Biodiversity-ecosystem service relationships in degraded and recovering ecosystems

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Abstract

Biodiversity loss is occurring at an unprecedented rate and most of this loss is due to human induced pressure. This loss in biodiversity had led to concerns that the provision of ecosystem services that humans depend upon might be negatively affected. As such much modern conservation science focusses on preserving biodiversity whilst protecting priority ecosystem services. However, there may be spatial and temporal trade-offs between these services and the biodiversity that is considered important. Characterisation of such the relationships between biodiversity and ecosystem services is vital in order to improve management and policies which aim to protect and restore both biodiversity and ecosystem services.

The broad aims of the thesis were to explore biodiversity-ecosystem service relationships in (1) ecosystems invaded by non-native plant species and (2) tropical forests affected by human exploitation and disturbance. Specifically this thesis aimed to answer the questions:

1. What effect do non-native plant invasions have on aboveground carbon storage, belowground carbon storage, carbon sequestration, water quality and water provision?
2. How do changes in species richness affect this ecosystem service provision?
3. How do these changes relate to the woodiness and traits of invasive and native dominant species, and the type of ecosystem invaded?
4. What factors drive differences in residual stand damage, biomass loss and species richness change following selective logging?
5. After deforestation how long do carbon stocks and plant biodiversity take to recover in tropical forests?
6. Do carbon and plant biodiversity differ in their recovery rates?
7. Which areas are priorities for restoration of tropical carbon?

All chapters in this thesis make use of large datasets that I collated from the literature and other authors in order to draw broad conclusions about trade-offs and relationships between services and biodiversity

In the section concentrating on invasive species my results suggest that non-native invasive plants generally increase the storage of carbon, whilst reducing water quality and availability. This may indicate a fundamental trade-off between services where increased biomass of plants results in higher evapotranspiration and thus water loss, while also enhancing the carbon cycle and nitrogen production of microorganisms. In addition my

results suggest that aboveground carbon storage increases as species richness is reduced, showing the opposite relationship to that shown in many biodiversity ecosystem functioning experiments. This is the first time any such relationship has been found between community change and ecosystem level impacts in the context of species invasions. However, it seems likely that this relationship depends on the identity and traits of the species, with invasions in open habitats by woody species likely to drive a negative relationship between richness change and biomass change with the opposite true when grassy species invade woodlands. This result presents a trade-off between conservation priorities that managers will need to consider.

In Chapter 3 I investigated the possibility of predicting the impact of non-native invasive plant impacts on ecosystem services by using characteristics and functional traits of both invasive and native species. This work suggested that aboveground carbon storage is most easily predicted by traits and characteristics of native and non-native species, with few other ecosystem services well explained by models. Results suggested that transition from woody to non-woody dominant species resulted in most dramatic changes in aboveground carbon storage. However, interestingly aboveground carbon storage also tended to increase where native species were replaced by species of similar woodiness. Similarly, given that woodiness and size of species are related, there was a positive relationship between the invasive species height and increases in aboveground carbon storage. However, all other ecosystem services were poorly predicted by species traits and characteristics. This work suggests that the most dramatic changes in carbon storage may result from shifts in ecosystems that resemble regime shifts. Future work addressing invasive species from this perspective is warranted as many invasions resemble such shifts.

In Chapter 4 I investigated the relationships between logging intensity and methods and residual stem damage, biomass loss and species richness change in tropical logged forests. Many syntheses of the logging literature have made little distinction between logged sites, and only one has explored any of the mechanisms that may drive heterogeneity in logging impacts. This is particularly surprising given that Reduced Impact Logging (RIL) has been implemented relatively widely principally to reduce carbon loss from logged forests. My results from this chapter suggest that the principal driver of logging impacts is the intensity at which logging is carried out, showing broadly negative relationships with biomass and tree species richness change and a positive relationship with residual stem damage. Interestingly, RIL appeared to reduce residual stem damage slightly but evidence for this effect was weaker in other analyses. These analyses also suggest a slight increase in tree species richness at low logging intensities, showing some similarities to intermediate disturbance hypothesis type relationships. This is suggestive of a complex relationship between tree species richness and biomass changes during logging that deviated substantially from that suggested in grassland biodiversity-ecosystem function experiments. This is as far as I know the first time this relationship has been suggested in the context of logged forests. The result from this chapter also suggest that there is weak support that RIL reduces logging damage at low intensities but little evidence that this is reflected by changes in biomass. Further studies are needed to discern the effect of RIL over a wide range of logging intensities.

Chapter 5 investigates tropical forest recovery following agricultural clearance. In this chapter I aimed to identify the recovery times of different above and belowground carbon pools and tree and epiphyte species richness as well as tree species composition using studies that had paired mature forest sites as comparators. Surprisingly this chapter represents the first attempt to generalise about this recovery rate. The results suggest that following clearance carbon and species richness of plants recovers relatively quickly (<100 years), but species indicative of old forests are rarely present in recovering forests and show few signs of recovery. Thus, while carbon recovery goals may be achievable full recovery of plant biodiversity may require centuries. This slow recovery may be aided by active restoration.

Finally in Chapter 6 I investigated which areas should be considered as priorities when restoring tropical forests for carbon storage and bird biodiversity. In this chapter I found evidence of spatial trade-offs between carbon storage and bird species recovery. Empirical models suggested that carbon is accumulated most rapidly in forests with long growing seasons, while probability of bird species presence was primarily driven by habitat specificity, range size and forest cover. Model projections suggested that areas that should be considered a priority for restoration targeting carbon storage are found in the wet tropics while priorities for restoration of bird biodiversity are found in mountainous areas. These analyses indicated that there was no relationship between the two goals, but that by using model projections it was possible to identify areas that maximised both.

In summary work in this thesis provides the best synthesis of the relationships between biodiversity and ecosystem services in the context of non-native invasive plants, and selective logging and recovery from tropical forest clearance to date. This is of particular value because such relationships have rarely been explored in these contexts despite widespread and of global importance for conservation.

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Author’s declaration

I confirm that this thesis is my own work, with the exceptions of the manuscripts below. As senior author on all the papers below, I led all aspects, including idea development, data collection, analysis and interpretation. I also led the preparation of these manuscripts. The only exception to this is the collection of data on bird biodiversity for Chapter 6 that was undertaken by Catherine Sayer as part of an MSc project I supervised. Where other sources of data were used in this thesis this is acknowledged and referenced accordingly.

Chapter 2 is in review and was written in collaboration with my supervisors as: Martin, P.A., Newton, A.C. & Bullock, J.M. Positive and negative effects of plant invasions on ecosystem services and interactions with native species loss: a meta-analysis, Global Ecology and Biogeography.

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Chapter 1

1 Introduction

This thesis explores the effects of ecosystem degradation on biodiversity and ecosystem services and the relationship between the two in these systems. In this introduction I briefly discuss the impact of human induced ecosystem change on biodiversity, how these changes may relate to changes in ecosystem function and services, the evidence base for this and finally how my research aims to address identified research gaps.

1.1 Human degradation of natural ecosystems and biodiversity loss

Over the past century humans have altered ecosystems massively as a result of rapid population growth and consumption (CBD 2010). Much recent loss of biodiversity[1] has been driven by conversion of natural ecosystems[2], largely as a result of the expansion of agriculture (Foley et al. 2005; Gibbs et al. 2010). However, a significant number of ecosystems have been degraded[3] either as a direct result of human exploitation, such as selective logging (Sodhi et al. 2004) or hunting (Bennett and Robinson 2000), or as an indirect result of human activity, such as by climate change (Heller and Zavaleta 2009) or invasion of non-native species (Sanders et al. 2003). The combined pressures of habitat loss and degradation have resulted in steep declines in a large number species' populations

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[1] Biodiversity in this thesis refers to the broad definition by the Conventional on Biological Diversity (CBD) as ' the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (CBD 2010).

[2] In this thesis ecosystem conversion refers transformation of an ecosystem into a human land use such as agricultural fields, mines or urban areas. This transformation involves the complete loss of biota considered characteristic to the given ecosystem (Keith et al. 2013).

[3] Degradation in this thesis refers to the reduction in conservation value or ecosystem service provision up until the point at which the ecosystem is considered as converted to human land use, such as agriculture (Sasaki and Putz 2009)

over the last century, with only few showing increases during the same period (Fuller et al. 1995; Houlahan et al. 2000; Craigie et al. 2010). Consequently approximately a quarter of all species are considered to be threatened with global extinction (CBD 2010).

Biodiversity changes following degradation tend to be less dramatic than those following ecosystem conversion (Sasaki and Putz 2009; Thomas 2013), but understanding their causes and consequences is vitally important given that: (i) much species conservation is now undertaken in degraded ecosystems (Chazdon et al. 2009); (ii) these degraded systems are often home to human populations that may rely on them for provision of ecosystem services[4] (Cincotta et al. 2000; Bateman et al. 2013); and (iii) positive feedbacks between drivers of degradation show the potential to cause widespread species extinction (Sodhi et al. 2004).

1.1.1 Why do species' extinction risks differ?

The long-term persistence of a species in an ecosystem ultimately depends on the survival of individuals and their ability to reproduce and their ability to re-colonise if they become locally extinct. Not all species have an equal likelihood of persistence following ecosystem degradation, and these differences may be related to functional traits[5] (Sodhi et al. 2008). For example relatively large species tend to be more likely to become locally extinct because they usually have smaller populations, lower reproductive rates and can be targeted directly by humans, e.g. large trees during selective logging (Sodhi et al. 2004) or large animals as a result of hunting (Bennett and Robinson 2000). The traits that influence survival of plants following degradation are relatively poorly understood (Stork et al. 2009), but work on the response of woody plants to disturbances suggests that the ability of species to resprout may be key to their survival (Bond and Midgley 2001; Poorter et al. 2010). Providing that species are still present following the initial degradation of a system their long-term persistence depends on their ability to reproduce. Species which have generally high rates of reproduction per generation and short generation times appear to be the most likely to recruit successfully in degraded ecosystems (Gaston and Blackburn 1995; Newbold et al. 2013), but successional theory

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[4] In this thesis ecosystem services are considered to be the elements of ecosystems used to generate human well-being (Fisher et al. 2009)

[5] In this thesis functional traits are defined as measures of the morphological, physiological or phenological characteristics of an organism affecting its individual performance (Violle et al. 2007)

suggests that over time without further disruption these species should be replaced by those with longer generation times (Guariguata and Ostertag 2001). At a larger scale the long-term persistence of species in a landscape depends on the ability of individuals or seeds to disperse to new areas, particularly in fragmented landscapes (Thomas 2000; Van Dyck and Baguette 2005).

1.1.1 How do species losses affect ecological communities?

These losses in individuals or populations result in changes in the composition of ecological communities. Losses of large numbers of populations will result in ecological communities having very different structure to communities found prior to degradation, and more intense degradation probably leads to greater changes in community structure (Cleary et al. 2006; Moura et al. 2013). These changes have been shown to lead to a reduction in the distinctiveness – i.e. decreased β diversity – of a wide range of ecological communities (McKinney and Lockwood 1999; Keith et al. 2009). In addition to community structure the number of species in a given area, the species richness, can also change as a result of degradation (Murphy and Romanuk 2014, but see Vellend et al. 2013). However, in the case of species richness the effects of degradation are not always negative, with some suggestions that slight degradation can lead to increases in species richness (Bongers et al. 2009; but see Fox 2013).

Since the structure and richness of communities can be altered by degradation it logically follows that the abundance and variety of functional traits found in a community can change. This can lead to alteration in functional diversity, which put simply, is diversity described in terms of what species do in an ecosystem rather than their taxonomy (Petchey and Gaston 2006). There are numerous metrics of functional diversity, which can include trait differentiation between individuals within a population, between species within communities, or between functional groups (Hillebrand and Matthiessen 2009) as well as mean per capita weighted trait values (Lavorel and Garnier 2002; Lavorel et al. 2011; Lavorel and Grigulis 2012). Much as community composition is more sensitive to degradation when compared to species richness, functional composition[6] changes appear to be

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[6] Functional composition refers to measure used by Baraloto et al. (2012) in which multiple traits were used to produce a measure equivalent to those used for community composition

more readily detected than changes to functional richness[7] (Baraloto et al. 2012). Such changes in functional diversity are thought to have possible consequences for ecosystem function (Díaz et al. 2007; Díaz et al. 2013).

1.2 Biodiversity-ecosystem function relationships

Pacala and Kinzig (2002) distinguish between 3 different groups of ecosystem function: stocks of energy and materials (e.g. biomass), fluxes of energy (e.g. productivity, decomposition) and stability of rates or stocks over time. All ecosystem functions depend upon various aspects of biodiversity for their maintenance though the exact relationships for specific functions differs. It has been suggested that the dramatic alteration of biodiversity by humans over the past century may have far reaching consequences for these functions, as well as the aspects of ecosystems on which humans depend, termed ecosystem services (Cardinale et al. 2012; Mace et al. 2012). There is experimental evidence for relationships between species or functional richness, and primary productivity, resource use, decomposition, multifunctionality and ecosystem stability in numerous systems (Cardinale et al. 2012). These results underpin the theory of how changes in biodiversity can impact ecosystem function and ultimately ecosystem services.

The most widely tested of the ‘biodiversity-ecosystem functioning’ (hereafter referred to as BEF) relationships is that between plant species richness and primary productivity (Hooper et al. 2005). Large numbers of controlled experiments conducted in grasslands suggest that as plant richness increases, productivity also tends to increase, plateauing in rich communities (Hooper et al. 2012). A recent large synthesis of the topic suggests that on average diverse polycultures attain ca. 1.4 times the biomass of monocultures, with aquatic ecosystems and grasslands showing most pronounced responses (Cardinale et al. 2011). However, the same synthesis by Cardinale et al. (2011) also indicated that effects of richness on forest productivity were less obvious, partly because of a relative lack of studies.

Similarly, Cardinale et al. (2011) also indicated that in 86% of experiments in which the impact of changes in producer species richness on nutrient concentration was tested, net diversity effects were negative. In addition, nutrient concentrations in the most diverse polycultures were on average 48% lower than those in monocultures (Cardinale et al. 2011). Approximately 94% of the information on the

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[7] Functional richness is the number of different functional groups found in an area of interest (Petchey et al. 2009)

resource use efficiency of communities identified by Cardinale et al. (2011) comes from temperate grasslands. It has been suggested that this effect may be mediated both by direct uptake as well as the effects of plants on soil microbial dynamics (Hooper and Vitousek 1997; Hooper and Vitousek 1998).

In addition to the impacts of species richness on productivity and resource use, there is also some suggestion that increases in diversity result in increased rates of decomposition. 62% of 84 experiments showed lower litter mass in polycultures than monocultures (Cardinale et al. 2011). However, when compared to productivity and resource use impacts appear to be relatively modest with only a 5% increase in decomposition in the most diverse polycultures compared to monocultures (Cardinale et al. 2011).

As well as increasing primary productivity, resource use and decomposition rates there is increasing evidence that species richness is positively related to stability of these through time (Isbell et al. 2011; Cardinale et al. 2012). Similarly, more species are needed to maximise multiple ecosystem functions (Isbell et al. 2011). This suggests that as the number of contexts, functions and temporal scale increase the number of species needed to maximise functions also increases (Isbell et al. 2011).

Though the patterns of BEF relationships are clear for aquatic and grassland ecosystems they are relatively uncertain for many other ecosystems (Waide et al. 1999) because of the relative difficulty in manipulating species rich assemblages, especially those that contain shrubs or trees. As such, the nature of BEF relationships is poorly characterised for most ecosystems, particularly for assemblages that are naturally very species rich such as those found in the tropics (but see Hector et al. 2011; Bruelheide et al. 2014 for examples of this).

1.2.1 Why *should* species richness affect ecosystem function?

Given that some ecosystem functions co-vary with plant species richness, there has been much debate on the likely reasons for this pattern. Current research suggests that these relationships are likely to be attributable to differences among species expressed in terms of their traits (Hillebrand and Matthiessen 2009). Since trait diversity can be correlated with species diversity, this helps to explain some of the observed relationships in BEF experiments. A number of hypotheses have been suggested which aim to explain the relationships seen between plant species richness and ecosystem functions, all of which rely on assumed trait variation between species.

The ‘complementarity effect’ hypothesis states that resource partitioning leads to greater total resource use (Loreau and Hector 2001) and has been suggested as a means of explaining the relationship between species richness and ecosystem functions. However, this relationship does not rely on species richness *per se*, but rather is driven by differences in the species traits which determine resource uptake and conversion to biomass. The ‘selection effect’ hypothesis has also been suggested as means of explaining the relationship between species richness and productivity, and states that species rich communities have a greater chance of containing more productive species (Loreau and Hector 2001). Mechanistically, this relationship must again rely on trait differences between species since it presumes that some species are more productive than others.

There are three different hypotheses that concerning the effects of species richness on temporal stability of ecosystem productivity: over-yielding, statistical averaging and compensatory dynamics (Cardinale et al. 2012). Over-yielding occurs when species mixtures perform better than expected and as a result in increases in productivity relative to variability (Hector et al. 2010). Statistical averaging occurs when stochastic variation in species populations reduces variability of ecosystem functions (Doak et al. 1998). Compensatory dynamics are the result of competition between species and/or differences in the response of species to changes in environmental conditions, which lead to asynchrony of species responses to changes. Though these three different mechanisms have been suggested as a means of explaining diversity-stability relationships, their relative importance is currently unclear (Cardinale et al. 2012).

1.2.2 Relevance of BEF experiments for biodiversity conservation

Though both species and functional richness, as well as particular traits, are likely to aid the maintenance of particular ecosystem services, the relevance of experimental BEF work for real world systems has been questioned by some (Schwartz et al. 2000; Srivastava and Vellend 2005; Thompson and Starzomski 2007). Firstly, the assemblages used in these experiments are often relatively species poor and bear little resemblance in composition to real world systems (Schwartz et al. 2000). This is of particular concern since BEF relationships in experiments are more likely to be log-linear than linear (Srivastava and Vellend 2005), meaning that increases in species richness result in increases in productivity before plateauing (Cardinale et al. 2006). This suggests that even in relatively species poor assemblages many species could be lost before function is appreciably reduced (Wardle 2002). However, when multiple functions, and contexts are considered this relationship tends to plateau later suggesting a greater number of species are needed to maintain a wide variety of functions (Isbell et al. 2011).

Secondly, alterations in species diversity are generally random in BEF experiments, whereas in natural systems extinctions are not random and are often linked to particular traits (Cardillo and Bromham 2001; Duncan et al. 2011). Research has indicated that realistic extinction scenarios can produce very different effects on ecosystem functions to those seen in random extinctions, and are likely to be driven by the degree to which the roles of species lost can be replaced by other similar species (Gross and Cardinale 2005; Larsen et al. 2005; Schläpfer et al. 2005).

1.3 Biodiversity-Ecosystem service relationships

Much BEF research has informed the relatively new area of ecosystem services. Fisher et al. (2009) define ecosystem services as the elements of ecosystems used directly and indirectly to produce human well-being, and the concept is seen as a powerful advocacy tool for biodiversity conservation (e.g. Daily et al. 2009) . Though there are other definitions, that of the United Kingdom's National Ecosystem Assessment (UK NEA, 2011), which adapted the framework of Fisher et al. (2009), is amongst the most practical since it also defines a conceptual supply-chain for ecosystem services (Figure 1). Using this definition ecosystem processes underpin final services which are those used directly by humans (UK National Ecosystem Assessment 2011). Ecosystem goods are considered to be the result of these final services and normally require some input from human infrastructure (UK National Ecosystem Assessment 2011). For example, maintenance of bee populations could be considered an ecosystem process, pollination of almond crop a final service and almonds to be the good (Fisher et al. 2009; UK National Ecosystem Assessment 2011). This makes it easier to define different stages which could be important in supplying the ecosystem benefits on which humans depend, although it obviously greatly simplifies relationships.

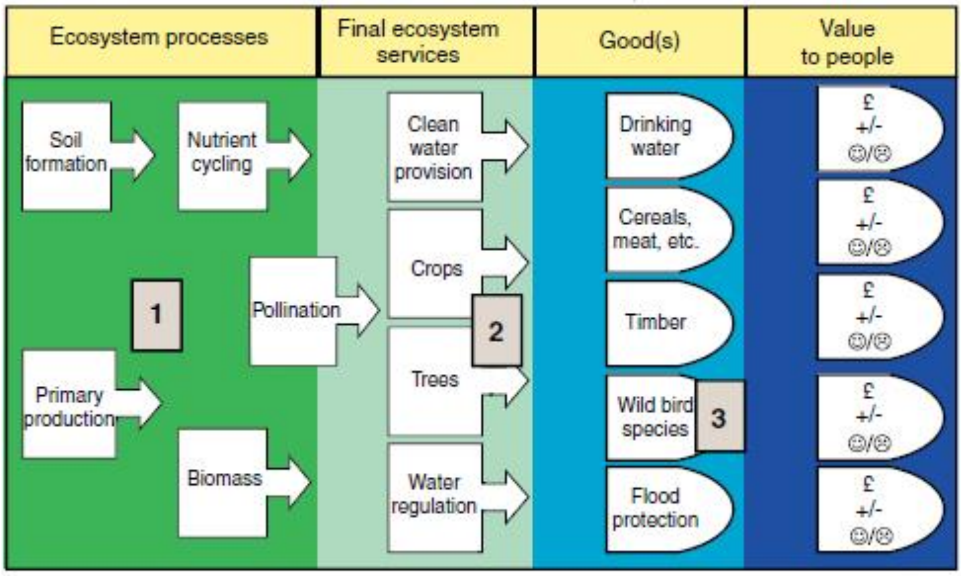

Figure 1 – Conceptual relationship between ecosystem process, final ecosystem services and ecosystem goods and the values they generate adapted from Mace et al. (2012). Final ecosystem services are the outcomes of ecosystems that directly lead to the good(s) that are valued by people, the full value is not only generated by the ecosystem but depends on the addition of inputs from society and the value is often context dependant. The final value of a good is therefore attributable to both the ecosystem and human inputs. The final value of the good is therefore attributable to both the ecosystem and human inputs. Values may be monetary (£), quantitative and non-monetary (+/-) or non-monetary (☺/☹). Using this framework biodiversity can have roles as (1) a regulator of ecosystem services e.g. a pollinator, (2) a final ecosystem service e.g. crops or trees (3) as a good that has its own value e.g. wild bird species that have cultural or aesthetic value.

In practice many ecosystem functions can be considered as ecosystem services, provided that humans benefit from them in some way. For example, soil carbon storage can be considered as an ecosystem service as well as an ecosystem function since this storage results in avoided carbon emissions which might otherwise accelerate global climate change (Lal 2004). However, the key issue of defining beneficiaries for a potential ecosystem service based on the scale at which they are provided has meant that measuring ecosystem services is generally difficult (Fisher et al. 2009; Peh et al. 2013), and proxy measures are often employed. The exceptions to the use of proxies are ecosystem services which provide tangible benefits such as food, timber, firewood and water, which are relatively easy to measure as well as to define beneficiaries (Millennium Ecosystem

Assessment 2005). In addition climate regulation through carbon storage and sequestration is also relatively easily assessed, since the scale of the provision of this service is global and thus it is argued that all humans benefit from it (Fisher et al. 2009).

The relationship between biodiversity and ecosystem services is a complex one. Early work on ecosystem services emphasised that biodiversity underpins many ecosystem services, using BEF experiments as evidence for this (Millennium Ecosystem Assessment 2005). However, recent work has suggested that biodiversity has key roles at all levels of the ecosystem service hierarchy: as a regulator underpinning ecosystem function, as a final ecosystem service and as a good (Figure 1; Mace et al. 2012). As discussed above, biodiversity has an obvious role in ecosystem functions that underpin ecosystem services by promoting greater productivity, more efficient resource use, greater stability and multi-functionality (Cardinale et al. 2012). However, biodiversity can also be a final ecosystem service such in the case of genetic diversity of plants for use in medicine or for improvement of crop cultivars (Mace et al. 2012). Finally, biodiversity can also be a good itself, either in the form of direct use via harvesting or because of cultural (Clark et al. 2014) and aesthetic appreciation (Lindemann-Matthies et al. 2010).

The complexity of this relationship between biodiversity and ecosystem services has sometimes been glossed over by conservation biologists and the perceived positive relationship between has been widely used as means of promoting biodiversity conservation, despite warnings against this (Schwartz et al. 2000; Thompson and Starzomski 2007). With the recent move in conservation towards a focus on ecosystem services many of the debates stemming from BEF research have been re-framed to argue that greater species richness results in greater ecosystem service provision (e.g. Balvanera et al. 2006). However, as I show below, it is clear that this is not true for all ecosystem services and we lack information on such relationships for most services in most ecosystems.

1.4 Evidence for biodiversity-ecosystem service relationships

Biodiversity conservation is becoming more holistic, attempting to maintain and enhance ecosystem service provision, whilst, at the same time, limiting species declines and extinctions (Soulé 2013; Doak et al.). As such, determining the linkages between different elements of biodiversity, ecosystem functions, final services and ecosystem goods are vitally important issues (Cardinale et al. 2012). However, we currently know relatively little about these relationships in many ecosystems (Mace et al. 2012) and it seems unlikely that they will be characterised in the near future. Ultimately the degree to which changes in biodiversity are linked to changes in ecosystem service provision depends how the two are linked. As such relationships are highly sensitive to how ecosystem service and biodiversity priorities are defined. To explore this I will focus on three key ways that biodiversity may be linked to changes in ecosystem service provision.

1.4.1 Functional links

One way in which biodiversity can be related to ecosystem service provision is via a functional link, where changes in the measure of biodiversity results in a change in the ecosystem service. The most tangible functional links are BEF relationships, such as primary productivity and nutrient cycling (Cardinale et al. 2012). While increasing productivity is of little importance to most biodiversity conservation, such relationships are potentially important in contexts where productivity for fodder (Cardinale et al. 2012) or carbon sequestration are goals (Srivastava and Vellend 2005). Pollination services are also widely seen as an example of such functional relationships, where increasing pollinator species richness, functional diversity and abundance appears to result in greater fruit set that is also less variable, and better quality fruit for a wide number of crops (Klein et al. 2003; Hoehn et al. 2008). In addition there is some evidence that decreases in species richness can result in increased disease transmission between animals and humans (Keesing et al. 2010; Johnson et al. 2013), as a result of increased encounters between infected and susceptible hosts, though this relationship is hotly debated (Lafferty and Wood 2013; Ostfeld and Keesing 2013; Salkeld et al. 2013). Thus in cases where the biodiversity that is of conservation concern shows a strong functional link to ecosystem service priorities, targeting one is likely to benefit the other. However, many relationships between ecosystem services and conservation priorities are not like this, given that humans tend to favour the conservation of large, charismatic, vertebrate species (Morse-Jones et al. 2010; Morse-Jones et al. 2012) that are not necessarily important for service provision. However, there can still be apparent relationships and spatial overlaps between biodiversity and ecosystem service priorities, even when there is no function linkage.

1.4.2 Spatial concordance

Ecosystem services and biodiversity priorities can appear to be related when they are in fact driven by different processes due to spatial overlaps of areas considered important for the two. For example, it has long been observed that the tropics exhibit high species richness and endemism when compared to temperate and boreal regions (Pianka 1966; Gaston 1996). The reasons for this pattern are unclear but hypotheses include greater energy availability, and more stable climate during ice-ages (Davies et al. 2007). As a result of recent increases in human population growth in the tropics many of these species are now threatened with global extinction (CBD 2010; Gibbs et al. 2010). The tropics also contain some of the most carbon dense forests in the world (Saatchi et al. 2011), largely as a result of hot, wet climate enabling in high productivity (Slik et al. 2013). Many projects have attempted to target vertebrate biodiversity conservation priorities and retention of carbon stocks in locations where the two coincide (Strassburg et al. 2010; Thomas et al. 2013). For example, a recent study showed a strong relationship between areas of high priority for jaguar conservation and carbon stock in Brazil (De Barros et al. 2014). However, the two are not directly related to each other but are purely linked because of overlap of jaguar range and forests that are highly carbon dense. There are many similar cases when spatial concordance of patterns leads to apparent relationships which form the basis of a number of schemes to protect both biodiversity and ecosystem service priorities (Venter et al. 2009). However, because they are not based on a functional relationship, such patterns are likely to be idiosyncratic.

1.4.3 Lack of linkage

Finally, it is possible that there is no functional linkage between biodiversity and ecosystem service provision and drivers of the two differ in their spatial concordance. The best examples of this come from spatial analyses such as that of Anderson et al. (2009) who showed that the recreational value of an area in the UK had very little to do with the number of species considered a national conservation priority. Further work has suggested that this is because in the UK recreational value is largely driven by the presence of streams and lakes as well as proximity to the public (Bateman et al. 2013). Biodiversity priority areas on the other hand tended to be located in areas of low human population (Anderson et al. 2009). Similar weak geographic concordance between biodiversity and ecosystem service priorities have been noted in California (Chan et al. 2006), British Colombia (Chan et al. 2011) and South Africa (Egoh et al. 2009). Thus while the functional role of biodiversity may be important in some cases, many biodiversity priorities do not show these functional links.

In cases where provision of ecosystem services and conservation of biodiversity priorities are goals it is important to identify potential trade-offs as well as situations in which both goals can be achieved. This is analogous to the idea that not all ecosystem services can be maximised in any given landscape and that trade-offs between them are inherent (Foley et al. 2005). Examples of the potential mechanisms by which these trade-offs between ecosystem services and biodiversity priorities can occur are given in Figure 2. Win-win situations will occur either when there is some functional link between the biodiversity managers are aiming to conserve and provision of the ES or when there are common drivers which positively influence both the biodiversity and the ecosystem service in question. Trade-offs can occur when there is no functional link between the biodiversity and ecosystem service objectives, or where aiming to reach one objective harms the ability of managers to achieve the other objective (Bullock et al. 2011). Acknowledgement of these trade-offs has been used by some in the conservation community as an argument for the abandonment of the ES concept since it may potentially endanger species conservation efforts (Redford and Adams 2009; Gómez-Baggethun and Ruiz-Pérez 2011; Büscher et al. 2012). As such, for the ES concept to be integrated with more traditional conservation goals investigation of these potential trade-offs is vitally important.

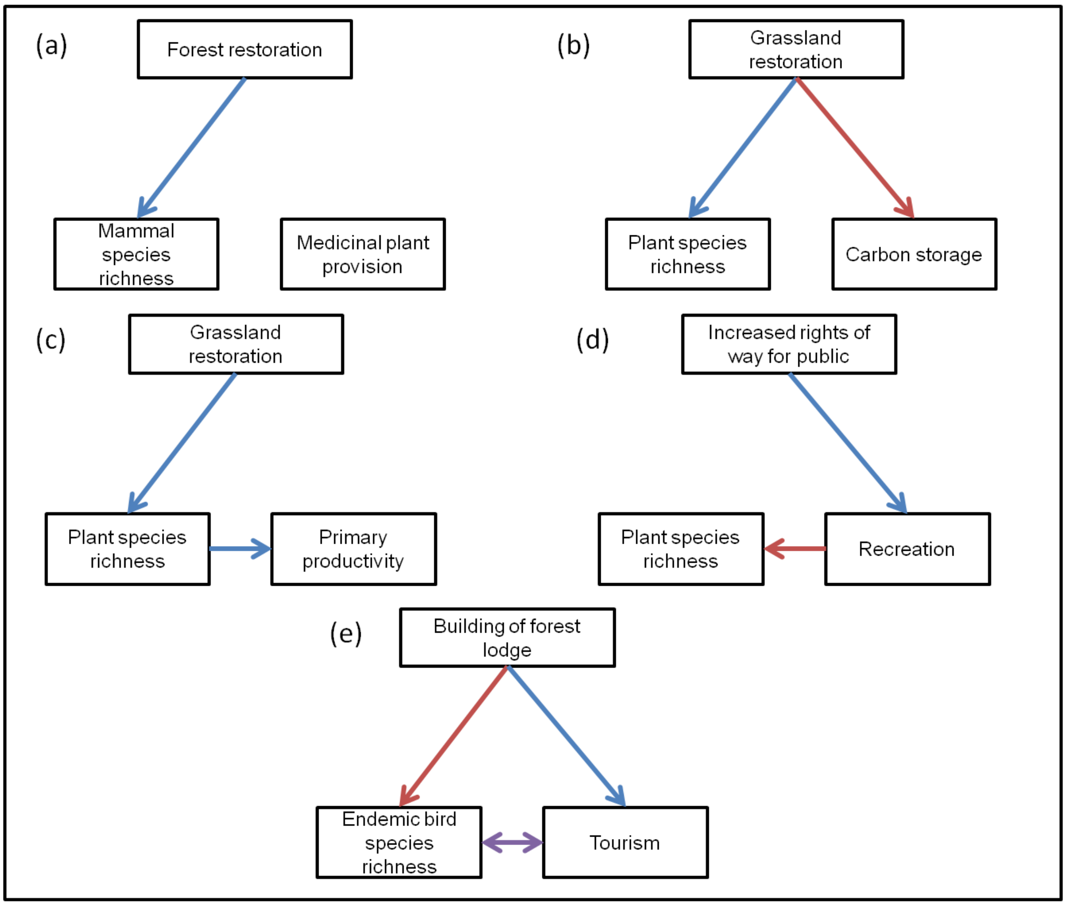

Figure 2 –Potential trade-offs and synergies between biodiversity conservation and ecosystem service priorities. In each diagram (a-e) arrows represent interactions between driver of change (top box), and biodiversity priorities (bottom left box) and ecosystem services (bottom right box), or interactions between biodiversity priorities and ecosystem services. Blue, red and purple arrows represent positive, negative and a mixture of negative and positive impacts respectively. In (a) forest restoration has a positive effect on mammal species richness but has no effect on the provision of medicinal plants. In (b) grassland restoration leads to an increase in plant species richness but a decrease in carbon storage. In (c) grassland restoration leads to an increase in plant species richness which in turn has a positive effect on primary productivity. In (d) increased rights of way for the public leads to an increase in recreation but this has a negative impact on plant populations as a result of increased disturbance. In (e) building of a forest lodge negatively effects endemic bird species richness but leads to an increase in tourism, however this increase has further negative impacts on bird richness which may result in a reduction in tourism.

1.4.4 The importance of spatial scale

A key issue when examining almost any relationship between variables in ecology is that of spatial scale, both at the level of the sample unit (termed ‘grain’) and at the level of the area of interest of a study (‘extent’). Both of these elements of scale influence the relationships observed between biodiversity priorities and ecosystem service provision. Below this is illustrated using the examples of biodiversity relationships with carbon, at local, regional and global scales.

To explore biodiversity-carbon relationships I will use the example of relationships between bird biodiversity and aboveground carbon storage. This relationship is relatively well characterised, but determining their relationships at different grains and extents reveals how relationships can apparently change when the scale at which they are examined changes. While there is no causal relationship between the two, at a local scale there is likely to be a statistical relationship due to common drivers where there is a gradient of forest degradation/deforestation (Moura et al. 2013; Ferreira 2014). Both biomass and species richness are strongly affected degradation and deforestation, and thus the two are linked via this driver (Moura et al. 2013; Ferreira 2014). However, in landscapes with large areas of undisturbed forest there appears to be little relationship between bird species richness and carbon storage since because of the negligible effect of the common driver of human disturbance (Ferreira 2014).

As the extent of study increases the importance of larger scale environmental drivers in governing such relationships will become more important. For example, at global and regional scales vegetation biomass appears to be highest in areas with high rainfall and high annual temperatures (Slik et al. 2013) since these allow high rates of primary productivity and biomass is less likely to be constrained by water stress (Stegen et al. 2011). In addition biomass is likely to be highest in areas with less human disturbance. In contrast, global scale patterns of bird biodiversity appear to be driven by heterogeneity in elevation and energy availability (Davies et al. 2007). However, at a global scale biomass and bird species richness show a weak positive relationship because of congruence of areas with these features (Strassburg et al. 2010). Examining the relationships between bird biodiversity and carbon storage at these two different scales indicates the variety of different ways in which ecosystem services and biodiversity can be inter-related.

Almost all studies that have assessed trade-offs between biodiversity and ecosystem services have done so using spatial data to identify overlaps between the two (Anderson et al. 2009; Egoh et al. 2009; Chan et al. 2011; Thomas et al. 2013). Very few however, have attempted to identify such trade-offs at a finer grain. By determining these relationships a more nuanced view of trade-offs between priorities is possible, revealing mechanisms that may not be apparent in coarser scale analyses. This thesis aims to deal with such trade-offs between biodiversity and ecosystem service priorities at a variety of different scales using previously published data, as well as identifying mechanisms for links where they exist.

1.5 Using systemic reviews and meta-analysis to assess evidence

Systematic review and formal meta-analysis is an objective way to assess the evidence for relationships between biodiversity and ecosystem services. Systematic review is seen as the ‘gold standard’ by which evidence is synthesised in medicine since it is a transparent, repeatable and unbiased assessment of treatment effectiveness (Borenstein et al. 2009). Prior to the widespread use of meta-analyses in ecology, statistical significance of treatments was often used in reviews to assess evidence for or against a theory (Hillebrand and Cardinale 2010). This approach, termed vote-counting, is statistically invalid since significance is purely a product of sample size, variability and differences between groups (Koricheva et al. 2013). Meta-analysis aims to improve synthesis by weighting studies, where possible, such that more accurate studies provide more weight (Koricheva et al. 2013). In addition the use of effect sizes, a measure of the magnitude of changes between control and treatment groups, represents an important progression from the arbitrary use of P values in vote counting approaches (Koricheva et al. 2013). In ecology meta-analysis has been used to address questions as diverse as impacts of land-use on soil carbon (Guo and Gifford 2002a), the effect of warming on arctic plant communities (Arft et al. 1999) and the relationships between biodiversity and ecosystem service provision during restoration (Rey Benayas et al. 2009).

Despite its numerous benefits for synthesising evidence, meta-analysis has been heavily criticised by some (Lindenmayer and Likens 2011; Whittaker 2011; Lindenmayer and Likens 2013). However, though some implementation of meta-analysis has been naïve, the movement of ecology away from a focus on individual case studies has aided immensely our ability to generalise (Hillebrand and Cardinale 2010; Koricheva et al. 2013). Meta-analyses can provide us with baselines against which future studies can be compared, they can aid debate by indicating reasons for differences in results between similar studies and in many cases they can identify what we do not know, thereby stimulating further research

(Hillebrand and Cardinale 2010). This thesis aims to do all of the above in the context of biodiversity-ecosystem service relationships in degraded ecosystems, using meta-analysis and related techniques to draw broad generalisations.

1.6 Aims of this thesis

The broad aims of this thesis are to explore the general research questions:

(i) How does degradation and recovery from degradation affect ecosystem service provision?
(ii) How are biodiversity and ecosystem service provision related in degraded ecosystems?
(iii) What are the mechanisms explaining these relationships?

Prior to starting work on the thesis I undertook an assessment of the evidence base for changes in biodiversity and ecosystem services for a wide range of drivers of degradation to identify cases in which evidence was lacking and whether it was feasible to conduct a meta-analysis to address questions related to the broad aims of the thesis based on the quantity of data available (Table 1)

Table 1 – Potential topics to be covered by this thesis addressed prior to commencement of work, detailing the potential availability of data from primary studies, any previous reviews or syntheses on the topic and the novelty of a topic and feasibility of undertaking a quantitative synthesis

Type of degradation	**Data availability**	**Previous syntheses**	**Novelty**	**Feasibility**
Nitrogen deposition	Lots of data from nitrogen addition experiments.	Meta-analysis of nitrogen addition (Lu *et al.* 2011)	Low	Medium
Harvesting of species	Relatively few studies looking at the consequences of hunting.	Estes et al (2011) review trophic downgrading consequences for ecosystems.	High	Low
Invasive species	Lots of work looking at ecosystem consequences of invasive species	Some reviews (Pejchar and Mooney 2009) but no quantitative syntheses	High	High
Climate change	Lots of data on experimental manipulation of CO_2 and temperature.	Meta-analysis of ecosystem consequences of CC (Wu *et al.* 2011).	Low	Medium
Connectivity & networks	Little work empirically testing this. (Staddon *et al.* 2010).	None	High	Very low
Land use change	Potentially lots of data	Syntheses on carbon (Don, Schumacher, & Freibauer 2011) and on pollinators (Kremen *et al.* 2004)	Low	Medium

Table 1 - Continued

Type of degradation	Data availability	Previous syntheses	Novelty	Feasibility
Recovery following degradation land/use change	Lots of work on recovery in forests, especially the tropics (Chazdon et al. 2009)	Meta-analysis of wetland recovery (Moreno-Mateos et al. 2012) and reviews of forest recovery (Guariguata and Ostertag 2001)	High	High
Forest degradation	Lots of work on carbon and biodiversity impacts of different types of degradation in forests	Large synthesis of tropical forest degradation impacts on biodiversity (Gibson et al. 2011), but nothing on carbon or other ecosystem services	High	High

Following this assessment I identified two areas that lacked evidence of the effects on ecosystem services and the relationships between biodiversity and ecosystem services in these degraded systems. These were (i) degradation of ecosystems as a result of non-native plant invasion and (ii) degradation and recovery in tropical forests. These were specifically selected because they lacked syntheses of their impacts on ecosystem services and biodiversity and there were an adequate number of studies from which to extract data.

The specific research questions that I address in this thesis relating to these topics are:

1.1.2 Invasive species (Chapters 2 and 3)

8. What effect do non-native plant invasions have on aboveground carbon storage, belowground carbon storage, carbon sequestration, water quality and water provision?

H0. Non-native species invasions do not have a consistent effect on any of these ecosystem services.
H1. Non-native plant invasions lead to increases in aboveground and belowground carbon, and carbon sequestration.
H2. Water quality is reduced by non-native plant invasions.
H3. Water provision is reduced by non-native plant invasions.

9. How do changes in species richness affect this ecosystem service provision?

H0. Changes in species richness as a result of non-native plant invasion are not related to changes in aboveground or belowground carbon storage or changes in water quality.
H1. Reductions in species richness lead to increases in aboveground and belowground carbon storage and reduced water quality.
H2. Reductions in species richness lead to reductions in aboveground and belowground carbon storage and increased water quality.

10. How do these changes relate to the woodiness and traits of invasive and native dominant species, and the type of ecosystem invaded?

H1. Where invasions involve transition from woody to non-woody dominant species change in aboveground and belowground carbon storage, water provision and water quality will be more pronounced than where invasion is by a species of similar woodiness.
H2. Where there is invasion by a species with similar woodiness there will be no change in ecosystem service provision
H3. Where there is invasion by a species with similar woodiness some ecosystem service provision will be altered
H4. Inclusion of detail on native ecosystem type along with that of invader woodiness result in a more parsimonious model.
H5. Invasive plant height is positively related to change in aboveground carbon storage and belowground carbon storage, and negatively related to water provision and water quality.
H6. Root depth of invasive plant species is negatively related to water provision changes.

H7. Accounting for differences in effect trait values improves predictive ability of models when compared to those that only consider invasive species traits

1.1.3 Tropical forest degradation and recovery (Chapters 4,5 and 6)

11. What factors drive differences in residual stand damage following selective logging of tropical forests?

H1. Residual stand damage increases with logging intensity.
H2. Residual stand damage increases with logging intensity but begins to plateau at higher intensities
H3. Residual stand damage increases with logging intensity but when forests are logged using RIL they cause lower damage for a given intensity.
H4. Residual stand damage increases with non-linearly with logging intensity but when forests are logged using RIL they cause lower damage for a given intensity.

12. What factors drive the differences in biomass loss following selective logging?

H1. Biomass loss increases with logging intensity.
H2. Biomass loss increases with logging intensity but forests logged using RIL have a less steep slope than those of conventionally logged forests.

13. What factors drive changes in tree species richness following selective logging?

H0. Tree species richness change is not related to logging intensity or method.
H1. Tree species richness loss increases with logging intensity.
H2. Tree species loss increases with logging intensity but forests logged using RIL show a less steep slope.
H3. Tree species richness increases at low intensities and decreases at higher intensities.

14. After deforestation how long do carbon stocks and plant biodiversity take to recover in tropical forests?
15. Do carbon and plant biodiversity differ in their recovery rates?
16. Which areas are priorities for restoration of tropical carbon?

Which areas are priorities for restoration of tropical bird biodiversity?
Are these areas complementary or are there signs of a spatial trade-off?

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Chapter 2

2 Positive and negative effects of plant invasions on ecosystem services and interactions with native species loss: a meta-analysis

2.1 Abstract

There are fears invasive species may affect the provision of ecosystem services on which humans depend, in addition to negatively impacting native biodiversity. However, there has been little quantitative work on this topic. To estimate the general impacts of invasive plant species on ecosystem services I carried out a random effects meta-analysis of 199 studies to determine the general impact of invasive species on aboveground carbon storage, belowground carbon storage, carbon sequestration, water quality, and water provision. Both above and belowground carbon storage increased following invasions, while water quality and water provision were reduced. Carbon sequestration showed no consistent trend. Reductions in species richness were related to increases in aboveground carbon storage, but showed no relationships with belowground carbon storage and water quality. My analysis suggests that invasive plant species have broadly positive effects on carbon storage but negative effects on water provision and quality. This is suggestive of a trade-off between carbon and water provision, possibly as a result of increased evapotranspiration from plants with higher biomass. The increase in aboveground carbon storage with reductions of species richness is likely to be as a result of increasing dominance of invasive species which tend to have higher productivity. Interestingly this work is the first study to suggest such a relationship, going against much biodiversity ecosystem functioning research which suggests that opposite relationship is generally true. However, this relationship is likely to differ depending on the characteristics of the invasive and native species with woody invaders of grasslands likely to result in a negative species richness-carbon relationship and grassy invaders of woodland a positive relationship. This analysis suggests that invasive plant species can affect ecosystem services both positively and negatively. Thus, it is important that the potential negative impacts of any invasion are weighed against the potential benefits rather than assuming non-natives will cause environmental damage.

2.2 Introduction

Invasive species generally have a negative effect on native biodiversity by reducing local species richness (Vilà et al. 2011). Possibly as a result of changes to native communities invasions by plant species can also alter ecosystem processes and functions (Ehrenfeld 2003; Levine et al. 2003), such as primary productivity (Vilà et al. 2011), evapotranspiration (Cavaleri and Sack 2010) and nutrient cycling (Ehrenfeld 2003). Indeed, the effects of plant species invasions on ecosystem function are relatively well-studied and there have been a number of meta-analyses summarising these impacts (Morales and Traveset 2009; Cavaleri and Sack 2010; Vilà et al. 2011). These syntheses indicate that invasive plant species tend to increase ecosystem productivity (Vilà et al. 2011), have higher water use (Cavaleri and Sack 2010), and reduce pollination of native plants (Morales and Traveset 2009). Certain ecosystem functions underpin final ecosystem services, such as carbon storage and water provision, that provide benefits to humans and ultimately enable human well-being. Thus there is a fear that effects of non-native species on ecosystem functions may lead to reduced provision of ecosystem services (Pejchar and Mooney 2009; Vilà et al. 2009). Despite this fear there has been relatively little quantitative work assessing the effects of invasions on ecosystem services in general or how these interact with biodiversity losses.

It is common to frame impacts of non-natives in purely negative terms (e.g. Pyšek et al. 2012). Indeed, there has been a long and heated debate as to whether species introductions should always be perceived negatively (Shackelford et al. 2013), and such judgements are often subjective. To avoid this problem an ecosystem services framework is a useful – although not the only – approach to assessing the impact of invasions. This approach interprets ecosystem changes using objective criteria based on whether they increase or decrease the provision of particular services. Indeed, some invasive species may be beneficial to humans (Gozlan and Newton 2009; Schlaepfer et al. 2011). For example, invasive acacias in South Africa are used by many rural communities as a source of firewood (Pejchar and Mooney 2009) and there are numerous cases of invasive plant species increasing carbon storage (Dickie et al. 2011). Given that many invasive plant species have been introduced to countries specifically to enhance services such as timber production (Pimentel et al. 2005) and aesthetic appreciation (Hulme 2011), it is likely that some invasive species could have positive effects on ecosystem service provision. It is clear, however, that there are many cases in which invasive species negatively affect ecosystem services (Le Maitre et al. 2002; Le Maitre et al.

2011), such as the severe crop losses and human allergenicity caused by invasive ragweed *Ambrosia artemisiifolia* in Europe (Bullock 2012).

Though there are fears that alteration of ecological communities by non-native invasive plant species may change ecosystem function and service provision, these relationships are poorly understood (Levine et al. 2003; Strayer 2012). However, based on ecological theory drawn from biodiversity-ecosystem function studies it is possible to produce hypotheses regarding these relationships. Firstly invasive plant species often appear to reduce species richness (Vilà et al. 2011; but see Vellend et al. 2013). Given that community productivity tends to be positively related to increases in species richness (Cardinale et al. 2011; Cardinale et al. 2012) it is possible that reductions in richness as a result of invasions lead to reductions in productivity and alteration of services linked to the carbon cycle. However, one of the explanations for the positive species richness-productivity relationship is the ‘selection effect’ which states that communities with more species are more likely to contain highly productive species than species poor communities (Loreau and Hector 2001). Since many non-native invasive species appear to have greater productivity than native species (Vilà et al. 2011) it is possible that communities dominated by these species may have higher biomass than more diverse ecosystems prior to invasion. Since changes in biomass linked to alteration of carbon, nutrient and water cycles it is possible that changes in these are also correlated with alteration of species richness.

To provide an assessment of the impacts of plant invasions on ecosystem services and how this relates to changes in native plant communities I carried out a systematic review and meta-analysis of published studies on non-native plant invasions to answer the questions and hypotheses:

What effect do non-native plant invasions have on aboveground carbon storage, belowground carbon storage, carbon sequestration, water quality and water provision?

1. Non-native species invasions do not have a consistent effect on any of these ecosystem services.
2. Non-native plant invasions lead to increases in aboveground and belowground carbon, and carbon sequestration.
3. Water quality is reduced by non-native plant invasions.
4. Water provision is reduced by non-native plant invasions.

How do changes in plant species richness following invasion relate to changes in ecosystem services?

5. Changes in species richness as a result of non-native plant invasion are not related to changes in aboveground or belowground carbon storage or changes in water quality.
6. Reductions in species richness lead to increases in aboveground and belowground carbon storage and reduced water quality.
7. Reductions in species richness lead to reductions in aboveground and belowground carbon storage and increased water quality.

2.3 Materials and methods

2.3.1 Systematic review

I used a systematic review methodology to locate studies of the ecosystem impacts of invasive species following standard methodologies (Pullin and Stewart 2006). To do this I searched the online databases Web of Knowledge, Science Direct and Wiley-Blackwell as well as the internet search engine Google (last accessed 1/08/2011, see Table S1 for search terms). Following this, accounts of invasive plant species were examined at the Global Invasive Species database (www.issg.org/database) and the CABI Invasive species compendium (http://www.cabi.org/isc) and potentially relevant literature was noted. This search method ensured that both papers published in scientific journals and ‘grey’ literature were assessed. The reference lists of papers meeting the inclusion criteria (see below), as well as those of previous reviews (e.g. Liao et al. 2008; Cavaleri and Sack 2010; Vilà et al. 2011), were checked for additional relevant studies.

To qualify for inclusion in the meta-analysis studies had to fulfil three criteria. (i) The species studied were invasive, rather than solely non-native. As such species had to be described as non-native and invasive in the study, and/or the species was classified as invasive by the Global Invasive Species database or the CABI Invasive species compendium. (ii) Quantitative measurements were supplied of the effects of invasive plant species on ecosystem processes, functions or properties that could be considered as proxies for services (see below for more detail). (iii) Details were given of replicated measurements of ecosystem processes, functions or properties at one or more invaded site and a relevant un-invaded control. Any invaded sites which differed in management or anthropogenic disturbance from un-invaded sites were excluded since these differences could confound the effects of invasive species. Any sites that were subject to deliberate establishment of invasive species, such as plantations, were not considered since this represents a change in land use and management as well as in species composition.

2.3.2 Data extraction and analysis

For each included study the mean; standard error, standard deviation, or confidence interval; and sample size for relevant measures were extracted for invaded and un-invaded systems. Where data were presented in graphs they were extracted using the program datathief (Tummers 2006). I then used a similar methodology to previous studies (Balvanera et al. 2006; Rey Benayas et al. 2009) to relate the ecosystem properties, processes and functions measured in the selected studies to specific ecosystem services (Table 1). Those studies which had measures I considered not to be proxies for ecosystem services were excluded from further analyses. In doing this, I included only measures that were tightly related to the service and examined the context of each study to ensure the interpretation of the measure in terms of the specific service was relevant to that context. For example, while impacts of invasives on pollination has been the subject of several studies (Morales and Traveset 2009), almost all consider pollination of wild species, not of domesticated plants providing produce for human use; and so in the former cases I considered pollination not to be a proxy for an ecosystem service. Furthermore, several services were represented by too few studies to allow meaningful analysis – for example erosion control– and these were not considered further.

The following ecosystem service classes were well represented by measures in the literature, and these were used in the meta-analysis: aboveground carbon storage, belowground carbon storage, carbon sequestration, water provision and water quality (Table 1). To explore the connection between changes in plant communities and ecosystem services, data describing species richness in invaded and un-invaded ecosystems were also extracted, where available. The data were subsequently used to calculate the log response ratio of an ecosystem service measured in an invaded ecosystem compared to that in an un-invaded system, along with the standard error of the effect size (Borenstein et al. 2009). Some measures have a negative relationship with the ecosystem service – e.g. increased soil nutrient content leads to poorer water quality – while others have a positive relationship – e.g. more aboveground biomass indicates greater carbon storage. I therefore gave each response ratio a positive or negative sign to reflect the relationship of the measure to the service (Table 2).

When calculating mean effect sizes the true magnitude of differences between invaded and un-invaded ecosystems were presumed to differ between studies and thus a random effects model was used (Borenstein et al. 2009). The weight assigned to each study was the inverse of the within-study variance plus the between-studies variance, so more precise studies were more heavily weighted. If 95% confidence intervals for changes in an ecosystem service did not overlap zero, invasion was deemed to result in a statistically significant change. To test for heterogeneity of effect sizes in each meta-analysis the Q statistic was calculated, and where $p<0.05$, heterogeneity was considered to be greater than would be expected to occur at random.

Table 2 –Classification of ecosystem measures as proxies for ecosystem services based on previous similar assessments (Balvanera et al. 2006; Rey Benayas et al. 2009). The sign after each measure indicates whether it has a negative (-) or positive (+) relationship with the service

Ecosystem property, process or function	**Ecosystem service classification**
Aboveground biomass (+)	Aboveground carbon storage
Belowground biomass (+), soil carbon content (+), leaf litter mass (+)	Belowground carbon storage
Soil carbon sequestration (+), carbon sequestration in biomass (+)	Carbon sequestration
Soil nutrient content (nitrogen, nitrate, phosphorus, ammonia) (-), water nutrient content (-)	Water quality
Water table depth (-), soil moisture (+), evapotranspiration rate (-)	Water provision

Meta-regression was used to examine the relationship between proportional changes in plant species richness and those of individual ecosystem services. Meta-regression is a similar to regression but differs in that it is weighted by the inverse of study variances plus between study variance (Borenstein et al. 2009). This aims to characterise between study variance, but cannot account for all sources of variability as is the case in regression used in primary studies (Borenstein et al. 2009). To determine the fit of meta-regression models the R^2 analogue was calculated as:

$$R^2\ analogue = 1 - \left(\frac{T^2_{residual}}{T^2_{total}}\right)$$

where T^2_{total} is the total between study variance and $T^2_{residual}$ is the residual variance of the model after independent variables have been accounted for. All analyses were carried out in R 2.15.0 (R Development Core Team 2011) using the metafor package (Viechtbauer 2010). Following all analyses, effect sizes were back-transformed to present percentage change relative to un-invaded ecosystems.

2.4 Results

537 measurements of ecosystem function that could be related to ecosystem services were identified from 102 studies at 199 different sites, which included a range of ecosystem types. The ecosystems most commonly investigated were grassland, broadleaf woodland, coastal dunes and scrubland. (see Table S1). The majority of sites for which I extracted data were located in North America and Europe, with relatively few found in the Southern hemisphere or the tropics (Figure 3). The studies summarised the impact of 70 invasive plant species with a relatively equal representation of forbs, grasses, trees and shrubs.

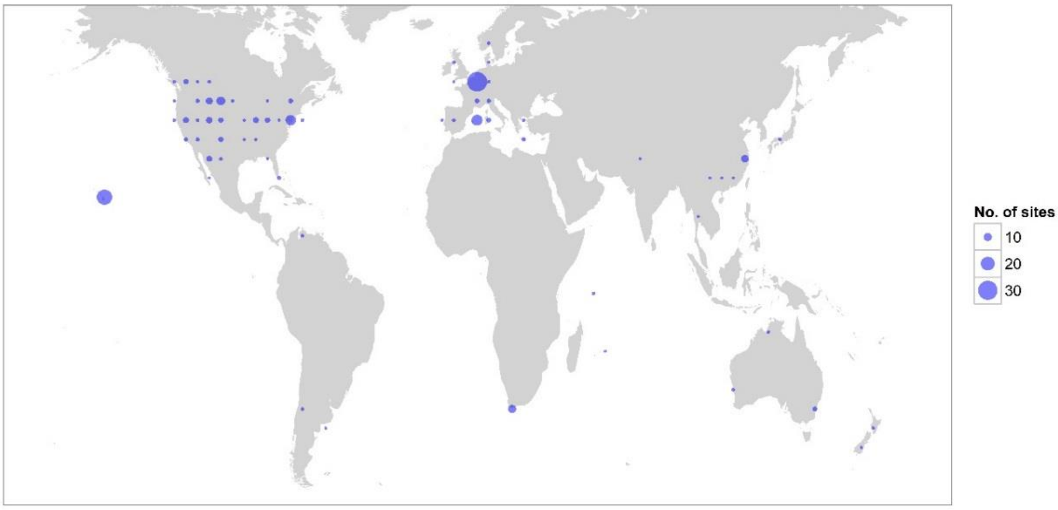

Figure 3 – Map of sites providing data for the meta-analysis. Sites are binned to a 4 by 4 decimal degree grid for ease of interpretation. Point size represents the number of sites in each 4 by 4 grid cell.

2.4.1 Effect of invasive plants on ecosystem services

Aboveground and belowground carbon storage were both significantly ($P<0.05$) higher in invaded sites, while water provision and water quality were lower (Figure 4). Carbon sequestration showed no effects of invasion. The largest change was in aboveground carbon storage, which was 41% higher in invaded sites, while belowground carbon storage was 13% higher. Proxies related to water provision were 28% lower and those related to water quality 12% lower in invaded sites. All variables showed significant heterogeneity in effect sizes ($p<0.001$), indicating that there was large variation in the magnitude of the effects of invasions among studies.

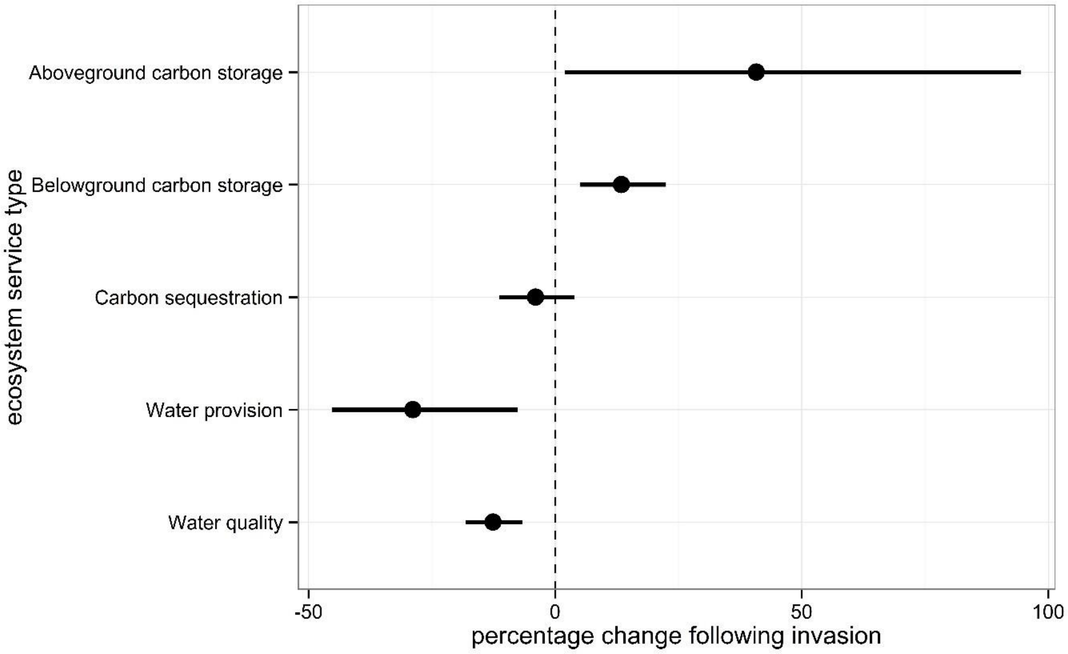

Figure 4 – Weighted mean effect of non-native plant species invasion on ecosystem services. Points represent weighted mean for each separate analysis and bars represent the 95% confidence intervals of these estimates.

2.4.2 Relationship between changes in species richness and ecosystem services

Not all studies had paired measurements of changes in species richness and ecosystem services, and so it was not possible to investigate relationships between changes in species richness and those of carbon sequestration and water provision. Differences in aboveground carbon storage were negatively related to differences in species richness between invaded and un-invaded sites ($P<0.05$, Figure 5) and this variable explained approximately 22% of between-study variation. Although this model showed a reasonable fit there was still a large amount of variation among studies in the effects of invasions once the effect of changes in species richness were accounted for ($Q=3983$, df=24, $P<0.001$). However, changes in belowground carbon or water quality were not correlated with changes in species richness (Figure 5, $P>0.05$).

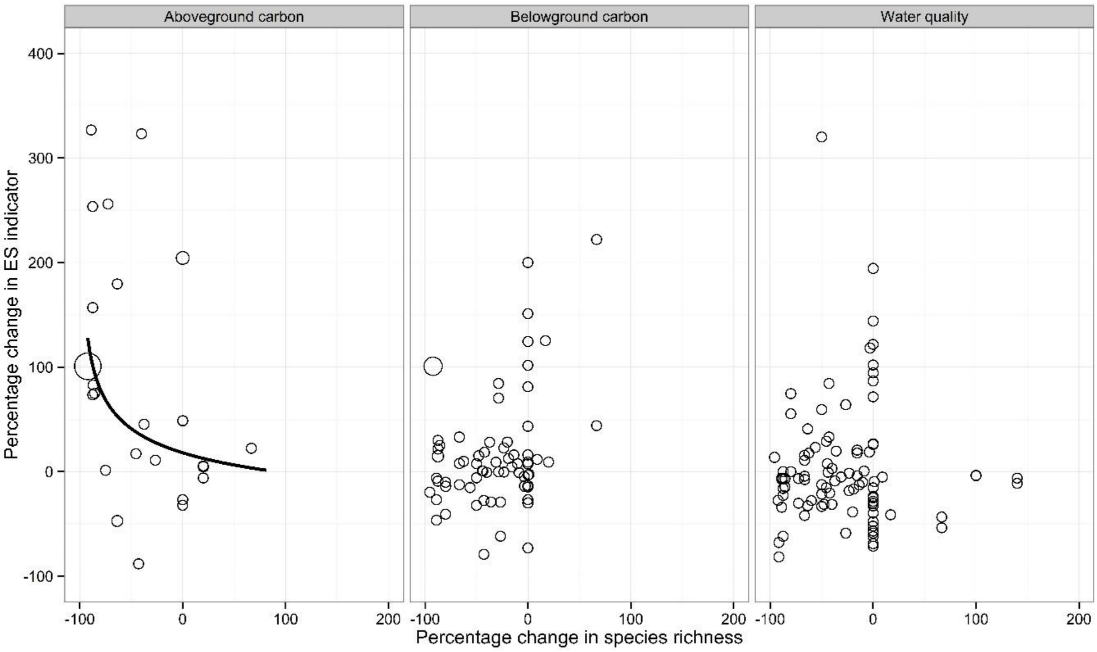

Figure 5 – Relationship between changes in species richness and those in ecosystem services. Solid line represents predictions where percentage change had a significant effect (P<0.05) effect on an ecosystem service. Note: neither belowground carbon storage or water quality showed any relationship to changes in species richness.

2.5 Discussion

My meta-analysis indicates that ecosystems around the world invaded by non-native plant species tend to exhibit improvements in some ecosystem services (higher above- and below-ground carbon storage), but deterioration in others (reduced water provision and quality) compared to paired un-invaded sites. The rate of carbon sequestration showed no consistent trend. Thus apart from the null hypothesis hypotheses 2-4 were well supported. Counter to hypotheses 5 and 7 predicted positive relationships between changes in species richness and ecosystem services, I found a negative relationship for changes in above-ground carbon and no relationship for changes in belowground carbon or water provision. As such hypothesis 6 had mixed support.

2.5.1 Effects of invasive plant species on ecosystem services

My finding that invaded ecosystems tend to have increased carbon storage both above- and below-ground is supported by the findings of previous meta-analyses of ecosystem functioning. Both Liao et al. (2008) and Vila et al (2011) indicated increases in productivity (133% and 56% respectively) following invasion. As such, the estimate of a 41% increase in aboveground carbon storage is likely to be as a result of invasive plant species having higher primary productivity. Similarly, the finding that belowground carbon pools increase by 13% are likely to be driven by the same phenomenon with increases in aboveground biomass leading to greater root biomass and increases in carbon inputs to the soil. Two mechanisms in particular may lead to general increases in carbon storage following non-native plant invasion. Firstly, non-native plant species may be able to compete more effectively for resources outside of their native range because of a lack of natural enemies (Keane and Crawley 2002). Secondly, successful invaders may possess traits, such as rapid relative growth rate, which allow local dominance (Firn et al. 2011).

The impacts of individual invasive plant species on water provision are well known, with particularly high-profile examples in the US Midwest and South Africa (Di Tomaso 1998; Le Maitre et al. 2011). The finding of decreased water provision in invaded systems is supported by Cavaleri and Sack (2010), who found that invasive species tend to have higher evapotranspiration rates than the native plants. Indeed, changes in water provision may be driven by invasive species having greater biomass, and therefore consuming more water, than co-occurring natives (Cavaleri and Sack 2010). This mechanism suggests a potential trade-off between carbon storage and provision of water as a result of invasions. This trade-off has been observed previously following establishment of plantations resulting in an increase in carbon storage, but reduced stream flow (Jackson et al. 2005). The meta-analysis suggests that this relationship may be widespread.

The negative impact of plant invasions on water quality is likely to be a result of increases in soil nutrient concentrations. Previous studies have regularly noted these increases and they are thought in part to relate to increases in carbon pools and consequent increases in carbohydrate availability to the microbial community (Ehrenfeld 2003). Thus increases in carbon stocks may be related to decreases in water quality. However, my results should be interpreted with some caution as very few studies in this meta-analysis measured changes in water quality directly, with the majority measuring changes in soil nutrients in wetland or riparian areas from which I inferred changes in water quality.

2.5.2 Relationships between changes in species richness and ecosystem services

Many species richness-productivity studies have suggested that increases in richness lead to higher community biomass, probably because communities become more likely to contain individual species with higher productivity and/or resources are more efficiently partitioned between species (Hooper et al. 2005). In the case of non-native plant invasions, this relationship appears to be reversed. My meta-analysis suggests that when invasive non-native plant species reduce plant species richness, aboveground biomass – and thus carbon – tends to increase. This study is the first to indicate such an empirical relationship between changes in plant communities and ecosystem services following invasion. I propose that the primary process driving this relationship is the ability of non-native invasive species to achieve higher productivity than native plants (Liao et al. 2008), which leads to increased dominance and a resulting loss of native species (Hillebrand et al. 2008). This supports the view that species identity (i.e. the presence of competitive non-natives with high growth rates) is more important than species richness per se in driving ecosystem functions and services in the case of non-native species invasion (Hooper et al. 2012).

Though my study indicated a negative relationship between changes in species richness and aboveground carbon storage this may be dependent upon the type of ecosystem invaded and the traits of the invasive species. For example when the functional traits of an invasive species differ markedly from those of those of native species its effects on biodiversity and ecosystem functions is hypothesised to be more dramatic than when they are similar (Ricciardi and Atkinson 2004; Ricciardi et al. 2013). As such though there are logical reasons why the negative relationship I observed in my study is likely to be generally true a mechanistic understanding of this relationship may require the characteristics of both invader and native species and ecosystems to be accounted for. For example some studies used for this chapter showed both a reduction in species richness and a loss of aboveground carbon storage (Figure 5). In these cases it is likely that a species that stored large amounts of carbon was outcompeted by smaller invasive species. As such the shape of the species richness-carbon storage relationship may depend on the characteristics of the invasive species. Thus woody invasions of open habitats may result in a negative relationship, as has been seen in some studies (Dickie et al. 2011), with grass invasions of woodlands showing the opposite relationship.

It has previously been suggested that species richness affects a wide variety of ecosystem services (Isbell et al. 2011). However, apart from the negative correlation between changes in richness and aboveground carbon, I found no relationship with changes in belowground carbon or water quality. I hypothesise that this is because the impact of invasive plant species on these ecosystem services is more variable than the effects on above-ground carbon storage. As such, the extent of changes in these ecosystem services may depend to a much greater extent on the identity of the invasive species, rather than purely its abundance or effect on the plant community. Thus the impacts of invasive species are likely to be better predicted by analyses using the traits or characteristics of both invasive and native dominant species.

The negative relationship between changes in aboveground carbon storage and those in species richness suggests that trade-offs between achieving goals of maximising carbon storage and conservation value in the context of non-native invasions may be more widespread than previously thought. If conservation managers intend to maximise plant species richness by controlling invasives, this may be at the cost of carbon storage. This conflict between the two goals - as has happened in New Zealand (Dickie et al. 2011) – is likely to occur throughout the globe, particularly when grass or shrublands are invaded by woody non-natives (Pejchar and Mooney 2009; Eldridge et al. 2011). Management of such situations will require careful consideration about which goal is a greater priority.

2.5.3 Caveats in analysing invasion studies

One of the biggest problems in any meta-analysis of invasive species is determining how representative the sites studied are of all sites affected by invasive species. To assess this it is necessary to understand geographic patterns in invasions, the type of ecosystems likely to be affected and the taxonomy and traits of the invasive species. Both Europe and North America appear to have high numbers of invasive species, but this is possibly due to relatively high recorder effort. Similarly there is little understanding of the types of ecosystem likely to be affected or the species that are likely to be invasive (Hulme et al. 2013).

In addition my meta-analysis inherently incorporated the assumptions of the primary studies. One such assumption is that the differences between uninvaded and invaded ecosystems were driven primarily by the invasive species. I excluded studies with obvious differences in land-use history between the paired sites, but there may have been subtle differences not noted by the researchers in the included studies. Indeed, MacDougall and Turkington (2005) suggested that invasive species may be the consequence as well as the cause of changes in ecosystems. While I have suggested mechanisms by which invasions may have led to the general impacts I found on ecosystem services, experiments will allow a better understanding of the processes involved.

The negative relationship between species richness and aboveground carbon storage I observed in this study is the result of comparing between studies but I caution against presuming there is necessarily a similar relationship within a given landscape. To my knowledge no study has attempted to link changes in ecosystem services and species richness at this scale. This is probably because the invasive species literature has traditionally focussed on comparisons between heavily invaded and un-invaded ecosystems, ignoring the transition between these two states. This must change if we wish to link changes in ecological communities to changes in ecosystem services. The use of environmental gradients in ecology has provided many valuable insights (Körner 2007; Kreyling et al. 2014) and I suggest that more studies of invasive plant species would benefit from viewing invasion in a similar manner.

2.6 Conclusions

It is clear from this study that invasive plant species can affect ecosystem services both positively and negatively. Thus, it is important that the potential benefits of any invasion are weighed alongside the potential negative impacts rather than assuming non-natives will cause environmental damage. I hypothesise that differing effects on the services I was able to study may be the result of fundamental trade-offs during invasions. Thus, invasive species grow faster and utilise resources more efficiently than co-occurring natives, which leads to increased carbon storage. The faster growth leads to higher water use and so decreased water provisioning, and increased soil carbon affects nutrient dynamics leading to decreased water quality. It also appears likely that there are trade-offs between carbon storage and species richness, which may have implications for conservation management. It must be noted that this meta-analysis is subject to caveats, including possible biases in which locations and species have been studied (Pyšek et al. 2008; Hulme et al. 2013) so it is not yet possible to generalize with confidence about the impacts of invasive species or possible trade-offs.

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Chapter 3

3 Can the impact of invasive plant species on ecosystem services be predicted using species and ecosystem characteristics?

3.1 Abstract

It has been a long-held goal of invasion biology to be able to predict which species are most likely to become invasive. Though there has been progress on this over the last two decades, invasiveness of plant species appears to have little to do with their ecological impacts, suggesting a need to identify correlates of this separately. To identify such correlates I used characteristics and traits of invasive and native plant species (woodiness, plant height and root depth) to predict post-invasion changes in ecosystem services. This analysis showed that invasive plant height predicts changes in aboveground carbon and water quality well but that other ecosystem service changes are poorly predicted. Rather than being suggestive of a lack of effects of traits on changes in ecosystem services this result is likely to reflect the need for greater detail on traits from uninvaded communities. However, given that prediction of impact prior to invasion is the ultimate aim of invasion biology methods that maximise the usefulness of currently available trait data, such as by phylogenetic imputation, may aid in this.

3.2 Introduction

Mechanistic models of community assembly state that in order for a species to become established in a location it must first pass through a number of environmental filters (Belyea and Lancaster 1999). Firstly, a species must have the ability to reach a site via dispersal and then overcome abiotic filters, such as climate or soil type, and biotic filters such as competition with other species (Belyea and Lancaster 1999; Lebrija-Trejos et al. 2010). The response traits of species, such as those relating to fecundity, regeneration and dispersal, determine their response to environmental pressures and thus their ability to overcome these filters (Suding et al. 2008). Following establishment the effect traits of plant species, such as leaf nutrient content or leaf toughness, are thought to determine ecosystem functioning (Lavorel and Garnier 2002). The theory surrounding community assembly has informed much of the work in invasion biology, one of the major goals of which is determining the traits and characteristics of non-native plant species that enable them to overcome environmental and biotic filters in order to become invasive (Van Kleunen et al. 2010).

Previous studies of invasive plants have suggested that response traits can be used to predict the likelihood of a species becoming invasive, with species that produce large numbers of easily transportable seeds likely to be those that are transported to areas outside of their native range (Lockwood et al. 2005). Following arrival of propagules in new locations, species that show either high phenotypic plasticity (Richards et al. 2006) or rapid evolution (Buswell et al. 2011) appear to establish more successfully. Such studies have helped to determine which species are more likely to become invasive and are now being used to aid risk assessments (Keller et al. 2007), though the usefulness of such assessment is strongly debated (Thompson and Davis 2011; van Kleunen et al. 2011). In addition to predicting which species will become invasive in the future another major aim of invasion biology is predicting the impact of invasive species once they colonise new areas (Ricciardi et al. 2013). However, the invasiveness of a species seems to be largely independent of its ecological impact (Ricciardi and Cohen 2007), implying a lack of linkage in response and effect traits as previously suggested by Suding et al. (2008). Given this there is a need for analyses to identify correlates of invasive species impact.

Following establishment, the impacts of invasive species on communities are largely thought to be driven by their ability to compete against other species for resources (Van Kleunen et al. 2010). Factors that increase the competitive ability of invasive species are hypothesised to include: (i) different resource use to native species (Vitousek 1996); (ii) a lack of natural enemies from their native range (Pimm 1987); (iii) release of novel defensive chemicals (Bais et al. 2003); and (iv) differences in effect traits between native and non-native species (Van Kleunen et al. 2010; see Ricciardi et al. 2013 for a review of current hypotheses). This increased competitive ability of invasive species can lead to reduction in native species population size, resulting in the simultaneous addition and removal of species traits (Wardle et al. 2011). These shifts in the traits present in a community may alter species interactions and thus ecosystem function and ultimately ecosystem services (Lavorel and Garnier 2002; Díaz et al. 2007).

Despite the perceived importance of attempts to generalise about mechanisms by which the impact of invasive species are governed, studies addressing the topic are rare. A recent analysis by Pyšek et al. (2012) attempted to determine characteristics of invasive species that governed impacts of invasions on biodiversity and ecosystem function. While this work was a welcome addition to the debate on the mechanisms underlying invasive species impacts it had two major limitations. Firstly, the work used statistical significance of individual studies as a measure of impact. This not only assumes that the direction of change of a variable caused by an invasive species is unimportant, it is also statistically invalid showing similarities to the widely discredited ‘vote-counting’ approach, which meta-analysis has attempted to eliminate (Koricheva et al. 2013). Secondly, the study lacked hypotheses and apparently fitted approximately 40 parameters for each statistical test. Such overfitting of models increases the likelihood of achieving a false positive. Exploratory analyses of this subject are unwarranted given that there are a wide range of hypotheses regarding the impact of non-native invasive species (Ricciardi et al. 2013) and the impact of plant community change in other contexts (Díaz et al. 2007; Suding et al. 2008).

The flaws in the study of Pyšek et al. (2012) mean that we currently have little idea about how the characteristics of invasive species influence their impacts, or how this interacts with features of native ecosystems. However, much work has been done outside of the field of invasion biology investigating the relationship between species characteristics or effect traits and ecosystem function or ecosystem services (Díaz et al. 2007). The basis for much work on links between ecosystem traits and function, the mass ratio hypothesis, states that the most abundant species are those that determine ecosystem function (Grime 1998). Given that invasive species can often become dominant in ecosystems this hypothesis may have particular relevance in this context. One of the recurrent hypotheses in invasion biology is that species that have ‘novel’ characteristics or differ in their traits from native species are likely to be those that have strongest impacts on ecosystems (Levine et al. 2003; Ricciardi and Atkinson 2004), and similar views have been expressed by people using functional traits to predict ecosystem function change in other contexts (Lavorel and Garnier 2002). These hypotheses suggest that species identity is more important in determining changes in ecosystem function than changes in species richness. This suggests that the ‘selection effect’ hypothesis, which states that more species rich communities have higher productivity and resource use, may not be relevant for all types of biodiversity change. Indeed in the case of invasive species it appears likely that because invasive species often show higher productivity than native species (Vilà et al. 2011) that species poor invaded ecosystems have higher carbon storage than uninvaded, more species rich ecosystems (Chapter 2). In this chapter I aim to test the hypothesis that invasive species which differ in their characteristics from native species are those that have strongest effects on ecosystem services.

Studies have indicated the importance of effect traits in governing decomposition (Cornwell et al. 2008), soil properties (Garnier et al. 2007; Grigulis et al. 2013) and water cycles (Gross et al. 2008) in a number of contexts. In particular this work has pointed to the potential role of plant height in governing carbon, nutrient and water cycling as it is strongly related to productivity (Diaz et al. 2004), increases in which may in-turn increase soil nutrient content (Ehrenfeld 2003) and water use (Jackson et al. 2005). In addition there is evidence that root depth of species determines soil moisture and water provision (Eviner 2004; Gross et al. 2008). Thus, there is evidence to suggest that both plant height and root depth may prove useful in predicting the impacts of community change on ecosystem functions and services.

While invasive species' effect traits may be related to post-invasion changes in ecosystem services, it is probable that these changes are dependent upon the traits of species in a recipient ecosystem (Wardle et al. 2011). The native species traits determine ecosystem service provision prior to invasion and as such changes in mean community trait values are likely to be driven by difference between invasive species and other species in the community. As such when the traits of an invasive species differ markedly from the traits of species in an uninvaded system the impact of invasion is likely to be large (Ricciardi et al. 2013). Thus accounting for the difference in the trait values between invaders and native species should enable a better prediction of ecosystem service impacts than merely considering invasive traits in isolation.

However, effect trait values for species are not always available (Swenson 2014) and so characteristics such as species woodiness can be used as an alternative (Castro-Díez et al. 2014). Though these classifications are not strictly functional traits they can be used as proxies where no other measurements are available. For example woody species tend to have greater leaf area, seed mass and height than non-woody species, while non-woody species tend to have thicker, tougher leaves (Diaz et al. 2004). Increases in the abundance of woody species appears likely to increase above and belowground carbon, while potentially reducing water availability, and thinner leaves may increase the speed at which nutrients can be transferred to soils (Díaz et al. 2007; Castro-Díez et al. 2014). As such invasive species which are woody or non-woody are likely to differ in how they alter ecosystem function and service provision and this may depend upon the woodiness of native species in the recipient ecosystems. However, greater detail on native ecosystem types may also aid in determining more nuanced effects of invaders by providing a more precise proxy of the trait values of native species prior to invasion.

Given the current lack of knowledge surrounding the mechanisms of invasive plant species impacts on native ecosystems and their services, use of these traits as a first step in predicting impact seems rational. Thus, in this study I use mean trait values for both dominant native and invasive species from the TRY global plant traits database (Kattge et al. 2011) along with the woodiness of native and non-native species, and ecosystem classification to test the following hypotheses:

Impacts of invasive and non-native woodiness on ecosystem services

1. Where invasions involve transition from woody to non-woody dominant species

change in aboveground and belowground carbon storage, water provision and water quality will be more pronounced than where invasion is by a species of similar woodiness.

2. Where there is invasion by a species with similar woodiness there will be no change in ecosystem service provision
3. Where there is invasion by a species with similar woodiness some ecosystem service provision will be altered
4. Inclusion of detail on native ecosystem type along with that of invader woodiness result in a more parsimonious model.

Effect trait impacts on ecosystem services

5. Invasive plant height is positively related to change in aboveground carbon storage and belowground carbon storage, and negatively related to water provision and water quality.
6. Root depth of invasive plant species is negatively related to water provision changes.
7. Accounting for differences in effect trait values improves predictive ability of models when compared to those that only consider invasive species traits

3.3 Methods

Data on the impacts of non-native plant invasions on ecosystem services were taken from the systematic review conducted in Chapter 2. Along with this I recorded data on woodiness of invasive and native species for use in analyses of impacts. Almost all studies contained sufficient data on species woodiness resulting in 454 datapoints that could be used in analyses (36 aboveground carbon storage, 108 belowground carbon storage, 20 carbon sequestration, 39 water provision, 251 water quality). To test hypotheses 1, 2, 3 and 4 I performed sub-group meta-analyses for each ecosystem service of interest. For these analyses the effect of invasive and dominant native species woodiness and the interaction term between these was tested along with all possible additive models. Alongside this models containing ecosystem type (wetland, grassland, forest, mixed – where more than one type of ecosystem was investigated in a study, and open – consisting of coastal dune and desert) were also tested. Model selection was undertaken using an information theoretic approach (Anderson et al. 2000) which is detailed below.

I also collated data on relevant traits of invasive and native plant species from the TRY global database of plant traits (Kattge et al. 2011). This database is a collation of over 3 million trait values for more than 69,000 plant species, and is the most comprehensive database of its type (Kattge et al. 2011). I used the R package taxonstand (Cayuela et al.

2012), which matches species names to The Plant List - a standardised taxonomy for all known plant species (see http://www.theplantlist.org/ for more details). This ensured taxonomic consistency between databases. I subsequently modified trait data to ensure consistent units of measurement (e.g. conversion from inches to cm). Where more than one trait measurement for a species was available I calculated the mean. These data were then linked to data from Chapter 2 so that each species at each site was assigned the appropriate trait value where it was available. This resulted in a dataset with a total of 314 assessments of ecosystem service changes at paired invaded and uninvaded sites for which invasive trait values were available and 98 paired sites for which measures of both invasive and native traits were available. This represented approximately 60% and 20% of the dataset used in Chapter 2 respectively (for site locations see Figure 6). Although there is some evidence of within species trait plasticity (Richards et al. 2006; Funk 2008), for the purposes of this work I assumed that traits did not vary within a species, as other analyses using trait databases have done (Cornwell et al. 2008).

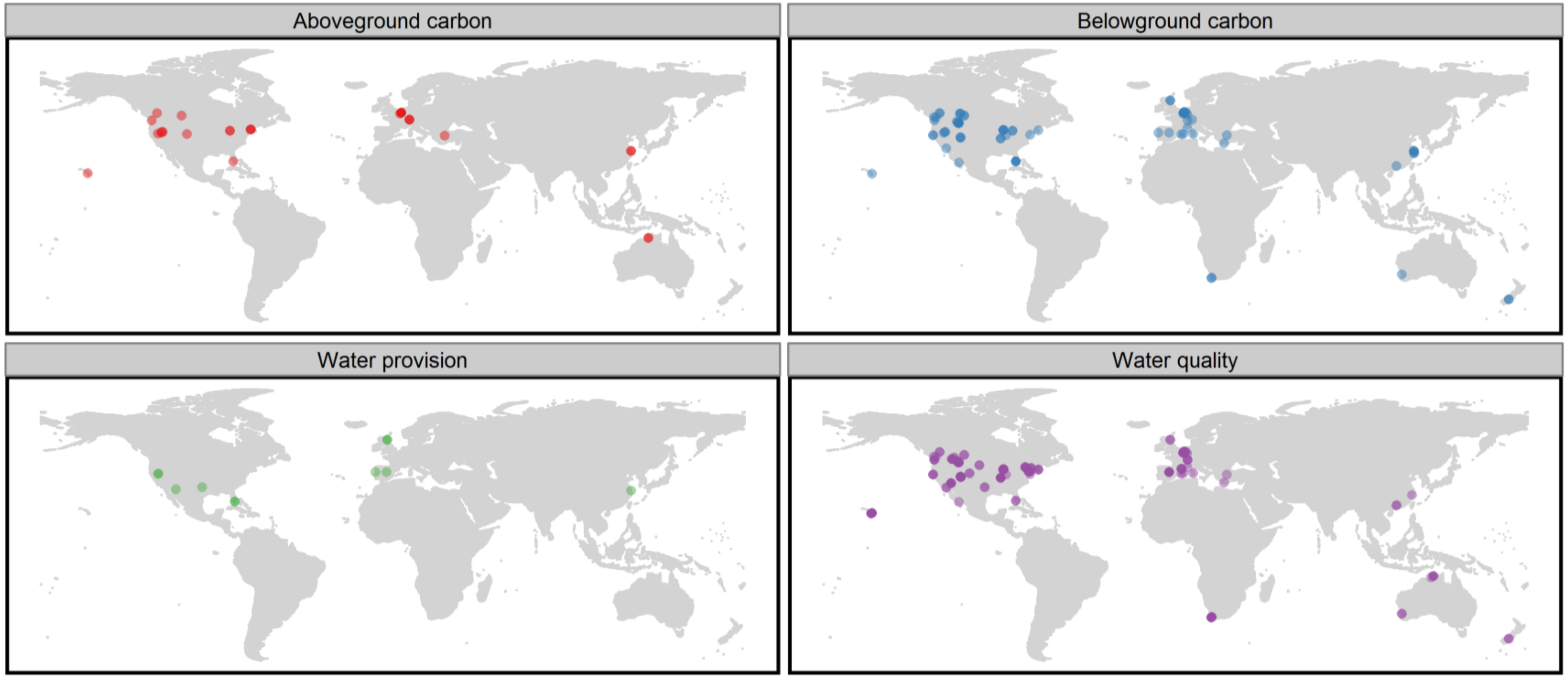

Figure 6 – Location of studies used for analysis of each ecosystem service that had invasive plant species for which traits were available in the TRY database (Kattge et al. 2011

To test the influence of these traits on aboveground carbon, belowground carbon, water provision and water quality I performed a meta-regression analyses in two stages. First I did meta-regressions using just invasive species traits to determine the relationship between these traits and the ecosystem services in question. Secondly, for the sub-set of studies that had data on both the invasive and native species traits I re-ran analyses to investigate changes as a function of invasive species traits and as a function of the log response ratio (Hedges et al. 1999) of differences between native and invasive species traits. For water provision the TRY database did not contain enough data on plant height or root depth values for native species and so I did only the first step of analysis. In all cases I also computed a null model. Evidence supporting each hypothesis was assessed by examining the AICc of each model and its difference from the most parsimonious model (termed ∆AICc - Anderson et al. 2000; Burnham et al. 2011). When models had a ∆AICc >7 they were considered to have little support (Burnham et al. 2011). All analyses were undertaken in R version 3.0.2 with meta-regression performed using the metafor package (Viechtbauer 2010) and all figures were produced using ggplot2 (Wickham 2009).

3.4 Results

3.4.1 Using woodiness and ecosystem type to predict impact

The most parsimonious model for the impacts of invasive species on aboveground carbon storage was a model that included terms for both non-native invasive woodiness and native species woodiness. Invasion by woody species in ecosystems with non-woody dominant species experienced a very large increase in aboveground carbon storage that averaged 1219%, while invasions by non-woody species to systems dominated by woody species saw a drop of 70% (Figure 7). Where woodiness of invasive and native dominants did not differ there was an increase in aboveground carbon storage with 41% and 189% increases for woody and non-woody invasive and native species respectively (Figure 7). This model also showed good explanatory value with an R^2 of 0.54. The model including invasive woodiness and ecosystem type was poorly supported with a ΔAICc=9.58 when compared to the most parsimonious model.

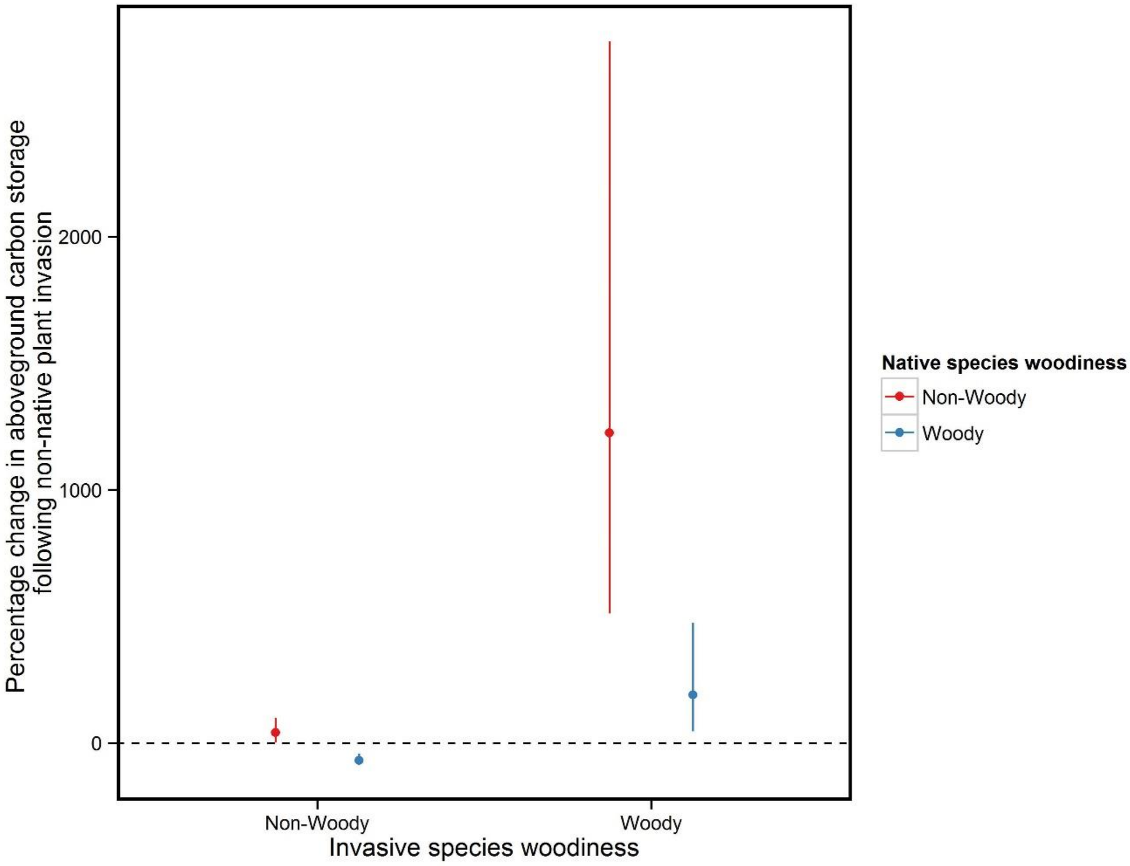

Figure 7 - Changes in aboveground carbon storage following woody or non-woody invasion in systems dominated by woody or non-woody species native species (n=36). Red points represent when the dominant native species prior to invasion was non-woody and blue when the dominant native species was woody. Bars represent 95% confidence intervals for model. Dashed line represents zero difference between invaded and uninvaded systems. R^2 of model was 0.54.

The model that best explained changes in belowground carbon storage suggested that changes were driven by whether invasive species were woody, but not by whether native species were woody or not. This model suggested that woody invaders increase belowground carbon storage by 38% while non-woody invaders cause increases of 18% but the confidence intervals for these two groups overlapped meaning that despite being the most parsimonious model the two groups could showed no statistically significant differences. The model explanatory value was low with a R^2 of 0.05. As with aboveground carbon storage the model including species woodiness and ecosystem type was relatively poorly supported with a ΔAICc=3.99 when compared to the most parsimonious model. When looking at models explaining carbon sequestration and water provision the null intercept only models were considered to be the most parsimonious with all other models having a ΔAICc>4.

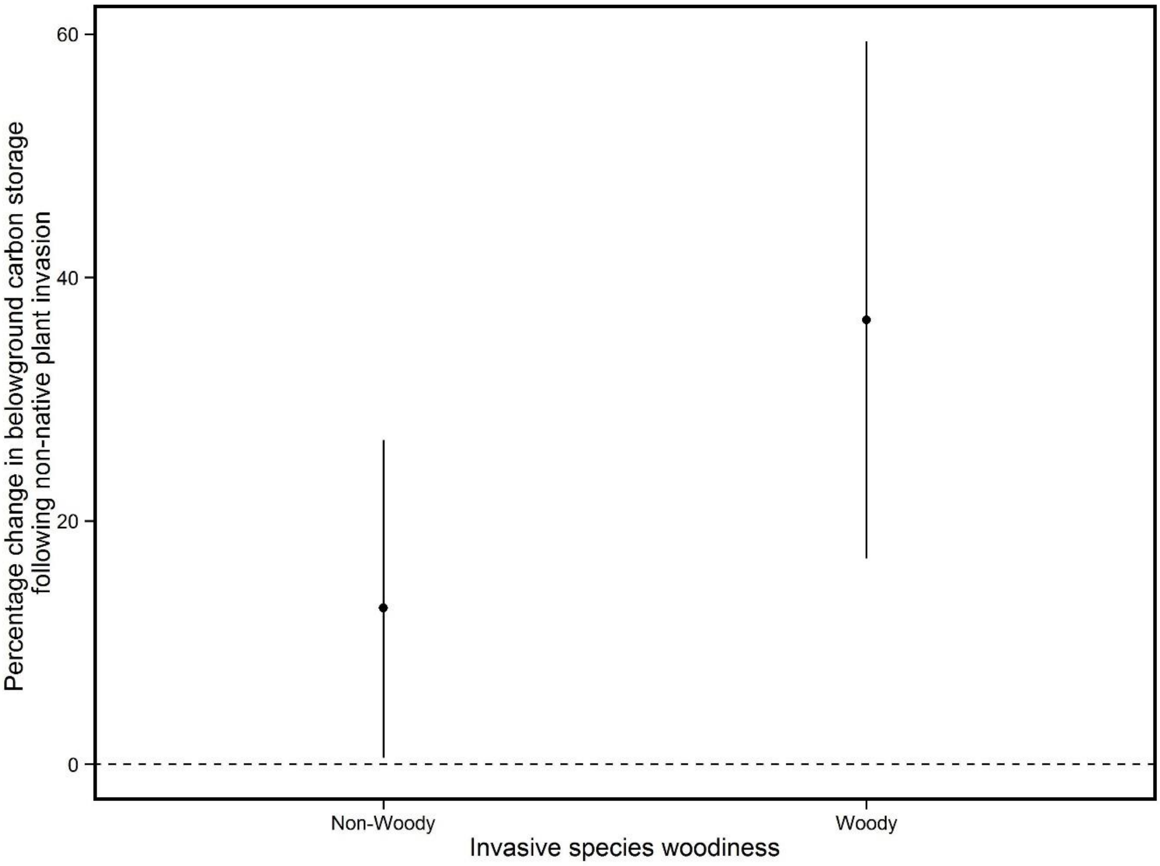

Figure 8 – Changes in belowground carbon storage as a result of invasion by non-woody or woody non-native species (n=108). Bars represent 95% confidence intervals for model. Dashed line represents zero difference between invaded and uninvaded systems. R^2 of model was 0.05.

Regarding changes in water quality a model including interaction terms between invasive species and native species woodiness was the most parsimonious. However, this model had relatively little explanatory power with an R^2 of 0.06. This model suggested woody invaders in systems with woody dominant species resulted in greater decreases in water quality than other transitions, but these differences were not statistically significant (Figure 9). In ecosystems dominated by non-woody native species there was little difference in the effect of woody or non-woody invasive species on water quality (Figure 9). Again inclusion of a term describing ecosystem type did not result in a more parsimonious model, with this model having a ΔAICc of 7.25.

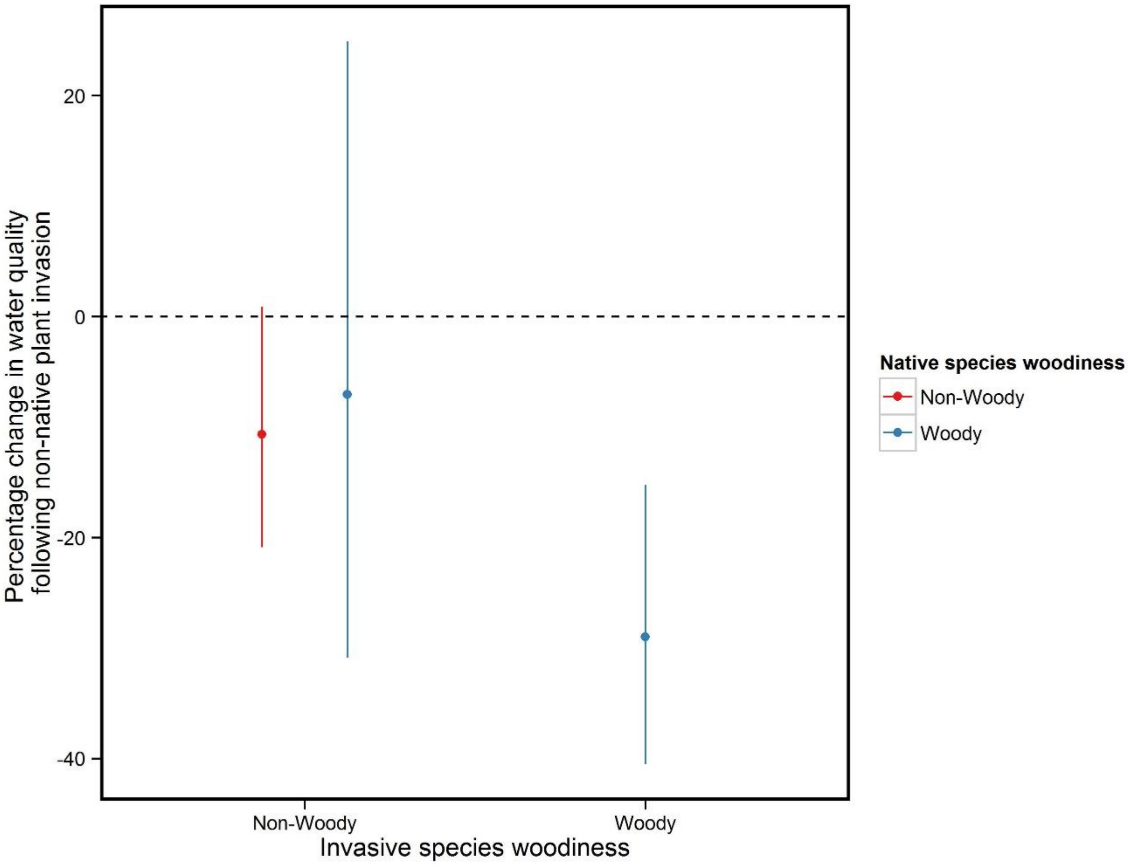

Figure 9 – Changes in water quality following non-native plant invasion by non-woody or woody non-native species, in ecosystems previously dominated by woody or non-woody species. Bars represent 95% confidence intervals for model. Dashed line represents zero difference between invaded and uninvaded systems. R^2 of model was 0.06.

3.4.2 Using invasive species traits to predict impact

Invasive species height was a good predictor of change in aboveground carbon storage following invasion (R^2=0.32). This model suggested a positive relationship between invasive plant height and changes in aboveground carbon storage (Figure 10). The model had much stronger support than the null model, which had a ΔAICc=9.76 (Appendix I – Table A2). Plant height was a poor predictor of changes in belowground carbon storage, with the null model having greater support (Appendix I – Table A3). However, plant height was a good predictor of changes in water quality (R^2=0.33) and was much better supported than the null model which had a ΔAICc=8.84 (Appendix I– Table A6). The model predicted a positive relationship between invasive species height and water quality, with greatest confidence in predictions for invasive species of <5m in height, which represented the majority of the data (Figure 11).

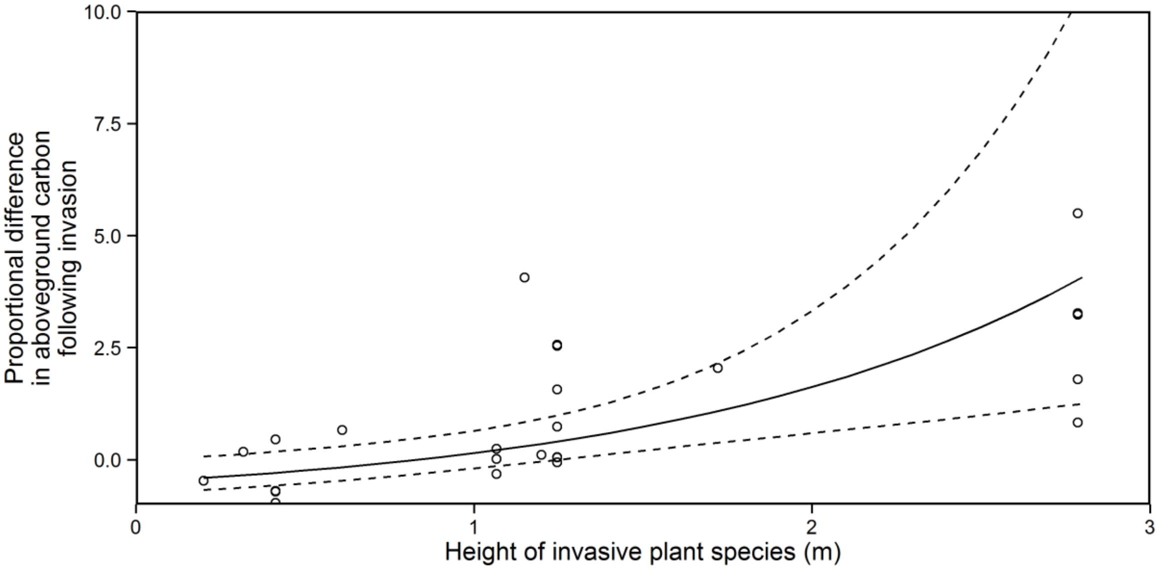

Figure 10 – Relationship between changes in aboveground carbon storage and the height of invasive non-native plant species (n=26). The solid line represents the predictions of the model with lowest AICc and the dashed lines are the 95% confidence intervals of this prediction.

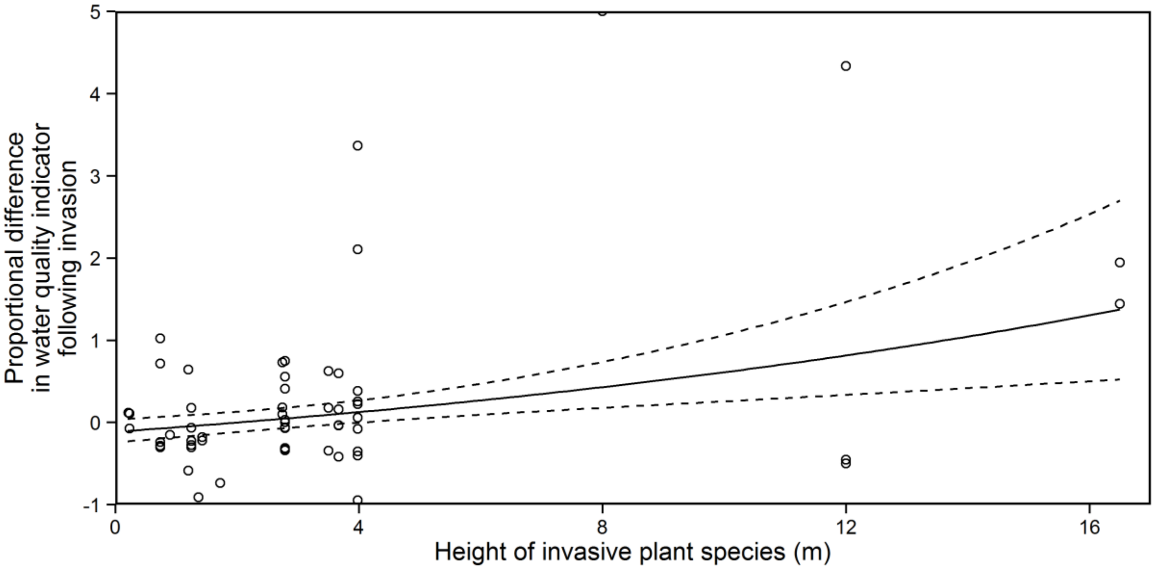

Figure 11 - Relationship between changes in water quality indicator and the height of invasive non-native plant species (n=76). The solid line represents the predictions

of the model with lowest AICc and the dashed lines are the 95% confidence intervals of this prediction.

Though plots of the relationship between invasive species height and change in water provision were suggestive of a negative relationship between invasive species height and water provision (Figure 12), the null model was more highly supported (Appendix I - Table A4), possibly as a result of small sample size (n=10). In addition an influence of root depth on water provision was poorly supported (Appendix I - Table A5).

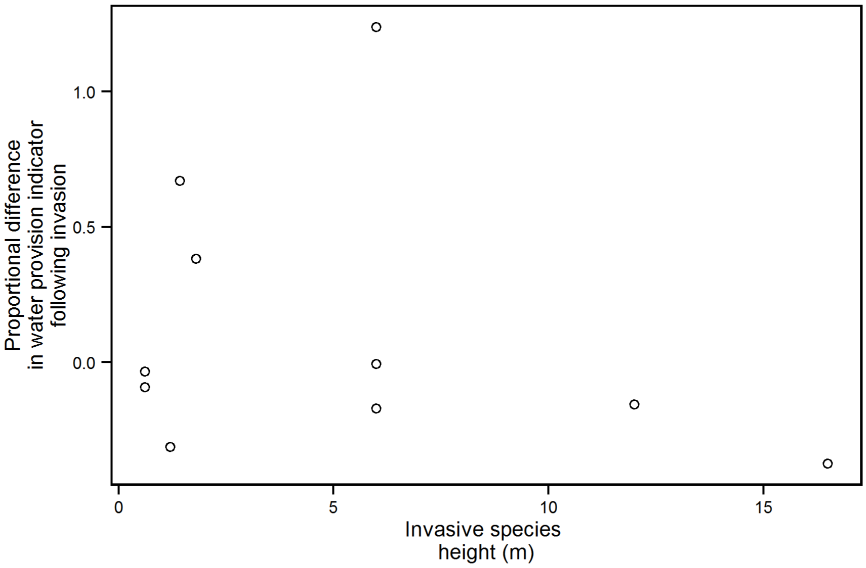

Figure 12 – Changes in water provision plotted against the height of invasive non-native plants (n=10).

3.4.3 Predictive ability of trait differences between invasive and native species

The hypothesis that including differences between native and non-native species' traits improved model parsimony compared to including only invasive species traits had mixed support. Only the model of belowground carbon storage indicated improved parsimony while aboveground carbon storage and water quality did not (Appendix I - Tables A7-A9). Proportional change in belowground carbon appeared to show a slight negative relationship with the proportional difference in height between invasive and native species (Figure 10). This model had relatively weak explanatory power (R^2=0.11) and had only slightly greater support than the null model (AICc 28.01 and 28.04 respectively). In the case of aboveground carbon storage invasive species height was a better predictor (Appendix – Table 6) and for water quality the null model had greatest support (Appendix – Table 8).

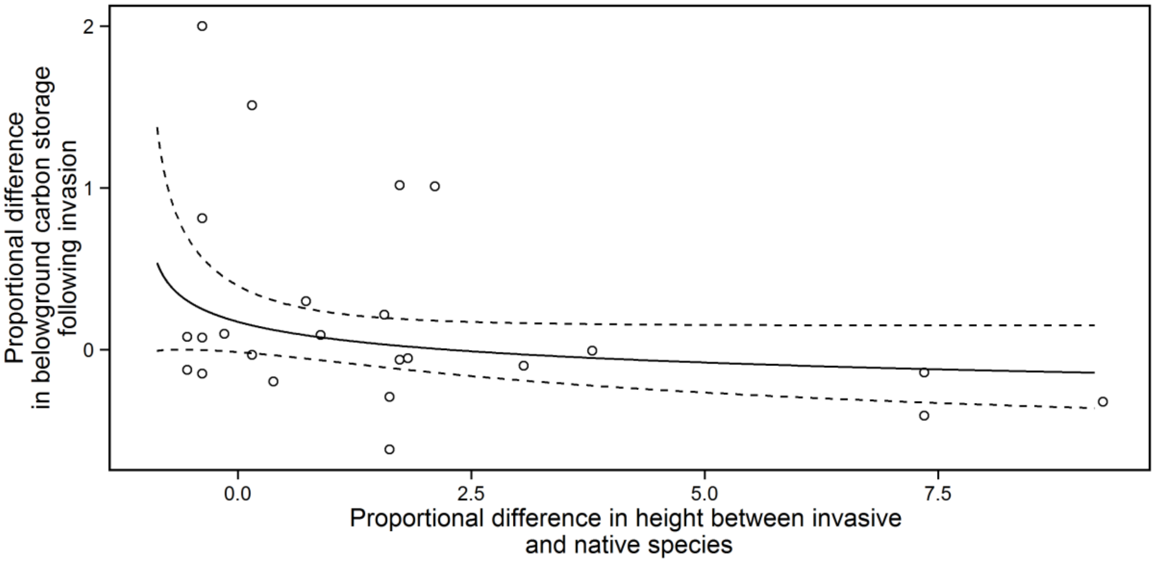

Figure 13 – Relationship between changes in belowground carbon storage and the proportional difference between the height of invasive non-native plant species and native plants (n=23). The solid line represents the predictions of the model with lowest AICc and the dashed lines are the 95% confidence intervals of this prediction.

3.5 Discussion

This study indicates a variety of relationships between impacts of invasive species on the selected ecosystem services and species woodiness. Aboveground carbon showed large increases following invasion by woody plants where native dominant species were none woody, and decreases where invasive were non-woody and natives were woody. However, there were also increases when native and invasive species woodiness did not differ. While models of belowground carbon storage suggested great increases in carbon following invasion by woody plants than non-woody plants this model had little explanatory value. Similarly changes in water quality, provision and carbon sequestration were poorly predicted by the woodiness of native and non-native species. This observation supports hypothesis 1 and 3 for aboveground carbon storage since transitions from woody to non-woody dominant species resulted in more pronounced changes than where invasion was by a species of similar woodiness; but invasion by a species with similar woodiness still resulted in ecosystem service change. Hypothesis 4, that adding details of ecosystem type to analysis would result in greater parsimony, was poorly supported and most of these models had much higher AICc values than the most parsimonious model.

Changes in aboveground carbon storage showed a positive relationship with invasive species height, while belowground carbon storage showed a negative relationship as invasive species height increased relative to native species. Water quality increased with increasing invasive species height while water provision showed little relationship. As such there was only partial support for hypothesis 4. Root depth did not predict change in water provision well and as such hypothesis 5 is not supported by this work. In addition it appears that hypothesis 6 that including data on the traits of native species improves model fit is poorly supported since it was only true in one case.

3.5.1 Relationships between invasive and native woodiness and impact

Change in aboveground carbon storage as a result of non-native plant invasion was the only ecosystem service which was well predicted by the woodiness of native and non-native species in this study. Where native species were non-woody and invasive species were woody there was a very large increase in aboveground carbon of approximately 1200%. Similarly when invasive species were non-woody and native dominant species were woody there was a large decrease in aboveground carbon storage of 70%. Both of these observations are likely to be driven by woody plants tending to be taller and having broader stems than non-woody plants and (Windham and Lathrop 1999) thus any transition between the two causes dramatic change in aboveground carbon storage (Gaertner et al. 2014). However, it is interesting to note that even when the woodiness of native and invasive species was the same aboveground carbon storage tended to increase after invasion. This may be the result of number of factors. First it is possible that a continuous trait might capture this relationship more effectively, since species of similar woodiness may still differ in important traits such as height or wood density. Secondly, it is possible that invasive species may have a competitive advantage over native species due to a lack of natural enemies allowing them to grow more quickly and achieve higher biomass.

Apart from aboveground carbon storage all other services were poorly predicted by native or invasive species woodiness and/or ecosystem type, with

$R^2<0.10$. This is in part as a result the classification scheme used for ecosystem services in this study. For example belowground biomass and soil carbon storage were both classed as belowground carbon storage in this study, even though the processes controlling the two may differ considerably. Taking this approach inevitably added noise to the dataset making relationships harder to discern. As such future work that aims to generalise about links between changes in biodiversity, ecosystem function and ecosystem services should be careful to make sure that metrics used in different studies are as similar to each other as possible to allow more meaningful comparisons.

The addition of ecosystem type to models did not result in greater parsimony in any of the ecosystem service changes modelled. This is likely to be because the majority of variation amongst ecosystem types is due to different native species assemblages, which may be well characterised by defining native dominant species as woody or non-woody in other models. Thus in contrast to previous studies (e.g. Gaertner et al. 2014) my chapter suggests that ecosystem impacts of non-native invasion, especially on aboveground biomass, are not necessarily ecosystem specific and can be described more parsimoniously by native and non-native species woodiness.

3.5.2 Relationships between height and carbon storage

The effects of invasive species plant height on carbon stocks differed for aboveground and belowground carbon storage. Invasion of taller non-native plants was linked to greater increases in aboveground carbon. This is likely to be because taller plants tend to have higher individual plant biomass, so that when the number of taller plants in a community increases so does the biomass (Windham and Lathrop 1999). As such an ecosystem invaded by a tall species is likely to increase in community biomass, particularly when this species is highly abundant as is the case in many studies of invasive plant species (Firn et al. 2011). Plant height is positively correlated with lignin content of plant stems (Diaz et al. 2004) and as such increases in carbon are likely to occur when woody species invade areas with less woody natural vegetation (Dickie et al. 2011), as was often the case in this study.

Potential reasons for reductions in belowground carbon with increasing relative height of invasive species are less obvious. Ecosystems invaded by tall invasive species would be expected to increase in aboveground carbon and this is likely to lead to increases in leaf litter and other organic material inputs into soil (Schlesinger and Lichter 2001). Previous meta-analyses have suggested that this in turn is likely to lead to increases in belowground carbon storage (Liao et al. 2008).

However, the finding that the best model in this chapter suggested a negative relationship may indicate prevalence of a ‘priming effect’ in the context of invasive species. Priming occurs when an increase in leaf litter stimulates microbial activity in the soil, leading to faster decomposition (Sayer et al. 2011). This can result in no net addition of carbon to the soils or in some cases loss of carbon (Sayer et al. 2011). Woody species also often possess thinner leaves that decompose more rapidly than those of smaller, tougher leaved species (Diaz et al. 2004) pointing to another mechanism that may explain this relationship. Given that woody invasive plant species can increase rates of decomposition (Ashton et al. 2005; Casas et al. 2013) this mechanism may explain some of the variation changes to belowground carbon storage. Loss of belowground carbon has been recorded previously in woody invasions, with greater losses occurring at wetter sites, suggestive of possible trait-climate interactions (Jackson et al. 2002).

In addition to plant height, specific leaf area (SLA) is important in determining changes in ecosystem carbon (Diaz et al. 2004), though there was not enough data on this trait in the TRY database to allow analyses in this study. SLA is negatively correlated with leaf thickness and toughness and positively related to leaf size (Diaz et al. 2004). Since tough, thick leaves require longer to decompose (Diaz et al. 2004; Cornwell et al. 2008) inclusion of this trait into analyses is likely to aid the study of interactions between invasive plants and soil properties. SLA is also positively correlated with growth rate of plants (Diaz et al. 2004) and as such is likely to play a role in determining changes in aboveground carbon storage following invasion. Plant height and SLA represent two of the major axes used to divide species into functional types and as such any future trait analyses should incorporate them into analyses.

3.5.3 Relationships between traits and nutrient and water cycles

As in Chapter 2 it was difficult to explain variation in the impacts of invasive plant species on water provision. Previous studies have indicated that water provision may be related to changes in community biomass (Jackson et al. 2005; Cavaleri and Sack 2010) and thus it is surprising there was no obvious relationship in this study with plant height. It is possible root depth of invasive species may influence water obscuring differences as a result of changes in plant height (Canadell et al. 1996; Eviner 2004; Gross et al. 2008), though this study found little evidence of this probably as a result of small sample sizes.

In contrast to water provision, water quality appeared to be increased by invasion of larger non-native plants. This is counter to my hypothesis and previous studies that have suggested taller species increase nitrogen pools (Castro-Díez et al. 2014) and would therefore be expected to reduce water quality. However, like belowground carbon storage there is evidence that the effect of this trait is dependent upon climate with higher changes in nitrogen occurring in hotter, wetter locations, which may warrant further investigation (Castro-Díez et al. 2014).

3.5.4 Using characteristics and traits of invasive and native species to predict impacts

A number of hypotheses state that the impacts of changes in plant community composition on ecosystem functions and services are governed by changes in the functional traits in the community (Grime 1998; Díaz et al. 2007). However, in the context of invasion of non-native plant species this study found mixed support for this general theory. Height of invasive species was the best predictor of impact on aboveground carbon and water quality, difference in height between invasive and native species was the best predictor of belowground carbon change and in the case of water provision neither variable was a good predictor. From the perspective of testing theory this study shows only weak support for the mass ratio hypothesis of Grime (1998). From a practical perspective it seems that invasive species height may be a useful predictor of impact on carbon storage, and water quality but not for water provision. Further analyses using a wider range of traits, particularly leaf traits that influence decomposition and thus nutrient flux (Diaz et al. 2004) may aid further understanding of such impacts.

3.5.5 Lack of relationships

Many studies have attempted to explain ecological patterns using data from plant trait databases, with some success (Cornwell et al. 2008). However, one difficulty of such an approach is that of missing trait data for some species (Swenson 2014). This is a problem that I also encountered with this study. Although I extracted data from a large number of studies for the meta-analyses in Chapter 2, only around 20% of these had complementary data on native species traits in the TRY database (Kattge et al. 2011). This consequently reduced the statistical power of my analyses. More worryingly if the studies that were missing data were not a random selection of the population of all studies, as often appears to be the case in ecology, parameter estimates and conclusions can biased (Nakagawa and Freckleton 2008). However, given that around 60% of the paired site comparisons from Chapter 2 had complementary trait data for invasive species, lack of relationships when just using these data is likely to be the result of other factors.

The lack of data is a common problem when using data from trait databases such as TRY (Swenson 2014). However, recent developments allowing researchers to produce phylogenies for a wide range of plant and animal species (e.g. Pearse and Purvis 2013) point to potential solutions that may prove valuable to the study of invasive species in the future. Swenson (2014) suggested one way of avoiding this problem is to impute trait values using phylogenetic relationships, given that traits often show a phylogenetic signal (Díaz et al. 2013). Techniques such as this show the great potential for increasing statistical power in analyses such as this study by reducing the number of missing cases. While imputation is not ideal, similar techniques have been shown to produce less bias than excluding records with missing data (Nakagawa and Freckleton 2008).

As well as the problems of missing data on traits very few studies gave an indication of the abundance or cover of the invasive species. The mass ratio hypothesis states that the most abundant species or those with highest biomass in a community determine ecosystem functioning to the greatest degree (Grime 1998). In the case of this chapter I used data on the species that were considered dominant in invaded and uninvaded systems by the researchers. This added another element of inaccuracy to the analysis since it was unclear whether the trait values of the most dominant species were representative of the mean values of the entire community. Examination of such relationships in the context of non-native invasive plant species has rarely been investigated, but in order to develop a more nuanced understanding of invader impacts they should be. However, given that invasion biology aims to predict the impact of species prior to their invasion use of easily available data, such as the traits of invasive species, appear to be the most feasible way of doing this. Given the mixed predictive ability of effect traits in this chapter, such predictions may be elusive.

One other approach that could prove useful is a combination of the different analyses I used in this study by using information on invasive species traits along with that on the woodiness of native species or type of ecosystem invaded. Doing this would give a more nuanced picture of how differences in invasive traits interact with those of native species to govern ecosystem level changes, particularly in the context of changes in aboveground and belowground carbon which were most effectively explained in this study. This approach would, for example, allow identification of the height of invasive species that are likely to result in increases in carbon in different ecosystems. Such an approach would allow a stronger test of the hypothesis that invader impacts depend on the characteristics of both invasive and native species, as discussed by Ricciardi et al. (2013). This method would allow the amount of data that can be used in analyses to be maximised, while using continuous effect traits that are generally favoured in such analyses (Díaz et al. 2007).

In addition there is a need for further studies of invasive species using trait based analyses. Although hypotheses of the effects of invasive species given their traits can be made based on our knowledge of community change in other contexts, there are a number of features which make invasive species in their non-native range different. For example, the relative lack of natural enemies may drive invasive species to have greater primary productivity than would be expected from a native species with similar traits (Keane and Crawley 2002). In addition, the apparently high phenotypic plasticity of some invasive species (Richards et al. 2006) may result in widespread variation in the traits that the exhibit. For example, there is evidence that invasive plant species tend to be taller outside of their native range (Blossey and Kamil 1996), suggesting that even invasive species of apparently similar height to native species may cause increases in aboveground biomass.

3.5.6 How this work informs theory

Work on species invasions has commonly states that the novelty of species characteristics and traits may drive their impacts on ecosystems (Ricciardi and Atkinson 2004). This work has found mixed support for this general hypothesis with only aboveground carbon storage well predicted by models including characteristics of both invasive and dominant native plant species. In addition most analyses using species traits suggested that inclusion of details on both native and non-native traits did not improve parsimony, apart from in the case of belowground carbon storage. However, rather than indicating that novelty of species traits or characteristics do not drive greater change in ecosystem services the results of this study indicate that it is much easier to predict changes in carbon cycling than other ecosystem changes. To predict changes in water and nutrient cycles it may be easier to disaggregate the measures used in this study so that similar ecosystem properties are analysed together rather than by ecosystem service type.

From this chapter it is clear that of all changes in ecosystem services those in aboveground carbon storage were the most easily predicted. Analyses that investigated relationships between species woodiness and changes in aboveground carbon storage revealed that even when species have similar woodiness biomass can increase, suggesting potential differences in traits or mechanisms relating to enemy release as potential drivers of change. Further research is needed to inform the mechanisms that drive differences in biomass when species are apparently similar. Analyses of species both in their native ranges and non-native ranges would allow researchers to distinguish whether which biomass is a product of inherent characteristics or lack of competitors (Firn et al. 2011).

However, the most dramatic changes in aboveground carbon storage were observed when the woodiness of invasive species and native species differed. It is unclear how common such dramatic differences between invasive and native species are but it is clear that such changes are potentially analogous to regime shifts (Gaertner et al. 2014). Regime shifts are dramatic, rapid and often unpredictable changes in ecosystems caused by can be external pressures following which ecosystems can remain in relatively stable states as a result of positive feedbacks (Scheffer and Carpenter 2003). Following a regime shift these feedback loops can make it extremely difficult to restore ecosystems to their prior state, as is often be the case in invasions (Suding et al. 2004). An example of such a feedback is the ability of many non-native invasive species to rapidly accumulate biomass (Vilà et al. 2011) and produce a large number of seeds (Holmes et al. 1987) encouraging persistence and dominance of the invasive species in the system once it has been invaded (Gaertner et al. 2014). Similarly non-native invasive plant species can alter fire regimes (Brooks et al. 2004), soil nitrogen (Vitousek et al. 1987) and leaf litter (Allison and Vitousek 2004) in a manner that can encourage the persistence of invasive species and encourage further invasions (Gaertner et al. 2014).

Despite the acknowledgement by some that invasion may result in regime shifts the topic has been the subject of relatively few empirical studies (Gaertner et al. 2014). Given that such regime shifts by their nature are extremely difficult to reverse further study of them in the context of non-native invasions is warranted (Suding et al. 2004). In particular it is important to identify the conditions which increase the probability of an ecosystem under which regime shifts are most likely to occur. Research has suggested that shifts between woody and non-woody native species are likely to occur in areas with high temperatures and intermediate rainfall on the fringes of savannah or forest ecosystems in the tropics (Hirota et al. 2011). It is possible that regime shifts that result in dominance of non-native invasive plant that differ in their woodiness when compared to species in native ecosystems may follow this same general pattern. However, given that it has been suggested that non-native invasive plants may not be the initial driver of change in many cases (MacDougall and Turkington 2005), any such analyses will likely require human disturbances prior to invasion to be taken into account.

3.5.7 Implications for invasive species management

This study has shown that height of invasive plant species appear to predict their impact on carbon stocks and water quality following invasion, even though relationships are relatively weak. However, changes in water provisioning showed little relationship to plant height. In order to gain a clearer picture of the impacts of invasive species further trait based studies are encouraged using a wider variety of traits such as leaf traits that have been linked to carbon flux and soil nutrient changes (Cornwell et al. 2008). However, given that trait data is not always available for all species of interest, imputing trait values using phylogenetic imputation may aid future predicts of impact.

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Chapter 4

4 Residual tree damage, carbon storage and species richness driven by intensity and method of selective logging in tropical forests: a meta-analysis

4.1 Introduction

Over 400 million hectares of forest have been designated as permanent logging concessions, making selective logging – the removal of selected trees from a stand – one of the most widespread human disturbances in tropical forests (Asner et al. 2009). Tropical logging currently produces approximately one eighth of global timber (ITTO 2012) and is important for many local economies. However, current logging practices can have negative impacts on biodiversity (Berry et al. 2010) and lead to increased carbon emissions (Cochrane et al. 1999; Fox et al. 2010). Current practices also endanger the long-term sustainability of timber production (Gourlet-Fleury et al. 2013) with evidence suggesting that we may be approaching so-called 'peak timber' in the tropics (Shearman et al. 2012).

The mechanisms that underlie logging impacts at the stand and ecosystem scales are ultimately driven by its effects on mortality and recruitment of trees and thus forest structure. Mortality of large trees in selectively logged forests is high compared to undisturbed forests since these trees are usually those with highest timber value and are thus likely to be harvested (Lindenmayer et al. 2013). However, mortality of smaller non-timber trees is also increased in logged forests when compared to undisturbed forests since harvesting and transportation of logs can result in damage to non-target trees (Picard et al. 2012). These increases in mortality result in a reduction in biomass (Putz et al. 2012) and leads to changes in tree community composition when species recruited are not the same as those lost or when recruitment cannot keep pace with mortality (Baraloto et al. 2012; Gourlet-Fleury et al. 2013). However as recent meta-analyses have shown the effects of selective logging in tropical forests on biomass and biodiversity is highly variable.

On average, selective logging of tropical forests leads to a 25% reduction in aboveground biomass and a 5% reduction in species richness (Putz et al. 2012).

However, biomass losses have been reported to vary between 4 and 66% while tree species richness changes can vary between -53% to +27% of that found in unlogged forests (Putz et al. 2012). This variation is likely to be partly attributable to the different methods used to extract logs (Pinard and Putz 1996). However, previous meta-analyses of the impacts of selective logging on tropical carbon and tree biodiversity did not explore potential causes of these differences (Clark and Covey 2012; Putz et al. 2012).

Though rarely explored in meta-analyses the variation in residual tree damage, aboveground biomass and tree biodiversity are likely to be strongly related to logging intensity (the volume of wood extracted per hectare). As logging intensity increases the number of trees harvested increases and a greater proportion of residual trees are damaged by harvesting (Picard et al. 2012). As such higher logging intensity is likely to lead to greater reductions in aboveground biomass, as seen in a number of field studies (Sist et al. 1998; Mazzei et al. 2010). The relationship between logging intensity and species richness appears to be more complex with the potential colonisation of generalist species leading maintenance or increases in species richness with low intensity logging and reductions of richness at higher intensities. Such relationship have been seen for birds, but changes in richness for other vertebrates tend to be linear reductions (Burivalova et al. 2014).

Differences in the methods used in logging are another important source of variation that affect logging impacts. Due to concern about unsustainable logging practices reduced impact logging (RIL) has been advocated as a means to reduce the negative consequences of logging for biodiversity and carbon (Pinard and Putz 1996). RIL involves techniques such as cutting lianas prior to logging, felling trees in directions selected to cause least impact to surrounding forest, and limiting road construction (Pinard and Putz 1996) . Such techniques may reduce residual tree damage compared to conventional logging, reducing impacts on tree biomass and biodiversity (Gullison and Hardner 1993; Pinard and Putz 1996). Some studies have suggested that RIL can be carried out at similar intensities (i.e. the volume of wood removed during logging) to those of conventional logging while causing less damage to residual stands (Pinard and Putz 1996; Putz et al. 2001; but see Sist et al. 2003). If this is true, RIL may be able to achieve similar timber yields to conventional methods whilst reducing losses of biodiversity and carbon. However, this claim is supported by relatively little evidence and has never been tested by meta-analysis.

Previous meta-analyses on the impacts of selective logging on forest structure, biomass and biodiversity have failed to account for differences that may be driven by logging intensity or differences in logging methods (e.g. Gibson et al. 2011; Clark and Covey 2012; Putz et al. 2012; but see Burivalova et al. 2014). In this chapter I explore whether logging intensity and differences in logging methods explain the variation in impacts on residual stand damage, aboveground biomass and tree species richness using a systematic review and meta-analysis. Specifically I address the following questions and hypotheses:

1. What factors drive differences in residual stand damage following selective logging of tropical forests?

H1. Residual stand damage increases with logging intensity.
H2. Residual stand damage increases with logging intensity but begins to plateau at higher intensities
H3. Residual stand damage increases with logging intensity but when forests are logged using RIL they cause lower damage for a given intensity.
H4. Residual stand damage increases non-linearly with logging intensity but when forests are logged using RIL they cause lower damage for a given intensity.

2. What factors drive the differences in biomass loss following selective logging?
H1. Biomass loss increases with logging intensity.
H2. Biomass loss increases with logging intensity but forests logged using RIL have a less steep slope than those of conventionally logged forests.

3. What factors drive changes in tree species richness following selective logging?
4.
H0. Tree species richness change is not related to logging intensity or method.
H1. Tree species richness loss increases with logging intensity.
H2. Tree species loss increases with logging intensity but forests logged using RIL show a less steep slope.
H3. Tree species richness increases at low intensities and decreases at higher intensities.

These analyses provide robust evidence for policy interventions, such as the reducing emissions from deforestation and degradation (REDD+) initiative (Miles and Kapos 2008), which aim to mitigate the impacts of climate change by incentivising sustainable forest management to improve carbon storage and biodiversity conservation.

4.2 Methods

I defined selectively logged tropical forests as native forests between the latitudes of 40’N and 40’S (Newbold et al. 2013) that have been subjected to the selective removal of trees for timber. I undertook a systematic review using standard methods (Pullin and Stewart 2006). I used the terms ("biomass" OR "carbon" OR "basal area" OR "damage" OR "snag" OR "non-target" OR "tree" OR "growth" OR "recruitment" OR "seedlings" OR "species richness" OR biodiversity) AND (selective logg* OR felling OR timber extraction OR reduced-impact logging OR degradation) AND tropical forest to search Web of Knowledge, Wiley Blackwell and Science Direct and used appendices of Gibson et al. (2011), Putz et al. (2012a), Clark and Covey (2012) and Picard et al. (2012) to locate studies. To minimise bias arising from the lack of publication of negative results (Pullin and Stewart 2006) I used the same search terms in Google to find relevant grey literature, though I found no studies that were relevant. I also contacted researchers working on this subject directly to identify any unpublished datasets and added datasets on the recommendation of reviewers of a manuscript based on this chapter.

Once the search was undertaken I discarded irrelevant papers. My inclusion criteria were: (i) studies should present data on residual stand damage following logging or aboveground tree biomass and/or species richness of trees from at least one undisturbed forest and one logged forest site, (ii) sites should have spatially replicated measures of the metrics of interest in both logged and unlogged sites with at least three plots present in each. This rule was relaxed for the studies of residual stand damage since very few were replicated or had comparisons with unlogged sites, (iii) logged sites could not be affected by confounding multiple disturbance types, such as fire. Studies carried out outside of moist lowland forest, where most logging in the tropics occurs, were included to improve generality of the meta-analysis. From each included article which focussed on biomass or species richness changes I extracted the mean, standard deviation and sample size of metrics in both logged and unlogged forests. For studies of forest damage I extracted the mean of each metric used to assess damage. I recorded the geographic location (latitude and longitude), region (Americas, Africa, or Asia), method of logging used (RIL or conventional selective), years since logging, number of logging cycles and volume of wood extracted (m^3ha^{-1}) and/or number of trees felled per hectare. For estimates of species richness I recorded whether these were made using rarefaction or not. For details of studies used see the appendix for this chapter.

4.2.1 Statistical analyses

Prior to analyses of differences caused by logging intensity or methods it was necessary to standardise the metrics of stand damage and logging intensity I used for this study. There is no universally accepted measure of residual stand damage following logging but the metrics can be broken down into two groups, tree-based measurements and area-based measurements (Picard et al. 2012). Tree-based measures attempt to identify the number or proportion of trees damaged per hectare or per tree felled. Similar measurements include the basal area damaged or the proportion of total basal area damaged. Area based measurements aim to identify the area or proportion of total area of plots in which trees have been damaged. Conversion between the two types of metric is difficult since they show non-linear relationships (Picard et al. 2012) and so for this study I concentrated on studies that measured damage of trees directly.

To allow conversion for to a common metric of stand damage, in this study the proportion of residual trees damaged, linear mixed models were used to produce scaling coefficients between this metric and the number of trees damaged per tree extracted and the number of trees damaged per hectare. The continent on which studies were undertaken was included in these models since forest stem density and tree size varies considerably across the tropics (Slik et al. 2013), and thus the slopes of these relationships could be expected to vary by continent. This method was then used to predict the proportion of residual trees damaged in studies where such data was not directly available. A similar process was undertaken to convert metrics of logging intensity to the metric used in this study, m^3 wood removed ha^{-1}. The number of trees harvested per hectare was the only other metric commonly used and thus a linear mixed model of the relationship between this and the volume of wood removed, accounting for continent level differences in this relationship was produced. Again where data on volume of wood removed was not available from a study this was predicted using coefficients from this model.

To determine the effect of logging intensity and different logging methods on the proportion of residual trees damaged an unweighted linear mixed model was used. Prior to model fitting the response variable was logit transformed so values were constrained between 0 and 1. Random effects were used to identify data drawn from the same study since their response may be more similar than data from drawn from other studies. The hypotheses tested related to how logging volume affected the proportion of residual trees damaged, and whether logging method changed the slope of this relationship. Previous work (e.g. Picard et al. 2012) has suggested that the relationship between logging damage and intensity is non-linear and so models with quadric and log terms were also tested.

For the analysis of the impact of logging intensity and logging methods on changes in aboveground biomass and species richness a weighted approach was used. Where standard errors of the mean were missing from studies, they were estimated using imputation methods (Koricheva et al. 2013) which are likely to bias results less than excluding studies with incomplete information (Nakagawa and Freckleton 2008). To do this, the relationship between the coefficient of variation for logged and unlogged sites for tree richness or biomass and plot size at which data was collected at was estimated using linear models. The literature on human-disturbed forests suggests that smaller sampling plots result in greater between sample variation and thus higher coefficients of variation, meaning that this approach is empirically supported (Wagner et al. 2010). Unweighted linear models were then used to predict the coefficient of variation for studies missing this data and missing standard deviations calculated by multiplying this prediction by the value of richness or biomass measured at the site.

To analyse the effects of logging on carbon pools and tree species richness, the log response ratio of differences between plots was calculated and models weighted by the inverse of pooled study variance so that more precise studies had more weight (Hedges et al. 1999; Borenstein et al. 2009). I fitted a random effects mixed model to account for pseudoreplication at the level of individual studies when the same unlogged site was used as a comparator for multiple logged sites. In the analyses of richness, estimation method (rarefied or not rarefied) was included as a random effect since this has been shown to cause between study differences in the past (Cannon et al. 1998; Gotelli and Colwell 2001), but was not of interest in the analysis which aimed to investigate the mechanisms underlying any differences. In the analyses, I explored the effects of logging method and logging intensity in determining post-logging biomass. For sites that had been logged twice, I calculated logging intensity as the sum of the volume extracted over both cycles, following Edwards et al. (2013). I explored the effects of logging intensity and logging method on species richness using the same method. In addition to the logging intensity and method it is possible that then number of years since a site was last logged and the location of study may play a role in determining impacts as an indicator of successional recovery or due to differences in forest structure respectively (Burivalova et al. 2014). As such these variables were also included in models. All possible models that had >3 data points per parameter were assessed and importance and R^2 values were calculated.

Model selection in all cases followed an information theoretic approach. To determine the relative importance of each variable in explaining differences, all models were run and their AICcs (Anderson et al. 2000; Burnham et al. 2011) calculated. AICc was subsequently used to determine the relative likelihood of a model being the ‘best model’ using the AICc weight. The relative importance of each model parameter, the ‘importance value,’ was calculated by summing the AICc weight for all models containing the parameter (Anderson et al. 2000). For the models of logging damage all models with a ΔAICc<7 were averaged to produce coefficient estimates (Burnham et al. 2011). Since this is not possible for the weighted analyses of impact on biomass and species richness the model with the lowest AICc was chosen as the most parsimonious model. All statistical analyses were performed in R 3.0.2 (R Development Core Team 2011), with weighted analysis carried out using the package metafor (Viechtbauer 2010) and all figures drawn using ggplot2 (Wickham 2009).

4.3 Results

The systematic review yielded 62 studies, from which I extracted data on residual tree damage from 24 sites, biomass differences between logged and unlogged sites at 32 paired, spatially replicated sites and species richness of trees at 9 paired, replicated sites. Median logged-site age for those sites where biomass was measured was 4.5 years (min=0, max=30) and for sites where richness was measured it was 5 years (min=0, max=50). Sites were mostly located in Asia and South America, with relatively few in Africa (Figure 14).

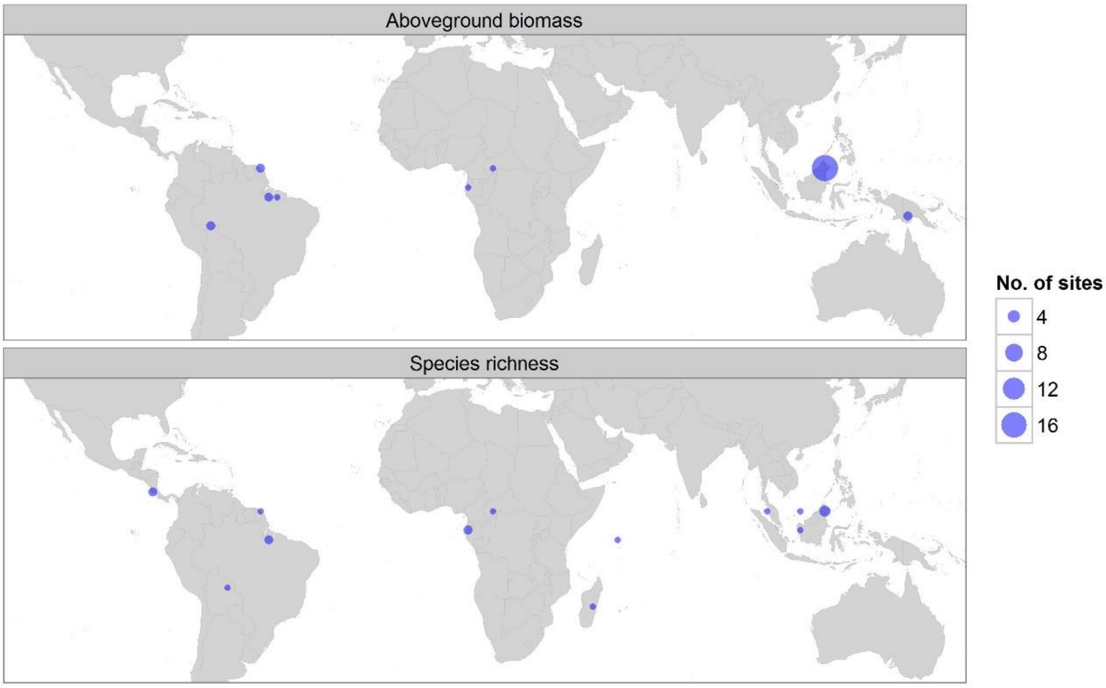

Figure 14 – Location of studies used for analyses of change in aboveground biomass and species richness.

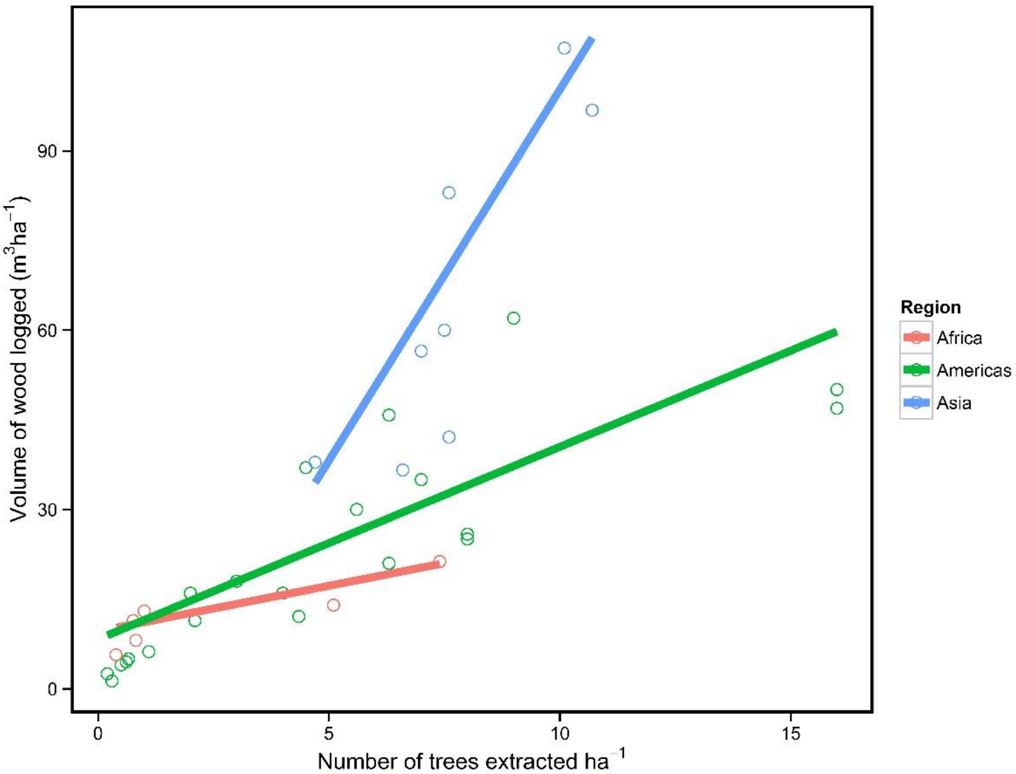

Figure 15 – Relationship between the number of trees extracted per hectare and the volume of wood logged per hectare (n=33). Points refer to individual sites, with red points representing sites from Africa, green points sites from the Americas, and blue points sites from Asia. Solid lines represent fit of the model with lowest AICc which was much better than any other model, with all other models having a ΔAICc>7.

4.3.1 Scaling coefficients for measures of stem damage and logging intensity

The most parsimonious model for predicting the volume of wood logged per hectare was a model that consisted on the number of trees extracted per hectare and the continent where studies were undertaken. This model indicated that for each tree removed a greater volume of wood was removed in Asia than in Africa or the Americas (Figure 15), and had a very good fit with an R^2 of 0.93. The most parsimonious model for converting from the number of trees damaged per hectare to the proportion of trees damaged per hectare did not require inclusion of study location as a variable and showed a very good fit with a R^2 of 0.95 (Figure 16).

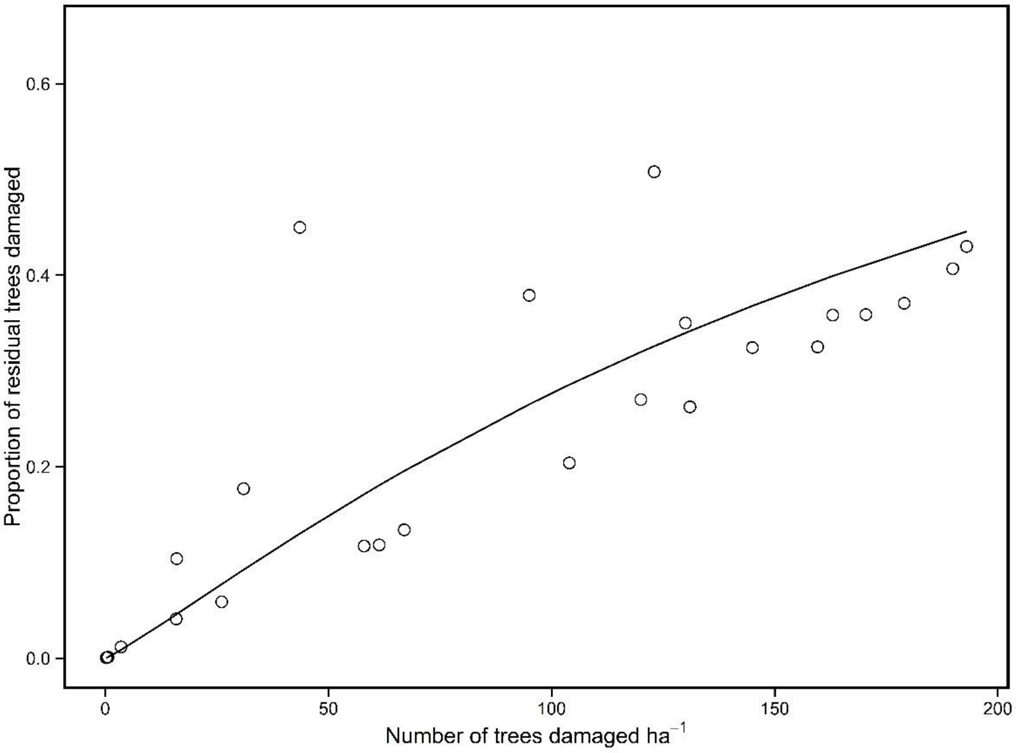

Figure 16 – Relationship between the number of trees damaged per hectare and the proportion of trees damaged per hectare (n=24). Points refer to individual sites. The solid line represent fit of the model with lowest AICc which was much better than any other model, with all other models having a ΔAICc>7.

4.3.2 Logging damage to residual trees

The model that best explained the proportion of residual tree stems that were damaged included and interaction between the logarithm of logging intensity and the logging method and this had an R^2 value of 0.32. Only one other models had a ΔAICc <7, which contained only logging method as an explanatory variable (R^2=0.09). Predictions using model averaged coefficients suggested that damage to the residual logging stand increased as a function of the logarithm of the logging intensity. The interaction between logging method and logging intensity suggested that at low logging intensities RIL tended to cause less residual damage than conventional logging but at high intensities the two methods became more similar in the residual damage they caused (Figure 17). However, the 95% confidence intervals for predictions were very wide indicating large variation in damage on residual tree stems for both methods.

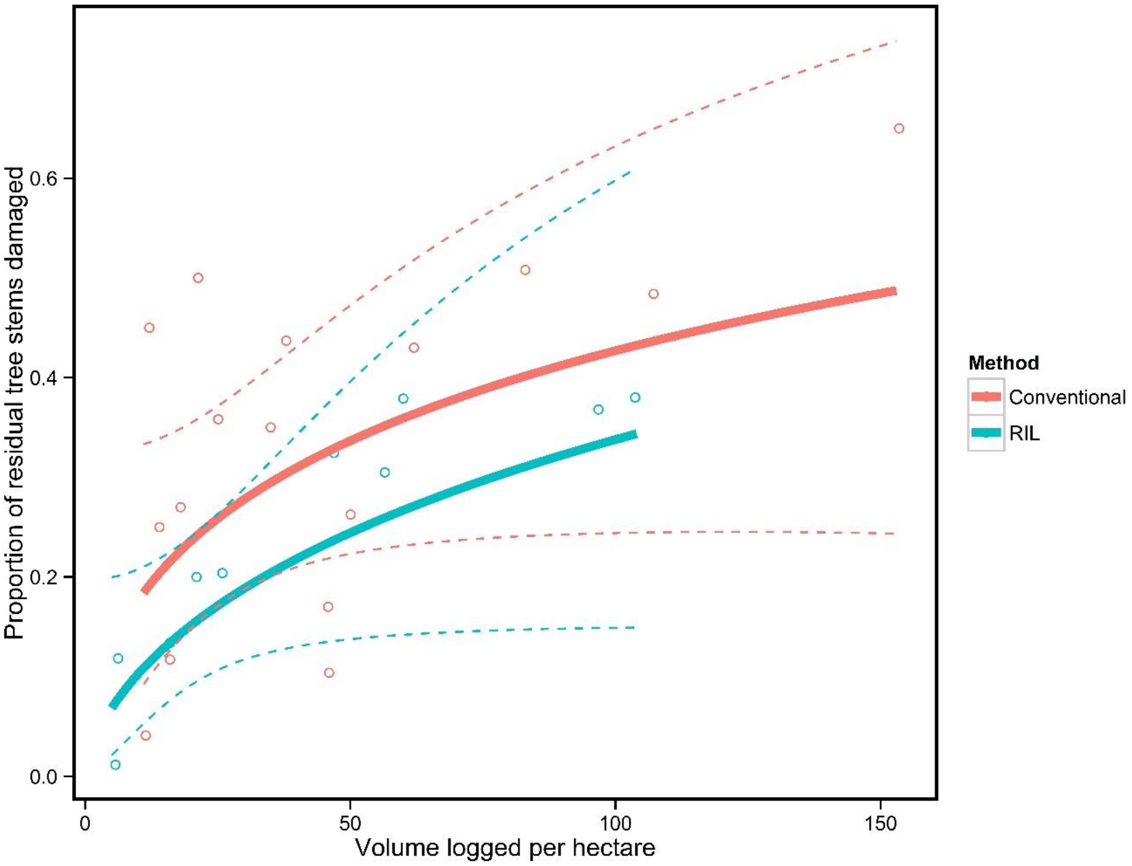

Figure 17 – Impact of logging intensity and method on the proportion of residual tree stems damaged following selective logging in tropical forests (n=24). Points represent single sites, solid lines are the predictions from the model with lowest AICc and dashed lines represent the 95% confidence intervals of these estimates. Red points and lines refer to sites where conventional harvest methods were used and blue points and lines where RIL techniques were used.

4.3.3 Impacts of logging intensity and method on biomass and species richness

For the second set of analyses, increased logging intensity led to reduced post-logging biomass with suggestions that the slope of this relationship differed between RIL and conventional methods (Figure 18). The model explaining variation in biomass effect size with greatest support (R^2=0.88, Table S3) suggested a linear relationship between logging intensity and differences in biomass and an interaction between this and logging method. The model indicated that RIL techniques may result in lower biomass losses per m^3 of wood removed per hectare, at intensities >50m^3ha^{-1} but this relationship was driven largely by a single data point at which volume logged was >100 m^3ha^{-1} (Figure 17).

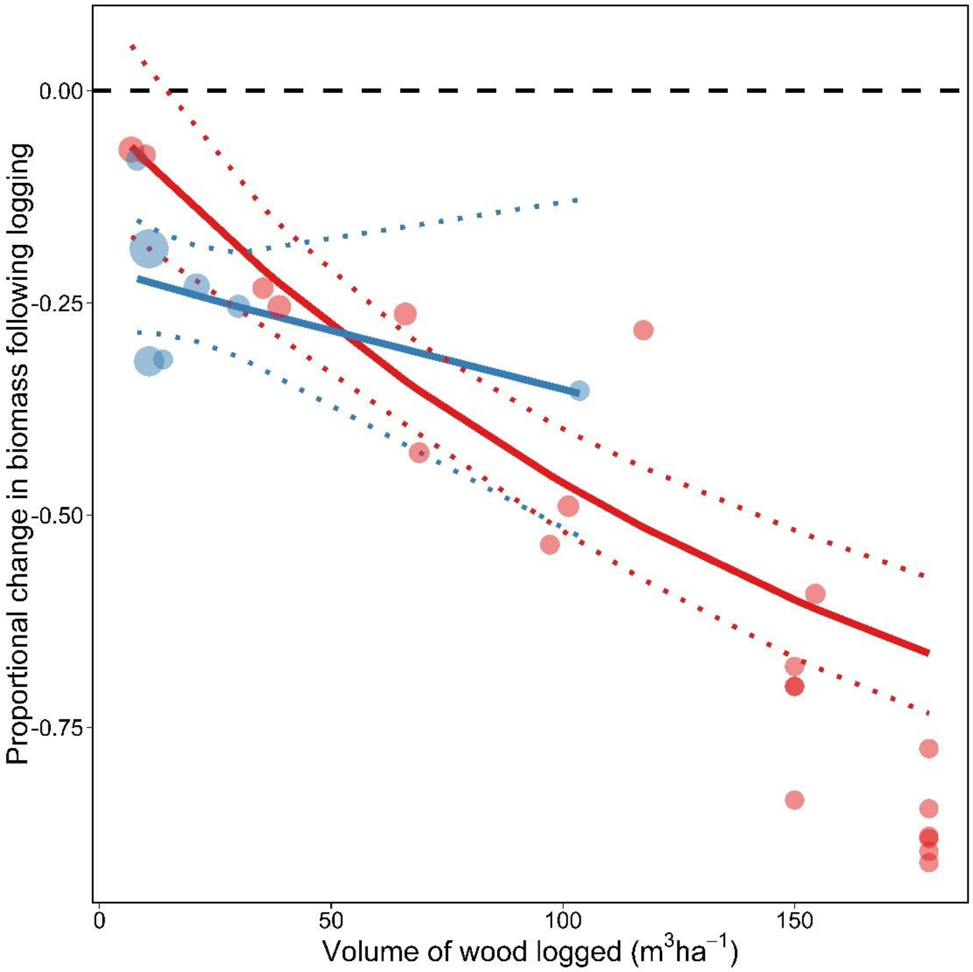

Figure 18 – Impacts of logging intensity on changes in aboveground biomass (n=32). Blue symbols are those sites where RIL was carried out, red symbols correspond to conventionally logged sites. The solid lines represents the predictions from the models with lowest AICc, and the dotted lines the corresponding 95% confidence intervals. The horizontal dashed line indicates when there is no difference between logged and unlogged sites. Note that RIL sites tend to logged at a lower intensity than conventionally logged sites.

The model that explained variation in tree species richness effect size most effectively, suggested a negative positive relationship with intensity of logging (Figure 19, Table S4). All other models had a ΔAICc>7 and the most parsimonious model had an R^2 of 0.36. Too few studies assessed the impact of RIL on species richness to conduct an analysis of its effect relative to conventional logging.

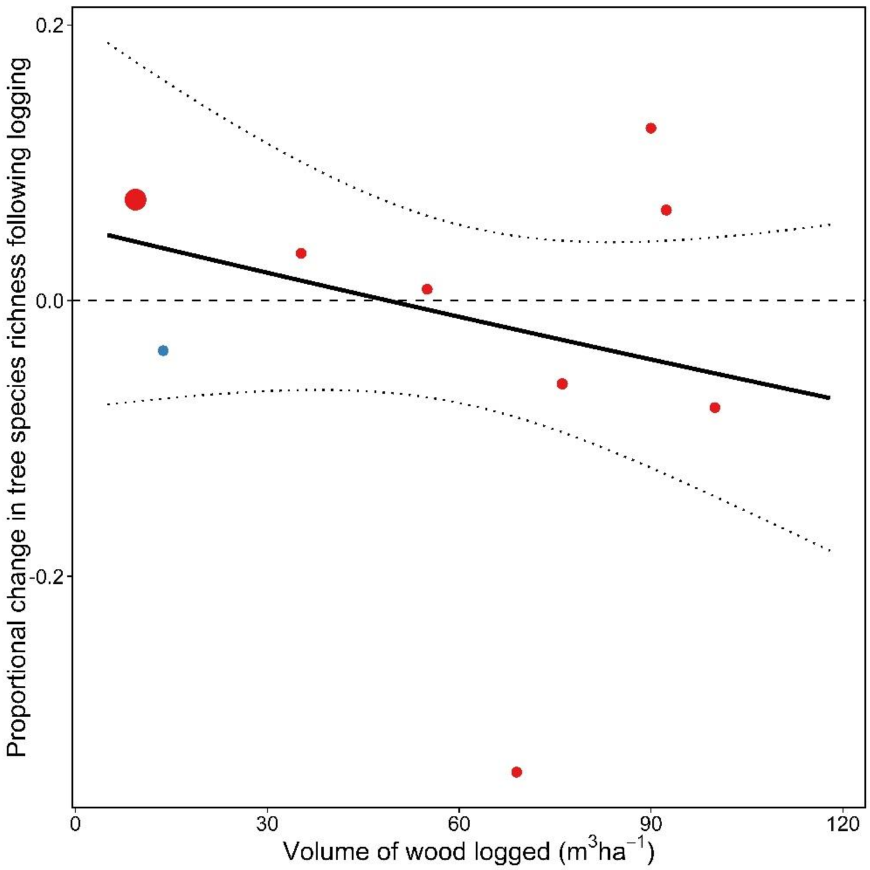

Figure 19 – Impacts of logging intensity in tree species richness (n=9) following logging. Blue symbols are those sites where RIL was carried out, red symbols correspond to conventionally logged sites. The solid line represents the predictions from the models with lowest AICc, and the dotted lines the corresponding 95% confidence intervals. The horizontal dashed line indicates when there is no difference between logged and unlogged sites.

4.4 Discussion

4.4.1 Effects of logging on non-target trees

This work suggests that logging intensity is the primary driver of differences in non-target tree damage in selectively logged tropical forests, as previously noted in other studies (Sist et al. 1998; Picard et al. 2012). However, my results also suggest that there is weak support for RIL techniques resulting in lower damage to residual trees than conventional logging, especially at lower intensities. Similar observations have been made at the site scale by Sist et al. (1998) who indicated that RIL reduced residual damage by around 50% when logging was carried out <8 trees ha^{-1} in Indonesian Borneo. My work suggests that this observation may be more generally true. Given that residual damage to trees is likely to account for the majority of carbon losses as a result of selective logging this indicates that RIL may be useful in reducing carbon losses at the stand scale. However, there is a large amount of variation in the impacts of logging intensity and methods on stem damage which suggests either that other variables that are important have not been considered in our model, or more likely that the methods used to assess stem between studies is extremely variable.

4.4.2 Effects of logging on aboveground biomass

This chapter shows that when considering the effects of logging on aboveground biomass it is vital to take account of the intensity at which harvesting is undertaken to understand results. The volume of wood removed per hectare was by far the best predictor of changes in biomass following timber harvest. Logging intensity varies by region (Figure 20 & Putz et al. 2001), and is relatively high in SE Asia & Australasia (mean 91.8 m^3 ha^{-1} in this study) compared to South America and Africa (mean 33.0 and 30.7 m^3 ha^{-1} respectively). This varying intensity is probably because SE Asian forests are often dominated by dipterocarp trees, which have high timber value (Corlett and Primack 2005), meaning there are a greater number of timber trees per hectare than in other regions.

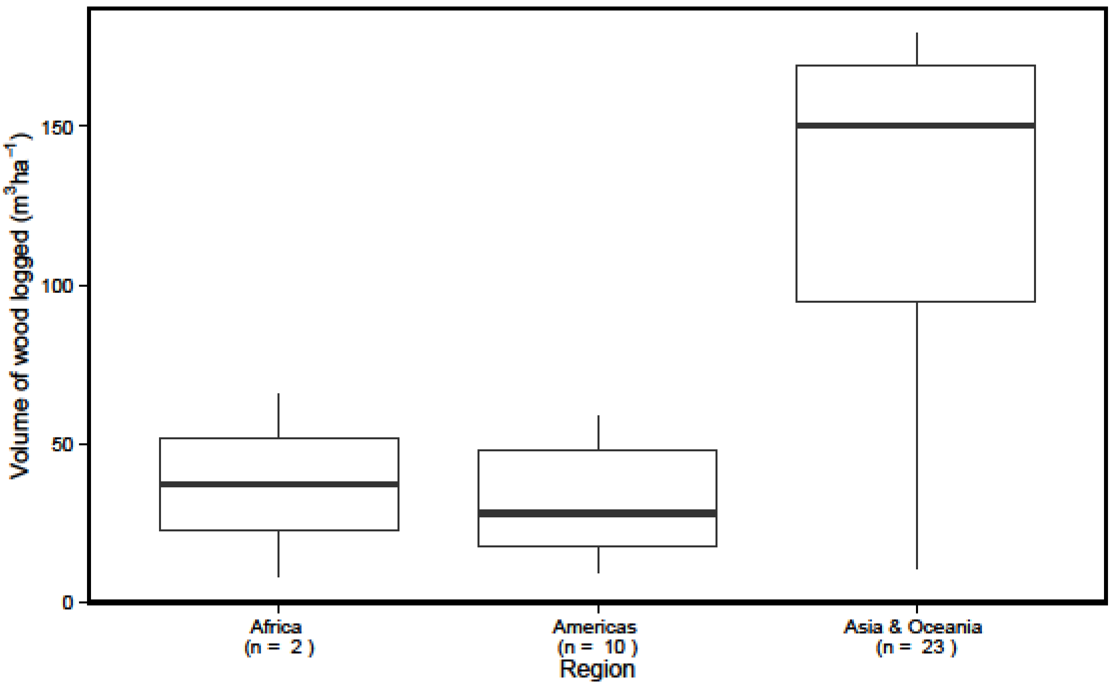

Figure 20 – Variation in selective logging intensity by study region. Data is taken from those studies that supplied data on logging intensity included in this research.

As shown in this study besides direct biomass removal, high logging intensity leads to greater damage to non-target trees. Given that aboveground carbon storage in logged forests appears to recover primarily through growth and recruitment of these non-target trees, reducing damage to them is of paramount importance (Mazzei et al. 2010; Gourlet-Fleury et al. 2013). Biomass recovery has been reported to take 7-24 years (Gourlet-Fleury et al. 2013; West et al. 2014), and more heavily logged areas appear to show slower recovery (Mazzei et al. 2010). This observation is largely supported by individual-based modelling studies of logging disturbances, though these also point to the length of time between cutting cycles as vital, with short cycles resulting in positive feedbacks causing greater mortality and reduction in biomass (Pinard and Cropper 2000). In this chapter, the best supported model suggests a linear relationship between changes in biomass and logging intensity. While this relationship may hold when comparing forests from different regions, it may not reflect relationships between volume and biomass loss in an individual forest. Further studies that compare a range of extracted volumes in single forests are needed to determine the exact nature of this relationship and identify potential tipping points.

This study also only found weak support that the impacts of RIL and conventional selective logging on post-logging biomass differ. Any effect was extremely difficult to discern since RIL generally involves relatively low logging intensities when compared to conventional selective logging (Figure 5). The observed difference in slopes is entirely driven by a single data point from the study of Pinard and Putz (1996) in which >100m^3ha^{-1} of wood was removed, with all other RIL carried out at relatively low intensities. While it appears possible that from my study that RIL may reduce residual damage to forests, unless studies of RIL are carried out at a similar range of intensities to conventional selective logging, its carbon benefits independent of reduced logging intensity are almost impossible to assess.

4.4.3 Effects of logging on tree species richness

As for aboveground biomass, the intensity of logging best explained differences in tree species richness due to logging. However, unlike for aboveground biomass, the slope of this relationship was much less steep, with an apparent initial increase in species richness at low intensities. The most plausible explanation for this increase is an influx of generalist species from surrounding non-forest areas (Carreno-Rocabado et al. 2012) leading to an initial post-harvest increase in richness as proposed by the intermediate disturbance hypothesis (Sheil and Burslem 2003). Similar relationships have recently been observed between logging intensity and bird species richness, while other vertebrates showed a decline even at low intensities (Burivalova et al. 2014). However, more studies of the effect of logging on tree species richness are needed in order to better understand this relationship since this meta-analysis only included 9 paired logged and unlogged sites despite an extensive literature search.

This work suggested that logging has a relatively modest effect on tree species richness, and even at high intensities richness was only reduced by ~10%. Since most logged forests had been logged relatively recently (median=5 years), it is possible that they exhibit an ‘extinction debt’ because of reduced recruitment of new individuals as a result of logging-induced degradation (Hylander and Ehrlén 2013). Despite this, it is also possible for biodiversity to recover following logging as a result of recolonisation from surrounding unlogged forest. However, this recovery may be dependent upon logging intensity, as shown by Chapman et al. (2000) who found that primate populations recovered relatively well 28 years after low intensity logging, but that forest logged at high intensities showed few signs of recovery.

Understanding of the long term dynamics of logged forests is currently hindered because, once logged, a forest is much more likely to be converted for agricultural use than an undisturbed forest (Asner et al. 2006).

The results of this study suggest that species richness may be relatively insensitive to subtle changes in forest cover (Ghazoul 2002). However, changes in species richness tell us nothing about the identity and function of individual species. Community composition is likely to be impacted by selective logging, with rare forest-dependent species sensitive to disturbance, which are often of conservation concern, becoming less abundant or locally extinct (Sheil et al. 1999) and generalist species increasing in abundance (Baraloto et al. 2012; Carreno-Rocabado et al. 2012). However, analysis of logging impacts on community composition is hindered because most studies of logging are spatially pseudoreplicated leading to biased estimates of change (Ramage et al. 2013).

4.4.4 Tree biodiversity-biomass relationships in logged tropical forests

Theory derived from biodiversity-ecosystem functioning experiments suggests that losses in plant species richness can result in reduced productivity (Cardinale et al. 2011; Hooper et al. 2012). While some studies of tropical forests have suggested such a relationship (Cavanaugh et al. 2014) the results of this chapter suggest that in case of logged forest this appears not to be the case. This is because at low logging intensity tree species richness may actually increase before dropping while any intensity of logging results in a loss of biomass. As such the relationship between species richness and biomass is complex and may resemble the humped relationship some have described between productivity and species richness with highest richness at intermediate levels of productivity (Huston 2014). As such it appears that general theories about the importance of species richness for productivity and carbon storage are not particularly useful for predicting change in logged forests.

This relationship is likely to exist because in logged forests the individual trees that are most important for carbon storage are often those lost first since they also tend to be the ones with highest timber value (Lindenmayer et al. 2013; Sist et al. 2014). These species may subsequently be replaced by pioneer species specialised to more open habitats (Ouédraogo et al. 2011) resulting in a maintenance or increase in species richness at low logging intensities. As such in order to understand the relationships between tree biodiversity and aboveground biomass in tropical logged forests it is preferable to use an approach that accounts for the changes in the functional traits found in tree communities (e.g. Díaz et al. 2007) rather than species richness. However, studies at which species number and identity are experimentally manipulated such as the Sabah biodiversity experiment (Hector et al. 2011) and the TreeDivNet experiments (http://www.treedivnet.ugent.be/)will help to further disentangle these relationships.

4.4.5 Improving assessment of logging impacts

This study and those of Ramage et al. (2013) and Burivalova et al. (2014) have identified clear methodological problems with current studies of logging impacts on forest structure, biomass and biodiversity, namely that nearly all studies show signs of spatial pseudo-replication, that logging intensity has largely been ignored by authors and that methods for assessing damage are very variable. There are a number of potential means to address these problems that would improve the robustness of the assessments of logging impact in the future. Firstly, the design of studies of logging impacts should be improved. Currently, most studies of logging sample spatially distinct logged and unlogged forests, resulting in artificially inflated statistical power since it is difficult to determine how much variation in measurements between logged and unlogged areas is due to variation in space and, how much, due to the selective removal of trees (Figure 21). As Ramage et al. (2013) note, this is a particular problem for detection of changes in community composition because ecological communities decline in similarity with increasing distance (Condit et al. 2002), even with no human disturbance, and tropical forests have extremely high beta diversity.

While less of a concern for aboveground biomass estimates and species richness, pseudoreplication also results in underestimation in variation in these cases. To remedy this problem, studies should aim to have fully randomised designs. This is however difficult to achieve since experimental manipulation of tropical forests is expensive and most commercial logging is usually undertaken in large blocks as harvesting of small areas is more expensive. Where statistically robust experimental design is not possible studies, should attempt to account for spatial pseudoreplication in analyses by assessing variation between plots based on the distance between them. Such an assessment would provide more robust measures of change and could potentially be used in syntheses in the future to partition variation arising from spatial differences and that arising from differences in disturbance (see Newbold et al. 2012 for an example of a project aiming to do this)

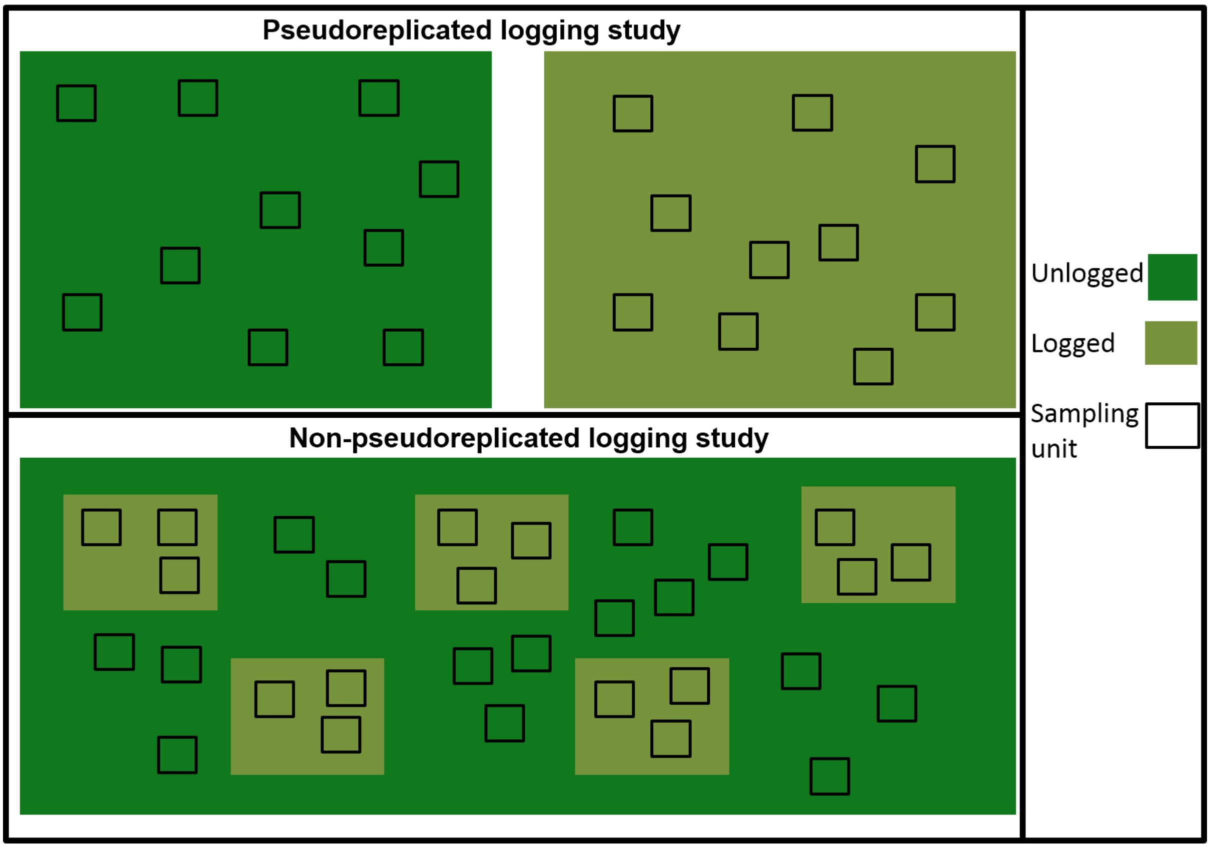

Figure 21 – Examples of pseudoreplicated (top) and non-pseudoreplicated (bottom) study designs for assessing the impacts of logging on a forest. Dark green areas indicate those that have not been logged, light green areas those that have been logged and black squares represent sampling plots.

In addition to spatial arrangement of sampling units, when assessing changes in forest structure the size of plots is also vital. My work and that of Wagner et al. (2010) indicated that studies with smaller plots tend to have a higher coefficient of variation and, thus, reduced statistical power in detecting changes in forest structure. This is likely to occur when impacts of human disturbance on forests is patchy, as in the case with selective logging, resulting in large differences between smaller plots, while larger plots capture greater variation in forest structure at the level of the sampling unit. Wagner et al. (2010) suggest that plot sizes for tropical forests should be >2 ha, but few used in the current study achieved this. I agree with the observation of Wagner that increased plot size should be considered a priority for logging studies, to increase precision of estimates of change. Doing this would also aid the attempts to determine the mechanism underlying these changes by increasing the statistical power of any analyses.

It is also clear from this study that logging intensity is important in explaining differences in carbon and biodiversity amongst sites and landscapes. However, it is sometimes difficult to obtain statistics on the volume of wood removed from an area (P. Saner, pers comm) and, when this is available, it is often only available as a mean volume removed per hectare for the entire study area. This means that identification of the role of logging intensity between plots is extremely difficult. Since volume of wood removed is difficult to obtain, other indicators of logging intensity may be useful. Previous studies have used number of trees logged per ha or basal area logged per ha as alternative measures (Mazzei et al. 2010). Of these two possibilities, basal area of cut trees is likely to be the most useful since the height and diameter (Feldpausch et al. 2011), and consequently biomass of individual trees, varies greatly throughout the tropics (Slik et al. 2013), thus limiting comparison amongst different landscapes. Measurement of basal area of cut trees and of those remaining would allow for comparison amongst plots and landscapes, enabling a greater understanding of the interplay between logging methods and intensity in determining logging impacts.

Regarding the damage to residual trees following logging it was clear during this study as well as that of Picard et al. (2012) that there are a wide variety of different measures used to assess damage. While I used coefficients to convert between different measures to maximise the value of available data this method inevitably introduces inaccuracies in to syntheses such as this chapter. In addition it is not always easy to convert between these different measures such as when studies assess damage as the percentage of an area damaged, which are not easy to convert to the proportion of trees damaged (Picard et al. 2012). The different measures used are probably a reflection of the different aims of studies or whether studies used ground surveys or remote sensing to assess damage. However, I suggest that assessments of damage should be carried out at the tree scale rather than assessing the area affected. In addition by reporting the proportion of remaining basal area that is damaged extra information of the potential impacts on the biomass in the forest can be made. Further stratifying logging damage by tree size class would allow an assessment of its potential demographic effects and would thus aid our understanding of the recovery of logged forests.

4.4.6 Reducing the negative impacts of logging

The results from this meta-analysis suggest that the most obvious way of reducing the negative impacts of tropical logging is to reduce local logging intensity.

However, given that more than 400 million hectares of tropical forest have already been designated for logging (Asner et al. 2009), this reduction in local intensity, and thus yield, may encourage expansion into previously unlogged areas. This mirrors the situation in agricultural landscapes where the biodiversity benefits of high-yield farming over small areas as opposed low-yield, extensive farming is heavily debated (Phalan et al. 2011; Benayas and Bullock 2012). A recent study indicates that high intensity logging over a smaller area (‘land sparing’) has better outcomes for tropical forest species than low-intensity extensive timber extraction (‘land sharing’) in Borneo (Edwards et al. 2013). I suggest that this sparing/sharing framework may prove useful to assess the potential value of differing land-use strategies in landscapes used to provide provisioning ecosystem services such as food and timber (Millennium Ecosystem Assessment 2005).

Reduced Impact Logging is widely advocated as a means of improving the long term sustainability of logging in tropical forests (Pinard and Putz 1996; Putz et al. 2008; Putz et al. 2012). My work found weak support that RIL can reduce damage to non-target trees in logged forests and potentially reduce carbon losses as a result, but any benefits of RIL compared to conventional selective logging are obscured by variation in logging intensity which is strongly linked to losses in aboveground biomass and changes in species richness. This is a classic example of a hidden treatment in an ecological experiment where an experimental manipulation has multiple components, only one of which is identified as an experimental treatment as identified by Huston (1997).This can lead to false conclusions about the cause and effect nature of such relationships because the actual cause of any observed response may be ignored in the interpretation of results (Huston 1997). This is currently the case in almost all studies that have aimed to assess the benefits of RIL when compared to conventional logging (but see West et al. 2014).

Though reductions in logging intensity may reduce impact, the high demand for timber requires novel solutions that do not drastically reduce current yields but reduce impacts on forest ecosystems. Methods such as silvicultural thinning techniques to remove pioneer species may aid recovery of floral community composition, carbon and timber stocks but further work is needed to assess their effectiveness (Ouédraogo et al. 2011; Gourlet-Fleury et al. 2013). Although RIL may also provide an appropriate solution, further evidence is required to verify this. I recommend further research to be undertaken to quantify the impacts of differing logging methods and intensities for the management of biodiversity, carbon pools and other ecosystem services. Such research is critical to inform policies to improve management of the vast area of tropical forest designated for permanent production.

4.4.7 Opportunities for further research

In addition to methodological issues in the study of logged forests, there are a number of key issues which appear to be relatively understudied; these relate to the long-term dynamics of logged forests after logging and investigation of techniques which provide an alternative to RIL in reducing the negative impacts of logging on biodiversity and carbon storage. When compared to secondary tropical forests relatively little is known about recovery of biomass and biodiversity in logged forests. This is likely to be a result of the increased risk of deforestation following logging (Asner et al. 2006), meaning that monitoring the dynamics of such sites is fraught with difficulties. The main method for monitoring post-logging dynamics has been experimental manipulation of forests under the control of research organisations. This has resulted in valuable detailed studies of dynamics of forests in French Guyana (Baraloto et al. 2012; Sist et al. 2012), the Brazilian Amazon (Mazzei et al. 2010) and the Central African Republic (Gourlet-Fleury et al. 2013). However, there seems to be a relative paucity of monitoring in SE Asian logged forests, where logging intensity is highest. Attempts to improve long term monitoring in Asian and Oceanian forests (Priyadi et al. 2005) must succeed to assess the sustainability of different logging strategies in this region.

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Chapter 5

5 Carbon pools recover more quickly than plant biodiversity in tropical secondary forests

5.1 Abstract

Although increasing efforts are being made to restore tropical forests, little information is available regarding the timescales required for carbon and plant biodiversity to recover to the values associated with undisturbed forests. To address this knowledge gap, we carried out a meta-analysis comparing data from >600 secondary tropical forest sites with nearby undisturbed reference forests. Above-ground biomass approached equivalence to reference values within 80 years since last disturbance, whereas below-ground biomass took longer to recover. Soil carbon content showed little relationship with time since disturbance. Tree species richness recovered after about 50 years. In contrast, epiphyte richness did not reach equivalence to undisturbed forests. The proportion of undisturbed forest tree and epiphyte species found in secondary forests was low and changed little over time. Our results indicate that carbon pools and biodiversity show different recovery rates under passive, secondary succession, and that colonisation by undisturbed forest plant species is slow. Initiatives such as the Convention on Biological Diversity and REDD+ should therefore encourage active management to help achieve their aims of restoring both carbon and biodiversity in tropical forests.

5.2 Introduction

Tropical forests contain between half and two thirds of terrestrial global biodiversity (Gardner et al. 2010) and approximately 37% of the global terrestrial carbon pool (Dixon et al. 1994). These forests also provide vital ecosystem services at local, regional and global scales (Foley et al. 2007; Gardner et al. 2009). Despite these benefits, tropical forests are undergoing widespread loss, largely as a result of agricultural expansion (Gibbs et al. 2010). These losses have led to increased carbon emissions, species extinctions and structural alteration of the majority of tropical forests worldwide (Foley et al. 2007; Gardner et al. 2009).

To combat these on-going losses, many projects have been implemented in different countries over the past two decades with the aim of restoring millions of hectares of tropical forest (Sayer et al. 2004; Calmon et al. 2011). The need for tropical forest restoration is recognised in international policy through the Convention on Biological Diversity (CBD) and REDD+ initiatives (CBD 2010; Alexander et al. 2011). The 2020 targets of the CBD aim to enhance biodiversity and carbon stocks, by restoring 15% of the world's degraded ecosystems (CBD 2010). In addition, REDD+ aims to enhance carbon stocks partly through forest restoration, using funding from carbon credits (Alexander et al. 2011). However, despite the perceived importance of restoring tropical forests for both carbon storage and biodiversity, information is lacking on their patterns and rates of recovery following disturbance.

To determine the relative value of recovering forests as carbon pools and for biodiversity conservation, comparison with a reference forest is required, such as a site that is relatively free of human disturbance. Previous studies of carbon accumulation in tropical secondary forests (e.g. Silver et al. 2000; Marín-Spiotta and Sharma 2012) have not undertaken comparisons against such reference systems. As such, these syntheses provide limited information about the recovery of carbon pools in tropical forests, but rather examine the factors explaining differences in biomass and soil carbon among tropical secondary forest sites, with climate emerging as a major driver (Johnson et al. 2000; Anderson et al. 2006; Marín-Spiotta and Sharma 2012).

As biomass recovers following disturbance, it is to be expected that forest ecosystems should accumulate carbon pools with time (Brown and Lugo 1990; Silver et al. 2000). In the case of secondary tropical forests, little information is available regarding the time period required for recovery of these carbon pools to the values of undisturbed forests. The most studied of these pools is that associated with aboveground biomass, for which recovery appears to become asymptotic over time (Saldarriaga et al. 1988; Hughes et al. 1999; Read and Lawrence 2003; Cifuentes-Jara 2008). However, the time required for this pool to recover completely has been hypothesised to be anywhere between 50 and 200 years (Hughes et al. 1999; Cifuentes-Jara 2008). Below-ground biomass has been studied less frequently, but may require similar periods for complete recovery, with Saldarriaga et al. (1988) suggesting an interval of over 80 years.

Changes in soil carbon in secondary forests are less well documented than biomass recovery. A transition from agricultural use to secondary forest generally results in an increase in soil carbon content (Guo and Gifford 2002b), but the evidence for soil carbon accumulation during secondary succession is conflicting. Recovery of soil carbon in secondary tropical forests to values similar to those in undisturbed forest can take 20-100 years (Rhoades et al. 2000; Neumann-Cosel et al. 2011), but some secondary forests have higher soil carbon than undisturbed forest (Saynes et al. 2005).

In contrast to studies of carbon pools, there have been a number of syntheses of biodiversity recovery in secondary tropical forests. These suggest that faunal species richness recovers relatively quickly during succession (Dunn 2004), but more than 150 years may be required for community composition to reach equivalence to undisturbed forests (Dent and Wright 2009). However, relatively little is known about changes in plant communities during secondary succession in tropical forests. The only previous synthesis – albeit of only eight locations across Central and South America – of plant biodiversity in secondary forests suggests that they may take longer to become equivalent to undisturbed forest than faunal communities, with only 40% of undisturbed forest species having colonised secondary forests after 80 years of recovery (Chazdon et al. 2009).

No integrated meta-analysis of the recovery of both carbon pools and plant biodiversity in tropical forests has been undertaken previously. Such information is urgently required to inform policy and management practice. To address this knowledge gap, we address the following questions by conducting a meta-analysis based on systematic review:

(i) At what age following forest clearance do carbon pools in secondary tropical forests reach equivalent values to those of undisturbed forest?

(ii) At what age following forest clearance do plant species richness and the proportion of undisturbed forest species in secondary tropical forests reach equivalent values to those of undisturbed forest?

(iii) How do the rates of recovery of biodiversity and carbon pools compare, and what are the consequences for tropical forest restoration policy?

5.3 Methods

5.3.1 Systematic review

We defined tropical secondary forest as a previously forested area undergoing secondary succession following total or near total removal of trees

(Corlett 1994), located between the latitudes 40° N and 40° S (Newbold et al. 2013). To collate relevant studies a systematic review was carried out using standard methodologies (Pullin and Stewart 2006). The online databases Web of Knowledge, Wiley Blackwell and Science Direct were searched, along with the Society for Ecological Restoration International website, and the internet search engine Google. Search terms were combinations of the keywords: tropical AND (*forest* OR wood* OR jungle*) AND (restor* OR reforest* OR recov* OR rehabilitat* OR secondary OR swidden OR slash* OR degrad*) AND (plant* OR carbon OR biomass OR litter OR rich* OR biodiversity OR function* OR service*). Records of all studies were downloaded to an Endnote database and the last date of access was 17th October 2012.

Irrelevant articles were excluded, first if titles were deemed irrelevant, and then by examining abstracts. The remaining articles were read and retained only if they met the inclusion criteria. Where there was evidence that relevant data had been collected but were not presented in the publications, data were requested from the authors. Data on aboveground biomass, belowground biomass, soil carbon, plant species richness and plant community composition were extracted from the retained studies and stored in a database.

Where data were presented in tables they were simply transferred to the database, but when data were graphical the program datathief (vIII) (Tummers 2006) was used to extract them.Where a range was given for the age of a forest the median value was recorded. Where soil carbon was given as % organic matter or % soil carbon this was converted to Mg ha^{-1} using standard equations (Guo and Gifford 2002b; Marín-Spiotta and Sharma 2012). Where soil bulk density (required to calculate carbon stocks) was not reported we used equations from (Guo and Gifford 2002b) and multiplied organic matter content by 0.5 to estimate carbon concentrations (Marín-Spiotta and Sharma 2012).

Studies were retained if they included: (i) at least one measurement of either above-ground biomass, below-ground biomass, soil carbon content, plant species richness and / or plant species community composition in both a secondary tropical forest and a reference undisturbed forest (following Gibson et al. 2011); (ii) the time since last disturbance for secondary forests; and (iii) definition of the type of disturbance prior to secondary succession, which included conversion to pasture, cropland or small-scale shifting agriculture. In addition, we extracted data on forest type determined by Holdridge life zone (Holdridge 1967) (hereafter referred to as forest type), and geographic location. Although methodologies differed amongst studies, measurements in secondary and undisturbed forests within a study were carried out using the same methods and using the same plot sizes.

Almost all of data we collated came from chronosequence studies where secondary forest stands of different ages were used to infer successional dynamics. One of the assumptions of chronosequences is that all sites have been subject to the same environmental conditions, though in practice this condition is rarely met (Johnson and Miyanishi 2008). For the purposes of our study we also assumed that undisturbed forests had stable carbon pools and species composition. This assumption is again unlikely to be met since many undisturbed forests are known to be increasing in biomass (Baker et al. 2004) and undergoing changes in biodiversity, but we consider these changes to be less dramatic than those caused by secondary succession. As such our study is reflective of the wider secondary forest literature which tends to make similar assumptions about chronosequences.

5.3.2 Statistical analysis

We calculated secondary forest carbon pool and species richness recovery using the equation:

$$logit\frac{\left(\frac{\bar{X}_{Sec}-\bar{X}_{Ref}}{\bar{X}_{Ref}}\right)+1}{2}$$

where $\bar{X}_{Sec}$ is the mean of a measurement in a secondary forest and $\bar{X}_{Ref}$ is the mean of the same measurement in the corresponding undisturbed reference site. This is a logit transformation of the proportional difference between secondary and undisturbed forests that conforms to the assumptions of linear models. Following model fitting, predicted values were converted to proportions relative to reference forests by calculating the inverse logit and multiplying by two.

Since most studies did not provide estimates of variation along with measurements of carbon pools or species richness, an unweighted analysis was used. Although this technique gives equal weight to studies that may differ in quality and accuracy, it has been used frequently in the ecological literature (Rey Benayas et al. 2009; Moreno-Mateos et al. 2012), where data reporting standards are very variable. A linear mixed model was constructed for each variable of interest using time since last disturbance, disturbance type and forest type as explanatory variables. We included quadratic or log relationships with time since disturbance where our hypotheses suggested there may be non-linear changes during succession. A random factor was included to group secondary forests which shared a undisturbed forest reference site eliminating the problems of pseudoreplication at the study scale (Bolker et al. 2009). In addition, random variables were included to account for differences in study methods, such as in measurement depth for soil carbon and whether allometric equations for calculation of biomass were locally derived or represented general multi-species allometries (e.g. Chave et al. 2005). Random variables accounting for the difference in minimum diameter at breast height (DBH) of trees included in assessments of species richness were also considered, but were found to add little explanatory value and thus were excluded from models (see Table S 15 for details of different minimum DBH used in studies). The proportion of the undisturbed forest plant species found in secondary forests was used as a metric of changes in community composition (see Barlow et al. 2007; Chazdon et al. 2009) and was analysed using a binomial generalised linear mixed model with logit link. While there are techniques which are better suited to determining whether species are undisturbed forest specialists (e.g. Chazdon et al. 2011), they require detailed data for each study to which we did not have access.

All possible additive models were computed using restricted maximum likelihood methods. Model comparison was based on AICc, excluding all models with Δ AIC$_C$ ≥7 (Burnham et al. 2011). We estimated the goodness of fit of each model by calculating the marginal R^2 using the equations developed by Nakagawa and Schielzeth (2013). Coefficients were derived from the weighted mean of all models with Δ AIC$_C$≤7. The importance of variables in explaining recovery of carbon pools and plant biodiversity was assessed by summing the weight of all models that included the variable (Burnham et al. 2011). Analyses were performed in R 2.15.3 (R Development Core Team 2011), with model averaging using the MuMIn package (Barton 2013), and all graphs produced using the ggplot2 package (Wickham 2009).

5.4 Results

The systematic review yielded data for 607 secondary forest sites from 74 studies describing aboveground biomass, belowground biomass, soil carbon, plant species richness or plant species composition, with comparable data for a reference undisturbed forest (further details in Appendix - Table 1). The majority of these sites were relatively young, with mean ages of between 20 and 30 years for each variable of interest (Appendix - Figure 1). Thus biomass and carbon recovery was measured for forests up to 85 years old. Biodiversity data was available for forests up to a little over 150 years old, although virtually all sites were under 100 years old. Most sites were in Central or South America (Figure 22), with few sites in Africa or Asia.

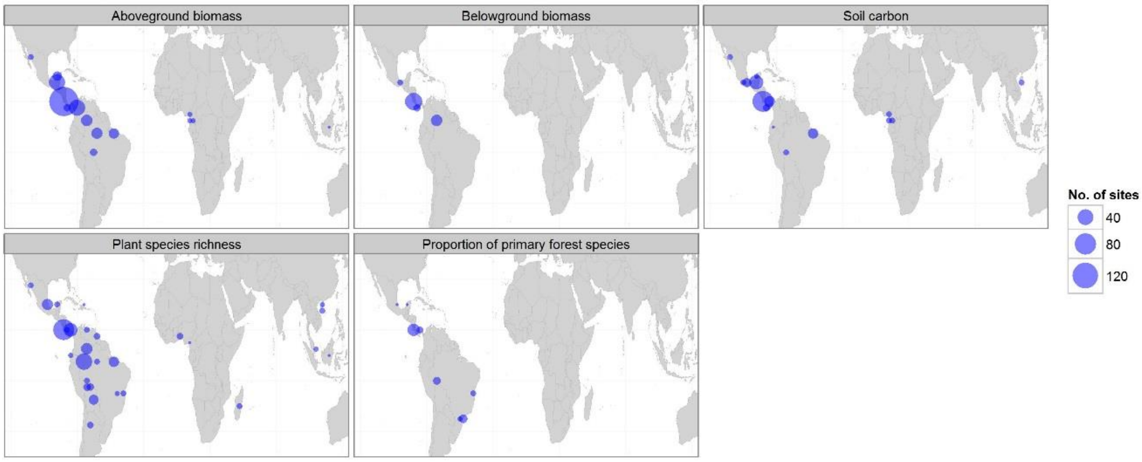

Figure 22 – Locations of studies from which data on aboveground biomass, belowground biomass, soil carbon, plant species richness and proportion of primary froest species were extracted. Data is summarised as the number of sites per 1 degree grid cell.

Model selection suggested that the best model describing aboveground biomass recovery in secondary forests included only a log relationship with time since disturbance. This model predicted recovery of aboveground biomass to slow over time and to be about 83% of that of undisturbed forests after 85 years (Figure 23). This model had an AICc weight of 0.57 and a marginal R^2 of 0.56 (Appendix III-Table A16). The relationship between relative biomass recovery and age was much more important than those of forest type and prior land use (Appendix III - Table A28).

Below-ground biomass increased more slowly than above-ground biomass as a function of forest age. As with aboveground biomass there was a log relationship with time since disturbance; after 80 years stocks in sites previously subject to shifting agriculture were still only about 50% of those in reference forests (Figure 23). Forests established on pastures appeared to recover below-ground biomass more rapidly than those following shifting agriculture, with recovery to 76% of reference levels in approximately 80 years. Forest type was not important in explaining differences between undisturbed and secondary forests (Importance value=0, Appendix III - Table A28). Models with Δ AIC$_C$≤7 had marginal R^2 values of 0.60-0.64 (Appendix III - Table A17).

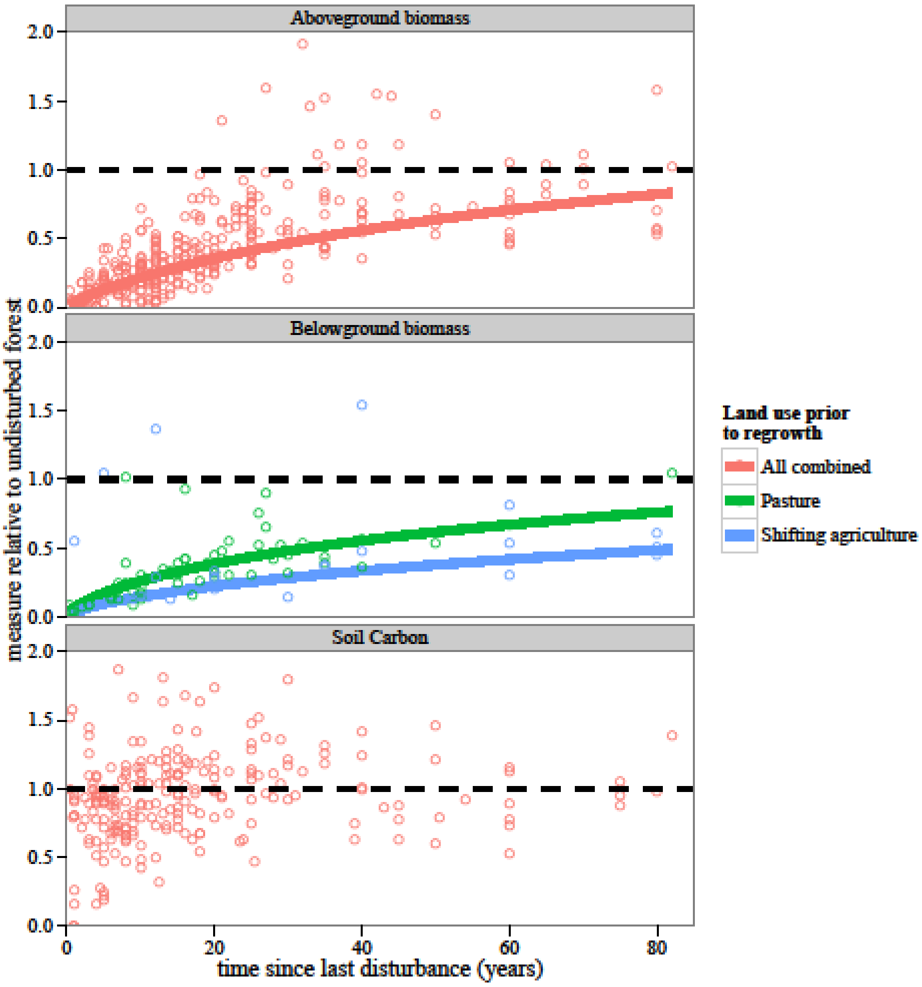

Figure 23 – Recovery of aboveground biomass (n=326), belowground biomass (n=76) and soil carbon (n=185) in secondary tropical forests, relative to undisturbed reference forests. Solid lines represent model predictions, with different colours representing different disturbance types. Parameters included in figures have AICc importance values >0.5. The horizontal dashed line represents no difference between secondary and undisturbed forests.

Soil carbon stocks showed very weak relationships with all variables; an intercept only model had the most support (AICc weight=0.43, Appendix III- Table A19). However, models predicting slight increases in soil carbon with time since disturbance were also supported, although these had extremely small marginal R^2 of ≤0.01 (Appendix III - Table A20).

Plant species richness increased with time since last disturbance – again following log relationships – with epiphyte richness showing slower recovery than tree richness (Figure 24). Tree species richness was predicted to recover after approximately 50 years, while epiphyte richness was predicted to take longer than 100 years. Model fits of tree species richness were also much better than those for epiphytes, with marginal R^2 of 0.24-0.26 and 0-0.08 respectively (Appendix III - Tables 21 and 22). In contrast, a relationship between time since last disturbance and proportion of species associated with undisturbed forest was relatively poorly supported (Importance value=0.35). The proportion of species associated with undisturbed forest was generally low, with a mean of 26% of species also being found in secondary forest (Upper CI=67%, Lower CI=6%; Figure 25; Appendix III - Tables A21 and A27).

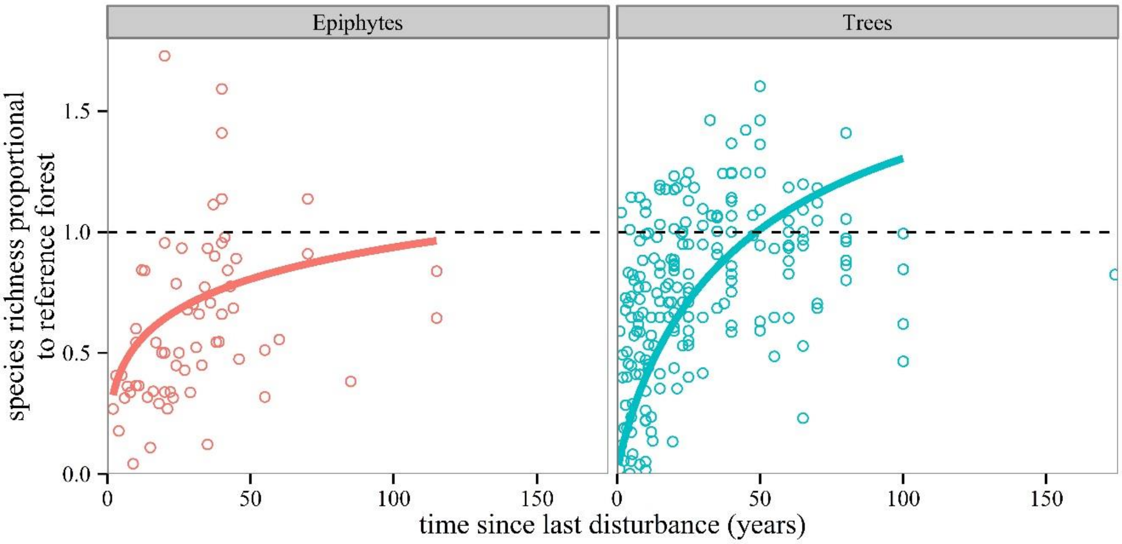

Figure 24 – Recovery of epiphyte (n=65) and tree (n=204) species richness in secondary tropical forests, relative to undisturbed reference forests. Solid lines represent model predictions, with different colours representing different disturbance types. Parameters included in figures have AICc importance values >0.5. The horizontal dashed line represents no difference between secondary and undisturbed forests.

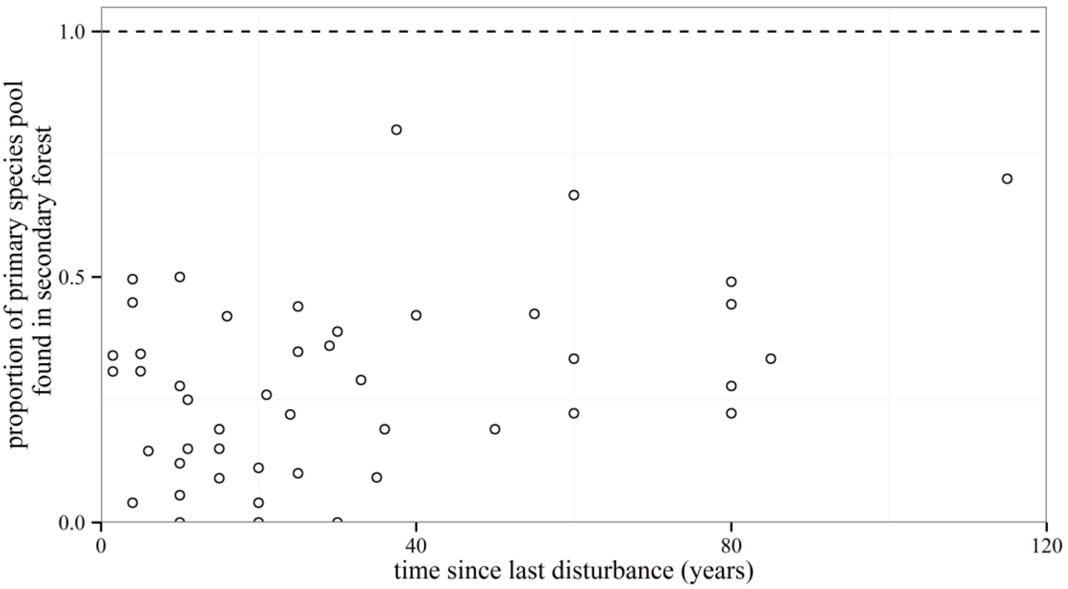

Figure 25 –Recovery of species associated with undisturbed tropical forest in secondary forest (n=50). The horizontal dashed line represents no difference between secondary and undisturbed forests.

5.5 Discussion

This study is the first to assess the recovery of both carbon pools and plant biodiversity across a large number of secondary tropical forest sites. Our results indicate that the various carbon pools and measures of biodiversity recover at different rates. Above-ground biomass approaches recovery 85 years after the last disturbance. Below-ground biomass also increases over time, with former pastures recovering 75% of belowground biomass after about 80 years, while areas affected by shifting agriculture take longer to recover. Soil carbon remained largely unchanged over time. In terms of biodiversity, tree species richness reached equivalence to reference forests after approximately 50 years and epiphyte richness only approached recovery after 100 years while the recovery of undisturbed forest species in secondary forests was limited and showed little relationship with time.

5.5.1 Recovery of carbon pools

Although previous work has suggested that rates of biomass accumulation differ between dry, moist and wet tropical forests (Saatchi et al. 2011) as well as among disturbance types (Silver et al. 2000), our study indicates that these factors are largely unimportant in determining the rate of recovery towards the state of undisturbed forests. Our estimated time required for above-ground biomass to reach approximately 85% of undisturbed forest levels is similar to suggested rates for basal area recovery in the neotropics (Guariguata and Ostertag 2001). While our results and previous observations (Guariguata and Ostertag 2001) suggest that forest biomass approaches that of undisturbed forest within a century, full recovery may take substantially longer. This is because many secondary forests are often composed of relatively small stemmed trees and lack the very large trees characteristic of old-growth forest, which can have very high biomass (Lindenmayer et al. 2013). However, without more data from older secondary forests it is difficult to determine how long full recovery takes. One important caveat regarding aboveground biomass recovery is that allometric equations used for its estimation are usually derived from undisturbed forest plots (van Breugel et al. 2011). As a result of this measurements in secondary forests, which are often dominated by trees with low DBH, may overestimate their biomass (van Breugel et al. 2011) possibly because of differences in secondary forest height:diameter relationships (Montgomery and Chazdon 2001). This is a potential bias in all the individual studies we used and we suggest that further research should aim to develop and test allometries designed for use in secondary forests to characterise recovery more accurately.

Belowground biomass represents an average of 19% of total biomass in tropical forests (Cairns et al. 1997), although root:stem ratios tend to be higher in younger forests (Fearnside and Guimarães 1996; Mokany et al. 2006). Thus, we would expect belowground biomass to recover more rapidly than those of aboveground biomass and it is surprising that we found the opposite pattern. However this effect may be an artefact because those sites for which we had belowground biomass data had lower aboveground biomass than other forests of similar age (Appendix - Figures 3 and 4).

We found that secondary tropical forests have soil carbon contents similar to undisturbed forests, contradicting a recent meta-analysis (Don et al. 2011), which suggested lower soil carbon in secondary forests. The differences between our study and that of Don et al. (Don et al. 2011) result from differing definitions of secondary forest, which they considered to be forests affected by any human disturbance. That definition conflates different types of disturbance and covers human-impacted forests and plantations as well as those undergoing secondary succession. As such we believe that our study more accurately represents soil carbon content in secondary forests as more usually defined – those that are recovering from near total removal of tree cover (Corlett 1994). Our findings do however support those of Marín-Spiotta et al. (Marín-Spiotta and Sharma 2012), who also found similar soil carbon pools in secondary and undisturbed tropical forests. These results indicate either that soil carbon in tropical forests is resilient to moderate, short term land use change or that carbon is accumulated rapidly following abandonment of farmland. However, as with belowground biomass, further research is required to explain the drivers of differences in soil carbon between sites. Given that the world's soils contain two to three times the carbon stored in aboveground biomass (Marin-Spiotta et al. 2009) such research should be considered a priority.

Former land use had an inconsistent effect on recovery of carbon pools in our study: there was no effect on above-ground biomass or soil carbon, but below-ground biomass recovered faster in former pastures than following shifting agriculture. The intensity and length of time under previous land-use influence factors such as soil nutrient content and undoubtedly play important roles in biomass recovery (Chazdon et al. 2007). For example, research has suggested that above-ground biomass is lower in secondary tropical forests that have experienced multiple cycles of conversion for shifting agriculture (Lawrence 2005; Eaton and Lawrence 2009). However, such detailed data were not collected for the majority of studies we analysed, and future studies should do so to aid our understanding of the factors that control carbon stocks in secondary forests.

Overall, these findings suggest that when attempting to restore carbon pools on tropical forest sites cleared for agriculture, the greatest gains are likely to be made in plant biomass as soil carbon appears to be relatively insensitive to moderate land use change. Independent of forest type, carbon pools in secondary forest sites could be expected to be 77-81% of those of undisturbed forests approximately 80 years after disturbance, given that aboveground biomass has been estimated as 5 times that of belowground biomass in tropical forests (Cairns et al. 1997).

5.5.2 Recovery of species richness and community composition

We found that tree species richness recovered within 50 years compared to >100 years for epiphyte richness. We have less confidence in the prediction of a continuing increase after 50 years, which is likely to be an artefact of the steep increase in younger forest and the relatively few data for older forests meaning that the shape of the log-relationship was constrained. Indeed, the data suggest relatively little increase after 50 years and our model tends to over-predict tree richness in older forests. In addition to differing recovery rates, our model of tree species richness change also showed a much better fit than that of epiphyte richness. These differences in recovery and our ability to explain changes in richness are likely to be driven by contrasting dispersal traits and requirements for establishment. Secondary tropical forest tree communities are initially dominated by short lived pioneer tree species and these are sequentially replaced by longer lived species (Guariguata and Ostertag 2001). Some secondary forests may be isolated from seed sources leading to an impeded recovery of richness, but our results, and the observations of others (Guariguata and Ostertag 2001), suggest that this is relatively rare. In contrast, epiphyte dispersal is largely local and propagation is often restricted to individual trees (KÖSter et al. 2009). In addition, epiphytes seem to occur more commonly on large trees (Woods and DeWalt 2013). These factors may lead to relatively poor recovery of epiphyte species since many secondary forests are fragmented and tend to consist of smaller stemmed trees (Guariguata and Ostertag 2001). An important caveat of our analysis is that few estimates of species richness were rarefied by either number of individuals or area sampled. It is possible that since secondary forests almost always have higher stem densities that our analysis overestimates species richness recovery. However, from a conservation perspective, given that plot size was equal for the secondary and undisturbed plots in all pairwise comparisons, our estimation of species per unit area remains valid.

Although tree species richness recovers relatively well in secondary forests, there was little or no accumulation of species associated with the reference undisturbed forests. This contrasts with the more rapid colonisation rates of animal species, communities of which may attain similarity to those of undisturbed forests within 150 years (Dent and Wright 2009). The poor recovery plant community composition is likely to be the result of a number of interacting mechanisms. Firstly, small secondary forest patches are likely to be subject to greater edge effects than larger undisturbed patches, making them less likely to be colonised by species adapted to old-growth forest conditions (Benitez-Malvido 1998). Secondly, patches of secondary forest can be distant from undisturbed forests (Turner and T. Corlett 1996) and thus receive few seeds from them. Finally, the extent of degradation of the landscape surrounding secondary forests will also influence seed dispersal processes, such as the behaviour of frugivorous birds (Chazdon et al. 2007).

In addition to these ecological mechanisms that might explain differences in the responses of species richness and community composition in secondary tropical forests, our study is subject to some of the limitations of the literature we used in our analyses. The most important factor is likely to be associated with distance-decay in community similarity (Condit et al. 2002). Sites used in this study are likely to vary in their distance from undisturbed reference sites and thus the proportion of species shared with undisturbed forests would be expected to vary, even without any human disturbance (Condit et al. 2002; Ramage et al. 2012). Unfortunately, very few studies give details of distances between secondary and reference sites. We hope that future studies might record such landscape metrics. Despite this our findings suggest that natural colonisation alone may not be sufficient to restore tropical forest plant biodiversity effectively in less a century.

5.5.3 Comparative rates of carbon and biodiversity recovery

Our results indicate that carbon pools and tree species richness recover more quickly than epiphyte species richness, while undisturbed forest plant species do not accumulate over time in secondary forests. Analyses of the carbon and biodiversity benefits of avoided deforestation have often suggested synergistic relationships between these goals due to overlap of priority areas for biodiversity conservation and carbon storage (Ebeling and Yasué 2008; Venter et al. 2009). In contrast, reforestation schemes that have the primary aim of carbon sequestration have often been criticised as they may support relatively little forest biodiversity (Bekessy and Wintle 2008). Our study suggests a more nuanced relationship between biodiversity and carbon in secondary tropical forests: while both carbon storage and conservation value increase as secondary forests age, the trajectories of these increases differ. As a result of this, tropical forests recovering from agricultural conversion are likely to have greater value for carbon storage and sequestration than for biodiversity, especially during the first 100 years of development. These differing rates of recovery should be acknowledged by policies targeting the recovery of biodiversity and carbon in tropical forests.

The failure of species associated with undisturbed forest to colonise secondary forests effectively is worrying for those aiming to conserve biodiversity in tropical forest landscapes subject to human disturbance. These species are likely to be adapted to old-growth conditions and thus are likely to be sensitive to human disturbance, have small ranges and populations (Gardner et al. 2007) and as a result they are likely to face greater threats of extinction (IUCN SSC 2001). This result clearly indicates that old growth forests are vital for the conservation of some specialist species but also that if goals to conserve species in human disturbed ecosystems are to be achieved we require novel solutions and further research.

5.6 Conclusion

This study is the first integrated meta-analysis of both plant biodiversity and carbon pool recovery in tropical secondary forests. We have shown that the recovery periods for the two differ markedly. This has important implications for policies that target recovery of both carbon and biodiversity, such as the Convention on Biological Diversity and REDD+. Carbon pools may take approximately 80 years to recover following disturbance, faunal biodiversity 150 years (Dent and Wright 2009) and plant biodiversity well over 100 years. Thus, initiatives aiming to support recovery of both biodiversity and carbon should not assume that the two are closely coupled. Enhancement of carbon stocks to the values associated with local undisturbed forests appears possible through passive restoration. However, in many situations active restoration involving human interventions (e.g. planting trees) or other strategies such as increasing seed dispersal across the non-forest matrix by creating woodland islets (Rey Benayas et al. 2008) may be required to enable long-term recovery of plant species community composition. In addition further research into active restoration of tropical forests is required to identify novel solutions to this problem.

5.7 References

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Chapter 6

6 Identifying priority areas for tropical forest restoration: trade-offs between carbon and biodiversity

6.1 Abstract

Ecological restoration of tropical forests is seen as means of addressing the problems associated with deforestation and degradation. Both the Convention on Biological Diversity (CBD) and Reducing Emissions from Deforestation and Degradation (REDD+) aim in part to incentivise the restoration of biodiversity and carbon in degraded and deforested areas. However, these initiatives appear to assume that areas that maximise carbon storage and biodiversity value coincide, an assumption that is untested. Given that there have been numerous costly forest restoration failures these assumptions need to be tested to identify the potential for trade-offs and win-win situations for the two goals. To do this I produced statistical models of carbon accumulation and bird species presence using data from previous studies. Following model selection and averaging I projected these models to predict carbon accumulation and bird presence in secondary forests throughout the tropics. Each bird species was weighted by the inverse of its global range so that species with smaller distributions were considered more important. Areas that accumulated most carbon tended to be located in the wet tropics, particularly the Western Amazon and the Indonesian Archipelago. Bird biodiversity value was maximised in areas where species had small ranges, particularly around mountain ranges. My results suggested that there was no relationship between the two goals, but that areas which maximised both goals could be identified. This suggests that in the case of tropical forest restoration carbon and biodiversity do not act as proxies for each other and explicit consideration of the two is needed to maximise the returns from investment in restoration.

6.2 Introduction

Tropical forests contain between half and two-thirds of all terrestrial biodiversity (Gardner et al. 2009) and approximately one-third of terrestrial carbon (Dixon et al. 1994). In addition, these forests are a principal source of multiple ecosystem services at local, regional and global scales (Foley et al. 2007). However, despite the benefits they provide, tropical forests are rapidly being cleared for agriculture (Gibbs et al. 2010), and face widespread degradation - largely as a result of logging (Asner et al. 2009). Ecological restoration of tropical forests is seen as one way of addressing these problems (Lamb et al. 2005; Chazdon 2008) and initiatives have been set up to incentivise this (CBD 2010; Alexander et al. 2011). Both the Convention on Biological Diversity (hereafter CBD) and Reducing Emissions from Deforestation and Degradation (REDD+) initiatives aim, in part, to encourage the restoration of biodiversity and carbon in degraded and deforested areas (CBD 2010; Alexander et al. 2011). However, these initiatives implicitly assume that areas that will maximise carbon storage, will also maximise biodiversity conservation. In the case of forest restoration this assumption is untested despite good knowledge of the factors that affect recovery of both carbon and biodiversity in tropical forests.

Previous studies have shown that forest restoration can be effective in improving conservation value and ecosystem service provision of degraded areas, with some older sites resembling old-growth forest (Gilroy et al. 2014a). While this restoration can often be cost effective (Birch et al. 2010), recovery of sites varies widely (Martin et al. 2013) as does their suitability for restoration. This has led to the costly failure of many restoration programmes (Jones and Schmitz 2009), resulting in perverse outcomes for both biodiversity and ecosystem services (Bullock et al. 2011). Examples of this include China’s Grain to Green project in which trees were planted in areas unsuitable for forest growth leading to increased erosion and negative biodiversity impacts (Cao et al. 2009). If such mistakes are to be avoided in the future and returns from restoration are to be maximised prioritisation of areas for forest restoration is important (Holl and Aide 2011) and, as such, it is seen as a research priority (Sutherland et al. 2009).

Spatial prioritisation aims to address how to allocate funding for conservation most effectively in space and time (Moilanen et al. 2009). Previous forest restoration prioritisation has been undertaken from local (Llewellyn et al. 1996) to global scales (Newton and Kapos 2003), and has had many different aims from restoration of habitat for individual species to increased ecosystem services provision (Birch et al. 2010). There is a much disagreement about the indicators that should be used to identify forest restoration priorities (Orsi et al. 2011) but criteria broadly fall into one of two groups: (a) those that identify the potential benefits that forest restoration may provide and (b) those that relate to the likelihood of success of a restoration project. In any forest restoration scheme it is vital these sets of criteria are addressed.

Areas that are likely to benefit from forest restoration are usually determined by identifying previously forested areas that have been deforested or degraded (Humphrey et al. 2000; Newton and Kapos 2003; Twedt et al. 2006; Orsi et al. 2011). Following this the presence of rare or endemic species, or species richness in the surrounding area have often been used as criteria for further prioritisation (Newton and Kapos 2003; Newton 2011; Orsi et al. 2011). While identification of species rich areas is intuitive as a means of prioritisation, conservation planning suggests that the irreplaceability of an area, which is reflective of the number of locations at which the same species are likely to be present, is preferred in conservation prioritisation (Moilanen et al. 2005). For example, an individual area that contains only species that occur in many other sites has low irreplaceability, while a site with species that occur at a few sites has higher irreplaceability. Thus, defining priority sites by their irreplaceability favours species rich communities which consist of species with restricted ranges (Moilanen et al. 2009), since these are at highest risk of extinction (IUCN SSC 2001).

The likelihood of a restoration scheme achieving these benefits is the result of an interaction between landscape characteristics and pressures from human population. Landscapes that have a large area of remnant forest are relatively close to intact forests, and have low levels of fragmentation are considered more likely to show a positive biodiversity recovery (Newton and Kapos 2003) since these benefit colonisation by forest taxa (Cordeiro and Howe 2001; Cordeiro and Howe 2003).

While such criteria are useful for guiding restoration of forests they are usually selected by expert opinion, which can lead to misidentification of important factors (Martin et al. 2012). Thus an approach to assessing a landscapes’ potential for meeting restoration targets based on empirical relationships is preferable. However, neither REDD+ nor the CBD define how sites should be prioritised or make a distinction between the criteria by which sites should be selected for restoration of carbon or biodiversity, even though the processes that drive them appear to differ.

Carbon accumulation appears to be driven by climate and it is greatest in hot, wet climates (Johnson et al. 2000; Zarin et al. 2001), with maximum forest biomass limited by precipitation (Stegen et al. 2011). Regarding biodiversity, of all taxa, birds probably have the most well understood response to forest recovery (Dent and Wright 2009). Presence of a bird species at a site is likely to be a result of interactions between landscape structure and species traits and characteristics. Landscapes that have high forest cover and low fragmentation appear likely to retain a greater proportion of those species originally present. In addition, those species that have high dispersal ability (Şekercioğlu et al. 2002), are less dependent on forest (Newbold et al. 2013) and that are abundant throughout their range (Gaston et al. 2000) appear to be more likely to persist in disturbed forest landscapes. Thus, landscapes that have relatively intact forest and contain a high proportion of species with these characteristics are likely to show the greatest potential for the recovery of bird biodiversity. Given that different processes drive carbon accumulation and biodiversity recovery, it is potentially dangerous to assume that both co-benefits can be maximised and strategic targeting is likely to be required to meet goals.

Despite our understanding of the ecology underlying carbon accumulation and bird biodiversity responses in recovering forests, there has been little attempt to identify areas that may deliver the best results for biodiversity and carbon storage as a result of tropical forest restoration – even though these are aims of two major global conservation initiatives. Without prioritisation, it is unclear whether such a scheme would deliver win-win situations (with an overlap of priority areas for recovery of carbon and biodiversity) or whether there would be little overlap resulting in strong trade-offs. To address this issue in this chapter I (i) have produced statistical models to explain variation of aboveground biomass and bird presence in secondary tropical forests; (ii) used these to predict aboveground biomass and bird presence in secondary forests across the tropics and; (iii) in turn used these predictions to identify priority areas for achievement of REDD+ and CBD goals, examining evidence for synergies and trade-offs.

6.3 Methods

6.3.1 Data sources

The majority of data on aboveground biomass in recovering secondary tropical forests were obtained during a previous study in which I undertook a systematic review to collate data from all relevant sources (Martin et al. 2013). I supplemented these with additional data on aboveground biomass collected from reviews of carbon accumulation in secondary forests (Johnson et al. 2000; Zarin et al. 2001; Anderson et al. 2006). The majority of these data came from studies conducted in Central and South America, with relatively few sites in Africa or Asia (Figure 25). To explain differences in the biomass of different secondary forest sites, I used data from worldclim (www.worldclim.org; Hijmans et al. 2005) on mean monthly rainfall and mean monthly temperature. I also obtained data from the harmonized world soils database (http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/; Nachtergaele et al. 2012) to allow an assessment of the coarseness of soils found at each site. These variables have all previously been identified as possible drivers of biomass differences (Johnson et al. 2000; Zarin et al. 2001; Anderson et al. 2006). I also noted the age of secondary forests as well as the type of allometric equation used to calculate biomass (see Martin et al. 2013; Chapter 5 - this thesis). Data were restricted to forests <40 years old since biomass accumulation often becomes non-linear after this (Martin et al. 2013). Furthermore modelling of younger forests may be more informative for policy makers since early rapid accumulation may be of greater interest than long term storage. In addition the majority of studies are on younger sites, predicting accumulation in these forests is likely to be more accurate than over longer periods of time.

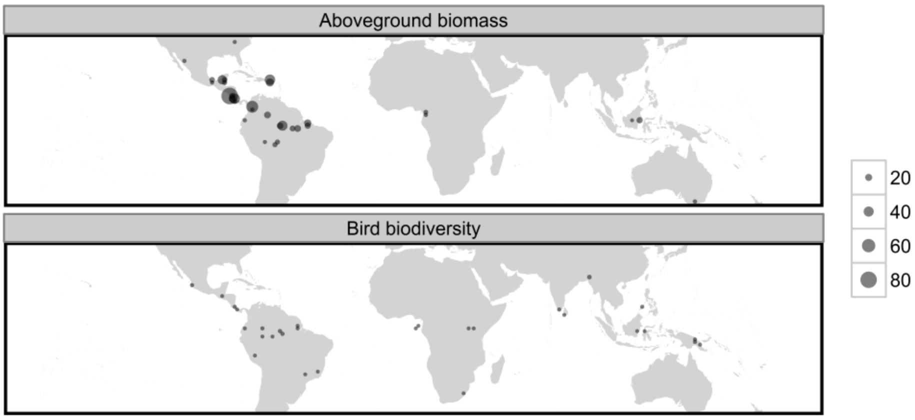

Figure 26 – Location of sites used for aboveground biomass and bird biodiversity models. Point size is relative to number of sites falling within a 2 degree grid square. Data taken from primary studies, for references see appendix.

Data on bird community composition in secondary forest sites were also taken from a previous study carried out by a master's student under my supervision (Sayer et al. 2013; for data on methods see appendix). These data had a more homogenous spread across the tropics compared to that of biomass, with a relatively even number of sites from each continent (Figure 26). To explain the differences in the likelihood of a species being present in secondary forest I collected data on forest cover, species traits and characteristics, and global range maps. I obtained percentage forest cover data from the Global Land Cover Facility (DiMiceli 2011) which I used to calculate forest cover statistics within a buffer with a radius 0.05 decimal degrees (an area of roughly 35km^2) since this was the finest resolution at which analyses could be carried out. The species traits and characteristics I used were dispersal distance, forest dependency of a species (none, low, medium or high), and global range size measured as the extent of occurrence. In addition, I used global range maps of species to determine likely local species pools within a grid composed of two degree cells, (an area of roughly 50,000km^2 at the equator), since at higher resolutions expert opinion maps misrepresent species pools (Hurlbert and Jetz 2007). All data on traits, characteristics and range maps were supplied by Birdlife International (2008; for more details of traits and characteristics used see Newbold et al. 2013).

6.3.2 Analyses

To test hypotheses about the recovery of aboveground biomass and bird biodiversity, I constructed a series of linear mixed models and used model averaging to produce parameter estimates. The model averaging approach I used followed the recommendations of Anderson et al. (2000) with all models considered biologically meaningful run, their AICc calculated and models ranked by AICc. I then calculated the difference in model likelihood as the difference between the best model's AICc and that of all other models, termed the ΔAICc (Burnham et al. 2011). I excluded all models with a ΔAICc > 7 from model averaging (Burnham et al. 2011). Following this, I undertook model averaging so that models with the lowest AICc provided more weight to parameter values and calculated importance values to determine the relative importance of individual variables in explaining variation in the response variable.

For the models of biomass recovery, the explanatory variables I used were based on equations provided by Johnson et al. (2000) and Anderson et al. (2006). First, I defined the number of annual growing season hours as the sum of the average number of daylight hours in each month (using the equations of Forsythe et al. 1995) where precipitation was >100mm in areas with an average annual temperature of >18°C, and with precipitation >40mm and monthly average temperatures >0°C for areas with an average annual temperature of <18°C. I defined growing season in this way for a number of reasons: (i) photosynthesis only occurs during daylight hours which therefore limits the time available for carbon accumulation (Anderson et al. 2006); (ii) average transpiration in tropical moist forests is ca. 100mm per month (Walsh 1996) and growth would be limited when precipitation drops below this amount (Doughty et al. 2014); and (iii) in cooler forests transpiration has been recorded at around 40mm per month during growing season (Cienciala et al. 1997; Wullschleger et al. 2001). I multiplied this annual growing season hour value by the time since last disturbance to produce an estimate of total growing hours – 'accumulated growing season hours' – following Anderson et al. (2006).

I tested the relationship between accumulated growing season hours and aboveground biomass along with mean temperature during the growing season, total precipitation during the growing season and soil coarseness. In order to do so, I assessed all models using these variables and two-way interactions with accumulated growing season hours. I could not use standard means of accounting for spatial autocorrelation as many sites had the same coordinates as each other, and so a random variable was used to identify sites drawn from the same chronosequence and study. Inclusion of this random factor eliminated problems of considering each data point to be independent. In addition, I included a random term to account for differences between the different allometric models used to calculate biomass since the selection of different allometric models can cause differences in biomass estimation (van Breugel et al. 2011).

For bird species recovery, I considered probability of presence as a function of percentage forest cover, species dispersal ability, species global range size and habitat specificity. As with biomass, I used a random term for sites drawn from the same study. I defined local species pools by whether a species was present or absent from a grid square using global range maps. I considered species to be absent if they were present in the species pool but not at the site and present if they were found at the site. Since I modelled likelihood of species presence given their presence in the species pool, any species not in the species pool was ignored. I used a random effect to identify each species so that models represented a generalised response of a bird species to the variables of interest. Thus, I used this model to estimate what determines bird species presence in secondary tropical forests, given their presence in the wider local species pool.

I used the modelled parameter values to project the accumulation of biomass and probability of species presence across the wider tropics that were considered suitable for forest growth. To do this, I modelled the biomass accumulation to be expected after 20 years since last disturbance using the gridded data on climate. I undertook a similar process for the model of bird biodiversity and predicted the probability of presence for a species in a hypothetical secondary forest in each grid square. I restricted projections to areas that were considered as suitable for forest growth under the BIOME model (Prentice et al. 1992), thereby reducing the probability of selecting areas, such as savannahs, where planting of trees may result in perverse outcomes for biodiversity and ecosystem services (Parr et al. 2014). I conducted analyses of the priority areas for bird biodiversity at a resolution of two degrees. Projections for biomass were made at the finer scale using wordclim climate data and then aggregated to a coarser resolution for comparison with the bird models.

I used the model projections as inputs for the Zonation spatial planning program (Moilanen et al. 2005). This program attempts to produce optimal planning strategies when given explicit goals. Using Zonation, I produced a map of priority areas for carbon and one of bird biodiversity priorities by summing the probability of species' occurrence, where species were weighted by the inverse of their global extent of occurrence so that species with small ranges were more heavily weighted. This method is recommended in the spatial planning literature when aiming to prevent global extinctions, though other approaches are available dependent upon explicit goals (Moilanen et al. 2005; Moilanen et al. 2009). I ranked grid cells from highest (1) to lowest (0) priority for forest restoration for the two goals separately. Following this, I ran a correlation analysis to determine the relationship between the rankings for carbon and for biodiversity. All analyses were done in R version 3.0.2 (R Development Core Team 2011), model averaging done using MuMIn (Barton 2013) and plots produced using ggplot2 (Wickham 2009).

6.4 Results

6.4.1 Biomass accumulation

My analyses of biomass accumulation produced one model that was much better supported than any other, with all other models having a ΔAICc>7. This model suggested that accumulated growing seasons hours was by far the most important variable in determining biomass accumulation and showed good fit to the data (R^2=0.53). Biomass tended to increase linearly with accumulated hours of growing season, with non-linearity suggested in Figure 27 a result of Box-Cox transformation of the response variable. Variations in soil texture, growing season precipitation and growing season temperature explained little variation and were not included as explanatory variables in any well supported models.

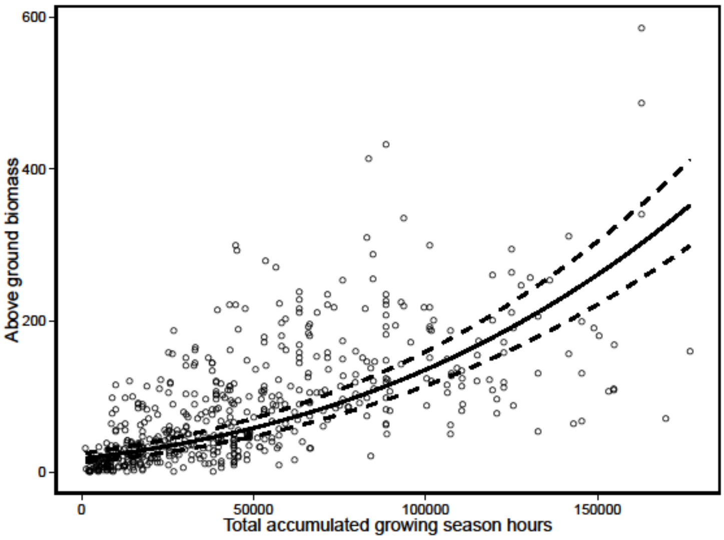

Figure 27 – Relationship between total accumulated growing season hours and aboveground biomass of forest sites. Points represent measurements at individual forest sites. The solid line represents prediction based on model parameters. Dashed lines represent the upper and lower confidence intervals of the prediction. Non-linearity is a result of a Box-Cox transformation of the response variable.

6.4.2 Probability of bird species presence

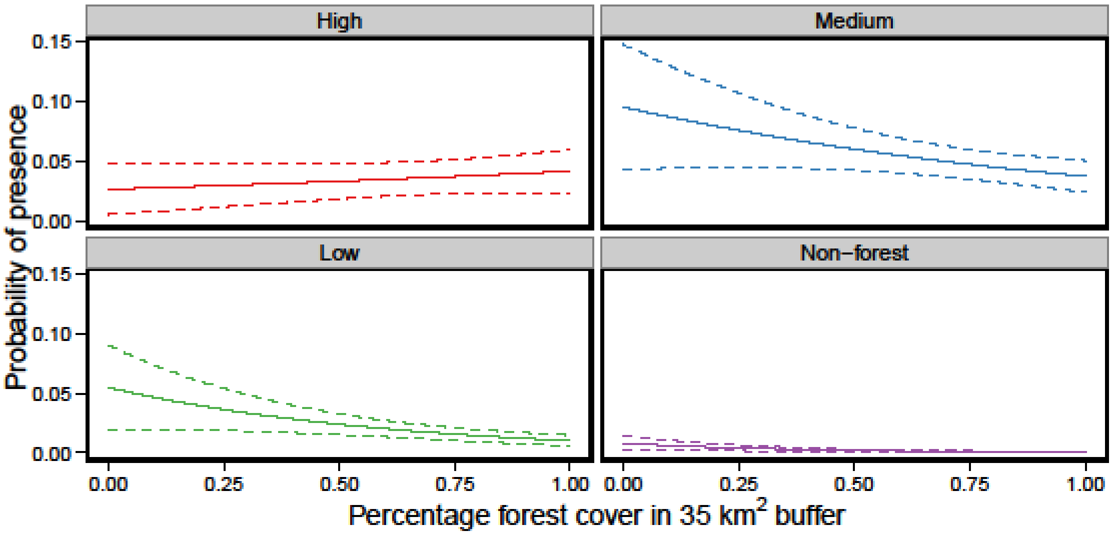

Figure 28 – Relationship between probability of presence of bird species and percentage forest cover in a 35km^2 buffer around site for birds with different dependence upon forest. Solid lines represent model predictions and dashed lines are the 95% confidence intervals around these predictions.

Only two models of bird presence had a ΔAIC<7 and both included species' forest dependency, percentage forest cover, species' range size (extent of occurrence) and an interaction between forest cover and forest dependency. The only difference between the two models was that the best model, with lowest AICc, also contained an interaction between range size and forest dependency. Models showed poorer fit to the data (R^2=0.22-0.19) than those for biomass. Model averaged coefficients suggested a gradient of responses to forest cover across different species dependencies with (a) non-forest species showing little response; (b) species with low and medium dependence on forest showing a negative response; and (c) species highly dependent on forest showing an increase in probability of presence with forest cover. (Figure 28) Similarly a species' extent of occurrence had little effect on presence for non-forest and species with low forest dependency, while for species with medium and high forest dependence, there was an increase in probability of presence with increasing extent of occurrence (Figure 29).

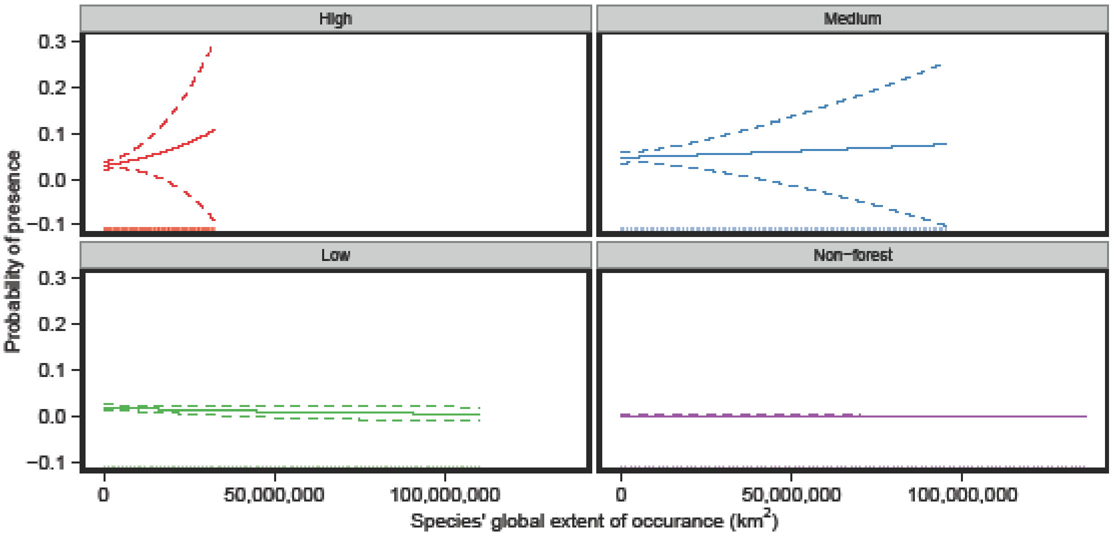

Figure 29 – Relationship between probability of presence of bird species and species' global extent of occurrence or birds with different dependence upon forest. Solid lines represent model predictions and dashed lines are the 95% confidence intervals around these predictions.

6.4.3 Identifying priority areas for forest restoration

Mapping of priority ranks over the area of the tropics suitable for forest growth showed clear differences in geographic patterns between priorities for biomass accumulation and bird biodiversity. Biomass accumulation was forecast to be highest in the wet tropical forests of Eastern Amazonia, Central Africa and the Indonesian Archipelago (Figure 30). Bird biodiversity priorities, however, were found in mountainous regions such as the Andes, Himalayas and East African mountain chains, as well as Central America and the Indonesian Archipelago (Figure 30).

There was no correlation between the ranking of areas for each goal; indeed, the rankings of the two priorities seem random with respect to each other (Figure 31). As a consequence, there were areas identified as high priority for both goals and these were largely found in the Andes and Southern Central America, and to a lesser extent in the Indonesian Archipelago, particularly New Guinea (Figure 32).

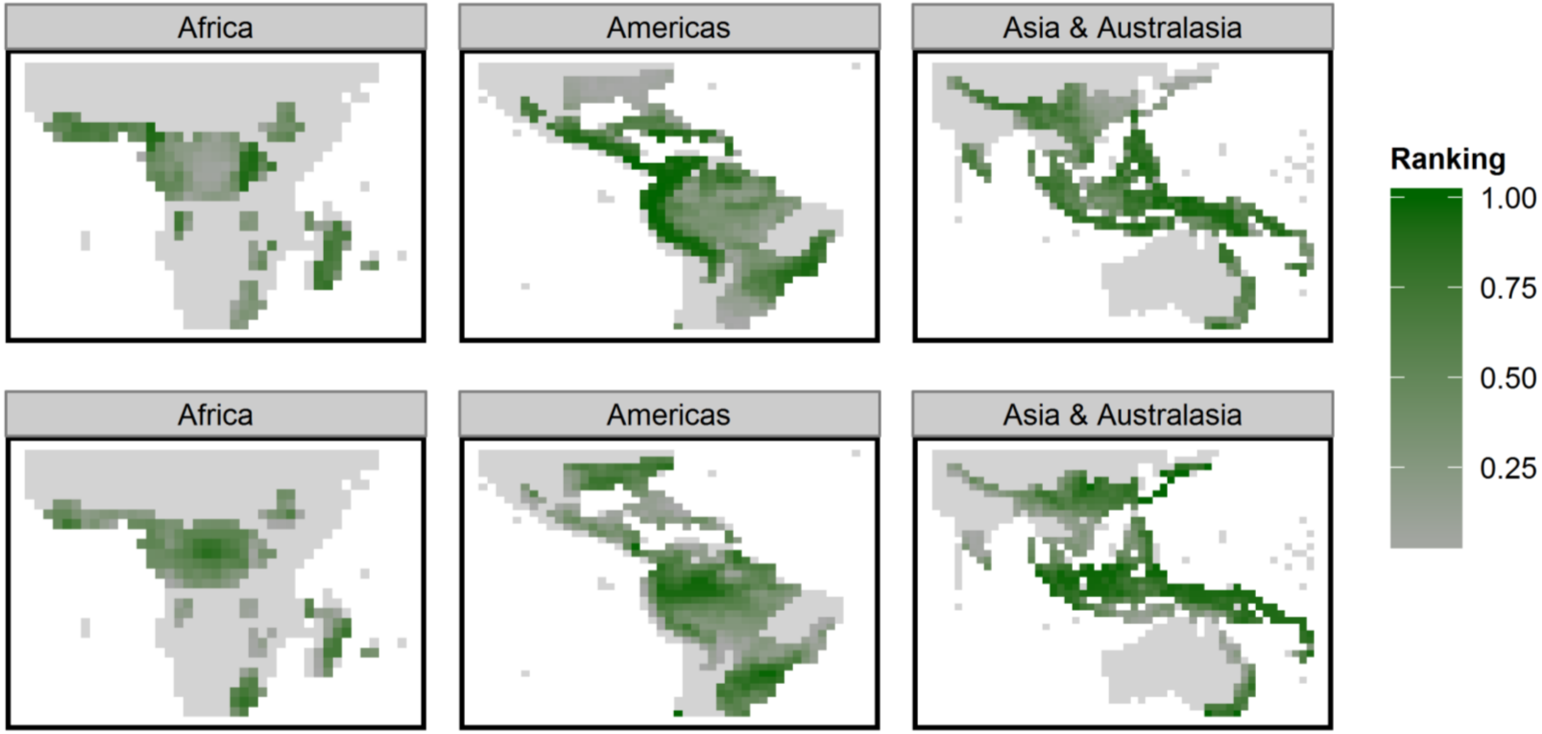

Figure 30 – Priority areas for forest restoration targeting biomass accumulation and bird biodiversity. Dark green represents areas that were ranked high, with dark grey areas those that were ranked low. Light grey areas were not considered in the analysis because they are not suitable for forest growth.

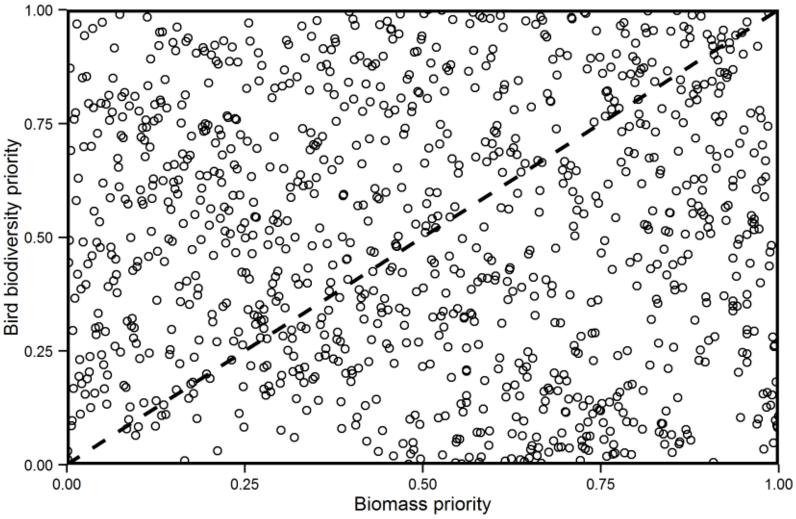

Figure 31 – Relationship between priority of area for biomass accumulation and its priority for bird biodiversity restoration, each point representing a 2x2 degree cell. The dashed line shows a 1:1 relationship between the two variables

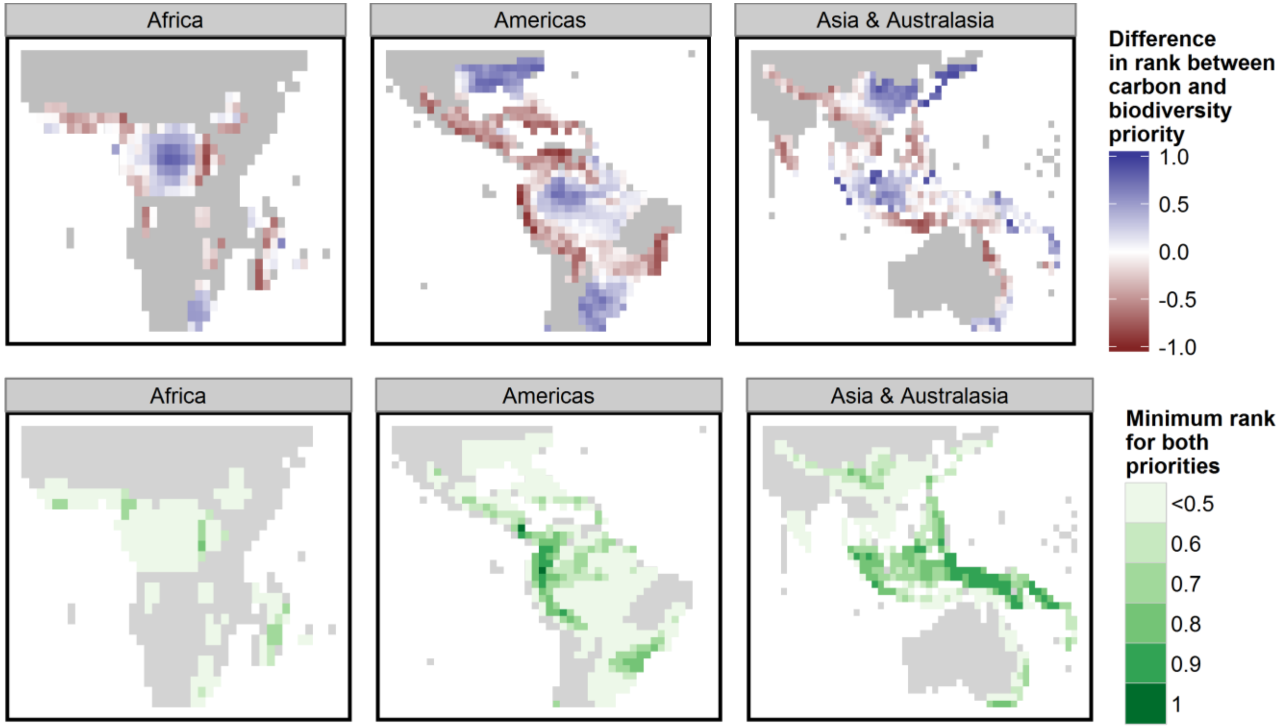

Figure 32 – Trade-offs between goals and overlap of priority areas. In the first plot, colours represent differences between the ranking in priority for the two goals with those coloured red ranked highly for restoration targeting bird biodiversity but not biomass accumulation and those coloured blue ranked highly for biomass accumulation but not bird biodiversity. In the second plot, colours represent ranking of areas for both goals, with those in dark green indicating high ranking for both. In both plots, dark grey areas are those not considered to be suitable for forest growth so were not considered in the analysis.

6.5 Discussion

This study indicates that following restoration, biomass is expected to accumulate most rapidly in areas with longest growing seasons, namely those with high year round temperatures but low water limitation. As a result, areas in the Western Amazon and in the Indonesian archipelago have highest potential gains for forest restoration aiming to maximise carbon sequestration. Presence of bird species in secondary forest was dependent upon the extent to which they depend on forest, the proportion of forest cover found in an area and the global extent of occurrence of a species. To generate priority areas for restoration each species was weighted by the inverse of its global range size, resulting in the Andes, Central America and the Indonesian archipelago having highest priority for restoration seeking to maximise retention of bird biodiversity. There was little evidence that the goals of carbon storage and biodiversity restoration, as defined by the measures developed in this chapter, were correlated. However, there was evidence of areas where both goals could be met in the Andes, Central America and New Guinea.

6.5.1 Biomass accumulation

The overriding driver of biomass accumulation in this study was length of accumulated growing season - the number of hours of growth each forest stand had that were not limited by temperature, water supply or light (Anderson et al. 2006). However, my study did not suggest that forests with sandy soils showed reduced biomass accumulation as Johnson et al. (2000) indicated. It is possible that this disagreement is due to differences in methods of statistical analyses, since (Johnson et al. 2000) did not use random effects to group studies, which leads to falsely inflated statistical power. In addition, Johnson et al. (2000) used soil data taken directly from the individual studies, which may have resulted in more accurate characterisation of soils at the site. Previous studies have suggested that soil characteristics are likely to be important in determining the maximum biomass of mature forests (Slik et al. 2013), but my work suggests that in secondary forests, at a pan-tropical scale, they are relatively unimportant in determining young secondary forest biomass. The inclusion of older secondary forests in such an analysis along with finer scale data on soils may help to resolve this apparent disparity.

The definition of growing season in this study used a combination of the methods of Anderson et al. (2006) and Johnson et al. (2000), and though it fit the data well, it is biologically simplistic. For example, I constrained my model by considering periods of precipitation <100mm per month in areas with mean annual temperature >18C and those with precipitation <40mm per month where mean annual temperature was <18C as being outside of the growing season, following Johnson et al. (2000). This parameterisation is based on observations in moist lowland tropical forests as well as montane forests and, while similar approaches have been used in the past (Johnson et al. 2000; Doughty et al. 2014), it is simplistic. For example, biomass change during secondary succession shows a strong non-linear pattern (Martin et al. 2013), increasing rapidly before reaching an asymptote. This maximum biomass has been suggested to be constrained by a lack of water since as a tree increases in height, and thus biomass, it requires more water (Ryan and Yoder 1997; Ryan et al. 2006). This may lead to areas with high year round rainfall and non-sandy soils being able to achieve higher maximum biomass (Stegen et al. 2011; Slik et al. 2013). As such, there is likely to be a gradient in water requirements for different forest types, depending on their age and composition. In order to more accurately parameterise such a model, greater information is needed about the water requirements of forests subject to different climatic conditions.

My projection of model values gave results that looked qualitatively realistic with highest accumulation predicted in the wet tropics, though it is interesting to note that the Congo basin showed relatively low biomass accumulation potential despite being the area of highest biomass stocks in intact forest in the tropics (Slik et al. 2013). However, it is difficult to determine whether this observation is inaccurate since no data on forests recovering from agricultural clearance are available for the area

6.5.2 Probability of bird presence

This study suggested that the probability of a bird species being present in secondary forest was dependent on its degree of forest dependency, forest cover surrounding the location and the extent of occurrence of the species. Forest dependency has previously been shown to be important in predicting species presence and abundance in degraded forest (Newbold et al. 2013) and, in my study, non-forest species and highly dependent forest species were least likely to be present, with those of low and medium dependency the most likely. This result is intuitively realistic since secondary forests often resemble an intermediate stage between forest and savannah ecosystems (Barlow et al. 2007; Barlow and Peres 2008) and, as such, both specialists of forest and open ecosystems may be absent (Newbold et al. 2013). Similarly, increasing extent of occurrence increased the likelihood of presence of species that had high and medium forest dependency. This is likely to be in part due to species with large ranges tending to have greater local densities than species with smaller ranges (Gaston 1996; Gaston et al. 2000). It is also possible that this variable allowed further separation of highly specialist species with small ranges from those of generalist species with larger ranges, since species with larger ranges appear to be more tolerant of secondary forest than small ranged species (Dunn and Romdal 2005; Sayer et al. 2013).

All species, apart from those highly dependent on forest, showed a reduction in probability of presence with increasing forest cover in the landscape. It is unsurprising that species with different dependencies on forest differ in their response to landscape forest cover, but it is surprising that only species classed as having high forest dependency increased in probability of presence. This relationship could be the result of a lack of precision in location data for each study since they did not provide the precise location of each individual site and, as such, the statistics of forest cover were the same for all sites taken from a single study. This resulted in a reduced ability to detect effects of variation in forest cover since variation between sites appeared smaller than in reality. In addition, relatively few sites exhibited forest cover <20% meaning that this extreme of the forest cover gradient was poorly characterised. The relationship could also reveal issues relating to the lack of data on forest fragmentation, which can reduce the probability of presence and the abundance of bird species independently of landscape forest cover (Villard et al. 1999).

6.5.3 Identification of priority areas

Projections of the biomass and bird biodiversity models produced maps that highlighted different areas as priorities for forest restoration that aimed to maximise those goals. Biomass was predicted to accumulate most rapidly in the wet tropics, while restoration targeting bird biodiversity had highest priority in areas possessing species with small global ranges such as mountain regions and the Indonesian archipelago. Strikingly there was no suggestion of a relationship between the two goals. Previous work supports this observation, with Strassburg et al. (2010) showing a very weak positive relationship between richness of small ranged species, which had most weight in the analyses in this study, and carbon storage. This lack of a relationship may be because small ranged species often occur in areas with high topographic variability (Davies et al. 2007) where carbon accumulation may be restricted as a result of low temperatures at high elevations or ‘rain shadow’ resulting in low rainfall surrounding mountains. This suggests that selection of sites to achieve the goals of REDD+ and the CBD for forest restoration based on only one goal is unlikely to result in optimal returns for the other goal.

These patterns gave rise to trade-offs between the two goals, with strongest trade-offs in parts of the Andes, Central America and mountainous areas of the Eastern Congo, which had high biodiversity but low carbon priority, and many areas of the sub-tropics, which had high carbon but low biodiversity priority. However, my analysis also identified areas where both goals could be maximised, largely located around the fringes of the Andes and in the Indonesian archipelago. Importantly, in order to target restoration with the goals of maximising carbon and bird biodiversity benefits, information on both is needed as one does not act as a proxy for the other. Restoration of forests in the Indonesian archipelago is likely to result in greatest increase in carbon storage relative to current levels because of the widespread logging and agricultural conversion currently going on in the area (Sodhi et al. 2009). However, restoration on the fringes of the Andes is likely to lead to greater probability of forest persistence because of the relatively low human population of the areas. In order to better assess the benefits of restoration, my analysis could be improved by further consideration of how restoration may enhance current carbon stocks, for which recently produced pan-tropical carbon maps could be used as a baseline (Saatchi et al. 2011; Baccini et al. 2012). In addition this study could also be improved by consideration of the potential persistence of any forest related to human population density, land-use and roads which have all been shown to be related to forest clearance (Nelson and Hellerstein 1997; Rosa et al. 2013).

6.5.4 Caveats and priorities for future research

These results represent a first attempt to identify priority areas across the tropics for forest restoration targeting carbon storage and bird biodiversity and, as such, there are a number of caveats associated with the approach. Firstly, the models of biomass and biodiversity may be a limited reflection of reality because of lack of data. In order to improve the model of biomass, more data is required from montane forests and possibly temperate and boreal areas, to characterise relationships between climate and biomass accumulation more generally. Currently, the lack of such data mean that any predictions for accumulation in montane forests may well be inaccurate, though recent publications of accumulation in the Colombian Andes may aid future models (Gilroy et al. 2014a; Gilroy et al. 2014b). In addition, the model would benefit from better determination of the degree to which precipitation limits growth in regions with different climates, since currently the model is overly simplistic. Similarly, the model of bird presence would benefit from more data from a wider set of sites in order to determine relationships more precisely. The inclusion of fragmentation metrics into models of bird presence would also undoubtedly improve the realism of predictions.

Model projections to locations in which variables fall outside of the range of values used to parameterise models may also have led to inaccurate predictions. For aboveground biomass accumulation there seems to be relatively little evidence for this given that all values of accumulated growing season hours fell within the range of data used to parameterise the model (Figure A7 – Appendix IV). However, given that this model is simplistic it is possible that predictions are inaccurate for locations where little data was available, such as colder, montane forests. Models of the probability of bird species presence were more problematic with suggestions of extrapolation outside of the range of data used to parameterise the models, particularly for species highly dependent upon forest and non-forest species (Figure A8 – Appendix IV). These extrapolations resulted in predictions for species that had an extent of occurrence greater than those used in model parameterisation. While this is likely to have resulted in inaccurate predictions, given that each species was weighted by the inverse of its extent of occurrence, it is unlikely to have affected prioritisation results.

As well as a lack of data that may have led to inaccurate predictions there are a number of assumptions that I made during the modelling of both biomass and bird biodiversity that may not accurately represent true ecological relationships. Firstly, I did not attempt to account for differences in age between secondary forests when modelling bird biodiversity. However, it is likely that bird assemblages change during the course of succession with a shift from communities dominated by generalist species to one with a higher number of forest specialists in late succession. I chose not to represent this because while it is obvious that there is species turnover at individual landscapes it is not clear that changes in animal diversity are well predicted by forest age, since age is purely a proxy for successional status. Despite this it is clear that a model that incorporated variables that aimed to account for the potential changes in bird communities during succession would present a more ecologically realistic picture than the model presented here.

Similarly I artificially truncated the maximum age used in my model of forest biomass to avoid modelling more complex non-linear relationships as other previous studies have also done (Johnson et al. 2000; Anderson et al. 2006). This is clearly a simplification of the successional process in which increases in biomass have repeatedly been shown to be non-linear with a general rapid increase followed by a gradual plateauing in older stands (Martin et al. 2013). Theory suggests that the rate of initial biomass increase is likely to be highest when both annual mean temperature and precipitation are high, thus enabling photosynthesis to occur rapidly throughout the entire year (Johnson et al. 2000; Anderson et al. 2006). It has previously been suggested that during succession biomass plateaus when constrained by a lack of water since as a tree increases in height, and thus biomass, it requires more water (Ryan and Yoder 1997; Ryan et al. 2006). In order to explore this non-linearity in greater detail future models should attempt to define which factors determine the slope of the initial rapid increase and the maximum biomass of stands when biomass accumulation plateaus. Doing so would improve our ability to model the potential for carbon storage in areas that are currently deforested or degraded.

In addition to potential problems with the models used in this chapter, it is possible that the relatively coarse grain size of this analysis (2x2 decimal degree squares) meant that finer scale relationships were poorly characterised, as noted previously by Strassburg et al. (2010). This problem stems from the use of range maps produced by experts as part of the Red List process (Rodrigues et al. 2006), which previous studies have shown do not represent real communities well at resolutions finer than two decimal degrees (Hurlbert and Jetz 2007). The inability to use maps based on expert opinion at the scales generally suitable for conservation management is recognised as a major problem for identification of conservation priorities (Hurlbert and Jetz 2007), and methods of fine scale presence of species using coarse scale range data are an area of active research (Keil et al. 2013; Keil and Jetz 2013). Such models are vital in order to target conservation and restoration actions more precisely than is currently possible.

Another caveat of this study is that bird biodiversity is not necessarily a good indicator of wider biodiversity since they are highly mobile and are able to disperse long distances. Bird biodiversity generally tends to be relatively poor as an indicator of changes in species richness of other taxonomic groups but are relatively good predictors of changes in composition (Westgate et al. 2014), and similar results have been shown in tropical degraded forests (Gardner et al. 2008). However, across a recent meta-analysis of the ecological literature on indicator taxa showed that there is extremely high variability in cross-taxon congruence and that it is relatively rare that any taxonomic group will serve as an effective surrogate for another (Westgate et al. 2014). Thus any work which attempts to address the potential biodiversity value of sites for restoration in the future should attempt to model the recovery of a wider suite of taxa than I have in this study, however this will be difficult since taxa tend to respond differently to alteration of forest ecosystems (Barton et al. 2014).

Despite these caveats, this study represents an improvement on the only previous study that aimed to prioritise areas for carbon and biodiversity recovery (Greve et al. 2013). That study did not attempt to model the degree to which restoration might benefit biodiversity as the researchers looked at the spatial overlap between current biodiversity priorities and the potential for carbon storage in sub Saharan Africa (Greve et al. 2013). Thus, this study represents an ecologically more realistic assessment of the potential benefits of tropical forest restoration for carbon and biodiversity recovery.

6.6 Conclusions

Both the Convention on Biological Diversity and REDD+ initiatives aim to increase carbon storage and conservation value of landscapes in part through forest restoration. Despite the caveats associated with this study, I have shown that these dual goals are unlikely to be achieved if restoration locations are selected using prioritisation based on one goal alone. Thus, if restoration aims to achieve multiple goals, prioritisation must model the potential impact of restoration on these goals since, in the case of carbon and bird biodiversity, they are poor proxies for each other.

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Chapter 7

7 Discussion

During this discussion I summarise the main findings of each chapter of the thesis before addressing the broad themes for the thesis (i) impacts of degradation on ecosystem services, (ii) biodiversity-ecosystem service relationships in degraded ecosystems and (iii) the potential mechanisms driving these relationships. Following this I discuss common themes in this thesis that I have not dealt with directly, such as the usefulness of gradients in degradation for ecological research, the need for more empirical studies of ecosystem services and the potential for improvements to research based on meta-analysis. I then discuss themes marginal to this thesis that present possible valuable research opportunities, before summarising the major contributions to knowledge this thesis has made.

7.1 Major findings of this thesis

The impacts of ecosystem degradation on biodiversity and ecosystem services are relatively poorly understood when compared to those of habitat conversion. The impacts of ecosystem degradation may be less dramatic than conversion of natural systems to agriculture, but understanding its consequences is vital given the importance of many of these systems for biodiversity conservation and ecosystem service provision in an increasingly human-dominated world (Chazdon et al. 2009). Experimental work has suggested that there are relationships between changes in plant species richness and ecosystem functions (Hector and Bagchi 2007; Cardinale et al. 2012), which may result in change to ecosystem services on which humans depend. However, the degree to which this is true in real-world systems has been questioned, as has the relevance of such research for biodiversity conservation (Srivastava and Vellend 2005). Since biodiversity that is perceived to be of conservation importance varies in its connection to ecosystem services, the two are not always related, even though they are both of societal concern (Mace et al. 2012). As such, there may be cases in which there is a trade-off between biodiversity and ecosystem service priorities (Bullock et al. 2011; Mace et al. 2012). To address this issue, I investigated biodiversity-ecosystem service relationships in the context of ecosystems degraded by non-native plant invasion, selective logging and tropical secondary forests recovering from deforestation, using meta-analyses to form generalisations.

7.1.1 Impacts of invasive non-native plant species on ecosystem services

Invasive non-native species tend to affect species richness negatively (Vilà et al. 2011), and changes in invaded communities can lead to alteration of ecosystem functions (Levine et al. 2003). Despite suggestions that invasive species pose a threat to ecosystem services (Pejchar and Mooney 2009), relatively little quantitative work has assessed this threat. In addition impacts on biodiversity and ecosystem services have been presumed to be linked in the context of non-native invasions (Vilà et al. 2009) but there is relatively little proof of this (Strayer 2012). In order to address these knowledge gaps, I undertook a meta-analysis with the aims of assessing (i) the impact non-native plant invasion on ecosystem services (ii) links between these impacts and changes in plant communities.

Following a meta-analysis of the available evidence, it is clear that non-native invasive plant species can have positive as well as negative effects of ecosystem services. On average non-native plant invasion led to increases in aboveground and belowground carbon storage and reductions in water provision and quality. While the potential positive impacts of invasive species has previously been noted (Pejchar and Mooney 2009), this is the first analysis to suggest that positive effects are common. Though this result is likely to be controversial, it is also intuitive given that some invasive plant species have been introduced specifically to enhance particular services (Hulme 2011). However, this observation should be balanced by noting that these positive changes were also accompanied by negative changes in other services. In addition, very few studies measured multiple ecosystem services and, therefore, trade-offs between services were difficult to assess. Further work must be undertaken to assess these trade-offs at the site scale.

Results from Chapter 2 also suggested that the impact of invasive plant species on aboveground carbon storage was negatively correlated with community richness change – so that communities that experienced greatest reductions in species richness showed greatest increases in aboveground biomass. This result was surprising as it suggests the opposite relationship to that seen in many biodiversity-ecosystem function experiments, where reduction in species richness results in reduced biomass (Cardinale et al. 2011). The negative relationship in my study is likely to be reflective of increased dominance of invasive plants in invaded ecosystems, rather than changes in species richness *per se*. This increased dominance is likely to cause reduced community richness and, since invasive species tend to show high productivity (Vilà et al. 2011), this results in increased aboveground carbon storage. However, the relationship between changes in species richness and aboveground carbon storage was relatively weak and no other ecosystem services showed any relationships to changes in species richness. Given that previous studies have suggested that species' effect traits can govern ecosystem services (Díaz et al. 2007), it appeared likely that this was also the case in the context of non-native plant invasions.

To investigate the hypothesis that species effect traits could be used to explain the ecosystem service impacts of non-native plant invasion, I used data collected during Chapter 2 along with trait data from the TRY plant traits database (Kattge et al. 2011). Though there were hints at the potential importance of effect traits (those traits hypothesised to have an effect on ecosystem functions) in governing the impact of invasive species on ecosystem services, attempts to predict impacts had mixed success. Invasive species height was a good predictor of changes in aboveground carbon, and a weaker predictor of changes in water quality. All other trait-impact relationships were poorly supported. These results suggest that predicting invasive plant species from their effect traits is likely to prove elusive. However, rather than suggesting that invasive species traits play no role in driving impacts on ecosystem services, it appears likely that more detailed data are needed to predict these impacts. Previous studies have suggested that in order to link community change to changes in ecosystem services, abundance of all species and their traits must be taken into account (Díaz et al. 2007). Thus, in order to predict the impact of invasive plant species identification of ecosystems likely to be invaded, the species present in them, the potential abundance of the invader following invasion and, traits of invasive and native species are needed. Given the level of detail, required it appears unlikely that such predictions will be possible in the near future.

7.1.2 Impacts of logging on carbon storage and biodiversity

Selective logging is one of the most widespread forms of forest degradation in the tropics with over 400 million hectares designated for permanent timber production (Asner et al. 2009). The only previous synthesis of the impacts of selective logging on biodiversity and carbon storage by Putz et al. (2012) identified wide-scale variation in effects, suggesting that Reduced Impact Logging (RIL) may reduce negative impacts compared to conventional logging. However, Putz et al. (2012), did not test this statistically or identify any other mechanisms for this variation. To address this I undertook a meta-analysis and systematic review to identify (i) the impact of selective logging on species richness and aboveground carbon storage in tropical forests, and (ii) the mechanisms related to logging method that may explain differences.

Results of my study indicated that carbon storage was strongly negatively affected by logging, while species richness only showed small declines. These results suggested that logging may have greater impacts on carbon than previously thought, with a mean reduction of 43% compared to previous estimates of 25% (Putz et al. 2012). Changes in species richness were similar to those reported by Putz et al. (2012), with my study suggesting reductions of 9% compared to their estimates of 10%. Given that my study was weighted by study accuracy and accounted for study level pseudoreplication, unlike that of Putz et al. (2012), it is likely to be the most accurate estimate of the general effects of logging to date.

My study also revealed that there is large variation in logging impacts on aboveground biomass and species richness, and that these differences are most effectively explained by variation in the volume of wood removed during logging operations. Analyses suggested that as logging intensity increased, biomass loss increased while species richness tended to increase. Importantly, there was relatively little evidence that reduced impact logging (RIL) differed in its impacts on biomass or species richness when compared to conventional logging. This was because RIL tended to be carried out at lower intensities and, thus, its effect independently of logging intensity was almost impossible to characterise.

These results suggest that further work at a greater range of intensities must be done in order to characterise the potential benefits of RIL. In addition, my results were suggestive of a trade-off in which during logging carbon storage is strongly reduced but species richness declines very little. However, further work is needed to identify how logging may impact community composition, given that species richness tells us nothing about identity of species and, thus, whether apparent lack of change in species richness is as a result of an influx of generalist species. However, in order to be able to do this studies must be undertaken to reduce spatial pseudo-replication which is widely prevalent in logging studies (Ramage et al. 2013).

7.1.3 Recovery of carbon and biodiversity in tropical secondary forests

Following clearance of tropical forest for farmland and subsequent abandonment carbon appeared to recover more quickly than plant biodiversity. Aboveground biomass increased rapidly before reaching a plateau and was predicted to be approximately 80% that of mature forests after 82 years. Soil carbon in secondary forests did not differ from mature forests and belowground biomass appeared to take longer to recover than aboveground biomass, though this was likely to be attributable to relative lack of data. Tree species richness also increased rapidly and recovered after ~50 years, while epiphyte richness showed slower recovery. However, despite increases in plant species richness there appeared to be little recovery of forest specialists with the proportion of mature forest species remaining low for most secondary forests. Indeed, on average secondary forests only contained approximately 25% of those species found in mature forests.

Thus, this is suggestive of a temporal trade-off in ecosystem service and biodiversity value, in which forests <100 years old are likely to be more valuable for carbon storage than for biodiversity conservation, especially given that faunal composition is likely to take >150 years to recover (Dent and Wright 2009). The results of my study also suggest that passive restoration may be enough to achieve restoration of carbon in forests but forest specialist species may require active restoration in order for them to become established, possibly due to impeded dispersal in highly fragmented tropical forest landscapes. Measures such as the planting of tree islands throughout the wider landscape may aid dispersal between forest patches and encourage such recovery (Rey Benayas et al. 2008).

While at a local scale there are temporal trade-offs between the carbon and biodiversity value of secondary forests, my analyses suggest that there are also spatial trade-offs between areas that should be considered a priority for carbon sequestration or for biodiversity recovery (Chapter 6). Empirical models suggested that biomass accumulation should be highest in the wet tropics, particularly in the western Amazon and the Indonesian archipelago. However, models suggested that the bird biodiversity value of restoration could be maximised in areas where species had small global ranges, in mountainous regions and in areas of the Indonesian archipelago. There was a lack of relationship between the two targets and trade-offs were just as likely as win-win situations. However, analyses showed that both goals could be maximised in a number of areas. Though there were caveats related to the models used for projections in this chapter, it appears clear that restoration projects that are located to maximise carbon sequestration or bird biodiversity value are unlikely to maximise both goals. In order for this to occur, project planning requires consideration of multiple goals to target policy effectively.

7.2 Common themes across chapters

Previous studies have suggested that drivers of biodiversity loss, particularly changes in species richness, also affect ecosystem functions and ecosystem services (Hooper et al. 2012). However, many biodiversity-ecosystem service relationships are unclear. Here I synthesise findings from a range of meta-analyses, including those undertaken as part of this thesis, to address the broad aims of this thesis, by assessing the evidence of (i) ecosystem degradation impacts on ecosystem services, focussing on carbon and water, (ii) the relationship between changes in species richness and ecosystem service provision in these degraded ecosystems and (iii) the possible mechanisms that explain differences in effects amongst different types of degradation.

7.2.1 How does ecosystem degradation affect ecosystem services?

Since drivers of degradation differ in their specific effects on ecosystems, changes in biodiversity and ecosystem service provision would be expected to differ amongst degradation types. In order to estimate the impact of different drivers of ecosystem degradation on ecosystem services, I collated data from previous meta-analyses (Gibson et al. 2011; Barlow et al. 2012; Hooper et al. 2012) along with that from Chapters 2, 4 and 5 of this thesis. Synthesis of these studies makes it obvious that the magnitude of impacts of differs markedly amongst different types of degradation (Figure 1). Invasive species and climate warming lead to increased aboveground carbon storage, with nitrogen addition on average also leading to increases though these were too variable to distinguish from no change (Figure 33). However, degradation that was associated with direct removal of biomass either directly by humans (logging or secondary forest) or as a result of dramatically increased mortality (fire or drought) led to sharp decreases in aboveground carbon storage (Figure 33). A gradient in the impacts of different disturbance types is also apparent, with more severe disturbances resulting in greater aboveground carbon losses.

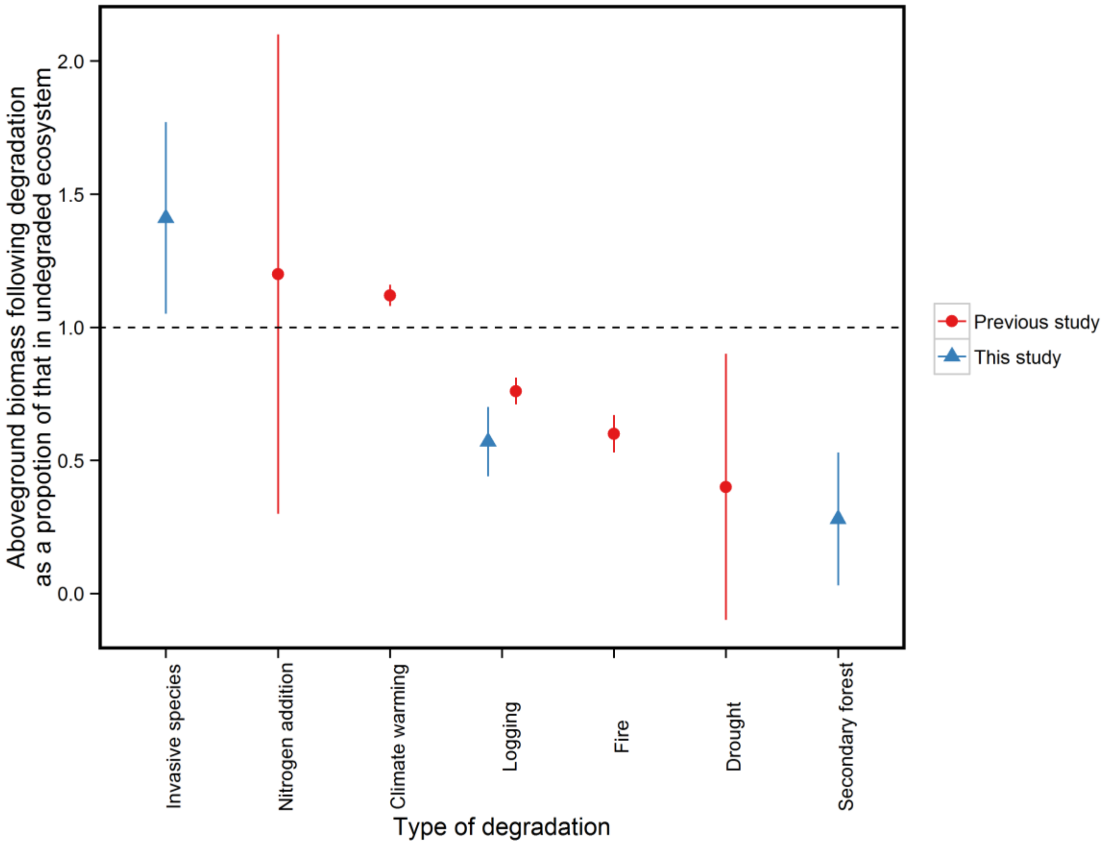

Figure 33 – Effect of difference types of ecosystem degradation on aboveground carbon storage. Results from previous meta-analyses are indicated by red circles and those from this thesis by blue triangles. Bars represent 95% confidence intervals and the dashed line indicates where carbon pools in degraded and undegraded ecosystems are the same. Data for meta-analyses not undertaken as part of this thesis were taken from Barlow et al. (2012), Hooper et al. (2012) and (Putz et al. 2012).

Regarding the other ecosystem services assessed in Chapter 2, water quality and water provision, the picture is less clear since they have rarely been subject to quantitative meta-analysis. Degrading activities thought to result in reductions in water quality as a result of increased nutrient inputs into rivers include logging (Lal 1997), overgrazing (Smith et al. 2013) and nitrogen deposition (Aber et al. 1989). My work added the possibility that invasive non-native plants may also reduce water quality, since they tend to increase nutrient content of soils (Ehrenfeld 2003; Vilà et al. 2011). These different degrading activities either remove barriers to run-off (e.g. logging or overgrazing) or lead to an increase in nutrient inputs, such as nitrogen deposition (Hooper et al. 2012) and invasion by non-native plants. However, compared to other drivers of changes in water quality, it appears likely that the changes that invasive non-native plants cause may be relatively modest although this topic requires further research.

There have also been relatively few studies of the impact of ecosystem degradation on water provision, making comparison difficult. There does however, appear to be a trend showing that increases in biomass in an ecosystem result in reduced water provision. Examples of this include increased stream flow following harvesting of trees (Lal 1997) and reduced stream flow following increases in forest cover (Jackson et al. 2005). Given that invasive species tended to increase community biomass, this is likely to be the mechanism by which non-native plants cause a reduction in water provision. Indeed, conservation management in South Africa specifically targets reducing non-native species biomass to increase water provision (Van Wilgen et al. 1998). There is a widespread recognition of the trade-off between carbon storage and water provision but there appears to be relatively little work quantifying it. Further work is required to provide quantitative assessments of this trade-off.

7.2.2 How are ecosystem services and biodiversity related in degraded systems?

Given that alteration in species richness has been suggested as being related to changes in productivity and, therefore, carbon storage (Cardinale et al. 2011), where degradation negatively affects species richness a reduction in carbon storage would be expected. However, for some types of degradation this is clearly not the case. While ecosystems degraded by fire, logging and forests recovering from clearance all show reduction in both carbon and species richness when compared to undisturbed ecosystems, nitrogen addition and invasive species both appear to cause a reduction in species richness, but an increase in aboveground carbon storage (Figure 34). These differences are likely to be due to the mechanisms which govern species richness-carbon relationships in the particular contexts. For example, invasive species outcompete native species and so reduce local richness (Vilà et al. 2011), but the species that invade tend to be highly productive, leading to increases in community biomass. Nitrogen addition meanwhile enhances productivity, but leads to the loss of species that are unable to take advantage of these increased resources (Bobbink et al. 2010).

In the cases of fire, logging and forest recovering from clearance, ecosystems show much smaller reductions in species richness than in carbon storage (Figure 32). This is possible evidence for particular species being important for the provision of the service of carbon storage and that these are either lost rapidly following degradation or regained slowly. In the case of logging, larger trees may be lost because they are selectively removed for use as timber. In the case of fire, there is evidence to suggest that some large trees show disproportionately large increases in mortality (Barlow and Peres 2008). In the case of secondary forest recovery following clearance, results from this thesis, and the work of others, suggest that these forests may lack long lived, large trees resulting in reduced carbon storage (Guariguata and Ostertag 2001; Martin et al. 2013). However, despite general trends in the effects of different drivers of degradation, there is much variation among studies of each type of degradation, as I have shown in this thesis. Identification of reasons for this heterogeneity is important if we are to gain a more nuanced picture of ecosystem degradation.

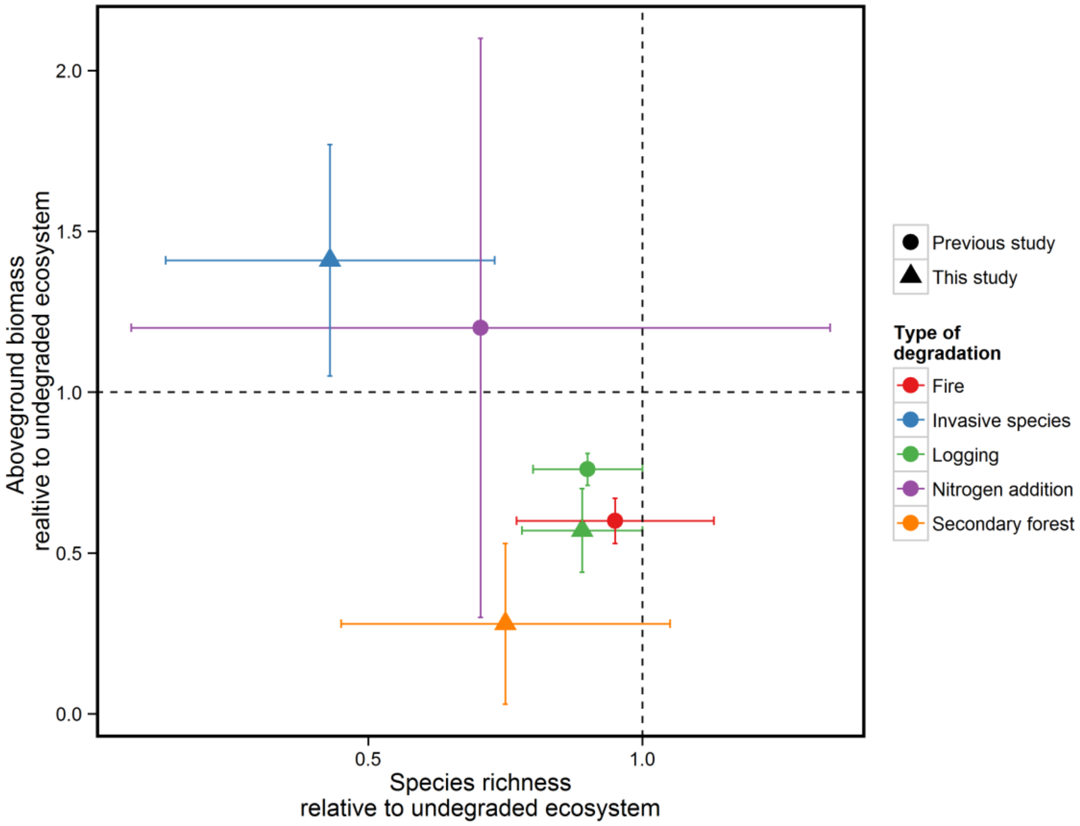

Figure 34 – Relationship between reductions in aboveground biomass and plant or tree species richness for a range of different types of ecosystem degradation. Triangular points represent results from this thesis while circular points represent the results from previous meta-analyses. Bars represent 95% confidence intervals for estimates of change, and dashed lines indicate where carbon pools or species richness is the same in degraded and undegraded ecosystems.

7.2.3 What mechanisms explain these biodiversity-ecosystem service relationships?

All the types of ecosystem degradation I have investigated in this thesis seem to affect biodiversity and ecosystem services via different mechanisms. Although there appear to be relationships between ecosystem service provision and species richness in each case, it is unlikely that changes in ecosystem service provision were caused directly by changes in richness *per se*. However, the most obvious explanations for relationships between biodiversity and ecosystem services provision from this thesis relate to the traits or characteristics of the species lost and gained as a result of degradation.

In the case of invasive non-native plant species there is an apparent negative relationship between changes in species richness and those in aboveground biomass. This relationship is suggestive of a situation in which the ecosystem is losing species with low productivity and gaining species with higher productivity, possibly because of effect trait differences between native and non-native species. However, the chapter in which I attempted to predict changes in ecosystem services using non-native invasive species' traits provided a mixed picture. Invasive height predicted changes in aboveground carbon storage and water quality but other relationships were poorly supported.

In the cases relating to tropical forest degradation explored in this thesis the fact that there was a greater loss of aboveground biomass than species richness suggests that the species that were being lost were disproportionately important for providing the service. These tree species are likely to be large, slow growing species that were either directly removed for timber in logged sites or had yet to colonise secondary forests (Guariguata and Ostertag 2001). This is suggestive of a strong link between response traits and effect traits in these cases with the species most likely to be lost from undisturbed systems also likely to be those that provide a disproportionately large carbon pool. Recent work suggests that such species may be lacking from human-disturbed forests in the Amazon, with very little recruitment of species with high wood density, which is positively associated with carbon storage (Berenguer 2013). However, further work is needed in order to be able to predict the long-term consequences of such disturbances.

7.3 Common themes across chapters that I have not dealt with directly

7.3.1 Gradients of degradation

Much of the work in this thesis has required the use of gradients of degradation to explain changes in carbon and biodiversity. The use of natural gradients has a long history in ecological research (Körner 2007) and much work has used land-use gradients that run from undisturbed ecosystems to those converted to human use (Maestas et al. 2003). However, few studies have identified how the impacts of individual drivers of degradation (e.g. logging) are affected as the intensity of degradation changes. This is surprising since it is clear from my work that the impacts of certain types of degradation on biodiversity and ecosystem services can vary massively. For example, in Chapter 2 impacts of non-native invasion on aboveground carbon storage ranged from a 90% reduction to a 325% increase. Similarly in Chapter 4, impacts of logging on biomass ranged from a 10% increase to an 85% reduction in aboveground carbon storage. Variation in both of these cases was partially explained by the intensity of degradation, namely impact of invasive species on community species richness and intensity of logging. However, the literature on invasive species and logging has rarely considered the importance of such intensity gradients (but see Sist et al. 1998). Almost all observational work that deals with ecosystem degradation would benefit from consideration of where sites lie on the degradation spectrum study. Not only would this consideration aid synthesis, it would also help to place studies in the context of the wider literature, thus, aiding interpretation of results.

In order to identify gradients in degradation, metrics need to be identified which accurately reflect the major changes associated with specific drivers. These metrics may be specific to the degrading activity but it would be beneficial if such metrics are applicable across disturbance classes. Many indicators of ecosystem condition have been suggested but these are largely applicable to monitoring schemes (Pereira et al. 2013; Thompson et al. 2013) and are generally of little use for identification of ecological gradients. The most practically useful indicators are likely to be those related to ecosystem structure, since increasing amount of degradation tend to drive simplification of ecosystem structure (Sasaki and Putz 2009). Here I use the examples of non-native invasive species and selective logging of tropical forest to elucidate such an approach.

Much invasive species research compares uninvaded and heavily invaded ecosystems (Lowry et al. 2013). However, in invaded ecosystems it is likely that the abundance of the invasive species varies markedly between plots. As such, an obvious gradient to use in many cases is the percentage cover of the invasive plant species of interest. However, given that invasive plant species represent many different functional plant types, ranging from grasses to trees, an assessment of the biomass of the invasive species in each plot would be more informative. This would present a relatively simple way to allow comparison between invasive species of different functional forms across different studies. In addition, this would help to address the long held goal of invasion biology of identifying the ‘per capita impact’ of an invasive species and allow for cross study comparison of these impacts (Brooks et al. 2004). Such an approach would enable the identification of species that have a greater than expected impact, given their biomass, on biodiversity and ecosystem functions. This would also aid trait based studies given that the use of such approaches depends on the relative abundances of species in plant communities (Lavorel and Garnier 2002).

In reference to identifying variation in degradation between different areas affected by selective logging, some studies have used number of trees removed and basal area cut as indicators (Mazzei et al. 2010). Of these two, the basal area cut is likely to be the most effective indicator for allowing effective synthesis since tree height and diameter and, thus, biomass are very variable across the globe (Slik et al. 2013). Using the basal area cut as a gradient would allow researchers to address applied questions, such as the potential differences in logging impact of reduced impact logging and conventional logging, which are currently unclear (Chapter 4).

Use of such gradients would undoubtedly aid in identifying nuanced effects of ecosystem degradation of which we are currently unaware. Gradient approaches could be used to identify potential non-linear regime shifts in terrestrial ecosystems that have previously been suggested in aquatic systems (Folke et al. 2004). Investigation of how well such indicators correlate with biodiversity or ecosystem service priorities could also help to determine their usefulness as proxy measures of degradation

7.3.2 Need for work investigating trade-offs in ecosystem services and biodiversity at the site scale

In this thesis I have summarised previous research on the impacts of different types of degradation on biodiversity and ecosystem services. However, the majority of ecosystem service data used in this thesis was related to carbon storage. While this storage is undoubtedly important for climate regulation, its common use in ecosystem service research is largely because of the relative ease with which it is measured when compared to less tangible services. Without the measurement of other ecosystem services at the site scale, it is impossible to determine trade-offs between ecosystem services as a result of changes in ecosystems. The use of trade-offs is one of the most important concepts in ecosystem service research (Foley et al. 2005), but currently much work that examines trade-offs uses GIS data to produce proxies of ecosystem services (e.g. Raudsepp-Hearne et al. 2010). Previous work has suggested that such proxies may poorly represent the real value of areas for ecosystem service provision (Eigenbrod et al. 2010). Thus, it is imperative that more field based studies attempt to quantify a wider variety of ecosystem services to validate models and identify links to biodiversity.

Ecosystem services that I attempted to address in this thesis, but found little data about, were the changes in water provision and quality related to ecosystem degradation. Even where I assessed these I had to use proxies of these services as few direct measures were available. As Mace et al. (2012) note, it is perhaps unsurprising that the ecology research community has focussed less on these topics because links between these services and changes in biodiversity are likely to be less tangible. However, lack of investigation of such services runs the risk of poor estimation of such services in ecosystem service assessments, or worse still ignoring them entirely. For example, it has been claimed that selective logging can reduce water quality as a result of increased run-off and sediment entering streams but, to my knowledge, there is only one quantitative assessment of these changes (Lal 1997). Changes in water provision in the context of land-use change have been studied (Jackson et al. 2005), but there is still relatively little evidence of the changes associated with degradation. While these changes may have relatively little direct link to changes in biodiversity, water provision is arguably a more basic human need than climate regulation which has received much attention.

Another area of ecosystem service research that has been particularly neglected is cultural services. Although there is evidence to suggest that humans value and place importance on biodiversity, there is little understanding how these values may be affected by biodiversity change (Clark et al.). The most relevant evidence that we do have for linking biodiversity to cultural services suggests that habitat and plant diversity have been found to be linked positively to peoples' preferences for undertaking recreation in an area (Fuller et al. 2007). Similar relationships have been found for aesthetic appreciation (Lindemann-Matthies et al. 2010) and self-reported general well-being of individuals depending on whether they live in areas with diverse faunal communities or not (Dallimer et al. 2012). The only evidence relating to change in cultural values associated with environmental degradation suggests that it can lead to increases in depression and distress (Speldewinde et al. 2009; Stain et al. 2011). However, studies that investigated this degradation looked at responses associated with drought and flooding, and not biodiversity loss *per se*. Though the studies cited here provide some of the best evidence of the links between biodiversity and cultural ecosystem services they are isolated examples and may not represent general rules since cultural context is likely to be important in our perception of nature (Daniel et al. 2012; Clark et al.

2014). This lack of data is emphasised by a recent systematic review (Lovell et al. 2014) which was unable to make any strong statements about relationships between biodiversity and cultural services, highlighting the need for greater research into the linkages.

Only by quantifying these less commonly assessed services in different ecosystems can we gain a realistic picture of the trade-offs amongst services which is seen as a cornerstone of the ecosystem service approach (Mace et al. 2012). This is not an easy task and will require multidisciplinary research. However, a number of research projects have recently been funded that in part aim to cover a broader range of ecosystem services than previous studies and how changes in ecosystem degradation can affect these services (Ewers et al. 2011; Gardner et al. 2013). These studies will provide the basis of our understanding of potential trade-offs and should result in more realistic estimation of how degradation effects service provision.

7.3.3 The value of meta-analysis and potential for improvements

Meta-analysis allows statistical analyses of entire fields of research and, as such, it is a powerful tool to assess evidence that is replacing case-study based understanding in ecology. Since they were first used in ecology in the early 1990s meta-analyses have evolved greatly and methods now exist to account for study-level pseudoreplication (Viechtbauer 2010) – though these are commonly ignored such as in the meta-analyses of Vilà et al. (2011) and Putz et al. (2012) which cover subjects similar to those covered in this thesis. While such methods accounting for study design have received much attention, there are still many ways in which meta-analysis in ecology could be improved that include methodological as well as cultural changes to how synthesis is conducted.

One of the most obvious ways in which meta-analysis in ecology could be made more meaningful is the increased investigation of sources of heterogeneity, which is still relatively rare (Koricheva et al. 2013). Given that many ecological studies are observational in nature, and that ecological experiments are much less controlled than those in the medical and physical sciences (Koricheva et al. 2013), such exploration of differences is particularly important. Exploration of this heterogeneity can largely be classified as that relating to differences in study methodology or that related to ecological processes. Explaining such variation can lead to improvement of methods in primary studies, as well as identifying important ecological reasons for differences that individual studies may have been unable to discern. Of particular importance to meta-analyses are the scale at which studies were carried out (Whittaker 2011), climatic differences between sites (Castro-Díez et al. 2014) and other ecological gradients such as those identified in this thesis.

In addition to heterogeneity in effects, the selection of study sites in ecology is biased (Martin et al. 2012a) and, as such, nearly all areas of ecological research show some clustering of study sites (e.g. Pyšek et al. 2008). Using data derived from these causes problems for meta-analyses sites since sites closer to each other may be expected to have similar effect sizes, thus potentially violating statistical assumptions of independence (Dormann 2007). In this thesis I ignored this problem, as have all previous ecological meta-analyses to my knowledge since at present there is no recognised technique to deal with this problem. Accounting for such spatial auto-correlation would improve the generality of ecological meta-analyses, making their results more useful. In addition to meta-analyses conducted at the site scale, there is a growing number of meta-analyses that have used plot level data (Martin et al. 2013; Newbold et al. 2013). Given the wide scale prevalence of spatial pseudo-replication in observational ecological studies (see Ramage et al. 2012 for an example of this), the ability to partition variance caused by treatments and spatial variation would also help enormously in aiding our ability to answer both applied and basic ecological questions.

Finally, there is a need for a cultural change amongst the research community if the value of meta-analyses is to be maximised. Currently, studies that provide the data for meta-analyses tend not to be cited in articles, meaning that authors of these articles essentially receive no credit for their work. Presumably, omission of these studies from the references is to save print space but given that most journals are now accessed online their exclusion now seems unwarranted. At the very least this situation is unfair and, at worst, breeds antagonism between field-based researchers and those undertaking meta-analyses. This has led to meta-analysts being characterised as ‘data parasites’ that undertake ‘bad science’ by some (Lindenmayer and Likens 2011; Lindenmayer and Likens 2013). Undertaking this thesis has made me much more aware of this issue and discussions surrounding the publication resulting from Chapter 5 (Martin et al. 2013) directly led to the Royal Society altering its policy so that studies included in meta-analyses published in their journals receive credit in the same way as other citations. However, in many situations a more collaborative approach to meta-analysis may be necessary by which data providers are offered co-authorship, particularly when additional meta-data are provided as is the case for the manuscript resulting from Chapter 4. Ecology will advance more quickly if theory is based on empirical results but this requires synthesis. To do this, the development of an academic culture that values data produced from experimental and field based studies is vital (Kueffer et al.).

7.4 Themes marginal to this thesis but that need more attention

This section includes thoughts on themes that I touched on when reviewing literature that require further research in some way. I briefly review the background of each subject, why they are interesting and identify potential areas for future research.

7.4.1 Loss of large trees

Like large, long lived animals, large long lived tree species appear to be particularly vulnerable to local extinction (Lindenmayer et al. 2012b). This elevated extinction can occur as a result of selective removal or because large trees possess characteristics, such as greater water requirements or slow growth (Ryan and Yoder 1997), that result in increases in mortality and decreases in recruitment following degradation. Large trees are perceived as critically important features of many ecosystems, providing multiple microhabitats for species (Lindenmayer et al. 2012a) as well as storing large amounts of carbon (Slik et al. 2013) and having great significance for some cultures (Salick et al. 2007). As such, their potential loss is of great conservation concern.

Recent reviews by Lindenmayer et al (2012; 2014) have suggested that there is a widespread loss of large old trees from many ecosystems across the globe. Though it is obvious that there is a loss of large trees as a result of human activity in some locations, it is unclear how widespread these losses are, where they are likely to occur or what drivers are most severe. The reviews of Lindenmayer et al do not attempt to quantify changes but claim to prove that these losses are a world-wide phenomenon. Such presumptions may be misguided as these reviews may be subject to cherry picking of studies to support the authors' viewpoint. As such, their claims require further scrutiny.

These losses of large trees as described by Lindenmayer et al can be the result of two basic processes, mortality of young, small trees (either seedlings or saplings) or that of large, old trees (Figure 35). Large scale mortality of young trees could potentially lead to an extinction debt in long lived trees over long time periods since their recruitment is required to maintain species populations (Fischer et al. 2009). Removal of large trees immediately changes ecosystems dramatically and potentially removes sources of seeds that would otherwise allow recruitment of these species. Both of these processes can occur as a result of human disturbance, with potential feedbacks between the two as well as between different disturbances. Here, I briefly review the evidence for the claims of Lindermayer et al and identify priority areas for further research on the topic.

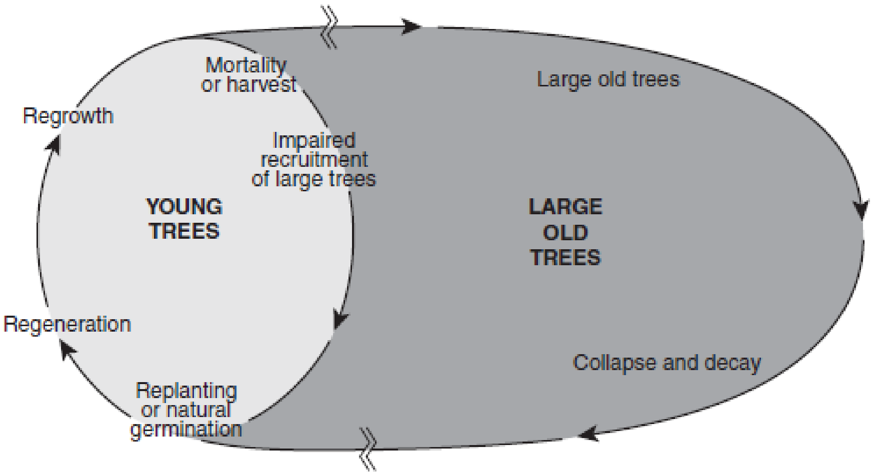

Figure 35- Conceptual model of the drivers of recruitment failure and increased loss of large trees, taken from Lindenmayer et al. (2014).

Large trees can suffer from increased mortality by two basic processes: selective removal or increased die-off as a result of changes in environmental conditions. The most obvious means by which large trees are directly removed is selective logging which is widespread throughout the tropics (Asner et al. 2009) varying from relatively low intensity in South America and Africa, to high intensity in South East Asian forests (Chapter 4; Putz et al. 2001). Selective logging removes trees of high timber value, leaving the remaining trees standing. Trees of highest timber value tend to be large and slow growing and, thus, it is clear that this practice tends to result in loss of large trees which is in turn linked to the large impact of selective logging on the biomass storage of forests. In addition, there is evidence that large trees are being lost from some urban environments because of fears for human safety (Carpaneto et al. 2010); although it is unclear how widespread this practice is.

Processes which can result in widespread increases in large tree mortality include fire, drought and fragmentation. Repeated frequent fires have been shown to result in forests resembling young secondary forests with increased mortality of large trees and recruitment of shade-intolerant pioneer species (Barlow and Peres 2008). This shift in composition has also been suggested to represent an alternative stable state with increased stem density and dryness of burnt forests promoting repeated fires (Barlow and Peres 2008; Lindenmayer et al. 2011). Similar die-off can be induced by fragmentation and drought which can both lead to changes in local environmental conditions. Fragmentation has been shown to increase mortality of large trees at forest edges, driving patches to resemble early successional states (Laurance et al. 2000). This loss of large shade-tolerant species has been shown to result in a collapse in biomass in forest fragments with reduction of between 30 and 60% at edges compared to the centre of fragments (Laurance et al. 2000). Drought has also been suggested to reduce large tree survival due to the greater water requirements of these trees (Nepstad et al. 2007), resulting in large potential biomass losses (Phillips et al. 2009).

Grazing effects on wooded landscapes largely involve recruitment limitation as a consequence of livestock browsing resulting in elevated seedling mortality (Fischer et al. 2009; Fischer et al. 2010). This reduction in recruitment represents a case of extinction debt since without removal of grazing pressure numerous tree species could be expected to become locally extinct. Indeed, Fischer et al. (2010) indicated that this could drastically reduce tree cover in an entire landscape if current unsustainable grazing practices are maintained. Fire has also been shown to reduce survival of shade-tolerant species, resulting in increases in pioneer species and shifts in community structure (Barlow and Peres 2008). In addition, logging and fragmentation can reduce survival of shade-tolerant species as canopy damage or edge effects can lead to rapid colonisation by shrubs which outcompete seedlings.

The most serious loss of large trees are likely to occur when there are synergistic effects between drivers of degradation. Previous research in the tropics suggests that such synergies can occur in areas where logging roads have been constructed, leading to reduction in moisture in forest edges next to roads, which increases the probability of fire (Cochrane et al. 1999; Cochrane 2001).

Though the potential for large tree loss from the drivers discussed is clear, the quantitative impacts of the drivers and where such losses are likely to be most severe is not. Given the large number of publications of the impacts of human disturbance on forests and savannah ecosystems throughout the world along with numerous international and national forest monitoring schemes, such quantification should be possible. Only by carrying out such an analysis will it be clear whether the claims of Lindenmayer et al. (2014) are an accurate reflection of reality. However, more importantly such quantification would allow differences in impacts between degrading activates to be identified as well as pinpointing areas in which policies to encourage tree regeneration should be a priority.

7.4.2 Improving generalisation in ecology

In this thesis, I have largely undertaken syntheses of disparate datasets in the form of meta-analyses. While this is useful for producing generalities, setting baselines and identifying potential new areas of research (Hillebrand and Cardinale 2010), meta-analyses can also be hampered by methodological differences between studies (Whittaker 2011), spatial pseudoreplication (Ramage et al. 2012) and missing data (Chapter 4 – This thesis). While meta-analysis can be used to explore the implications of differences in study methodologies, differences can also hamper the ultimate aim of meta-analysis, generalisation. However, recent developments in collaborative research have sought to overcome these problems and may offer a means of drawing generalisations that represents an intermediate between single site studies and meta-analyses. These collaborations can largely be divided into two groups: collaborative distributed experiments (CDEs) and collaborative observation networks (CONs).

The major features of CDEs in ecology, as identified by Fraser et al. (2012), are that (i) they represent hypothesis-driven experimental studies, (ii) they are multi-site investigations, (iii) they have a standardised research design, (iv) they collect standardised data (v) have common agreements on data sharing, (vi) have synchronised data collection, (vii) have multiple investigative teams and (viii) are low cost and low maintenance. The fact that these represent multi-site investigations allows broad generalisations to be made that were previously impossible due to the limited scope and scale of studies that focussed on single sites or a group of sites in single regions. The most important advantage of CDEs over meta-analyses is that they use standardised methodologies at a wide variety of sites (Fraser et al. 2012). Standardisation of methodologies means that analyses do not need to account for methodological differences, thus, making statistical tests much more powerful. Standardised methodologies also mean that statistical analyses can be much simpler than those used by meta-analyses, often employing mixed-effect models to group measurements at individual sites (Fraser et al. 2012). While the experimental nature of CDEs perhaps presents the most effective means of inferring cause-and-effect relationships in ecology today, it is not always feasible due to economic constraints associated with manipulation of certain ecosystems such as those containing woody species. In these cases, CONs play a vital role.

CONs share many of the features of CDEs but importantly are not hypothesis-driven experimental studies. These networks largely aim to monitor changes in ecosystems using standardised methodologies to allow data synthesis across sites. The most high profile CON is probably the US National Ecological Observatory Network (NEON) which is a continental scale network of 76 sites that aims to monitor changes associated with climate change, land-use change and nitrogen deposition (Kampe et al. 2010). There are many other similar networks throughout the globe from tropical forests (Lopez-Gonzalez et al. 2011), to both polar regions (Lee et al. 2010). While these networks are extremely valuable, they are also costly to run and, as such, contribution to data collection and studies is much less open to external collaboration when compared to CDEs.

These types of networks attempt to infer causality either through experimental approaches or observation. While these are both useful there are cases in which manipulation is either not possible or very costly, but studies still aim to infer causality related to local processes. Thus, an alternative approach to CBEs and CONs could use an observational approach to investigate changes over gradients or other natural experiments. Using standardised approaches across a series of gradients distributed throughout the globe would allow stronger inference than currently that acheived by single location studies currently. Specifically these networks could be used to address knowledge gaps identified by this thesis, and help answer questions such as: How does the impact of non-native invasive plant species change with their abundance? Do the impacts of Reduced Impact Logging and conventional logging differ when logging intensity is controlled for? To my knowledge no such networks currently exist but represent a potentially powerful tool in situations where CDEs are not suitable.

Probably the most difficult obstacle to increasing the number of collaborative networks is obtaining funding (Fraser et al. 2012). While much less expensive than CONs, CDEs require money to set up, to enable collation of data and help organise meetings to strengthen collaborations (Fraser et al. 2012). Currently it appears that few funding agencies support collaborative intercontinental ecological projects, though the growth of interest in the topic may increase as collaborative networks become more common. The major goal of ecology is generalisation and such networks represent the best way to improve this. Thus it is vital that more networks are created to address a broader range of questions.

7.5 Broad contribution to knowledge of this thesis

In this thesis, I aimed to (i) generalise about the impact of different types of ecosystem degradation on ecosystem services; (ii) understand how these relate to change in biodiversity and (iii) synthesise data collected in primary studies to contribute new knowledge to this broad research area. The size of the datasets used provided amongst the best syntheses of the subjects to date and helped to identify trends and gaps in current research. The most obvious research gap is the relative lack of data relevant to ecosystem services other than carbon storage. This must be filled if we are to form a clearer picture about how biodiversity change may impact ecosystem provision and how these changes trade-off against each other. Despite these limitations, I have presented the first syntheses of the effects of non-native invasive species, logging in tropical forests and tropical secondary forest recovery on ecosystem services and biodiversity.

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Appendix I – Information in support of Chapters 2 and 3

Effect size calculation

The effect size we used in this study was the log response ratio which was calculated as:

$$lnR = \ln(\bar{X}_{logged}) - \ln(\bar{X}_{unlogged})$$

Where $\bar{X}_{logged}$ represents the mean value of aboveground biomass or species richness in a logged stand and $\bar{X}_{unlogged}$ represents the equivalent value in an unlogged stand with the standard error of each paired site combination calculated as:

$$SE_{lnR} = \sqrt{V_{lnR}} = \sqrt{S_{pooled}^2\left(\frac{1}{n_1(\bar{X}_{logged})^2} + \frac{1}{n_1(\bar{X}_{unlogged})^2}\right)}$$

Due to the inherent differences between studies in the ecological literature true effect sizes were presumed to differ between studies and to test for heterogeneity between studies the weighted sum of squares, *Q,* was calculated as:

$$Q = \sum_{i=1}^{k} W_f g^2 - \frac{\left(\sum_{i=1}^{k} W_f g\right)^2}{\sum_{i=1}^{k} W_f}$$

This statistic was subsequently used to determine the weighted means of differences between logged and unlogged sites using a random effects model. Thus the weight (W_r) assigned to each study was the inverse of the within-study variance plus the between-studies variance:

$$W_r = \frac{1}{V + T^2}$$

T^2 was calculated as:

$$T^2 = \frac{Q - df}{C}$$

where

$$df = number\ of\ independent\ datasets - 1$$

$$C = \sum W_f - \frac{W_f^2}{W_f}$$

As such the weighted mean was calculated as:

$$M_r = \frac{\sum_{i=l}^{k} W_r g}{\sum_{i=l}^{k} W_r} \text{ or } M_r = \frac{\sum_{i=l}^{k} W_r LnR}{\sum_{i=l}^{k} W_r}$$

with the standard error of the mean effect size calculated as:

$$SE_r = \sqrt{\frac{1}{\sum_{i=1}^{k} W_r}}$$

and the upper and lower 95% confidence intervals for both effect sizes calculated as:

$$UL_{M_r} = M_r + 1.96 \times SE_r$$

$$LL_{M_r} = M_r - 1.96 \times SE_r$$

Goodness of fit was estimated by calculating the pseudo-R^2

$$pseudo\ R^2 = 1 - \left(\frac{T_{unexplained}^2}{T_{total}^2}\right)$$

Where $T_{unexplained}^2$ is the variance left unexplained after fitting a model and T_{total}^2 is the total variance when fitting an intercept only model.

Table A1 – The number of sites used in the study classified by broad ecosystem type

Ecosystem type	Number of sites used in meta-analyses
Grassland	72
Broadleaf forest	53
Coastal dune	15
Scrub	12
Mixed	8
Coastal wetland	8
Freshwater wetland	4
Cropland	3
Coniferous forest	3
Desert	1

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Statistical tables for Chapter 3

Table A2 - Model comparison for models of change in aboveground carbon that included only invasive height and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Invasive trait	74.17	0	31.91	131.47	0.99
Null model	83.93	9.76	0	1	0.01

Table A3 - Model comparison for models of change in belowground carbon that included only invasive height and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Null model	66.21	0	0	1	0.64
Invasive trait	67.37	1.16	0.01	0.56	0.36

Table A4 - Model comparison for models of change in water provision that included only invasive height and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Null model	15.86	0	0	1	0.85
Invasive trait	19.28	3.42	0.09	0.18	0.15

Table A5 - Model comparison for models of change in water provision that included only invasive root depth and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Null model	13.81	0	0	1	0.98
Invasive trait	21.68	7.87	39.28	0.02	0.02

Table A6 - Model comparison for models of change in water quality that included only invasive height and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Invasive trait	190.81	0	31.43	83.22	0.99
Null model	199.66	8.84	0	1	0.01

Table A7 - Model comparison for models of change in aboveground carbon that included invasive height, differences between invasive and native species and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Invasive trait	32.32	0	0.17	2.26	0.55
Null model	33.95	1.63	0	1	0.24
Invasive and native traits	34.31	2.00	0.10	0.83	0.20

Table A8 - Model comparison for models of change in belowground carbon that included invasive height, differences between invasive and native species and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative likelihood	AICc weight
Invasive and native traits	28.01	0	0.11	1.01	0.44
Null model	28.04	0.03	0	1.00	0.43
Invasive trait	30.64	2.63	<0.01	0.27	0.12

Table A9 - Model comparison for models of change in water quality that included invasive height, differences between invasive and native species and the model intercept

Model variables	AICc	ΔAICc	R^2	Relative liklihood	AICc weight
Null model	105.94	0	0	1	0.44
Invasive trait	106.26	0.32	0.02	0.85	0.37
Invasive and native traits	107.56	1.62	0.01	0.44	0.19

Appendix II – Information in support of Chapter 4

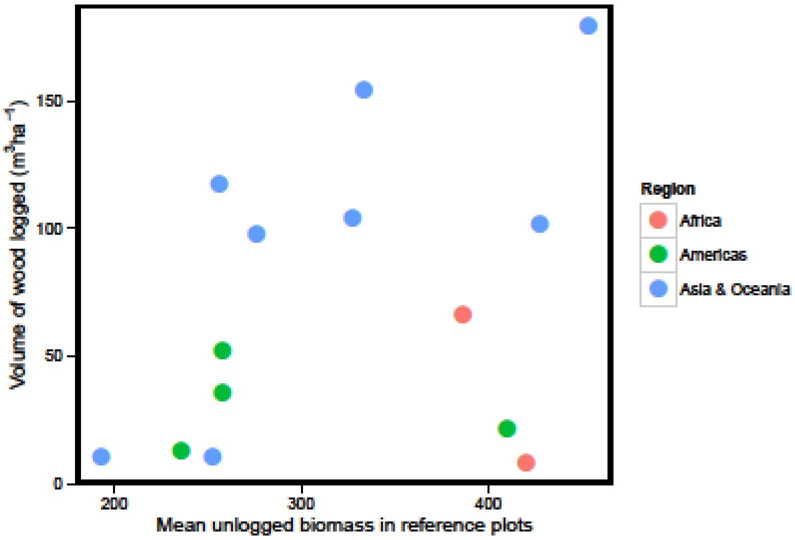

Figure A1 - Variation in the volume of logged wood in forests with differing non-logged biomass and by region

Table A10 - Models explaining changes in aboveground biomass following selective logging with delta AICc≤7 for studies with no information on logging intensity

Model rank	Variables in model	AICc	AICc delta	Model weight	R^2
1	Region + logging method	51.30	0	0.73	0.35
2	Region	53.93	2.64	0.19	0.30
3	Logging method	56.87	5.57	0.04	0.03
4	Null_model	57.42	6.13	0.03	0

Table A11 – Models explaining changes in species richness following selective logging with delta AICc≤7 for studies with no information on logging intensity

Model rank	Variables in model	AICc	AICc delta	weight	R^2
1	Null	27.95	0	0.62	0
2	Method	29.84	1.89	0.24	0.12
3	Region	32.18	4.23	0.08	0.16
4	Method + Region	32.79	4.84	0.06	0.18

Table A12 – Models explaining changes in aboveground biomass following selective logging with delta AICc≤7 for studies with details of logging intensity

Model rank	Variables in model	AICc	AICc delta	Model weight	R^2
1	Volume+Volume^2	16.31685	0	1	0.88

Table A13 – Models explaining changes in species richness following selective logging with delta AICc≤7 for studies with details of logging intensity

Model rank	Variables in model	AICc	AICc delta	Model weight	R^2
1	Volume	-7.00	0	0.77	0.34
2	None (Null model)	-4.16	2.84	0.19	0
3	Logging method	-1.25	5.75	0.04	0.12

Table A14 – Importance values for variables assessed during modelling of changes in aboveground biomass and species richness following selective logging. Where a variable was not considered in a set of models it is labelled NC.

Variable	Biomass – without volume	Biomass with volume	Richness – without volume	Richness – with volume
Volume	NC	1	NC	0.77
Volume^2	NC	1	NC	NC
Rarefied	NC	0	0.53	NC
Region	0.92	0	0.13	0
Logging method	0.77	0	0.30	0.04
Taxonomic group	NC	0	0.03	0

Papers used in meta-analyses of logging

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Appendix III – Information in support of Chapter 5

Peer-reviewed studies from which data were collated for the meta-analysis of recovery of carbon pools and plant biodiversity in tropical secondary forests

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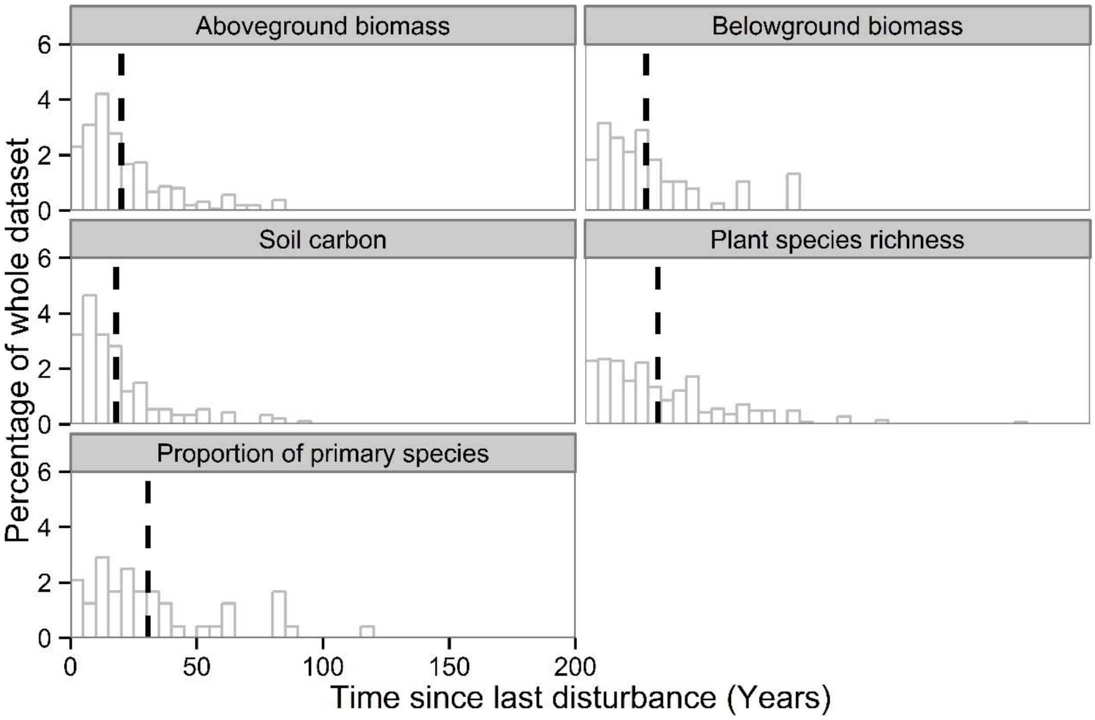

Figure A3 –Distribution of forest ages by metric for the 678 sites represented in the meta-analysis. Vertical dashed lines represent mean ages for each metric type.

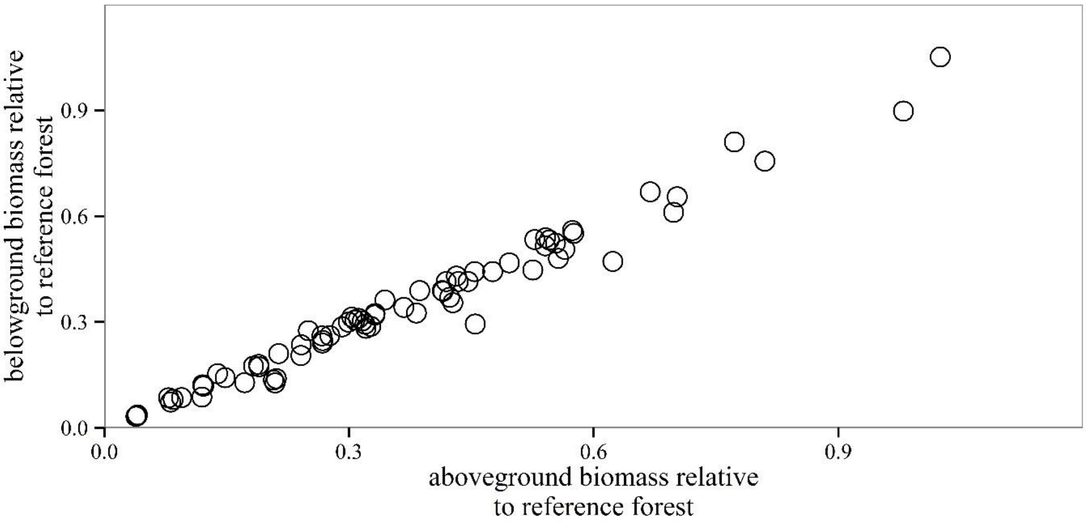

Figure A4 – Relationship between relative above and relative belowground biomass in locations where both measures were available.

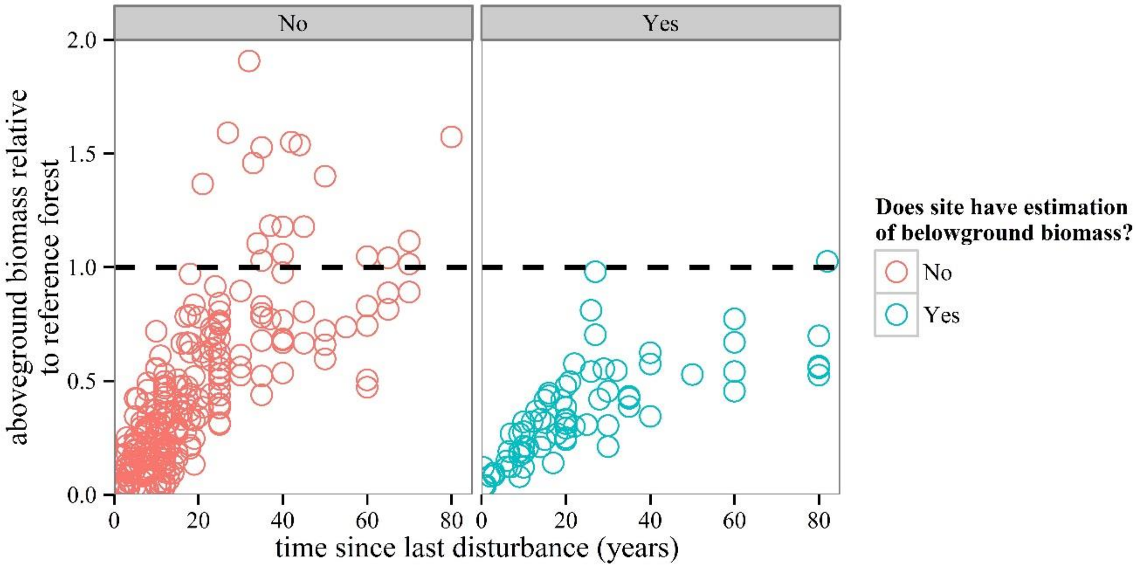

Figure A5 – Change of aboveground biomass over time since disturbance showing relative difference between studies that had information on belowground biomass and those that did not

Table A15 – Number of sites for each metric used in this study including the number of sites shared between different metrics

	Aboveground biomass	Belowground biomass	Soil carbon	Species richness	Shared species
Aboveground biomass	326				
Belowground biomass	73	76			
Soil carbon	104	54	185		
Species richness	111	19	0	283	
Shared species	5	0	0	23	50

Table A16 – Variables included in models of aboveground biomass recovery with ∆ AICc <7, models are ranked by AICc with weight representing the likelihood that individual models are the most parsimonious

Variables included in model	df	AICc	∆ AICc	Weight	Marginal R^2
Intercept+log(Age)	7	654.32	0	0.57	0.56
Intercept+log(Age)+Disturbance	9	655.34	1.01	0.35	0.56
Intercept+log(Age)*Disturbance	11	659.11	4.78	0.05	0.56
Intercept+log(Age)+Forest type	10	660.29	5.97	0.03	0.56

Table A17 – Variables included in models of belowground biomass recovery with ∆ AICc <7, models are ranked by AICc with weight representing the likelihood that individual models are the most parsimonious

Variables included in model	df	AICc	∆ AICc	Weight	Marginal R^2
Intercept+log(Age)	6	125.66	0	0.47	0.64
Intercept+log(Age) +Disturbance	7	125.83	0.17	0.43	0.61
Intercept+log(Age)*Disturbance	8	128.8	3.14	0.1	0.61

Table A18 – Variables included in models of soil carbon recovery with ∆ AICc <7, models are ranked by AICc with weight representing the likelihood that individual models are the most parsimonious

Variables included in model	df	AICc	∆ AICc	Weight	Marginal R^2
Intercept only (null model)	6	334.23	0	0.43	0
Intercept+Age+Age^2	8	335.85	1.62	0.19	0.01
Intercept+Age	7	336.18	1.95	0.16	<0.01
Intercept+ Disturbance	8	337.28	3.05	0.09	0.01
Intercept+Age+Age^2 +Disturbance	10	337.84	3.62	0.07	0.03
Intercept+Age*Disturbance	9	338.64	4.41	0.05	0.02
Intercept+Age+Disturbance	6	334.23	0	0.43	<0.01

Table A19 – Variables included in models of tree species richness recovery with ∆ AICc <7, models are ranked by AICc with weight representing the likelihood that individual models are the most parsimonious

Variables included in model	df	AICc	∆ AICc	Weight	Marginal R^2
Intercept+log(Age)	6	499.1	0	0.7	0.25
Intercept +log(Age+Disturbance	8	501.61	2.51	0.2	0.26
Intercept+log(Age)+log(Age)^2	7	503.83	4.73	0.07	0.23
Intercept+log(Age)+log(Age)^2+ Disturbance	9	505.57	6.47	0.03	0.26

Table A20 – Variables included in models of epiphyte species richness recovery with ∆ AICc <7, models are ranked by AICc with weight representing the likelihood that individual models are the most parsimonious

Variables included in model	df	AICc	∆ AICc	Weight	Marginal R^2
Intercept+log(Age)	6	150.75	0	0.56	0.07
Intercept only (null mode)	5	152.31	1.56	0.26	0
Intercept+log(Age)+log(Age)^2	7	152.96	2.22	0.18	0.09

Table A21 – Variables included in models of primary forest species recovery with ∆ AICc <7, models are ranked by AICc with weight representing the likelihood that individual models are the most parsimonious

Variables included in model	df	AICc	∆ AICc	Weight	Marginal R^2
Intercept only (Null model)	2	13.52	0	0.42	0
Intercept+Age	3	14.6	1.08	0.24	0.13
Intercept+Disturbance	3	15.77	2.25	0.14	0.03
Intercept+Age+Disturbance	4	16.95	3.43	0.08	0.15
Intercept+Type	4	17.07	3.55	0.07	0.02
Intercept+Age+Type	5	18.78	5.26	0.03	0.17
Intercept+Disturbance+Type	5	19.56	6.04	0.02	0.04

Table A22- Parameter estimates for models of aboveground biomass with delta≤7 calculated by multiplying the estimates for individual models which contain parameters by their weights. Note that units represent the transformation used for model fitting

Parameter	Estimate	Standard error of estimate	Lower confidence interval	Upper confidence interval
Intercept	-4.08	0.29	-4.65	-3.52
Log(Age)	0.85	0.07	0.7	0.99
Disturbance - Pasture	-0.01	0.24	-0.49	0.46
Disturbance - Shifting agriculture	0.19	0.28	-0.36	0.74
Disturbance – Pasture*logAge	0.07	0.2	-0.31	0.46
Disturbance - Shifting agriculture*logAge	0.16	0.22	-0.28	0.6
Type - Moist	0.06	0.19	-0.31	0.43
Type - Montane	-0.11	0.75	-1.58	1.36
Type - Wet	-0.04	0.16	-0.35	0.26

Table A23- Parameter estimates for models of belowground biomass with with delta≤7 calculated by multiplying the estimates for individual models which contain parameters by their weights. Note that units represent the transformation used for model fitting

Parameter	Estimate	Standard error of estimate	Lower confidence interval	Upper confidence interval
(Intercept)	-3.48	0.23	-3.93	-3.02
Disturbance - Shifting agriculture	-0.65	0.64	-1.91	0.6
log(Age)	0.68	0.06	0.56	0.8
Disturbance - Shifting agriculture*log(Age)	0.11	0.34	-0.55	0.76

Table A24- Parameter estimates for models of soil carbon with delta≤7 calculated by multiplying the estimates for individual models which contain parameters by their weights. Note that units represent the transformation used for model fitting

Parameter	Estimate	Standard error of estimate	Lower confidence interval	Upper confidence interval
(Intercept)	-0.2	0.2	-0.6	0.2
Age	0.01	0.01	-0.01	0.02
Age^2	0	0	0	0
DisturbancePasture	0.18	0.21	-0.23	0.58
DisturbanceShifting agriculture	0.34	0.25	-0.15	0.82

Table A25- Parameter estimates for models of tree species richness with delta≤7 calculated by multiplying the estimates for individual models which contain parameters by their weights. Note that units represent the transformation used for model fitting

Parameter	Estimate	Standard error of estimate	Lower confidence interval	Upper confidence interval
(Intercept)	-3.41	0.34	-4.08	-2.73
log(Age)	0.88	0.12	0.65	1.11
Disturbance - Pasture	0.17	0.21	-0.24	0.59
Disturbance - Shifting agriculture	-0.2	0.23	-0.65	0.26
log(Age)^2	-0.06	0.04	-0.15	0.02

Table A25- Parameter estimates for models of epiphyte species richness with delta≤7 calculated by multiplying the estimates for individual models which contain parameters by their weights. Note that units represent the transformation used for model fitting

Parameter	Estimate	Standard error of estimate	Lower confidence interval	Upper confidence interval
(Intercept)	-1.91	1.04	-3.94	0.13
log(Age)	0.39	0.31	-0.22	0.99
Log(Age)^2	0.06	0.1	-0.13	0.25

Table A27- Parameter estimates for models of primary forest species with delta≤7 calculated by multiplying the estimates for individual models which contain parameters by their weights. Note that units represent the transformation used for model fitting

Parameter	Estimate	Standard error of estimate	Lower confidence interval	Upper confidence interval
(Intercept)	-1.01	0.88	-2.73	0.7
Age	0.01	0.01	-0.01	0.04
Disturbance - Shifting agriculture	-0.02	0.69	-1.37	1.33
Type - Tropical moist forest	-0.1	2.15	-4.32	4.12
Type - Tropical rainforest	-0.85	2.07	-4.9	3.2

Table A28– Importance values for explanatory variables in corresponding models. These values are the sum of the AICc weight for different models with Δ AICc <7

	Model name					
Explanatory variable	Aboveground biomass	Belowground biomass	Soil Carbon	Tree species richness	Epiphyte species richness	Proportion of undisturbed forest species
Age – linear	0	0	0.47	0	0	0.35
Age – quadratic	0	0	0.26	0	0	0
log(Age)	1	1	0	1	0.74	0
log(Age) - quadratic	0	0	0	0.093	0.18	0
Disturbance type	0.40	0.52	0.21	0.22	0	0.23
Forest type	0.02	0	0	0	0	0.12

Appendix IV – Information in support of Chapter 6

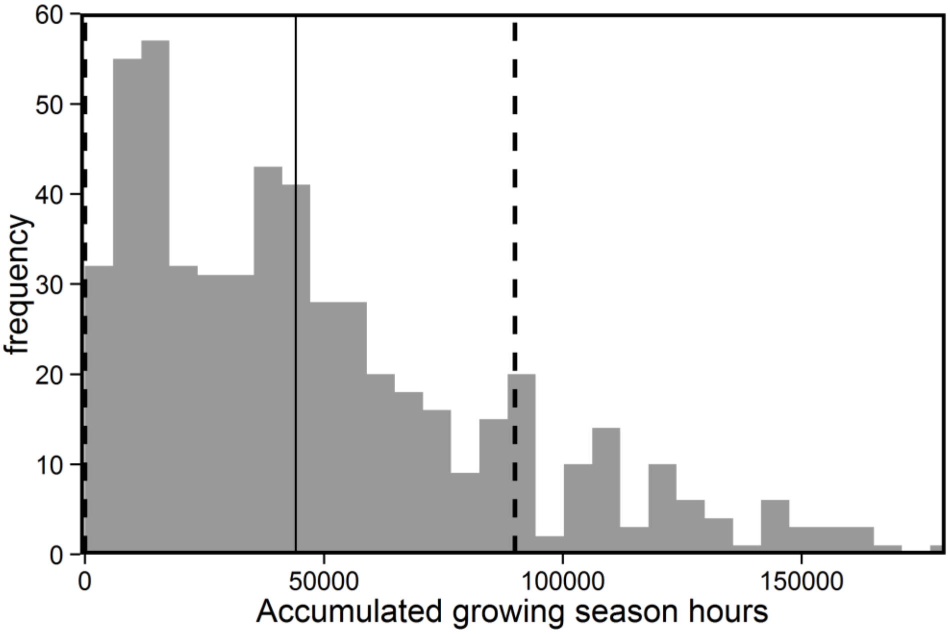

Figure A6 –Data used in aboveground biomass model, showing the range and frequency of data used to parameterise the model. Dashed lines represent minimum and maximum values for which model projections were made, with the solid line representing the median value for which projections were made

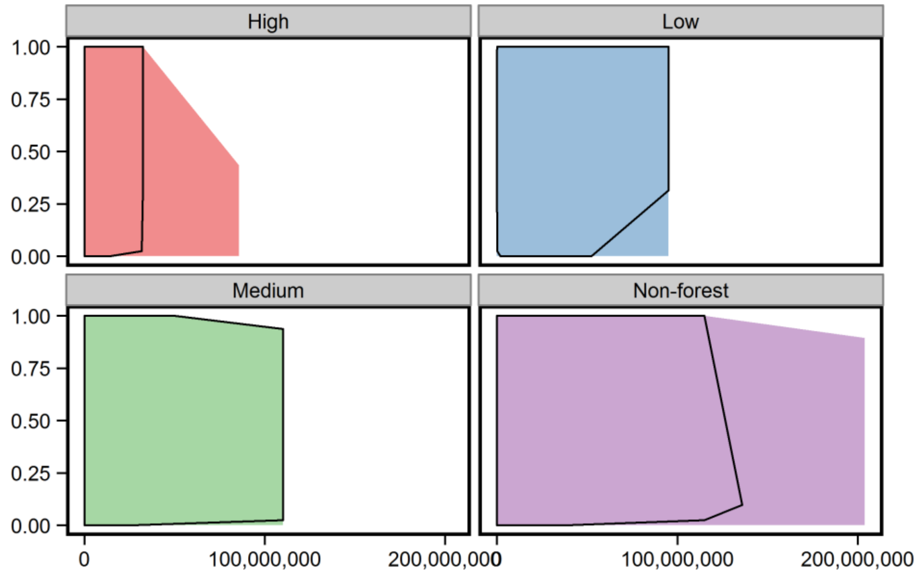

Figure A7 – Data used in model of species presence, with each panel representing species with differing species dependence on forest. Solid lines represent the convex hulls of the variable values used to parameterise the model and coloured polygons the convex hulls of values over which models were projected. The figure shows some signs of extrapolation of models that may lead to inaccurate predictions of probability of species presence, particularly for highly forest dependant species and for non-forest species.

Methods used to collate bird data from primary studies

A systematic review of the literature in was conducted in May 2013 by searching Thomas Reuters Web of Knowledge with the terms bird* AND (secondary or disturb*) AND forest AND tropic*. Additional studies were found in the references of reviews (Barlow et al., 2007; Bowen et al., 2007; Chazdon et al., 2009; Dent and Wright, 2009; Gardner et al., 2007).

Studies were selected if they included details of avian community composition in (at least) one secondary forest site and a reference undisturbed primary forest site. Secondary forest was defined as a naturally forested area where there had been discontinuity in forest cover (Corlett, 1994). Following Newbold et al. (2013), studies from the tropics and sub-tropics between the latitudes of 40°N and 40°S were included. Forests that had previously been selectively logged were excluded, as selectively logged sites recover differently to those converted for agriculture (Corlett, 1994; Dunn, 2004).

Data on bird species present in forest sites were extracted from the articles, in addition to species abundance data where provided. Authors were contacted to request this data when articles suggested that it had been collected but it was not presented. Additionally for each secondary forest site, the age, whether the site was continuous or discontinuous with primary forest and whether the site’s disturbance history prior to secondary succession left remnants of the original forest vegetation (e.g. slash-and-burn agriculture, pasture) or not (e.g. arable agriculture, plantation) were noted. Where age and disturbance history were not presented, authors were contacted to request the information. The median age of secondary forest was recorded when a range of values was given. Methodologies used to sample bird communities was consistent within studies but differed between them. However, sampling method does not affect the reported response of birds to disturbance in tropical forests (Hill and Hamer, 2004) so these differences are unlikely to bias results.

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