The role of trophic interactions in shaping tropical tree communities

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Summary Abstract

Tropical rainforests contain exceptionally high biodiversity and account for >30% of the world's carbon fixed by photosynthesis. Consequently, there are compelling reasons to deepen our understanding of the mechanisms that maintain these highly diverse forests and of the potential long-term threats to their preservation. An important process shaping tropical plant communities is negative density dependence (NDD). NDD occurs when plant performance is negatively impacted by increased neighbourhood density. Reduced performance at high neighbourhood density is thought to arise through ecological interactions between plants and their natural enemies. Thus in a healthy ecosystem, trophic interactions play vital roles as mechanisms driving NDD and are important as dispersers facilitating escape from NDD mortality. However, interruption to ecological processes caused by human activities, such as hunting, can perturb NDD interactions and cause cascading effects throughout an ecosystem. In my thesis I investigate the role of dispersal and mortality in NDD dynamics of tropical tree communities, as well as investigating local and global impacts of removing ecological interactions in tropical rainforests.

In my thesis, I begin by addressing the presence and variation in strength of NDD among tree species and ontogenetic stages, the mechanisms driving NDD, and the role of trophic interactions in this process. The Janzen-Connell hypothesis predicts that host-specific natural enemies drive NDD by selectively reducing conspecific density, and increase diversity by suppressing competitive exclusion, thus allowing heterospecifics to persist. In chapters 2 and 3 of this thesis, I show that mortality driven by conspecific NDD is prevalent at the early life stages, and this effect is considerably stronger during the year after germination. Furthermore, this process is driven exclusively by host-specific fungal pathogens, which cause mortality selectively among conspecifics and drive diversity. As seedlings age beyond their first year, NDD interactions become less impacted by conspecifics but are impacted by closely related neighbours or by general neighbourhood density, representing changes in the mechanism driving NDD as seedlings age, and a decline in host-specificity of natural enemies. Equally, relative growth rates (RGR) are reduced under high neighbourhood density irrespective of species identity. Results suggest insect herbivores are the strongest driver of reduced RGR but not mortality under increased neighbourhood density. As a consequence of stronger inter than intra-specific NDD effects on RGR, insects had no impact on seedling diversity in the short term. This study supports assertions that regionally rare species experience stronger NDD than common species, accounting for the high variability in species relative abundance in the tropics.

In the second part of my thesis, I address the role of large vertebrate dispersers in shaping tropical tree communities and the consequences of defaunation for tree assemblage and carbon storage. Dispersal allows seeds to escape NDD and persist to reproductive maturity and is therefore vital for the maintenance of diversity. Vertebrates disperse the seeds of more than 70% of neo-tropical tree species. However, many large vertebrates are becoming scarce due to widespread hunting. The decline of large vertebrates and their role as dispersers is predicted to alter tree community composition. Additionally, large vertebrates are responsible for the dispersal of large-seeded species, which are linked to species with high wood density. With wood density positively associated with carbon storage, there is a potential cascading influence of defaunation on global carbon storage. We investigate the consequences of declining large vertebrate mortality agents in chapter 3, and the consequences of declining large vertebrate dispersers in chapters 4 and 5. Although community composition is altered in a defaunated forest, species dispersed by extirpated fauna do not appear to drive this. In fact we find that many species thought to be heavily reliant on extirpated fauna manage to persist. Although it is thought that the simultaneous loss of seed predation from large terrestrial vertebrates may create compensatory effects, we found little support for this, with an absence of large terrestrial vertebrates driving only temporary changes to species diversity. Neither a loss of large frugivores or large-seeded species lead to declines in species with high wood density, but we detect a worrying decline in large stemmed species, which has negative implications for carbon storage.

Overall, my thesis highlights the importance of NDD and trophic interactions, particularly fungal pathogens, at the early life stages in shaping tropical tree communities and in maintaining diversity. I provide evidence that the removal of trophic interactions among larger natural enemies and dispersers does not impact community assemblage in the directional manner found in previous studies. I provide evidence for the variability in response to trophic interactions among species and ontogenetic stages. I show disproportionate relative importance among natural enemies and dispersers in the maintenance of tropical tree assemblage, with implications for conservation and for assessing the consequences for tree diversity under the influence of degradation.

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Chapter 1

General Introduction

1.1 Tropical forests

“Instead of endless repetitions of the same forms of trunk such as are to be seen in our pine, or oak, or beechwoods, the eye wanders from one tree to another and rarely detects two together of the same species. All are tall and upright columns, but they differ from each other more than do the columns of Gothic, Greek, and Egyptian temples.”
(Wallace 1891)

Wallace’s (1891) description of the variety and intrigue of tropical flora and fauna has since inspired ecologists to ask why and how this immense diversity persists in tropical forests. A single hectare of tropical rain forest may support over 280 tree species with a DBH ≥10 cm (Valencia et al. 1994, Oliveira and Mori 1999), with as many as 10 times the number of tree species in tropical compared to temperate zones (Latham and Ricklefs 1993). Tropical forests have been intrinsically linked to global carbon storage, with the Amazon alone accounting for ~23% of carbon stored by vegetation (Dixon et al. 1994), and comprising 40% of global tropical forest (Grace et al. 1995). With the acceleration of habitat and species declines in tropical forests in recent decades (Wright and Muller-landau 2006, Dirzo et al. 2014), understanding the mechanisms that maintain diversity in tropical forests has become crucial to conservation efforts. Ecologists are currently only scratching the surface in addressing the myriad ways in which forest degradation may impact diversity and climate change.

1.2 Shaping plant communities

Plant community assembly is often referred to as the relative contribution of a regional pool of species to the formation of a local plant community (HilleRisLambers et al. 2012). Understanding the mechanisms that drive plant community assembly is essential for managing ecosystems and developing conservation strategies (Hubbell and Foster 1986, Duru et al. 2015), and informing strategies on rare species conservation (DeCesare et al. 2010) and the impacts of climate change (Chu et al. 2016). Stabilizing mechanisms have been the focus of much research in recent decades (Aldler et al. 2018), and are essential for species coexistence in diverse communities (Chesson 2000). Stabilizing mechanisms rely on stronger intra- than inter-specific negative interactions among plants, such that species limit their own performance more than their competitors, thereby limiting competitive exclusion (Chesson 2000, Wright 2002).

Stabilizing mechanisms specify a multitude of processes (Palmer 1994, Wright 2002), including abiotic niche partitioning wherein species thrive only in particular micro-habitats (Silvertown 2004, Levine and HilleRisLambers 2009, Metz 2012) and negative density dependent (NDD) interactions that generate species specific mortality and promote survival of locally rare species (Harms et al. 2000, Comita et al. 2010, LaManna et al. 2017). Substantial evidence has been found for both niche and NDD processes in tropical tree communities (Adler et al. 2010, Metz 2012, Comita et al. 2014, Zhu et al. 2015a). Whether abiotic niche partitioning or NDD plays a dominant role in shaping community assembly can depend on relative species abundance (Wang et al. 2012), ontogenetic stage (Piao et al. 2013), or functional traits (Kobe and Vriesendorp 2011, Inman-Narahari et al. 2016, Lebrija-Trejos et al. 2016), and studies now show that these processes are working in combination (Chen et al. 2010, Bagchi et al. 2011, Kobe and Vriesendorp 2011, McCarthy-Neumann and Ibáñez 2013, Johnson et al. 2017).

1.3 Trees and the early life stage

Mechanisms that shape tree community assemblage are frequently attributed to the seed and seedling stage of a tree’s life (Metz et al. 2010, Comita et al. 2014, Green et al. 2014, Zhu et al. 2015b). Seeds and seedlings occur at high densities compared to saplings and mature trees, where they are clustered close to the parent tree (Nathan and Muller-landau 2000), generating a high occurrence of frequency dependent mortality among conspecifics (Terborgh 2012). Furthermore at this early stage, trees are vulnerable to attack by host-specific pathogens or herbivory (Clark and Clark 1985, Gilbert et al. 1994). For this reason most studies have focussed on the seed or seedling stage when measuring mechanisms that shape tropical forest community assemblage (Harms et al. 2000, Mangan et al. 2010, Bagchi et al. 2014, Comita et al. 2014). Many studies categorize all seedlings in the same age class (Harms et al. 2000, Bagchi et al. 2014, Zhu et al. 2015a), however, considering a seedling may remain in the seedling size class for over a decade, it is beneficial for studies to focus specifically on the first year after germination (Metz et al. 2010, Lebrija-Trejos et al. 2014), extracting the effect of age among seedlings.

1.4 Abiotic niche partitioning

Some ecologists argue that abiotic niche partitioning drives species community assembly among plants (Silvertown 2004, Kraft et al. 2008, Metz et al. 2010). Species differ in the light, water and soil nutrients they require for successful germination and survival (Grubb

1977), and availability of these resources may temporally or spatially vary. Abiotic niche partitioning generates coexistence by partitioning resources at a micro- and macro-scale, allowing each species to thrive in its preferred micro-habitat, thereby avoiding competitive exclusion (Silvertown 2004). In a tropical forest, this process requires a great many different micro-habitats to facilitate the large number of species that coexist, and studies assessing abiotic niche partitioning have shown that this process alone is not sufficient to drive community assembly (Webb and Peart 2000, Harms et al. 2001, Queenborough et al. 2007a), although it may be more prevalent in less species rich biomes (Lamanna et al. 2016). Nevertheless, some studies show convincing evidence for abiotic niche partitioning to be a dominant factor in shaping community assembly in tropical forests (Kraft et al. 2008, Metz 2012), and it is therefore important to consider the contribution of abiotic niche partitioning in shaping tree communities.

1.5 Negative density dependence

Negative density dependence (NDD) refers to a decline in individual performance with increasing neighbourhood density. While NDD is frequently linked with plant diversity, alone it cannot drive diversity. To meet the requirements laid out by Chesson (2000), intraspecific NDD must be stronger than interspecific NDD in order to supress competitive exclusion and maintain diversity. Freckleton and Lewis (2006) proposed that NDD can be compensating (mortality is proportional to density) or overcompensating (mortality is greater than proportional to density). In a compensatory NDD scenario, higher densities will not change the probability of mortality, although overall mortality will increase at the same rate as density. In an over-compensatory NDD scenario, probability of mortality will increase with higher densities, eventually resulting in 100% mortality at high densities, for example seed rain under a parent tree (Alvarez-Loayza and Terborgh 2011). To facilitate coexistence in a community, NDD must be over-compensatory, only in this way would competitive exclusion be sufficiently minimised to allow recruitment of locally rare species (Freckleton and Lewis 2006, Bagchi et al. 2010b).

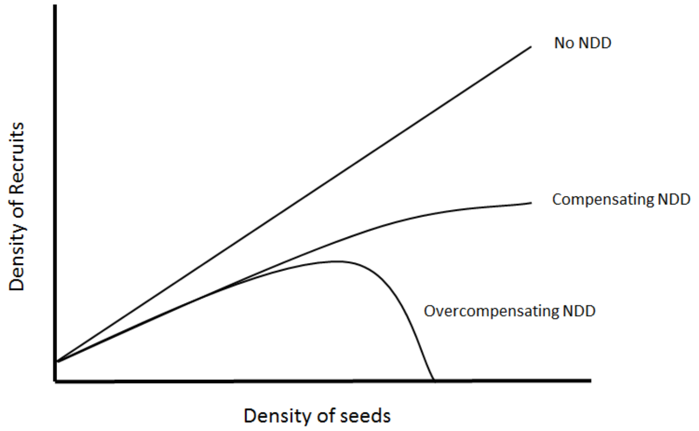

Figure 1.1 Probability of recruitment predicted by seed density. Presenting negative density dependence as posited by Bagchi et al. (2010b).

Diversity is maximised under overcompensating NDD, since high density of seeds are not permitted to dominate the community of seedling recruits and do not exclude heterospecifics.

1.5.1 Mechanisms driving negative density dependence

Negative density dependence as a driver of community assembly among tropical trees has received considerable support over recent decades (Connell et al. 1984, Harms et al. 2000, Wright 2002, Terborgh 2012, Comita et al. 2014, Zhu et al. 2015a, Lamanna et al. 2016). The mechanisms that drive NDD interactions, however, have been widely debated (Paine et al. 2008, 2016, Bagchi et al. 2014, Comita et al. 2014, Zhu et al. 2015b). NDD interactions are widely attributed to one of two mechanisms; resource competition among neighbouring plants (Yoda et al. 1963) and natural enemies that reduce plant performance or cause mortality (Janzen 1970, Connell 1971), both of which can be intra- or inter-specific. We discuss these mechanisms in more detail below.

1.5.2 Competitive negative density dependence

Plants compete among neighbours for limited resources such as light, water and soil nutrients. Yoda et al. (1963) proposed that resource competition imposed negative effects on growth and survival among neighbouring plants within a trophic level (self-thinning). Self-thinning has been traditionally studied in temperate regions with low species richness (Yoda et al. 1963, Pretzsch 2006), but has rarely been associated with tropical regions (Pillet et al. 2018). Competitive interactions may be driven by either conspecific or heterospecific neighbourhoods. However, to promote diversity and shape community assemblage, competition among conspecifics must be more intense than among heterospecifics (Chesson 2000). Since we expect early life stages to be highly important in shaping species communities in the tropics, we expect competitive interactions that shape tree communities to be both conspecific and among seedlings. While studies have found evidence for resource competition between mature or juvenile trees and seedlings (Lewis and Tanner 2000), there has been little evidence for competition among seedlings (Paine et al. 2008, Svenning et al. 2008). Consequently, competitive interactions have often been disregarded in studies addressing NDD interactions among tropical seedlings. Although there is little evidence supporting resource competition at the early life stages of trees, there is evidence that competition among older plants within an ontogenetic stage (Stoll and Newbery 2005, Piao et al. 2013), though it is unclear to what extent processes at this late stage contribute to shaping community assemblage.

1.5.3 Natural Enemies and negative density dependence

Janzen (1970) and Connell (1971) first independently hypothesized that density dependent mortality among seedlings is driven by host specific natural enemies. Seed dispersal is leptokurtic, with the majority of seeds remaining undispersed and landing in close proximity to the parent tree. This creates dense aggregations of conspecific seeds and seedlings close to the parent tree. Natural enemies aggregate at this abundant food source and can, in some cases, cause 100% mortality among seeds or seedlings (Alvarez-Loayza and Terborgh 2011). Where natural enemies are host specific, conspecifics experience negative density dependence while heterospecifics persist, minimising competitive exclusion and generating diversity (Wright 2002).

Host specificity is an essential component of conspecific NDD, and natural enemies in the smaller size class are frequently host specific or have narrow host ranges (Terborgh 2012), implicating insects, fungal pathogens and oomycota (Novotny and Basset 2005, Gilbert and Webb 2007). Fungal pathogens in particular have received strong support from the literature: studies monitoring plant-soil feedback in the presence and absence of soil biota collected from beneath the parent tree strongly implicated pathogens in NDD interactions (Packer and Clay 2000, McCarthy-Neumann and Kobe 2010, Mangan et al. 2010). Other studies used fungicides to exclude pathogens at high densities or close to the parent tree, again finding strong links between fungal pathogens and NDD interactions (Bell et al. 2006, Bagchi et al. 2014, Krishnadas and Comita 2018). Studies investigating insect herbivores have yielded mixed results: exclusion studies using either physical barriers or insecticide found associations between insects and NDD interactions (Connell et al. 1984, Bagchi et al. 2014, Fricke et al. 2014), and others found no association (Bagchi et al. 2010a, Gripenberg et al. 2014) or variable results depending on the species (Greiling and Kichanan 2002). Bagchi et al. (2014) were the first to compare the effects of fungal pathogens and insects on seedling communities using pesticide treatments, and while they found NDD was driven by both natural enemies, diversity and community composition was only driven by fungal pathogens. García-Guzman & Dirzo (2001) investigated interacting natural enemy attacks, and found that leaf herbivory driven by insects exacerbated the rate of fungal infection. Mammals have less frequently been studied, but have also been associated with NDD interactions. Theimer et al. (2011) and Beck et al. (2013) found NDD interactions driven by large mammals, but no further association with diversity or plant community composition. Paine et al. (2016) compared the effect of large and small mammals on NDD interactions, and found NDD was driven by small and medium sized mammals but not large mammals, leading to higher beta diversity. The missing link among these studies is a comparison of all natural enemy groups thought to be associated with NDD interactions among seedlings, which we investigate in Chapter 3.

Figure 1.2 Pathogen attack on newly germinated *Calatola microcarpa* seedling causing mortality in under 6 months.

1.5.4 Host-specificity and density dependence

Host specificity is often assumed to be characteristic of enemies driving NDD (Wright 2002, Freckleton and Lewis 2006, Terborgh 2012). Some studies, however, have questioned the degree of host specificity among natural enemies (Novotny et al. 2002, 2010, Gilbert and Webb 2007), and whether high host-specificity is necessary for NDD processes (Liu et al. 2012, Paine et al. 2012b, Sedio and Ostling 2013, Zhu et al. 2015b). In a review by Novotny and Basset (2005), a small proportion of insect herbivores were found to feed on a single species, though many were restricted to congenerics, and a later paper found that host-specificity in insects varied along a gradient of monophagy to highly generalist (Novotny et al. 2010). Gilbert and Webb (2007) studied host-specificity in plant pathogens, and found results parallel to studies of insect herbivores, with a range from monophagy to generalist. Species that share morphological or chemical traits are those most likely to share natural enemies (Sedio et al. 2012), which leads to the assertion that enemies are shared among closely related species (Gilbert and Webb 2007, Bagchi et al. 2010a).

Conventionally, the Janzen-Connell hypothesis assumes that natural enemies must be host specific to drive negative density dependence and to shape community assemblage among plants (Janzen 1970, Connell 1971), but can generalist natural enemies drive this process? Sedio and Ostling (2013) used a simulation approach to show that natural enemies that consume a wide host clade can be sufficient to maintain a similar species richness to that driven by monophagous natural enemies. Investigations have shown that phylogenetic relatedness drives density dependent interactions among seedlings, wherein mortality rates are higher in closely related neighbours (Webb et al. 2006, Liu et al. 2012, Paine et al. 2012b), suggesting the true monophagy may be unimportant in generating diversity through NDD. Zhu et al. (2015b), however, found support for phylogenetically driven NDD only at later ontogenetic stages, and Lebrija-Trejos et al. (2014) found that phylogenetic relatedness drove positive density dependent interactions at the early life stage. The question of whether phylogenetic relatedness drives NDD interactions is still open to discussion, and further insight into variation in response to phylogenetic NDD among species may offer answers.

1.5.5 NDD and among species variation

In a species rich community such as a tropical forest there is substantial variation in relative abundance among species, with many rare and few common species. Indeed, approximately 1.4% of species comprise 50% of individuals in a tropical plant community (ter Steege et al. 2013). Mouillot et al. (2013) showed that rare species, particularly among tropical trees, play a vital role in supporting vulnerable ecosystem functions and thus their importance in maintaining functional and taxonomic diversity. Understanding the drivers of such a high number of rare species is therefore key to understanding drivers of diversity (Preston 1948, Gaston 1996). The maintenance of exceptionally high numbers of rare species is often explained as NDD disproportionately impacting rare species over common species (Hubbell et al. 2001, Comita et al. 2010, Johnson et al. 2012). If this is the case NDD may be responsible for shaping not only local but regional community assemblages. Studies have found evidence for variation among species in response to conspecific NDD (Zhu et al. 2015b), with stronger NDD effects among rare species (Hubbell et al. 2001, Comita et al. 2010, Johnson et al. 2012), and some have linked this variation among species to trophic interactions (Klironomos 2002, Mangan et al. 2010, Xu et al. 2015).

Studies have also found support for opposing trends, with stronger NDD for common species (Queenborough et al. 2007b, Zhu et al. 2015a). NDD could be lower in rare species if rare species occur at such low densities that they cannot sustain host specific natural enemies (Novotny et al. 2007). Furthermore, Lamanna et al. (2016) showed that if NDD was stronger for rare species then diversity was reduced, and the reverse when NDD was stronger in common species, suggesting that NDD at the early life stage may not be important in shaping regional species communities. This may be caused by increased extinction risk of rare species when subjected to high NDD mortality, though this effect may be negated if conspecific density is lower for rare species (Johnson et al. 2012). The debate surrounding these contradictory hypotheses continues, as it is, by definition, difficult to obtain sufficient sample sizes of rare species to conduct a comprehensive study. A further possibility is that variation in NDD among species is unconnected to regional species abundance, if they are influenced by habitat affinity and resource use (Comita et al. 2010), where there is sufficient correlation between these traits and rarity that non-causational effects are detected.

1.6 Dispersal

There is substantial evidence for conspecific negative density dependence for tropical tree seeds and seedlings (Connell et al. 1984, Harms et al. 2000, Wright 2002, Comita et al. 2014, Zhu et al. 2015a, Lamanna et al. 2016), and this is particularly evident under the canopy of the parent tree (Swamy et al. 2011, Terborgh 2012). Undispersed seeds fall directly beneath the parent tree and result in high densities of conspecific seeds or seedlings, attracting high densities of natural enemies (Janzen 1970, Connell 1971) or elevating competitive interactions among seedlings (Tanner et al. 2005) or between adults and seedlings (Lewis and Tanner 2000). NDD processes, therefore, make it vital that seeds are able to disperse for successful germination and survival past the seedling stage.

Dispersal syndromes can be broadly categorised into abiotic (e.g. anemochory, autochory) or biotic (zoochory) means (Howe 2016). Primary seed dispersal refers to the removal of seeds directly from the parent tree for distribution elsewhere, in zoochorous species this usually involves animals consuming the seeds and defecating or regurgitating the seeds away from the parent tree (Vander Wall and Longland 2004, de Barros Leite et al. 2012). Primary dispersal is considered to be highly important for seed germination and plant survival (Howe and Smallwood 1982, Vander Wall and Longland 2004), however many studies have addressed the importance of secondary dispersal (Andresen 1999, Vander Wall et al. 2005). Secondary dispersal is the movement of seeds after they have left the parent tree, either after falling undispersed beneath the parent tree or following primary dispersal (Vander Wall and Longland 2004). Studies have shown that ants (Bottcher et al. 2016), dung beetles (Lawson et al. 2012), rodents (Hirsch et al. 2012, Jansen et al. 2012) and carnivores (Hamalainen et al. 2017) act as secondary dispersers. Scatter hoarding rodents are frequently implicated in secondary dispersal of large seeds, wherein rodents remove seeds and bury them (sometimes multiple times) to consume later (Jansen et al. 2012). These seeds are often abandoned and permitted to germinate, either because the animal has forgotten the location, or because the animal has died. Recent studies have shown that scatter hoarding rodents may be vital for the persistence of some large seeded species (Cao et al. 2011, Hirsch et al. 2012, Jansen et al. 2012, Geng et al. 2017). Furthermore, if a primary disperser is lost, scatter hoarding rodents may in some cases take on the role of primary disperser (Vander Wall and Longland 2004), and are thought to be responsible for the persistence of plant species that evolved dispersal mechanisms for extinct megafauna (Guimaraes Jr et al. 2008, Jansen et al. 2012).

1.7 Defaunation

Defaunation was coined by Dirzo and Miranda (1991), to refer to the loss of fauna through human activities. Redford (1992) expanded on this with what he termed ‘the empty forest’, referring to forests that are floristically intact but have lost much of the vertebrate fauna beneath the canopy. These studies responded to a global defaunation crisis, with anthropogenic impacts causing global declines in vertebrate species throughout the tropics (Milner-Gulland et al. 2003, Corlett 2007, Peres and Palacios 2007, Wright et al. 2007c, Harrison 2011, Abernethy et al. 2013, Dirzo et al. 2014). A review by Dirzo et al. (2014) estimated a global decline of 28% of vertebrates in 40 years. Fa and Peres (2001) estimated 60% of large forest mammals in their study were being unsustainably harvested in the Congo Basin, and in the neo-tropics Peres and Palacios (2007) found that 22 of 30 harvest sensitive species had populations significantly impacted by hunting.

Hunting has accelerated over recent decades due to improved access to guns and to remote areas (Robinson and Bennett 2000, Milner-Gulland et al. 2003, Fa and Brown 2009). While hunting is often for sustenance, driven by a need for protein, there is also an expanding market for bushmeat, animal products for medicine and for illegal pets, and demand for these products is driving hunting far beyond sustainable levels (Milner-Gulland et al. 2003). Hunting disproportionately targets larger vertebrates that provide better sustenance or financial reward (Galetti and Dirzo 2013). In the neo-tropics, this puts particularly high hunting pressure on frugivores (Peres and Palacios 2007). Smaller mammals in the neo-tropics, not often targeted by hunters, have increased in abundance at hunted sites (Peres and Palacios 2007), once their competitors for shared resources have been extirpated (Peres and Dolman 2000, Wright 2003).

1.7.1 Defaunation and plant community assemblage

Vertebrates in tropical communities are responsible for ecological processes including seed dispersal, seed predation and herbivory (Beck 2006, Wright et al. 2007c, Stoner et al. 2007), and these trophic interactions are highly important in maintaining plant community assemblage (Wright 2003). Increased defaunation in recent decades has seen a decline in large bodied vertebrates (Dirzo et al. 2014), and many ecologists believe this is impacting ecological processes that maintain species assemblages in tropical forests (Wright et al. 2007c, Stoner et al. 2007, Terborgh et al. 2008, Harrison et al. 2013, Peres et al. 2015).

Along latitudinal and climatic gradients, the relative abundance of dispersal syndrome among plants shifts, with plant species reliant on vertebrate dispersers increasing in tropical and wet zones (Howe and Smallwood 1982, Gentry 1995). 76% of seed dispersal was zoochorous at a site in Panama (Muller-Landau and Hardesty 2005), and

Peres and van Roosmalen (2002) found 87-90% of tree species relied on zoochorous dispersal in Brazil and Suriname, with 40% dispersed by primates. Large frugivores in particular are unique in their ability to disperse large seeds, since they are able to swallow large seeds whole (Galetti et al. 2013). The loss of large frugivores under the pressure of hunting has been connected with declines in tree species reliant on large frugivores for dispersal (Wright et al. 2007c). Terborgh et al. (2008) compared sapling and mature tree community assemblage in a hunted and a nonhunted forest, finding reduced recruitment of large-seeded species and increased recruitment of abiotically dispersed species, resulting in altered species relative abundance at a hunted site. Other studies have backed Terborgh et al. (2008), finding altered tree species community assemblages (Wright et al. 2007c, Nuñez-Iturri et al. 2008, Stevenson et al. 2008, Harrison et al. 2013) and in some cases declines in diversity (Nuñez-Iturri and Howe 2007, Kurten 2013) under influence of hunting.

Frugivory, however, is not the only role large mammals play in shaping plant communities; seed predation and herbivory drive NDD interactions that shape community assemblage (Dirzo and Miranda 1991, Wright et al. 2007b, Poulsen et al. 2013, Beck et al. 2013). In a combined observation and manipulation study, Kurten et al. (2015) found that the simultaneous loss of large vertebrate dispersers and predators had compensatory effects, with large seeded species simultaneously benefitting from the loss of predators and impaired by the loss of dispersers under hunting pressure. Wright et al. (2007b) preceded this, finding that although small seeded and abiotically dispersed species were increasing under hunting pressure, large seeded species were favoured due to the decline in predation from large terrestrial mammals, in opposition to other contemporary studies (Nuñez-Iturri et al. 2008, Stevenson et al. 2008, Terborgh et al. 2008). There is, however, contradictory evidence indicating that large mammals do not play a strong role in shaping tree species communities (Brocardo et al. 2013, Paine et al. 2016), and Terborgh (2013) suggests that compensation for the loss of seed predators is more common than compensation for loss of dispersers. The latter studies suggest that it is unlikely that the loss of large terrestrial mammal predation alone can compensate for the loss of dispersers. Evidence for some compensatory mechanisms taking place in defaunated forests (Wright et al. 2007b, Kurten et al. 2015) could be related to secondary dispersal (Cao et al. 2011, Hirsch et al. 2012, Jansen et al. 2012, Geng et al. 2017). If this is the case, secondary dispersal could hold the answers to altered community assemblage, and may be an important factor in predicted changes to tree community assemblage in defaunated forests.

1.7.2 Defaunation and carbon storage

There is substantial evidence for impacts of defaunation on tree communities at the local scale (Wright et al. 2007c, Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Harrison et al. 2013), and recent studies have revealed implications for impacts of defaunation at the global scale, with consequences for carbon storage in defaunated forests (Brodie and Gibbs 2009, Peres et al. 2015). Tropical forests play an irreplaceable role in global carbon storage (Cao and Woodward 1998, Pan et al. 2011), responsible for 14% of carbon fixed by photosynthesis and 17% of terrestrial vegetation carbon stock (Zhao and Running 2010, Feldpausch et al. 2012). The amount of carbon a tree stores is positively associated with size, age and wood density (Chave et al. 2005, Lindner 2010, Stephenson et al. 2014), furthermore, the largest 10% of species are responsible for up to a third of forest biomass (Fauset et al. 2015). Species with high wood density usually have large seeds (Peres and van Roosmalen 2002, Diaz et al. 2004, Wright et al. 2007a). Since large seeds are thought to be reliant on large frugivores for dispersal (Galetti and Dirzo 2013), the decline of these dispersers in defaunated forests could lead to cascading consequences for wood density and thereby carbon storage (Poulsen et al. 2013, Bello et al. 2015, Peres et al. 2015). Peres et al. (2015) used both field data and simulations to predict long term changes in carbon storage in defaunated neo-tropical forests, and found that in some cases up to 37.8% of biomass loss could be driven by defaunation, backed up by studies finding similar trends, with severe consequences for carbon storage (Bello et al. 2015, Kurten et al. 2015). The consequences of the loss of large-seeded species was intensified when Fauset et al. (2015) considered the comparative contribution of carbon storage within the tree community, with 50% of carbon storage represented by only 1% of Amazonian tree species, indicating that a reduction of a small number of species could have drastic implications for global carbon storage.

1.8 Site Descriptions

1.8.1 The Cocha Cashu Biological Station

The Cocha Cashu biological station is a lowland tropical moist forest site in the north-eastern region of Peru at 11°88’S and 71°41’W, at 340 m elevation with young alluvial soil. Approximately 2500 mm annual rain falls mainly between November and May (Terborgh 1990). Although located in the Manu National Park, the site was founded before the creation of the national park in 1969-70. A trail system surrounds an oxbow lake covering 52 km, incorporating successional to mature floodplain forest. The data in this thesis was collected in mature floodplain forest only. It was particularly noted when the site was initially used by biologists that there was high abundance and diversity of fauna and flora (Terborgh 1990); including >1400 plant species, with 350 tree species >10 cm diameter (Foster 1990), >70 non-flying mammal species, >60 fish species, 528 bird species, and 82 amphibian species.

The site has not been subjected to hunting, logging or mining in the last 100 years (Terborgh 1990), and the only anthropogenic disturbance before its occupation by biologists were the occasional visits from non-contacted indigenous groups, carrying out small scale subsistence hunting for short periods of time. The site therefore provides an ideal baseline ecosystem for biologists to study, with no confounding effects from anthropogenic disturbance.

1.8.2 Boca Manu

Boca Manu is a village located in the peripheral zone of the Manu National Park, the site used in this study was located a short distance from the village across an oxbow lake at 12°16’S and 70°54’W, 90 km from the Cocha Cashu biological station (Terborgh et al. 2008). The village of Boca Manu was founded in 1972-3 close to a small indigenous village, when a petroleum exploration camp was established (Cities Service Corporation). The increased population in the area spurred the bushmeat market, and intensive hunting of large vertebrates commenced until 1976, after which the petroleum company left and steady but less intensive hunting continued in the area to the current day (Terborgh et al. 2008). The surrounding forest is now depleted of large birds and mammals, with particular declines in large primates (*Ateles paniscus, Alouatta seniculus*) and large terrestrial mammals (*Tapirus terrestris, Tayassu sp.* Terborgh et al. 2008, Chapter 4). The forest in this study is lowland tropical moist forest on mature floodplain, with very similar elevation, soil type and rainfall to the Cocha Cashu biological station. Valuable commercial species have been selectively logged from the area surrounding the village, but much of the forest has been unimpacted by heavy logging, and for the duration of the study represented in this thesis (from 2004 to 2015) there was no logging in the tree plots.

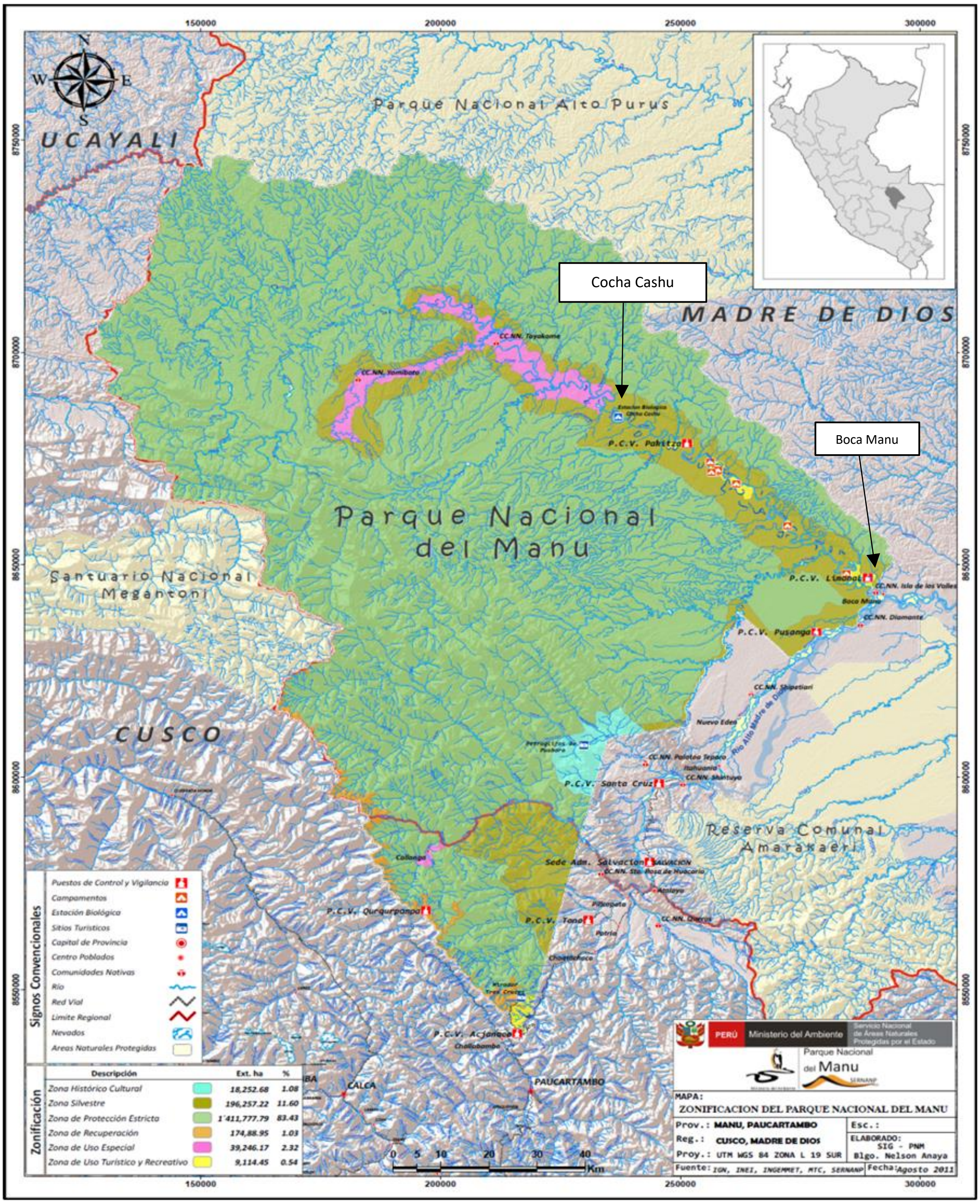

Figure 1.3 The Manu National Park, Madre de Dios, Peru. Source: Ministerio del Ambiente, Peru.

1.9 Aims and Objectives

Negative density dependence is a fundamental process among plants in tropical forests, but there is continued debate in the literature concerning the relative importance of this process and the mechanisms that drive it (Wright 2002). Trophic interactions are key to maintaining tree species community assemblage through NDD, with implications for predation or herbivory (Janzen 1970, Connell 1971), and seed dispersal (Howe and Smallwood 1982). This study aims to understand the community-wide relevance of NDD processes among tropical trees and the mechanisms that drive them, and to further assess the impacts of removing trophic interactions from a forest community. A better knowledge of processes that maintain tree community assemblage informs conservation and strategies from the local to the global scale, and contributes to the array of studies attempting to unravel the basic principles that maintain such high diversity in the tropics. My aims were addressed in four chapters as follows:

Chapter 2: Neighbourhood identity and ageing drive density dependence interactions in tropical seedlings.

I assess the influence of negative density dependence on seedling communities. I investigate the effect of species identity, phylogenetic relatedness, age and species relative abundance on NDD interactions among seedlings, and assess the influence of NDD plant performance in terms of mortality or relative growth rates.

Chapter 3: Fungal pathogens, insects and mammals differentially cause negative density dependence and increase diversity in tropical seedling communities.

In this chapter I address the mechanisms that drive NDD among seedlings, assessing the influence of natural enemies. Furthermore I compare the relative contribution of natural enemy groups to NDD interactions, separating out the effects of fungal pathogens, insects, and small and large mammals. I further assess the influence of natural enemies on diversity, and investigate links between diversity and NDD processes.

Chapter 4: Dispersal limitation in defaunated forests and changing tree community structure

Given that trophic interactions shape tree community assemblage at the seedling stage, it is important to understand the implications of removing some of these interactions. In this chapter I address the impacts of defaunation on tree community composition. I investigate shifts in relative species abundance in terms of dispersal syndrome and seed mass, to link tree compositional changes to changes in the disperser community.

Chapter 5: Simulating the next generation of a tree community in a defaunated landscape: the impact of disperser loss

The lifespan of a tree far exceeds the timespan of a PhD study. In this chapter I use simulations to predict long-term changes in tree community assemblage under the influence of defaunation. Given the vital role tropical forests play in carbon storage, it is important to understand how changes to tree community assemblage impact carbon storage potential. I investigate long-term changes in wood density under the influence of defaunation, in order to make predictions about the effect of dispersal loss on carbon storage in tropical forests.

Chapter 2

Neighbourhood identity and ageing drive density dependent interactions in tropical seedlings

K. Hazelwood & C. E. T. Paine

2.1 Abstract

Density dependent interactions can promote species coexistence through competitive interactions between neighbours or interactions with natural enemies. We investigated negative density dependence (NDD) in tropical seedlings in a lowland rainforest in south-east Peru over a 14-year period. We investigated the interactive effects of species identity, seedling age, and neighbourhood crowding on both mortality and relative growth rate, and the impact of phylogenetic relatedness on mortality and relative growth rate. We found that in the first year of a seedling's life, conspecific density drives mortality, but that in subsequent years, the effect of heterospecific crowding and phylogenetic crowding intensify, although overall mortality rates declined. Thus, mechanisms driving NDD change as a seedling ages. We interpret the strong conspecific mortality in very young seedlings as a host-specific enemy mediated process, but mechanisms become less host-specific as seedlings age, with NDD effects driven by a broad range of species in the seedling neighbourhood. Relative growth rates varied with heterospecific and phylogenetic crowding irrespective of age, but were not affected by conspecific crowding. We infer that mechanisms affecting growth and mortality differ, since NDD growth responses are slower than NDD mortality. Finally, we tested for difference in the strength of NDD among species, and assessed the effect of adult species abundance on NDD. Conspecific NDD mortality was stronger in rare species, but heterospecific NDD mortality did not differ among species. This may be due to different mechanisms driving NDD for common and rare species, though it is not clear in what way they differ. Our results support a growing consensus that conspecific NDD drives variation in performance among young seedlings, but we emphasize that community dynamics at the seedling stage cannot be assigned to a single mechanism or process.

2.2 Introduction

In highly diverse tropical regions, stabilizing mechanisms are required to maintain species coexistence (Chesson 2000), and for decades ecologists have sought to understand these mechanisms (Wright 2002, HilleRisLambers et al. 2012). Stabilizing mechanisms within plant communities have been studied extensively at early life stages (Green et al. 2014, Inman-Narahari et al. 2016), specifying niche partitioning (Silvertown 2004, Levine and HilleRisLambers 2009) and density dependent interactions (Harms et al. 2000, Comita et al. 2010, LaManna et al. 2017). Negative density dependence (NDD) generates species specific mortality and promotes persistence of locally rare species when negative conspecific interactions are stronger than heterospecific interactions (Webb and Peart 1999, Chesson 2000). Many studies support the idea that density dependence is a key stabilizing mechanism in tropical tree communities (Harms et al. 2000, HilleRisLambers et al. 2012, Terborgh 2012, Comita et al. 2014, Zhu et al. 2015a), but recently studies have shown variation in the strength or drivers of NDD among species and among ontogenetic stages (Queenborough et al. 2009, Comita et al. 2010, Piao et al. 2013, Lebrija-Trejos et al. 2014, 2016, Zhu et al. 2015a, 2018, Choo et al. 2017).

Density dependent stabilizing mechanisms can drive changes in plant performance and maintain coexistence through competition or through host-specific natural enemies (Janzen 1970, Connell 1971, Bell et al. 2006, Liu et al. 2012, Terborgh 2012). Competition among seedlings drives resource limitation, slows growth rates and impacts survival (Yoda et al. 1963). Little evidence has been found for intraspecific competition among similar sized tropical tree seedlings (Paine et al. 2008, Svenning et al. 2008), and without comparatively strong intraspecific competition this mechanism would not promote coexistence (Chesson 2000). Host-specific natural enemies, such as pathogens and insects, promote diversity by putting selective pressure on locally common species and allowing locally rare species to succeed (Wright 2002). Natural enemies have been posited as a species specific driver of reduced seedling performance, but equally generalist predators may cause density dependent mortality or degradation (Sedio and Ostling 2013).

At a larger scale, it has been posited that NDD disproportionately affects regionally rare species (Hubbell et al. 2001, Comita et al. 2010, Johnson et al. 2012), making it an important generator of the variation in abundance among species. Conversely, studies have suggested that common species will experience stronger NDD (Queenborough et al. 2007b, Zhu et al. 2015a), either because strong NDD in rare species could increase extinction risk and therefore decrease diversity (Johnson et al. 2012), or because rare species are not sufficiently abundant to support host-specific natural enemies (Novotny et al. 2007).

Although highly diverse regions have greater species richness of host-specific natural enemies (Arnold et al. 2000, Baldeck et al. 2013, Forister et al. 2015), it is unlikely that all these species are truly host-specific (Novotny et al. 2010). Many studies classify neighbouring individuals into conspecifics and heterospecifics to test for conspecific NDD (Comita et al. 2010), but due to variation in host-specificity among natural enemies (Novotny et al. 2010), this method may be too crude (Uriarte et al. 2004). Recent studies have instead measured a gradient of phylogenetic relatedness among seedling neighbours, showing that host ranges of natural enemies can be predicted by phylogenetic signal (Webb et al. 2006, Novotny et al. 2010, Bagchi et al. 2010a), but results have indicated both negative (Metz et al. 2010, Liu et al. 2012, Paine et al. 2012b) and positive (Baraloto et al. 2012, Lebrija-Trejos et al. 2014, Zhu et al. 2015b) influences on seedling performance of close relatives. Drivers of phylogenetic NDD could be driven by competition or trophic interactions, since close relatives are likely to share the traits that facilitate these interactions (Gilbert and Webb 2007). Phylogenetic positive density dependence (PDD), however, results from close relatives sharing habitat associations, supporting the niche partitioning theory (Sedio et al. 2012).

Many studies have assessed the effects of NDD at the early seedling stage, when plants are highly vulnerable and likely to be susceptible to non-random mortality processes (Swamy and Terborgh 2010, Bai et al. 2012, Bagchi et al. 2014, Green et al. 2014, Zhu et al. 2015a, Johnson et al. 2017), but few have assessed ontogenetic shifts from newly germinated to more established seedlings of similar size. In an unusual study, Metz et al. (2010) found that a diverse phylogenetic neighbourhood improved survival after a seedling's first year, when strong conspecific mortality effects had subsided, but Zhu et al. (2015b) and Lebrija-Trejos *et al.* (2014) found that negative impacts of phylogenetic relatedness were strongest at later ontogenetic stages, and that closely related heterospecific neighbours cause positive density dependence. Host-specific natural enemy driven NDD is most likely to occur in the very early stages of a seedlings life (Metz et al. 2010, Green et al. 2014), when seeds are aggregated at high densities close to parent trees (Alvarez-Loayza and Terborgh 2011), most likely in the first year after germination. If, however, NDD is driven by interspecific competition or by generalist predators, i.e. if species identity is unimportant, the process will likely be size dependent, with smaller seedlings suffering higher mortality than larger seedlings (Tanner et al. 2005). Size effects may be correlated with age but the effect would vary considerably among species with different initial sizes at germination. Additionally if younger seedlings are thinned out due to conspecific NDD, this may clear the way for competitive interactions in older seedlings. Intraspecific competition may be size dependent, but, equally, younger seedlings may be more vulnerable and be more susceptible to competitive exclusion, meaning both size and ontogenetic stage may impact seedling performance.

Monitoring seedling communities in an Amazonian floodplain region for 14 years has allowed us the unique opportunity to assess density dependent interactions and ageing in seedlings. Whereas many studies have included all seedlings of a certain height in the same age category, we have partitioned the effects of seedling height and age, and assessed their relative interactions with NDD. In this study we address the following questions: *1) what are the comparative effects of conspecific and heterospecific density on mortality and relative growth rate (RGR)?* Where there are negative effects on seedling performance from conspecific but not heterospecific density, indicating stronger intraspecific than interspecific mechanisms, we implicate intraspecific NDD in the maintenance of species diversity. *2) To what extent does phylogenetic relatedness predict mortality and RGR?* With a range of host breadth among natural enemies that drive NDD, we expect closely related neighbours to drive NDD interactions. *3) Do causes of NDD change as seedlings age?* We expect NDD interactions among ageing seedlings to vary irrespective of seedling size, with strong conspecific NDD following the initial germination. *4) Is there variation in the strength of density dependent interactions among species?* Rare species are expected to experience stronger NDD than common species, thereby shaping community assemblage. To answer these questions we used seedling plots from a diverse lowland Amazonian site, monitored 7 times over a 14 year period, and make inferences concerning the mechanisms driving these trends.

2.3 Methods

2.3.1 Study Site

Seedling plots were located at the Cocha Cashu Biological Station (CCBS), situated in the Manu National Park in Amazonian South-East Peru. The lowland tropical moist forest (Holdridge 1947) stands at 11°51’S, 71°19’W, 350m elevation, and annual precipitation averages at 2200mm. The site has exceptionally high diversity with over 350 tree species with a diameter >10 cm DBH (Foster 1990), and as a remote site it has experienced little anthropogenic influence with no hunting, logging or mining, (see Chapter 1 and Terborgh (1990) for site description).

2.3.2 Data Collection

Seedling plots were set up in 2003-04, with 24 transects randomly assigned a location within a 4 km^2 CCBS trail system in mature floodplain forest. Each transect was assigned a random compass bearing along which 24 circular 1 m^2 plots were located, with plots spaced between 5 and 10 metres apart, avoiding trails and new treefalls (for details see Paine and Harms (2009)). Within each plot, all woody seedlings >10 cm and <1 m high were identified, tagged, and height and number of leaves were recorded. Plots were censused yearly from 2003 to 2006, and again in 2010, 2015 and 2017.

Adult species abundances were taken from tree plot data assimilated by Pitman et al. (1999) from 10 sites in the Manu National Park (including CCBS), extracting data from mature floodplain forest only, to match the forest used in this study. For analyses, we used the mean number of individuals per hectare for each species over 10 mature floodplain sites, to assign adult species abundance to each species.

2.3.3 Data Analysis

Since some species do not occur frequently enough to have many conspecific neighbours, the dataset for analyses included only species whose mean per-plot abundance over all censuses was greater than 1. The species list included morphospecies labelled with a unique non-taxonomic species name, which allowed us to detect the influence of conspecific neighbours even if the individual was not identified with a binomial species name. Individuals that were not identifiable to the genus level were excluded. The resulting dataset consisted of 160 unique names. Datasets were cut down to exclude seedlings that were present before the onset of the study, since the age of these seedlings is unknown.

For each individual, the total number of conspecific and heterospecific neighbours were summed at each location and census (individuals not included in the species list were also counted). Crowding indices were calculated to quantify the joint effects of the density and sizes of neighbouring seedlings (Canham et al. 2004). Neighbourhood crowding indices (NCI) were calculated per plot and census as:

Equation 1

$$NCI_k = \sum \frac{height_n}{height_k}$$

Where *k* is the focal individual, and *n* are the neighbouring seedlings. This was calculated for conspecific and heterospecific neighbours.

Phylogenetic relatedness was obtained using branch lengths from a phylogeny of 32223 plant species worldwide (Zanne et al. 2014) using phylomatic (Paradis et al. 2004, Chamberlain 2016), in which branch lengths represented the number of million years since the divergence of two species. For individuals identified only to genus, we used an available branch length from a closely related species in the same genus (n=94), or were assigned a mean branch length for species within the genus. Phylogenetic relatedness between each seedling and all neighbouring seedlings was summed in each plot and census. Phylogenetic crowding indices (PCI) were calculated as:

Equation 2

$$PCI_k = \sum \frac{1}{P_{kn}} * \frac{height_n}{height_k}$$

Where *P* is the phylogenetic dissimilarity between focal seedling *k* and each neighbouring seedling (*n*). Phylogenetic crowding indices were calculated with phylogenetic relatedness to each seedling neighbour for heterospecific neighbours only.

Mortality was modelled against log transformed crowding indices (heterospecific, conspecific, and phylogenetic crowding) using generalized linear mixed effect models with binomial error. Models were offset by logged time (years) between census and complementary log-log links were used, this accounted for differences in the amount of time between censuses (Egli and Schmid 2001). To assess changes in the effects of crowding indices on mortality for seedlings of different height and age, an interaction between crowding indices and log-transformed height or age was included and the significance of the interactions was tested using analysis of covariance to compare models with and without the interactions. Height and age were modelled separately to prevent the confounding effect of multicollinearity.

Relative growth rates (RGR) were modelled as log-transformed seedling height predicted by age using linear mixed effect models. A linear relationship between height and age indicates that growth does not change with seedling age. Although this would be unrealistic over the entire lifespan of a tree (Paine et al. 2012a), over the small portion of a tree's lifespan investigated in this study, relative growth rate does not slow with age (Fig. S2.2). Crowding indices were added as interacting fixed effects, to test the impact of crowding on relative growth rates.

Seedling plots were uniquely labelled and entered the models as random intercepts in all models to allow for spatial variation in mortality and growth. Species also entered as random intercepts with heterospecific or conspecific density as random slopes. Models with and without random slopes were compared using analysis of covariance, to assess the strength of among-species variation in density dependent interactions. Where the addition of random slopes improved the model fit, the term was retained. We assessed the prevalence of density dependence in seedlings among species with regards to adult relative abundance using random slope coefficients modelled against regional adult species abundance in linear models. To ensure sufficient species data were available for predictions in this analysis, the dataset was cut to include only species that had a range of conspecific and heterospecific crowding indices >1 among both surviving and perishing seedlings (Zhu et al. 2015a). The final dataset included 61 species.

All analyses were performed in R 3.5.0 (R Core Team 2017), using packages lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), effects (Fox 2003), and ggplot2 (Wickham 2009).

2.4 Results

Over a 14 year period with 7 censuses, we monitored 10995 seedlings from 295 species. 64.9% of individuals were identified to species level, 86.5% were identified to genus, 94.5% were identified to family, and 5.5% were not identified. Of the 160 unique names used in the reduced dataset in this analysis (6709 individuals), 76% were identified to species level and the remaining 24% were identified to genus level.

Overall probability of mortality was greatest in the early stages of a seedling's life ($P < 0.001$), with predicted mortality rates declining from 32% for one year old seedlings to 14% for 10 year old seedlings (Fig. S2.1b), with only 1.5% reaching 1 m in height. Mortality rates significantly decreased with seedling height, with mortality rates decreasing from 45% to 24% in seedlings growing from 10 to 20 cm, and decreasing to

9% in seedlings of 50 cm (Fig. S2.1a). Seedling height increased significantly with age ($P < 0.001$), and the relationship between height and age was exponential (Fig. S2.2).

2.4.1 Density dependent Interactions

Seedling mortality was modelled as a function of heterospecific and conspecific crowding, assessing the effects of species identity on mortality. Heterospecific crowding had no significant impact on mortality rates ($P = 0.78$). High densities of conspecifics significantly increased mortality rates, with mortality increasing from 18% to 24% with crowding increasing from 0 to 10, and increasing to 29% at a crowding index of 50 ($P < 0.001$, Fig. 2.1). High phylogenetic crowding, wherein heterospecific neighbours were more closely related, had no significant impact on seedling mortality ($P = 0.37$), with no effect of phylogenetic crowding on mortality even from very close relatives ($P < 0.001$, Fig. 2.1).

Relative growth rates were negatively influenced by heterospecific crowding ($P < 0.001$), with higher numbers of heterospecifics reducing growth rates irrespective of species identity, while conspecific crowding had no effect on relative growth rates ($P = 0.24$, Fig. 2.2). Relative growth rates decreased from 1 to 0.2 $\text{cm}\cdot\text{cm}^{-1}\cdot\text{y}^{-1}$ with an increase in heterospecific crowding index 0 to 10 and decreased to -0.3 $\text{cm}\cdot\text{cm}^{-1}\cdot\text{y}^{-1}$ at heterospecific crowding index of 50. Following a similar pattern to heterospecific crowding, phylogenetic crowding negatively impacted RGR ($P < 0.001$, Fig. 2.2), with closely related neighbours reducing RGR.

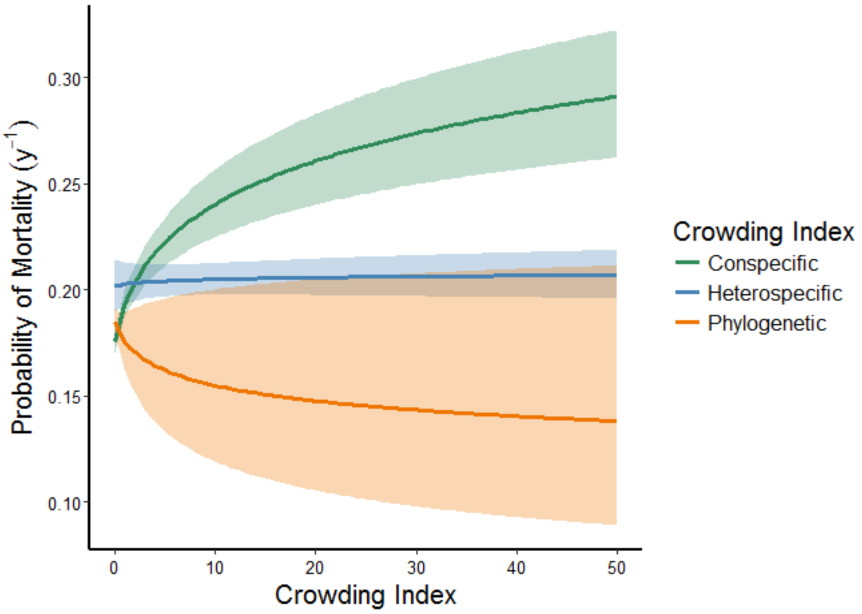

Figure 2.1 Model predictions showing the effect of crowding indices on mortality.

Green represents conspecific crowding indices and blue represents heterospecific crowding indices, with high crowding indices representing a high density of neighbours. Orange lines represents phylogenetic crowding indices, with high crowding indices representing a high density of closely related neighbours.

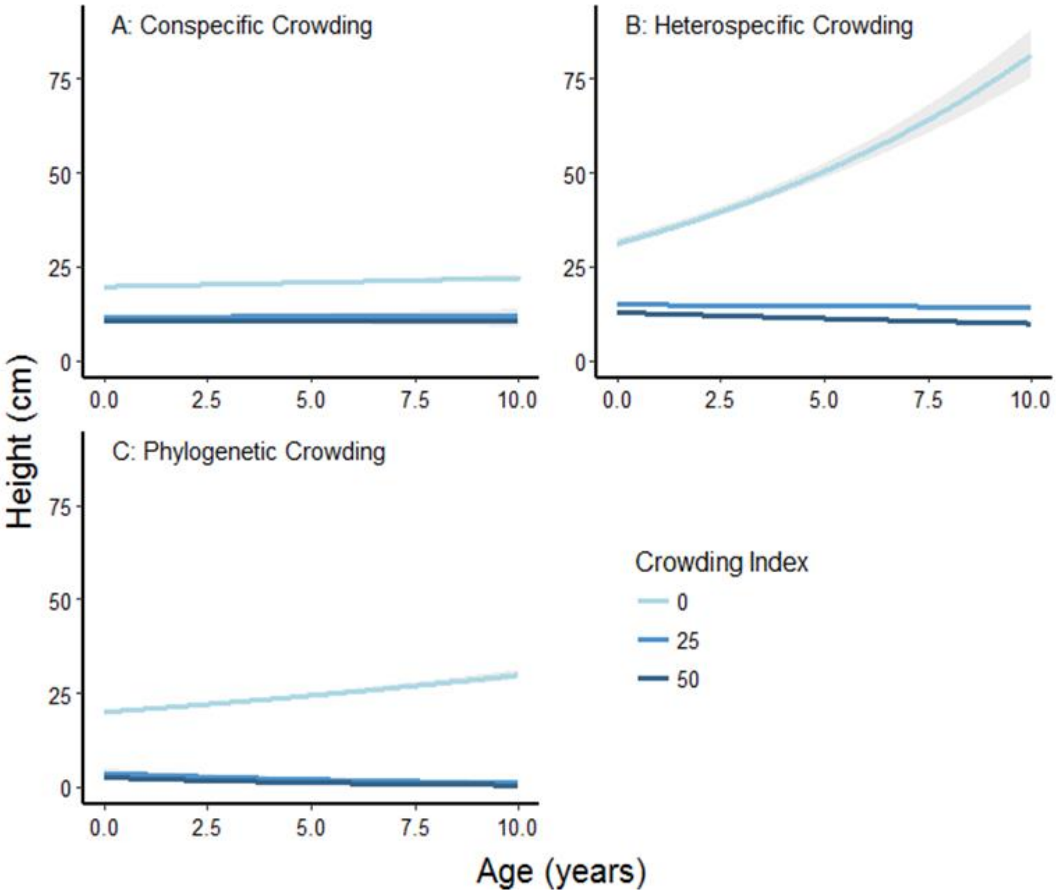

Figure 2.2 Model predictions showing relative growth rates (RGR) as height predicted by age under the influence of A) conspecific, B) heterospecific and C) Phylogenetic crowding.

Colours represent minimum, median and maximum crowding indices. Difference in slope indicates a difference in RGR among crowding indices, with steep lines represent high RGR. RGR decreases with increased crowding index for heterospecific and phylogenetic crowding.

2.4.2 Density dependence and ageing

We next assessed whether crowding effects on mortality varied with seedling height or age. Neither conspecific nor heterospecific crowding changed mortality with differing seedling height, with non-significant interaction terms (conspecific: *P* = 0.16, heterospecific: *P* = 0.67); although mortality rates decreased with increasing seedling height (Fig. S2.1a), this effect was not driven by crowding indices (Fig. S2.3). As seedlings aged, the effect of conspecific crowding on mortality decreased (*P* = 0.006), with a stronger relationship between conspecific crowding and mortality for younger seedlings, particularly those in the very early stages (Fig. 2.3a). Contrastingly, the effect of heterospecific crowding on mortality intensified as seedling aged (*P* < 0.001); Fig. 2.3b shows that while mortality was higher overall for younger seedlings, the relationship between heterospecific crowding and mortality became stronger as seedlings aged. Seedling height did not impact the relationship between phylogenetic relatedness of heterospecifics and mortality (*P* = 0.86, Fig. S2.3), smaller seedlings experience generally higher mortality but this was not driven by phylogenetic crowding. As seedlings aged, however, the effect of phylogenetic relatedness on mortality within heterospecifics increased (*P* = 0.004, Fig. 2.3c).

2.4.3 Variation among species

We tested whether the impact of conspecific and heterospecific crowding on plant performance varied among species. Including conspecific and heterospecific crowding as random slopes in mortality models significantly improved the model fit (conspecifics: *P* = 0.01, heterospecific: *P* = 0.02), though this was not the case for phylogenetic crowding (*P* = 0.42). This indicates that the strengths of conspecific and heterospecific crowding differ among species. Conspecific, heterospecific or phylogenetic crowding did not significantly improve RGR models, indicating no variation among species in density dependent RGR (*P* > 0.1 for all models).

We measured the association of adult species abundance with species specific NDD. Adult species abundance was negatively associated with slope coefficients representing mortality driven by conspecific crowding (*P* = 0.03), where species that were more abundant as adults experience weaker conspecific NDD mortality (Fig. 2.4). There was no association between slope coefficients representing mortality driven by heterospecific crowding and adult abundance (*P* = 0.6), with density dependent mortality similar among common and rare species (Fig. 2.4).

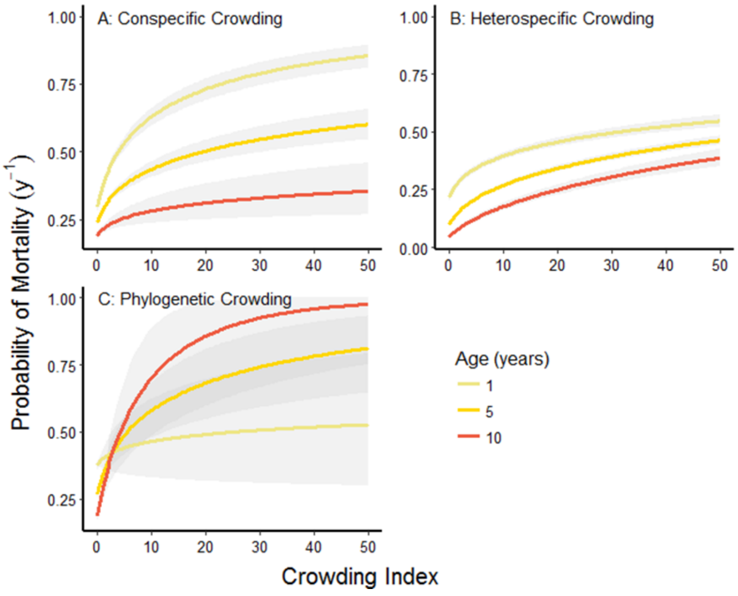

Figure 2.3 Model predictions showing predicted by A) conspecific, B) heterospecific and C) Phylogenetic crowding for ageing seedlings.

Colours represent seedlings at 1, 5 and 10 years old. Difference in slope indicates a difference in density dependent mortality, with steep lines representing high density dependent mortality. density dependent mortality is strongest in 1 year old seedlings under conspecific crowding, but stronger in 10 year old seedlings under heterospecific and phylogenetic crowding.

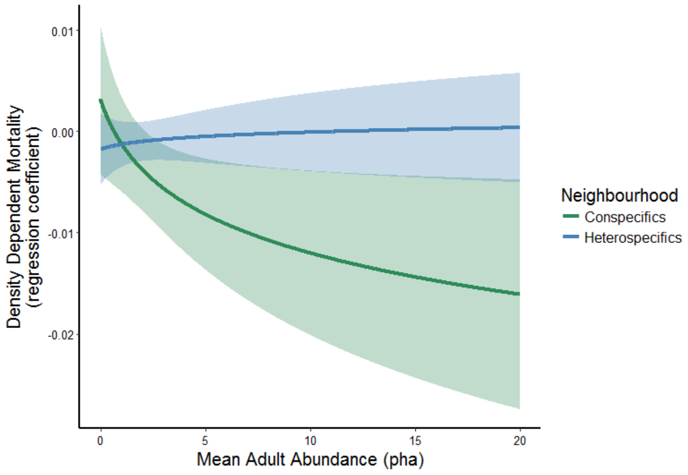

Figure 2.4 Model predictions showing the effect of mean adult species abundance (pha) on density dependent mortality driven by conspecifics and heterospecifics crowding indices.

Response variables are random slope coefficients extracted from models assessing the impact of crowding indices on mortality.

2.5 Discussion

This study examined the effects of density dependent growth and mortality in seedling communities using data from 6709 seedlings of 160 species over a 14 year period. The timescale of this study allowed us to robustly assess the influence of NDD interactions among seedlings, to determine the importance of intra- and inter-specific interactions in seedling communities, and to detect changes in density dependent interactions as seedlings age. Overall, conspecific crowding drove mortality to a greater degree than heterospecific crowding, but the effect of heterospecific and phylogenetic crowding increased as seedlings aged beyond their first year. Growth did not reflect this mortality pattern, with heterospecific and phylogenetic crowding negatively impacting RGR, but no change in RGR among seedlings of different age or size (see Table S2.1 for results summary). This study offers a unique insight into NDD interactions as seedlings age, and extracts key differences between measurements of NDD performance; mortality and growth, that have previously been considered equivalent under NDD pressure.

2.5.1 Density dependent crowding

The effect of density dependent interactions among seedlings and the association with species identity was assessed by monitoring the effects of seedling crowding on mortality and RGR. Heterospecific crowding had no effect on mortality, but we found strong support for the effect of conspecific crowding, signifying high seedling density alone does not drive NDD mortality but that NDD interactions are species specific. Previous studies have found evidence for similar patterns in conspecific density dependence mortality among seedlings (Wills et al. 2006, Bagchi et al. 2010a, Johnson et al. 2012, Terborgh 2012, Piao et al. 2013). Where negative density dependence is driven by species specific interactions, as in this case, likely drivers are intraspecific competition (Levine and HilleRisLambers 2009) or host-specific natural enemies (Comita et al. 2014), but without further examining these processes it is difficult to determine which of these drivers is causing conspecific NDD mortality in this case.

Conspecific crowding had no impact on RGR, contrasting previous studies that found a negative effect on growth from conspecific neighbours (McCarthy-Neumann and Kobe 2010, Mangan et al. 2010). Heterospecific crowding significantly reduced RGR, relating growth to non-species specific density dependent interactions. This negative effect on RGR could be driven by interspecific competition (Tanner et al. 2005), with a high heterospecific density creating higher competition for resources shared among many species. Tanner et al. (2005) found evidence for reduced RGR driven by competitive interactions among seedlings.Some studies, however, have shown that competition among seedlings is unlikely (Paine et al. 2008, Svenning et al. 2008), since comparatively small neighbours are unlikely to provide a significant amount of shading compared to mid and canopy plants. Another possibility is that the driver of mortality in high densities of seedlings is not competition among seedlings but generalist natural enemies. Generalist natural enemies, including pathogens, insects and mammals (Sedio and Ostling 2013), would likely be attracted to high densities of host species, resulting in non-species specific density dependent plant damage that would be reflected in the reduced growth rates we detect in this study.

There is a disparity between the influence of crowding on mortality and RGR; while mortality is only driven by conspecific crowding, heterospecific crowding reduces RGR without causing mortality. This implies that density dependent effects of conspecific crowding cause rapid mortality and we therefore were unable to detect any change in growth rates before seedlings perished. Likely drivers of rapid NDD mortality are natural enemies, particularly fungal pathogens or oomycote (Augspurger 1983, Bagchi et al. 2010b), while competition may cause mortality over a longer timescale (Zhu et al. 2018) and would therefore be detected in reduced RGR that we do not detect in this study. Effects of heterospecific crowding on RGR but not on mortality implicate mechanisms that impact plant health but do not necessarily cause mortality, though a decline in health may in the long-term cause mortality outside the timescale of this study. Both competition and generalist natural enemies may have a slow but non-fatal impact on seedlings (Murrell 2009, Theimer et al. 2011), and it is possible that either or both of these mechanisms are driving reduced RGR. It is clear from these results that there are differing mechanisms driving conspecific and heterospecific density dependent effects, and this study reveals the importance of measuring both mortality and growth.

2.5.2 Density dependence and ageing

When we assessed the interaction between seedling age and crowding indices, we found that while heterospecific crowding effects on mortality were absent in first year seedlings, the effect increased in older seedlings, although overall mortality in young seedlings was exceptionally high. Conversely, conspecific mortality was strongest in younger seedlings. We expect smaller seedlings to experience higher mortality from competitive effects when they are out competed for resources (Tanner et al. 2005), and we further expect younger seedlings to be smaller, and therefore to see similar mortality patterns in both age and height models. However, unlike age, seedling height did not interact with heterospecific or conspecific effects on mortality and this disparity indicates that crowding effects seen in ageing seedlings were driven by age alone and not seedling size.

Conspecific NDD mortality was strongest in younger seedlings. Although this reflects results in similar studies (Metz et al. 2010, Lebrija-Trejos et al. 2014), neither of these studies looked at seedlings older than 3 years, and were unable to detect the shift in NDD drivers evident in this study. Studies have further shown that non species specific interactions are driving community dynamics at later ontogenetic stages and not at the early seedling stage (Lebrija-Trejos et al. 2014, Zhu et al. 2018), but until now, no study has addressed the change in dynamics as seedlings age but remain similar sizes. The apparent increase in species independent interactions among older seedlings within the seedling stage implies that drivers of density dependent dynamics are becoming less intraspecific only a few years after germination. Since seedlings can remain in the seedling size class for over 10 years (95% of the seedlings that survived more than 10 years remained smaller than 1 m in height) this is a surprisingly early shift in drivers of seedling mortality within the lifespan of tree.

2.5.3 Phylogenetic crowding

We tested the assertion that closely related neighbours are important drivers of density dependent mortality, utilizing phylogenetic relatedness among seedling neighbourhoods. Studies assessing the density dependent effects of phylogenetic relatedness to date have shown both positive, negative and non-significant associations (see Lebrija-Trejos *et al.* 2014). Our study supports negative associations with close relatives, with a negative effect of phylogenetic crowding on mortality and RGR, though the impact on mortality was present only for older seedlings. These negative associations may be driven by shared natural enemies where host clades are selected in phylogenetically similar individuals (Novotny et al. 2010), or shared resources, with increasing competitive interactions among close relatives (Novotny et al. 2010, Liu et al. 2012, Paine et al. 2012b). Our results reflect the effects found by Metz et al. (2010) who found that phylogenetic distance improved survival one year after germination, though we expand upon this study with an age range of up to ten years. Zhu et al. (2015b) found that phylogenetic relatedness caused NDD interactions only at later sapling and mature tree stages, and although our study does not incorporate these ontogenetic stages, it appears that our results lead in a similar direction. We do not detect the corresponding positive association that are detected in the papers mentioned above, where survival improves in high densities of closely related young seedlings, that are indicators of habitat association (Lebrija-Trejos et al. 2014, Zhu et al. 2015b).

Although both conspecific and phylogenetic crowding drive mortality, it is likely that different mechanisms are associated with these interactions since these mechanisms are impacting seedlings at different ages. Highly host-specific natural enemies are drivers where conspecifics and not close relatives cause NDD mortality, while enemies driving phylogenetic NDD mortality are evidently less host-specific as these enemies will also attack close relatives (Novotny et al. 2010). Further, if enemies are influencing RGR in close relatives but not conspecifics, they are likely those that cause damage that decreases plant health, but does not drive rapid mortality (Clark and Clark 1985). It is possible that the effect of phylogenetic crowding on mortality in young seedlings exists but was undetected due to low incidence of closely related neighbours landing in close proximity. Conspecifics maintain a high likelihood of landing in close proximity because of the locality of a fruiting adult (Alvarez-Loayza and Terborgh 2011), but this is not the case for close relatives. Our species pool is large and our plot areas are small, this may mean that the likelihood of two closely related individuals landing in the same plot are small enough that no effect is detected. It could further be argued that it would therefore not be profitable for a natural enemy to target multiple hosts unless the host range is very wide, since the likelihood of encountering two closely related hosts in a highly diverse ecosystem is minimal.

2.5.4 Variation among species

While in all models overall mortality varied among species, the addition of conspecific and heterospecific density as a random slope indicated that density dependent interactions varied among species. It has been posited that conspecific density dependence does not impact all species equally, particularly that it may differentially impact common and rare species (Hubbell et al. 2001, Comita et al. 2010, Lamanna et al. 2016). Our results support a trend in the literature that hypothesizes that rare species are rare because they experience comparatively higher conspecific negative density dependence (Hubbell et al. 2001, Comita et al. 2010, Johnson et al. 2012), while heterospecific neighbours experience density dependent mortality similarly for common and rare species. NDD prevents both common and rare species from dominating the adult stand, however with rare species experiencing stronger negative effects from conspecific neighbours, common species are permitted to maintain a higher relative abundance (Comita et al. 2010). Our results suggest that contrary to some suggestions, even at low densities rare species are able to sustain host-specific enemies (Novotny et al. 2007). Furthermore, there appears to be no increased risk of extinction for rare species experiencing stronger NDD (Lamanna et al. 2016), possibly because conspecific density tends to be lower for rare species (Johnson et al. 2012).

2.5.5 Conclusions

Our study provides strong support for negative density dependent processes in tropical seedlings, but emphasizes that the mechanisms driving NDD change as seedlings persist beyond initial germination and into established seedlings. After the initial germination stages, seedlings experience strong conspecific NDD mortality, which is likely driven by host-specific natural enemies. Natural enemies that cause mortality without any implications for deteriorating growth rates and attack conspecifics and not close relatives are likely to be both truly host-specific (or with a very narrow host range) and to cause rapid mortality, traits most often found in fungal pathogens and oomycota (Augspurger 1983).

If seedlings survive this initial high-mortality stage, the drivers and mechanisms become more varied. Overall mortality and conspecific NDD mortality diminish, and although conspecific crowding remains a strong driver of NDD, other drivers begin to emerge. Both heterospecific and phylogenetic crowding effects on mortality become more apparent as seedlings age, from which we surmise that mechanisms underlying NDD effects become less species specific in older seedlings. Furthermore, growth rates are negatively impacted by heterospecific and phylogenetic crowding for seedlings of any age. Mechanisms driving NDD growth cause slow degradation, reducing RGR, as opposed to causing rapid mortality. Where heterospecific crowding drives mortality or reduces RGR, mechanisms could be interspecific competition (Murrell 2009) or generalist natural predators (Theimer et al. 2011), though a more in depth mechanistic study is needed to separate these effects, as shown in Chapter 3. Where phylogenetic relatedness drives mortality or RGR, mechanisms are most likely natural enemies with host clades rather than one specific host (Novotny et al. 2010), and those that reduce health rather than those that cause mortality, an example of which could be insectivorous herbivory (Novotny et al. 2002).

The assertion that natural enemies or competitive interactions are driving NDD in seedlings is well supported (Wright 2002, Comita et al. 2014, Johnson et al. 2017), but it is an error to assume that one is more important than the other, or that all natural enemies impact seedling cohorts equally. Although it appears likely that, as shown by Bagchi et al. (2014), natural enemies are disproportionately contributing to NDD interactions, our evidence shows that drivers of seedling mortality and health are variable across a relatively short timescale of the seedlings life, and among common and rare species. We support indications that NDD drivers are both competitive and natural enemy driven, and that these mechanisms are highly diverse.

2.6 Acknowledgements

We thank Roxana Arauco and the staff at Cocha Cashu Biological Station for their support, enabling the data to be collected and Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP) for permitting research to be conducted in the Manu National Park. Natural Environment Research Council (NERC) and supported this research. Mario Vallejo-Marin provided improvements to the manuscript.

2.7 Supplementary Figures

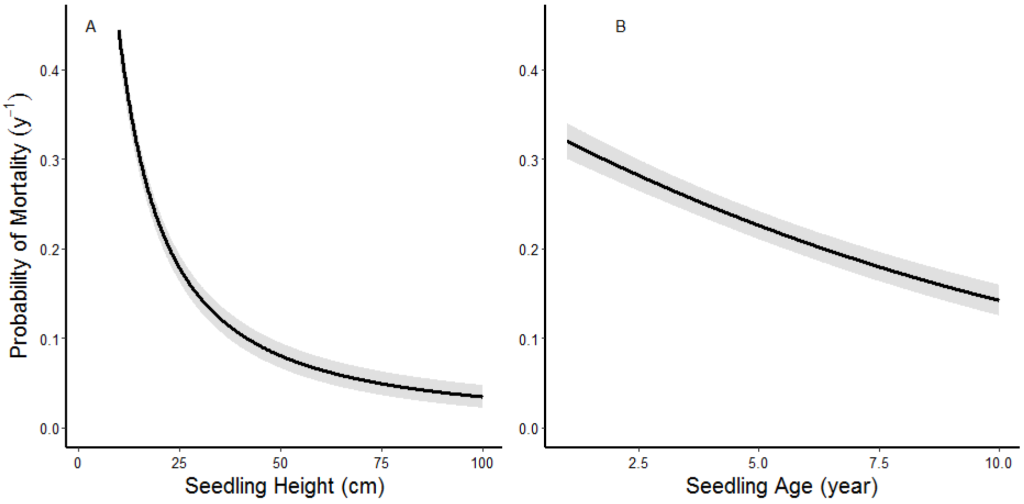

Figure S2.1 Probability of mortality predicted by A) seedling height (cm) and B) seedling age (years).

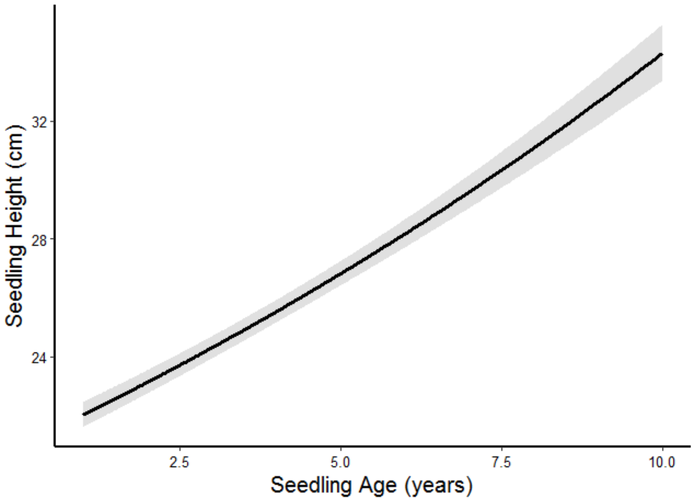

Figure S2.2 Seedling height (cm) predicted by age (years) representing linear relative growth rates among seedlings.

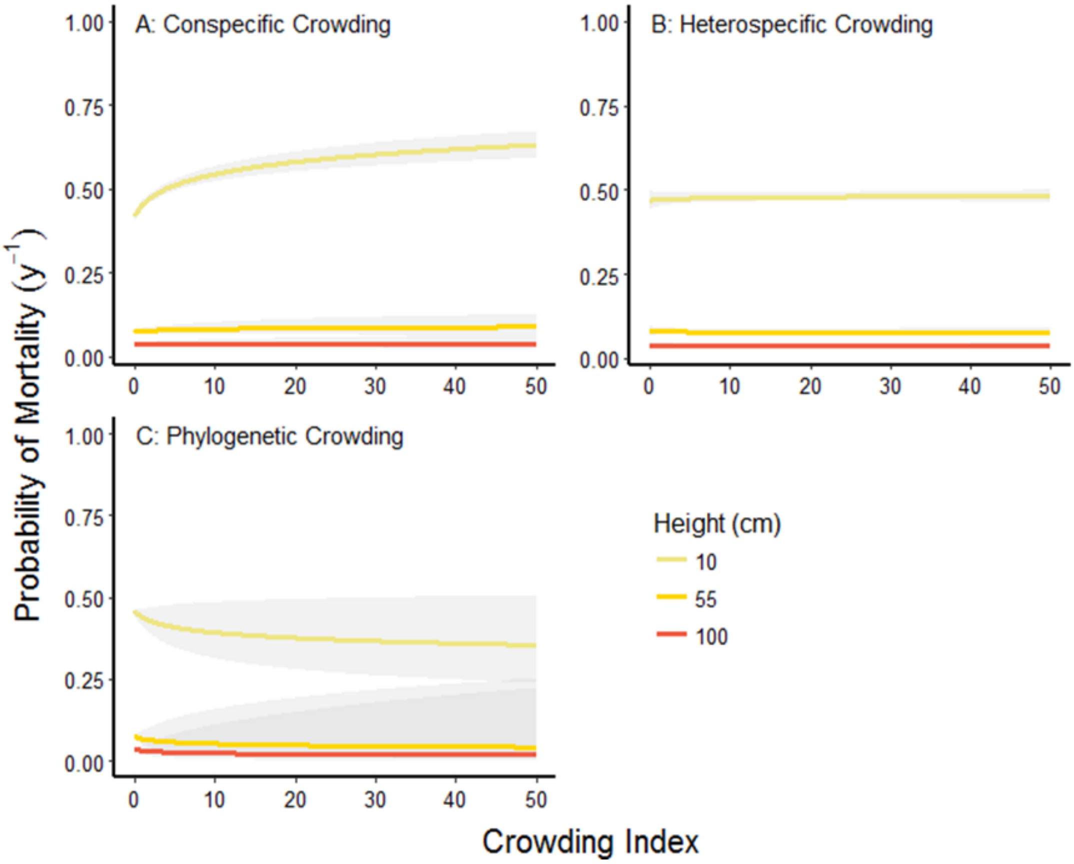

Figure S2.3 Model predictions showing predicted by A) conspecific, B) heterospecific and C) Phylogenetic crowding for seedlings of different heights.

Colours represent seedlings at 10, 55 and 100 cm. Difference in slope indicates a difference in density dependent mortality, with steep lines representing high density dependent mortality. density dependent mortality does not differ for seedlings of different heights.

Table S2.1 Summary of results in two response variables (mortality and relative growth rates (RGR), three crowding indices (conspecific, heterospecific and phylogenetic), and interactions between crowding indices and seedling height or age for mortality models.

Response	**Predictor**	**AIC**	**DF**	**Significance**
Mortality	Conspecific Crowding	13332	12969	***
Mortality	Heterospecific Crowding	13332	12969	NS
Mortality	Phylogenetic Crowding	13452	13838	NS
-	-	-	-	-
RGR	Conspecific Crowding	8251	7565	NS
RGR	Heterospecific Crowding	8251	7565	***
RGR	Phylogenetic Crowding	10971	10943	***
-	-	-	-	-
Mortality	Conspecific Crowding * Height	13334	12967	NS
Mortality	Heterospecific Crowding * Height	13334	12967	NS
Mortality	Phylogenetic Crowding * Height	13452	13838	NS
-	-	-	-	-
Mortality	Conspecific Crowding * Age	13829	12967	***
Mortality	Heterospecific Crowding * Age	13829	12967	***
Mortality	Phylogenetic Crowding * Age	14214	13834	**

Akaike Information Criterion (AIC), Degrees of Freedom (DF) and Significance codes presented.

Significance codes: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Chapter 3

Fungal pathogens, insects and mammals differentially impact tropical seedling communities and diversity

K. Hazelwood, H. Beck, C. E. T. Paine

3.1 Abstract

Fungal pathogens, insects and mammals have been implicated as agents of negative density dependent (NDD) performance in tropical tree seedlings, but their relative contributions to NDD and the maintenance of diversity are largely unknown. We assessed the influence of natural enemies on density dependent interactions among tropical seedlings by monitoring seedling survival and relative growth rates for 31 months, in plots that excluded four groups of natural enemies separately and in conjunction: fungal pathogens, insects, and small and large mammals. Fungal pathogens alone drove density dependent mortality, and the exclusion of fungal pathogens reduced species diversity. Insects reduced relative growth rates in high densities of seedlings. This was, however, driven by overall neighbourhood density and species identity was unimportant, consequently, insects had little net effect on species diversity. While small mammals did not drive NDD or diversity, large mammals temporarily supressed diversity via non-NDD interactions. We found that diversity is re-stabilised after 31 months in the absence of large mammals, but mechanisms that facilitated this re-stabilisation were not driven by other natural enemies. This indicates that diversity is maintained by a combination of natural enemies and other means. Our study presents evidence that both fungal pathogens and insects drive NDD interactions, but insects are less host-specific and decrease growth rates without altering diversity. Only fungal pathogens increase seedling diversity through conspecific negative density dependence, and are consequently highly important in shaping tree community assemblages.

3.2 Introduction

Tropical forests facilitate the coexistence of a greater number of species per hectare than most other biomes (Dirzo and Raven 2003), where up to 300 species of tree may occupy a single hectare of forest (Valencia et al. 1994). The maintenance of such high diversity is a topic that has generated the interest of community ecologists for many years (Wright 2002, Terborgh 2012, Valladares et al. 2015). Minimising competitive exclusion is central to the continued persistence of rare species, and although several mechanisms of species coexistence are extensively debated in the literature (Wright 2002), negative density dependence (NDD) is one that has received extensive support (Wills et al. 2006, Swamy and Terborgh 2010, Liu et al. 2012, Comita et al. 2014, Zhu et al. 2015a). NDD promotes coexistence by negatively impacting individual performance at high conspecific density, thereby favouring rare species (Harms et al. 2000). The seedling stage, with high mortality rates, is an especially important determinant of tree community assemblage (Metz 2012, Green et al. 2014). Mechanisms that drive NDD are widely debated (Wright 2002, Terborgh 2012), and are attributed to one of two mechanisms (Swamy and Terborgh 2010): competitive interactions among neighbouring plants for shared resources (Yoda et al. 1963), and frequency dependent mortality driven by host specific natural enemies (Janzen 1970, Connell 1971).

Studies in the tropics have found evidence for resource competition between mature or juvenile trees and seedlings (Lewis and Tanner 2000), but little evidence for competition among seedlings (Paine et al. 2008). Many studies, however, implicate natural enemies in this process (Packer and Clay 2000, Bell et al. 2006, Mangan et al. 2010, Terborgh 2012, Bagchi et al. 2014, Paine et al. 2016). Janzen (1970) and Connell (1971) first hypothesised that natural enemies facilitated NDD by disproportionately killing locally common species and allowing rare species to succeed, thereby increasing diversity. This theory rests on the assumption that the natural enemies driving this process are host specific, thereby reducing conspecific density but remaining ineffectual against heterospecifics. The most commonly proposed driving mechanism is pathogenic fungi or oomycota (referred to as fungal pathogens hereafter) (Bell et al. 2006, Mangan et al. 2010), since they are commonly highly host specific, or have a limited host range (Gilbert et al. 2012). Packer and Clay (2000) showed that pathogens had a higher likelihood of attacking seedlings in soils closer to the conspecific parent, and Bagchi et al (2010b) later used fungicide treatments to show that mortality in treated seedlings was less density dependent than controls. Insects have also been implicated in NDD processes (Connell et al. 1984, Bagchi et al. 2014, Fricke et al. 2014) though their contribution to

NDD interactions is debated (Bagchi et al. 2010a, Gripenberg et al. 2014). There is evidence for NDD associations between mammals and seed or seedling communities (Theimer et al. 2011, Beck et al. 2013), but studies have shown limited consequences for diversity (Paine et al. 2016). Considering the widespread defaunation taking place in tropical regions worldwide (Milner-Gulland et al. 2003, Peres and Palacios 2007, Abernethy et al. 2013, Dirzo et al. 2014), there are serious implications regarding the contribution of mammals to the generation of species diversity (Paine et al. 2016). With the loss of large vertebrate seed or seedling predators under hunting pressure there may be altered plant community composition (Theimer et al. 2011) and declining plant diversity (Peres and Palacios 2007, Paine et al. 2016).

Many studies have observed NDD patterns in seed or seedling communities to date (Comita et al. 2010, Swamy and Terborgh 2010, Bai et al. 2012, Zhu et al. 2018), and a few have elucidated the mechanisms by which the process is working (Packer and Clay 2000, Bell et al. 2006, Bagchi et al. 2010b, Liu et al. 2012), but very few studies have compared the relative contribution of different taxonomic groups to NDD (Bagchi et al. 2014, Gripenberg et al. 2014, Paine et al. 2016). Bagchi et al (2014) compared NDD effects from fungal pathogens and insect herbivores in neo-tropical seedlings, finding a NDD effect from both natural enemies, but changes in diversity only from fungal pathogens. Paine et al. (2016) compared NDD effects on seeds from three different size classes in mammals, finding NDD mortality and consequential diversity caused by small and medium, but not large mammals. No comparative study to date, however, has compared the contribution of mammals of different sizes to seedling community dynamics, or conducted comparisons among pathogenic, insectivorous and mammalian groups. In this study we address a missing link in the literature; a comparison of natural enemies between all of these functional groups. Moreover, we compare the degree to which pathogens, insects, and small and large mammals generate to NDD in growth and mortality.

This study assessed the comparative contribution of different natural enemies to the generation of NDD interactions on seedling performance. We split natural enemies into four categories: fungal pathogens, insects, small mammals and large mammals. We expect all natural enemy groups to drive NDD (Packer and Clay 2000, Sullivan 2003, Paine et al. 2016), but that natural enemies in the smaller size classes will drive stronger NDD interactions (Swamy and Terborgh 2010, Bagchi et al. 2014), since these tend to be host specific (Gilbert et al. 2012). Additionally, by using combinations of three treatment types, our study is able to assess the interacting effect of natural enemies. We assess two different measures of seedling performance; NDD mortality and NDD relative growth rates (RGR) in conspecific and heterospecific neighbourhoods. Chapter 2 indicates that RGR can be reduced by general crowding (i.e. heterospecific crowding) and not by species-specific interactions, we therefore expect this to be driven by generalist natural enemies such as insects (Novotny et al. 2002) and mammals (Paine et al. 2016). Mortality, however, is more strongly driven by conspecific crowding (Comita *et al.* 2010, Chapter 2), and we therefore expect mortality drivers to be the more host specific fungal pathogens (Augspurger 1983, Gilbert et al. 2012). This study asks three questions: 1) which natural enemy groups drive seedling mortality under the influence of high conspecific and heterospecific neighbours, 2) which natural enemy groups impact seedling RGR under the influence of high conspecific and heterospecific neighbours, and 3) do natural enemy groups impact diversity over the experimental period, and do processes discussed in questions 1 and 2 reflect changes in diversity.

3.3 Methods

3.3.1 Study Site

This study was carried out at the Cocha Cashu Biological Station (CCBS). CCBS is located in Amazonian South-East Peru in lowland tropical forest, at 11°51'S, 71°19'W, 350 m elevation, and 2200 mm average annual precipitation. The site is in a highly diverse and remote area of the Manu National Park, with over 350 tree species with a diameter >10 cm DBH (Foster 1990), and has not experienced any hunting, logging or mining (see Terborgh (1990) and Chapter 1 for site description).

3.3.2 Experimental Design

Circular 1 m^2 experimental seedling plots were spread throughout a 4 km trail system in mature floodplain forest (see Chapter 2 for plot setup). Out of a total of 24 transects, each with 24 plots, experimental treatments were applied to 16 randomly selected transects. Within each transect 8 plots were randomly selected on which 8 different treatment types were applied. These treatments included 7 exclusion types: fungi, insects, large mammals, all mammals, and combined fungi and insects, all mammals and fungi, and all mammals and insects, plus an 8th control plot. Within each experimental plot all woody seedlings >10 cm high and <1 cm dbh were identified, tagged, and had their height and number of leaves recorded over four censuses from 2014 to 2017. Censuses were between 294 and 330 days apart.

In order to assess the effects of pathogenic fungi on seedlings, we applied the fungicide Amistar (Syngenta Ltd, active ingredient: azoxystrobin), providing a broad spectrum of protection against fungal attack and low toxicity in non-target organisms, and found to be effective by Bagchi *et al.* (2014). To exclude insects we used the insecticide Karate (Syngenta Ltd. active ingredient: lambda cyhalothrin), protecting against a broad spectrum of insect herbivores, leaving low rates of residue and low impact on non-target organisms. Pesticides were applied according to manufacturer's instructions, mixing 1.25 ml of pesticide with 1 litre of water, and applying 50 ml of the mixture to 1 m^2 plot. Mammals were excluded using 2x2 cm wire mesh exclosures, 150 cm high, held out by iron rebar and tied down by wire, with a 50 cm strip around the perimeter of each plot inside the exclosure to reduce germination bias from perching birds. Half of the mammal exclosures allowed entry of small mammals with holes cut into the base of the mesh large enough to allow an agouti (*Dasyprocta sp.*) or smaller rodent to enter, but too small for a peccary (*Tayassu sp.*), deer (*Mazama Americana*) or tapir (*Tapirus terrestris*). Exclosures that excluded all mammals were constructed flush to the ground. In non-pesticide plots water was applied to account for the extra water received by seedlings in pesticide-treated plots. Pesticides or water were applied to treatment plots every 10 days – 2 weeks, in equal amounts over 31 months, with some treatment breaks where it was not possible to apply treatments (max 1 month).

3.3.3 Data Analysis

Over a 31 month period with 4 censuses, 4637 seedlings were monitored from 437 unique names, plus 762 individuals that were unknown or identifiable only to family, the latter were excluded from the analysis. Rarer species that do not occur frequently enough to have many conspecific neighbours were removed from the dataset by including only species that had a mean conspecific neighbourhood density of >1. The resulting dataset consisted of 174 unique names, with 71% identified to species level and the remaining 29% identified to genus level.

To compare model responses between treatment types the eight treatments were split into four groups: 1) non-combination plots; exclusion of fungi, insects, large mammals and all mammals, 2) exclusion of fungi, insects and both combined, 3) exclusion of all mammals, fungi, and both combined, and 4) exclusion of all mammals, insects, and both combined. Controls, where water was applied were included in all groups. Non-experimental seedling plots where no treatment was applied were also monitored. Mortality and RGR were modelled against conspecific and heterospecific neighbourhood density in control plots (where water was applied) and non-treatment plots (with no experimental interference) and no significant difference was found between control and non-treatment plots in mortality models (conspecific density: $P = 0.68$, heterospecific density: $P = 0.61$) or RGR models (conspecific density: $P = 0.16$, heterospecific density: $P = 0.79$), we therefore combined control and non-treatment plots for all treatment comparisons.

Both conspecific or heterospecific neighbourhood density, and neighbouring seedling size may impact mortality or RGR, we therefore calculated a neighbourhood crowding index for each seedling (Canham et al. 2004). Neighbourhood crowding indices (NCI) were calculated per plot and census as:

$NCI_k = \Sigma(\text{height}_n / \text{height}_k)$

Where k is the focal individual, and n are neighbouring seedlings. Indices were calculated separately for conspecific neighbours and heterospecific neighbours. Seedlings that were excluded from the dataset for analytical purposes were counted among heterospecific neighbours.

To assess NDD mortality, we used generalised linear mixed effect models with mortality predicted by interacting conspecific crowding and treatment, and heterospecific crowding and treatment. Larger seedlings experience lower mortality (Chapter 2), therefore log-transformed seedling height was included in these models as a fixed effect. Models were offset by logged time (years) between census and complementary log-log links, to account for differing census intervals. RGR was assessed using linear mixed effect models, in which log-transformed seedling height was predicted by seedling age, and model coefficients represented relative growth rates (Paine et al. 2012a). Seedling RGR was considered to be exponential since growth rates do not decline until trees reach a height far exceeding that of 1 m (Fig. S3.1). Model coefficients from interactions between age, crowding indices (conspecific and heterospecific) and treatment indicated RGR for each treatment and their association with crowding indices.

Fungicide, insecticide, all mammal and large mammal treatments were each compared to control plots. To assess the impact of small mammals, large mammal and all mammal treatments were included in one model as separate treatment levels and in a second model as a single combined treatment level. ΔAIC for the two models were compared (Burnham and Anderson 2004), the significance of these separate treatments was compared using analysis of variance. Combination treatments (e.g. fungicide and insecticide treatments in one plot) were compared to control and to each constituent non-combination treatment (e.g. fungicide & insecticide treatments compared to 1) control, 2) fungicide and 3) insecticide treatments).

Species was included as a random intercept in all models to account for different mortality or RGR among species. Crowding indices were included as a random slope to assess whether the strength of NDD varied among species (Chapter 2). The inclusion of random slopes was assessed using model ΔAIC comparisons (Burnham and Anderson 2004). Model fits were better with the inclusion of random slopes for conspecific crowding for all mortality models. In the growth models, model fit was better with the inclusion of random slopes for both conspecific and heterospecific crowding.

Diversity was measured using exponential Shannon-Weiner diversity indices for each plot at each census. Change in diversity was calculated as the within-plot difference in Shannon-Weiner diversity index from one census to the next per census interval, measuring from the second census, 0.8 years after the initiation of treatments. Change in diversity was modelled against the number of days since the initiation of the experiment, interacting with treatment. Shannon-Weiner diversity was included as a random intercept to allow for differences in diversity among plots at the outset of the study.

Analyses were performed in R 3.5.0 (R Core Team 2017), using packages lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), effects (Fox 2003), vegan (Oksanen et al. 2017), and ggplot2 (Wickham 2009).

3.4 Results

Over 31 months and four censuses, we monitored 3262 seedlings from 174 species. For seedlings in all treatments, mortality rates were around 18% per year in the absence of conspecific neighbours. Mortality increased with conspecific crowding in control plots ($P = 0.008$, Fig. 3.1), with a doubling of conspecific crowding resulting in a 2% increase in the annual probability of mortality. Heterospecific crowding had no impact on mortality ($P = 0.36$, Fig. 3.1). RGR declined with both conspecific and heterospecific crowding (both $P \leq 0.001$), though the decline was stronger with heterospecific crowding (Fig. 3.2). Mortality and RGR irrespective of neighbourhood density were not significantly different among treatments.

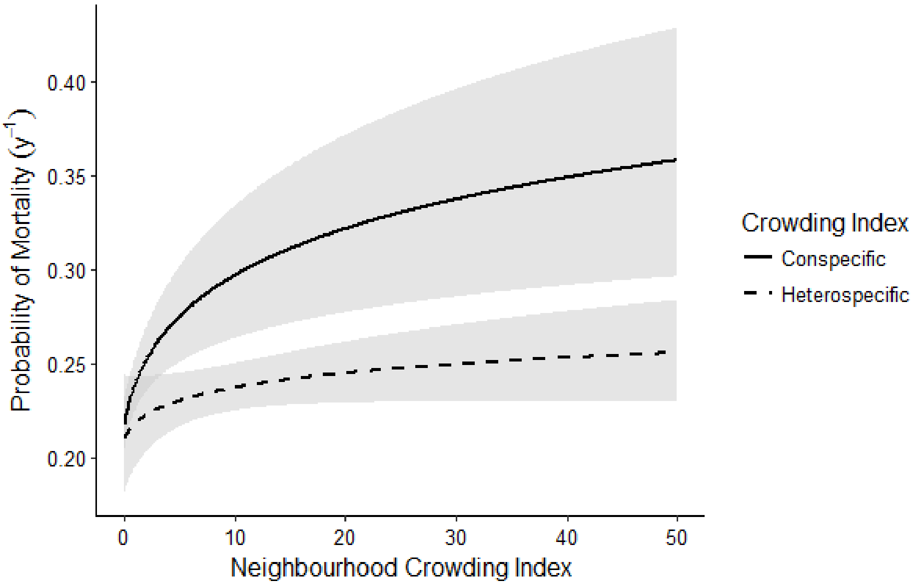

Figure 3.1 Predicted neighbourhood crowding effects on probability of mortality (y^{-1}) in control plots. Conspecific but not heterospecific crowding lead to higher mortality rates.

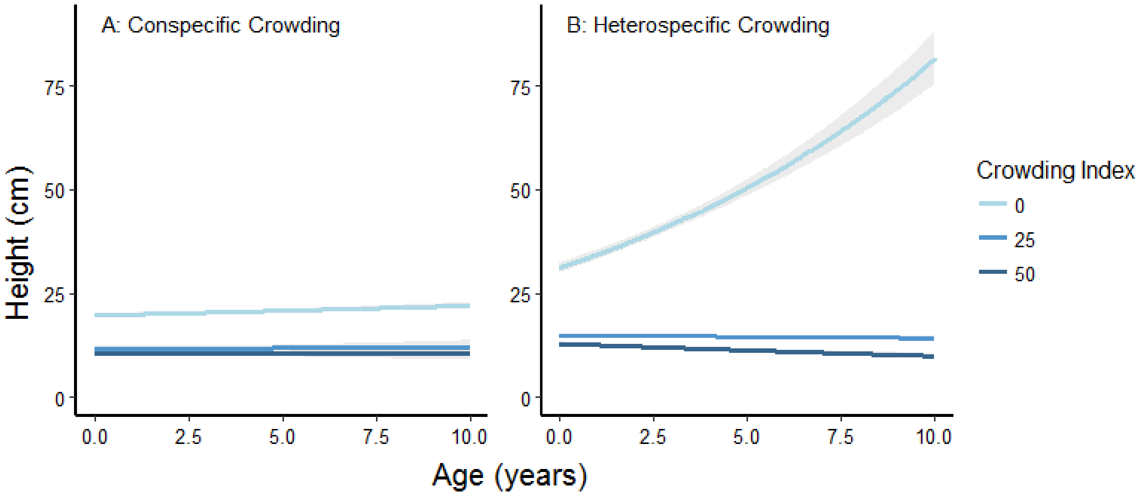

Figure 3.2 Model predictions showing relative growth rates (RGR) as height predicted by age under the influence of A) conspecific and B) heterospecific crowding.

Colours represent minimum, median and maximum crowding indices. Difference in slope indicates a difference in RGR among crowding indices, with steep lines represent high RGR. RGR decreases with increased crowding index for heterospecific crowding only.

3.4.1 Mortality

The impact of neighbourhood density on mortality was assessed for each different natural enemy exclusion treatment. The effect of conspecific crowding on mortality was significantly reduced by fungicide application ($P = 0.01$, Fig. 3.3), with a doubling of conspecific crowding resulting in a 2% *decrease* in mortality. We compared models with large mammal and all mammal treatments separate and pooled to assess the effects of small mammals. There was no significant difference between models, indicating that small mammals did not influence mortality under altered conspecific crowding ($P = 0.37$, Fig. 3.3). No change in mortality was seen in relation to heterospecific crowding in any treatments ($P > 0.1$ for all treatments, Fig. S3.2), nor was heterospecific crowding a driver of mortality in control plots ($P = 0.36$, Fig. 3.1). Combination treatments, in which two natural enemy groups were simultaneously excluded, did not significantly differ from insecticide or mammal treatments when mortality was interacting with conspecific or heterospecific crowding effects ($P > 0.05$ for all combination treatments, Fig. 3.4). Plots that excluded fungi in combination with other treatments were significantly or near significantly different from fungicide only plots when mortality interacted with conspecific crowding (Fungicide & Insecticide: $P = 0.01$, Fungicide & Mammals: $P = 0.06$) and heterospecific (Fungicide & Mammals: $P = 0.01$) crowding. Unlike control plots however, no combination treatment showed any evidence of conspecific crowding driving mortality, with exceptionally high variance in mortality rates (Fig. 3.4).

3.4.2 Relative Growth Rates

Relative growth rates were negatively impacted by conspecific crowding (Fig. 3.2), and this did not change under any exclusion treatments (Fig. S3.3). High heterospecific crowding negatively impacted RGR ($P < 0.001$), and this effect was significantly weakened by the application of insecticide ($P = 0.003$, Fig. 3.5c). In control plots, a doubling in heterospecific crowding reduced RGR by 5%, whereas RGR was reduced by only 1% in plots from which insects were excluded. Under the influence of heterospecific crowding there was no effect of excluding fungal pathogens, large mammals or all mammals on RGR ($P = 0.11$, $P = 0.89$, $P = 0.18$ respectively, Fig. 3.5), and no effect of small mammals ($P = 0.37$). Plots in which insects are excluded in combination with other treatments showed a reduced effect of heterospecific crowding on RGR compared to control plots (insects and fungi: $P = 0.005$, insects and mammals: $P < 0.001$, Fig. S3.4.

The effect of heterospecific crowding on RGR in combined fungi and mammal exclusion treatments was not significantly different to control plots (*P* = 0.69).

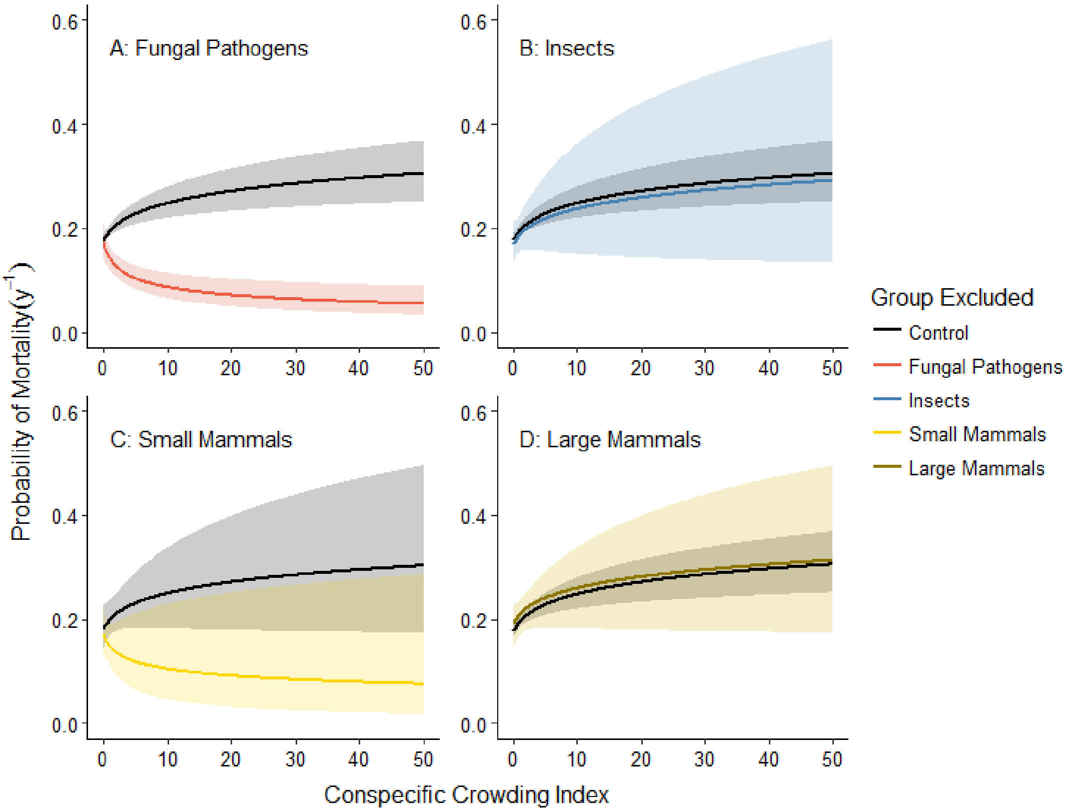

Figure 3.3 Probability of mortality (y^{-1}) predicted by conspecific crowding indices under the exclusion of fungal pathogens, insects, small mammals and large mammals.

Coloured lines represent the excluded group of natural enemies. Only plots excluding fungal pathogens significantly reduced mortality at high conspecific crowding.

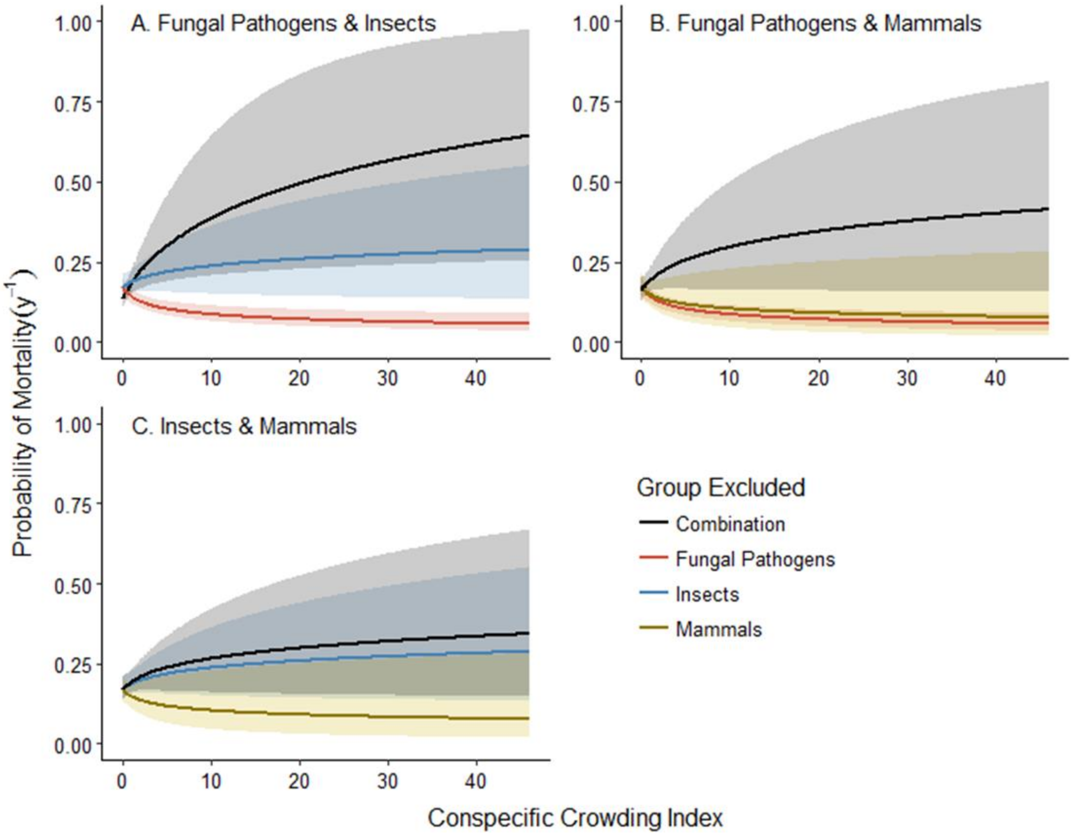

Figure 3.4 Mortality driven by conspecific crowding indices for plots excluding A) fungal pathogens and insects, B) mammals and fungal pathogens, and C) mammals and insects.

Coloured lines represent the excluded group of natural enemies. Combination treatments are indicated in the plot heading. Conspecific crowding influences mortality under control treatments, but does not significantly impact mortality under any combination treatments.

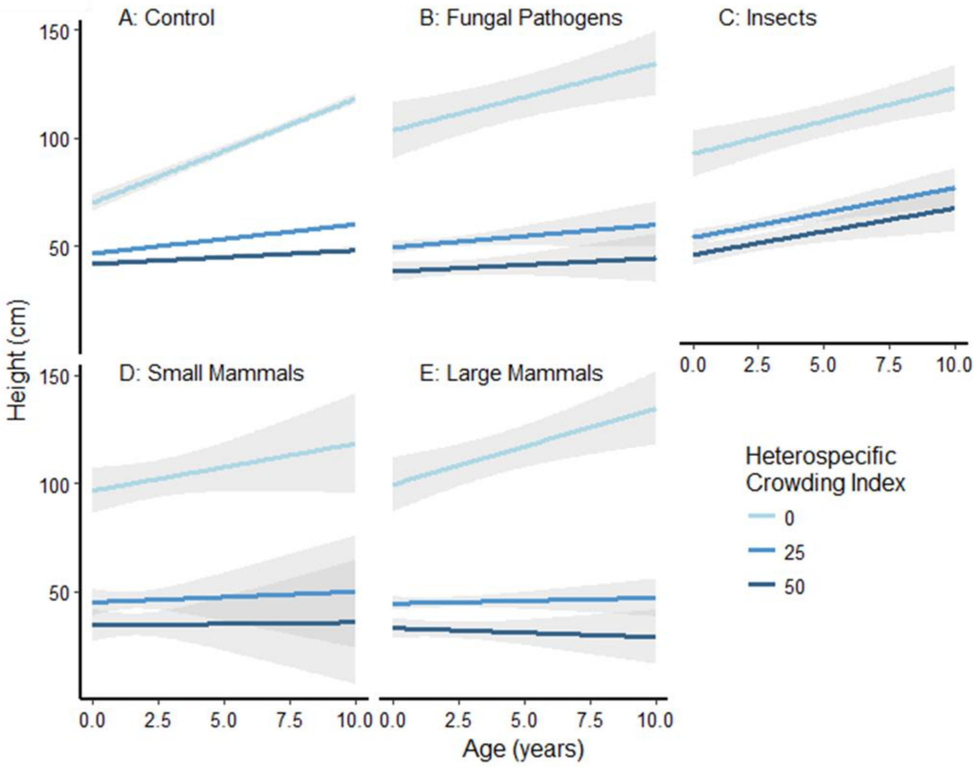

Figure 3.5 Model predictions showing relative growth rates (RGR) as height predicted by age under the influence of heterospecific crowding in A) control plots and under the exclusion of B) fungal pathogens, C) insects, D) small mammals and E) large mammals.

Colours represent minimum, median and maximum heterospecific crowding indices. Difference in slope indicates a difference in RGR among crowding indices, with steep lines represent high RGR. RGR decreases with increased heterospecific crowding in all plots except those in which insects were excluded.

3.4.3 Diversity

The effect of exclusion treatments on diversity was monitored using the change in Shannon-Weiner diversity index per plot for the duration of the experiment. Control plots showed very little change in diversity throughout the experiment (*P* = 0.32). The application of fungicide lead to a decrease in diversity over the experimental period (*P* = 0.006, Fig. 3.6a). Diversity significantly increased in large mammal plots (*P* = 0.006), declining again after the first census period (Fig. 3.6a). The model with all mammals and large mammals separate, and the model with the treatments combined were not significantly different (*P* = 0.96), indicating that small mammals were not a significant driver of declining diversity. The exclusion of insects lead to a similar pattern in diversity as large mammals, with a small initial increase followed by a decline, but this change was not significant (*P* = 0.16). When treatments were combined, diversity decreased significantly in plots where mammals were excluded in combination with fungi (*P* = 0.005) or insects (*P* = 0.05, Fig. 3.6b). The combined exclusion of fungi and insects had no significant effect on diversity in comparison to control plots (*P* = 0.22).

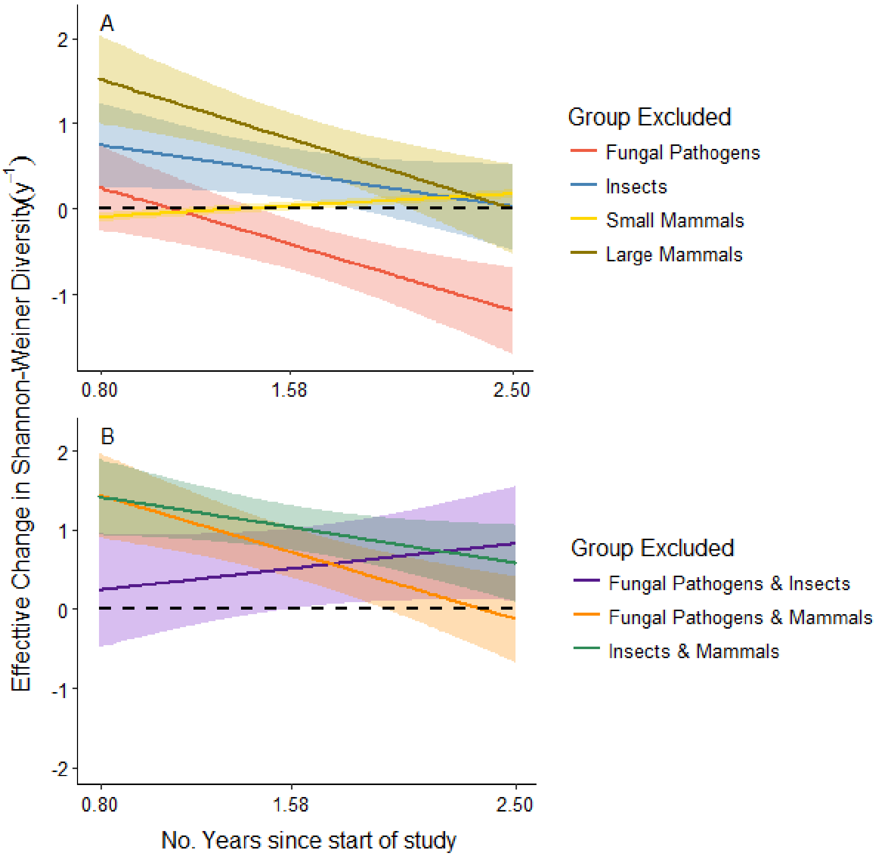

Figure 3.6 Effective change in Shannon-Weiner Diversity index under the exclusion of A) fungal pathogens, insects, small mammals and large mammals, and B) combination treatments.

Diversity change is within plot over time from 0.8 years after the initial application (the second census), x axis tick marks are at the third (1.58 years) and fourth (2.5 years) censuses. Treatment effects are represented as the ratio of Shannon diversity in treatment vs. control plots. Small mammal effects are represented as the ratio of Shannon diversity in all mammal vs. large mammal plots.

3.5 Discussion

Natural enemies have frequently been associated with NDD processes in seedlings (Bell et al. 2006, Mangan et al. 2010), and while these mechanisms have been tested individually (Packer and Clay 2000, Sullivan 2003, Bagchi et al. 2010b), this study is among very few that have compared these natural enemies (Paine and Beck 2007, Bagchi et al. 2014, Gripenberg et al. 2014, Fricke et al. 2014). Further, this is the only study to date that has compared four natural enemy groups. We find strong evidence that fungal pathogens generate more NDD mortality than insects, consistent with results found by Bagchi *et al.* (2014). Our study expands upon theirs, being the first to compare NDD among seedlings driven by mammals of different size classes. Further, the comparison of four natural enemy groups, gives this study a unique perspective regarding the relative contributions of all of these natural enemies within this trophic level. We build on previous NDD mortality studies with the assessment of RGR and NDD among natural enemy groups; while density dependent mortality is driven by fungal pathogens (exclusively in this study), density dependent RGR among seedlings is driven by insects, and while fungal pathogens drive conspecific NDD, insects drive heterospecific NDD. Only fungal pathogens, however, drive changes in diversity through NDD. This clarifies the difference between drivers of diversity, and shows that while NDD among plants may have multiple drivers, not all are important in maintaining diversity.

It has been widely demonstrated that NDD is a strong driver in structuring tree species communities at early life stages (Harms et al. 2000, Comita et al. 2010, Green et al. 2014). Here, we show that conspecific interactions are the primary contributor to NDD mortality, consistent with previous research (Zhu *et al.* 2018, Swamy & Terborgh 2010, Chapter 2). The presence of NDD in control plots allowed us to test the driving mechanism using treatment plots, where natural enemy groups are excluded. Our results indicate that fungal pathogens alone are the key drivers of conspecific NDD mortality. These results are consistent with studies that found strong associations between NDD and fungal pathogens (Packer and Clay 2000, Bell et al. 2006, Bagchi et al. 2014), and validate a mechanism originally proposed by Janzen (1970). Fungal pathogens are often highly host specific (Gilbert and Webb 2007), it is this host specificity that allows pathogens to pass between hosts effectively under high conspecific crowding, rapidly causing mortality to conspecifics and allowing heterospecifics to persist. Where fungal pathogens were excluded in this study, mortality at high conspecific crowding not only decreased but reversed the trend, indicating that, once released from the negative effects of fungal pathogens, the environmental conditions are favourable enough for high densities of conspecifics to thrive. This further supports the argument that intraspecific competition among seedlings is unlikely to drive NDD interactions (Paine et al. 2008). A comparable study by Bagchi *et al.* (2014) showed NDD mortality driven by both fungal pathogens and insects, while we found no evidence for insect driven NDD mortality. Both studies used robust and similar methods, and insect mortality was detected in insecticide treated plots, verifying the efficacy of the treatment. Differing biotic and abiotic conditions among experimental sites may account for this difference, however it would be beneficial to extend studies excluding insects to monitor long term effects. NDD interactions driven by fungal pathogens in this study are driving changes in diversity through the suppression of competitive exclusion in seedling communities (Harms et al. 2000). This process is key to the maintenance of diversity in seedling communities (Wright 2002, Comita et al. 2010), and our study presents strong evidence that fungal pathogens are by far the strongest driver of this process.

Relative growth rates are negatively impacted by overall crowding effects, with RGR diminished under both high conspecific and heterospecific crowding, and seedling neighbour identity remaining unimportant. With fungal pathogens driving mortality but not RGR under high conspecific crowding, it appears that seedling mortality driven by fungal pathogens is rapid, with little time for deterioration of health before mortality occurs (Augspurger 1983, Bell et al. 2006). The exclusion of insects increased RGR significantly under high heterospecific crowding, an effect that did not consequently reduce mortality during this study. It is, however, possible that negative effects on RGR lead to mortality in the long-term, reducing plant health until they are unable to compete successfully, but such long-term effects were beyond the scope of this 3- year study. Although many insect herbivores are host-specific (Barone 1998, Forister et al. 2015), insects more commonly consume a host clade, which can be variable in breadth (Novotny et al. 2002, Gilbert et al. 2015). With this semi-generalist nature, insects are generating non species-specific NDD RGR, and thereby not generating a significant change in diversity, since diversity is elevated only when intraspecific effects are stronger than interspecific effects (Chesson 2000).

García-Guzman & Dirzo (2001) found that insect herbivores can accelerate rates of pathogen infection by creating wounds by which pathogens can attack. To test this, we experimentally combined treatment groups, expecting to find stronger NDD processes in combined herbivore (insects or mammals) and fungal pathogen exclusion plots. Surprisingly, not only did we detect no change in rates of NDD mortality, the effect of excluding fungal pathogens alone was lost. We found, however, that in all cases the simultaneous exclusion of multiple natural enemy groups lead to an overall loss of conspecific NDD mortality, with highly variable mortality rates under any conspecific crowding. In theory this is because removing multiple deterministic mechanisms simultaneously (e.g. fungi impacting mortality and insects impacting RGR) makes the occurrence of mortality highly stochastic, or at least unconnected to the biotic neighbourhood. Combined treatments impacted RGR similarly to plots with individual exclusions; in plots excluding insects in combination with other treatments, the effect of heterospecific crowding on RGR was diminished as with plots excluding insects alone. We conclude that insects alone are driving the change detected in combination plots. Our results show that natural enemies are not interacting to influence NDD, and are therefore impacting different sections of the seedling community. This provides evidence for variation among species in vulnerability to natural enemy attack, and thereby vulnerability to NDD.

There was no change in mortality or RGR under the influence of crowding after the exclusion of large or small mammals. This is in contradiction with Paine *et al.* (2016), who found that small and medium sized mammals contribute to NDD interactions and increase beta diversity in a seed removal experiment. However Paine *et al.* (2016) did not consider fungal pathogens or insects, and our study indicates that the effects of mammals are minimal compared to the prevailing effects of natural enemies in the smaller size classes. Small mammals preferably predate seeds over seedlings (Asquith et al. 1999, Wright et al. 2000) and impact recruitment, therefore data on seed arrival would improve the scope of this study, and allow us to detect recruitment rates. With studies implicating mammalian predators in structuring tree communities (Demattia et al. 2006, Paine et al. 2016), it is possible this study overlooks a component of NDD interactions at the seed stage. However we do not detect any changes in diversity driven by small mammals, so where recruitment effects are present but undetected, they are not sufficient to impact diversity.

A caveat in this study is the unusually low densities of *T. pecari* (white lipped peccary) at the site during this experiment. *T. pecari* populations undergo large fluctuations, becoming locally scarce for years at a time (Reyna-Hurtado et al. 2009). During periods of high densities of *T. pecari,* the species moves about in large groups both consuming seeds and destroying plants as they move (Beck 2005), without these species present our study lacks the potentially powerful effect of this species on seedling mortality, which could account for the contrasting results found by Beck *et al.* (2013) and Theimer *et al.* (2011), who found that large mammals contributed to NDD interactions. Despite the absence of this important species however, we detect a change in diversity where large mammals are excluded. Diversity initially increases after the first year, implying that large mammals suppress diversity when present, though this effect diminishes during the following 2 years. We did not detect NDD in large mammal plots, and it is unlikely that NDD would suppress diversity, so we must assume that large mammals are suppressing plant diversity via alternative mechanisms. Large mammals cause mortality and mechanical damage to seedlings through grazing or trampling (Terborgh and Wright 1994, Wright 2003), and when plants are released from this effect survival and recruitment improve (Beck et al. 2013). While improved overall survival may not influence diversity per se, this may benefit species differentially and increase the likelihood of competitive exclusion in, for example, faster growing species, and thereby decrease diversity. Initial disruption to community dynamics are followed by a gradual return to stable diversity. Similarly, Beck *et al.* (2013) found that overall seedling density, survival and recruitment was higher when large mammals were excluded during the first 2 years of the experiment only. A secondary mechanism appears to be stabilizing diversity after the initial release from herbivory, though as with Beck *et al.* (2013), this takes a few years to re-stabilize. Where mammals and fungal pathogens were simultaneously excluded, diversity increased initially as with large mammal exclusion, showing no signs of the significant decline seen in fungicide treated plots (Fig. 3.6b), indicating the diversity effects of large mammals are more powerful than the effects of fungal pathogens. Moreover, there is a subsequent decline in diversity in large mammal plots in the presence and absence of fungal pathogens or insects, it is therefore unlikely that fungal pathogens or insects are causing the re-stabilizing effect on diversity through NDD interactions.

Large mammals initially have a stronger impact on diversity than small mammals, contrasting with studies that indicate small mammals are more likely to drive NDD interactions (Demattia et al. 2006, Paine et al. 2016), or show little evidence for altered diversity in relation to large mammals (Theimer et al. 2011). Large vertebrates suffer population declines in hunted forests (Endo et al. 2010) and defaunated forests have seen substantial changes in tree community assemblage (Wright et al. 2007c, Terborgh et al. 2008, Peres et al. 2015). Our results indicate that the extirpation of large terrestrial mammals would have little effect on tree diversity, with the initial boost in diversity after the loss of large mammals levelling out before trees reach reproductive age. This does not negate impacts of hunting however, since hunting impacts both terrestrial and arboreal mammals (Peres and Palacios 2007, Endo et al. 2010), and many trees are heavily reliant on arboreal frugivores for seed dispersal (Peres and van Roosmalen 2002). While the loss of large terrestrial mammals has minimal consequences for tree communities, hunting conceivably alters community assembly in hunted forests due to a loss of large frugivores (Wright et al. 2007c, Terborgh et al. 2008).

3.5.1 Conclusions

Our study demonstrates that while fungal pathogens and insects drive NDD interactions, diversity is impacted under the influence of fungal pathogens. Diversity is also driven by large mammals; but while fungal pathogens maintain diversity through NDD, large mammals temporarily suppress diversity through non-NDD processes. Furthermore, after a loss of large mammals de-stabilizes diversity, fungal pathogens are not associated with the following re-stabilization. In response to this we emphasize two points; 1) NDD is not the only, or the most important driver of diversity in tropical seedling communities, and 2) in the absence of large mammals, disruption to tree diversity is not compensated for by natural enemies, implying abiotic mechanisms play an essential role in maintaining diversity. While our results suggest that diversity is maintained by multiple drivers and should not be assigned a single mechanism, we present strong evidence that fungal pathogens are uniquely important in shaping tropical tree communities above other groups of natural enemies, and are disproportionately important drivers of diversity in tropical forests.

3.6 Acknowledgements

Natural Environment Research Council (NERC) and Harald Beck supported this research. We thank Adrian Torres-Paucar, Noemie Darloy, Alex Adonis Caceres Muna, Simona Clausnitzer, Fortunato Jaime Rayan, Moises Huarankashi and Juan Kapeshi for their unwavering assistance in the field that enabled the experiment to run. We also thank Roxana Arauco and the staff at Cocha Cashu Biological Station for their support, without whom we could not have constructed and managed the experiment. We thank Mario Vallejo-Marin for improvements to the manuscript, Daisy Dent for conceptual input and Patricia Alvarez-Loayza for assistance with seedling and pathogen identification.

3.7 Supplementary Figures

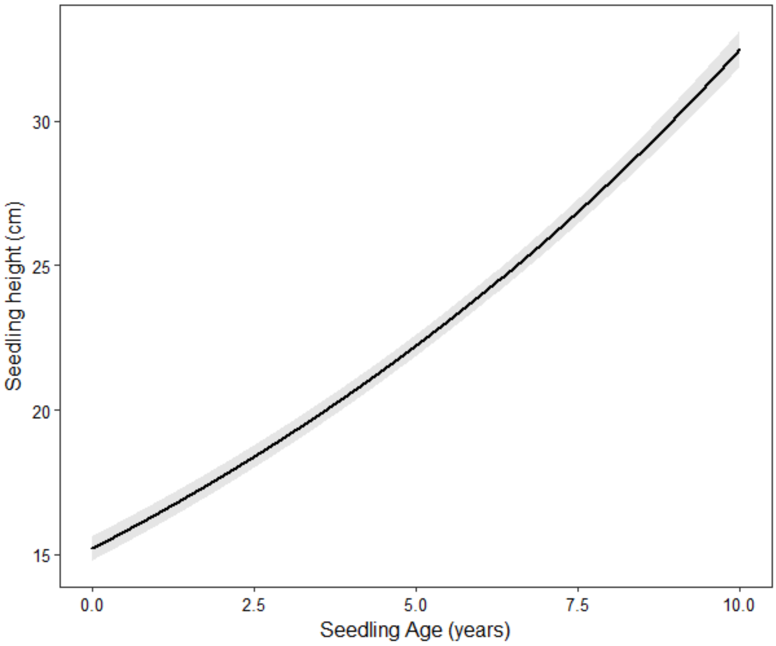

Figure S3.1 Seedling relative growth rates represented by height (cm) predicted by age in control plots only.

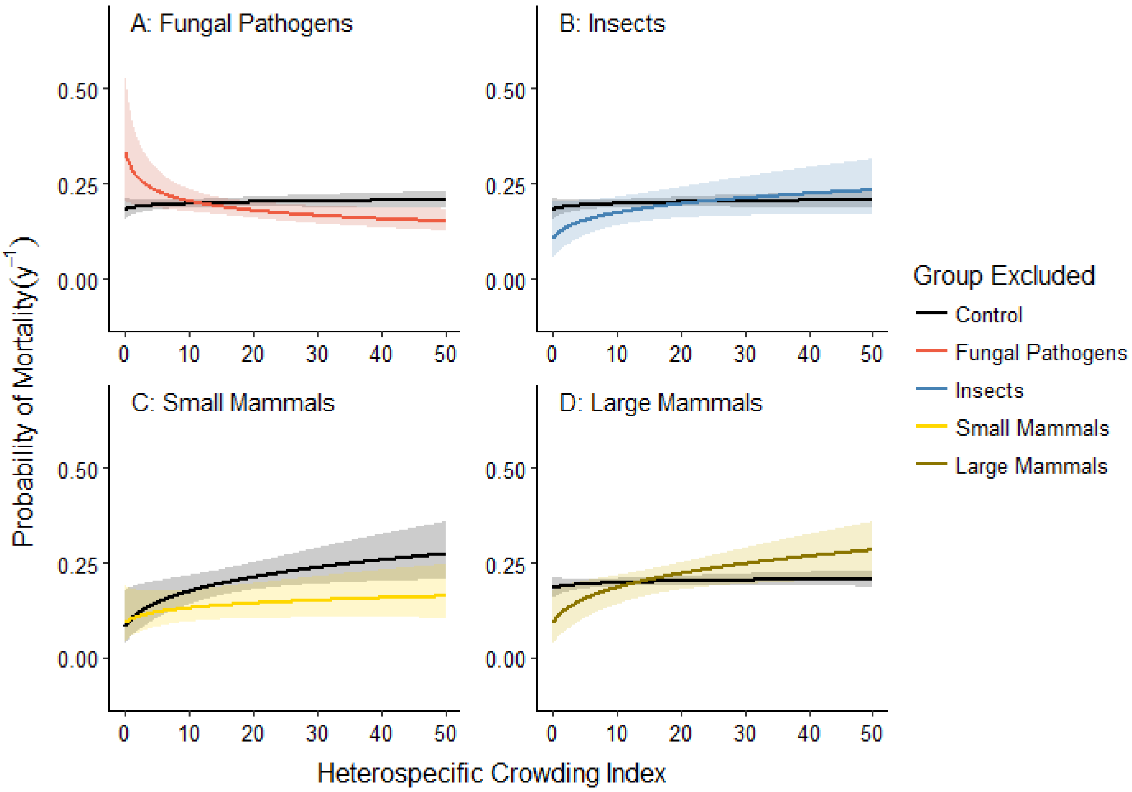

Figure S3.2 Probability of mortality (y^{-1}) predicted by heterospecific crowding indices under the exclusion of fungal pathogens, insects, small mammals and large mammals.

Coloured lines represent the excluded group of natural enemies.

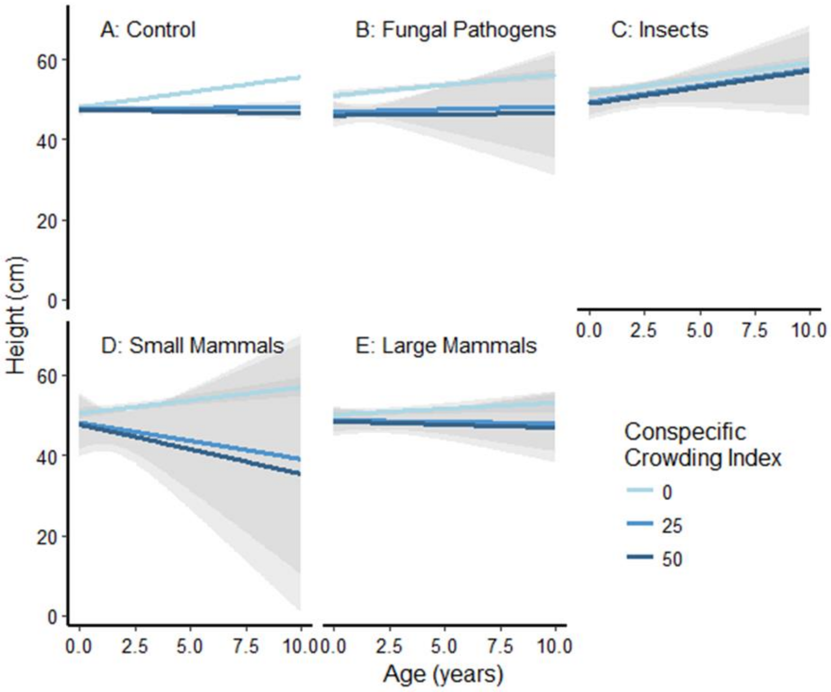

Figure S3.3 Model predictions showing relative growth rates (RGR) as height predicted by age under the influence of heterospecific crowding in A) control plots and under the exclusion of B) fungal pathogens, C) insects, D) small mammals and E) large mammals.

Colours represent minimum, median and maximum heterospecific crowding indices. Difference in slope indicates a difference in RGR among crowding indices, with steep lines represent high RGR.

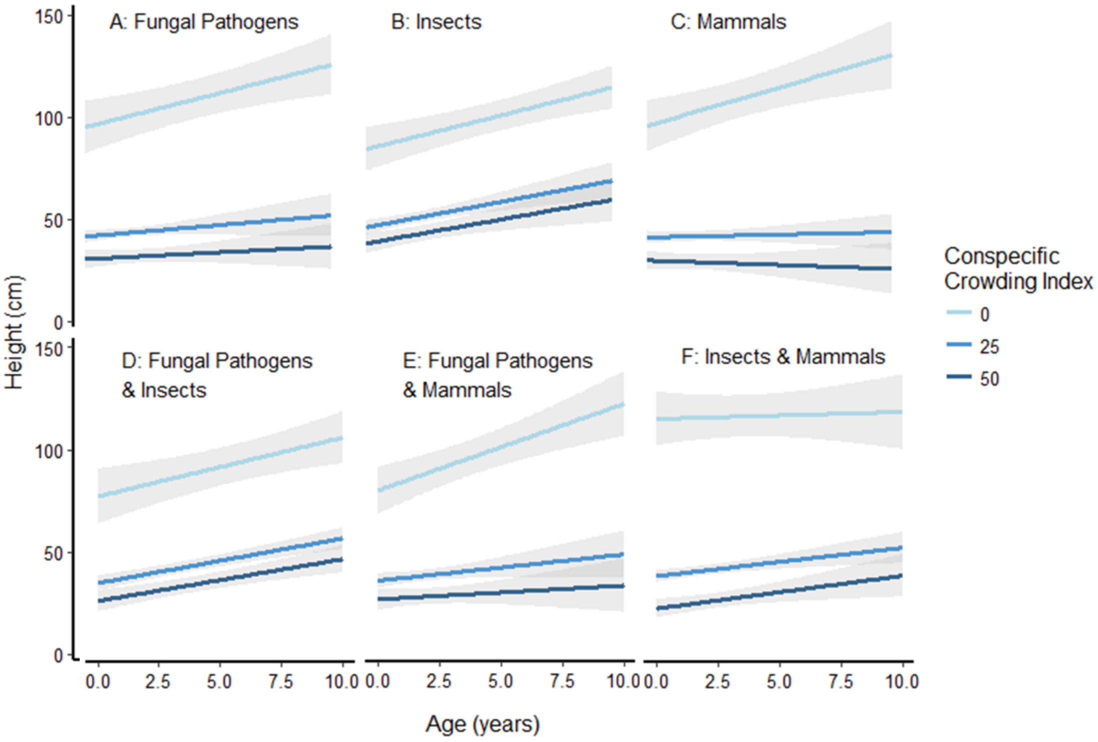

Figure S3.4 Model predictions showing relative growth rates (RGR) as height predicted by age under the influence of heterospecific crowding under the exclusion of A) fungal pathogens, B) insects, C) mammals, D) fungal pathogens and insects, E) fungal pathogens and mammals, and F) insects and mammals.

Colours represent minimum, median and maximum heterospecific crowding indices. Difference in slope indicates a difference in RGR among crowding indices, with steep lines represent high RGR.

Chapter 4

Changing tree community structures in defaunated forests are not driven only by dispersal limitation

K. Hazelwood; C. E. T. Paine; F. H. Cornejo Valverde, E. G. Pringle; H. Beck; J. Terborgh

4.1 Abstract

Bushmeat hunting has reduced population sizes of large frugivorous mammals and birds throughout the tropics, thereby reducing the dispersal of seeds. This is believed to affect tree population dynamics, and therefore community composition, because seed dispersal of large-seeded trees depends upon large-bodied arboreal vertebrates, which are preferentially hunted. We report on a long-running study of the effect of defaunation on a tropical tree community. With three censuses over 11 years, we assessed sapling recruitment to determine the extent to which species composition is changing through time at nearby, comparable hunted and nonhunted sites. We expected to find a decline in the tree species that rely on large frugivores for dispersal at the hunted site, and altered community structure as a consequence. Although community composition at the hunted site diverged from that at the nonhunted site, the changes in community composition were independent of dispersal syndrome. Evidence suggests that the loss of large-bodied dispersers has not generated the changes in tree community composition we expected. Rather, many species that rely on large-bodied frugivores for dispersal are recruiting without their dispersers. The presumption that forests depleted of large-bodied dispersers will experience rapid, directional compositional change is not fully supported by our results. Altered species composition at the hunted site, however, indicates that defaunation may be connected with changes to the tree community, but the nature of these changes are not as unidirectional as previously assumed. It will be difficult to predict how defaunation will affect tree community composition without a deeper understanding of the driving mechanisms at play and of differences among species in response to defaunation.

4.2 Introduction

Bushmeat hunting has caused population declines in many species of large vertebrates in forests throughout the tropics (Milner-Gulland et al. 2003, Corlett 2007, Peres and Palacios 2007, Wright et al. 2007b, Harrison 2011, Abernethy et al. 2013, Dirzo et al. 2014). This has given rise to a proliferation of defaunated 'empty forests' (Redford 1992), which, though they appear structurally intact, have suffered dramatic changes in ecosystem function (Wright et al. 2007c, Harrison et al. 2013, Peres et al. 2015). As animals impact plant communities through herbivory, seed predation, pollination and seed dispersal, removing any of these functions can alter the community dynamics of plants and have a cascading effect through the ecological community (Palmer et al. 2008, Terborgh 2013).

Hunting in the Neotropics targets large-bodied vertebrates, including many frugivores (Peres and Palacios 2007) that play an essential role in seed dispersal of trees (Levey et al. 1994, Peres and van Roosmalen 2002). Large-seeded tree species are most likely to rely on large-bodied frugivores for dispersal because smaller animals are unable to swallow the seeds. Thus, any loss of large-bodied frugivores is likely to impact dispersal function (Forget and Jansen 2007, Wang et al. 2007). Janzen (1970) and Connell (1971) suggested that undispersed seeds or seedlings experience increased mortality, caused by denser aggregations of host specific natural enemies near conspecific adults. Evidence has shown that effects of the Janzen-Connell hypothesis can be strong drivers of tree community structure, especially in Neotropical forests (Comita et al. 2010, Swamy and Terborgh 2010, Bagchi et al. 2010b). We would therefore expect lower recruitment of species that experience reduced dispersal and, as a consequence, changes in plant community composition.

To date, there have been considerable inconsistencies in the results from studies that address those questions, with many suggesting that the loss of large-bodied frugivores could have severe consequences for many tree species, including extinction (Nuñez-Iturri et al. 2008, Stevenson and Aldana 2008, Terborgh et al. 2008, Peres et al. 2015). Whereas others making more moderate assertions (Brocardo et al. 2013, Kurten et al. 2015, Bagchi et al. 2018). Numerous studies have assessed the effects on plant community composition in defaunated forests at a single point in time (Nuñez-Iturri and Howe 2007, Stevenson and Aldana 2008, Bello et al. 2015, Peres et al. 2015), whereas others have conducted manipulative experiments over a longer time period at the seed or seedling level (Brocardo et al. 2013, Beck et al. 2013, Kurten et al. 2015). Very few studies, however, have examined population dynamics in detail across ontogenetic stages over a period of more than 3 years, with the notable exception of Harrison et al. (2013), who found significant changes in tree community composition 15 years after the onset of hunting in the Paleo-tropics. Studies that address transitional changes between ontogenetic stages are important for determining community structure in the long term, and our understanding of these changing forest dynamics is essential to making large-scale or long-term predictions about changing tree communities.

In a thorough evaluation of the effects of defaunation, Terborgh et al. (2008) compared the sapling and mature tree populations between a hunted and a nearby nonhunted neotropical forest, and concluded that defaunation had strongly impacted tree community dynamics. However, because their study was conducted at a single point in time, its ability to detect directional change in composition was limited. Furthermore, their primary response metric for tree recruitment was the species-specific ratio of saplings to adults at each site. As individual stems may potentially remain in the sapling layer for decades (Connell and Green 2000, Hubbell 2004, Green et al. 2014), many of the saplings they investigated may have dispersed and germinated prior to the commencement of hunting (32 years previous to the study). In the current study, we build upon the work of Terborgh et al. (2008) with three census periods of the same hunted and nonhunted forest sites over 11 years, allowing finer temporal resolution to assess the effects of defaunation on tropical tree communities.

We hypothesized that defaunation would induce changes in mature tree community structure. In particular, due to the loss of large-bodied dispersers, we predicted a decline in large-seeded tree species in hunted areas (Levey 1987). To test this prediction, we first evaluated the comparability of the two sites, including a comparison of mature tree community structure and light availability at the two sites. We then examined whether there were differences in vertebrate abundance that could be caused by hunting. Next, we examined the degree to which species composition is changing between sapling and mature-tree communities, and, finally, whether changes in species composition could be attributed to dispersal syndrome and/or to seed mass. Our study uses trees from the small-sapling stage (>1 m height and <10 cm DBH) to the >10 cm dbh stage that were monitored three times over an 11-year period. The sapling layer should be an early predictor of the adult layer that it will eventually replace. With the use of multiple ontogenetic stages and repeated observations, we robustly assess the changes in the relative abundance of tree species in a defaunated forest, as well as the potential for directional changes in the community assemblage through time.

4.3 Methods

4.3.1 Study Site

The study took place at two sites in the Department of Madre de Dios, south-east Peru. The intact site, which has not been subjected to hunting in the last 100 years, was the Cocha Cashu Biological Station (CCBS), in the core zone of the Manu National Park (11°54' S, 71°22’ W). The hunted site is near the settlement of Boca Manu in the designated peripheral buffer zone of the national park (12°16' S, 70°54’ W). The two sites, 100 km apart, are highly comparable, located in young alluvial soils of the Manu River floodplain, and neither has experienced commercial logging. Condit et al (2002) indicated that tree communities under 100 km vary very little in South America, we therefore expect tree communities at the two sites to be similar had there been no anthropogenic disturbance. The site near Boca Manu has been hunted since the establishment of the settlement in 1972, resulting in severely depleted communities of large mammals and birds (Terborgh et al. 2008). Because the mature trees present at the outset of the study probably recruited before hunting began (i.e. they had germinated more than 32 years previously), we expect the mature trees at both sites to be products of forests with fully intact disperser communities. For this reason, the mature tree stands at the two sites should be similar in species composition and abundance (Terborgh et al. 2008). In contrast, saplings currently recruiting at the hunted site should display the effects of defaunation.

4.3.2 Tree Plots

Tree and sapling plots were surveyed in 2004, 2009 and 2015 at the hunted site, and in 2002, 2006, 2010 and 2015 at the nonhunted site. Tree plots covered 4 ha with a central square 1 ha or 1.08 ha sapling plot, at the hunted and nonhunted site respectively. In each census, every individual was identified, tagged and mapped, DBH was measured for trees (>10 cm DBH) and large saplings (>1 cm DBH, <10 cm DBH), and height was measured for smaller saplings (>1 m height, <1 cm DBH). Over the three censuses at both sites, 94.6% of the individuals were identified to species level, 4.9% were identified to family or genu, and 0.5% of trees could not be identified.

We wanted to maximize the extent to which the saplings used in the study had germinated after hunting began. Because some individuals can remain in the sapling stage for longer than 32 years (when hunting began) (Connell and Green 2000, Green et al. 2014), we define ‘recruits’ as individuals that recruited into the sapling layer (i.e., have reached 1 m in height) between the first and second or the second and third censuses. It is unlikely that these recruits are older than 32 years, and likely, therefore, that these germinated after the onset of hunting. Focussing on recruits, as opposed to on the whole sapling community, should yield a more accurate portrayal of the effect of hunting on the tree community.

4.3.3 Light

To assess the effects of light availability on sapling growth and recruitment, canopy cover was measured throughout the sapling plots using methods similar to those used in Welden et al. (1991) and Terborgh et al. (2008). Parallel lines 5 m apart were walked across each sapling plot, starting 1 m into the plot to eliminate any effects of cutting along grid lines, with measurements taken every 5 m along the line. Each measurement assessed the presence or absence of canopy cover below 5m, between 5 m and 20 m, and above 20 m. Presence of canopy cover below 5 m gave a score of 1, between 5 m and 20 m a score of 2, and above 20 m a score of 3, these scores were summed resulting in a score between 1 and 6 for each measurement. Light scores were compared between sites using a Pearson’s Chi-squared test of independence.

4.3.4 Mammal Transects

Densities of hunted fauna were assessed at both sites in 2004 and 2015 using line transects, where all mammals and large birds (those that are targeted by hunters) were recorded. At both sites, transects were 4 km, except for transects at the nonhunted site in 2015, which were 3 km. Transects were carried out during the day and the night in the dry season, and were walked at a speed of 1 km/hr as in the methods of Peres (1999). Recordings for each sighting included group size, species (or functional group if the species was unknown), and perpendicular distance from the transect line to the centre of the group. Data from 2004 were published in Terborgh et al. (2008), data from 2015 are analysed for a repeat comparison in this study.

4.3.5 Data Analysis – Mammal Transects

For analysis, species were categorised into one of eight functional groups: large primates; small primates; nocturnal arboreal mammals, including night monkeys (*Aotus nigriceps*); large birds, including guans (*Penelope jacquacu*), curassows (*Mitu tuberosum*) and trumpeters (*Psophia leucoptera*); large terrestrial mammals, including ocelots (*Felis pardalis)*, armadillos (*Priodontes maximus, Dasypus novemcinctus*), deer

(*Mazama americana*), tapir (*Tapirus terrestris*) and peccary (*Tayassu tajacu*); large rodents, including agouti (*Dasyprocta variegata*) and paca (*Cuniculus paca*); small nocturnal mammals (small rodents and opossums, *Marmosa spp., Didelphis spp., Marmosops spp.*); and squirrels (*Sciurillus* spp., *Microsciurus* spp). Primates that were detected acoustically only at large distances were excluded from the analysis because it was impossible to quantify group size. Bats were not counted in mammal transects because of the complicated nature of detection, though we do not expect bat abundance to be impacted by hunters.

Analyses were performed using the Distance package in R 3.3.0 (Miller 2016; R Core Team 2017). Detection function models, in which probability of detecting an animal decreases with distance from the transect line, were performed separately for each functional group. We tested each functional group model with size and species as potential covariates, selecting models on an AIC basis. Densities were compared between sites using z-tests, p values were obtained using Satterthwaite approximations for effective degrees of freedom.

4.3.6 Dispersal Syndromes

Tree species were assigned to primary dispersal syndromes based on data collected over many years of observation at CCBS; 48% of classifications were derived from published data (Terborgh 1983, Foster and Janson 1985, Romo 1996, Swamy et al. 2011), complemented by unpublished data and personal observations for 41% of classifications (11% of species). Where the dispersal syndrome was unknown, a species was assigned the same dispersal syndrome as other species in the same genus. Tree species were assigned to one of six dispersal categories: abiotic (wind or autochorus), 11%; birds or bats, 32%; large primates (*Ateles sp.*or *Alouatta sp.*), 22%; small arboreal mammals (e.g. small primates, squirrels, nocturnal arboreal mammals), 21%; terrestrial mammals (rodents, peccary's, tapirs), 3%; and unknown, 11%.

Heavier seeds are more likely to rely on large bodied dispersers because smaller dispersers are unable to handle or swallow them, so seed mass was assigned to each species. Seed mass was sourced from local data collected at CCBS (Pringle et al. 2007, Terborgh et al. 2011, 2014), and supplemented by published data collated on the Royal Botanic Gardens, Kew Seed Information Database (Royal Botanic Gardens Kew 2017). Out of 641 tree species identified, 96% were assigned a seed mass. A seed mass was assigned to 37% of species at species level, 42% at genus level, and 17% at family level.

4.3.7 Data Analysis – Tree Plots

Mature tree communities were compared to assess the similarity between the two sites and their suitability for comparison. High similarity indicates that the dynamics of tree recruitment in the pre-hunted era at the hunted site were similar to those of the nonhunted tree community. Species abundances were compared using a major axis regression using package smatr (Warton *et al.* 2012, R Core Team 2017), comparing the number of individuals per species at each site.

To confirm similarities between mature tree communities and to assess differences in sapling communities since the onset of hunting, Bray-Curtis (B-C) dissimilarity was used to assess differences in species composition at the two sites. Communities were compared between (1) sites, (2) census years and (3) growth stages, taking into account both full communities at each growth stage, as well as only the new recruits to the sapling stage at each of the latter two censuses. Non-metric multi-dimensional scaling (NMDS) ordinations were used to visualise the distance between community structures using the vegan package (Oksanen et al. 2017; R Core Team 2017). Differences were then tested for significance using a permutational multiple analysis of variance (MANOVA) using the Adonis function in the vegan package.

Linear mixed effect models were used to assess the causes of differences in species assemblage between the two sites using the lme4 package in R (Bates et al. 2015; R Core Team 2017). Site (hunted or nonhunted) and dispersal syndrome category or seed mass were interacting fixed effects. To assess the similarity between mature tree communities across dispersal syndromes, mature-tree density per ha was used as a response variable. Because the mature-tree layers are similar at the two sites but the sapling layer at the hunted site may have been influenced by hunting, we used the new-sapling to mature-tree ratio (per species and within site) as the response variable to detect differences driven by hunting. Species were allowed to have random intercepts since overall abundance and sapling to mature tree ratios may vary among species for other reasons. Ratios were log-transformed to reduce heteroscedasticity. The model was weighted by the population size of each species over the two sites, with more common species having a stronger weight in the model than rarer species. The significance of the interaction was tested through parametric bootstrapping (Halekoh & Hojsgaard 2014; R

Core Team 2017), in which residuals and random effects are resampled to obtain estimated F values on which to base p-values (Halekoh and Hojsgaard 2014).

For all analyses listed here, species that did not occur as both mature trees and saplings, and species occurring at a density of <1 mature tree/ha were excluded, as were species that are known to mature <10 cm DBH (final species pool: N=97).

Analyses were carried out in R 3.3.0 (R Core Team 2017).

4.4 Results

4.4.1 Site comparison

The hunted and nonhunted sites were similar with regards to the density, basal area, species richness, species composition, and representation of dispersal syndromes of mature trees (Supplementary Table S4.1). The species composition of mature trees did not differ between the sites at any census (permutational MANOVA of Bray-Curtis dissimilarity: $R^2 = 0.08$, $P = 0.24$). A major axis regression indicated that species abundance was similar at the two sites ($R^2 = 0.42$, $P < 0.001$), with a positive correlation between abundance within species at the two sites (Fig. S4.1). The density of mature trees did not differ significantly between the two sites in any of the six dispersal categories (linear mixed effect model: $X^2 = 22.99$, $P = 0.14$; Fig. S4.2).

Comparison of canopy openness as a proxy for light availability showed there was higher light availability at the hunted site ($X^2 = 10.24$, $P = 0.006$). Terborgh et al. (2008) found no difference in canopy openness in 2004, so it is likely that this difference is a recent change resulting from a large treefall in the hunted plot in recent years.

4.4.2 Mammal Transects

In 2015, a total of 182 km of transect were walked at the two sites, split equally between day and night, with 503 sightings recorded. The majority of sightings fell into the small rodent/opossum category, with >115 small rodents/opossums$\cdot$km^{-2} at both sites (Table S4.2). The functional groups expected to be most affected by hunting are large primates and large birds (Peres and Palacios 2007). Some large terrestrial mammals might be impacted but as their densities are very low even at nonhunted sites across Manu National Park (Endo et al. 2010), no inferences could be made about large terrestrial mammals.

Mammal and large bird densities were estimated for the hunted and nonhunted site for eight functional groups (Fig. 4.1). The estimated population size of large primates was almost 50 times smaller at the hunted site than at the nonhunted site (0.82 and 40.23 individuals·km^{-2}, respectively; $Z = -3.65$, $P < 0.001$, Fig. 4.1a), with only one group of large primates (*Ateles paniscus*) recorded at the hunted site. Large bird density estimates were also significantly lower at the hunted site ($Z = -3.05$, $P = 0.008$. Fig. 4.1d), consistent with Terborgh et al. (2008). Squirrel densities were significantly higher at the hunted site ($Z = -3.51$, $P = <0.001$. Fig 4.1h).

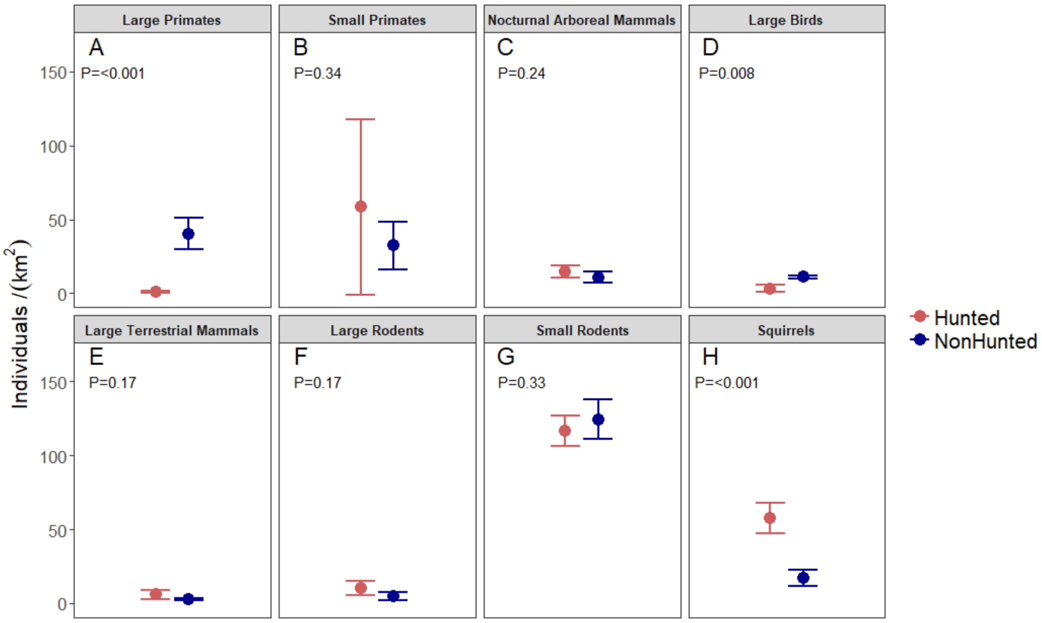

Figure 4.1 Density estimates (/km2) for mammals and large birds divided into 8 functional groups for hunted (red) and nonhunted (blue) sites. Error bars represent standard errors. Large primate and squirrel abundance are significantly different between hunted and nonhunted sites.

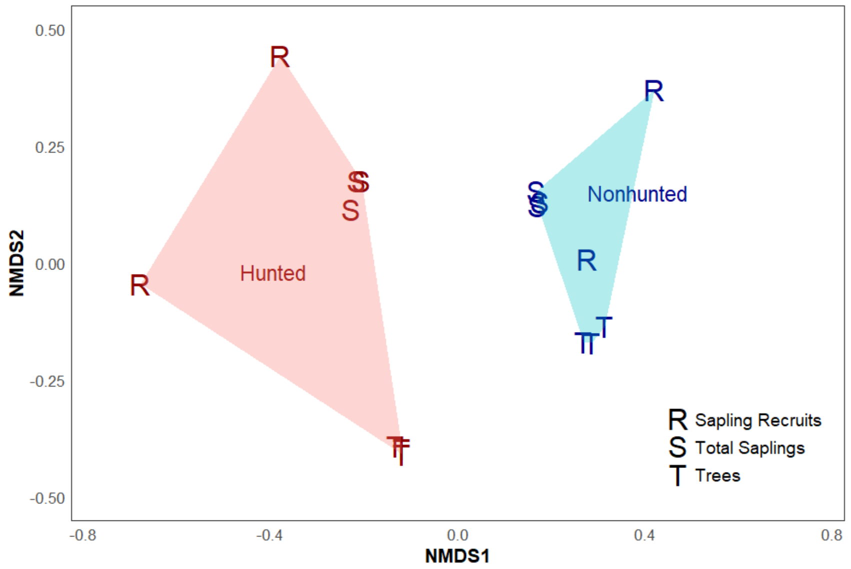

Figure 4.2 Non-metric multi-dimensional scaling plot showing Bray-Curtis dissimilarities between a) sites (hunted: red, non-hunted: blue), b) census, and c) growth stage. Tree communities at the hunted site have greater dissimilarities between the mature tree and sapling communities than at the non-hunted site. This dissimilarity is driven by the sapling recruits. Points clustered together for Trees and Total Saplings are data points for each of three censuses. Stress value is 0.03.

4.4.3 Species compositional dissimilarity

Species composition differed between sapling and mature tree stages ($R^2 = 0.78$, $P < 0.001$, Fig. 4.2). Dissimilarity was significantly greater between sapling recruits and mature trees at the hunted site ($R^2 = 0.96$, $P < 0.001$). This means that new sapling recruits at the hunted site, which probably dispersed after the onset of hunting, are driving a change in community composition that was not seen at the nonhunted site. The dissimilarity between sapling recruits and mature trees was increasing within the hunted site over time (Table S4.1).

4.4.4 Dispersal Syndromes

To assess the degree to which defaunation-induced changes in seed dispersal have generated the observed change in sapling recruitment, we examined sapling-to-adult density ratios from the 2009 and 2015 censuses. Although the sapling-to-adult ratio for species dispersed by large primates was slightly higher at the nonhunted site, this difference was not significant ($SE = 0.16$, $P = 0.06$; Fig. 4.3a). Moreover, dispersal syndrome as a whole did not predict differences in sapling-to-adult ratios between sites (X^2 = 12.53, *P* = 0.46, Fig. 4.3). Seed mass also failed to predict sapling-to-adult ratios (Fig. 4.4); the sapling-to-adult ratio of larger seeded species was only marginally lower at the hunted site than at the nonhunted site (X^2 = 3.39, *P* = 0.2).

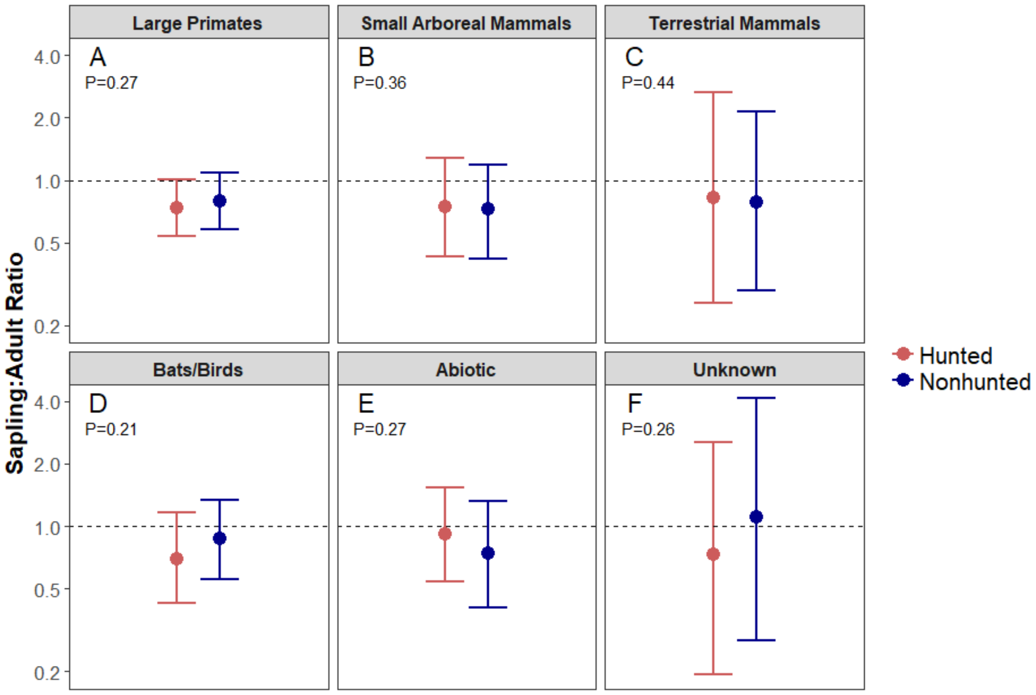

Figure 4.3 Predicted values from a linear mixed effect model showing species-specific log sapling-to-adult ratio by assigned dispersal mechanism for each site, with species as a random effect.

Error bars represent standard errors. Model results show no significant difference between the two sites within any dispersal syndrome.

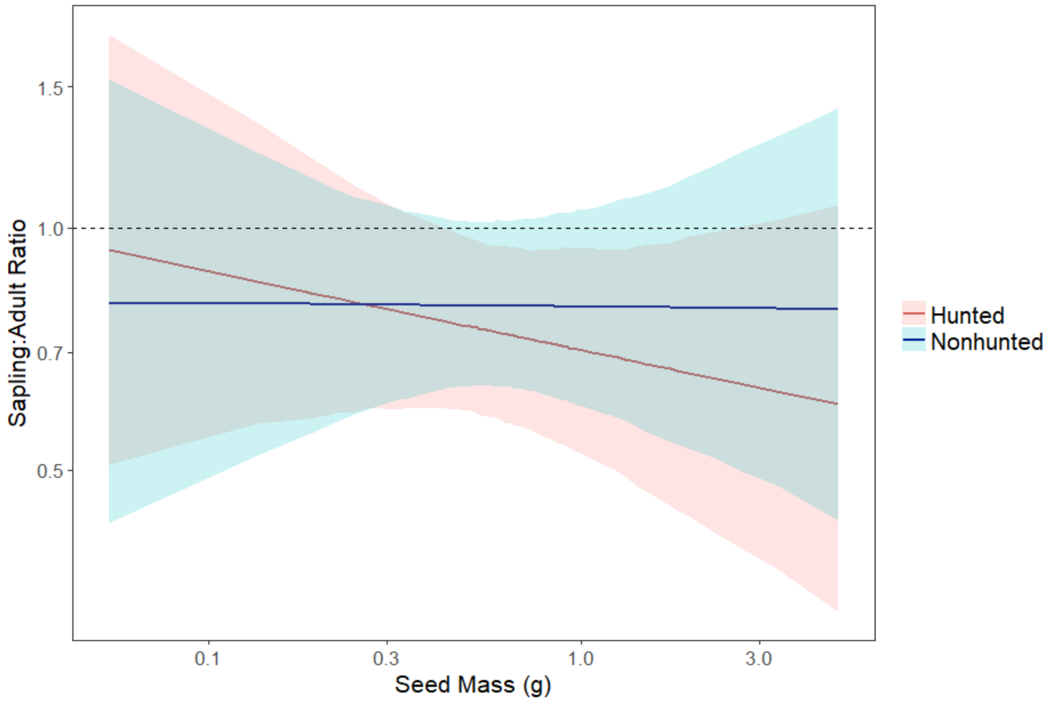

Figure 4.4 Predicted values from a linear mixed effect model showing species-specific sapling-to-adult ratio as predicted by seed mass (g) for each site, with species as a random effect.

Model results show no significant difference in sapling-to-adult ratio where sites and seed mass are interacting effects (P=0.26).

4.5 Discussion

A static comparison of these sites led to the strong conclusion that defaunation had affected tree species composition (Terborgh et al. 2008). Static data in this context, however, must be regarded with caution. Since many trees take over 30 years to mature (Connell and Green 2000, Green et al. 2014), studies with no temporal aspect may be based on saplings of uncertain age, including those that germinated both before and after the onset of hunting. The results presented here are not consistent with studies that have demonstrated defaunation reduces the recruitment of large-primate-dispersed tree species (Wright et al. 2007c, Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Effiom et al. 2013, Galetti and Dirzo 2013, Harrison et al. 2013, Kurten et al. 2015, Peres et al. 2015). Few of the studies addressing this question, however, have examined various ontogenetic stages or extended over more than 3 years. The repeated censuses in our study allowed us to assess sapling recruitment, and the period of 43 years since the onset of hunting gives us confidence that the community of young saplings germinated in a hunted forest. Moreover, because these findings contradict those of the previous static study by Terborgh et al. (2008), the temporal extension of the study has had a profound impact on the patterns we are detecting.

Although the mature tree communities were similar between sites (Table S4.1, Fig. S4.1 & S4.2), the densities of key functional groups in the faunal communities differed (Fig. 4.1). In the 2015 census reported here, large primates showed much lower densities at the hunted site, as did large birds to a smaller degree. Terborgh et al. (2008) conducted surveys using an identical survey technique in the year of the first census at both sites. They found a similar difference in large primate abundances, but a much higher abundance of large birds at the nonhunted site. Because there has been no human interference at this site for the duration of the study, this is likely due to natural fluctuations in these populations. These results are supported by previous studies carried out in Amazonia (Peres and Palacios 2007, Endo et al. 2010), which also found reduced populations of large primates at hunted sites when compared to nonhunted sites. Furthermore, we found a higher abundance of squirrels at the hunted site, likely a result of a relief from competition under reduced abundance of large primates. Canopy cover differed between the sites in 2015 but not in 2004, likely due to a large treefall prior to the 2015 census, which could influence tree communities. However, we expect light to influence tree survival and growth at the germination and early seedling stage and we are uncertain of light conditions at this time. Altered light availability is a likely to effect both sites during the 40 years since the onset of hunting, and although we cannot rule out the influence of light, we do not expect it to play a strong role in shaping tree communities at these sites.

We hypothesized that the severe reduction in large frugivorous dispersers would impact tree community structure by reducing the opportunities for tree species that rely on extirpated fauna to disperse, and thereby to survive the vulnerable early ontogenetic stages. Our results confirmed that tree community structure is changing in the defaunated forest (Fig. 4.2), which is consistent with the results of many other studies (Nuñez-Iturri et al. 2008, Kurten et al. 2015). Notably, the saplings that recruited after the start of the study showed higher dissimilarity to mature trees at the hunted site than at the nonhunted site, and this dissimilarity increased over the 11 years of our study (Fig. 4.2). This increasing dissimilarity over time between the community of the newest saplings and that of the mature trees suggests not only that community structure is likely to change in the next generation, but also that this change is temporally directional. This is the first time that a community assemblage in a hunted forest has been observed over such an extended time period, up to 43 years after the onset of hunting. The utilisation of new sapling recruits as a community separate to the full sapling community is unique to this study, and allows us to eliminate the potential confounding effects of a time lag present in a statically sampled sapling community composed of trees of unknown age. A combination of an extended period of study and a better knowledge of the age of recruiting saplings means we can be confident that saplings in the cohorts of new recruits were dispersed after the onset of hunting.

Neither dispersal syndrome nor seed mass could explain the observed variation in sapling to mature tree ratio between hunted and nonhunted sites (Fig. 4.3 & 4.4, Text S4.1). Like Bagchi et al. (2018) we found that, contrary to our predictions, the survival of large-primate dispersed species are not uniformly limited by the loss of large primates. In fact, there were tree species that rely on large primates for seed dispersal that appeared to be increasing in abundance at the hunted site (e. g., *Pseudolmedia laevis* and *Theobroma cacao*): these are species that appear to be able to germinate and recruit into the sapling layer in the absence of their presumed principal disperser. There are two potential explanations for these results: 1) species thought to be reliant on extirpated fauna for dispersal are managing to disperse by alternative means, or 2) species reliant on extirpated fauna for dispersal are managing to escape mortality beneath the parent tree and survive, which may eventually lead to clumped species distributions.

The persistence in this study of some large-primate dispersed species, while others decline may reflect these differences among species in the presence and extent of secondary dispersal. Secondary dispersal is an important mechanism shaping tree communities (Vander Wall and Longland 2004, Hirsch et al. 2012). Few studies have quantified the proportion of species that rely on secondary seed dispersal, though it is now thought to play an essential role in the successful germination of many plant species (Andresen 1999, Guimaraes Jr et al. 2008, Hamalainen et al. 2017). Species usually considered to play minor roles in seed dispersal, such as squirrels, who have a higher abundance at the hunted site, may opportunistically compensate for missing large primate dispersers (Bagchi et al. 2018). Or, if more undispersed seeds fall to the ground, they may be dispersed by nonhunted rodents, including agoutis and squirrels (Hirsch et al. 2012). Indeed pacas (*Cuniculus paca*) and agoutis (*Dasyprocta variegate*) are known to preferentially scatterhoard large seeds, and seed survival of scatterhoarded seeds is substantially higher than those left on the surface (Galetti et al. 2010). This suggests that scatterhoarding may favour survival of large seeds and effectively compensate germination and survival in the absence of a primary disperser. The extent to which these interactions can maintain a stable population for any plant species is unknown, but some studies addressing the continuing survival of plant species that rely on extinct mega-fauna have suggested that compensatory secondary dispersal can be long-lasting and effective (Janzen & Martin 1982; Guimaraes Jr et al. 2008). It is unlikely, however that these compensatory mechanisms are effective for all species that are impacted by the loss of a primary disperser, and it is not clear whether these mechanisms can maintain species at their current densities and distributions. The fact that we have been surprised by some aspects of the results is a clear indication that there is much yet to be learned about alternative pathways of seed dispersal in tropical forests.

Although the focus of this study has mainly been on the loss of frugivorous dispersers, hunting can also impact populations of seed predators (Wright et al. 2000, Galetti et al. 2006, Beckman and Muller-Landau 2007, Corlett 2007). Simultaneous removal of dispersers and seed predators can have compensatory effects, in that seeds that remain undispersed due to disperser loss also remain un-predated, escaping density-dependent mortality (Dirzo et al. 2007, Stoner et al. 2007, Kurten et al. 2015). An important mammalian seed predator in the Manu region is the white-lipped Peccary (*Tayassu pecari*) (Beck 2005). Due to natural fluctuations in population densities of white-lipped peccary (Richard-Hansen et al. 2014), none were present at either the hunted or the nonhunted site in the 2015 mammal surveys. However, prior to a mass die-off in 2012, white-lipped peccaries were abundant throughout the region, at these times mammal surveys showed significantly higher densities of white-lipped peccaries at nonhunted sites (Terborgh et al. 2008, Endo et al. 2010). If we assumed that large mammals were the main seed predators for undispersed large seeds, this compensatory effect may to some extent explain the lack of difference in large-seeded tree species between the hunted and nonhunted site that we detect in this study. There is a large body of evidence, however, that suggests that large mammals play a comparatively minor role in density-dependent mortality of undispersed seeds, when compared to pathogen or insect attack, or small mammals (Notman and Villegas 2005, Beck et al. 2013, Paine et al. 2016), and since these smaller natural enemies may be presumed to have similar densities at the hunted and nonhunted sites, they are unlikely to contribute to any compensatory seed predation effects. It is unlikely therefore that any compensatory effects of reduced large mammal seed predators could be strong enough to counteract the loss of large-bodied dispersers.

Our species-by-species assessment of community dynamics across different ontogenetic stages allows insight into changes in tree community structure, but our replication is low. Extrapolation from these results, therefore, should be done with caution. It should also be noted that better predictions can be made regarding species that have short-lived seed banks or rapid growth during early ontogenetic stages. Slow-growing species, and those with long seed banks will take comparatively longer to experience changes in their population densities, and such changes could remain undetected even at the timescale of our study. It is unlikely however that there will be a significant proportion of the plant community that set seed more than forty years ago and still have not reached 1 m in height (Connell and Green 2000, Green et al. 2014), so we remain confident that the majority of the saplings recruiting into this community have been subject to the effects of defaunation. These difficulties render long-term studies such as this one essential to the understanding of changing ecological processes in natural systems that are becoming rapidly more susceptible to defaunation and other human induced impacts (Peres 2000, Abernethy et al. 2013, Dirzo et al. 2014).

Our detailed study into the interactions between plant communities and their overlapping animal communities suggests that there are complex and species-specific mechanisms that are driving changes in community structure. In light of these results, it seems unlikely that the outcome for plant communities where hunting is taking place will be completely black and white, with all large-seeded species or species dispersed by large-bodied frugivores declining. Instead it appears that tree communities will change in as yet unpredicted ways, and that understanding these changes will require more detailed insights into ecological processes and species interactions. Our study also suggests that previous studies may overestimate the impacts of defaunation by assuming there is there will be unmitigated declines in the recruitment of large-seeded species following the loss of large primates (Peres et al. 2015, Bello et al. 2015), and that some of the assumptions made in such studies could be far from reality of complex ecosystems. While we detect no link between defaunation and long-term changes in forest structure, the greatest difference between the two forests is a decline of large-primates. It is therefore likely that defaunation was altering tree species communities, but that variation among species in ability to compensate in an altered dispersal community means that some species are able to persist while others decline, masking the true link between defaunation and community assemblage. Predictions about long-term changes to tropical tree communities and the cascading effects that arise from defaunation will not be sufficiently accurate when impacts are assumed to be identical across all species, and we hope that further investigations into the processes associated with disperser loss could shed some light on what directional changes we should expect in a defaunated landscape.

4.6 Acknowledgements

We thank Yuri Huillca, Walter Flores Casanova, Manuel J. Marca Zevallos, Antonio Guerra Rosas, Alexsandre Quispe Naupa, Pamela Olarte and Zenayda Aleli who worked tirelessly in the tree plots, and the countless essential field workers who conducted the censuses in previous years. We also thank Patricia Alvarez-Loayza for her fieldwork contribution and seed mass and dispersal syndrome data. The research was supported by Natural Environment Research Council (NERC) and extensively by personal financial contributions from researchers.

4.7 Supplementary Figures

Table S4.1 Comparison of mature adult stands between hunted and nonhunted sites and comparison of sapling recruits and mature trees within site at all three censuses.

Bray-Curtis dissimilarities are bounded between 0 and 1.

	Census 1		**Census 2**		**Census 3**	
	Hunted	Non-Hunted	Hunted	Non-Hunted	Hunted	Non-Hunted
Adult Density	1912	1900	1945	1967	1944	2023
Adult Basal Area (m2)	115.5	108.5	114.2	102.9	114.8	111.9
No. Species	225	256	234	262	244	271
Bray Curtis Dissimilarity between sites within a census	0.39		0.39		0.4	
Bray Curtis Dissimilarity between sapling recruits and mature tree communities within sites	-	-	0.68	0.65	0.76	0.63

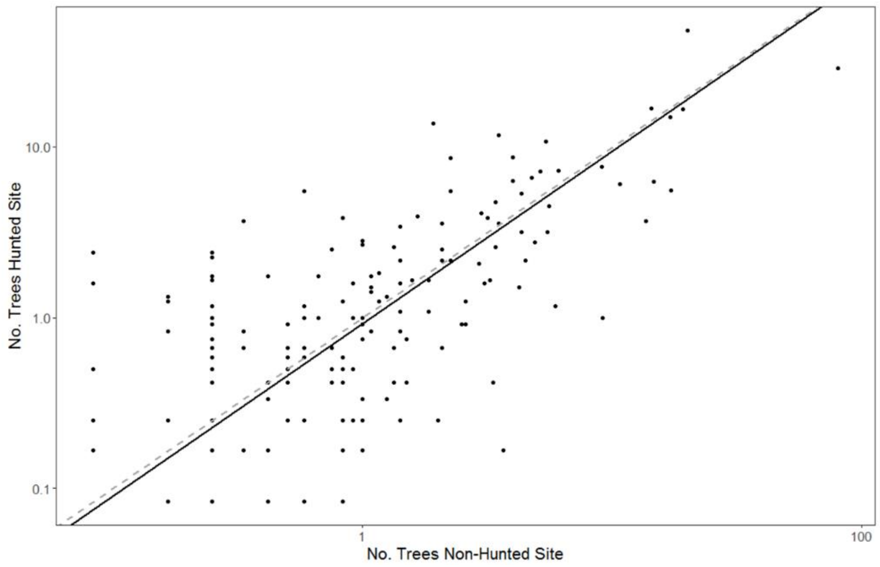

Figure S4.1 Comparison of adult tree abundance between hunted and non-hunted sites by species.

Solid line represents major axis (MA) regression fit, dashed line shows regression where slope = 1 and intercept = 0. Axes are on the logit scale. Species abundances are similar at the two sites.

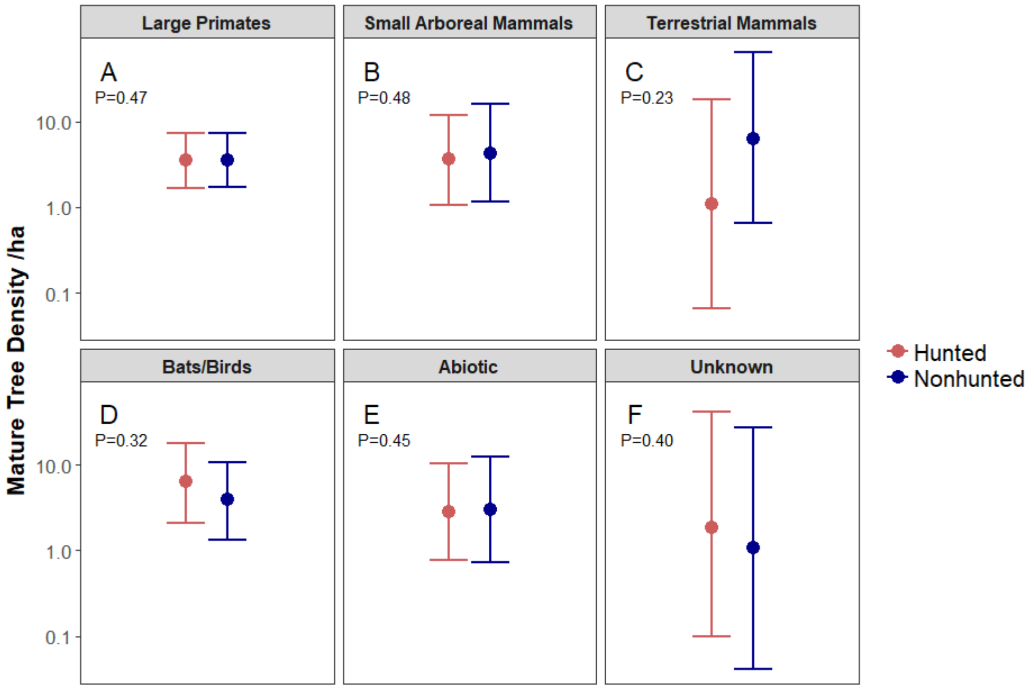

Figure S4.2 Linear mixed effect model predictions showing mature tree density per hectare by dispersal syndrome at hunted (red) and non-hunted (blue) sites.

Results show no significant difference between dispersal syndrome distribution between the two sites, indicating strong similarities between the mature tree communities.

Table S4.2 Density estimates (/km^2) for mammals and large birds divided into 8 functional groups for hunted and non-hunted sites.

Estimates are given for individuals /km^2 .

Functional Group	**Hunted Site**		**Non-Hunted Site**		**z-value**	**p-value**
	Individuals /km^2	SE	Individuals /km^2	SE		
Large Primates	0.82	0.72	40.23	10.77	-3.65	0.0001
Small Primates	58.53	59.45	32.31	16.13	0.43	0.66
Nocturnal Arboreal Mammals	14.86	4.20	10.81	3.81	0.71	0.76
Large Birds	3.03	2.38	10.96	1.06	-3.05	0.008
Large Terrestrial Mammals	5.83	3.08	2.82	0.82	0.95	0.66
Large Rodents	10.14	4.59	5.02	2.78	0.95	0.83
Small Nocturnal Rodents	116.70	10.53	124.48	13.56	-0.45	0.33
Squirrels	57.58	10.18	17.14	5.43	3.51	0.99

Text S4.1: Results based on a single assigned disperser (Figure 3) could face some bias due to the coarse groupings of dispersal syndromes, when many species experience compensatory effects from secondary dispersal. To account for this we also assigned dispersal syndromes separately for species that rely on one disperser alone and for those that rely on a disperser among one or more other dispersers. When modelled against sapling-to-adult ratio using a linear mixed effect model there was still no significant effect of dispersal syndrome, (X^2=18.72, p=0.57**).** Even when a species is reliant solely on large primates for dispersal, the reduced abundance of dispersers at the hunted site did not appear to be impacting recruitment (Figure S3-a).

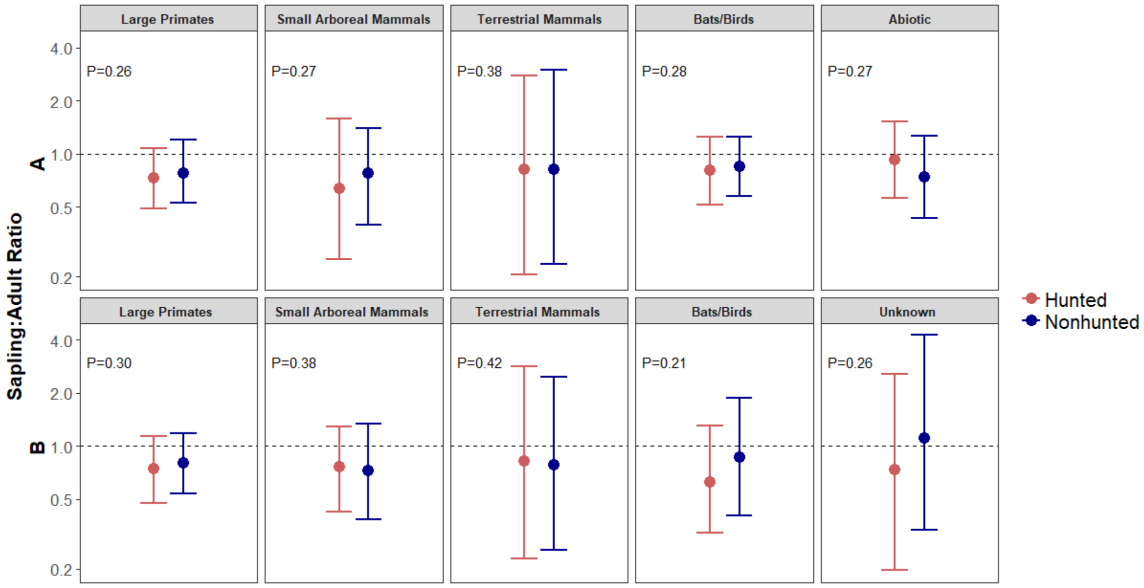

Figure S4.3 Predicted values from linear mixed effect model showing species specific log sapling-to-adult ratio by assigned dispersal mechanism for each site, with species as a random effect.

Species are divided into (a) those that have only one named disperser and (b) those for which the named disperser is the primary but not the only disperser. Model results show no significant difference between the two sites within any dispersal syndrome.

Chapter 5

Simulating the next generation of a tree community in a defaunated landscape

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5.1 Abstract:

Defaunation has caused declines in population sizes of large vertebrates throughout the tropics, with consequential impacts on seed dispersal and predation. If defaunation differentially affects recruitment among tree species, tree community composition could experience slow but substantial transformations. Furthermore, species dispersed by hunted fauna tend to have high wood density, so defaunation could negatively affect carbon storage. Where large primates are hunted we expect to see tree declines in large primate dispersed species, large seeded species, and species with higher wood density. Using a simulation approach, we projected tree community composition 200 years into the future to assess changes to the tree community composition, using 11 years of data on sapling and tree performance at hunted and non-hunted sites in South-East Peru. We predict changes in community structure at the hunted site, with the ratio of large to small stemmed species decreasing. These changes are not, however, linked to a decline in large primate dispersed species, large seeded species, or species with high wood density. In contradiction to previous studies, we predict that many species that we had expected to experience reduced dispersal through defaunation are recruiting, and maintain their populations. It is unclear from our results whether changes to the community structure are influenced by abiotic means and that defaunation is unrelated, or whether large-primate-dispersed species are persisting through secondary dispersal. The causal links between defaunation and tropical tree community structure may be mechanistically complex, with differing impacts among species within large primate dispersed species communities. The decline of large stemmed species is a notable and concerning trend in the hunted forest, and while we do not detect a link to a decline in large primate dispersers, a deeper understanding of the causes and mechanisms driving this change is essential to the continued persistence of large trees that are essential for carbon sequestration in tropical forests.

5.2 Introduction

The role of tropical forests in carbon storage is well established (Cao and Woodward 1998, Pan et al. 2011), with the Amazon basin alone responsible for ~23% of tropical vegetation carbon storage (Dixon et al. 1994). Forest degradation in Latin America constitutes 54% of global deforestation emissions (Harris et al. 2012), but recent studies have suggested that bushmeat hunting may also contribute in unforeseen ways (Bello et al. 2015, Peres et al. 2015). Hunting in the Neotropics disproportionately targets large bodied vertebrates, in particular large primates (Peres and Palacios 2007), with consequential declines in hunted species (Wright et al. 2000, Dirzo et al. 2014). Large vertebrates preferentially consume large seeds, and are believed to be primarily responsible for the dispersal of many large-seeded tree species (Levey et al. 1994, Peres and van Roosmalen 2002). There is now mounting evidence that the decline of large bodied dispersers may instigate long term alterations to the tree communities (Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Galetti and Dirzo 2013), and be further linked to a decline in carbon storage (Peres et al. 2015).

Globally, seed size is positively associated with wood density in trees (Thompson and Rabinowitz 1989, Diaz et al. 2004, Wright et al. 2007a), and wood density is a key component of terrestrial carbon storage in vegetation (Chave et al. 2005). As large-seeded tree species often rely on large vertebrates for dispersal (Stevenson 2011), these species are likely to be most affected by the loss of dispersal function. Consequently hunting may impose substantial long term implications for carbon storage. Since the Amazon alone accounts for 14% of the planet’s terrestrial carbon fixation (Zhao and Running 2010), it is important that we understand the long term impacts of declines in large vertebrates and the trees that depend on them. However, it is not clear whether the relationships between seed size or dispersal syndrome and wood density consistently hold true in a tropical tree community. In the case that this assumption does not hold true, the implications for carbon storage could be very different to previous predictions (Bello et al. 2015, Peres et al. 2015).

There have been two notable weaknesses in previous studies that have assessed changes in carbon stocks as a response to defaunation. The first are in studies that assess forest stands at a single point in time, as static comparisons do not allow for age differences within sapling communities (Nuñez-Iturri and Howe 2007, Terborgh et al. 2008, Bello et al. 2015, Peres et al. 2015). Many individuals can remain in the sapling layer more than 30 years (Connell and Green 2000, Green et al. 2014), therefore a static sample of the sapling layer will likely include a mix of individuals from pre- and post-defaunated forests. A second weakness occurs in studies that investigate saplings or mature trees but do not allow sufficient lag time between the onset of defaunation and the outset of the study (Harrison et al. 2013). There is mounting evidence that the transition from seedling recruit to sapling (>1 m height) can take anywhere from one year to over a decade (Connell and Green 2000, Kurten and Carson 2015, Chapter 2). In order to ensure that study communities are influenced by defaunation, therefore, there must be an effective lag time between the onset of hunting and the start of a study incorporating a sapling community, to allow the generation of seedling recruits germinated under defaunation to reach sapling status.

Using simulations, we address these issues in a study that expands on work by Terborgh et al (2008, and Chapter 4), monitoring sapling and tree communities over an 11 year period, up to 43 years after the onset of hunting. The simulation approach allows us to project the change in tree species communities detected during the study period beyond the scope of time for this study, and visualise a complete tree community turnover, which can take over 200 years (Chambers et al. 1998, Fichtler et al. 2003). Our simulation uses species specific recruitment and mortality rates obtained from consecutive censuses, and applies these parameters to site specific populations to predict the annual turnover of saplings and trees over 200 years. We hypothesize that the loss of large frugivorous vertebrates in defaunated forests will result in a long term change in tree community structure. More specifically we predict a decrease in the abundance of tree species dispersed by large primates, a decrease in the abundance of large seeded tree species, and a decrease in wood density throughout the tree community.

5.3 Methods

5.3.1 Study Site

Two sites were surveyed in the Department of Madre de Dios, Peru. Boca Manu (12°16' S, 70°54’ W), in the peripheral zone of the Manu National Park, has been subjected to hunting since its establishment in 1972. Cocha Cashu Biological Station (CCBS, 11°54' S, 71°22’ W), in the core zone of the national park, has not experienced any hunting in the last 100 years (Terborgh 1990). Commercial logging has not taken place at either site, and both are located in the floodplain of the Manu River, on young alluvial soil (Terborgh 1990). Mature tree communities at the two sites are similar, as the mature trees at the hunted site are likely to have recruited before the onset of hunting in 1972.

Younger sapling communities, having recruited after hunting began, will show the effects of hunting.

5.3.2 Tree Plots

Three censuses were undertaken between 2002 and 2015 at hunted and non-hunted sites. In each census every individual was marked and identified, and DBH (individuals >1 cm DBH) or height (individuals <1 cm DBH) measured in 1 ha sapling (individuals <10 cm DBH and >1 m height) plots and DBH measured in 4 ha tree (individuals >10 cm DBH) plots. Saplings were split into small (<1c m DBH and >1 m in height) and large (>1 cm DBH and <10 cm DBH) size classes. For details see methods as in Chapter 4.

5.3.3 Traits

Tree species were assigned to one of six dispersal syndrome categories: abiotic (wind or autochorus), birds or bats, large primates (*Ateles sp.* or *Alouatta sp.*), small arboreal mammals (smaller primates, squirrels, nocturnal arboreal mammals), rodents and unknown (11% of species). 48% of classifications were obtained from published data (Terborgh 1983, Foster and Janson 1985, Romo 1996, Swamy et al. 2011), 41% were taken from unpublished data and field observations. Where a species was categorised with more than one disperser, only the primary disperser was assigned.

Wood density data were obtained from trees at the study sites by taking sapwood samples using a 5 mm diameter tree corer from up to three individuals of each species for 84% of species. Where wood density data were missing, it was supplemented with data from Chave et al (2005) (5% of species). Where wood density data was unobtainable at the species level, we used genus (9%) or family (2%) level means. Seed mass was assigned to each species from data collected at the non-hunted site (Pringle et al. 2007, Terborgh et al. 2011, 2014), accounting for 60% of species. Missing seed masses were supplemented by published data collated by the Royal Botanic Gardens, Kew, Seed Information Database (Royal Botanic Gardens Kew 2017, 11% of species). We were unable to obtain seed mass data for 29% of species, in these cases we used the genus (21%) or family (8%) level means from local data. Seeds > 1.5 g were categorised as ‘large seeds’ since this is the mean seed mass for large primate dispersed species for species represented in this study.

5.3.4 Simulation

We simulated tree community composition for each site over 200 timesteps, representing a new adult tree community since most adults trees will die and be replaced in under 200 years (Fichtler et al. 2003). A ‘timestep’ represents one year, in which a representative sample of individuals from each of the three size classes (small saplings, large saplings and adults) die and recruit. Individuals subject to mortality at each timestep were randomly selected based on species specific abundance and mortality rates, calculated separately for each size class (see below). At the mature tree stage new recruits equated the sum of the basal area of those that have died, with equivalent total basal area maintained over at each timestep. At both sapling stages new recruits equated the number of stems of those that have died in that size class. Individuals recruiting into each size class were selected based on species specific recruitment rates and species-specific abundance in the previous size class, which were estimated from the field data. Immigration was allowed for species that were present in the 4 ha tree plot but not in the 1 ha tree and sapling plot from which the simulation is sampled. Species not present at a timestep were able to recruit from a species pool of the number of adults per hectare present at the outset of the simulation.

To calculate rates of recruitment and mortality, per ha/year species specific recruits and deaths were used from each ontogenetic stage for each site. Rates were calculated as:

$$Recruiment = \frac{{N\ recruits_{stage\ 2,i}}\Big/{N\ present_{stage\ 1,i}}}{Census\ Interval}$$

$$Mortality = \frac{{N\ dead_{stage\ 2,i}}\Big/{N\ present_{stage\ 2,i}}}{Census\ Interval}$$

Where *i* indicates species, *census interval* is the number of years between censuses, *stage.1* is the stage the individual is recruiting from, and *stage.2* is the layer an individual is recruiting into. For example, for the recruitment of mature trees, *stage.2* = mature tree stage and *stage.1* = large sapling stage.

A null simulation, in which all species were assigned equivalent mortality and recruitment rates, tested the capability of the simulation to detect changes to the species community, and the validity of using the non-hunted site as a control. The initial mature tree community in the null simulation was equivalent to the non-hunted site, and sapling abundances were initialised at a ratio of 1:2:3 for mature trees, large saplings, and small saplings, respectively, for all species. Recruitment and mortality rates were equivalent to each other and across all species, using median recruitment rates for each ontogenetic stage in the non-hunted community.

The null simulation was altered to test the simulation's ability to detect the effects of hunting on tree composition, the simulation was run with recruitment rates of 0 at the small sapling stage for species dispersed by large primates, and for large seeded species (seeds >1.5 g). In both simulations, all individuals that were already present at the start of the simulation were permitted to recruit to the mature tree layer. These simulations are hereafter referred to as 0LP simulation (simulation where large primate dispersed species are unable to recruit) and 0LS simulation (simulation where large seeded species are unable to recruit). This simulated the loss of dispersal for species that are reliant on large primates or those with large seeds, assuming that a tree cannot recruit if it is not dispersed and allowed us to assess links between these depleted communities and seed mass, wood density, and changing community structure.

Tree demographic data from the hunted and non-hunted sites were used as input for two further simulations. These simulations tested the trends in species turnover based on real data, and assessed likely changes to the species community after 200 years. All rates were species- and site-specific at all stages. Species that were rare, and therefore provided insufficient data to calculate recruitment and mortality parameters were removed from the species pools, leaving a site specific community composition of 95 species. All simulations were run with 1000 replicates.

5.3.5 Statistical Analysis

To detect changes in species composition we used the Bray-Curtis dissimilarity index to measure dissimilarity between the initial mature tree community and the mature tree community at each subsequent timestep in each of the five simulations (null, 0LP, 0LS, non-hunted and hunted). Linear models assessed the difference between simulations by comparing change in dissimilarity between the initial and final timestep among simulations.

We assessed the difference between the first and last timestep for stem density, community weighted mean (CWM) seed mass and CWM wood density, and evaluated the difference between simulations using linear models. To detect changes in proportional representation of dispersal syndromes in tree communities over time, we used linear models to predict the change in mature tree abundance at each timestep by interacting dispersal syndrome and simulation (non-hunted, hunted, 0LP or 0LS).

We evaluated the expectation that wood density is predicted by seed mass and dispersal syndrome with linear models, using wood density, seed mass and dispersal syndrome data for the species in the simulation at either site where data were available from the study site (127 species for seed mass and 128 species for wood density). Tukey's Honest Significant Difference (HSD) test was used to assess relative significant differences between dispersal categories.

In each of the above models, null simulations were compared to non-hunted simulations, to assess the validity of assigning the tree community at the non-hunted site as stable. Where differences between the null simulation and the non-hunted simulation were non-significant, the non-hunted simulation was used as a control comparison for 0LP, 0LS and hunted simulations.

Due to the uninformative nature of p-values when using large datasets, r-squared values were used to assess the percent variance explained in the model by the explanatory variable. Analyses were carried out in R 3.4.1 (R Core Team 2017), using packages vegan (Oksanen et al. 2017) and lme4 (Bates et al. 2015).

5.4 Results

Over 11 years and three censuses at two sites, one hunted and one non-hunted, 306 unique species were identified in the mature tree and saplings layers, 95 of which were sufficiently abundant to yield recruitment and mortality rates at sapling and mature tree stages. These sites were used to assess the long term impacts of hunting on tree community composition, with the non-hunted site used as a control against which to predict changes in community structure at the hunted site. The assumption that the non-hunted site was an effective control site was assessed using a null simulation, in which recruitment and mortality rates were equal for all species. Any changes to the species community in the null simulation were due to random variation implicit in the simulation and were therefore minor and did not cause large changes in community structure. The null simulation and the simulation of the non-hunted site were consistently similar, in terms of stem density, CWM seed mass and CWM wood density ($R^2 = 0.04$ / < 0.01 / 0.02 respectively; Fig. S5.1a and S5.3). Bray-Curtis dissimilarity increased through time for all simulations (Fig. S5.1b). The non-hunted simulation changed in community structure to a greater degree than the null simulation, with a 12% greater change in dissimilarity at the non-hunted site ($R^2 = 0.25$). This is expected since the 1 ha scale used in this study is small compared to the total forest size, and only a small proportion of species are represented, with a lot of room for emigration and immigration of species.

The rate of change in community composition in the non-hunted simulation is used as a comparative baseline from which to compare other simulations. The relative abundance of species dispersed by abiotic means declined moderately in the non-hunted simulation, whereas the relative abundance of species across dispersal syndromes remained steady in the null simulation (Fig. S5.2). Nevertheless, the number of abiotically dispersed species is comparatively small, so this increase did not cause substantial changes in the community structure ($R^2 = 0.02$).

Mature tree stem density increased marginally by 18% in the 0LS simulation ($R^2 < 0.001$) and the 0LP and non-hunted simulations maintained a similar stem density over time (< 10% change in stem density, $R^2 < 0.001$). Stem density at the hunted site increased by 40%, compared to the non-hunted site ($R^2 = 0.7$), a greater increase than any other simulation (Fig. 5.1a). Since basal area is kept constant throughout each run in the simulation, a higher stem density indicates there are more trees with smaller basal areas.

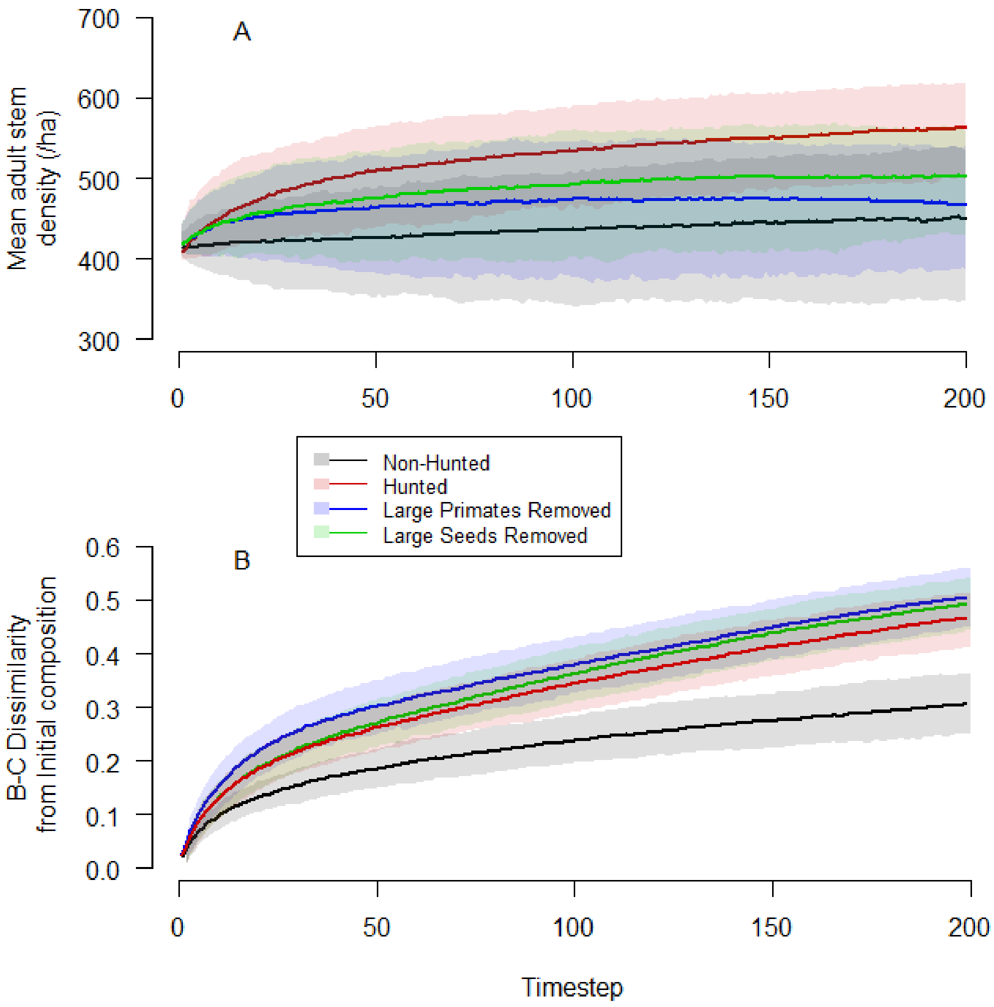

Figure 5.1 (A) Mean adult stem density, and (B) Bray-Curtis dissimilarity between initial community at timestep 1 and each subsequent timestep.

Colours represent large primates removed (0LP), large seeds removed (0LS), non-hunted and hunted simulations. Confidence intervals are the variation among simulation repetitions.The 0LS and hunted simulations see an increase in stem density, though the increase is most apparent in the hunted simulation (R^2=0.7). The 0LP, 0LS and hunted simulation with all change in community composition to a greater degree than the non-hunted simulation, though with little significance (R^2=0.03/0.01/0.04 respectively).

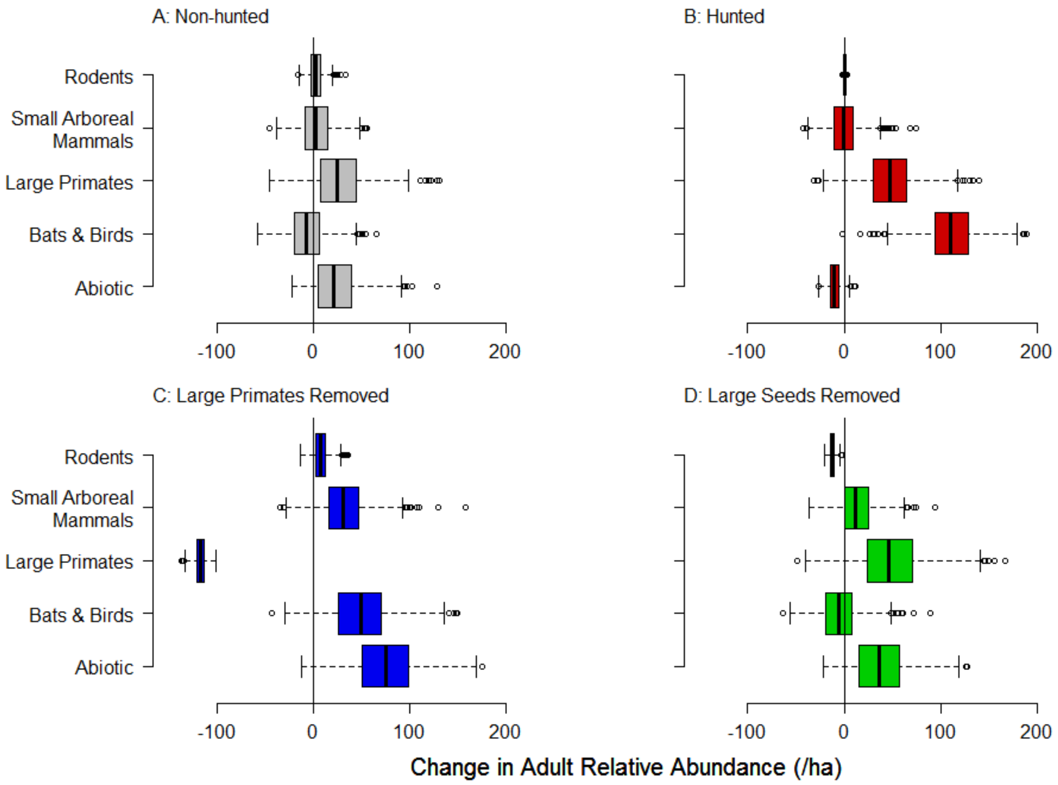

Figure 5.2 Change in adult relative abundance: difference between initial and final timesteps in number of adults per hectare in each dispersal category.

Results presented for A) Non-hunted, B) hunted, C) large primates removed (0LP), and D) large seeds removed (0LS) simulations. The 0LP simulation declines as expected in large primate dispersed species (Large Primates: P=0.03, R^2=0.09). In the 0LS simulation (R^2=-0.02) and the hunted simulation (R^2=-0.02) there are some non-significant increases in some dispersal groups. The hunted simulation remains stable in all dispersal categories (R^2=0.02).

Bray-Curtis dissimilarity was measured as the difference between the initial mature tree species community and the species community at each subsequent timestep (Fig. 5.1b). Dissimilarity increased by 41% in the non-hunted simulation ($R^2 = 0.69$), all other simulations increased to a greater degree than the non-hunted simulation, with the greatest increase, by 50%, in the 0LP simulation (0LP: $R^2 = 0.64$, 0LS: $R^2 = 0.42$).

We monitored the relative abundance of trees in each dispersal syndrome over the course of each simulation. In the 0LP simulation, large primate dispersed species declined, as expected ($P = 0.03$, $R^2 = 0.1$). Most primate-dispersed species went locally extinct, and species of all other dispersal syndromes concomitantly increased in abundance (Fig. 5.2a). In 0LS, non-hunted and hunted simulations there was little change in the relative abundance of any dispersal syndrome (Fig. 5.3b, c & d, 0LS: R^2 = 0.03, hunted: R^2 = 0.02), though there were some marginal changes that reflected the fluctuating species community composition in all simulations. There were only three rodent-dispersed species at the hunted site, and it is not possible to extract any statistical changes to species in this dispersal category.

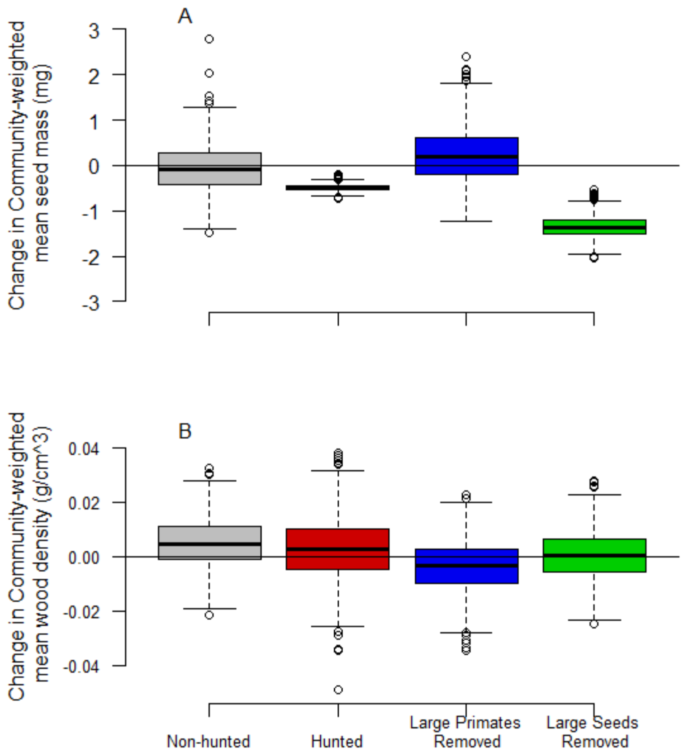

Figure 5.3 Change in community weighted mean seed mass (A) and community weighted mean wood density (B) measured as the difference in community weighted means between initial and final timesteps.

Results presented for non-hunted, hunted, large primates removed (0LP) and large seeds removed (0LS) simulations. A: 0LS and hunted simulations decline in seed mass, though only the 0LS simulation changes significantly (0LS: R^2=0.73, hunted: R^2=0.08) non-hunted and 0LP simulations remain stable. B: No simulations change significantly (R^2=<0.1 for all simulations).

CWM seed mass changed by less than 10% between the beginning and end of the non-hunted and 0LP simulations ($R^2 = 0.05$; Fig. 5.3a). CWM seed mass declined in both hunted and 0LS simulations, by 39% and 54% respectively, only the 0LS simulation changes substantially (0LS: $R^2 = 0.73$, hunted: $R^2 = 0.08$). In all simulations, CWM wood density remained stable in all simulations, changing by <1% at the final timestep (0LP: $R^2 = 0.18$, 0LS: $R^2 = 0.06$, hunted: $R^2 = 0.01$; Fig. 5.3b).

Dispersal syndrome was modelled against CWM seed mass and wood density, to assess the assumption that larger seeds and species with higher wood density are dispersed by large vertebrates. Dispersal syndrome were compared in a linear model ($R^2 = 0.21$) using Tukey HSD tests, these indicate that larger seeds are more likely to be dispersed by rodents or by large primates than by bats, birds or abiotic means (rodents: $P < 0.001$, large primates: $P < 0.001$, Fig. 5.4a), but this relationship is not apparent when wood density is predicted by dispersal syndrome, with no difference in wood density among dispersal syndromes ($P > 0.1$ for all dispersal syndromes, Fig. 5.4b).

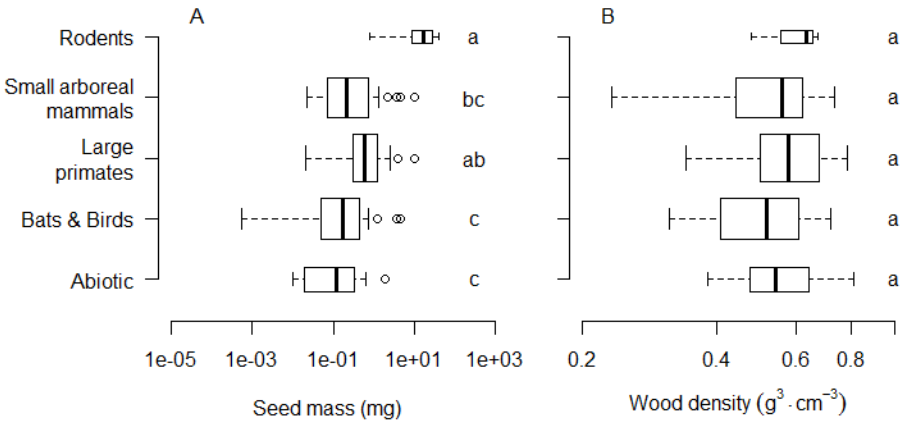

Figure 5.4 Community weighted mean seed mass (A) and wood density (B) predicted by dispersal syndrome for all simulation species.

Letters indicate Tukey HSD values from linear models; categories that share a Tukey HSD letter are non-significantly different. Seed mass is likely to be higher in species dispersed by terrestrial mammals or large primates compared to species dispersed by bats, birds or by abiotic means. Wood density is not significantly different in any dispersal category.

5.5 Discussion

Many studies have investigated the impacts of defaunation on tree communities using static or short-term data (Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Peres et al. 2015), with inevitable drawbacks. There is a great variety in growth strategies among trees (Denslow 1987, Ruger et al. 2011), including wide variation among species in age at first reproduction (Connell and Green 2000, Wright et al. 2005). Accounting for this variation is problematic, with the slowest growing trees maturing only after 40 years old (Lieberman and Lieberman 1987). Simulations allow us to extrapolate from an 11 year study to predict long term tree community turnover, using saplings from a defaunated forest and mature trees from a pre-defaunated forest at the same site.

This study challenges assumptions made in previous defaunation studies. Dispersal syndrome is not always a good indicator of high wood density (Fig. 5.4b), and defaunation does not necessarily reduce the abundance of trees with high wood density (Fig. 5.3b) as other studies have predicted (Bello et al. 2015, Kurten et al. 2015). In fact, many species with high wood density persist throughout the hunted simulation. As few individual trees survived through the 200-year duration of the simulations, this indicates that high-wood-density species are recruiting even in the face of anthropogenic defaunation. Our study suggests that many species dispersed by hunted fauna will be able to persist without their primary disperser, and that declines or extinctions of these species may not be apparent throughout the community as seen in previous studies (Terborgh et al. 2008, Effiom et al. 2014, Peres et al. 2015). This is a trend that can be seen among species that rely on extinct neo-tropical megafauna, with species whose disperser was lost centuries ago managing to persist to the current day (Guimaraes Jr et al. 2008, Jansen et al. 2012).

As a result of defaunation, we expected to see declines in tree species that are dispersed by large vertebrates and in species that have larger seeds. To monitor this effectively, the 0LP simulation eliminated sapling recruitment of species that are dispersed by large primates, and the 0LS simulation eliminated sapling recruitment of species with larger seeds. These simulations generated outcomes we had expected to see as a result of defaunation, with declines of large primate dispersed species (0LP simulation) or large seeded species (0LS simulation) respectively (Fig. 5.2c and 5.3a). This indicates that our model is capable of simulating substantial changes in species composition, and further supports our inference that defaunation at the hunted site is not predicted to lead to the local extinction of primate-dispersed or large-seeded tree species. These results link to previous findings, with changing community structure detected in hunted forests, with a similar, though less distinct change detected in our simulation of a hunted forest (Terborgh et al. 2008, Galetti and Dirzo 2013, Harrison et al. 2013).

Adult stem density in the 0LP simulation remained similar to the non-hunted simulation, while 0LS and hunted simulations increase in stem density (Fig. 5.1a). The increase was especially strong in the hunted simulation. Since basal area is kept constant throughout the simulation, an increase in stem density is an indication that larger stems are being replaced by multiple smaller stems. Larger stems are associated with more effective carbon storage (Lindner 2010, Sillett et al. 2010), and Stephenson et al. (2014) showed that the amount of carbon stored in a mid-sized tree can be sequestered in a single year by some of the largest trees. Furthermore, because there is no change in wood density at the hunted site, a decrease in large stems is not being offset by an increase in wood density. With a decline of large stemmed species in hunted forests therefore, there could be severe consequences for carbon storage, with hunted forests storing substantially less carbon than a forest with an intact faunal community.

To relate changes in the community structure to the depleted faunal community at the hunted site, we monitored relative abundance of species across dispersal syndromes (Fig. 5.2). Studies have found a reduction in species dispersed by large primates in hunted forests (Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Bagchi et al. 2018). In our simulation of the hunted forest, however, the relative abundance of mature trees across dispersal syndromes remained unexpectedly consistent (Fig. 5.2b). Large primates have been linked to the dispersal of large seeded species (Stevenson 2011), and studies have found that declines in large primates are reflected in a decline in large seeded species (Levey et al. 1994, Peres and van Roosmalen 2002). We see a decline in community weighted seed mass in the hunted simulation (Fig. 5.3a) that is marginally different from trends in the nonhunted simulation. Lack of support for declining populations of large primate dispersed species and large seeded species indicates that the predicted changes in community structure and stem density are not in fact driven by the loss of hunted fauna.

Since we are confident that large primates are severely depleted at the hunted site (Chapter 4), there must be alternative ecological processes facilitating the continued recruitment of large primate dispersed species. Fig. 5.4a shows that although many large seeds are reliant on large primates, the largest seeds are dispersed by rodents, which are not hunted at this site. Furthermore, large primate dispersed species are not declining in the 0LS simulation (Fig. 5.2d), and large seeded species are not declining in the 0LP simulation (Fig. 5.3a). We show that an assumed link between large primate dispersers and large seeds (Peres et al. 2015), is unfounded. Could rodents be playing a more important role in the dispersal of large seeded species than large primates? Scatter hoarding rodents are known to contribute to the dispersal of many large seeded species (Guimaraes et al. 2006, Galetti et al. 2010, Hirsch et al. 2012), but their relative contribution to dispersal within a plant community is unknown. It is becoming apparent that scatter hoarding rodents may have strong compensatory effects in the absence of primary dispersers, removing and caching undispersed seeds that are often not consumed and therefore germinate (Cao et al. 2011, Jansen et al. 2012). If this is the case there may be behavioural implications for scatter hoarding rodents; in order to fulfil the dispersal needs of a greater number and variety of tree species in a defaunated forest, they will need to increase not only their population size, as has already been observed (Peres 2000, Nuñez-Iturri et al. 2008), but also the diversity of species they target. Scatter hoarding rodents are not depleted at our hunted site (Chapter 4, Terborgh *et al.* 2008), but when both large primates and large rodents are hunted, or if hunting intensity is higher than our study site (Donatti et al. 2009, Kurten 2013) there could be reductions in the rodent populations, and thus severe consequences for tree communities.

A supplemental analysis of global wood density and seed mass showed that, although there is a weak positive relationship, there is substantial variation among species (Fig. S5.4). It is often assumed that large seeded species strongly predict high wood density (Peres and van Roosmalen 2002, Bello et al. 2015, Peres et al. 2015), but our study shows that this does not appear to be the case throughout the species community. The changes we observe due to the loss of large seeded species are not reflected in any change in CWM wood density (Fig. 5.3b). Further, we observed no direct relationship between wood density and dispersal syndrome (Fig. 5.4). These results reflect a disconnect between wood density and the loss of large vertebrate dispersers, and implies that using large seeds or dispersal syndrome as a metric for detecting changes in carbon storage potential may be unsuitable. Differences in severity of hunting may account for differences in results between this study and Peres et al. (2015) who found harsher consequences of defaunation. However, our study is the first to test the relationship between defaunation and a decline in large-seeded species or species dispersed by large primates where other studies have assumed the relationship exists (Bello et al. 2015, Peres et al. 2015).

The simulation approach gave us unique insight into species composition over a timescale that has not been replicated in real time, but the exclusion of a proportion of the species community due to insufficient data may create bias. 69% of species present in the total species pool were excluded from this study (22% of individuals) due to being too rare to obtain recruitment and mortality rates. The exclusion of rare species in the study gives some potential bias towards common species, as rare species are often more likely to be impacted by degradation, while common species become more common (Fauset et al. 2015). Furthermore, rare species have been connected to specialised and vulnerable ecosystem function (Mouillot et al. 2013), therefore the consequences of declines in rare species may be more severe than a decline of common species. Further research into whether negative impacts of defaunation are biased against rare species could reveal more about changing defaunated forest communities. Our simulation shows that although the loss of large primates has little impact on common species, there may yet be changes in defaunated forests that are difficult to predict and that could lead to instability in the tree community.

5.5.1 Conclusions

Using simple, well-parameterised simulations, we predicted long term changes to tree community composition in a hunted forest. We expected the loss of large primates to negatively impact recruitment of tree species that rely on them, negatively impact large seeded tree species, and for there to be further consequences for stem density, community composition and wood density. The hypothesized changes to stem density and community composition in our hunted simulation were apparent, with a greater increase in Bray-Curtis dissimilarity and in stem density in the hunted simulation than in the non-hunted simulations (Fig. 5.1). We did not, however, see the strong link between large primate dispersed species and changing community composition that we hypothesized. Rather, the model predicted similar patterns to those observed in Chapter 4; with relative abundance of dispersal syndromes in the tree community remaining surprisingly stable in the hunted forest, and large primate dispersed species persisting despite the loss of their primary dispersers. Our study suggests that, contrary to our predictions, there is no clear connection between changing tree species communities and the loss of large vertebrates through hunting in the long term.

We must presume that large primate dispersed species are recruiting despite their lack of dispersers. It cannot be ignored though, that in the hunted forest there appear to be directional changes to the tree community composition and a decreasing abundance of larger stems. There are two possible conclusions to consider: one is that the changing species community is unrelated to the loss of large primates as our results suggest, and that the changing tree community is influenced by other factors, likely abiotic. Another possibility is that the loss of large primates is affecting the rare species, but that many of the more common tree species are being dispersed by alternate means. This could result in a change in species community in favour of the more adaptable species that are able to find alternate means of dispersal, while those that rely on specialist dispersers decline (Fricke et al. 2018). In either scenario, the loss of large stems is a concerning outcome for the changing forest, since it is well documented that the larger trees are responsible for a disproportionate amount of carbon storage and fixation (Stephenson et al. 2014, Fauset et al. 2015, Lutz et al. 2018). It is therefore important that we try to gain a greater understanding of the processes driving the changing species community in hunted forests, and whether the main driver of these changes is defaunation itself, or the consequential meltdown of ecological processes in the forest system.

5.6 Acknowledgements

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5.7 Supplementary Figures

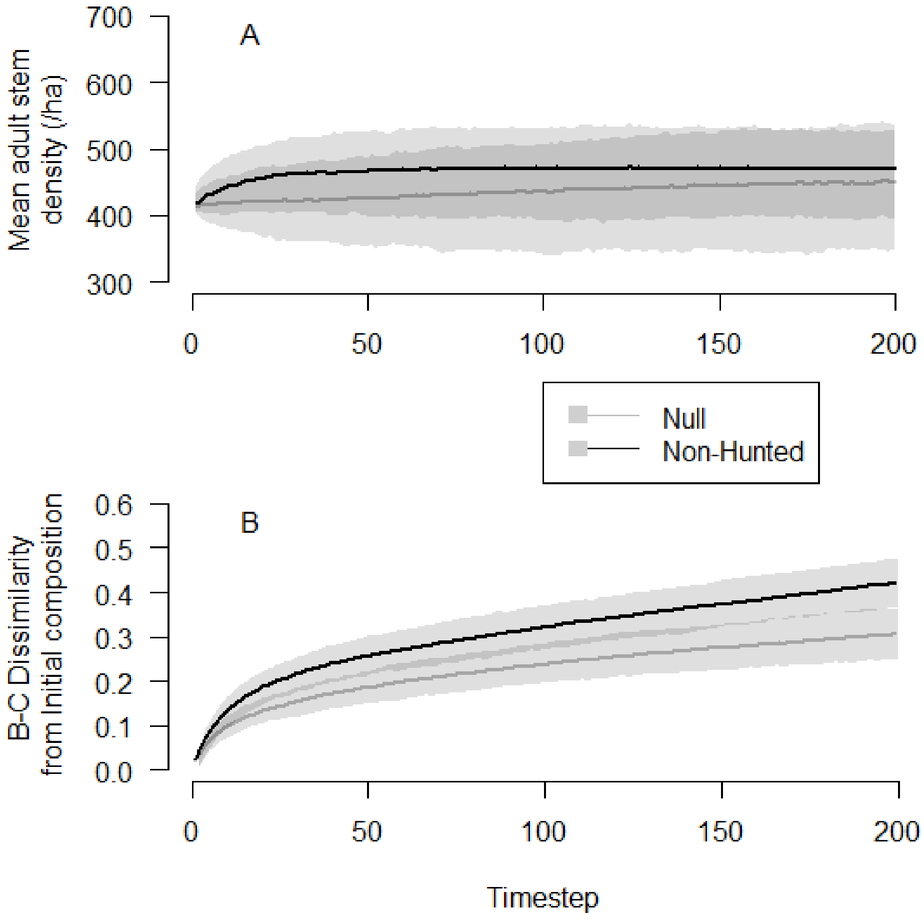

Figure S5.1 (A) Mean adult stem density, and (B) Bray-Curtis dissimilarity between initial community at timestep 1 and each subsequent timestep.

Shading represent the null simulation and the non-hunted simulation. Confidence intervals are the variation among simulation repetitions.

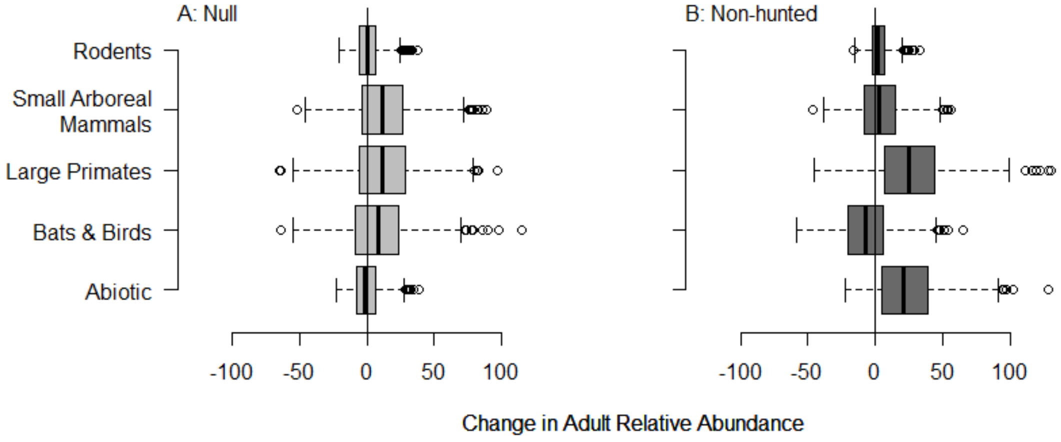

Figure S5.2 Change in adult relative abundance (abundance at start – abundance at final simulation) for species in each dispersal category for (A) the null simulation and (B) the non-hunted simulation.

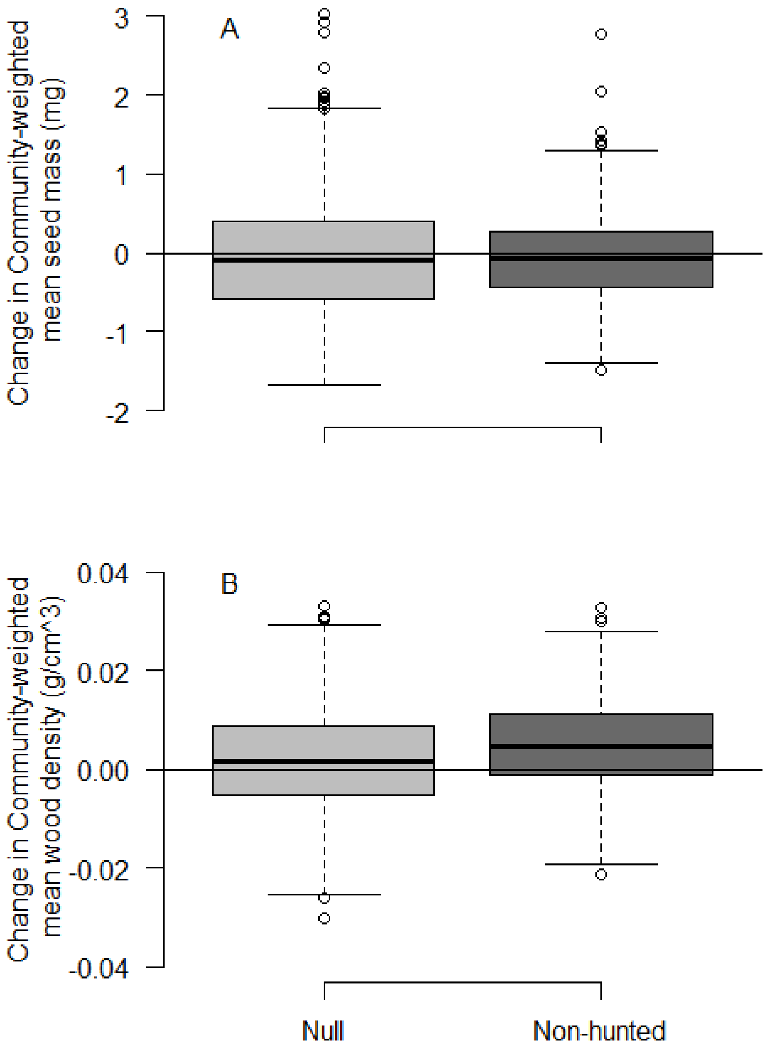

Figure S5.3 Change in (A) community weighted mean seed mass and (B) wood density for each simulation timestep for the null simulation and the non-hunted simulation.

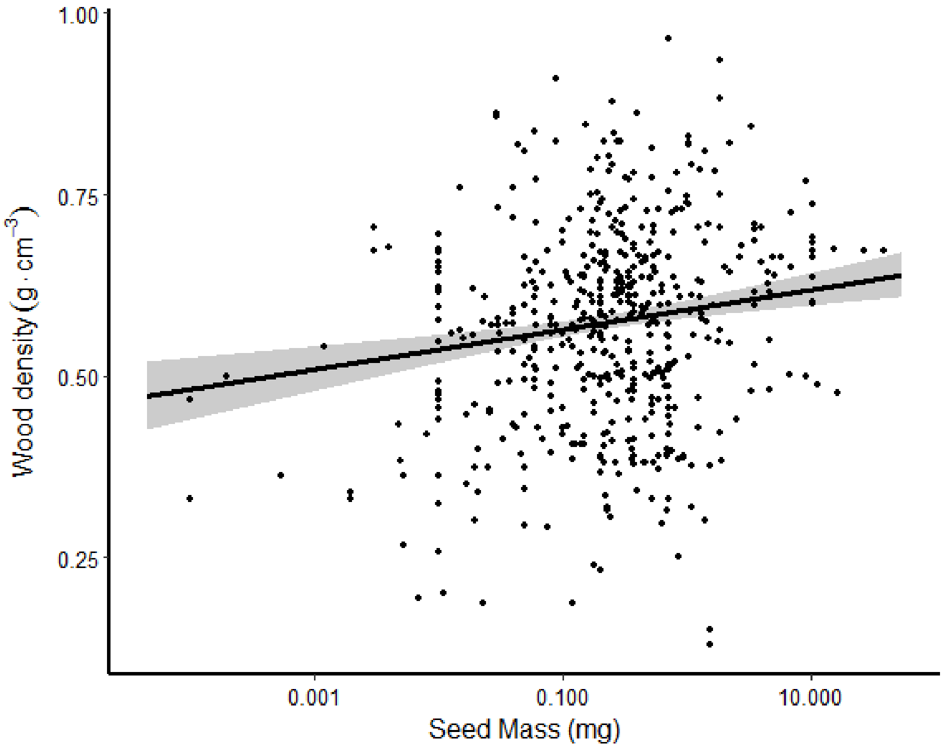

Figure S5.4 Wood density predicted by Seed mass using global trait data. The line represents linear regression.

Chapter 6

General Discussion

Ecologists have sought to unravel the drivers of exceptional plant diversity in tropical forests for many decades. Examining the local scale processes that generate species community structure contributes to an understanding of the broader scale community dynamics and ultimately the mechanisms that generate such high diversity. Moreover, with widespread anthropogenic impacts such as hunting impacting tropical regions (Dirzo et al. 2014), it is vital that we understand the consequences of perturbing the trophic interactions that are crucial to the maintenance of tree community assembly.

While a multitude of theories exist surrounding the mechanisms for species coexistence (Wright 2002), negative density dependence (NDD), whereby individual performance is negatively associated with conspecific density, is one that has received considerable support (Harms et al. 2000, Comita et al. 2014), and one that is potentially an important driver of diversity (Chesson 2000). Trophic interactions are critical both in the form of enemies that drive NDD (Janzen 1970, Connell 1971) and of dispersers providing a means to escape NDD mortality (Howe 2016). It is unclear, however, which guilds of natural enemies or dispersers are most influential to tree community assembly. Natural enemies, including fungal pathogens, insects and mammals, have been implicated in NDD processes individually (Connell et al. 1984, Packer and Clay 2000, Bell et al. 2006, Beck et al. 2013), and in some cases natural enemy groups have been compared (Bagchi et al. 2014, Fricke et al. 2014, Paine et al. 2016). There was a gap in our knowledge to date concerning the relative impact of fungal pathogens, insects and mammals on NDD among seedling communities, and their consequent link to diversity. This thesis addressed this gap in knowledge regarding the underlying mechanisms of NDD, and provides evidence for NDD at different ontogenetic stages, among species with different regional abundance.

Large frugivores and terrestrial mammals have been extirpated from many tropical regions under intensive hunting (Peres and Palacios 2007, Dirzo et al. 2014), thus the impacts of losing trophic interactions associated with these groups are of particular interest to ecologists. This thesis investigated the impacts of declines in natural enemies and dispersers in tree communities at multiple ontogenetic stages under hunting pressure. This thesis addressed issues surrounding defaunation in both local scale community impacts and global impacts concerning carbon storage. Overall, this study addressed NDD and the importance of trophic interactions, spanning demographic vulnerability to NDD among seedlings, to local and global impacts of removing ecological interactions associated with this process.

6.1 Negative density dependence shapes tropical tree communities

6.1.1 Conspecific negative density dependence

This thesis presents strong evidence for both the existence and the importance of negative density dependence (NDD) for shaping tree communities and maintaining diversity. We detected higher rates of mortality among seedlings with high conspecific neighbourhood densities in Chapters 2 and 3, supporting numerous studies finding similar patterns of NDD at this early life stage (Wills et al. 2006, Bagchi et al. 2010b, Johnson et al. 2012, Terborgh 2012). We expanded our study by showing that NDD interactions were exceptionally strong in the year following germination, with a mortality rate of over 75% at high conspecific crowding for the youngest seedlings, dropping to 50% after 5 years. While studies have indicated that NDD interactions take place at these early life stages (Green et al. 2014), it is important to note that NDD effects are particular to the very beginning of a seedling's life. Distance dependent mortality predicts that mortality is highest among seedlings close to the parent tree (Alvarez-Loayza and Terborgh 2011), though this effect would be reflected in measures of both distance and density dependence, since density of conspecific seedlings is highest close to the parent tree when undispersed seeds are dropped beneath the canopy (Terborgh 2012). With NDD strongest among the youngest seedlings (i.e. those that have recently germinated), it is likely NDD mortality takes place because seeds remain undispersed and accumulate at high densities beneath the parent tree. These observations signify the necessity of dispersers in maintaining tree community assembly, since only by achieving dispersal can a seed escape NDD mortality. I will return to the importance of dispersers in section 6.2.

Janzen (1970) and Connell (1971) predicted that following the deposition of seeds beneath the parent tree, conspecific NDD would be driven by host-specific natural enemies, thereby preventing competitive exclusion and maintaining diversity. Here I link three key findings from this thesis that uncover details of this process. 1) While studies have found evidence for NDD driven by fungal pathogens (Packer and Clay 2000, Bagchi et al. 2010b), insects (Sullivan 2003, Bagchi et al. 2014), and small and large mammals (Beck et al. 2013, Paine et al. 2016), this thesis includes the first comparison of all four natural enemy groups (Chapter 3). We show that fungal pathogens alone play a pivotal role in driving conspecific NDD, and that fungal pathogens are the only natural enemy that maintain diversity at the sites in this study. 2) Chapter 2 shows that conspecifics and not closely related neighbours drive NDD in young seedlings, indicating high host-specificity is necessary for NDD mortality and for generating of diversity. In contrast, previous studies have shown that closely related species may share traits, therefore natural enemies with host clades driven by phylogenetic signal impact NDD among seedlings (Metz et al. 2010, Liu et al. 2012, Paine et al. 2012b). 3) Conspecific NDD only impacts mortality and has no effect on relative growth rates (RGR), indicating that conspecific NDD occurs rapidly and is not driven by processes that increase mortality risk by slowing growth.

This thesis illustrates that fungal pathogens are uniquely responsible for driving conspecific NDD and diversity shortly after seedling germination, that they are highly host specific, and that they cause rapid mortality without limiting RGR. This places exceptionally high importance on pathogens as natural enemies and their unique host-specific interactions in the maintenance of diversity in tropical forests. Fungal pathogens, however, are a comparatively understudied taxonomic group, due to a combination of high species diversity and complex identification methods (Blackwell 2011). A deeper understanding of the maintenance of diversity in tropical forests may rely on improved understanding of pathogenic fungi and their specialised interactions with plants (Pringle et al. 2007, Álvarez-Loayza et al. 2011). This could allow studies to understand the underlying causes of diversity loss in tropical forests, and implications throughout the ecosystem of forest degradation.

6.1.2 Host-specificity among natural enemies

We show that natural enemies and specifically host-specific fungal pathogens are uniquely important in maintaining diversity among young seedlings. However it is clear that multiple NDD mechanisms are present throughout the seedling life stage. We detect reduced host-specificity as natural enemies shift from fungal pathogens to insects, and a shift from fungal pathogens to alternate mechanisms as seedlings age. Furthermore, we detect reduced host-specificity as seedlings age, making insects a possible driver of NDD in older seedlings. Reduced host-specificity in older seedlings was reflected in both general neighbourhood and phylogenetic NDD mortality and relative growth rates, whereas conspecific NDD only impacted mortality. Chapter 3 showed insects driving strong NDD growth among seedlings from heterospecific density, with the identity of neighbouring seedlings unimportant. This reflects evidence provided by Novotny et al. (2010) for variation in host-specificity among insects, and Gilbert and Webb (2007), who found generalist behaviour among fungal pathogens. This study, however, indicates that generalist natural enemies are unable to drive NDD. This could either be because they occur infrequently and the majority of fungal pathogens are host-specific, or that they do not drive detectable NDD effects compared to host-specific natural enemies.

Density dependent insect herbivory did not lead to changes in diversity among seedlings, which is unsurprising since effects were driven only by the heterospecific neighbourhood. Moreover, where insects are assumed to be the mechanism reducing growth rates through phylogenetic NDD (Novotny et al. 2010), it is unlikely that these phylogenetic effects are driving diversity. Chesson (2000) showed that negative effects must be stronger among conspecific than heterospecific neighbours in order to promote diversity, however recent studies have shown that phylogenetic density dependence can also promote diversity (Metz et al. 2010, Liu et al. 2012, Paine et al. 2012b), creating a grey area regarding connections between NDD and diversity. Assertions made in this thesis imply that only conspecific NDD maintains diversity, and phylogenetic relatedness, while driving NDD (Liu et al. 2012, Paine et al. 2012b), is not an important factor in the maintenance of diversity. Connections between phylogenetic NDD and diversity, however, are yet to be rigorously tested, and would benefit from a more thorough assessment. Overall, these results indicate that the mechanism driving NDD and diversity at the earliest life stage of a seedling is uniquely pathogenic and highly host-specific, while the mechanisms at later life stages or that don’t drive diversity vary in mechanism and host-specificity but are less powerful.

Unexpectedly, large mammals supressed diversity, though only briefly at the outset of the experiment. This change, however, revealed interesting aspects concerning the recovery of diversity. If fungal pathogens were the only driver of diversity, it is expected that the recovery of diversity after the loss of mammals would be impacted by fungal pathogens. Experimental exclusions of large mammals and fungal pathogens, however, revealed little evidence of this, and we must therefore assume that the recovery of diversity after the loss of large mammals is driven by abiotic forces not measured in the study. Importantly, this implies that while fungal pathogens are important agents for the maintenance of diversity, it is likely they are working in combination with other drivers, most likely associated with environmental filtering (Bai et al. 2012, Paine et al. 2012b, Adler et al. 2013).

Where multiple drivers are responsible for maintaining diversity in tropical forests, diversity may be sensitive to a variety of disturbances. Disturbance to the biotic community or interrupting vital trophic interactions (e.g. defaunation or deforestation) may reduce diversity, as could changes to the abiotic community (e.g. increasing light gaps or edge effects, or climate change) (Wright and Muller-landau 2006, Dirzo et al. 2014). For this reason it is important to monitor not only the direct impact of forest degradation caused by anthropogenic disturbance, but to assess the interlinked impacts that cascade through the ecosystem, and to consider the potential interactive effects of both biotic and abiotic disturbance.

6.1.3 Plant performance measures

Chapters 2 and 3 show that mortality and growth, two commonly used measures of plant performance (McCarthy-Neumann and Kobe 2010, Mangan et al. 2010, Bagchi et al. 2010b, Terborgh 2012, Inman-Narahari et al. 2016), respond to different NDD pressures and are driven by different mechanisms. NDD mortality, an important process among seedlings, is driven by different mechanisms as seedlings age, with an increase in less conspecific NDD in older seedlings. Relative growth rates (RGR) are not impacted by conspecific NDD at any age, though there are impacts from a wider species range of seedling neighbours. Importantly, this means that only NDD mortality maintains diversity, and studies connecting RGR and NDD may not be linked to species diversity. RGR, however is a slower process than mortality (Chapter 2), and this study only monitors RGR over the first decade of a seedlings life. If NDD RGR impacts continue into later ontogenetic stages the impact on community assembly may become more distinct, and diversity may be maintained by this slower process. It is important that, as some studies have done (Lebrija-Trejos et al. 2014, Zhu et al. 2015b), multiple ontogenetic stages are assessed simultaneously, and mechanisms that shape their communities are compared.

6.2 Defaunation

6.2.1 Defaunation and plant community assemblage

The importance of dispersal for escaping NDD mortality was introduced in section 6.1.1; While NDD is vital to the maintenance of plant diversity, some seeds must be able to escape this process in order to maintain a population (Terborgh 2012). Declines in large vertebrates in tropical forests (Peres and Palacios 2007, Dirzo et al. 2014), are thought to be altering tree community assemblage (Wright et al. 2007c, Terborgh et al. 2008, Peres et al. 2015). Chapters 4 and 5, however, show that while there are changes in tree community assemblage, this is not linked to the decline in large frugivores in a hunted forest. Vertebrates dominate dispersal syndromes in the neotropics, with over 70% of neotropical tree species reliant on zoochorous dispersal (Peres and van Roosmalen 2002, Muller-Landau and Hardesty 2005). Tropical forests are thought to be losing valuable ecosystem processes from a variety of trophic interactions, with large mammals influencing tree community assemblage through predation (Beck 2006, Kurten et al. 2015) and dispersal (Wright et al. 2007c, Stoner et al. 2007). However this study shows that many large-seeded species or species thought to be heavily reliant on large primates persist in a defaunated landscape. There are two potential explanations for this: 1) seeds are managing to find other means of dispersal, or 2) undispersed seeds are able to escape NDD mortality. These are discussed below.

6.2.2 Compensation and avoidance of the impacts of defaunation

Large primate dispersed species that are managing to persist in a defaunated landscape may be utilising alternate dispersers; scatter hoarding rodents in particular are thought to play a vital role in the dispersal of large seeded species (Hirsch et al. 2012, Jansen et al. 2012, Geng et al. 2017). If this is the case, dispersal by rodents may be more important than previously assumed. However, it is unlikely secondary dispersal fully compensates for all species that are losing dispersers, which may account for the change in community assemblage detected in Chapters 4 and 5 but variable response among species thought to be impacted by defaunation. Within the vertebrate dispersal category, the comparative importance of dispersers to maintaining species diversity is largely unknown; some tree species are thought to be reliant on only a few species of dispersers (Howe and Smallwood 1982, Vander Wall and Longland 2004), while many tree species utilise multiple species of dispersers (Vander Wall et al. 2005, Hirsch et al. 2012, Jansen et al. 2012). The breadth of dispersers may be critical in deciding the fate of a plant species after the loss of a primary disperser, with trees reliant on limited dispersers highly vulnerable to population declines in disturbed forest. Further study into the capacity for compensatory seed dispersal, particularly among rodents and small arboreal mammals, in defaunated forests may clarify contradictory results in this thesis.

For undispersed seeds to escape NDD in defaunated forests, they must either have some resilience to natural enemies or have their natural enemies removed (Wright et al. 2007b). The latter may be the case in a hunted forest where both large frugivores and large terrestrial seed predators and herbivores are extirpated (Kurten et al. 2015). Chapter 4, however, indicates that our defaunated forests maintained similar densities of trees dispersed by large terrestrial mammals, furthermore, in support of Paine et al. (2016), Chapter 3 indicates that large terrestrial mammals do not effectively drive NDD mortality. These two findings demonstrate that simultaneous removal of large vertebrate dispersers and predators will not drive compensatory effects as posited by Kurten et al. (2015).

Canopy openness was different at the defaunated site in the most recent survey, but similar in previous surveys, indicating inconsistency in light availability between the two sites. Light availability can play an important role in determining whether a seed successfully germinates and survives to maturity (Denslow 1987, Ruger et al. 2009). Saplings surveyed in the study will have been influenced most by light availability at the time of germination, and in many cases this will have been before the start of this study. We cannot be certain that light availability was similar at this time, and so cannot rule out the possibility of light as an influence on community assemblage. Equally we cannot be certain that other abiotic aspects did not influence the structuring of the sapling community. Considering we saw no evidence that defaunation is driving changes in the community structure, it is possible that these abiotic factors are comparatively strong drivers behind structuring tree communities.

This thesis indicates that secondary dispersal is a most likely candidate for compensatory effects in defaunated forests, however it is possible that all of the above assertions play a part in structuring the tree community in a defaunated landscape. It is important to consider, however, that there are yet directional changes in tree community assemblage at defaunated sites. More in depth study regarding the compensatory and NDD mechanisms are needed to assist our understanding of the underlying causes of these changes. While this study does not support a growing trend in the literature showing widespread declines of large seeded species in defaunated forests (Wright et al. 2007c, Stoner et al. 2007, Terborgh et al. 2008, Harrison et al. 2013, Peres et al. 2015), I do not dismiss any connection between large frugivorous dispersers and the tree community. Efforts to stem rising defaunation rates throughout the tropics should be maintained not only for the conservation of species targeted by hunters, but for the conservation of floral and faunal communities that may be unpredictably and irrevocably altered decades or even centuries after hunting pressure begins. The fact that the direction and underlying causes of these changes remains unclear does not diminish the importance of both understanding and attempting to slow this trend.

6.2.3 Carbon storage

Chapter 5 finds no link between a simulated decline in large-seeded or large primate dispersed species and wood density. Moreover, changes to the community structure at a defaunated site do not drive a decline in wood density. Large frugivores targeted by hunters (Peres and Palacios 2007) are linked to dispersal of large seeds (Galetti and Dirzo 2013), which are in turn associated with high wood density and larger stems (Peres and van Roosmalen 2002, Diaz et al. 2004, Wright et al. 2007a). Carbon storage is higher in species with high wood density and larger stems (Chave et al. 2005, Stephenson et al. 2014), and are thus responsible for a disproportionate amount of global carbon storage (Fauset et al. 2015). While our study finds little evidence to support this, there is a noteworthy decline in large stemmed species, which are important for carbon storage (Stephenson et al. 2014), and this decline in large stems is evidently not being compensated for by an increase in wood density. Although this trend does not relate to large-seeded or large primate dispersed species, it is important to further investigate this change and assess its drivers, since if this decline is widespread there could be implications for carbon storage. Overall, predicted declines in carbon storage as a result of defaunation are not supported in this thesis. Moreover, an assessment linking trees that are important for carbon storage to trophic interactions that maintain their species could reveal the type of anthropogenic disturbance that will impact carbon storage. However we should look most urgently to the direct loss of trees through deforestation to explain the rapidly declining tropical carbon sink (Grace et al. 2014, Rosa et al. 2016, Pearson et al. 2017).

6.3 Among species variation

Chapter 2 indicated that NDD varied in strength among species (Zhu et al. 2015b), with regionally rare species experiencing stronger NDD than common species (Hubbell et al. 2001, Comita et al. 2010, Johnson et al. 2012). In agreement with this study, a species-specific study by Gripenberg et al. (2014) found that NDD mortality was highly variable even among the few species she studied, and numerous studies have assessed the difference in NDD among species with different regional abundance (Hubbell et al. 2001, Comita et al. 2010, Johnson et al. 2012). With higher vulnerability to NDD rare species may be disproportionately suppressed within a community, maintaining their rare status while common species experiencing low NDD pressure are permitted to dominate the species stand (Comita et al. 2010). In a species community that consists of upwards of 300 species studies look for trends within the community in order to understand underlying mechanisms. It is important to note, however, that a diverse species community has a large variation in functional traits (Zhang et al. 2013), and there is no ‘one size fits all’ model to explain species coexistence.

When studying community trends in hyperdiverse communities such as the tropics, it is difficult to avoid a bias towards common species created by the disproportionately high number of rare species (Fauset et al. 2015). Community-wide trends are strongly driven by common species, since it is difficult to obtain enough data to detect trends in rare species. Moreover, since I show that rare species experience stronger NDD (Chapter 2), we may be missing vital elements when studying mechanisms and demographic patterns in NDD among seedlings. A study incorporating common and rare species and their associated NDD mechanisms may provide interesting insights into variation among species not only in strength of NDD but in the driving mechanisms.

In a defaunated landscape variation among species may be a key barrier to a comprehensive understanding of altered ecological processes. Altered tree community assembly under the influence of hunting detected in Chapters 4 and 5 is an indication that changes are occurring, but with species-specific responses to altered faunal communities, it becomes impossible to extract these responses at the community level. Differences in responses may be driven by species traits, e.g. larger seeds may be appealing to scatter-hoarding rodents (Hirsch et al. 2012, Jansen et al. 2012), or smaller fruits may attract small arboreal mammals in the absence of larger frugivores that would otherwise outcompete them. Furthermore, common species experience weaker NDD (Comita et al. 2010, Chapter 2) and these are the species available to assess under the impact of hunting. These common species could therefore be escaping NDD or experiencing low enough NDD that they persist in the absence of a disperser, while rare species subject to strong NDD are unable to persist but remain undetected in a community wide study.

An undetected decline in rare species may be critical problem facing changing tree community assemblage, with rare species collectively supporting a disproportionate degree of ecosystem function (Mouillot et al. 2013). Though individually each species comprises a small proportion of the community, together rare species comprise ~50% of the tree community (ter Steege et al. 2013), and contribute an exceptional proportion of diversity (Preston 1948, Gaston 1996). Fricke and Wright (2017) have started to examine these processes in more detail, however further efforts to understand the mechanisms that drive rarity and the persistence of rare species are necessary to aid an understanding of the fate of rare species under anthropogenic impacts.

6.4 Scope for further research

This thesis opens up a potential for a deeper understanding of mechanisms driving community assemblage. Reliable results are presented from the rigorous experimental study presented in this thesis, however the study of mechanisms spans only 3 years, a comparatively short time for a life form that may live for 100 years (Lieberman and Lieberman 1987), and may spend over a decade under 1m in height (Chapter 2). Chapter 2 shows that mechanisms of species coexistence are changing even within the first decade of a seedlings life, it would therefore be beneficial to clarify alternate mechanisms at later ontogenetic stages, since studies have shown that NDD interactions differ throughout ontogeny (Lebrija-Trejos et al. 2014, Comita et al. 2014, Zhu et al. 2015b, Inman-Narahari et al. 2016). It would further benefit studies such as that presented in Chapter 3 to include both seed and seedling stages, since seeds and seedlings are likely to differ in their response to natural enemies and abiotic factors (Swamy et al. 2011, Gripenberg et al. 2014, Paine et al. 2016). Moreover, while we detect mechanisms driving seedling diversity, there are few studies that consider whether diversity created at this early life stage dictates diversity in the mature tree community (but see Johnson et al. 2017, Rüger et al. 2018). This assumption, though logically formed, is not proven, and Chapters 4 and 5 of this study, disproving the assumed link between large seeds and high wood density, reiterates the importance of testing assumptions. Empirical evidence linking diversity created at the early life stages to diversity at the mature tree stage is necessary to complete this picture.

This thesis highlights extensive variation among species in NDD strength and mechanisms, and in response to anthropogenic changes to ecological processes. Insight into the nature of this variation may give a deeper insight into the comparative contribution of natural enemy driven NDD among seedlings, the comparative contribution of abiotic and biotic drivers of NDD among species, and the comparative contribution of dispersal syndromes within and among species. This would further assist understanding of the variable impacts of defaunation among tree species, and the nature of the changes to community assemblage detected in defaunated forests.

6.5 Conclusions

This thesis examines the comparative contribution of trophic interactions among tropical trees, considering both negative associations with natural enemies and positive associations of dispersers. Negative density dependence among seedlings is a prevalent process in a tree’s early life stages, and while there is demographic variation in driving mechanisms, mortality caused by fungal pathogens in the first year of a seedling’s life is shown to be uniquely important in the maintenance of diversity.

Disruption to the disperser community induces alterations to tree community assemblage, but these are not explained by declines in large frugivores. To further understand the nature of hunting induced changes to tree communities, among species variation in dispersal ability and in strength and drivers of NDD needs to be examined. Defaunation is severely impacting tropical forests worldwide (Milner-Gulland et al. 2003, Peres and Palacios 2007, Dirzo et al. 2014). While we recommend caution in connecting vertebrate declines to declines in diversity and carbon storage (Terborgh et al. 2008, Peres et al. 2015), there are changes in defaunated communities that have yet to be explained, and further insights are necessary before we can conclusively link defaunation to forest structure.

We provide evidence that trophic interactions in tropical forests are essential in shaping plant community composition, but that those most influential for high diversity are those least understood, that of pathogenic host-specific mortality. Understanding the remarkably high diversity in tropical forests and the long-term consequences of degradation is therefore inextricably linked to understanding these local scale processes, and interspecific variation at this scale. With diversity in tropical forests essential for ecosystem services (Hooper et al. 2005) and mitigating climate change (Pan et al. 2011), considering the local scale biotic interactions is vital both for a deeper understanding of the drivers of diversity and for conservation efforts in an extensively anthropogenically altered tropical ecosystem.

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