y. *et al.* (2007) ‘Estimation of individual leaf area, fresh weight, and dry weight of hydroponically grown cucumbers (Cucumis sativus L.) using leaf length, width, and SPAD value’, *Scientia Horticulturae*. Elsevier, 111(4), pp. 330–334. doi: 10.1016/j.scienta.2006.12.028.

Christenhusz, Maarten J M and Byng, J. W. (2016) ‘The number of known plants species in the world and its annual increase’, *Phytotaxa*, 261(3), pp. 201–217. doi: 10.11646/phytotaxa.261.3.1.

Christenhusz, Maarten J.M. and Byng, J. W. (2016) ‘The number of known plants species in the world and its annual increase’, *Phytotaxa*, pp. 201–217. doi: 10.11646/phytotaxa.261.3.1.

Cintra, R. and Horna, Æ. V. (1997) ‘Cintra, Horna_1997_Seed an seedling survival of the palm Astrocaryum murumuru and the legume tree Dipteryx micrantha in gaps in Amazonian forest.pdf’, *Journal of Tropical Ecology*, 13(2), pp. 257–277. doi: 10.1017/S0266467400010889.

Clark, D. A. and Clark, D. B. (1984) ‘Spacing Dynamics of a Tropical Rain Forest Tree: Evaluation of the Janzen-Connell Model’, *The American Naturalist*, 124(6), pp. 769–788. doi: 10.1086/284316.

Coates-Estrada, R. and Estrada, A. (1988) ‘Frugivory and seed dispersal in Cymbopetalim baillonii (Annonaceae) at Los Tuxles, Mexico’, *Journal of Tropical Ecology*, 4(2), pp. 157–172.

Coley, P. D. and Barone, J. A. (1996) ‘HERBIVORY AND PLANT DEFENSES IN TROPICAL FORESTS’, *Annual Review of Ecology and Systematics*. Annual Reviews 4139 El Camino Way, P.O. Box 10139, Palo Alto, CA 94303-0139, USA , 27(1), pp. 305–335. doi: 10.1146/annurev.ecolsys.27.1.305.

Comita, L. S. *et al.* (2014) ‘Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival’, *Journal of Ecology*, 102(4), pp. 845–856. doi: 10.1111/1365-2745.12232.

Connell, J. H. (1971) ‘On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees’, in *Dynamics of populations. Proceeding of the advanced study institute, Osterbeek, 1970.*, pp. 298–312. doi: 10.1890/07-2056.1.

Connell, J. H. (1978) ‘Diversity in Tropical Rain Forests and Coral Reefs High diversity of trees and corals is maintained’, *Science*, 199(4335), pp. 1302–1310. doi: 10.2307/1745369.

Connell, J. H., Green, P. T. and Feb, N. (2000) ‘Seedling Dynamics over Thirty-Two Years in a Tropical Rain Forest Tree SEEDLING DYNAMICS OVER THIRTY-

TWO YEARS IN A TROPICAL RAIN FOREST TREE', *Wiley Online Library*, 81(2), pp. 568–584. Available at: https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/0012-9658(2000)081%5B0568:SDOTTY%5D2.0.CO%3B2 (Accessed: 19 February 2019).

Cooper, N., Freckleton, R. P. and Jetz, W. (2011) 'Phylogenetic conservatism of environmental niches in mammals', *Proceedings of the Royal Society B: Biological Sciences*, 278(1716), pp. 2384–2391. doi: 10.1098/rspb.2010.2207.

Cooper, N., Thomas, G. H. and FitzJohn, R. G. (2016) 'Shedding light on the "dark side" of phylogenetic comparative methods', *Methods in Ecology and Evolution*. Edited by R. B. O'Hara. Wiley/Blackwell (10.1111), 7(6), pp. 693–699. doi: 10.1111/2041-210X.12533.

Crawley, M. J. and Long, C. R. (1995) 'Alternate Bearing, Predator Satiation and Seedling Recruitment in Quercus Robur L.', *The Journal of Ecology*, 83(4), p. 683. doi: 10.2307/2261636.

Curran, L. M. *et al.* (1999) 'Impact of El Nino and logging on canopy tree recruitment in Borneo', *Science*, 286(5447), pp. 2184–2188. doi: 10.1126/science.286.5447.2184.

Curran, L M and Leighton, M. (2000) 'Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae', *Ecological Monographs*, 70(1), pp. 101–128. doi: 10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2.

Curran, L. M. and Leighton, M. (2000) 'Vertebrate Responses To Spatiotemporal Variation in Seed Production of Mast-Fruiting Dipterocarpaceae', *Ecological Monographs*, 70(1), pp. 101–128. doi: 10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2.

Curran, L. M. and Webb, C. O. (2000) 'Experimental Tests of the Spatiotemporal Scale of Seed Predation in Mast-Fruiting Dipterocarpaceae EXPERIMENTAL TESTS OF THE SPATIOTEMPORAL SCALE OF SEED PREDATION IN MAST-FRUITING DIPTEROCARPACEAE', 70(1), pp. 129–148.

Dalling, J. W., Hubbell, S. P. and Silvera, K. (1998) 'Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees', *Journal of Ecology*, 86(4), pp. 674–689. doi: 10.1046/j.1365-2745.1998.00298.x.

Dayanandan, S. *et al.* (1999) 'Phylogeny of the tropical tree family Dipterocarpaceae based on nucleotide sequences of the chloroplast rbcL gene', *American Journal of Botany*, 86(8), pp. 1182–1190. doi: 10.2307/2656982.

Donoghue, M. J. (2008) 'Colloquium paper: a phylogenetic perspective on the distribution of plant diversity.', *Proceedings of the National Academy of Sciences of the United States of America*, (Suppl 1), pp. 11549–55. doi: 10.1073/pnas.0801962105.

Du, Y. *et al.* (2017) 'Intraspecific and phylogenetic density-dependent seedling recruitment in a subtropical evergreen forest', *Oecologia*. Springer Berlin Heidelberg. doi: 10.1007/s00442-017-3842-3.

Ducousso, M. *et al.* (2004) 'The last common ancestor of Sarcolaenaceae and Asian dipterocarp trees was ectomycorrhizal before the India-Madagascar separation, about 88 million years ago', *Molecular Ecology*. Wiley/Blackwell (10.1111), 13(1), pp. 231–236. doi: 10.1046/j.1365-294X.2003.02032.x.

Dudley, N., Jeanrenaud, J. and Sullivan, F. (2014) *Bad Harvest: The Timber Trade and the Degradation of Global Forests*. Available at: https://www.taylorfrancis.com/books/9781134164387 (Accessed: 13 December 2018).

Edwards, D. P. *et al.* (2014) 'Selective-logging and oil palm: Multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning', *Ecological Applications*. Nature Publishing Group, 24(8), pp. 2029–2049. doi: 10.1038/nature11318.

Faith, D. P. (1992) 'Conservation evaluation and phylogentic diversity', *Biological Conservation*, 61, pp. 1–10. doi: 10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2.

Faith, D. P., Reid, C. A. M. and Hunter, J. (2004) 'Integrating Phylogenetic Diversity, Complementarity, and Endemism for Conservation Assessment', *Conservation Biology*, pp. 255–261. doi: 10.1111/j.1523-1739.2004.00330.x.

Fearnside, P. M. and Laurance, W. F. (2004) 'TROPICAL DEFORESTATION AND GREENHOUSE-GAS EMISSIONS', *Ecological Applications*, 14(4), pp. 982–986. doi: 10.1890/03-5225.

Felsenstein, J. (1985a) 'Phylogenies and the Comparative Method', *The American Naturalist*. University of Chicago Press, 125(1), pp. 1–15. doi: 10.1086/284325.

Felsenstein, J. (1985b) 'Phylogenies and the Comparative Method', *The American Naturalist*. University of Chicago Press, 125(1), pp. 1–15. doi: 10.1038/sj.bjp.0701596.

Fisher, B., Edwards, David P., *et al.* (2011) 'Cost-effective conservation: Calculating biodiversity and logging trade-offs in Southeast Asia', *Conservation Letters*, 4(6), pp. 443–450. doi: 10.1111/j.1755-263X.2011.00198.x.

Fisher, B., Edwards, David P, *et al.* (2011) 'The high costs of conserving Southeast Asia's lowland rainforests', *Frontiers in Ecology and the Environment*. Wiley-Blackwell, 9(6), pp. 329–334. doi: 10.1890/100079.

Forget, P. (1992) 'Seed Removal and Seed Fate in Gustavia superba (Lecythidaceae) Author (s): Pierre-Michel Forget Published by : The Association for Tropical Biology and Conservation Stable URL : http://www.jstor.org/stable/2388611', *The Association for Tropical Biology and Conservation*, 24(3), pp. 408–414.

Forget, P. (1993) 'Post-dispersal predation and scatter hoarding of Dipteryx panamensis seed by rodents in Panama', *Oecologia*, 94, pp. 255–261.

Forrest, J. L. *et al.* (2015) 'Tropical deforestation and carbon emissions from Protected Area Downgrading, Downsizing, And Degazettement (PADDD)', *Conservation Letters*, 8(3), pp. 153–161. doi: 10.1111/conl.12144.

Freckleton, R. P. (2009) 'The seven deadly sins of comparative analysis', *Journal of Evolutionary Biology*. Wiley/Blackwell (10.1111), pp. 1367–1375. doi: 10.1111/j.1420-9101.2009.01757.x.

Freckleton, R. P., Harvey, P. H. and Pagel, M. (2002) 'Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence', *The American Naturalist*, 160(6), pp. 712–726. doi: 10.1086/343873.

Freckleton, R. P. and Lewis, O. T. (2006) ‘Pathogens, density dependence and the coexistence of tropical trees.’, *Proceedings. Biological sciences / The Royal Society*, 273(August), pp. 2909–2916. doi: 10.1098/rspb.2006.3660.

Fricke, E. C., Tewksbury, J. J. and Rogers, H. S. (2014) ‘Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition’, *Ecology Letters*, 17(5), pp. 593–598. doi: 10.1111/ele.12261.

Fritz, S. A. and Purvis, A. (2010a) ‘Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits’, *Conservation Biology*, 24(4), pp. 1042–1051. doi: 10.1111/j.1523-1739.2010.01455.x.

Fritz, S. A. and Purvis, A. (2010b) ‘Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits’, *Conservation Biology*, 24(4), pp. 1042–1051. doi: 10.1111/j.1523-1739.2010.01455.x.

Fukue, Y. *et al.* (2007) ‘Effects of flowering tree density on the mating system and gene flow in Shorea leprosula (Dipterocarpaceae) in Peninsular Malaysia’, *Journal of Plant Research*, 120(3), pp. 413–420. doi: 10.1007/s10265-007-0078-z.

Gamage, D. T. *et al.* (2006) ‘Comprehensive molecular phylogeny of the sub-family Dipterocarpoideae (Dipterocarpaceae) based on chloroplast DNA sequences.’, *Genes & genetic systems*, 81(1), pp. 1–12. doi: 10.1266/ggs.81.1.

Gardner, T. A. *et al.* (2009) ‘Prospects for tropical forest biodiversity in a human-modified world’, *Ecology Letters*, 12(6), pp. 561–582. doi: 10.1111/j.1461-0248.2009.01294.x.

Garzon-Lopez, C. X. *et al.* (2015) ‘Indirect interactions among tropical tree species through shared rodent seed predators: A novel mechanism of tree species coexistence’, *Ecology Letters*. Edited by M. Rejmanek, 18(8), pp. 752–760. doi: 10.1111/ele.12452.

Gaveau, D. L. A. *et al.* (2014) ‘Four decades of forest persistence, clearance and logging on Borneo’, *PLoS ONE*. Edited by K. Bawa. Public Library of Science, 9(7), p. e101654. doi: 10.1371/journal.pone.0101654.

Ghazoul, J. (2016) *Dipterocarp Biology, Ecology, and Conservation*. Available at: https://books.google.co.uk/books?hl=en&lr=&id=NX4eDQAAQBAJ&oi=fnd&pg=PP1&dq=jaboury+ghazoul+dipterocarp++biology+&ots=lVqwvuFHTR&sig=ZdtUNA9reG6NtkvVRkQVVi5Per0 (Accessed: 17 March 2017).

Ghazoul, J. and Sheil, D. (2010) *Tropical rain forest ecology, diversity, and conservation*. Available at: http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=sibe01.xis&method=post&formato=2&cantidad=1&expresion=mfn=027946 (Accessed: 14 January 2019).

Gilbert, G. S. (2005) 'Dimensions of plant disease in tropical forests.', *Biotic interactions in the tropics: their role in the maintenance of species diversity*, (Gause 1934), pp. 141–164. doi: 10.1017/CBO9780511541971.007.

Gilbert, G. S. and Webb, C. O. (2007) 'Phylogenetic signal in plant pathogen-host range', *Proceedings of the National Academy of Sciences*, 104(12), pp. 4979–4983. doi: 10.1073/pnas.0607968104.

Green, D. S. (1980) 'The Terminal Velocity and Dispersal of Spinning Samaras', *American Journal of Botany*, 67(8), pp. 1218–1224. doi: 10.2307/2442364.

Gurevitch, J. and Hedges, L. V. (1999) 'Statistical issues in ecological meta-analysis', *Ecology*, 80(4), pp. 1142–1149. doi: 10.1890/0012-9658(1999)080[1142:SIIEMA]2.0.CO;2.

Haase, D. L. (2008) 'Understanding forest seedling quality: measurements and interpretation', *Tree Planters' Notes*, 52(2), pp. 24–30. Available at: http://forestseedlingnetwork.com/media/15912/Understanding_Forest_Seedling_Quality_-_Measurements_and_Interpretation.pdf.

Hansen *et al.* (2013) 'High-resolution global maps of 21st-century forest cover change', *Science*, pp. 850–853. Available at: http://www.sciencemag.org/content/342/6160/850.full.pdf%5Cnhttp://ovidsp.ovid.com/ovidweb.cgi?T=JS&PAGE=reference&D=emed15&NEWS=N&AN=370277325 (Accessed: 12 December 2018).

Hansen, T. F. (1997) 'STABILIZING SELECTION AND THE COMPARATIVE ANALYSIS OF ADAPTATION', *Evolution*, 51(5), pp. 1341–1351. doi:

10.2307/2411186.

Hardin, G. (1960) ‘The competitive exclusion principle’, *Science*, pp. 1292–1297. doi: 10.1126/science.131.3409.1292.

Harms, K. E. *et al.* (2000) ‘Pervasive density-dependent recruitment enchances seedling diversity in a tropical forest’, *Nature*, 404(1997), pp. 493–495.

Harrison, F. (2011) ‘Getting started with meta-analysis’, *Methods in Ecology and Evolution*, 2(1), pp. 1–10. doi: 10.1111/j.2041-210X.2010.00056.x.

Hart, T. B. (1995) ‘Seed, seedling and sub-canopy survival in monodominant and mixed forests of the Ituri Forest, Africa’, *Journal of Tropical Ecology*, 11(03), p. 443. doi: 10.1017/S0266467400008919.

Harvey, P. H. and Pagel, M. D. (1991) ‘The comparative method in evolutionary biology’, *Trends in Ecology & Evolution*, p. 239. doi: 10.1016/0169-5347(92)90117-T.

Hawthorne, W. D. *et al.* (2011) ‘The Impact of Logging Damage on Tropical Rainforests , their Recovery and Regeneration an Annotated Bibliography’, *Forestry*, pp. 1–140. doi: ISBN 9780850741688.

Hille Ris Lambers, J., Clark, J. S. and Beckage, B. (2002) ‘Density-dependent mortality and the latitudinal gradient in species diversity’, *Nature*. Nature Publishing Group, 417(6890), pp. 732–735. doi: 10.1038/nature00809.

Hoffmann, A. A. and Sgró, C. M. (2011) ‘Climate change and evolutionary adaptation’, *Nature*. Nature Publishing Group, pp. 479–485. doi: 10.1038/nature09670.

Holmes, T. P. *et al.* (2002) ‘Financial and ecological indicators of reduced impact logging performance in the eastern Amazon’, *Forest Ecology and Management*, 163(1–3), pp. 93–110. doi: 10.1016/S0378-1127(01)00530-8.

Hubbell, S. P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press. Available at: https://press.princeton.edu/titles/7105.html (Accessed: 9 August 2018).

Hutchinson (1961) ‘paradox of the plankton.’, *The American Naturalist*, 95(882), pp. 137–145. doi: 10.1073/pnas.0803032105.

Hyatt, L. *et al.* (2003) ‘The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis’, *Oikos*, 103(April), pp. 590–602. doi: 10.1034/j.1600-0706.2003.12235.x.

Ishiyama, H. *et al.* (2008) ‘Demographic history and interspecific hybridization of four Shorea species (Dipterocarpaceae) from Peninsular Malaysia inferred from nucleotide polymorphism in nuclear gene regions’, *Canadian Journal of Forest Research*, 38(5), pp. 996–1007. doi: 10.1139/X07-218.

Itoh, A. *et al.* (1995) ‘Survivorship and growth of seedlings of four dipterocarp species in a tropical rainforest of Sarawak, East Malaysia’, *Ecological Research*, 10(3), pp. 327–338. doi: 10.1007/BF02347859.

Janzen, D. (1974) ‘Tropical Blackwater Rivers, Animals, and Mast Fruiting by the Dipterocarpaceae’, *Biotropica*, 6(2), pp. 69–103. doi: 10.2307/2989823.

Janzen, D. H. (1970) ‘Herbivores and the Number of Tree Species in Tropical Forests’, *The American Naturalist*, 104(940), pp. 501–528. doi: 10.1086/282687.

Janzen, D. H. (1971) ‘Seed Predation by Animals’, *Annual Review of Ecology and Systematics*. Annual Reviews 4139 El Camino Way, P.O. Box 10139, Palo Alto, CA 94303-0139, USA, 2(1), pp. 465–492. doi: 10.1146/annurev.es.02.110171.002341.

Johnson, D. J. *et al.* (2012) ‘Conspecific negative density dependence and forest diversity.’, *Science (New York, N.Y.)*, 336(6083), pp. 904–907. doi: 10.1126/science.1220269.

Jomo, K., Chang, Y. and Khoo, K. (2004) *Deforesting Malaysia. The Political Economy and Social Ecology of Agricultural Expansion and a Commercial Logging*, *Zed Books*. Available at: https://www.cabdirect.org/cabdirect/abstract/20056702120 (Accessed: 23 May 2018).

Jones, M. D., Durall, D. M. and Cairney, J. W. G. (2003) ‘Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging’, *New Phytologist*. Wiley/Blackwell (10.1111), pp. 399–422. doi: 10.1046/j.1469-8137.2003.00698.x.

Jones, R. H. *et al.* (2006) ‘Woody Plant Regeneration in Four Floodplain Forests’, *Ecological Monographs*, 64(3), pp. 345–367. doi: 10.2307/2937166.

Kamiya, K. *et al.* (2011) ‘Morphological and molecular evidence of natural hybridization in Shorea (Dipterocarpaceae)’, *Tree Genetics and Genomes*. Springer-Verlag, 7(2), pp. 297–306. doi: 10.1007/s11295-010-0332-8.

Katabuchi, M. *et al.* (2012) ‘Soil resource availability shapes community trait structure in a species-rich dipterocarp forest’, *Journal of Ecology*, 100(3), pp. 643–651. doi: 10.1111/j.1365-2745.2011.01937.x.

Keenan, R. J. *et al.* (2015) ‘Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015’, *Forest Ecology and Management*. Elsevier B.V., 352, pp. 9–20. doi: 10.1016/j.foreco.2015.06.014.

Kelly, D. and Sork, V. L. (2002) ‘Mast Seeding in Perennial Plants: Why, How, Where?’, *Annual Review of Ecology and Systematics*, 33(1), pp. 427–447. doi: 10.1146/annurev.ecolsys.33.020602.095433.

Kelly, D. and Sullivan, J. J. (1997) ‘Quantifying the benefits of mast seeding on predator satiation and wind pollination in Chionochloa pallens (Poaceae)’, *Oikos*, 78(1), pp. 143–150. doi: 10.2307/3545810.

Kessler, M. (2002) ‘The elevational gradient of Andean plant endemism: Varying influences of taxon-specific traits and topography at different taxonomic levels’, *Journal of Biogeography*. Wiley/Blackwell (10.1111), 29(9), pp. 1159–1165. doi: 10.1046/j.1365-2699.2002.00773.x.

King, D. A. *et al.* (2005) ‘Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia’, *Functional Ecology*. Wiley/Blackwell (10.1111), 19(3), pp. 445–453. doi: 10.1111/j.1365-2435.2005.00982.x.

King, D. A. *et al.* (2006) ‘The role of wood density and stem support costs in the growth and mortality of tropical trees’, *Journal of Ecology*. Wiley/Blackwell (10.1111), 94(3), pp. 670–680. doi: 10.1111/j.1365-2745.2006.01112.x.

Kleine, M. and Heuveldop, J. (1993) ‘A management planning concept for sustained yield of tropical forests in Sabah, Malaysia’, *Forest Ecology and Management*, 61(3–4), pp. 277–297. doi: 10.1016/0378-1127(93)90207-4.

Kobe, R. K. (1999) 'Light gradient partitioning among tropical tree species through differntial seedling mortality and growth', *Ecology*, 80(1), pp. 187–201. doi: 10.1890/0012-9658(1999)080[0187:LGPATT]2.0.CO;2.

Kobe, R. K. and Vriesendorp, C. F. (2011) 'Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest', *Ecology Letters*. John Wiley & Sons, Ltd (10.1111), 14(5), pp. 503–510. doi: 10.1111/j.1461-0248.2011.01612.x.

de Kok, R. P. J. *et al.* (2015) 'Identifying Targets for Plant Conservation in Harapan Rainforest, Sumatra', *Tropical Conservation Science*. SAGE PublicationsSage CA: Los Angeles, CA, 8(1), pp. 28–32. doi: 10.1177/194008291500800105.

Koricheva, J., Gurevitch, J. and Mengersen, K. (2013) *Handbook of meta-analysis in ecology and evolution*. Available at: https://books.google.co.uk/books?hl=en&lr=&id=y-BjX58AXsQC&oi=fnd&pg=PP1&dq=koricheva+meta+analysis&ots=_ihsLzCYmL&sig=RgtHESlIvNZI9nha8PmoAeJsKRE (Accessed: 12 December 2018).

Kormann, U. G. *et al.* (2018) 'Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization', *Journal of Applied Ecology*. Edited by M. Maron. John Wiley & Sons, Ltd (10.1111), 55(3), pp. 1288–1298. doi: 10.1111/1365-2664.13084.

Kreier, H. P. and Schneider, H. (2006) 'Phylogeny and biogeography of the staghorn fern genus Platycerium (Polypodiaceae, Polypodiidae)', *American Journal of Botany*, 93(2), pp. 217–225. doi: 10.3732/ajb.93.2.217.

Kummer, D. M. and Turner, B. L. (2009) 'The Human Causes of deforestation in Southeast Deforestation Asia is that of large-scale expansion', *Bioscience*, 44(5), pp. 323–328. Available at: http://www.jstor.org/stable/1312382 (Accessed: 23 May 2018).

Lee, S. L. *et al.* (2000) 'Genetic Diversity of a Tropical Tree Species, Shorea leprosula Miq. (Dipterocarpaceae), in Malaysia: Implications for Conservation of Genetic Resources and Tree Improvement 1', *Biotropica*, 32(2), pp. 213–224. doi: 10.1646/0006-3606(2000)032[0213:GDOATT]2.0.CO;2.

Levin, S. A. (1970) ‘Principle’, *The American Naturalist*, 104(939), pp. 413–423.

Liu, H. *et al.* (2012) ‘Phylogenetic niche conservatism in C4 grasses’, *Oecologia*, 170(3), pp. 835–845. doi: 10.1007/s00442-012-2337-5.

Liu, H. *et al.* (2016) ‘Uncovering the spatio-temporal drivers of species trait variances: A case study of Magnoliaceae in China’, *Journal of Biogeography*, 43(6), pp. 1179–1191. doi: 10.1111/jbi.12707.

Liu, X. *et al.* (2012) ‘Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest’, *Ecology Letters*, 15(2), pp. 111–118. doi: 10.1111/j.1461-0248.2011.01715.x.

Losos, J. B. (2011) ‘Seeing the Forest for the Trees: The Limitations of Phylogenies in Comparative Biology’, *The American Naturalist*. University of Chicago PressChicago, IL, 177(6), pp. 709–727. doi: 10.1086/660020.

Lyal, C. H. C. and Curran, L. M. (2000) *Seed-feeding beetles of the weevil tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) developing in seeds of trees in the Dipterocarpaceae*, *Journal of Natural History*. doi: 10.1080/00222930050122165.

Magrach, A. *et al.* (2016) ‘Selective logging in tropical forests decreases the robustness of liana – tree interaction networks to the loss of host tree species’.

Maguire, B. and Ashton, P. S. (1980) ‘Pakaraimaea dipterocarpacea II’, *Taxon*. International Association for Plant Taxonomy (IAPT), 29(2/3), pp. 225–231. doi: 10.1111/j.1469-8137.2006.01860.x.

Mangan, S. A. *et al.* (2010) ‘Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest.’, *Nature*. Nature Publishing Group, 466(7307), pp. 752–5. doi: 10.1038/nature09273.

Maryudi, A. (2016) ‘Choosing timber legality verification as a policy instrument to combat illegal logging in Indonesia’, *Forest Policy and Economics*. Elsevier, 68, pp. 99–104. doi: 10.1016/J.FORPOL.2015.10.010.

Massey, F. P. *et al.* (2006) ‘Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings’, *Journal of Ecology*, 94(3), pp.

646–655. doi: 10.1111/j.1365-2745.2006.01127.x.

Matthesius, A., Chapman, H. and Kelly, D. (2011) ‘Testing for Janzen-Connell Effects in a West African Montane Forest’, *Biotropica*, 43(1), pp. 77–83. doi: 10.1111/j.1744-7429.2010.00664.x.

Maycock, C. R. *et al.* (2012) ‘A Revised Conservation Assessment of Dipterocarps in Sabah’, *Biotropica*, 44(5), pp. 649–657. doi: 10.1111/j.1744-7429.2011.00852.x.

McGuire, K. L. (2008) ‘Ectomycorrhizal Associations Function to Maintain Tropical Monodominance’, in *Mycorrhizae: Sustainable Agriculture and Forestry*. Dordrecht: Springer Netherlands, pp. 287–302. doi: 10.1007/978-1-4020-8770-7_12.

Metz, M. (2007) *Spatiotemporal variation in seedling dynamics and the maintenance of diversity in an Amazonian forest*. Available at: http://search.proquest.com/openview/ac6bf2bbefe0f041a440ab6ccfbefff6/1?pq-origsite=gscholar&cbl=18750&diss=y (Accessed: 19 February 2019).

Metz, M. R., Sousa, W. P. and Valencia, R. (2010) ‘Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest’, *Ecology*. John Wiley & Sons, Ltd, 91(12), pp. 3675–3685. doi: 10.1890/08-2323.1.

Molina-Montenegro, M. A., Badano, E. I. and Cavieres, L. A. (2006) ‘Cushion Plants as Microclimatic Shelters for Two Ladybird Beetles Species in Alpine Zone of Central Chile’, *Arctic, Antarctic, and Alpine Research*, 38(2), pp. 224–227. doi: 10.1657/1523-0430(2006)38[224:CPAMSF]2.0.CO;2.

Molles, M. C. (2002) *Ecology : concepts and applications*. McGraw-Hill. Available at: https://www.gle-search.com/web/search?q=Molles, Manuel C., Jr. (2002). Ecology: Concepts and Applications (International ed.). New York: The McGraw-Hill Companies, Inc. pp. 586 pp. ISBN 0-07-112252-4.&source=1453d03b898a44cfa80c6914b060910d (Accessed: 22 February 2019).

Momose, K. *et al.* (1998) ‘Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest', *American Journal of Botany*, 85(10), pp. 1477–1501. doi: 10.2307/2446404.

Moreira, X. *et al.* (2015) 'Latitudinal variation in herbivory: influences of climatic drivers, herbivore identity and natural enemies', *Oikos*, 124(11), pp. 1444–1452. doi: 10.1111/oik.02040.

Nakagawa, M. *et al.* (2005) 'Predispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia', *Biotropica*, 37(3), pp. 389–396. doi: 10.1111/j.1744-7429.2005.00051.x.

Nock, C. A. *et al.* (2009) 'Wood density and its radial variation in six canopy tree species differing in shade-tolerance in western Thailand', *Annals of Botany*. Oxford University Press, 104(2), pp. 297–306. doi: 10.1093/aob/mcp118.

Norghauer, J. M. *et al.* (2006) 'An experimental test of density- and distant-dependent recruitment of mahogany (Swietenia macrophylla) in southeastern Amazonia', *Oecologia*, 148(3), pp. 437–446. doi: 10.1007/s00442-006-0395-2.

Notman, E., Gorchov, D. L. and Cornejo, F. (1996) 'Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed neotropical rain forest tree species', *Oecologia*, 106(2), pp. 221–227. doi: 10.1007/BF00328602.

Novotny, V. and Basset, Y. (2005) 'Host specificity of insect herbivores in tropical forests.', *Proceedings. Biological sciences / The Royal Society*, 272(1568), pp. 1083–90. doi: 10.1098/rspb.2004.3023.

NUSSBAUM, R. and HOE, A. L. (1996) 'REHABILITATION OF DEGRADED SITES IN LOGGED-OVER FOREST USING DIPTEROCARPS', in *Dipterocarp Forest Ecosystems: Towards Sustainable Management*. WORLD SCIENTIFIC, pp. 446–463. doi: 10.1142/9789814261043_0020.

Okuda, T. *et al.* (2003) 'Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia', *Forest Ecology and Management*. Elsevier, 175(1–3), pp. 297–320. doi: 10.1016/S0378-1127(02)00137-8.

De Oliveira, A. A. and Mori, S. A. (1999) 'A central Amazonian terra firme forest. I. High tree species richness on poor soils', *Biodiversity and Conservation*. Kluwer

Academic Publishers, 8(9), pp. 1219–1244. doi: 10.1023/A:1008908615271.

Oshima, C., Tokumoto, Y. and Nakagawa, M. (2015) ‘Biotic and abiotic drivers of dipterocarp seedling survival following mast fruiting in Malaysian Borneo’, *Journal of Tropical Ecology*, 31(2), pp. 129–137. doi: 10.1017/S026646741400073X.

Packer, a and Clay, K. (2000) ‘Soil pathogens and spatial patterns of seedling mortality in a temperate tree.’, *Nature*, 404(6775), pp. 278–81. doi: 10.1038/35005072.

Pagel, M. (1999) ‘Inferring the historical patterns of biological evolution’, *Nature*. Nature Publishing Group, pp. 877–884. doi: 10.1038/44766.

Paine, C. E. T. and Beck, H. (2007) ‘Seed predation by Neotropical rain forest mammals increases diversity in seedling recruitment.’, *Ecology*, 88(12), pp. 3076–87. doi: 10.1890/06-1835.1.

Palmer, C. E. (2001) ‘the Extent and Causes of Illegal Logging: an Analysis of a Major Cause of Tropical Deforestation in Indonesia’, *CSERGE Working Paper*, p. 33. doi: 10.1017/S0007114509993266.

Palmer, H. E. *et al.* (1998) ‘An economic evaluation of alternative genetic improvement strategies for farm woodland trees’, *Forestry*, 71(4), pp. 333–347. doi: http://dx.doi.org/10.1093/forestry/71.4.333.

Palmiotto, P. A. *et al.* (2004) ‘Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo’, *Journal of Ecology*, 92(4), pp. 609–623. doi: 10.1111/j.0022-0477.2004.00894.x.

Paoli, G. D., Curran, L. M. and Zak, D. R. (2006) ‘Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: Evidence for niche partitioning by tropical rain forest trees’, *Journal of Ecology*, 94(1), pp. 157–170. doi: 10.1111/j.1365-2745.2005.01077.x.

Pariona, W., Fredericksen, T. S. and Licona, J. C. (2003) ‘Natural regeneration and liberation of timber species in logging gaps in two Bolivian tropical forests’, *Forest Ecology and Management*, 181(3), pp. 313–322. doi: 10.1016/S0378-1127(03)00002-1.

Pavoine, S. and Bonsall, M. B. (2011) ‘Measuring biodiversity to explain community assembly a unified approach - Pavoine - 2010 - Biological Reviews - Wiley Online Library', *Biological Reviews*, 86(4), pp. 792–812. Available at: http://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2010.00171.x/full (Accessed: 25 May 2018).

Peay, K. G. *et al.* (2010) 'Potential link between plant and fungal distributions in a dipterocarp rainforest: Community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone', *New Phytologist*, 185(2), pp. 529–542. doi: 10.1111/j.1469-8137.2009.03075.x.

Peluso, N. L., Vandergeest, P. and Potter, L. (1995) 'Department of History , National University of Singapore Social Aspects of Forestry in Southeast Asia : A Review of Postwar Trends in the Scholarly Literature Author (s): Nancy Lee Peluso , Peter Vandergeest and Lesley Potter Published by : Cambridge Un', *Journal of Southeast Asian Studies*, 26(1), pp. 196–218.

Peña-Claros, M. *et al.* (2008) 'Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees', *Forest Ecology and Management*, 256(7), pp. 1458–1467. doi: 10.1016/j.foreco.2007.11.013.

Peres, C. a. and Baider, C. (1997) 'Seed dispersal, spatial distribution and population structure of Brazilnut trees (Bertholletia excelsa) in southeastern Amazonia', *Journal of Tropical Ecology*, 13(04), p. 595. doi: 10.1017/S0266467400010749.

Pianka, E. R. (1966) *Latitudinal Gradients in Species Diversity: A Review of Concepts*, *The American Naturalist*. Available at: http://biology.unm.edu/jhbrown/Documents/511Readings/Pianka1966.pdf (Accessed: 14 February 2019).

Pirard, R., Dal Secco, L. and Warman, R. (2016) 'Do timber plantations contribute to forest conservation?', *Environmental Science & Policy*. Elsevier, 57, pp. 122–130. doi: 10.1016/J.ENVSCI.2015.12.010.

Poore, D. (1991) 'An introduction to tropical rain forests', *Biological Conservation*, 56(3), p. 368. doi: 10.1016/0006-3207(91)90068-K.

Poorter, L. *et al.* (2010) 'The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species', *New*

Phytologist, 185(2), pp. 481–492. doi: 10.1111/j.1469-8137.2009.03092.x.

Potts, M. D. *et al.* (2002) ‘HABITAT PATTERNS IN TROPICAL RAIN FORESTS: A COMPARISON OF 105 PLOTS IN NORTHWEST BORNEO’, *Ecology*. John Wiley & Sons, Ltd, 83(10), pp. 2782–2797. doi: 10.1890/0012-9658(2002)083[2782:HPITRF]2.0.CO;2.

Press, M. C., Brown, N. D. and Barker, M. G. (1997) ‘Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning?’, *Oecologia*, 112(4), pp. 453–463. doi: 10.1007/s004420050332.

Preston, K. A., Cornwell, W. K. and DeNoyer, J. L. (2006) ‘Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms’, *New Phytologist*, 170(4), pp. 807–818. doi: 10.1111/j.1469-8137.2006.01712.x.

Primack, R. and Corlett, R. (2005) *Tropical rain forests: an ecological and biogeographical comparison*, *Oxford*. Available at: http://www.biosch.hku.hk/ecology/porcupine/por33pdf/por33-p20-21.pdf (Accessed: 14 January 2019).

Purvis, A. *et al.* (2005) ‘Correlates of extinction risk : phylogeny, biology, threat and scale’, in *Phylogeny and Conservation*, pp. 295–316. doi: http://dx.doi.org/10.1017/CBO9780511614927.013.

Putz, F. E. *et al.* (2008) ‘Reduced-impact logging: Challenges and opportunities’, *Forest Ecology and Management*, 256(7), pp. 1427–1433. doi: 10.1016/j.foreco.2008.03.036.

Qian, H. and Jin, Y. (2016) ‘An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure’, *Journal of Plant Ecology*, 9(2), pp. 233–239. doi: 10.1093/jpe/rtv047.

Qian, H. and Zhang, J. (2014) ‘Using an updated time-calibrated family-level phylogeny of seed plants to test for non-random patterns of life forms across the phylogeny’, *Journal of Systematics and Evolution*, 52(4), pp. 423–430. doi: 10.1111/jse.12086.

Rana, R. *et al.* (2009) ‘Functional anatomy of five endangered tropical timber wood species of the family dipterocarpaceae’, *Trees - Structure and Function*. Springer-Verlag, 23(3), pp. 521–529. doi: 10.1007/s00468-008-0298-4.

Redding, D. W. and Mooers, A. O. (2006) ‘Incorporating evolutionary measures into conservation prioritization’, *Conservation Biology*, 20(6), pp. 1670–1678. doi: 10.1111/j.1523-1739.2006.00555.x.

Roberts, J. T. and Heithaus, E. R. (1986) ‘Ants Rearrange the Vertebrate-Generated Seed Shadow of a Neotropical Fig Tree Author (s): J . Timmons Roberts and E . Raymond Heithaus Published by : Ecological Society of America Stable URL : http://www.jstor.org/stable/1939827 . ANTS REARRANGE THE VER’, *Ecology*, 67(4), pp. 1046–1051.

Roopsind, A. *et al.* (2018) ‘Trade-offs between carbon stocks and timber recovery in tropical forests are mediated by logging intensity’, *Global Change Biology*, 24(7), pp. 2862–2874. doi: 10.1111/gcb.14155.

Russo, S. E. *et al.* (2005) ‘Soil-related performance variation and distributions of tree species in a Bornean rain forest’, *Journal of Ecology*, 93(5), pp. 879–889. doi: 10.1111/j.1365-2745.2005.01030.x.

Sakai, S. (2002) ‘General flowering in lowland mixed dipterocarp forests of south-east Asia’, *Biological Journal of the Linnean Society*. Wiley/Blackwell (10.1111), 75(2), pp. 233–247. doi: 10.1046/j.1095-8312.2002.00016.x.

Sanchez-cordero, V. and Martinez-gallardo, R. (2010) ‘Postdispersal Fruit and Seed Removal by Forest-Dwelling Rodents in a Lowland Rainforest in Mexico Author (s): Victor Sanchez-Cordero and Roberto Martinez-Gallardo Published by : Cambridge University Press Stable URL : http://www.jstor.org/stable/2560001’, 14(2), pp. 139–151.

Sasaki, N. *et al.* (2016) ‘Sustainable Management of Tropical Forests Can Reduce Carbon Emissions and Stabilize Timber Production’, *Frontiers in Environmental Science*, 4. doi: 10.3389/fenvs.2016.00050.

Schemske, D. W. and Mittelbach, G. G. (2017) ‘“Latitudinal Gradients in Species Diversity”: Reflections on Pianka’s 1966 Article and a Look Forward’, *The*

American Naturalist, 189(6), pp. 599–603. doi: 10.1086/691719.

Schoener, T. W. (1974a) ‘Resource partitioning in ecological communities’, *Science*, 185(4145), pp. 27–39. doi: 10.1126/science.185.4145.27.

Schoener, T. W. (1974b) ‘Resource partitioning in ecological communities’, *Science*, 185(4145), pp. 27–39. doi: 10.1126/science.185.4145.27.

Schupp, E. W. and Jordano, P. (2011) ‘The full path of Janzen-Connell effects: Genetic tracking of seeds to adult plant recruitment’, *Molecular Ecology*, 20(19), pp. 3953–3955. doi: 10.1111/j.1365-294X.2011.05202.x.

Sedio, B. E. and Ostling, A. M. (2013) ‘How specialised must natural enemies be to facilitate coexistence among plants?’, *Ecology Letters*, 16(8), pp. 995–1003. doi: 10.1111/ele.12130.

Shamshuddin, J. and Fauziah, C. I. (2010) *Weathered tropical soils: the ultisols and oxisols*, *UPM Press, Serdang.* Universiti Putra Malaysia Press. Available at: http://agris.fao.org/agris-search/search.do?recordID=MY2014000389 (Accessed: 26 February 2019).

Silva Matos, D. M., Freckleton, R. P. and Watkinson, A. R. (1999) ‘The role of density dependence in the population dynamics of a tropical palm’, *Ecology*. Ecological Society of America, 80(8), pp. 2635–2650. doi: 10.1890/0012-9658(1999)080[2635:TRODDI]2.0.CO;2.

Singh, S. (2014) ‘Borderland practices and narratives: Illegal cross-border logging in northeastern Cambodia’, *Ethnography*, 15(2), pp. 135–159. doi: 10.1177/1466138112463805.

Sjöström, A. and Gross, C. L. (2006) ‘Life-history characters and phylogeny are correlated with extinction risk in the Australian angiosperms’, *Journal of Biogeography*, 33(2), pp. 271–290. doi: 10.1111/j.1365-2699.2005.01393.x.

Slik, J. W. F. (2006) ‘Estimating species-specific wood density from the genus average in Indonesian trees’, *Journal of Tropical Ecology*. Cambridge University Press, 22(04), pp. 481–482. doi: 10.1017/S0266467406003324.

Slik, J. W. F. *et al.* (2015) ‘An estimate of the number of tropical tree species’, *Proceedings of the National Academy of Sciences*, 112(24), pp. 7472–7477. doi: 10.1073/pnas.1423147112.

Smith, T. B. and Bernatchez, L. (2008) 'Evolutionary change in human-altered environments', *Molecular Ecology*, January, pp. 1–8. doi: 10.1111/j.1365-294X.2007.03607.x.

Smits, W. (1994) *Dipterocarpaceae: mycorrhizae and regeneration.* Available at: http://www.cabdirect.org/abstracts/19946797862.html.

Sodhi, N. S. *et al.* (2004) 'Southeast Asian biodiversity: An impending disaster', *Trends in Ecology and Evolution*, pp. 654–660. doi: 10.1016/j.tree.2004.09.006.

Soepadmo, E., Saw, L. G. and Chung, R. C. K. (2004) 'Tree Flora of Sabah and Sarawak', *Government of Malaysia*, 5, p. 335. doi: 10.1017/CBO9781107415324.004.

Sohngen, B., Mendelsohn, R. and Sedjo, R. (1999) 'Forest Management, Conservation, and Global Timber Markets', *American Journal of Agricultural Economics*, 81(1), pp. 1–13. doi: 10.2307/1244446.

Sork, V. L. (1993) 'Evolutionary ecology of mast-seeding in temperate and tropical oaks (Quercus spp.)', *Vegetatio*. Dordrecht: Springer Netherlands, 107–108(1), pp. 133–147. doi: 10.1007/BF00052217.

Steege, H. *et al.* (2015) 'Supplementary Materials for Estimating the global conservation status of more than 15 , 000 Amazonian tree species', 1500936(November), pp. 9–11. doi: 10.1126/sciadv.1500936.

Stevenson, P. R., Link, A. and Ramírez, B. H. (2005) 'Frugivory and seed fate in Bursera inversa (Burseraceae) at Tinigua Park, Colombia: Implications for primate conservation', *Biotropica*, 37(3), pp. 431–438. doi: 10.1111/j.1744-7429.2005.00057.x.

Stoll, P. and Newbery, D. M. (2005) 'Evidence of species-specific neighborhood effects in the dipteracarpaceae of a Bornean rain forest.', *Ecology*, 86(11), pp. 3048–3062. doi: 10.1890/04-1540.

Stotz, H. U. *et al.* (2000) 'Induced plant defense responses against chewing insects.

Ethylene signaling reduces resistance of Arabidopsis against Egyptian cotton worm but not diamondback moth', *Plant Physiology*, 124(3), p. 1007. doi: 10.1104/pp.124.3.1007.

Streng, D. R., Glitzenstein, J. S. and Harcombe, P. A. (1989) 'Woody Seedling Dynamics in an East Texas Floodplain Forest', *Ecological Monographs*. John Wiley & Sons, Ltd, 59(2), pp. 177–204. doi: 10.2307/2937285.

Sun, I. F. *et al.* (2007) 'Seed predation during general flowering events of varying magnitude in a Malaysian rain forest', *Journal of Ecology*, 95(4), pp. 818–827. doi: 10.1111/j.1365-2745.2007.01235.x.

Swamy, V. and Terborgh, J. W. (2010) 'Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest', *Journal of Ecology*, 98(5), pp. 1096–1107. doi: 10.1111/j.1365-2745.2010.01686.x.

Swinfield, T. *et al.* (2012) 'Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings', *Ecology and Evolution*, 2(7), pp. 1408–1413. doi: 10.1002/ece3.252.

Takeuchi, Y. and Nakashizuka, T. (2007a) 'Effect of distance and density on seed/seedling fate of two dipterocarp species', *Forest Ecology and Management*. Elsevier, 247(1–3), pp. 167–174. doi: 10.1016/j.foreco.2007.04.028.

Takeuchi, Y. and Nakashizuka, T. (2007b) 'Effect of distance and density on seed/seedling fate of two dipterocarp species', *Forest Ecology and Management*, 247(1–3), pp. 167–174. doi: 10.1016/j.foreco.2007.04.028.

Tange, T. *et al.* (2000) 'Responses of Shorea curtisii and Shorea leprosula seedlings to short-term flooding', *Journal of Tropical Forest Science*, 12(2), pp. 414–417. doi: 10.1086/324549.

Tedersoo, L. *et al.* (2007) 'Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native Vateriopsis seychellarum (Dipterocarpaceae) and Intsia bijuga (Caesalpiniaceae) to the introduced Eucalyptus robusta (Myrtaceae), but not P', *New Phytologist*, 175, pp. 321–33. doi: 10.1111/j.1469-8137.2007.02104.x.

Terborgh, J. *et al.* (1993) ‘Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest’, *Vegetatio*, 107–108(1), pp. 375–386. doi: 10.1007/BF00052236.

Terborgh, J. (2012) ‘Enemies Maintain Hyperdiverse Tropical Forests’, *The American Naturalist*, 179(3), pp. 303–314. doi: 10.1086/664183.

Tnah, L. H. *et al.* (2012) ‘DNA extraction from dry wood of Neobalanocarpus heimii (Dipterocarpaceae) for forensic DNA profiling and timber tracking’, *Wood Science and Technology*. Springer-Verlag, 46(5), pp. 813–825. doi: 10.1007/s00226-011-0447-6.

Tokumoto, Y. *et al.* (2009) ‘How does flowering magnitude affect seed survival in Shorea pilosa (Dipterocarpaceae) at the predispersal stage in Malaysia?’, *Plant Species Biology*. John Wiley & Sons, Ltd, pp. 104–108. doi: 10.1111/j.1442-1984.2009.00243.x.

Traveset, A. (1990a) ‘Post-dispersal predation of Acacia farnesiana seeds by Stator vachelliae (Bruchidae) in Central America’, *Oecologia*, 84(4), pp. 506–512. doi: 10.1007/BF00328167.

Traveset, A. (1990b) ‘Post-dispersal predation of Acacia farnesiana seeds by Stator vachelliae (Bruchidae) in Central America’, *Oecologia*, 84(4), pp. 506–512. doi: 10.1007/BF00328167.

Turner, W. R. *et al.* (2012) ‘Global Biodiversity Conservation and the Alleviation of Poverty’, *BioScience*, 62(1), pp. 85–92. doi: 10.1525/bio.2012.62.1.13.

Valencia, R., Balslev, H. and Paz Y Miño C, G. (1994) ‘High tree alpha-diversity in Amazonian Ecuador’, *BIODIVERSITY AND CONSERVATION*. Kluwer Academic Publishers, 3(1), pp. 21–28. doi: 10.1007/BF00115330.

Volkov, I. *et al.* (2005) ‘Density dependence explains tree species abundance and diversity in tropical forests’, *Nature*, 438(December), pp. 658–661. doi: 10.1038/nature04030.

Walsh, R. P. D. *et al.* (2011) ‘Long-term responses of rainforest erosional systems at different spatial scales to selective logging and climatic change’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, pp. 3340–3353.

doi: 10.1098/rstb.2011.0054.

Webb, C. . and and Peart, D. R. (1999) ‘Seedling density dependence promotes coexistence of Bornean rain forest trees’, *Ecology*, 80(6), pp. 2006–2017.

Weiblen, G. D. *et al.* (2006) ‘Phylogenetic Dispersion of Host Use in a Tropical Insect Herbivore Community Published by : Ecological Society of America content in a trusted digital archive . We use information technology and tools to increase productivity and facilitate new forms phyl’, *Ecology*, 87(7), pp. S62–S75.

Werner, S. (1999) *The Impact of management practices on species richness within productive rubber agroforests of Indonesia*, *Selected Proceedings of an International Workshop*.

Whitmore, T. C. (1984) ‘A Vegetation Map of Malesia at Scale 1:5 Million’, *Journal of Biogeography*, 11(6), pp. 461–471.

Whitmore, T. C. (1990) ‘An introduction to tropical rain forests.’, *An introduction to tropical rain forests.* Clarendon Press. Available at: https://www.cabdirect.org/cabdirect/abstract/19910646819 (Accessed: 11 January 2019).

Wiens, J. J. *et al.* (2006) *Evolutionary and Ecological Causes of the Latitudinal Diversity Gradient in Hylid Frogs: Treefrog Trees Unearth the Roots of High Tropical Diversity*, *Am. Nat*. Available at: http://www.wienslab.com/Publications_files/Wiens_et_al_AmNat_2006.pdf (Accessed: 14 February 2019).

Wiens, J. J. *et al.* (2010) ‘Niche conservatism as an emerging principle in ecology and conservation biology’, *Ecology Letters*, pp. 1310–1324. doi: 10.1111/j.1461-0248.2010.01515.x.

Wiens, J. J. and Graham, C. H. (2005) ‘Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology’, *Annual Review of Ecology, Evolution, and Systematics*, 36(1), pp. 519–539. doi: 10.1146/annurev.ecolsys.36.102803.095431.

Willis, C. G. *et al.* (2008) ‘Phylogenetic patterns of species loss in Thoreau’s woods are driven by climate change’, *Proceedings of the National Academy of Sciences*, 105(44), pp. 17029–17033. doi: 10.1073/pnas.0806446105.

Wright, J. S. (2002) ‘Plant diversity in tropical forests: a review of mechanisms of species coexistence’, *Oecologia*, 130(1), pp. 1–14. doi: 10.1007/s004420100809.

Wu, J. *et al.* (2016) ‘How does habitat filtering affect the detection of conspecific and phylogenetic density dependence?’, *Ecology*. doi: 10.1890/14-2465.

Yeong, K. L., Reynolds, G. and Hill, J. K. (2016) ‘Enrichment planting to improve habitat quality and conservation value of tropical rainforest fragments’, *Biodiversity and Conservation*. Springer Netherlands, 25(5), pp. 957–973. doi: 10.1007/s10531-016-1100-3.

Zakaria, M. *et al.* (2016) ‘Fauna Diversity in Tropical Rainforest: Threats from Land-Use Change’, in *Tropical Forests - The Challenges of Maintaining Ecosystem Services while Managing the Landscape*. InTech. doi: 10.5772/64963.

Zanne, A. E. *et al.* (2014) ‘Three keys to the radiation of angiosperms into freezing environments’, *Nature*, 506(7486), pp. 89–92. doi: 10.1038/nature12872.

Zhu, Y. *et al.* (2015) ‘Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest’, *Journal of Ecology*, 103(4), pp. 957–966. doi: 10.1111/1365-2745.12414.

Zhu, Y. *et al.* (2018) ‘Density-dependent survival varies with species life-history strategy in a tropical forest’, *Ecology Letters*. Edited by T. Coulson, pp. 506–515. doi: 10.1111/ele.12915.

Appendix A

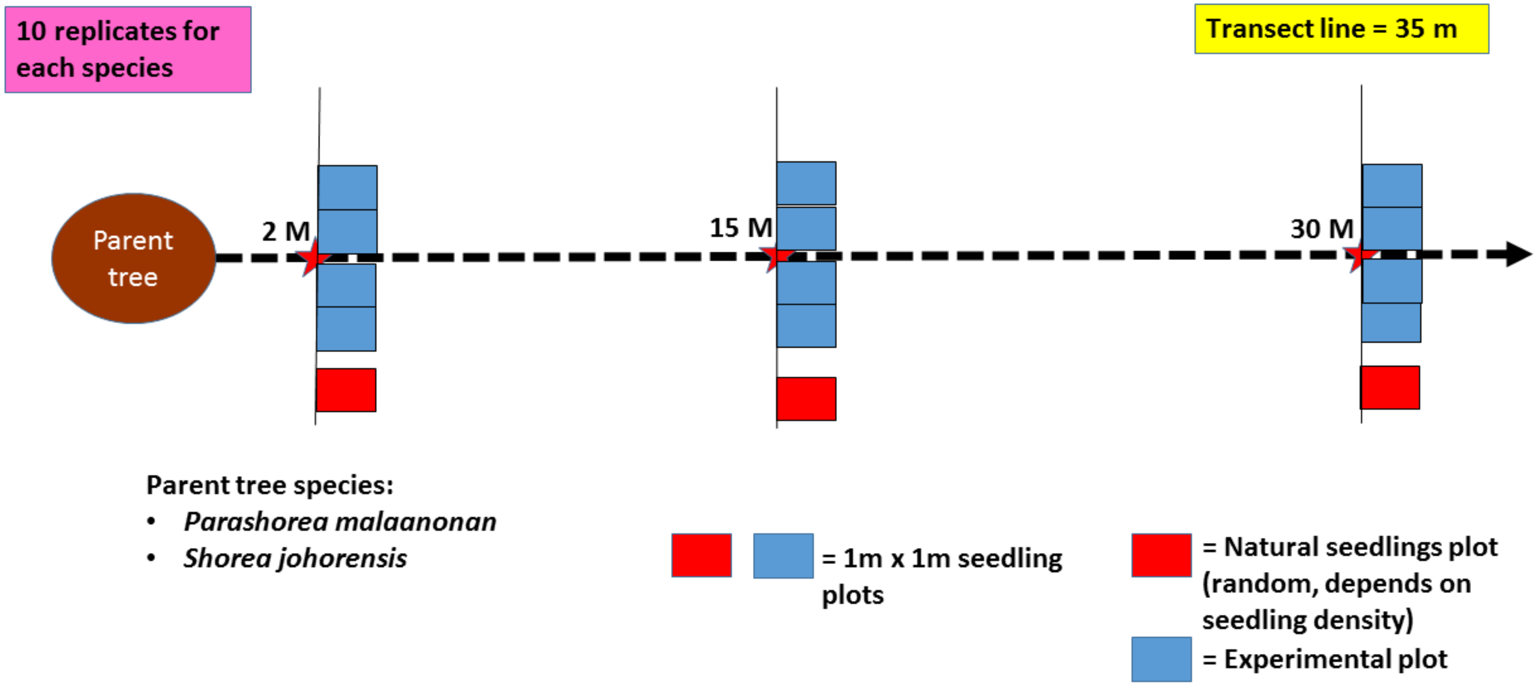
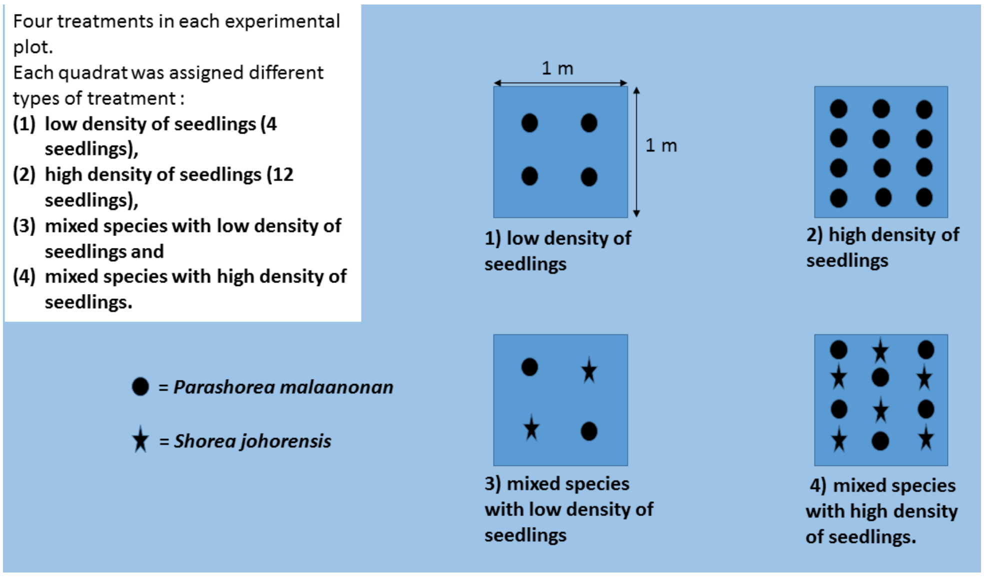


Figure S1: Study design of distance and density dependence experimental chapter



Four treatments in each experimental plot.
Each quadrat was assigned different types of treatment :
(1) low density of seedlings (4 seedlings),
(2) high density of seedlings (12 seedlings),
(3) mixed species with low density of seedlings and
(4) mixed species with high density of seedlings.

Figure S2: Planting treatment applied in the distance and density dependence experimental chapter

Parashorea malaanonan *Shorea johorensis*

Figure S3: Selected dipterocarp species in the distance and density dependence experimental chapter

Appendix B

Appendix B1: References for studies included in the meta-analysis of distance- and density-dependent survival.

Augspurger, C.K. & Kelly, C.K. (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia.

Augspurger, C.K. & Kitajima, K. (1992) Experimental studies of seedling recruitment from contrasting seed distributions. Ecology, 73, 1270-1284.

Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripenberg, S., Narayan, L. and Freckleton, R.P., 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. Ecology letters, 13(10), pp.1262-1269.

Bagchi, R., Philipson, C.D., Slade, E.M., Hector, A., Phillips, S., Villanueva, J.F., Lewis, O.T., Lyal, C.H., Nilus, R., Madran, A. and Scholes, J.D., 2011. Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1582), pp.3246-3255.

Bell, T., Freckleton, R.P. & Lewis, O.T. (2006) Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecology letters, 9, 569-574.

Bermejo, T., Traveset, A. & Willson, M.F. (1998) Post-dispersal seed predation in the temperate rainforest of Southeast Alaska. Canadian Field Naturalist, 112, 510-512.

Boman, J.S. and Casper, B.B., 1995. Differential postdispersal seed predation in disturbed and intact temperate forest. American Midland Naturalist, pp.107-116.

Boyd, R.S. (2001) Ecological benefits of myrmecochory for the endangered chaparral shrub Fremontodendron decumbens (Sterculiaceae). American Journal of Botany, 88, 234-241.

Brewer, S.W. & Webb, M.a.H. (2001) Ignorant seed predators and factors affecting the seed survival of a tropical palm. Oikos, 93, 32-41.

Burkey, T.V. (1994) Tropical tree species diversity : a test of the Janzen-Connell model. Oecologia, 97, 533-540.

Bustamante, R.O. & Simonetti, J.A. (2000) Seed predation and seedling recruitment in plants: the effect of the distance between parents. Plant Ecology, 147, 173-183.

Caccia, F.D. & Ballaré, C.L. (1998) Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (Pseudotsuga menziesii) in southwestern Argentina. Canadian Journal of Forest Research, 28, 683-692.

Casper, B.B. (1987) Spatial patterns of seed dispersal and postdispersal seed predation of Cryptantha flava (Boraginaceae). American Journal of Botany, 74, 1646-1655.

Casper, B.B. (1988) Seed predation may select for wind dispersal but not seed number per dispersal unit in Cryptantha flava. Oikos, 52, 27-30.

Castellanos, M.C. and Stevenson, P.R., 2011. Phenology, seed dispersal and difficulties in natural recruitment of the canopy tree Pachira quinata (Malvaceae). Revista de biologia tropical.

Chapman, C.A. & Chapman, L.J. (1996) Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. Journal of Tropical Ecology, 12, 491-504.

Cintra, R. & Horna, V. (1997) Seed and seedling survival of the palm Astrocaryum murumuru and the legume tree Dipteryx micrantha in gaps in Amazonian forest. Journal of Tropical Ecology, 13, 257-257.

Clark, C.J., Poulsen, J.R. and Levey, D.J., 2013. Roles of seed and establishment limitation in determining patterns of Afrotropical tree recruitment. PloS one, 8(5), p.e63330.

Coates-Estrada, R. & Estrada, A. (1988) Frugivory and seed dispersal in Cymbopetalum bailloni (Annonaceae) at Los Tuxtlas, Mexico. Journal of Tropical Ecology, 4, 157-172.

Curio, E., Reiter, J. & Tacud, B. (2003) Seedling mortality of six Phillpine rain forest tree species: a test of the 'escape hypothesis'. Ecotropica, 9, 59-70.

Dalling, J.W., Swaine, M.D. & Garwood, N.C. (1998) Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology, 79, 564-578.

DeSteven, D. & Putz, F.E. (1984) Impact of mammals on early recruitment of a tropical canopy tree, Dipteryx panamensis, in Panama. Oikos, 2, 207-216.

Forget, P.-M. (1993) Post-dispersal predation and scatterhoarding of Dipteryx panamensis (Papilionaceae) seeds by rodents in Panama. Oecologia, 94, 255-261.

Forget, P.M. (1992) Seed removal and seed fate in Gustavia superba (Lecythidaceae). Biotropica, 24, 408-414.

Fricke, E.C., Simon, M.J., Reagan, K.M., Levey, D.J., Riffell, J.a., Carlo, T.a. & Tewksbury, J.J. (2013) When condition trumps location: seed consumption by fruit-eating birds removes pathogens and predator attractants. Ecology letters, 16, 1031-1036.

Fricke, E.C., Tewksbury, J.J. and Rogers, H.S., 2014. Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. Ecology letters, 17(5), pp.593-598.

Fukasawa, Y. and Seiwa, K., 2016. Roles of pathogens on replacement of tree seedlings in heterogeneous light environments in a temperate forest: a reciprocal seed sowing experiment. Journal of Ecology, 104(3), pp.765-772.

Gripenberg, S., Bagchi, R., Gallery, R.E., Freckleton, R.P., Narayan, L. and Lewis, O.T., 2014. Testing for enemy-mediated density-dependence in the mortality of seedlings: field experiments with five Neotropical tree species. Oikos, 123(2), pp.185-193.

Gryj, E.O. & Domíguez, C.A. (1996) Fruit removal and postdispersal survivorship in the tropical dry forest shrub Erythroxylum havanense: ecological and evolutionary implications. Oecologia, 3041, 368-374.

Gustafsson, C. and Ehrlén, J., 2003. Effects of intraspecific and interspecific density on the demography of a perennial herb, Sanicula europaea. Oikos, 100(2), pp.317-324.

Hart, T.B. (1995) Seed, seedling and sub-canopy survival in monodominant and mixed forests of the Ituri Forest, Africa. Journal of Tropical Ecology, 11, 443-459.

Hautier, Y., Saner, P., Philipson, C., Bagchi, R., Ong, R.C. and Hector, A., 2010. Effects of seed predators of different body size on seed mortality in Bornean logged forest. PloS one, 5(7), p.e11651.

Hewitt, N. and Kellman, M., 2004. Factors influencing tree colonization in fragmented forests: an experimental study of introduced seeds and seedlings. Forest Ecology and management, 191(1-3), pp.39-59.

Holl, K.D. and Lulow, M.E., 1997. Effects of Species, Habitat, and Distance from Edge on Post-dispersal Seed Predation in a Tropical Rainforest 1. Biotropica, 29(4), pp.459-468.

Howe, H.F. (1993) Aspects of variation in a neotropical seed dispersal system. Vegetatio, 107, 149-162.

Howe, H.F., Schupp, E.W. & Westley, L.C. (1985) Early consequences of seed dispersal for a neotropical tree (Virola surinamensis). Ecology, 66, 781-791.

Hulme, P.E. (1996) Natural regeneration of yew (Taxus baccata L.): microsite, seed or herbivore limitation? Journal of Ecology, 84, 853-861.

Hulme, P.E. (1997) Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. Oecologia, 111, 91-98.

Huxham, M., Kumara, M.P., Jayatissa, L.P., Krauss, K.W., Kairo, J., Langat, J., Mencuccini, M., Skov, M.W. and Kirui, B., 2010. Intra-and interspecific facilitation in mangroves may increase resilience to climate change threats. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1549), pp.2127-2135.

Hyatt, L.A., 1998. Spatial patterns and causes of overwinter seed mortality in Phytolacca americana. Canadian Journal of Botany, 76(2), pp.197-203.

Itoh, A. (1995) Survival and growth of seedlings of four dipterocarp species in a tropical rainforest of Sarawak, East Malaysia. 327-338.

Janzen, D.H., 1982. Removal of seeds from horse dung by tropical rodents: Influnce of habitat and amount of dung. Ecology, 63(6), pp.1887-1900.

Kelly, D., Ladley, J.J. and Robertson, A.W., 2007. Is the pollen-limited mistletoe Peraxilla tetrapetala (Loranthaceae) also seed limited?. Austral Ecology, 32(8), pp.850-857.

Kolb, A. and Barsch, K., 2010. Environmental factors and seed abundance influence seedling emergence of a perennial forest herb. Acta Oecologica, 36(5), pp.507-513.

Kwit, C., Levey, D.J. and Greenberg, C.H., 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. Oikos, 107(2), pp.303-308.

Levi, T. and Peres, C.A., 2013. Dispersal vacuum in the seedling recruitment of a primate-dispersed Amazonian tree. Biological Conservation, 163, pp.99-106.

Liu, Y., Yu, S., Xie, Z.P. and Staehelin, C., 2012. Analysis of a negative plant–soil feedback in a subtropical monsoon forest. Journal of Ecology, 100(4), pp.1019-1028.

Lott, R.H., Harrington, G.N., Irvine, A.K. & McIntyre, S. (1995) Density-dependent seed predation and plant dispersion of the tropical palm Normanbya normanbyi. Biotropica, 14, 139-151.

Louda, S.M. and Zedler, P.H., 1985. Predation in insular plant dynamics: an experimental assessment of postdispersal fruit and seed survival, Enewetak Atoll, Marshall Islands. American Journal of Botany, 72(3), pp.438-445.

Mack, A.L., Ickes, K., Jessen, J.H., Kennedy, B. and Sinclair, R., 1999. Ecology of Aglaia mackiana (Meliaceae) Seedlings in a New Guinea Rain Forest 1. Biotropica, 31(1), pp.111-120.

Maetô, K. & Fukuyama, K. (1997) Mature tree effect ofAcer mono on seedling mortality due to insect herbivory. Ecological Research, 12, 337-343.

Maher, C.T., Barber, A.L. and Affleck, D.L., 2015. Shelter provided by wood, facilitation, and density-dependent herbivory influence Great Basin bristlecone pine seedling survival. Forest Ecology and Management, 342, pp.76-83.

Manson, R.H. and Stiles, E.W., 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. Oikos, pp.37-50.

Mariano, V. and Christianini, A.V., 2016. Reproductive phenology, seed removal and early regeneration in relation to distance from parental plants of a native palm in small Atlantic forest fragments. Acta Botanica Brasilica, 30(2), pp.176-182.

Masaka, K. and Seiwa, K., 2017. Leaf diseases drive the Janzen–Connell mechanism regardless of light conditions: a 3-year field study. Oecologia, 183(1), pp.191-199.

Masaki, T., Tanaka, H., Shibata, M. & Nakashizuka, T. (1998) The seed bank dynamics of Cornus controversa and their role in regeneration. Seed Science Research, 8, 53-63.

Massey, F.P., Massey, K., Press, M.C. & Hartley, S.E. (2006) Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. Journal of Ecology, 94, 646-655.

Matthesius, A., Chapman, H. & Kelly, D. (2011) Testing for Janzen-Connell effects in a West African montane forest. Biotropica, 43, 77-83.

Molofsky, J. and Fisher, B.L., 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. Ecology, 74(1), pp.261-265.

Myster, R.W. & Pickett, S.T.A. (1993) Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos, 66, 381-388.

Nichols, J.D. & Agyeman, V.K. (1999) Patterns of seedling survival in the tropical African tree Milicia excelsa. Journal of tropical …, 15, 451-461.

Norghauer, J.M., Grogan, J., Malcolm, J.R. & Felfili, J.M. (2010a) Long-distance dispersal helps germinating mahogany seedlings escape defoliation by a specialist caterpillar. Oecologia, 162, 405-412.

Norghauer, J.M., Malcolm, J.R., Zimmerman, B.L. & Felfili, J.M. (2006) An experimental test of density- and distant-dependent recruitment of mahogany (Swietenia macrophylla) in southeastern Amazonia. Oecologia, 148, 437-446.

Norghauer, J.M., Newbery, D.M., Tedersoo, L. & Chuyong, G.B. (2010b) Do fungal pathogens drive density-dependent mortality in established seedlings of two dominant African rain-forest trees? Journal of Tropical Ecology, 26, 293-293.

Norghauer, J.M., Free, C.M., Landis, R.M., Grogan, J., Malcolm, J.R. and Thomas, S.C., 2016. Herbivores limit the population size of big-leaf mahogany trees in an Amazonian forest. Oikos, 125(1), pp.137-148.

Notman, E., Gorchov, D.L. & Cornejo, F. (1996) Effect of distance , aggregation , and habitat on levels of seed predation for two mammal: dispersed neotropical rain forest tree species. Oecologia, 106, 221-227.

Nyiramana, A., Mendoza, I., Kaplin, B.a. & Forget, P.-M. (2011) Evidence for seed dispersal byrRodents in tropical montane forest in Africa. Biotropica, 43, 654-657.

Oliveira, A.D.S., Carvalho, M.L.M.D., Nery, M.C., Oliveira, J.A. and Guimarães, R.M., 2011. Seed quality and optimal spatial arrangement of fodder radish. Scientia Agricola, 68(4), pp.417-423.

Parker, M.A. (1982) Association with mature plants protects seedlings from predation in an arid grassland. Oecologia, 53, 276-280.

Peres, C.a., Schiesari, L.C. & Dias-Leme, C.L. (1997) Vertebrate predation of Brazil-nuts (Bertholletia excelsa, Lecythidaceae), an agouti-dispersed Amazonian seed crop: a test of the escape hypothesis. Journal of Tropical Ecology, 13, 69-79.

Pigot, A.L. & Leather, S.R. (2008) Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree Acer pseudoplatanus. Oikos, 117, 521-530.

Pizo, M.A. (1997) Seed dispersal and predation in two populations of Cabralea canjerana (Meliaceae) in the Atlantic Forest of southeastern Brazil. Journal of Tropical Ecology, 13, 559-559.

Poulsen, J.R., Clark, C.J. and Bolker, B.M., 2012. Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. Ecology, 93(3), pp.500-510.

Ramírez, B.H., Parrado-Rosselli, Á. and Stevenson, P., 2009. Seed dispersal of a useful palm (Astrocaryum chambira Burret) in three Amazonian forests with different human intervention. Colombia Forestal, 12(1), pp.5-16.

Rand, T.A. (2003) Herbivore-mediated apparent competition between two salt marsh forbs. Ecology, 84, 1517-1526.

Rausher, M.D. & Feeny, P. (1980) Herbivory , plant density , and plant reproductive success: the effect of BattuspPhilenor on Aristolochia reticulata. Ecology, 61, 905-917.

Reinhart, K.O. & Clay, K. (2009) Spatial variation in soil-borne disease dynamics of a temperate tree, Prunus serotina. Ecology, 90, 2984-2993.

Reinhart, K.O., Johnson, D. & Clay, K. (2012) Effects of trees on their recruits in the southern Appalachians, USA. Forest Ecology and Management, 263, 268-274.

Roberts, J.T. & Heithaus, E.R. (1986) Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. Ecology, 67, 1046-1051.

Rogers, H.S., Buhle, E.R., HilleRisLambers, J., Fricke, E.C., Miller, R.H. and Tewksbury, J.J., 2017. Effects of an invasive predator cascade to plants via mutualism disruption. Nature Communications, 8, p.14557.

Rolhauser, A.G., Chaneton, E.J. & Batista, W.B. (2011) Influence of conspecific and heterospecific adults on riparian tree species establishment during encroachment of a humid palm savanna. Oecologia, 167, 141-148.

Russell, S.K. & Schupp, E.W. (1998) Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of Cercocarpus ledifolius (Rosaceae). Oikos, 81, 434-443.

Sanchez-Cordero, V. & Martinez-Gallardo, R. (1998) No postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. Journal of Tropical Ecology, 14, 139-151.

Scheper, J. & Smit, C. (2011) The role of rodents in the seed fate of a thorny shrub in an ancient wood pasture. Acta Oecologica, 37, 133-139.

Schupp, E.W. (1988) Seed and early seedling predation in the forest understory and in treefall gaps. Oikos, 51, 71-78.

Schupp, E.W. & Frost, E.J. (1989) Differential predation of Welfia georgii seeds in treefall gaps and the forest understory. Biotropica, 21, 200-203.

Setterfield, S.A., 2002. Seedling establishment in an Australian tropical savanna: effects of seed supply, soil disturbance and fire. Journal of Applied Ecology, 39(6), pp.949-959.

Smith, B.H., Forman, P.D. & Boyd, A.E. (1989) Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. Ecology, 70, 1649-1656.

Souza, F.M., Franco, G.A.D.C. and Callaway, R.M., 2013. Strong distance-dependent effects for a spatially aggregated tropical species. Plant ecology, 214(4), pp.545-555.

Stevenson, P.R., Link, A. & Ramírez, B.H. (2005) Frugivory and seed rate in Bursera inversa (Burseraceae) at Tinigua Park, Colombia: implications for primate conservation. Biotropica, 37, 431-438.

Sugiyama, A. and Peterson, C.J., 2015. Transplant experiments reveal edge effects and inconsistent maternal effects on seedling performance in the pioneer tree Ficus tonduzii (Moraceae). Tropics, 24(3), pp.91-99.

Swamy, V. & Terborgh, J.W. (2010) Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. Journal of Ecology, 98, 1096-1107.

Takeuchi, Y. & Nakashizuka, T. (2007) Effect of distance and density on seed/seedling fate of two dipterocarp species. Forest Ecology and Management, 247, 167-174.

Terborgh, J., Losos, E., Riley, M.P. & Riley, M.B. (1993) Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. Vegetatio, 107, 375-386.

Traveset, A. (1990) Post-dispersal predation of Acacia farnesiana seeds by Stator vachelliae (Bruchidae) in Central America. Oecologia, 84, 506-512.

Urli, M., Brown, C.D., Narváez Perez, R., Chagnon, P.L. and Vellend, M., 2016. Increased seedling establishment via enemy release at the upper elevational range limit of sugar maple. Ecology, 97(11), pp.3058-3069.

Verdu, M. & Garcia-Fayos, P. (1996) Postdispersal seed predation in a Mediterranean patchy landscape. Acta Oecologica, 17, 379-391.

Webb, S.L. & Willson, M.F. (1985) Spatial heterogeneity in post-dispersal predation on Prunus and Uvularia seeds. Oecologia, 67, 150-153.

Wenny, D.G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecological Monographs, 70, 331-351.

Xu, M., Wang, Y., Liu, Y., Zhang, Z. and Yu, S., 2015a. Soil-borne pathogens restrict the recruitment of a subtropical tree: a distance-dependent effect. Oecologia, 177(3), pp.723-732.

Xu, M., Wang, Y. and Yu, S., 2015b. Conspecific negative density dependence decreases with increasing species abundance. Ecosphere, 6(12), pp.1-11.

Yamazaki, M., Iwamoto, S. & Seiwa, K. (2009) Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest. Plant Ecology, 201, 181-196.

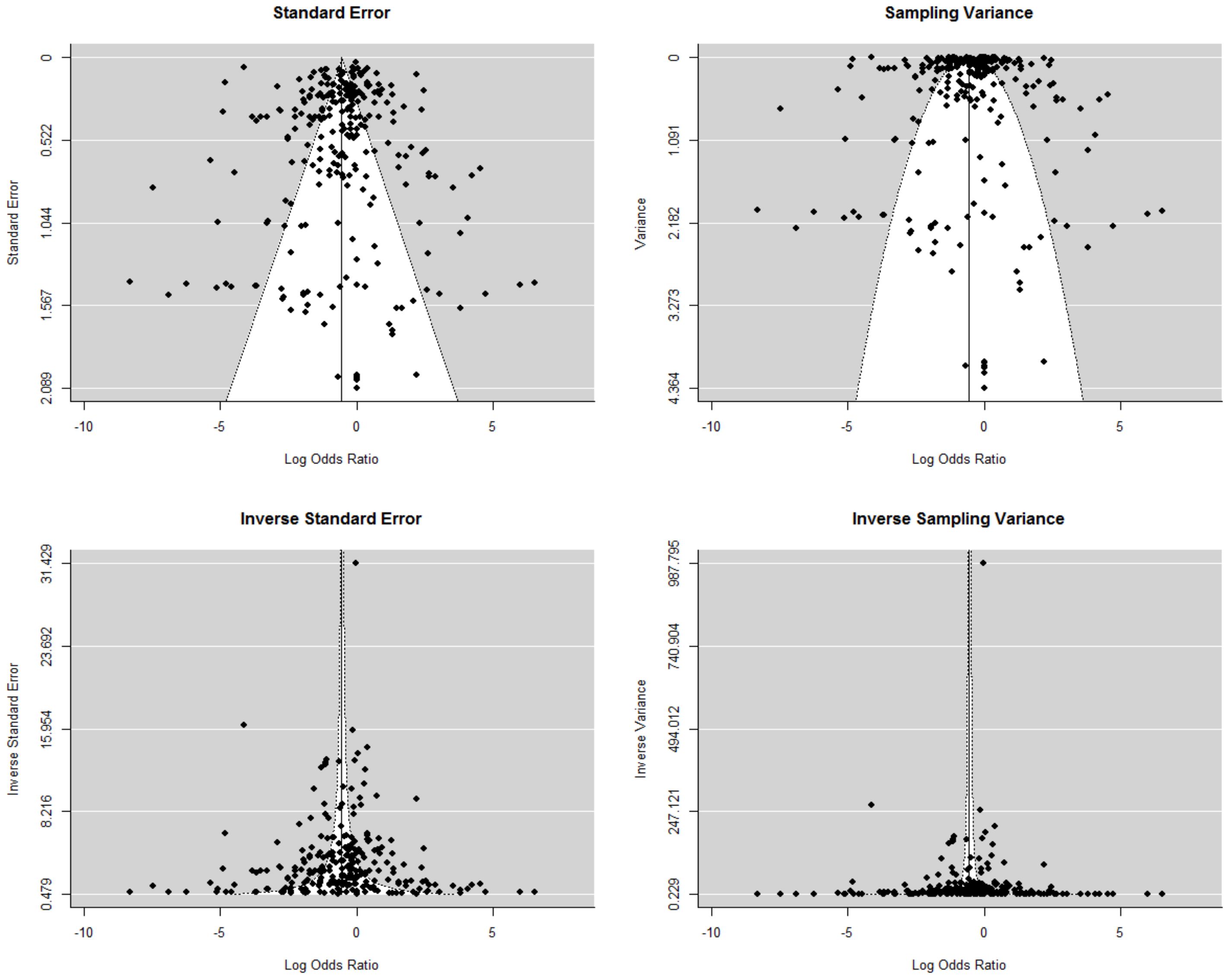


Figure S1: Funnel plot. No evidence of publication bias. Rank correlation test was not significant (Kendall' s tau = - 0.051, p-value = 0. 223)

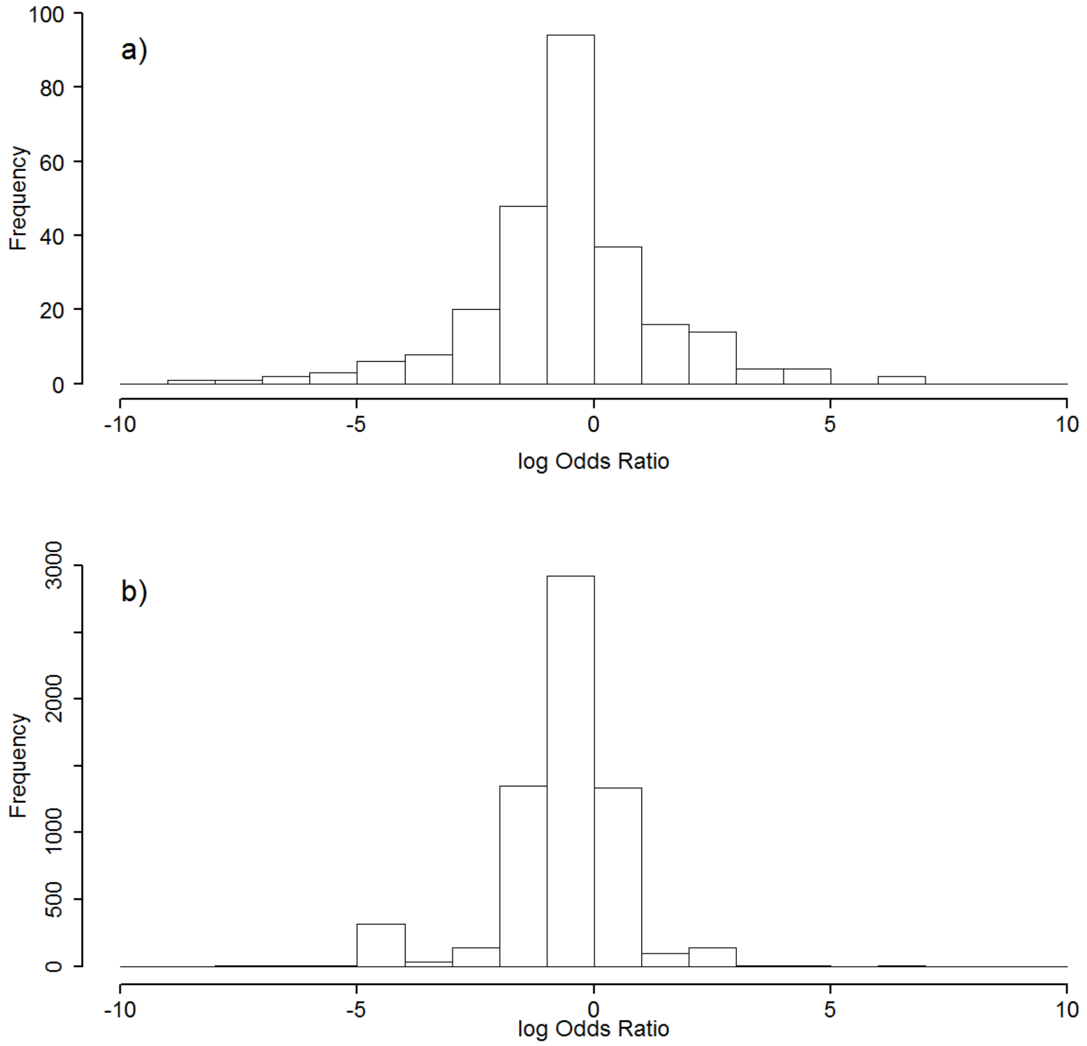


Figure S2: Check for publication bias. a) Histogram of logs odds ratios; b) histogram of log odd ratio weighted by 1/variance.

Appendix C: List of plant traits of dipterocarp species that have been used in this study

Traits	Definition	Units	Description of classes
Lower elevation limit	Low distance above sea level of species occurrence	m	Quantitative value
Upper elevation limit	High distance above sea level of species occurrence	m	Quantitative value
Endemism	Species that being unique to specific location		Qualitative (Widespread = 0, Endemic= 1)
Estimated Extent of Occurrence	"area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy", (IUCN 2001)	km^2	Quantitative value
Estimated Area of Occupancy	"area within its 'extent of occurrence' which is occupied by a taxon, excluding cases of vagrancy", (IUCN 2001)	km^2	Quantitative value
Habitat Soil type	Soil type that inhabited by plant (Voroney, 2007)		Qualitative (Soil type= Clay, Sandy, Loam, and Limestone Inhabiting? Yes= 1, No=0)
Height	Distance from ground level to the level top of the tree	m	Quantitative value
Diameter at breast height (DBH)	Measurement of tree stem at the height of 1.30 m	cm	Quantitative value

Growth rate	Girth increment per year	cm/per year	Quantitative value
Shade tolerance	Ability to tolerate low light level		Qualitative (Shade tolerant= 0, Intermediate= 1, Light demander= 2)
Leaf length	Length of the leaf in vascular plants from lamina tip to the petioles along lamina midrib (Cho *et al.*, 2007)	cm	Quantitative value
Flower size	Diameter of flower	mm	Qualitative (Small(<10mm) = 0, Medium(10—20mm) = 1, Large(>20mm) = 2)
Flower reward	Secretion or structure of the labellum that can be consumed or gathered by pollinators (Singer & Koehler 2004)		Qualitative (Type= Nectar, Pollen and Corolla, Produced? Yes= 1, No= 0)
Survival	Tree mortality	%	Quantitative value
Flowering frequency	Regularity of flowering in vascular plant		Qualitative (General= 0, Regular= 1)
Anthesis (Day)	Flowering period of plant (0600-1800)		Qualitative (Yes= 1, No= 0)
Anthesis (Night)	Flowering period of plant (1800-0600)		Qualitative (Yes=1, No=0)
Chromosome number	Number of DNA molecule that carry genetic information of plant (Battaglia, 1955)		Qualitative (Chromosome no x=7,10,11 and Polyploidy, Yes=1, No=0)
Outcrossing rate	Rates of crossing between different breeds	%	Quantitative value
Fruit length	Length of nut	mm	Quantitative value
Fruit width	Width of nut	mm	Quantitative value

Seed weight	Seed mass	seed per kilo	Quantitative value
Functional wing	Wings that involved in seed dispersal		Qualitative (Wing no= 0,2,3 and 5, Has? Yes= 1, No=0)
Functional wing length	Measurement of length of wings involved in dispersal	mm	Quantitative value
Wing loading	Fruit mass divided by wing surface area(Green, 1980)		Quantitative value
Wood type	Hardwood type classification		Qualitative (Light Hardwood=0, Medium Hardwood= 1, Heavy Hardwood= 2)
Wood densities	"Measurement of the ratio of oven-dry mass of wood divided mass of water displaced by its green volume " (Chave, no date)	g/cm^3	Quantitative value
Red List status	Species conservation status through criteria such as population size, rate of decline and geographic distribution as listed in IUCN Red List Categories (IUCN 2017)		Qualitative (Data Deficient= 0, Least Concern= 1, Near Threatened= 2, Vulnerable= 3, Endangered=4, Critically Endangered=5, Extinct in The Wild= 6)

Appendix C1: Dipterocarp species list used in the study

Anisoptera brunnea
Anisoptera costata
Anisoptera curtisii
Anisoptera grossivenia
Anisoptera laevis
Anisoptera marginata
Anisoptera megistocarpa
Anisoptera reticulata
Anisoptera scaphula
Anisoptera thurifera
Cotylelobium burckii
Cotylelobium lanceolatum
Cotylelobium lewisianum
Cotylelobium melanoxylon
Cotylelobium scabriusculum
Dipterocarpus acutangulus
Dipterocarpus alatus
Dipterocarpus applanatus
Dipterocarpus baudii
Dipterocarpus borneensis
Dipterocarpus bourdillonii
Dipterocarpus caudatus
Dipterocarpus caudiferus
Dipterocarpus chartaceus
Dipterocarpus cinereus
Dipterocarpus concavus
Dipterocarpus confertus
Dipterocarpus conformis
Dipterocarpus lowii
Dipterocarpus mannii
Dipterocarpus megacarpus
Dipterocarpus mundus
Dipterocarpus nudus
Dipterocarpus oblongifolius
Dipterocarpus obtusifolius
Dipterocarpus ochraceus
Dipterocarpus orbicularis
Dipterocarpus pachyphyllus
Dipterocarpus palembanicus
Dipterocarpus perakensis
Dipterocarpus pseudocornutus
Dipterocarpus retusus
Dipterocarpus rigidus
Dipterocarpus rotundifolius
Dipterocarpus sarawakensis
Dipterocarpus semivestitus
Dipterocarpus coriaceus
Dipterocarpus cornutus
Dipterocarpus costatus
Dipterocarpus costulatus
Dipterocarpus crinitus
Dipterocarpus cuspidatus
Dipterocarpus dyeri
Dipterocarpus elongatus
Dipterocarpus eurhynchus
Dipterocarpus fagineus
Dipterocarpus fusiformis
Dipterocarpus geniculatus
Dipterocarpus glabrigemmatus
Dipterocarpus glandulosus
Dipterocarpus globosus
Dipterocarpus gonopterus
Dipterocarpus gracilis
Dipterocarpus grandiflorus
Dipterocarpus hasseltii
Dipterocarpus hispidus
Dipterocarpus humeratus
Dipterocarpus indicus
Dipterocarpus insignis
Dipterocarpus intricatus
Dipterocarpus kerrii
Dipterocarpus kunstleri
Dipterocarpus lamellatus
Dipterocarpus littoralis
Dryobalanops fusca
Dryobalanops keithii
Dryobalanops lanceolata
Dryobalanops oblongifolia
Dryobalanops rappa
Dryobalanops sumatrensis
Hopea acuminata
Hopea aequalis
Hopea altocollina
Hopea andersonii
Hopea apiculata
Hopea aptera
Hopea auriculata
Hopea bancana
Hopea basilanica
Hopea beccariana
Hopea bilitonensis
Hopea brachyptera

Dipterocarpus stellatus
Dipterocarpus sublamellatus
Dipterocarpus tempehes
Dipterocarpus tuberculatus
Dipterocarpus turbinatus
Dipterocarpus validus
Dipterocarpus verrucosus
Dipterocarpus zeylanicus
Dryobalanops aromatica
Dryobalanops beccarii
Hopea cordata
Hopea cordifolia
Hopea coriacea
Hopea dasyrrhachis
Hopea depressinerva
Hopea discolor
Hopea dryobalanoides
Hopea dyeri
Hopea enicosanthoides
Hopea erosa
Hopea exalata
Hopea ferrea
Hopea ferruginea
Hopea fluvialis
Hopea forbesii
Hopea foxworthyi
Hopea glabra
Hopea glabrifolia
Hopea glaucescens
Hopea gregaria
Hopea griffithii
Hopea hainanensis
Hopea helferi
Hopea hongayanensis
Hopea inexpectata
Hopea iriana
Hopea jacobi
Hopea johorensis
Hopea paucinervis
Hopea pedicellata
Hopea pentanervia
Hopea philippinensis
Hopea pierrei
Hopea plagata
Hopea polyalthioides
Hopea ponga
Hopea pterygota
Hopea pubescens
Hopea bracteata
Hopea brevipetiolaris
Hopea bullatifolia
Hopea cagayanensis
Hopea canarensis
Hopea celebica
Hopea celtidifolia
Hopea centipeda
Hopea cernua
Hopea chinensis
Hopea jucunda
Hopea kerangasensis
Hopea kitulgallensis
Hopea latifolia
Hopea longirostrata
Hopea malibato
Hopea megacarpa
Hopea mengarawan
Hopea mesuoides
Hopea micrantha
Hopea mindanensis
Hopea modesta
Hopea mollissima
Hopea montana
Hopea myrtifolia
Hopea nervosa
Hopea nigra
Hopea nodosa
Hopea novoguineensis
Hopea nutans
Hopea oblongifolia
Hopea obscurinerva
Hopea odorata
Hopea ovoidea
Hopea pachycarpa
Hopea papuana
Hopea parviflora
Hopea parvifolia
Hopea treubii
Hopea ultima
Hopea utilis
Hopea vacciniifolia
Hopea vesquei
Hopea vietnamensis
Hopea wyatt-smithii
Marquesia acuminata
Marquesia excelsa
Marquesia macroura

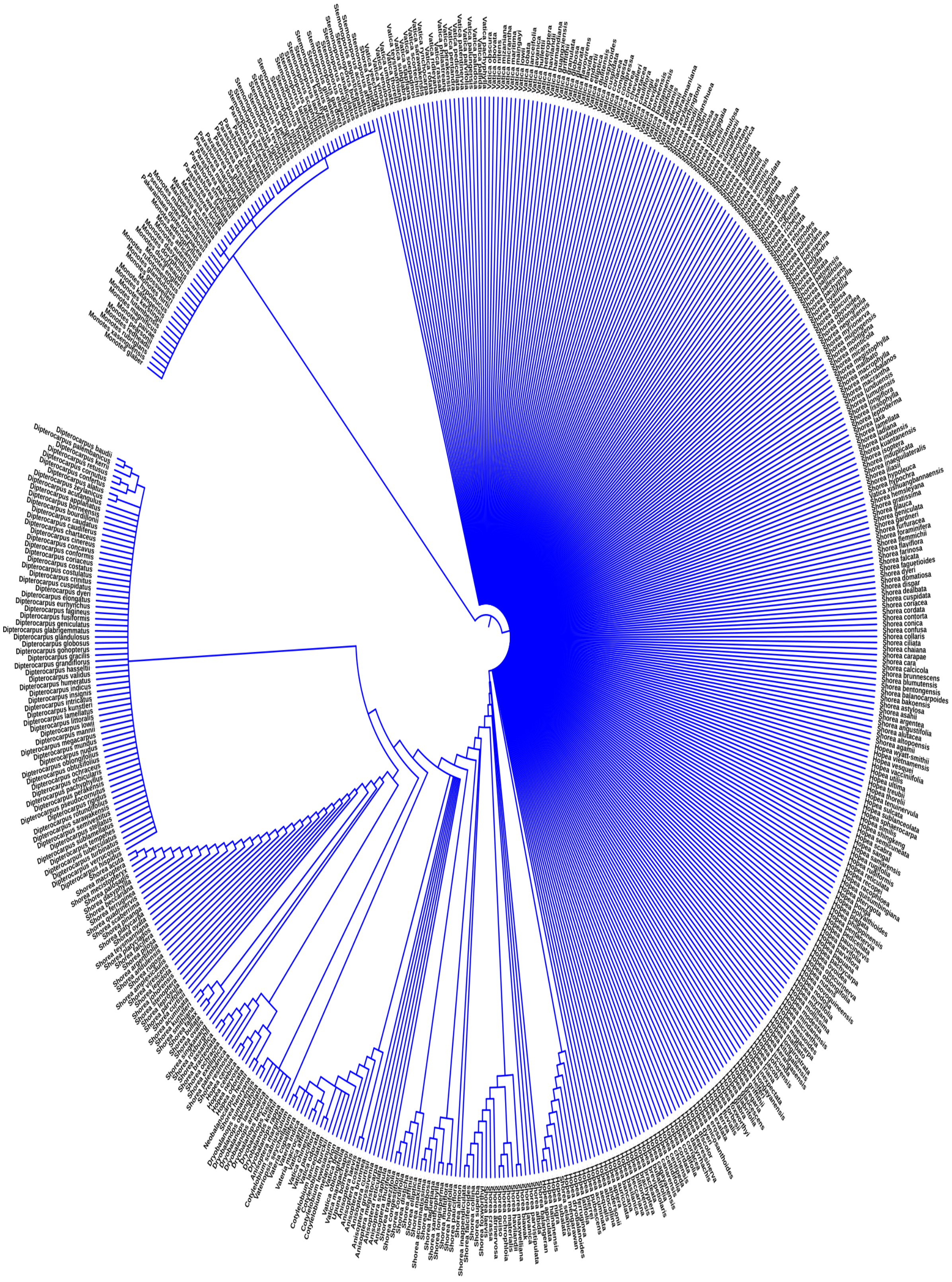
Hopea quisumbingiana
Hopea racophloea
Hopea recopei
Hopea reticulata
Hopea rudiformis
Hopea rugifolia
Hopea samarensis
Hopea sangal
Hopea scabra
Hopea semicuneata
Hopea shingkeng
Hopea similis
Hopea sphaerocarpa
Hopea subalata
Hopea sublanceolata
Hopea sulcata
Hopea tenuinervula
Hopea thorelii
Monotes pearsonii
Monotes redheadii
Monotes rubriglans
Monotes rufotomentosus
Monotes xasenguensis
Neobalanocarpus heimii
Pakaraimaea dipterocarpacea
Parashorea aptera
Parashorea buchananii
Parashorea chinensis
Parashorea densiflora
Parashorea dussaudii
Parashorea globosa
Parashorea lucida
Parashorea macrophylla
Parashorea malaanonan
Parashorea parvifolia
Parashorea smythiesii
Parashorea stellata
Parashorea tomentella
Parashorea warburgii
Pseudomonotes tropenbosii
Shorea acuminata
Shorea acuminatissima
Shorea acuta
Shorea affinis
Shorea agamii
Shorea albida
Shorea collina
Shorea confusa
Monotes adenophyllus
Monotes africanus
Monotes autennei
Monotes dasyanthus
Monotes doryphorus
Monotes duvigneaudii
Monotes engleri
Monotes glaber
Monotes glandulosus
Monotes gossweileri
Monotes hirtii
Monotes hypoleucus
Monotes katangensis
Monotes kerstingii
Monotes lutambensis
Monotes madagascariensis
Monotes magnificus
Monotes paivae
Shorea almon
Shorea altopoensis
Shorea alutacea
Shorea amplexicaulis
Shorea andulensis
Shorea angustifolia
Shorea argentea
Shorea argentifolia
Shorea asahii
Shorea assamica
Shorea astylosa
Shorea atrinervosa
Shorea bakoensis
Shorea balangeran
Shorea balanocarpoides
Shorea beccariana
Shorea bentongensis
Shorea biawak
Shorea blumutensis
Shorea bracteolata
Shorea brunnescens
Shorea bullata
Shorea calcicola
Shorea cara
Shorea carapae
Shorea chaiana
Shorea ciliata
Shorea collaris
Shorea flemmichii
Shorea foraminifera

Shorea congestiflora
Shorea conica
Shorea contorta
Shorea cordata
Shorea cordifolia
Shorea coriacea
Shorea crassa
Shorea curtisii
Shorea cuspidata
Shorea dasyphylla
Shorea dealbata
Shorea dispar
Shorea disticha
Shorea domatiosa
Shorea dyeri
Shorea elliptica
Shorea exelliptica
Shorea faguetiana
Shorea faguetioides
Shorea falcata
Shorea falcifera
Shorea falciferoides
Shorea fallax
Shorea farinosa
Shorea ferruginea
Shorea flaviflora
Shorea laevis
Shorea lamellata
Shorea laxa
Shorea lepidota
Shorea leprosula
Shorea leptoderma
Shorea lissophylla
Shorea longiflora
Shorea longisperma
Shorea lumutensis
Shorea lunduensis
Shorea macrantha
Shorea macrobalanos
Shorea macrophylla
Shorea macroptera
Shorea malibato
Shorea materialis
Shorea maxima
Shorea maxwelliana
Shorea mecistopteryx
Shorea megistophylla
Shorea micans
Shorea foxworthyi
Shorea furfuracea
Shorea gardneri
Shorea geniculata
Shorea gibbosa
Shorea glauca
Shorea gratissima
Shorea guiso
Shorea havilandii
Shorea hemsleyana
Shorea henryana
Shorea hopeifolia
Shorea hulanidda
Shorea hypochra
Shorea hypoleuca
Shorea iliasii
Shorea inaequilateralis
Shorea inappendiculata
Shorea induplicata
Shorea isoptera
Shorea javanica
Shorea johorensis
Shorea kuantanensis
Shorea kudatensis
Shorea kunstleri
Shorea ladiana
Shorea oblongifolia
Shorea obovoidea
Shorea obscura
Shorea obtusa
Shorea ochracea
Shorea ochrophloia
Shorea ovalifolia
Shorea ovalis
Shorea ovata
Shorea pachyphylla
Shorea palembanica
Shorea pallescens
Shorea pallidifolia
Shorea palosapis
Shorea parvifolia
Shorea parvistipulata
Shorea patoiensis
Shorea pauciflora
Shorea peltata
Shorea pilosa
Shorea pinanga
Shorea platycarpa

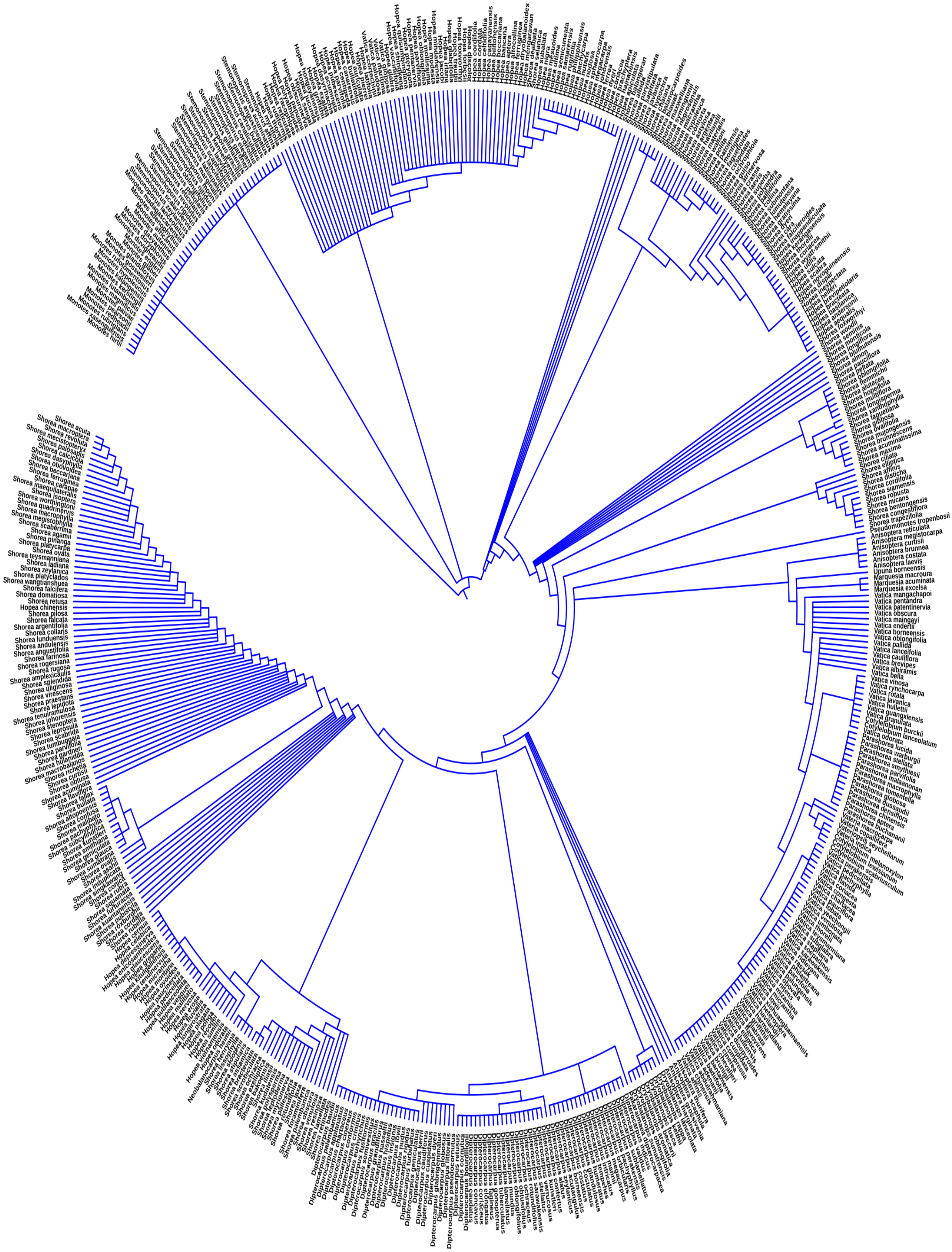
Shorea monticola
Shorea montigena
Shorea mujongensis
Shorea multiflora
Shorea myrionerva
Shorea negrosensis
Shorea quadrinervis
Shorea resinosa
Shorea retinodes
Shorea retusa
Shorea revoluta
Shorea richetia
Shorea robusta
Shorea rogersiana
Shorea rotundifolia
Shorea roxburghii
Shorea rubella
Shorea rubra
Shorea rugosa
Shorea sagittata
Shorea scaberrima
Shorea scabrida
Shorea scrobiculata
Shorea selanica
Shorea seminis
Shorea siamensis
Shorea singkawang
Shorea slootenii
Shorea smithiana
Shorea splendida
Shorea squamata
Shorea stenoptera
Shorea stipularis
Shorea subcylindrica
Stemonoporus kanneliyensis
Stemonoporus laevifolius
Stemonoporus lanceolatus
Stemonoporus lancifolius
Stemonoporus latisepalus
Stemonoporus marginalis
Stemonoporus mooni
Stemonoporus nitidus
Stemonoporus oblongifolius
Stemonoporus petiolaris
Stemonoporus reticulatus
Stemonoporus revolutus
Stemonoporus rigidus
Stemonoporus scalarinervis
Shorea platyclados
Shorea polita
Shorea polyandra
Shorea polysperma
Shorea praestans
Shorea pubistyla
Shorea submontana
Shorea sumatrana
Shorea superba
Shorea symingtonii
Shorea tenuiramulosa
Shorea teysmanniana
Shorea thorelii
Shorea trapezifolia
Shorea tumbuggaia
Shorea uliginosa
Shorea venulosa
Shorea virescens
Shorea waltoni
Shorea wangtianshuea
Shorea woodii
Shorea worthingtoni
Shorea xanthophylla
Shorea zeylanica
Stemonoporus acuminatus
Stemonoporus affinis
Stemonoporus angustisepalus
Stemonoporus bullatus
Stemonoporus canaliculatus
Stemonoporus cordifolius
Stemonoporus elegans
Stemonoporus gardneri
Stemonoporus gilimalensis
Stemonoporus gracilis
Vatica borneensis
Vatica brevipes
Vatica brunigii
Vatica cauliflora
Vatica chartacea
Vatica chevalieri
Vatica chinensis
Vatica cinerea
Vatica compressa
Vatica congesta
Vatica coriacea
Vatica cuspidata
Vatica diospyroides
Vatica dulitensis

Stemonoporus scaphifolius
Stemonoporus zeylanicus
Upuna borneensis
Vateria copallifera
Vateria indica
Vateria macrocarpa
Vateriopsis seychellarum
Vatica abdulrahmaniana
Vatica adenanii
Vatica affinis
Vatica albiramis
Vatica badiifolia
Vatica bantamensis
Vatica bella
Vatica lanceifolia
Vatica lobata
Vatica lowii
Vatica maingayi
Vatica mangachapoi
Vatica maritima
Vatica micrantha
Vatica mizaniana
Vatica nitens
Vatica oblongifolia
Vatica obovata
Vatica obscura
Vatica odorata
Vatica pachyphylla
Vatica pallida
Vatica paludosa
Vatica palungensis
Vatica parvifolia
Vatica patentinervia
Vatica pauciflora
Vatica pedicellata
Vatica pentandra
Vatica perakensis
Vatica philastreana
Vatica rassak
Vatica ridleyana
Vatica rotata
Vatica rynchocarpa
Vatica elliptica
Vatica endertii
Vatica flavida
Vatica flavovirens
Vatica glabrata
Vatica globosa
Vatica granulata
Vatica griffithii
Vatica guangxiensis
Vatica harmandiana
Vatica havilandii
Vatica heteroptera
Vatica hullettii
Vatica javanica
Vatica sarawakensis
Vatica scortechinii
Vatica soepadmoi
Vatica stapfiana
Vatica subglabra
Vatica teysmanniana
Vatica thorelii
Vatica umbonata
Vatica venulosa
Vatica vinosa
Vatica xishuangbannaensis
Vatica yeechongii

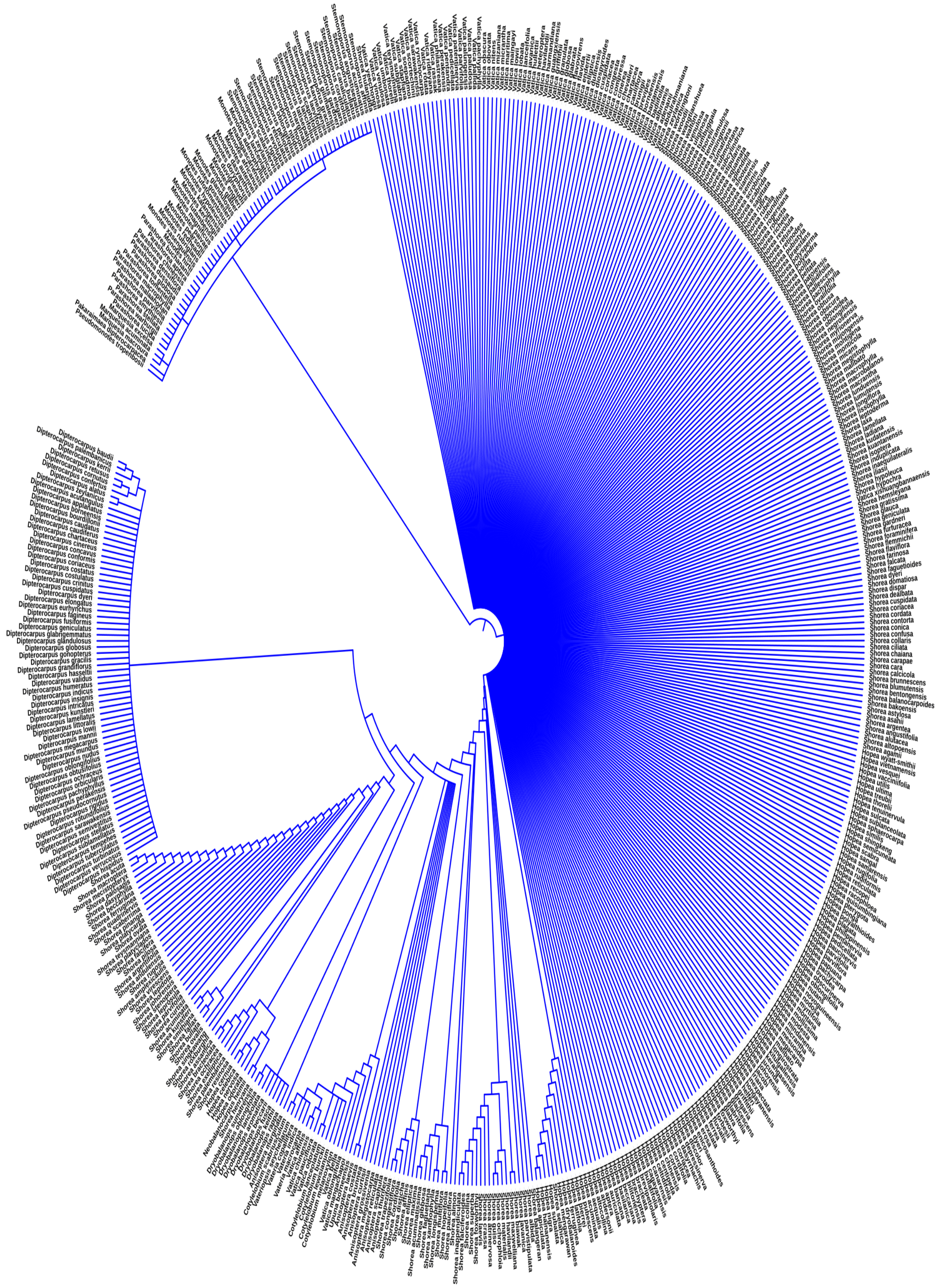
Appendix C2: Dipterocarp phylogeny in three scenarios. A) Scenario One; B) Scenario Two; C) Scenario Three



A) Scenario One



B) Scenario Two



C) Scenario Three