Legacies of tropical forest fragmentation and regeneration for biodiversity and carbon storage

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SUMMARY ABSTRACT

Expanding anthropogenic development within the tropical forest biome is driving the loss of an irreplaceable global resource. Mega-diverse tropical forests are vital for regulating the global carbon cycle, and are essential for climate change mitigation. Today, over half of the world's remaining tropical forest is degraded or regenerating secondary forest. Tropical forests are becoming increasingly fragmented through the expansion of agriculture and roads. Landscape-scale flooding of terrestrial habitats caused by dam construction is an emerging driver of habitat loss and fragmentation.

Much attention has been paid to the long-term impacts of tropical forest fragmentation for biodiversity, ecosystem functioning, and carbon emissions. Most of our understanding of the impacts associated with habitat fragmentation originates from systems in which the habitat matrix surrounding remnant forest patches is another, albeit low quality, terrestrial habitat. However, dam-induced habitat fragmentation results in remnant terrestrial biological communities becoming isolated on islands within a water matrix. A water matrix presents the worst-case scenario for remnant habitat fragments. In Chapter 2 I synthesise the results of numerous studies reporting the responses of taxonomic groups to isolation on reservoir land-bridge islands, and uncover a globally-applicable pattern of extinction debt acting upon remnant biological communities on reservoir islands. All islands, regardless of taxonomic group, habitat type, or island area lose species as island isolation time increases. Moreover, I show that contrary to existing ecological theory, once terrestrial habitat becomes isolated within a water matrix, it is effectively too isolated for species losses to be buffered by metapopulation dynamics.

Dam development is rapidly expanding in the largest remaining tract of intact tropical forest, the Amazon Basin. In Chapters 3 and 4 I study the Balbina mega-dam system in the central Brazilian Amazon. Here, I use detailed field inventories of trees and lianas on islands and in continuous mainland habitat to determine the impact of landscape-scale habitat fragmentation caused by reservoir creation on these taxonomic groups. I find that islands maintain tree communities at significantly lower densities, richness and diversity compared to continuous forest. Furthermore, tree communities on islands exhibit compositional divergence from those found in mainland continuous forest. Island tree assemblages are dominated by low-wood density species, and may be on a trajectory towards communities characteristic of early successional forests with reduced carbon storage capacity. In contrast, liana assemblages remain compositionally intact and are becoming increasingly dominant relative to trees. Thus, lianas appear robust to many of the negative impacts associated with landscape-scale habitat fragmentation. As insular tree communities continue to degrade through area- and edge-effects, lianas may become a key feature of this archipelagic landscape due to their competitive advantage over trees in disturbed forest habitats. Lianas significantly inhibit tree recruitment and carbon storage. Thus, findings from Chapters 3 and 4 provide strong evidence for additional, and currently unaccounted-for biodiversity and carbon impacts associated with tropical dams.

As development of tropical forest regions increases, there is an urgent need to reconcile the need for resources with the need for ecosystem service provision, such as carbon storage, particularly as we attempt to mitigate the impacts of rising atmospheric carbon. Recent studies have shown that secondary tropical forests have the potential to rapidly uptake atmospheric carbon, and act as a powerful tool in climate change mitigation policy. Broad-scale estimates of secondary forest carbon uptake are currently based on above-ground biomass alone. In Chapter 5 I present carbon stock estimates of additional tropical forest carbon pools - soil and dead woody biomass - in secondary forests ranging from 40-120 years. I find that soil fertility (nitrogen concentration) is key in determining carbon storage in secondary forests, and that the stability of carbon stocks held in dead woody biomass increases with secondary forest stand age. I highlight the need to integrate detailed site-specific information into broad-scale predictive models of secondary tropical forest carbon sequestration.

This thesis links ecological theory and landscape-scale field inventories, to provide new understanding of the long-term costs of tropical forest fragmentation for biodiversity conservation and carbon storage, and provides further evidence of the important role secondary tropical forests may play in carbon sequestration and climate change mitigation.

DECLARATION OF AUTHORSHIP

I, Isabel Louise Jones, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of the work carried out in collaboration with others.

Signed……………………………………………

Date………………………………………………

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Namaste

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CHAPTER 1

General introduction

1.1 TROPICAL FOREST BIODIVERSITY AND ECOSYSTEM SERVICE PROVISION

The tropical forest biome occupies 15 % of Earth's land surface, and contains more species than any other biome (Olson *et al.* 2001; Mace, Masundire & Baillie 2005). Tropical forests of the Amazon Basin are mega-diverse, containing approximately 11,000 species of canopy tree (Hubbell *et al.* 2008). A single hectare of Amazonian forest can contain ~300 tree species, often represented by a single individual (Gentry 1988; Pitman *et al.* 2001). Amazonian forests comprise 40 % of the world's tropical forest cover, representing the largest remaining tract of intact tropical forest (Laurance 2001). Aside from the intrinsic worth of tropical forests for biodiversity conservation, tropical forests provide globally important services such as climate regulation; the economic benefits derived from these services - including nutrient cycling, water supply, and raw materials - amount to over \$2,000 ha^{-1} $year^{-1}$ (Costanza et al 1997; Malhi & Grace 2000; Foley *et al.* 2007).

1.1.2 Tropical forest carbon storage and uptake

Due to high rates of net primary productivity, tropical forests uptake and sequester significant quantities of atmospheric CO_2, estimated at ~ 1.19 Pg $year^{-1}$ (Pan *et al.* 2011). Thus, tropical forests comprise the largest terrestrial store of carbon, containing 471 ± 93 Pg C or 55 % of global stocks, in contrast to other terrestrial biomes such as boreal forests that store 32 % and temperate forests that store 14 % (Pan *et al.* 2011). Within tropical forests, carbon is stored both above-ground in living and dead woody biomass, and below-ground in roots and soil. Over half of the total tropical forest carbon stock is held within trees, with around 30 % of the remaining stocks in soil (Jobbagy & Jackson 2000; Nascimento & Laurance 2002; Saatchi *et al.* 2011; Pan *et al.* 2011). The amount of carbon stored below-ground in roots corresponds to approximately 30 % of the carbon stock held in above-ground living biomass (Saatchi *et al.* 2011), while 7-25 % of the total above-ground carbon stock is contributed by dead woody biomass (necromass; Clark *et al.* 2002; Baker *et al.* 2007; Palace *et al.* 2012).

1.1.3 Carbon emission from deforestation

Deforestation of tropical forests results in significant carbon emissions, recently estimated at ~2 Pg year^{-1} (Grace, Mitchard & Gloor 2014; Rosa *et al.* 2016; Pearson *et al.* 2017). An estimated 12 % of anthropogenic CO_2 emissions are generated by deforestation and forest degradation (net loss of forest biomass; van der Werf *et al.* 2009). Carbon is released from tropical forests through burning and decomposition of biomass, and through the concurrent degradation of soil carbon stocks (van der Werf *et al.* 2009; Pearson *et al.* 2017). Considering just the loss of biomass, historical deforestation between 1950-2009 across Amazonia, Congo and S.E. Asia, has led to carbon emissions estimated at ~50 Pg C (Rosa *et al.* 2016). If carbon emissions associated with loss of soil carbon stocks were to be included, then these carbon emission estimates are likely to underestimate the full carbon emissions associated with deforestation.

1.1.4 Increasing global cover of degraded and secondary tropical forests

Persistent deforestation and land-use change means that globally approximately 50 % of tropical forest cover is now degraded or secondary forest rather than intact old-growth forest (FAO 2010; Mitchard *et al.* 2013; Achard *et al.* 2014). Intact tropical forests are irreplaceable for biodiversity and ecosystem functioning (Barlow *et al.* 2007; Gibson *et al.* 2011). However, due to the ongoing loss of old-growth forest cover, we are increasingly reliant on secondary tropical forests to deliver ecosystem services such as carbon storage, and habitat for tropical biodiversity (Wright & Muller-landau 2006; Gardner *et al.* 2009; Dent & Wright 2009; Dent 2010; Mendenhall *et al.* 2011; Anderson-Teixeira *et al.* 2016).

The carbon storage capacity of secondary tropical forests increases with forest stand development. For example, above-ground biomass rapidly accumulates during the first 20 years of secondary forest regeneration, actively taking up atmospheric carbon at a rate of ~3 Mg C ha^{-1} year^{-1}, which is 11 times the rate seen in intact primary forests (Poorter *et al.* 2016). The rate of carbon stock recovery differs between carbon pools such that up to 50 % of soil carbon stocks recover within ~30 years of forest regeneration (Don, Schumacher & Freibauer 2011), and necromass carbon stocks lag behind those of above-ground biomass (Anderson-Teixeira *et al.* 2016). Current broad-scale estimates of the atmospheric carbon uptake potential of secondary forests, are, however, based solely on above-ground biomass (Poorter *et al.* 2016) or soil carbon (Don *et al.* 2011) and do not include other important carbon pools such as necromass (Martin *et al.* 2013). Thus, we are likely to be underestimating the carbon uptake potential of secondary forests until broad-scale models incorporate all tropical forest carbon pools simultaneously (Chazdon *et al.* 2016).

1.1.5 The role of tropical forests in climate change and policy

Anthropogenic emissions of greenhouse gases drive changes in global climatic patterns, causing, for example, increases in extreme weather events such as drought and flooding, desertification of agricultural land, rising sea levels, and loss of endemic species and habitats (Vitousek *et al.* 1997; Sala *et al.* 2000; IPCC 2014). The threats posed by a changing climate are severe, and there is growing international pressure for countries to limit carbon emissions via signatory agreements following the 1997 UNFCCC Kyoto Protocol. Climate change mitigation strategies such as REDD+ (Reducing Emissions from Deforestation and Degradation) have advocated the cessation of tropical forest loss to maintain existing carbon stocks held within intact tropical forests, and reduce emissions associated with tropical land clearance and forest degeneration (Gullison *et al.* 2007; Gibbs *et al.* 2007). Increasing the cover of secondary tropical forests, in concert with halting deforestation of remaining intact forests, may provide a powerful, simple, and cheap tool in climate change mitigation policy (Chazdon *et al.* 2016; Poorter *et al.* 2016).

1.2 THREATS TO TROPICAL FORESTS

Approximately half of the original old-growth tropical forest cover has been lost to deforestation and permanent conversion to another land-use, or has been significantly degraded (FAO 2010; Houghton 2012). Agricultural expansion is the strongest driver of tropical deforestation, but logging, infrastructure development, mega-dams, and urbanisation all lead to tropical forest loss (Foley 2005; DeFries *et al.* 2010; FAO 2010; Houghton 2012; Finer & Jenkins 2012; Laurance, Sayer & Cassman 2014b; Newbold *et al.* 2015). National and global population growth, and increasing resource demand, spurs the anthropogenic advance into tropical forest frontier lands. The global population is projected to reach 11 billion during this century, with the highest population growth rates expected in developing countries (Laurance *et al.* 2014b). Developing countries are therefore increasing investment into projects to expand road networks and land available for agriculture, in efforts to provide resources for burgeoning populations and international markets. In parallel, the increasing demand for cheap energy is driving extensive development of hydropower schemes (Prado *et al.* 2016).

1.2.1 Development of the Brazilian Amazon

Over the past 50 years deforestation and development has largely been driven by increasing rural populations, logging, agricultural expansion and mining (Laurance 2001). More recently, global demand for GM-free soy products and raw materials for industry has galvanised large-scale Government projects such as Avança Brazil, and US$40 billion has been injected into the development of frontier areas of the Brazilian Amazon. Avança Brazil has involved the construction of roads, railways, power lines and river channelization initiated to transport goods for the international trade market (Laurance 2001; Peres 2001a; Laurance *et al.* 2002b, 2014b, Fearnside 2002b; c; Finer *et al.* 2008). Large-scale development projects such as Avança Brazil trigger forest loss and degradation at spatial scales exceeding those of the physical footprint of infrastructure itself. Approximately 75 % of deforestation occurs within 50 km of roads, and there is virtually no colonisation or deforestation of intact tropical forests without the presence of roads (Kirby *et al.* 2006). The construction of roads in the Brazilian Amazon is rampant, and the road network grew by 17,000 km in just three years between 2004 and 2006 (Kirby *et al.* 2006; Ahmed *et al.* 2013). A 400 km-wide swathe of deforestation in the eastern Amazon occurred in the wake of the 1970s construction of the 2000 km Belem-Brasilia Highway; the re-pavement of the Manaus-Porto Velho highway will likely cause a similar level of forest clearance, as it links the central Amazon to major population centres in the south of the Amazon (Laurance, Goosem & Laurance 2009).

Access to new land, facilitated by road construction, has caused a rapid increase in the population of the Brazilian Amazon, from around 7.5 million in 1970 to >20 million in 2000, with a mean growth rate of 3.35 % per annum (Laurance, Albernaz & Costa 2002a). The rural population of Amazonia is estimated at 2.4 million (12 % of Brazil's population; Pereira *et al.* 2010), and is predominantly comprised of farmers practicing small-scale shifting cultivation. Fires associated with shifting cultivation can lead to additional forest loss and degradation if they penetrate into remaining forest cover, which is a particular risk during droughts (Nepstad *et al.* 1999; Barlow & Peres 2008; Cochrane & Laurance 2008). Between 40,000 and 50,000 separate fires are typically detected each year in the Amazon (Laurance 1998; Cochrane & Laurance 2008). Increasing rural human populations can also intensify hunting in remnant forest, leading to unsustainable extraction of bush meat and loss of vertebrate seed dispersers (Peres & Lake 2003; Wright 2005; Cramer, Mesquita & Williamson 2007). Expansion of road networks can also increase animal mortality through road kills, particularly in Amazonia where animals are unaccustomed to the presence of vehicles (Laurance *et al.* 2009).

1.3 Habitat fragmentation

1.3.1 Habitat fragments as 'islands'

Any advance of human populations and development of frontier lands leads to direct removal of formerly continuous habitat, leaving behind a mosaic of remnant habitat patches (Fahrig 2003; Ewers & Didham 2006). These habitat fragments can therefore be thought of as 'islands' within a 'sea' of a different habitat type. Thus, the Island Biogeography Theory (IBT; MacArthur & Wilson 1967) has been used to understand species population dynamics in fragmented habitats, and in the design and evaluation of biological reserves for conservation (Lomolino 2000; Cook *et al.* 2002; Williams, ReVelle & Levin 2005; Watling & Donnelly 2006; Laurance 2008). The IBT was originally developed to explain variation in species richness across oceanic archipelagos, and proposes that the species richness of an island is determined by island area, and the degree of isolation from a mainland species source pool. According to the IBT, biological communities on islands accumulate and are sustained by processes of immigration, extinction, and evolution. Islands further from species source pools should have lower rates of species immigration, and small islands should have higher rates of local species extinction as there are fewer resources available to sustain many species. Rates of evolution of species capable of exploiting new niches on islands are dependent on time, environmental stability and resource availability (MacArthur & Wilson 1967; Lomolino 2000). The IBT assumes that species are equivalent in terms of both colonisation ability and ability to maintain a viable population on an island. Furthermore, the IBT assumes that no additional species migrate into islands from the surrounding habitat (Cook *et al.* 2002).

Fragmentation of existing habitat does not necessarily reflect the processes or assumptions underlying the IBT, namely that the species present in fragments are a product of immigration (Lomolino 2000; Ewers & Didham 2006). The communities within habitat fragments are relicts from a formerly continuous habitat that has been divided into smaller, isolated patches. Thus, due to the reduction of habitat area available, rather than a process of species 'assembly,' species are lost from fragments and communities are 'disassembled' through a process of ecological 'relaxation' until a new stable community is reached (Diamond 1972; Gonzalez 2000).

The habitat that is cleared and the habitat that remains following habitat fragmentation is non-random: habitat fragments are typically left in areas unsuitable for the land-use driving the habitat clearance. For instance, if habitat is being cleared for agricultural expansion, the most nutrient-rich and shallow-sloped areas will typically be cleared first. The habitat fragments left are a non-random subset of the original habitat, often occupying steep ground, hilltops and nutrient-poor land (Seabloom, Dobson & Stoms 2002; Laurance 2008). Within fragments, the loss of species during the 'relaxation' process is also non-random: species that are most vulnerable to local extinction tend to have low population sizes or high natural fluctuations in populations, low competitive ability and disturbance tolerance, and high micro-habitat specialisation (Watling & Donnelly 2006).

Thus, biological diversity, which can be measured at a range of scales, can be differentially affected within a fragmented system. At the landscape-scale, gamma (γ) diversity is the species richness and composition of the landscape as a whole, and is a product of alpha (α) and beta (β) diversity: α-diversity is the species richness of a particular site, while β-diversity relates to differences in community composition among sites (Whittaker 1972; Magurran & McGill 2011; Collins *et al.* 2016). The α- and β-diversity of habitat fragments therefore depends on species-level population dynamics (metapopulation dynamics), and community-level dynamics across the landscape (metacommunity dynamics). The amount and spatial configuration of habitat remaining after fragmentation influences α- and β-diversity levels because of the differential persistence of species populations within a remnant habitat patches (Hanski & Ovaskainen 2000). Species loss associated with diminished habitat area results in a reduction in α-diversity, and changes in β-diversity among fragments. If remnant habitat fragments within a landscape all undergo species losses, then broader-scale γ-diversity is also reduced (Kareiva & Wennergren 1995).

1.3.2 The importance of the habitat matrix and spatial configuration of fragments

The immigration of individuals from the habitat surrounding fragments may bolster the population of a particular species within a fragment, a process known as the 'rescue effect,' and allow insular populations to persist (Brown & Kodric-Brown 1977; Hanski & Gilpin 1991; Hanski & Ovaskainen 2000). The ability of a species to persist within a fragment may also be influenced by whether the species can use the surrounding matrix as an additional resource, such as for feeding or breeding, which may mitigate some of the detrimental effects of reduced habitat area (Kupfer, Malanson & Franklin 2006; Watling & Donnelly 2006). At the community-level, species assemblages may be supplemented by novel species entering fragments from the surrounding habitat matrix; thus, while species richness *per se* may not decline in fragments, the community composition of species within fragments may be modified (Ewers & Didham 2006). Similarly the spatial configuration and number of fragments also influences species persistence, as species-specific dispersal limitation can inhibit the ability of some species to migrate among fragments and maintain viable metapopulations (Ewers & Didham 2006; Watling & Donnelly 2006; Martensen *et al.* 2012; Fahrig 2013).

Given the importance of the surrounding habitat matrix in bolstering species populations within fragments, the degree to which the habitat fragment and the surrounding matrix differ is paramount in determining species persistence in fragments. For example, habitat patches surrounded by a similar, but lower quality habitat matrix, e.g. remnant old-growth forest surrounded by secondary forest, will maintain a greater proportion of the original species than a fragment surrounded by a more hostile matrix, due to increased resource use within the matrix for example (Ewers & Didham 2006; Mendenhall *et al.* 2011; Ruffell, Clout & Didham 2016). A high-contrast matrix, such as water, confers the least advantage to remnant communities within fragments, as open water can be too great a dispersal barrier for many species to cross successfully for example, leading to a breakdown in metapopulation dynamics and no 'rescue effect' (Moore *et al.* 2008; Mendenhall *et al.* 2014). However, fragments surrounded by another terrestrial matrix may be disadvantaged by negative matrix effects such as fires and invasive species penetrating into them from the matrix (Cochrane & Laurance, 2002).

1.3.3 Extinction debt

Overall, the fragmentation of terrestrial habitat has a negative impact on remnant communities isolated in fragments: a synthesis of 35 years of findings from seven different experimentally fragmented landscapes revealed that the level of biodiversity in fragments is reduced between 13 and 75 %, and ecosystem functioning such as carbon storage is acutely impaired (Haddad *et al.* 2015). The speed and magnitude of species loss from fragments as they undergo 'relaxation' to new equilibrium communities is mediated by fragment size, spatial configuration, and type of surrounding habitat matrix (Ewers & Didham 2006). Species losses from fragments can occur for generations following the initial fragmentation event i.e. species are subject to an 'extinction debt', which has been demonstrated for mammals, birds, amphibians, invertebrates, and plants (Tilman *et al.* 1994; Kuussaari *et al.* 2009; Wearn, Reuman & Ewers 2012; Halley, Sgardeli & Triantis 2014; Kitzes & Harte 2015). For example, a 30 year study of ground-foraging birds in eucalypt woodland (SW Australia) demonstrated that habitat loss that occurred >100 years prior to the study was still causing significant population declines. The population declines observed were primarily due to dispersal limitation between isolated populations, and altered biotic interactions including elevated nest predation (Ford *et al.* 2009). Extinction debts can be particularly prolonged for plants that have long generation times. For example, in a study of European woodland vascular plants species, an extinction debt was demonstrated for species inhabiting remnant fragments >100 years after habitat fragmentation, due to their slow rates of population turnover (Vellend *et al.* 2006).

Deforestation and fragmentation of tropical forests is also predicted to cause extinction debts for many species: in a recent study of historical deforestation across the Amazon Basin, Congo Basin and S.E. Asia between 1950 and 2009, 1.1 % of tropical forest-specific vertebrate species were estimated to have gone extinct (Rosa *et al.* 2016). But when the time lags of species' responses to fragmentation are considered, even if tropical forest deforestation halted in 2010, the payment of extinction debts - predicted for 144 of 4,125 species studied - would increase the number of known extinctions of tropical forest-specific mammals, birds and amphibians since 1900 by 120 %. Over 50 % of these predicted extinction debts are for vertebrate species within the Amazon Basin (Rosa *et al.* 2016).

1.3.4 Edge-effects

The isolation of remnant habitat fragments within a different habitat matrix causes changes to the abiotic and biotic conditions at the boundary of the fragment and the matrix, known as edge-effects (Murcia 1995). Edge-effects are various and in tropical forest ecosystems can include higher irradiance levels, desiccation and wind disturbance, which can extend to varying degrees into fragment cores (Laurance & Curran 2008; Briant, Gond & Laurance 2010). Furthermore, fires spawned from the surrounding habitat matrix are a pervasive threat to fragment edges, and can penetrate into fragments cores. Even remaining intact forest and large forest fragments are subject to fires penetrating up to 2.5 km into forest interiors (Nepstad *et al.* 1999; Cochrane & Laurance 2002; Barlow & Peres 2008).

1.3.5 Impacts of fragmentation on tropical forest dynamics and composition

Much of our understanding of the impacts of fragmentation on tropical forests comes from long-term experimentally fragmented systems such as the Biological Dynamics of Forest Fragments Project (BDFFP, Brazil; Bierregaard *et al.* 1992; Laurance *et al.* 2011). Extensive research has also been conducted in the Atlantic Forest, Brazil, an area which has undergone significant land-use conversion, fragmentation, and forest regrowth (see e.g. Tabarelli, Mantovani & Peres 1999; Tabarelli, Lopes & Peres 2008; Santos *et al.* 2008; Lôbo *et al.* 2011; Collins *et al.* 2016). Across these systems, fragmentation of tropical forest leads to increased mortality and turnover of trees, particularly in edge-dominated fragments, with rapid changes in tree community composition (Laurance *et al.* 2006a; b; Lôbo *et al.* 2011; Haddad *et al.* 2015).

Mortality of shade-tolerant trees at fragment edges opens gaps in the canopy, and fast-growing pioneer species able to exploit these high-light conditions tend to increase in abundance. For example pioneer tree species have been found to be relatively uncommon in continuous forests in Amazonia, yet following forest fragmentation and the creation of the BDFFP, pioneer trees species tripled in abundance, with sustained population increase over time (Laurance *et al.* 2006b). In the Atlantic Forest, pioneer tree species have been found to contribute >60 % of individuals in both the adult and sapling layers in fragments, leading to a long-term shift towards tree communities more representative of early-successional forest stands (Santos *et al.* 2008; Santo-Silva *et al.* 2016). Lianas (woody vines) are also ubiquitous in forest fragment edges and degraded forest stands, and the recruitment of lianas following fragmentation can increase >500 % (DeWalt, Schnitzer & Denslow 2000; Schnitzer & Bongers 2002; Benítez-Malvido & Martínez-Ramos 2003). Lianas compete with trees for above- and below-ground resources at all life stages (Alvarez-Cansino *et al.* 2015; Wright *et al.* 2015). Lianas can therefore further increase tree mortality in forest fragments, through both competition and structural damage (Ingwell *et al.* 2010). Furthermore, lianas can supress tree recruitment in canopy gaps, effectively stalling the successional process of forest stand development following disturbance, leading to long-term loss of forest biomass (Schnitzer, Dalling & Carson 2000; Schnitzer & Carson 2010).

Shifts in the presence and abundance of species in fragments can therefore fundamentally alter the forest community structure of remnant forest fragments (Laurance *et al.* 2011). Compositional shifts may lead to a breakdown in ecosystem functioning, including carbon storage, of remnant forest (Magnago *et al.* 2016). The amount of carbon a tree can store depends on its wood density, which is intrinsically linked to life-history trade-offs: fast-growing pioneer species tend to have lower wood density than slow-growing shade-tolerant species (Muller-Landau 2004; Chave *et al.* 2009; Visser *et al.* 2016). Thus in disturbed environments, such as fragment edges, community-level carbon storage can be reduced because fast-growing pioneer tree species and lianas have a competitive advantage over slow-growing high wood density species (Benítez-Malvido & Martínez-Ramos 2003; Laurance *et al.* 2006a; Magnago *et al.* 2016). For their biomass, lianas have a disproportionate influence on tree communities, and through competition and suppression of tree recruitment, liana proliferation can lead to further loss of ecosystem functioning and carbon storage capacity in forest fragments (Tobin *et al.* 2012; van der Heijden, Powers & Schnitzer 2015; Wright *et al.* 2015).

1.3.6 Carbon emissions as a result of tropical forest fragmentation

The deforestation and fragmentation of tropical forests and associated degradation of remaining forest leads to significant carbon emissions. Emissions associated with the creation of fragment edges can be in the region of 12-15 Mg C for every 100 m of forest edge created, and reductions in carbon storage capacity can extend up to 1.5 km into fragment cores due to biomass loss, leading to emissions 47 % higher than for deforestation alone (Nascimento & Laurance 2004; Asner *et al.* 2010; Chaplin-Kramer *et al.* 2015). Time lags in species loss from fragments i.e. extinction debts, and subsequent alterations in biotic and abiotic conditions, may also lead to an 'ecosystem function debt,' whereby changes in carbon storage capacity, for example, are delayed following habitat fragmentation. In experimentally fragmented systems including the BDFFP and The Wog Wog Fragmentation Experiment (Eucalypt forest; Australia), the loss of ecosystem functioning in fragments amounted to a 30 % reduction one year post-fragmentation, and after 10 years, small fragments showed a reduction in ecosystem functioning of 80 % (Haddad *et al.* 2015). Moreover, the time lag in carbon emissions from biomass loss from 1950-2009 has been predicted to result in a carbon emission debt of ~9 Pg C, the equivalent of 50-10 years of deforestation (Rosa *et al.* 2016).

1.3.7 Synergies determining fragmentation impacts

Changing climatic patterns could interact with edge-effects to exacerbate the deleterious consequences of fragmentation on biological communities (Travis 2003; Ewers & Didham 2006). Impacts from a changing climate, such as increased frequency and duration of drought, will likely act in synergy with edge-effects, putting further pressure on fragmented forest communities and increasing carbon emissions. For example the 2005 drought in Amazonia led to tree mortality and a loss of forest biomass, resulting in a loss of 1.2-1.6 Pg C (Phillips *et al.* 2009). Even within intact Amazonian forest, it has been predicted that 20-33 % of tree species will be extirpated under current scenarios of forest loss and climate change, with species that are already less able to cope with habitat fragmentation e.g. range-restricted habitat specialists being most threatened (Henle *et al.* 2004; Hubbell *et al.* 2008).

Other synergies arise from interactions between fragment area and edge-effects, and from the type and quality of the surrounding habitat matrix (Ewers & Didham 2006; Kupfer *et al.* 2006; Ewers, Thorpe & Didham 2007). A relatively benign matrix of similar habitat type, such as with the BDFFP system where forest fragments are surrounded by abandoned pasture and secondary forest regrowth, presents the best case scenario for fragmentation. Although even in this instance the impacts of fragmentation on remnant communities are severe, with the proliferation of pioneer tree species and lianas causing a non-random shift in tree communities at fragment edges away from those in fragment interiors (Laurance *et al.* 2006b, 2011). In contrast, fragments surrounded by a wholly different matrix, such as water, is the worst case scenario in terms of fragmentation effects: land-bridge islands created by inundation following the construction of dams results in such a landscape (Ewers & Didham 2006).

1.4 DAMS AS AN EMERGING DRIVER OF HABITAT LOSS AND FRAGMENTATION

Dams are an emerging driver of habitat loss and fragmentation, and globally over half of all large river systems, eight of which are the most biogeographically diverse, have been dammed (Nilsson *et al.* 2005). Following river impoundment, vast areas of terrestrial habitat can be inundated, for example following the construction of the Tucuruí dam in Brazil, ~2430 km^2 of land was flooded (Fearnside 2001). Dam-induced inundation can also cause extensive fragmentation of terrestrial habitats, creating archipelagos of former hilltops within reservoirs (Fig. 1.1). Such newly-formed reservoir islands are true land-bridge islands, as they have been created simultaneously from previously continuous habitat. The Balbina hydroelectric mega-dam in the Brazilian Amazon created >3500 land-bridge islands following the flooding of ~2360 km^2 of continuous old-growth tropical forest habitat (Fearnside 1989; Benchimol & Peres 2015a). These islands are surrounded by a water matrix, which provides no buffer to edge-effects that even a low-quality a terrestrial habitat matrix can provide. Thus, the impacts of habitat fragmentation on remnant biological communities are severe, and species loss from fragments in a land-water matrix is at a greater magnitude than from fragments within a terrestrial matrix (Ewers & Didham 2006). A study in Panama that explicitly compared bat communities in fragments embedded within a terrestrial ‘countryside’ matrix and those embedded within water, found striking differences in species richness, evenness and composition between the two landscapes: species richness on islands declined with island isolation distance, and the rate of species loss was higher on islands compared to fragments within the ‘countryside’ matrix (Mendenhall *et al.* 2014). Furthermore, islands were more unstable in terms of species evenness, and community compositions were significantly different between the two landscape systems (Mendenhall *et al.* 2014).

Fig. 1.1: Reservoir land-bridge islands. Island archipelagos are created from former hill-tops when terrestrial habitat is flooded after dam construction. For example, >3500 reservoir land-bridge islands were created when the Balbina hydroelectric reservoir (Brazil) flooded ~2360km^2 of continuous old-growth forest of central Amazonia in 1986. [Photo: E.M. Venticinque].

The impacts of dam creation on remnant biological communities on islands can be extreme, and can occur over short time-scales. In Thailand, islands within the Chiew Larn reservoir experienced near total extinction of small mammals within 26 years of island isolation, with 50 % of species locally extinct in <14 years (Gibson *et al.* 2013). In Lago Guri (Venezuela) local extinctions of top predators caused a trophic cascade, severely impacting tree regeneration because of increased herbivory (Terborgh *et al.* 2001, 2006). In Balbina (Brazil) a recent study highlighted the vulnerability of remnant tree communities to area- and edge-effects, including a severe fire, which have led to increased dominance of pioneer tree species at the expense of old-growth shade-tolerant species in <30 years of island isolation (Benchimol & Peres 2015a).

Indirectly, the construction of dams can also cause extensive additional forest loss due to human migration following the construction of access roads, and the initial phase of construction when labour is no longer required. Following dam construction, the inflated rural population increasingly relies upon forest resource extraction for subsistence, leading to logging and bush meat hunting, as well as the establishment of small-scale farming. Practices that lead to the degradation of remaining forest surrounding dams add to the ecological footprint of dam construction (Peres & Lake 2003; Fearnside 2008; Peres *et al.* 2010). For example, the 2016 completion of the Belo Monte dam in Brazil is predicted to trigger an additional 4000-5000 km^2 of forest loss by 2030, above the ~1500 km^2 of forest loss that will occur from reservoir creation itself (Barreto *et al.* 2011).

Other ecological impacts following river impoundment include loss of connectivity between the upper and lower reaches of rivers, with catastrophic impacts for migratory fish species and species reliant on seasonal flood pulses (Agostinho, Pelicice & Gomes 2008; Lees *et al.* 2016). Dams have been shown to cause significant reductions in the abundance, biomass, species richness, diversity and dominance in fish communities as river channels are changed from lentic to lotic habitats (Sá-Oliveira *et al.* 2015). Such changes have concurrent social impacts such as disruption to downstream fisheries, which can provide a vital source of protein to subsistence rural communities (Fearnside 1999). Perhaps the biggest social impact of dams is the loss of indigenous lands and the displacement of people who have no rights to compensation due to lack of land titles. One of the most controversial examples of the social and ecological impacts of dam construction is the Belo Monte dam (Brazil), where human rights and environmental impact have clashed with political power and corporate investment for decades (Fearnside 2006). An estimated 19,000 people have been forcibly removed and indigenous lands taken, to enable the construction of the ~$17 billion dollar project; the energy produced from Belo Monte will power iron ore and aluminium smelters owned by shareholders, and emissions from the dam are predicted to be four times the emissions of an equivalent-sized fossil-fuel thermal power plant (Fearnside 2006; International Rivers 2012).

1.4.1 Increasing global development of dams

As the global population increases so does energy demand, and global energy consumption is predicted to increase 56 % by 2040. Developing countries with emerging economies are predicted to increase energy consumption by 90 % during this period (EIA 2013). To meet energy demands, developing countries increasingly seek cheap and reliable energy generation sources, and hydropower is a logical option for tropical nations, considering the high precipitation and numerous rivers (Finer & Jenkins 2012). Furthermore, because hydropower is a renewable energy source, funding for hydropower projects can be garnered from international climate change mitigation funds and strategies, such as the Clean Development Mechanism and the World Bank (Haya, McCully & Pearson 2002). As of 2016 there are >58,000 large dams (dam height >15 m) in operation globally, which provide water predominantly for agriculture and hydropower generation (ICOLD 2016). The global demand for water is set to increase over the coming decades due to the increasing frequency of severe droughts. However, low water levels reduce hydropower outputs, increasing the need for energy generated from other power sources, including from fossil-fuel-powered thermal energy plants (Oki & Kanae 2006; Prado *et al.* 2016). In 2013 reservoir levels in Brazil reached their lowest levels since 2001 for example, necessitating an increase in thermal power generation. Furthermore, droughts are predicted to reduce any future hydropower production in Amazonia by 36 % (Prado *et al.* 2016).

While the production of energy using hydropower is in principle an excellent option for providing relatively cheap and reliable energy to growing populations, the reality is that most energy produced from hydropower in countries with emerging economies is not consumed by people, but by the extractive industry: for example, a single aluminium smelting plant in S.E. Brazil can use more power than the ~1.2 million population of Belém (Fearnside 1999). The decision to construct dams is heavily embroiled in large financial investment and political will, yet dams provide few long-term social benefits. For example employment opportunities tend to be limited, as few people are employed once dam construction is complete, and goods produced using power from dams are exported as a raw material, rather than providing employment in-country from production of high-value goods for the international market (Fearnside 2016a; Prado *et al.* 2016).

1.4.2 Carbon emissions associated with tropical dams

Emissions of CO_2 and CH_4 from tropical reservoirs begin at the construction phase (involving carbon emissions from cement production and vehicles for example) can persist for many years after inundation, and potentially over the entire lifetime of the dam (Table 1.1; Abril *et al.* 2005; Gibson, Wilman & Laurance, 2017). Dams constructed in topographically rugged areas with high rainfall are the most efficient in terms of the energy produced per unit area flooded (Finer & Jenkins 2012). However, of the 1096 GW installed energy generation capacity of dams globally in 2016, the energy generated for that year amounted to just 4.1 PWh (Gibson, Wilman & Laurance, 2017). When dams are constructed in areas of relatively shallow topography, such as the Amazon Basin, large areas of land must be flooded to provide enough water to power turbines (Fearnside 1989). Indeed, 10 million hectares of Amazonian forest is estimated to become flooded by hydropower expansion, leading to the direct loss of tropical forests and associated carbon stocks (Fearnside, 2006).

Tropical forests are rarely logged prior to inundation due to logistical and time constraints (Gilani & Innes 2017) and thus, all plant biomass is submerged. The decomposition of dead biomass below water level, combined with high levels of dissolved organic carbon entering reservoirs from tributaries, leads to significant emissions of CO_2 and CH_4 from reservoir surfaces, and as anoxic water layers are drawn through turbines and down spillways (Abril *et al.,* 2013). Seasonal exposure of the reservoir bottom during periods of low rainfall also results in a cyclical pulse of emissions from exposure of high-carbon tropical soils to the air, followed by rapid vegetation regrowth on exposed soil, re-submergence of vegetation and its subsequent decomposition (Fearnside 2002a; Demarty & Bastien 2011). Emissions are far larger from tropical reservoirs compared to those in more temperate climates due to high carbon stocks in soil and vegetation, and higher water temperatures increasing gaseous emissions from reservoirs (St. Louis *et al.* 2013). Annual emissions from the Tucuruí dam (Brazil) have been estimated to be more than the annual emissions generated by the population of São Paulo burning fossil fuels (Fearnside 2002a). Field-based quantification of carbon emissions from dams in Amazonia has shown that carbon emissions from decomposing submerged biomass and soil are the largest contributors to reservoir carbon emissions, with Petit Saut (French Guiana) emitting 22 % of the flooded carbon stocks over 10 years (Abril *et al.* 2005), and emissions from Tucuruí (Brazil) estimated at >28 Mg C year $^{-1}$ (Kemenes, Forsberg & Melack 2007). Carbon emissions from the Balbina dam (Brazil) exceed those of a thermal power plant that would generate the same amount of energy (Rosa *et al.* 2004). However there have been recent calls for more comprehensive quantification of carbon exchange from tropical reservoirs in general, to gain insight into whole-system carbon flux (Demarty & Bastien 2011; Gibson, Wilman & Laurance 2017). Accurate quantification of such carbon fluxes in hydroelectric systems is especially needed, as current policy to mitigate climate change via emission reductions favours sources of renewable energy such as hydropower. Yet, global emissions from hydroelectric reservoirs across all major habitat types have been estimated to range from 136-635 Tg for CH_4 and 176-301 Tg for CO_2 (Fearnside 2013; Deemer *et al.* 2016; Scherer & Pfister 2016; Winemiller *et al.* 2016).

1.4.3 Impact assessments and additional sources of carbon loss from tropical dams

Given the wealth of documented impacts of dams, there is a lack of appropriate environmental impact assessment prior to project approval; where impact assessments have been conducted, they are often inadequate in mega-diverse regions such as the Amazon basin, and regularly ignored in favour of political and financial gains (Peres 2005; Peres *et al.* 2010; Ritter *et al.* 2017). While some environmental mitigation measures, such as the development of protected areas surrounding dams, are suggested in "best practice guidelines" for dam developers (International Energy Agency 2006), there is no consensus or signatory international agreement on how to forecast, prevent, or mitigate the detrimental impacts of large dams (Kareiva 2012; Prado *et al.* 2016; Winemiller *et al.* 2016). Furthermore, when island archipelagos are created, their cumulative area is not included in impact assessments. Given the impact of habitat fragmentation on remnant terrestrial habitat and species, particularly when remnant habitat fragments are surrounding by water, the area of reservoir islands should be accounted for in any impact assessments of future dams. At present, reservoir islands are hailed as 'wildlife refuges' by dam developers, when in reality, local extinctions of taxa on islands are widely reported, and rescue efforts to save wildlife as reservoirs are filled are ineffective and result in significant mortality of rescued wildlife (Terborgh *et al.*

2001; Nakhasathien 2009; Gibson *et al.* 2013; Benchimol & Peres 2015b; Aurélio-Silva *et al.* 2016).

Current models of carbon emissions from dams do not consider long-term degradation of remnant tree communities on islands, nor do they include additional forest loss and degradation associated with dam construction. For example, on the Tapajos River and its tributaries, deforestation is predicted to increase by approximately 1 million ha by 2030 due to the construction of roads and powerlines, and the influx of people able to access forest resources (Barreto 2014). Even with these potential long-term sources of carbon emissions omitted from models, six out of 18 dams planned for construction in Amazonia have been predicted to have emissions comparable to thermal power plants, and higher emissions compared to solar or wind projects (de Faria *et al.* 2015). Models also predict that the 18 dams would lead to average total emissions of 9 to 21 Tg CH_4 and 21-310 Tg CO_2 over a hundred years (de Faria *et al.* 2015). A further source of carbon emissions associated with dam construction comes from dam developers themselves, encouraging deforestation of land surrounding reservoirs and tributary rivers to increase river flow. The irony in this practice is astounding considering the green energy credentials of hydropower (Haya *et al.* 2002; Fearnside 2013), and the fact that intact forests increase rainfall and river flow upon which hydropower generation relies. Using predicted levels of deforestation within the Amazon basin and rainfall models of the Xingu River basin (the location for the Belo Monte dam complex), deforestation was found to inhibit rainfall and decrease river discharge by 6-36 %, reducing projected power output of the Belo Monte dam by 75 % (Stickler *et al.* 2013).

Tropical forest fragmentation leads to loss of tree biomass and carbon emissions (Asner *et al.* 2010; Chaplin-Kramer *et al.* 2015). Thus the inclusion of forest degradation on reservoir islands in impact assessments is needed for better carbon accounting of dams, as loss of tree biomass on islands will doubtless lead to significant carbon emissions, on top of those already associated with tropical reservoirs (Fearnside & Pueyo 2012; Benchimol & Peres 2015a). Studies have shown that tropical tree communities isolated on reservoir land-bridge islands undergo rapid degradation, including loss of biomass, species richness, and alterations in community composition (Leigh *et al.* 1993;

Terborgh *et al.* 2001; Yu *et al.* 2012; Benchimol & Peres 2015a). If we consider the Balbina hydropower reservoir, 118,000 ha of formerly continuous forest now forms an archipelago of 3545 islands, and only 2% of this total island area is predicted to provide suitable habitat to support >75 % of the original vertebrate community (Benchimol & Peres 2015b). Assuming that depauperate vertebrate communities are indicative of forest degradation, carbon emissions due to forest degradation could therefore be in the region of 0.1 Pg CO_2 per year from islands. In addition, the 8992 km of island edge may also be a significant source of emissions (Nascimento & Laurance, 2004; Table 1.1). We have little understanding of how tree communities recruited on islands post-isolation correspond to remnant adult tree communities, and whether there is evidence for a shift from remnant tree communities towards future communities representative of early successional tree communities, with lower carbon storage capacity (Tabarelli *et al.* 2008; Lôbo *et al.* 2011).

Table 1.1: Potential additional sources of CO_2 emissions from dam construction and operation, and relative magnitudes of emissions

Geographic Area/ Case study	Main source of C flux	Emissions of CO_2 and/or CO_2 equivalent	Details and significance
Dam construction			
Three Gorges Dam, China	Cement production	36.59 Pg	Approximately 900kg CO_2 is produced per 1000kg cement (Mahasenan, Smith & Humphreys, 2003). The Three Gorges dam, China, used approximately 27 million m^3 of cement, requiring ~40,654,860,043 kg cement (Embassy of the People's Republic of China in the Unisted staes of America; undated). The total amount of CO_2 emitted from cement from the Three Gorges Dam can therefore be estimated at 36.59 Pg.
Itaipu	Transportation of materials	Unknown	The CO_2 emissions of trucks throughout the construction phase of dams could be significant. For example, the Itaipu dam in Brazil took 18 years to complete.
Dam operation			
Reservoirs globally & Amazonia	Emissions from reservoir surface, including bubbling	2.5 x10^{-7} Pg ha^{-1} year $^{-1}$	773.1 Tg CO_2 equivalent per year is estimated to be emitted from 0.31 x10^6 km^2 of reservoir surfaces globally (Deemer *et al.,* 2006), and thus, approximately 2.5 x10^{-6} Tg per km^2 which equates to 2.5^{-7} Pg CO_2 per ha of reservoir surface area. 10 million ha of forest will be flooded by proposed dam construction in Amazonia (Fearnside, 2006), which may therefore result in annual emissions of 2.5 Pg CO_2 per year from Amazonian reservoir surfaces and bubbling.
Reservoirs in Amazonia	Wood decomposition (flooded wood)	140-227 Pg ha^{-1} year $^{-1}$ of flooded forest	Over a 100 year period, an estimated 140-227 Pg CO_2 equivalent is emitted per km^2 Amazonian forest flooded (Abril *et al.,* 2013), equating to approximately 1.4-2.3 Pg per year per km^2, (converting to 140-227 ha^{-1} per year). In Amazonia, 10 million hectares of forests are expected to be inundated by dam development (Fearnside 2006). Using estimates for carbon emissions from flooded forest, this may give rise to annual emissions of between 14 – 22.7 Pt CO_2 from flooded Amazonian forests.

	Balbina, Brazil	Seasonal exposure of reservoir bottom	0.002 Pg year^{-1} (total exposed reservoir bottom; unknown area)	97,000 tonnes of methane have been estimated to be released annually from the seasonal exposure of the reservoir bottom in the Balbina dam (Demarty & Bastien, 2011). This equates to the CO_2 equivalent of 2,425,000 tonnes i.e. 0.002 Pg CO_2 equivalent year^{-1}
Collateral				
	Tropical and sub-tropical forests	Degradation of remnant forest (per hectare, per year)	9.36 x10^{-10} Pg ha^{-1} year $^{-1}$	Over the estimated 2.2 billion hectares of tropical and subtropical forest which is degraded from fire and resource extraction, 2.06 Pg of CO_2 is emitted per year (Pearson *et al.,* 2017), which converts to emissions of approximately 9.36 x10^{-10} CO_2 ha^{-1} year $^{-1}$. Considering Balbina has a total of 3546 islands of a combined area of 118,000 ha, and only 2 % of this island area (2360 ha) can harbour over 75% of species (i.e. appear to be least degraded), this means that ~115,640 ha of forest islands is degraded. Using the estimated C emissions from degraded tropical forest, emissions from degraded forest islands could be in the region of 0.0001 Pg CO_2 per year.
	Tropical forests	Forest edge creation	12-15 x10^{-8} Pg 100m^{-1}	Considering that the negative effects of forest edge creation on biomass and carbon storage can extend <1500m into forests away from forest edges, a cumulative emission of 12-15 Mg C 100m^{-2} has been estimated (Nascimento & Laurance, 2004). The creation of 3546 reservoir islands in Balbina has created 8992 km of island edge, which therefore may lead to emissions in the region of 0.001 Pg CO_2 (this estimate does not include the mainland edge, which would further increase emissions estimates).
	Belo Monte, Brazil	Deforestation surrounding reservoirs	1.5 x10^{-9} Pg carbon ha^{-1} year $^{-1}$	Deforestation surrounding the Belo Monte dam is predicted to reach 4000-5000 km^{2} by 2030 (Barreto *et al.,* 2011). Across 1949 million ha of tropical forests, 2.9 Pg carbon is lost from deforestation per year (Pan *et al.,* 2011).

1.5 THESIS AIMS

In this thesis I aim to assess the impacts of landscape-scale habitat fragmentation induced by mega-dams on local biodiversity carbon storage, and assess the potential of regenerating secondary forests to uptake carbon and mitigate carbon losses from deforestation.

Chapter 2: Is there a globally-applicable pattern in species responses to isolation on reservoir land-bridge islands?

Within Chapter 2 I present the findings of a global analysis of the impacts of reservoir creation on different taxonomic groups isolated on reservoir land-bridge islands, investigating patterns of species richness change on islands compared to nearby mainland continuous habitat. I discuss the relative importance of island area, isolation distance, and isolation time in governing rates of species loss from islands in the context of Island Biogeography Theory and extinction debt.

Chapter 3: What is the long-term impact of dam-induced fragmentation on tree communities?

Understanding the processes that govern responses of tree communities to fragmentation in the long-term will allow us to better predict the long-term carbon balance of tropical mega-dams. In Chapter 3, I examine the relationship between adult and sapling trees on islands within the Balbina hydroelectric mega-dam, Brazil, and discuss findings in the context of long-term floristic change and carbon loss from insular forest communities.

Chapter 4: How do liana communities respond to dam-induced fragmentation compared to trees?

Given that lianas are well-adapted to fragmented and degraded forest habitats, and play a disproportionate role in driving tree community dynamics, in Chapter 4 I present analyses relating to adult and sapling lianas and their community composition across the Balbina archipelagic landscape. I discuss differences in the responses of lianas and trees to landscape-scale fragmentation, with a particular focus on the additional role lianas may play in shaping future insular tree communities and carbon storage on reservoir islands.

Chapter 5: What contribution can soil and necromass carbon stocks make to broad-scale predictive models of secondary forest carbon uptake?

In Chapter 5 I present a study of soil and necromass carbon stocks across a chronosequence of secondary forest plots, ranging from 40 to 120 years, within the Barro Colorado Nature Monument (BCNM) Panama. Findings are discussed in terms of the importance of including detailed plot-level soil nutrient information in future predictive models of secondary forest carbon uptake, and the relative contributions of soil and necromass carbon pools to total forest carbon stocks.

CHAPTER 2

Extinction debt on reservoir land-bridge islands

A version of this chapter has been published as:

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IJ and DD formulated the research idea. IJ collected the data and performed analyses with advice from NB. All authors commented on draft versions of this manuscript, and the published version formatted for the thesis is presented here.

2.1 ABSTRACT

Large dams cause extensive inundation of habitats, with remaining terrestrial habitat confined to highly fragmented archipelagos of land-bridge islands comprised of former hilltops. Isolation of biological communities on reservoir islands induces local extinctions and degradation of remnant communities. “Good practice” dam development guidelines propose using reservoir islands for species conservation, mitigating some of the detrimental impacts associated with flooding terrestrial habitats. The degree of species retention on islands in the long-term, and hence, whether they are effective for conservation is currently unknown. Here, we quantitatively review species' responses to isolation on reservoir islands. We specifically investigate island species richness in comparison with neighbouring continuous habitat, and relationships between island species richness and island area, isolation time, and distance to mainland and to other islands. Species' responses to isolation on reservoir islands have been investigated in only 15 of the >58 000 large-dam reservoirs (dam height >15 m) operating globally. Research predominantly originates from wet tropical forest habitats and focuses on mammals, with species richness being the most widely-reported ecological metric. Terrestrial taxa are, overall, negatively impacted by isolation on reservoir islands. Reservoir island species richness declines with isolation time, and although the rate of loss is slower on larger islands, all islands exhibit depauperate species richness <100 years after isolation, compared to continuous mainland habitats. Such a pattern of sustained and delayed species loss following large-scale habitat disturbance is indicative of an extinction debt existing for reservoir island species: this pattern is evident across all taxonomic groups and dams studied. Thus, reservoir islands cannot reliably be used for species conservation as part of impact mitigation measures, and should instead be included in area calculations for land impacted by dam creation. Environmental licensing assessments as a precondition for future dam development should explicitly consider the long-term fate of island communities when assessing biodiversity loss vs energy output.

2.2 INTRODUCTION

There are 58 402 large dams (dam height >15 m) operating globally, constructed predominantly for irrigation and hydropower generation (ICOLD 2016). A growing human population is predicted to increase the demand for water by 2-3 % per year, and the demand for energy by >56 % globally between 2010-2040. Energy demand is estimated to rise by 90 % in increasingly industrialised countries with emerging economies over the same period (WCD 2000; EIA 2013). Concurrently, changing climatic and precipitation patterns, including severe droughts, will likely further increase demand for water and reduce hydropower generation from large reservoirs (Oki & Kanae 2006).

Hydropower is regarded as a renewable "green" energy source, and dams constructed in areas with steep topography and high rainfall produce the most energy per unit area (Finer & Jenkins 2012). However dams are often constructed in low-lying areas with high conservation value: for example 154 dams operate in the Amazon basin with a further 277 planned (Castello *et al.* 2013; Lees *et al.* 2016). The construction of dams directly impacts both terrestrial and freshwater ecosystems through inundation of habitat, compositional changes in biological communities, and the loss of structural and functional connectivity between upper and lower reaches of watersheds (Nilsson *et al.* 2005; Finer *et al.* 2008; Palmeirim, Peres & Rosas 2014; Sá-Oliveira *et al.* 2015; Lees *et al.* 2016).

Over 50 % of the world's large river systems and >60 % of the combined habitat area of tropical, subtropical and boreal forests, tropical and subtropical grasslands, savannahs and shrublands have been estimated to be impacted by dams (Nilsson *et al.* 2005). Inundation of terrestrial habitats, and tropical forests in particular, can result in significant carbon emissions from reservoirs in the form of CO_2 and CH_4, which can persist for many years after inundation and often over the lifetime of the reservoir (Fearnside 2002a; Abril *et al.* 2005; Demarty & Bastien 2011; Fearnside & Pueyo 2012). Direct social impacts arise from the loss of indigenous lands, displacement of communities, and disruption to local economies reliant on fisheries often concurrently affected by heavy metal accumulation (Fearnside 1999; Boudou *et al.* 2005). Additionally, increased access to previously undisturbed habitat can elevate levels of hunting and deforestation in areas surrounding reservoirs (Peres & Lake 2003; Kirby *et al.* 2006).

When dams are built, habitat is lost through inundation, with remnants of previously continuous terrestrial habitat confined to highly fragmented land-bridge island archipelagos comprised of former hilltops. "Good practice" guidelines (International Energy Agency 2006) for dam developers to mitigate ecological impacts from dam construction, include implementing protected areas covering land-bridge islands and habitat surrounding reservoirs. For example, the REBIO Uatumã (the largest Biological Reserve in Brazil) encompasses approximately half of the Balbina hydroelectric reservoir, including all islands east of the former left bank of the Uatumã river and mainland areas extending away from the eastern edge of the reservoir. Strictly-protected area status has largely deterred small-scale slash-and-burn agriculture and extraction of resources within the REBIO Uatumã, on both islands and within surrounding continuous forest (Benchimol & Peres 2015b; c). However, we do not know whether protecting reservoir islands is effective for biodiversity conservation, due to a lack of long-term monitoring. The International Energy Agency highlights the dearth of systematic evaluation of any mitigation, enhancement, and compensation measures currently being recommended to large dam developers (International Energy Agency 2000; Trussart *et al.* 2002).

Fragmentation of habitat causes a number of impacts to species, such as population reductions and local extinctions; the strength of fragmentation impacts differ depending on the taxonomic group and life-history traits of species (Turner 1996; Bender, Contreras & Fahrig 1998; Forman & Alexander 1998; Fahrig 2003). Previous studies of reservoir island archipelagos have shown that island taxa typically experience a novel hyper-disturbance regime, resulting in drastic shifts in species diversity and community composition through species turnover, and altered carrying capacity of the remaining habitat (Cosson *et al.* 1999b; Hanski & Ovaskainen 2000; Terborgh *et al.* 2001; Ferreira *et al.* 2012; Benchimol & Peres 2015a). Local species extinctions on reservoir islands have been observed for plants (Yu *et al.* 2012; Benchimol & Peres 2015a), invertebrates (Feer & Hingrat 2005; Emer, Venticinque & Fonseca 2013), birds (Yu *et al.* 2012), bats (Cosson, Pons & Masson 1999a), small-mammals (Lambert *et al.* 2003; Gibson *et al.* 2013), and midsized to large-bodied vertebrates (Benchimol & Peres 2015b; c). Populations of some species can become hyper-abundant on islands, and invasive species can establish, further impacting other taxa (Chauvet & Forget 2005; Feeley & Terborgh 2006; Lopez & Terborgh 2007; Gibson *et al.* 2013).

Changes in island communities may not occur immediately after inundation; instead, species may be subject to an "extinction debt" whereby a portion of species are initially lost, followed, potentially multiple generations later, by further species extinctions (Tilman *et al.* 1994; Kuussaari *et al.* 2009; Halley *et al.* 2014; Kitzes & Harte 2015). Thus, the effects of fragmentation and isolation can persist for years after initial habitat loss, as communities undergo "relaxation" towards a new equilibrium community (Diamond 1972, 2001; Terborgh *et al.* 1997; Ewers & Didham 2006; Feeley *et al.* 2007; Wang *et al.* 2009). The “relaxation” process is likely mediated by island area, with species losses faster on smaller islands, and a greater time-lag for species loss on larger islands (Diamond 1972; Gonzalez 2000). There are a number of empirical methods for calculating extinction debt (Wearn *et al.* 2012; Kitzes & Harte 2015), and here we consider a decline in species richness on islands over time, compared to mainland continuous habitat, as evidence of extinction debt. In the absence of extinction debt, we assume that all species extinctions would happen immediately, with no evidence of further degradation of insular biological communities through time (Kitzes & Harte 2015).

In the long-term it is unknown how reservoir island communities will continue change with increasing isolation time, as the creation of artificial archipelagos from dam construction has only occurred over the past century. Our present knowledge of ecological communities within artificial archipelagos comes from multiple snapshot studies from different countries, dams, habitats and taxa, at different time points since the originally continuous habitat was fragmented. Bringing these snapshots together enables identification of general trends across disparate studies, aiding development of policy-relevant recommendations in terms of the conservation value of reservoir islands.

Here, we quantitatively review peer-reviewed research detailing responses of terrestrial taxa to habitat fragmentation and subsequent isolation on reservoir land-bridge islands. We then analyse species richness data from 249 islands and adjacent continuous habitats through time. In particular, we ask: (1) is there evidence of an extinction debt existing for reservoir island species; i.e. compared to continuous habitat, does island species richness decrease with increasing island isolation time? and (2) how does island size, distance to continuous habitat and distance to other islands relate to patterns of species richness and rates of species loss?

2.3 METHODS

2.3.1 Literature summary

Dataset collation

We conducted a literature search using Web of Knowledge and Google Scholar search engines between January 2014 and June 2015 using the key words: hydropower or hydroelectric, reservoir or dam, island or land-bridge, and forest islands or fragments. Only full-text, peer-reviewed articles in English were retained; unpublished or grey literature was not included. Studies researching terrestrial species, guilds, taxonomic groups or communities on reservoir islands, attributing ecological responses observed to reservoir creation were retained. Experimental studies or those not explicitly stating an aspect of reservoir creation as a causal factor for the response observed were excluded. Studies which met the inclusion criteria were entered into a dataset (henceforth referred to as "dataset studies"). Literature cited in the dataset studies was also screened for inclusion, and searches for names of dams in dataset studies were performed. A total of 129 studies were assessed for inclusion in our study, 100 of which met the criteria to be retained.

Data extraction

Data such as the number of islands surveyed, island area, taxonomic groups investigated, and time since island isolation were extracted from studies (S2.1). Each study was assigned a broad habitat type (wet tropical forest, tropical grassland e.g. *cerrado*, subtropical forest, Mediterranean forest, boreal forest). Taxa investigated were broadly grouped into mammals, birds, invertebrates, herptiles, plants, and fungi. If multiple taxa were included within a study, data were extracted for each group separately due to the potential for different responses. The precise isolation time of islands is seldom reported, thus we estimated island isolation time as the year of dam closure minus the year of field data collection. In six studies field data collection dates were not reported, thus, data collection date was conservatively estimated as two years prior to publication date.

Assigning study response directions

For each study the authors' key results and conclusions were used to assign an overall response of the study taxa to isolation on islands (response: positive, negative, variable, or neutral; see S2.1). For example, a study reporting declining species richness on islands would be assigned an overall negative response. An overall positive response would be assigned if, for example, recorded sightings (e.g. presence/absence data) were higher on islands. Overall variable responses could result from research involving different species within the same taxon, e.g. two species of bat exhibiting divergent responses to isolation. Neutral responses would result if no differences or alterations in taxa on islands compared to mainland sites were reported. If authors did not draw a conclusion as to the response directions observed, we examined the data reported and assigned a response direction accordingly. If multiple response directions for the same taxa were observed over time, the predominant response direction (i.e. over most years) was used as the overall direction.

To account for within-study complexity i.e. inclusion of multiple taxonomic groups and/or ecological metrics, response directions were derived for each taxonomic group and ecological metric investigated (S2.1). Ecological metrics included species richness, population density, behaviour (e.g. foraging behaviour), community composition, presence/absence, fitness/recruitment (e.g. breeding output), genetic diversity, and functional diversity.

2.3.2 Species richness analysis

Estimates of species richness were the most widely-reported and accessible data available in the collated studies, and therefore we selected this ecological metric for in-depth analysis.

Data collection

Dataset studies presenting species richness data for islands and nearby continuous (control) habitat, as well as island areas and isolation time, were used to assess variation in species richness on reservoir islands compared to control habitat (S2.1). These data also allowed investigation of the relationships between species richness and island area, isolation time, distance to mainland and distance to nearest island. Of the 100 dataset studies, 17 presented species richness data for islands (n = 249; size range <1-1690 ha; isolation time <1-92 years) and control sites (n = 84), and were used for the in-depth analysis of species richness data (S2.1). If data for the distance to mainland or nearest island were not presented, then if possible these data were calculated from satellite imagery using Google Earth Pro (Google 2015). Geographically, the 17 studies suitable for species richness analysis originated from nine dams, located on three continents in three broad habitat types (wet tropical forest, subtropical forest, and tropical grassland).

Data analysis

For each study the average species richness for control sites was calculated. The ratio of island species richness to average control species richness (S_{RICH}) was then calculated for each site and used for analysis. If a study contained data over multiple years, and thus, multiple isolation times, then species richness for control sites over the same isolation time period was averaged. If a study had multiple species richness values for the same island size, taxon, and isolation time, species richness values were averaged to avoid pseudo-replication.

To normalise data, all data were logged (natural logarithm) prior to analysis. S_{RICH} values were modelled using linear mixed effects models (lmer using lme4; Bates et al., 2014), as a function of island isolation time (T_{ISO}), island area (AREA), distance to mainland (D_{MAIN}) and distance to nearest island (D_{ISLAND}) as fixed effects, with taxonomic group (TAXA), dam identity (DAM; a surrogate for location), and study (STUDY; to account for differing survey methods and survey intensity among studies) as random effects (Bunnefeld & Phillimore 2012). Interaction terms were included between AREA, T_{ISO}, D_{MAIN} and D_{ISLAND}, as well as between TAXA, DAM and STUDY; quadratic terms were also tested for.

Due to missing values for D_{MAIN} and D_{ISLAND} we reduced the dataset to only those data rows containing values for all variables being tested (n islands = 178) and used this dataset for linear regression and model selection in R (R Core Team 2016). Models were simplified following stepwise deletion of non-significant terms i.e. those with a *t*-value <2 and models compared using Chi-square tests in ANOVA (Crawley 2005; Table S2.2). Following model simplification, the final model did not include variables with missing values, thus, the final model was fitted to the whole dataset (n islands = 249). The best linear unbiased predictors (BLUPs) for each dam were extracted using the 'ranef' function within the lme4 R package (Bates *et al.* 2014). Each dam has a different intercept, which can fall above or below that of the overall model: positive BLUPs indicate that the dam has higher than expected levels of species richness estimated from the fixed effects, and those falling below the model average indicate that species richness is lower than expected (S2.3). A variance components analysis was carried out for the random effects (Crawley 2005).

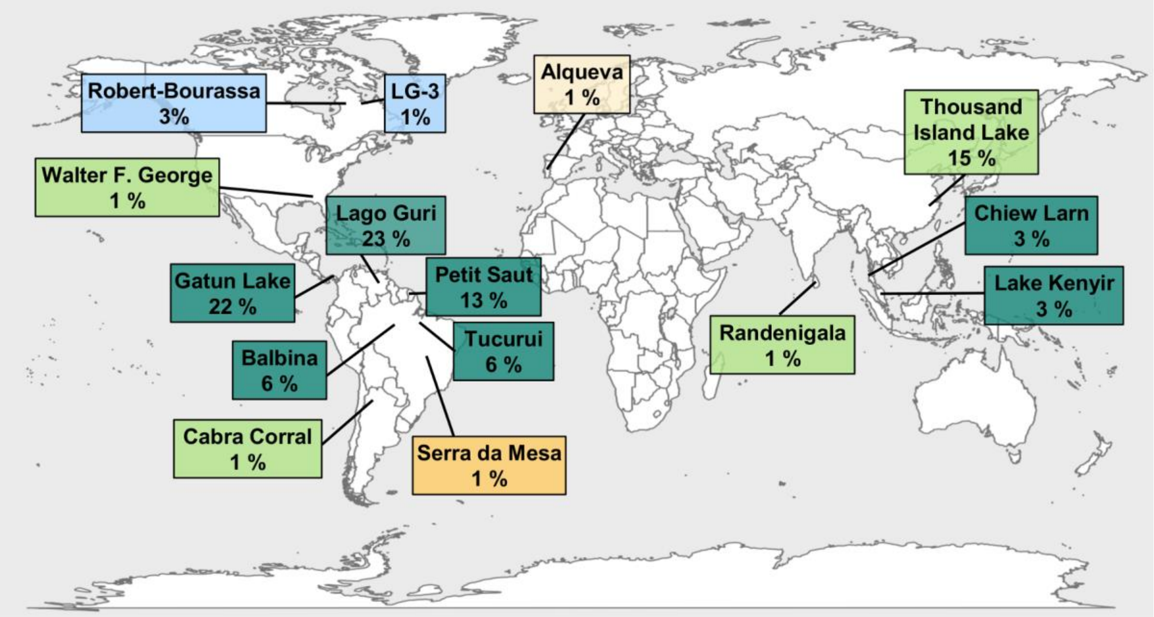

Fig. 2.1: Geography of research detailing responses of terrestrial taxa to isolation on reservoir land-bridge islands. Dam names and the percentage of total dataset studies (n = 100) originating from each are presented. Broad habitat type is indicated by colour: dark green = wet tropical forest; light green = subtropical forest; yellow = tropical grassland (e.g. *cerrado*); cream = Mediterranean forest; blue = boreal forest.

2.4 RESULTS

2.4.1 Literature summary

The 100 dataset studies examined here were predominantly from Neotropical forest habitats (Fig. 2.1; 2.2a). Mammals were the best-studied taxonomic group (Fig. 2.2b); responses of terrestrial taxa isolated on reservoir islands were most often expressed in terms of species richness and presence/absence, and rarely with regards to behaviour, genetic or functional diversity (Fig. 2.2c). An overall negative response of terrestrial taxa to dam creation was reported in >75% of studies, and these negative responses were seen across all habitat types, ecological metrics, and taxonomic groups investigated (Fig. 2.2a-c). Overall positive responses were confined to only two of the 100 studies (Fig. 2.2a), of which one reported increased and more stable population densities of small mammals (Adler 1996), and the second, increased food resources for a raptor due to prey being 'captive' on isolated islands (Benchimol & Venticinque 2010). Studies report results for islands isolated from <1 to 92 years, with the mean island isolation age of ~33 years (Fig. 2.2d).

2.4.2 Species richness analysis

The final model for analysis of S_{RICH} included T_{ISO} and AREA as fixed effects, and TAXA, DAM and STUDY as random effects (Table 2.1); D_{MAIN} and D_{ISLAND} had no significant effect on S_{RICH}, and no interaction terms were significant (S2.2). Of the random effects, 36% of variation was explained by STUDY, 17% explained by DAM, with 47% residual variance; TAXA did not explain any variance.

Table 2.1: Coefficient estimates for fixed effects in the most parsimonious model used for species richness analysis, with TAXA, DAM and STUDY as random effects; *t*-values >2 were treated as significant.

	Estimate	**Standard Error**	***t*-value**
Intercept	-0.514	0.237	-2.168
AREA	0.185	0.015	11.944
T_{ISO}	-0.244	0.067	-3.641

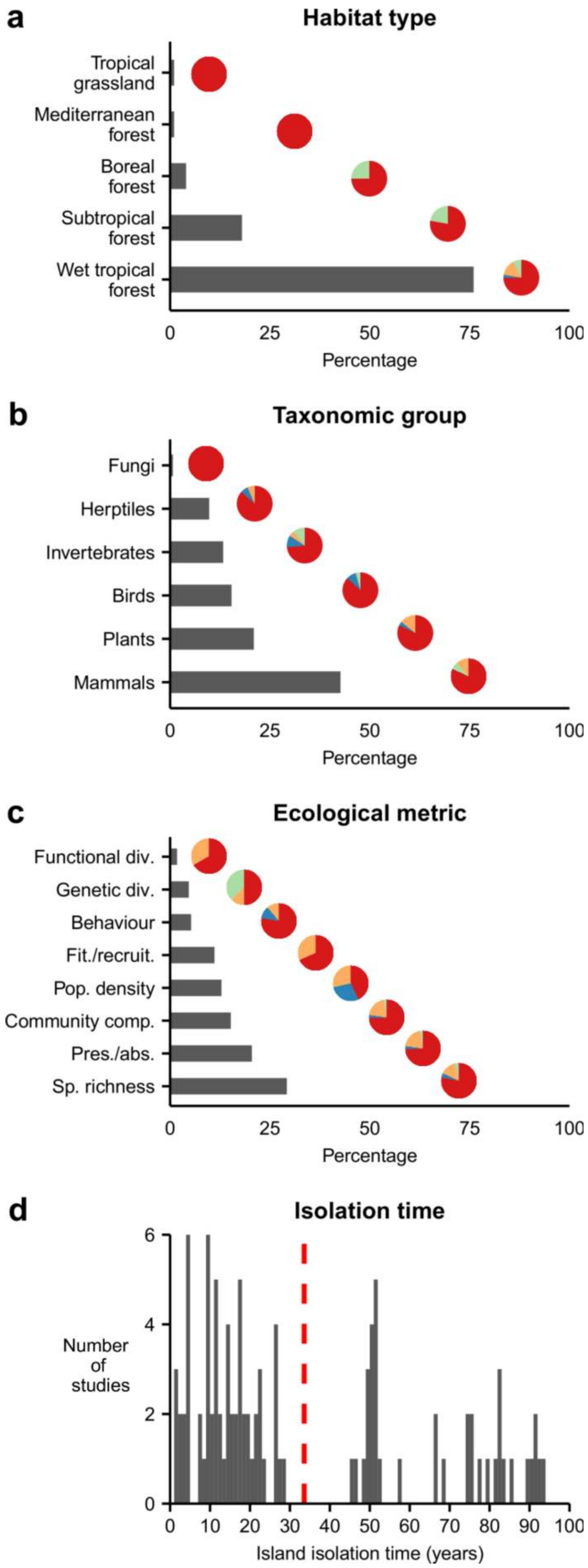

Fig. 2.2: Overview of research presented within dataset studies (n=100). 2a-c) present the proportion of total studies (black bars) for habitat type, ecological metric and taxonomic group investigated respectively; pie charts represent overall response directions (red = negative; blue = positive; green = neutral; yellow = variable). 2d) presents the distribution of studies through island isolation time (red dashed line represents mean island isolation time, ~33 years).

For all taxonomic groups and dams, species richness declined with island isolation time, but this effect was mediated by island size with larger islands retaining more species than smaller islands (Fig. 2.3). For example, predicted S_{RICH} on the largest island (1690 ha, within the Balbina hydroelectric dam, Brazilian Amazon) is predicted to be 3.2 at the mean isolation time of islands in the analysis, compared to a predicted S_{RICH} of 1.2 on the smallest island (0.17 ha, Cabra Corral, Argentina). In terms of island isolation time, even the largest island studied (1690 ha) exhibits reduced S_{RICH} in <30 years of isolation, and Barro Colorado Island (~1500 ha, Gatun Lake, Panama), which has been isolated for the longest period in our study (~92 years), similarly shows sustained species richness declines (Fig. 2.3).

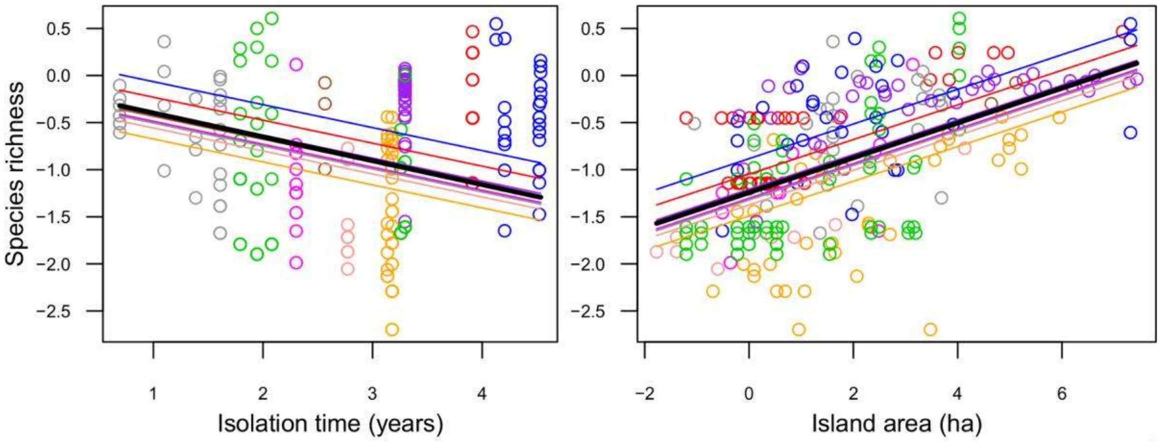

Fig. 2.3: Analysis of species richness (S_{RICH}) data from 249 islands and 84 control sites available from nine dams in three broad habitat types (wet tropical forest, subtropical forest, and tropical grassland), modelled with time since island isolation (T_{ISO}) and island area (AREA). Bold black lines represent the slope for the overall model, with individual lines for each dam fitted using the BLUPs extracted from random effects. Colour indicates dam identity: grey = Petit Saut; green = Chiew Larn; magenta = Lago Guri; brown = Randenigala; light pink = Cabra Corral; orange = Lake Kenyir; purple = Balbina; red = Thousand Island Lake; blue = Gatun Lake. Axes are on a natural log scale.

The estimates for the random effect of DAM (BLUPs) show that the majority of dams (66%) maintain lower than expected levels of species richness i.e. species richness values fall below those predicted by the overall model (Fig. 2.3; S2.3). Only islands in Gatun Lake, Balbina, and Thousand

Island Lake maintain higher species richness than predicted. Using our model we can predict S_{RICH} values for islands of mean area at a given isolation time, and islands of different areas at the mean isolation time, for each reservoir. For example, the S_{RICH} for mean island size within Gatun Lake reduces from 2.24 at five years of isolation to 1.49 after 90 years of isolation. In contrast, in Lake Kenyir which maintains the lowest expected species richness values, a small island of 5 ha (at mean island isolation time) has a predicted S_{RICH} value of 1.35, which is increased to just 2.23 on an island of 1000 ha. There was no evidence that islands located nearer other terrestrial habitat or mainland continuous habitat had reduced levels of species loss.

2.5 DISCUSSION

Our study finds that terrestrial taxa isolated on reservoir islands experience significant reductions in species richness in less than a century of isolation. Such sustained local species losses after the initial loss of habitat indicates that reservoir island species are subject to an extinction debt, which is evident across all dams, habitats, and taxa. All islands showed depauperate levels of species richness compared to continuous habitats, with smaller islands maintaining lower species richness than larger islands. Island isolation time and area, but not distance from other terrestrial habitat or the mainland, were the drivers of species richness patterns observed.

More broadly, we show that the majority of taxa are negatively impacted by reservoir creation across a range of other ecological metrics including behaviour and genetic diversity. Our current knowledge of the impacts of reservoir creation is disproportionately focussed on mammals, and originates predominantly from evergreen Neotropical forest habitats. While not all dams create archipelagic landscapes, research within our synthesis covers just 15 of the >58 000 large dams operating globally, representing a small and potentially biased sample of possible island systems. However, even with such limited data we clearly demonstrate the negative impact of dam creation on island species richness. Furthermore, we highlight the shortfalls in current conservation and impact mitigation strategies for dam development, particularly in terms of long-term biological costs, in addition to the immediate direct loss of lowland habitat during flooding.

2.5.1 Island species richness, area, and isolation time

Classic island biogeography theory (IBT; MacArthur & Wilson 1967) explains variation in island species richness through a balance of species immigration and distance from species source pools. In the artificial archipelagic systems we investigate in our analysis, rather than a process of species accumulation on islands, remnant communities of formerly continuous habitat undergo species loss ("relaxation") until a new equilibrium community is reached (Diamond 1972; Gonzalez 2000; Lomolino 2000).

Area was a significant predictor of species richness on islands within our analysis, as expected from the species-area relationship and IBT (MacArthur & Wilson 1967; Connor & McCoy 1979; Triantis, Guilhaumon & Whittaker 2012). However distance, both to the mainland and other islands, was not a significant predictor of island species richness: this represents a departure from the IBT, and suggests the reduced importance of metapopulation dynamics (Hanski & Gilpin 1991; With & King 2001) and the "rescue effect" (Brown & Kodric-Brown 1977) for maintaining insular populations in artificial archipelagic systems.

In the case of reservoir islands, remnant terrestrial habitat fragments are surrounded by a high-contrast, inhospitable water matrix, presenting a prohibitive dispersal barrier for certain taxa. Such an extreme dispersal barrier effectively renders all islands as too isolated for any "rescue effect" from wider species source pools to maintain island communities and species richness, and explains the lack of distance effects we find in our analysis (Watson 2002). The evolutionary history and traits of species resident in continuous habitats make many incapable of dispersing through open habitats, across large distances, or through a high-contrast matrix such as open water (see Fig. 2 in Ewers & Didham, 2006). For example, the ability of tropical understorey bird species to disperse across a water matrix between islands was tested in Gatun Lake, Panama, where some species were limited to <100m of flight (Moore *et al.* 2008); species reliant on continuous habitats can be averse to crossing even small clearings, such as logging roads, even when the forest canopy is closed (Develey & Stouffer 2001; Laurance, Stouffer & Laurance 2004).

Habitat fragments surrounded by water therefore represent a worse-case scenario in terms of fragmentation effects; aside from the dispersal barrier preventing species migration, islands are subject to extreme edge effects from e.g. increased UV and wind damage, often penetrating deep into islands leading to further degradation of island biota (Murcia 1995; Laurance & Curran 2008; Benchimol & Peres 2015c). Habitat fragments embedded within a more similar and potentially hospitable, but low-quality, terrestrial habitat matrix (e.g. forest fragments within an agricultural landscape) can retain higher levels of species diversity, with reduced local extinction rates (Mendenhall *et al.* 2011), when compared to reservoir islands of a similar size (Mendenhall *et al.* 2014).

We find a reduction in species richness on all islands with increasing time since initial habitat loss. Such a pattern of sustained and delayed species loss is indicative of extinction debt (Tilman *et al.* 1994; Kuussaari *et al.* 2009; Kitzes & Harte 2015). Extinction debts are especially high in areas subject to recent large-scale habitat loss, such as islands created by rapid flooding of terrestrial habitats (Hanski & Ovaskainen 2002). Our analysis illustrates that reservoir islands are of limited long-term conservation value, due to evidence of an extinction debt: species loss appears most rapid on smaller islands, but even the largest islands studied (~1690 ha) exhibited lowered species richness in under 30 years of isolation.

Ongoing species losses have been reported on another large island in our synthesis: Barro Colorado Island (BCI, ~1500 ha) has been isolated for 92 years since the formation of the Gatun Lake, Panama. In less than a century of island isolation, and despite strict environmental protection of BCI and surrounding peninsulas, 65 bird species (Robinson 1999) and 23 butterfly species (Basset *et al.* 2015) have become locally extinct, alongside long-term degradation of the tree community (Leigh *et al.* 1993). In the Balbina hydroelectric mega-dam system in Amazonia, Benchimol and Peres (2015c) calculated that a threshold island size of 475 ha was needed to conserve >80% of terrestrial and arboreal vertebrates on islands. However, only 25 out of 3546 islands in the Balbina archipelago meet this size criterion. Balbina is protected by the largest biological reserve in Brazil, and thus represents a best case scenario for biodiversity conservation within an artificial archipelago system. Species inhabiting other such systems, without protection, will therefore likely suffer not only from direct habitat loss through flooding and potential extinction debt, but additional human-mediated impacts such as deforestation, agriculture, hunting, and fire (Peres 2001b; Laurance 2008).

The data we use for analysis of species richness on reservoir land-bridge islands originate from 249 islands within 9 of the 15 dams presented in Fig. 2.1 and allow us to show patterns applicable to all dams and taxonomic groups, although we acknowledge that publication bias towards negative impacts of reservoir creation could influence the response patterns presented. While the data do not allow us to disentangle species richness patterns for individual taxonomic groups, dams and habitat types, we have addressed this shortcoming by using random effects in linear mixed effects models (Bunnefeld & Phillimore 2012). Similarly we cannot calculate the magnitude of extinction debts for individual taxonomic groups and/or habitat types, and instead highlight evidence that all reservoir islands are subject to an extinction debt, and therefore cannot be relied upon for long-term species conservation.

It is possible that the observed patterns of depauperate island species richness could be shaped by landscape attributes prior to inundation and non-random loss of more species-rich lowland habitat during flooding (Seabloom *et al.* 2002). Mainland species richness levels may have been elevated through surveying lowland habitats; such a potential sampling effect should be accounted for during survey site selection (e.g. Benchimol & Peres 2015a). In continuous habitats the greater availability of resources allows more species to inhabit a given area, compared to the same area of isolated habitat (Ewers & Didham 2006). Thus, sampling islands can inherently give lower species richness values than an equal area of continuous habitat (MacArthur & Wilson 1963; Gonzalez 2000; Crawley & Harral 2001; Halley *et al.* 2014).

Data for island taxa in artificial archipelagos come from snapshots of responses to isolation in <100 years of reservoir lifetime, across multiple taxa and habitat types. In addition, no studies monitored changes in insular community dynamics over a significant post-isolation time. Consequently, we cannot currently determine if the rates of local species loss are predictable beyond the relatively short time frame analysed here. Nor can we accurately quantify extinction debt to predict the eventual number of species able to persist in the artificial archipelago systems created due to the assumptions that would be required to do so. Further long-term monitoring of reservoir island biota is needed to allow these more detailed assessments to be made, since at present only Gatun Lake, Panama, provides data for a reservoir >90 years of age.

2.5.2 Conservation implications

Our study strongly suggests that islands within reservoir systems do not sustain full complements of flora and fauna in the long term; larger islands retain species for longer than smaller islands, but all island communities likely face an extinction debt. Given that degradation of island communities can be predicted to occur in all artificial archipelagic systems created by dam development, we emphasise that reservoir islands cannot be used for species conservation as part of impact mitigation strategies. The combined area of reservoir islands should be explicitly included in environmental impact assessments, in addition to the area of habitat directly lost through inundation.

Current policy to mitigate the negative impacts of dam creation on terrestrial environments consists of "good practice" guidelines with no statutory legislation requiring specific actions by developers (International Energy Agency 2006). Environmental legislation is highly variable among countries, and there is no signatory international agreement on how to forecast, prevent or mitigate the effects of large dams. Mitigation measures can take a multitude of forms, ranging from conducting wildlife inventories and environmental impact assessments before reservoir filling, creating new habitats such as wetland zones within the reservoir system, and conservation offsets such as strictly protecting land both within and surrounding reservoirs. There is however no long-term monitoring of such practices to assess whether these mitigation measures are effective (International Energy Agency 2000).

In light of the many dams that are planned to meet future water and electricity needs, especially in developing countries, we call for better trade-off calculations (Kareiva 2012) to be made for future dams, accounting for long-term species loss on islands created by flooding. In addition, enhanced protection of larger islands and surrounding non-fragmented habitats is essential to avoid biological collapse in artificial archipelagic systems. We highlight the potential for additional impacts from long-term degradation of high carbon-storing habitats such as tropical forests, where erosion of island tree communities (Benchimol & Peres 2015a) could lead to future carbon loss from tropical dams, exacerbating the greenhouse gas emissions already documented from this “green” energy source (Fearnside 2009; Demarty & Bastien 2011).

2.5.3 Conclusions

We have shown that there is an overall negative response of terrestrial species and communities to isolation on reservoir land-bridge islands. These trends are seen across a broad spectrum of taxonomic groups and ecological metrics. Species isolated on reservoir islands will likely experience extinction debt, and the rate of local extinctions is driven by island size and island isolation time, independently of distance from potential source populations within the landscape. Our synthesis of current literature allows broad conclusions about the ecological impacts of reservoirs through time, and highlights the need for further research from a greater number of reservoirs over the duration of their lifetime. Building upon the findings that we present here, investigation of the many other direct and indirect ecological impacts of reservoirs, such as loss of river habitats and connectivity, land tenure rights, and the impacts of wider infrastructure development on surrounding habitats, should be a priority for future research.

2.6 ACKNOWLEDGEMENTS

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S2 SUPPLEMENTARY INFORMATION

S2.1: Summary of sources and data included in Chapter 2. References for these studies follow in S2.1.2

Reference	Habitat type	Country	Dam	Isolation time (years)	Number of islands studied	Number of control sites	Island areas (ha)	Overall response reported by study	Study type	Response reported per study type	Taxonomic group(s) studied	Response of taxonomic group	Data used in species richness analysis
Benchimol and Venticinque, 2010	Wet tropical forest	Brazil	Balbina	20	1	0	no data	Positive	Population density	Positive	Mammals	Negative	No
									Behaviour	Positive	Birds	Positive	
Benchimol and Venticinque, 2014	Wet tropical forest	Brazil	Balbina	21	20	0	5-1815	Negative	Species richness	Negative	Mammals	Negative	No
									Presence/ absence	Negative			
Benchimol and Peres, 2015a	Wet tropical forest	Brazil	Balbina	26	34	12	<1-1690	Negative	Species richness	Negative	Plants	Negative	Yes
									Presence/ absence	Negative			
									Community composition	Negative			
Benchimol and Peres, 2015b	Wet tropical forest	Brazil	Balbina	26	34	12	<1-1690	Negative	Presence/ absence	Negative	Mammals	Negative	No
											Birds	Negative	
											Herptiles	Negative	
Benchimol and Peres, 2015c	Wet tropical forest	Brazil	Balbina	26	34	12	<1-1690	Negative	Presence/ absence	Negative	Mammals	Negative	No
									Community composition	Negative	Birds	Negative	
									Functional diversity	Negative	Herptiles	Negative	
Emer et al., 2013	Wet tropical forest	Brazil	Balbina	20	20	6	<15 - >2000	Negative	Species richness	Negative	Plants	Negative	No
									Community composition	Negative	Invertebrates	Negative	No
Bastos et al., 2010	Wet tropical forest	Brazil	Tucurui	17	2	2	no data	Neutral	Genetic diversity	Neutral	Mammals	Neutral	No

Carvalho et al., 2012	Wet tropical forest	Brazil	Tucurui	21	8	0	12.9-91.3	Neutral	Presence/ absence	Neutral	Invertebrates	Neutral	No
Ferreira et al., 2012	Wet tropical forest	Brazil	Tucurui	27	17	0	7.9-102.6	Negative	Species richness	Negative	Plants	Negative	No
									Community composition	Negative			
Lima et al., 2015	Wet tropical forest	Brazil	Tucurui	21	10	0	3-2140	Negative	Species richness	Negative	Herptiles	Negative	No
									Presence/ absence	Negative			
Silva and Ferrari, 2009	Wet tropical forest	Brazil	Tucurui	17	1	1	16.3	Negative	Genetic diversity	Negative	Mammals	Negative	No
									Fitness/ recruitment	Negative			
Veiga and Ferrari, 2006	Wet tropical forest	Brazil	Tucurui	19	1	1	18	Negative	Population density	Negative	Mammals	Negative	No
									Behaviour	Negative			
Cosson et al., 1999a	Wet tropical forest	French Guiana	Petit Saut	3	33	3	0.5-80	Negative	Community composition	Negative	Birds	Negative	No
											Herptiles	Negative	
											Mammals	Negative	
Cosson et al., 1999b	Wet tropical forest	French Guiana	Petit Saut	1	6	3	2-40	Negative	Species richness	Negative	Mammals	Negative	Yes
									Community composition	Negative			
Daleky et al., 2002	Wet tropical forest	French Guiana	Petit Saut	4	36	2	<1->20	Negative	Species richness	Negative	Mammals	Negative	No
Davies, 2002	Wet tropical forest	French Guiana	Petit Saut	3	10	3	0.2-80	Neutral	Species richness	Variable	Invertebrates	Neutral	No
									Presence/ absence	Variable			
Davies et al., 2003	Wet tropical forest	French Guiana	Petit Saut	4	10	3	0.35-80	Variable	Species richness	Variable	Invertebrates	Variable	No
									Community composition	Variable			
Feer and	Wet tropical	French	Petit Saut	4	7	3	1.1-25.5	Negative	Species richness	Negative	Invertebrates	Negative	Yes

Hingrat, 2005	forest	Guiana							Community composition	Negative	Mammals	Negative	
Granjon et al., 1996	Wet tropical forest	French Guiana	Petit Saut	1	10	1	0.35-30	Negative	Species richness	Variable	Mammals	Negative	Yes
									Community composition	Variable		Negative	
									Population density	Variable		Variable	
Granjon et al., 2002	Wet tropical forest	French Guiana	Petit Saut	4	33	0	0.1-8.5	Negative	Species richness	Negative	Mammals	Negative	No
									Presence/ absence	Negative			
Henry et al., 2007a	Wet tropical forest	French Guiana	Petit Saut	9	14	4	2-7.5	Variable	Behaviour	Variable	Mammals	Variable	No
									Fitness/ recruitment	Negative			
Henry et al., 2007b	Wet tropical forest	French Guiana	Petit Saut	9	14	4	0.8-7.5	Negative	Presence/ absence	Negative	Mammals	Negative	No
									Behaviour	Negative			
Henry et al., 2010	Wet tropical forest	French Guiana	Petit Saut	9	14	4	0.8-7.5	Negative	Species richness	Negative	Mammals	Negative	No
Pons and Cosson, 2002	Wet tropical forest	French Guiana	Petit Saut	2	16	1	<6-28	Neutral	Species richness	Neutral	Mammals	Neutral	Yes
Ringuet, 2000	Wet tropical forest	French Guiana	Petit Saut	1	35	1	0.2-60	Negative	Species richness	Negative	Mammal	Negative	No
									Presence/ absence	Negative	Herptiles	Negative	
Aponte et al., 2003	Wet tropical forest	Venezuela	Lago Guri	14	1	2	350	Negative	Population density	Positive	Herptiles	Negative	No
									Fitness/ recruitment	Negative			
Asquith et al., 1999	Wet tropical forest	Venezuela	Lago Guri	10	13	2	1-350	Negative	Species presence/ absence	Negative	Plants	Negative	No
									Community composition	Negative	Mammals	Negative	

Feeley, 2003	Wet tropical forest	Venezuela	Lago Guri	14	26	0	0.2-180	Negative	Species richness	Negative	Birds	Negative	No
Feeley and Terborgh, 2005	Wet tropical forest	Venezuela	Lago Guri	16	19		>0.2-<5	Variable	Community composition	Variable	Primates	Negative	No
											Plants	Negative	
Feeley and Terborgh, 2006	Wet tropical forest	Venezuela	Lago Guri	14	29	0	>2.5-<25	Variable	Species richness	Positive	Mammals	Neutral	No
									Population density	Positive	Birds	Positive	
Feeley et al., 2007	Wet tropical forest	Venezuela	Lago Guri	14	26	0	<2.5 - >25	Negative	Community composition	Variable	Birds	Negative	No
Feeley and Terborgh, 2008	Wet tropical forest	Venezuela	Lago Guri	17	11	0	<1 - >200	Negative	Species richness	Negative	Birds	Negative	No
									Presence/ absence	Negative			
Lambert et al., 2003	Wet tropical forest	Venezuela	Lago Guri	12	10	0	0.2-350	Negative	Species richness	Variable	Mammals	Negative	No
Larsen et al., 2005	Wet tropical forest	Venezuela	Lago Guri	17	29	3	0.16-181	Negative	Species richness	Negative	Invertebrates	Negative	No
									Community composition	Negative			
									Functional diversity	Negative			
Larsen et al., 2008	Wet tropical forest	Venezuela	Lago Guri	17	33	1	0.16-181	Negative	Species richness	Negative	Invertebrates	Negative	No
									Species presence/ absence	Negative			
									Population density	Negative			
Lopez et al., 2005	Wet tropical forest	Venezuela	Lago Guri	15	2	0	0.6-190	Negative	Behaviour	Negative	Mammals	Negative	No
									Fitness	Negative			
Lopez and Terborgh,	Wet tropical	Venezuela	Lago Guri	13	13	2	0.6-190	Negative	Community composition	Negative	Mammals	Negative	No

2007	forest								Fitness/ recruitment	Negative	Plants	Negative	No
Norconk and Grafton, 2003	Wet tropical forest	Venezuela	Lago Guri	16	1	0	12.8	Negative	Species presence/ absence	Negative	Mammals	Negative	No
									Population density	Negative	Plants	Negative	No
									Genetic diversity	Negative			
Peetz et al., 1992	Wet tropical forest	Venezuela	Lago Guri	4	1	0	70	Negative	Behaviour	Negative	Mammals	Negative	No
Rao, 2000	Wet tropical forest	Venezuela	Lago Guri	10	19	1	0.15-350	Variable	Population density	Variable	Invertebrates	Variable	No
Rao et al., 2001	Wet tropical forest	Venezuela	Lago Guri	9	12	3	0.3-350	Negative	Presence/ absence	Variable	Plants	Negative	No
									Fitness/ recruitment	Variable	Invertebrates	Negative	No
Shahabuddin et al., 2000	Wet tropical forest	Venezuela	Lago Guri	11	12	0	0.1-350	Negative	Presence/ absence	Variable	Invertebrates	Negative	No
Shahabuddin and Terborgh, 2000	Wet tropical forest	Venezuela	Lago Guri	11	11	11	0.1-1.15	Negative	Species richness	Negative	Invertebrates	Negative	No
									Population density	Negative			
Shahabuddin and Ponte, 2005	Wet tropical forest	Venezuela	Lago Guri	11	11	8	0.1-1.15	Negative	Species presence/ absence	Negative	Invertebrates	Negative	No
Terborgh et al., 1997a	Wet tropical forest	Venezuela	Lago Guri	9	12	1	1-350	Negative	Community composition	Variable	Birds	Negative	Yes
									Population density	Positive			
Terborgh et al., 1997b	Wet tropical forest	Venezuela	Lago Guri	9	12	1	1-350	Negative	Species richness	Negative	Birds	Negative	No
									Presence/ absence	Negative	Mammals	Negative	
									Population density	Variable	Herptiles	Negative	
											Invertebrates	Positive	

Terborgh et al., 2001	Wet tropical forest	Venezuela	Lago Guri	8	12	4	0.25->150	Negative	Presence/ absence	Negative	Invertebrates	Negative	No
									Community composition	Negative	Plants	Negative	
									Population density	Variable			
									Fitness/recruitment	Negative			
Terborgh et al., 2006	Wet tropical forest	Venezuela	Lago Guri	19	12	4	0.6-189.8	Negative	Presence/absence	Negative	Plants	Negative	No
									Fitness/ recruitment	Negative	Invertebrates	Negative	
Adler and Seamon, 1991	Wet tropical forest	Panama	Gatun Lake	75	50	0	0.3-17.1	Negative	Species presence/ absence	Negative	Mammals	Negative	No
Adler, 1994	Wet tropical forest	Panama	Gatun Lake	77	8	0	1.7-3.5	Variable	Fitness/ recruitment	Variable	Mammals	Variable	No
Adler (1996)a	Wet tropical forest	Panama	Gatun Lake	82	8	0	no data	Positive	Population density	Positive	Mammals	Positive	No
									Fitness/ recruitment	Variable			
Adler (1996)b	Wet tropical forest	Panama	Gatun Lake	75	50	0	0.3-17.1	Variable	Species presence/ absence	Variable	Mammals	Variable	No
Adler et al., 1997	Wet tropical forest	Panama	Gatun Lake	82	4	0	1.9-2.7	Variable	Population density	Variable	Mammal	Variable	No
									Fitness/ recruitment	Variable	Plant/tree/fungi	Variable	
Arnold and Asquith, 2002	Wet tropical forest	Panama	Gatun Lake	83	8	0	<1-1500	Negative	Fitness/ recruitment	Variable	Invertebrate	Negative	No
											Plants	Negative	
Asquith et al., 1997	Wet tropical forest	Panama	Gatun Lake	79	11	5	no data	Negative	Fitness/ recruitment	Negative	Plants	Negative	No
											Mammal	Negative	
Asquith and	Wet tropical	Panama	Gatun Lake	83	9	4	<2.2-17	Negative	Species richness	Negative	Plants	Negative	No

Mejía-Chang, 2005	forest								Community composition	Negative	Mammal	Negative	
Boyett et al., 2000	Wet tropical forest	Panama	Gatun Lake	81	12	0	1.7-3.7	Negative	Species richness	Negative	Mammal	Negative	No
									Presence/ absence	Negative			
									Population density	Negative			
Estrada-Villegas et al., 2010	Wet tropical forest	Panama	Gatun Lake	92	8	6	2.5-50	Variable	Species richness	Positive	Mammal	Variable	Yes
									Community composition	Negative			
									Behaviour	Negative			
Karr, 1982a	Wet tropical forest	Panama	Gatun Lake	68	1	1	no data	Negative	Species richness	Negative	Birds	Negative	No
									Species presence/ absence	Negative			
									Population density	Negative			
Karr, 1982b	Wet tropical	Panama	Gatun Lake	66	1	2	no data	Negative	Species richness	Negative	Birds	Negative	Yes
Karr, 1990	Wet tropical forest	Panama	Gatun Lake	74	1	1	no data	Negative	Presence/ absence	Negative	Birds	Negative	No
									Fitness/ recruitment				
Leigh et al., 1993	Wet tropical forest	Panama	Gatun Lake	66	7	4	no data	Negative	Species richness	Negative	Plants	Negative	Yes
Mangan et al., 2004	Wet tropical forest	Panama	Gatun Lake	85	6	3	<0.5-3.5	Variable	Presence/ absence	Variable	Fungi	Variable	No
Meyer and Kalko, 2008a	Wet tropical forest	Panama	Gatun Lake	91	11	6	2.5-50	Negative	Species richness	Negative	Mammals	Negative	Yes
									Community	Negative			
Meyer and Kalko, 2008b	Wet tropical forest	Panama	Gatun Lake	91	11	0	2.5-50	Negative	Presence/ absence	Negative	Mammals	Negative	No
Meyer et al., 2009	Wet tropical forest	Panama	Gatun Lake	90	11	3	2.5-50	Negative	Genetic diversity	Negative	Mammals	Negative	No

Milton et al., 2008	Wet tropical forest	Panama	Gatun Lake	90	1	0	1600	Neutral	Genetic diversity	Neutral	Mammals	Neutral	No
Robinson, 1999	Wet tropical forest	Panama	Gatun Lake	82	1	0	1600	Negative	Species richness	Negative	Birds	Negative	No
									Presence/ absence	Negative			
									Population density	Negative			
Willis, 1974	Wet tropical forest	Panama	Gatun Lake	57	1	0	1600	Negative	Species richness	Negative	Birds	Negative	No
									Community composition	Negative			
									Population density	Negative			
Wright et al., 1994	Wet tropical forest	Panama	Gatun Lake	74	1	1	1600	Neutral	Species richness	Neutral	Mammals	Neutral	No
Qie et al., 2011	Wet tropical forest	Malaysia	Lake Kenyir	23	24	3	<1-383.3	Negative	Presence/ absence	Negative	Invertebrates	Negative	Yes
									Community composition	Variable			
									Functional diversity	Variable			
Yong et al., 2010	Wet tropical forest	Malaysia	Lake Kenyir	22	6	2	<20->100	Negative	Species richness	Negative	Birds	Negative	Yes
									Community composition	Negative			
Yong et al.,	Wet tropical	Malaysia	Lake Kenyir	22	6	2	<20-	Negative	Species richness	Negative	Invertebrates	Negative	Yes
Gibson et al., 2013	Wet tropical forest	Thailand	Chiew Larn	26	16	1	0.3-56.3	Negative	Species richness	Negative	Mammals	Negative	Yes
									Presence/ absence	Negative			
Lynam, 1997	Wet tropical forest	Thailand	Chiew Larn	7	12	12	0.7-109	Negative	Species richness	Negative	Mammals	Negative	No
									Community composition	Variable			
									Functional diversity	Negative			

Lynam and Billick, 1999	Wet tropical forest	Thailand	Chiew Larn	7	12	12	0.7-109	Negative	Community composition	Variable	Mammals	Variable	No
Badano et al., 2005	Subtropical forest	Argentina	Cabra Corral	15	9	1	0.16-62.5	Negative	Species richness	Negative	Invertebrates	Negative	Yes
Brandao and Araujo, 2008	Tropical grassland	Brazil	Serra da Mesa	4	8	1	0.5-23	Negative	Presence/ absence	Negative	Herptiles	Negative	No
Ennen et al., 2011	Subtropical forest	USA	Walter F. George	45	2	8	no data	Variable	Population density	Variable	Herptiles	Variable	No
									Genetic diversity	Neutral			
									Fitness/ recruitment	Negative			
Rebelo and Rainho, 2009	Mediterranean woodland	Portugal	Alqueva	2	4	6	no data	Negative	Presence/ absence	Positive	Mammals	Negative	No
									Behaviour	Negative			
Weerakoon, 2001	Subtropical forest	Sri Lanka	Randenigala	12	6	5	2-167	Negative	Species richness	Variable	Herptiles	Negative	Yes
									Presence/ absence	Variable	Herptiles	Positive	
											Mammals	Negative	
Ding et al., 2013	Subtropical forest	China	Thousand Island Lake	50	41	0	<0.5->140	Negative	Species richness	Negative	Birds	Negative	No
Hu et al., 2011	Subtropical forest	China	Thousand Island Lake	49	154	0	0.02-1153.88	Negative	Species richness	Negative	Plants	Negative	No
Hu et al., 2012	Subtropical forest	China	Thousand Island Lake	49	152	0	no data	Negative	Species richness	Negative	Plants	Negative	No
Lu et al., 2011	Subtropical forest	China	Thousand Island Lake	48	50	0	<1->5	Variable	Species richness	Variable	Plants	Variable	No
									Presence/ absence	Variable			
Wang et al., 2009	Subtropical forest	China	Thousand Island Lake	49	42	7	0.67-1289.23	Negative	Species richness	Negative	Herptiles	Negative	Yes
Wang et al.,	Subtropical	China	Thousand	50	46	0	0.3-	Negative	Species richness	Negative	Birds	Negative	No

2010	forest		Island Lake				1289.23		Presence/ absence	Negative	Herptiles	Negative	
											Mammal	Negative	
Wang et al., 2011	Subtropical forest	China	Thousand Island Lake	50	46	0	0.3-1289.23	Negative	Community composition	Negative	Birds	Negative	No
Wang et al., 2012a	Subtropical forest	China	Thousand Island Lake	52	42	0	0.3-1289.23	Negative	Species richness	Negative	Birds	Negative	No
Wang et al., 2012b	Subtropical forest	China	Thousand Island Lake	51	20	0	0.8-1289.23	Negative	Species richness	Negative	Herptiles	Negative	No
Wang et al., 2012c	Subtropical forest	China	Thousand Island Lake	53	8	10	no data	Variable	Genetic diversity	Variable	Plants	Variable	No
Wang et al., 2012d	Subtropical forest	China	Thousand Island Lake	51	14	0	1.74-128.32	Variable	Behaviour	Variable	Herptiles	Variable	No
Yu and Lu, 2011	Subtropical forest	China	Thousand Island Lake	50	10	1	no data	Negative	Fitness/ recruitment	Variable	Plants	Negative	No
Yu et al., 2012	Subtropical forest	China	Thousand Island Lake	53	41	0	0.16-1153.9	Negative	Species richness	Negative	Plants	Negative	No
									Community composition	Negative	Birds	Negative	
Yuan et al., 2012	Subtropical forest	China	Thousand Island Lake	53	10	8	0.2-875	Negative	Genetic diversity	Negative	Plants	Negative	No
Zhang et al., 2007	Subtropical forest	China	Thousand Island Lake	48	31	1	no data	Negative	Presence/ absence	Negative	Plants	Negative	No
									Population density	Negative			
Crete et al., 1997	Boreal	Canada	LG-3	11	10	10	no data	Neutral	Species richness	Variable	Mammal	Neutral	No
									Community composition	Neutral	Birds	Neutral	
											Plants	Positive	
Bégin et al., 2010	Boreal	Canada	Robert-Bourassa Reservoir	30	16	0	no data	Negative	Fitness/ recruitment	Negative	Plants	Negative	No

Tremblay and Begin, 2000	Boreal	Canada	Robert-Bourassa Reservoir	18	1	0	no data	Negative	Fitness/ recruitment	Negative	Plants	Negative	No
Tremblay and Begin, 2005	Boreal	Canada	Robert-Bourassa Reservoir	18	1	0	no data	Negative	Fitness/ recruitment	Negative	Plants	Negative	No

S2.1.2: Full reference list for S2.1

Adler, G.H., 1994. Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. J. Anim. Ecol. 63, 903–911

Adler, G.H., Beatty, R.P.,1997. Changing reproductive rates in a Neotropical forest rodent, *Proechimys semispinosus*. J. Anim. Ecol. 66, 472–480

Adler, G.H., Seamon, J.O., 1991. Distribution and abundance of a tropical rodent, the spiny rat, on islands in Panama. J. Trop. Ecol. 7, 349–360. doi:10.1017/S0266467400005617

Aponte, C., Barreto, G.R., Terborgh, J., 2003. Consequences of Habitat Fragmentation on Age Structure and Life History in a Tortoise Population. Biotropica 35, 550–555

Arnold, A.E., Asquith, N.M., 2002. Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatun, Panama. Biodivers. Conserv. 11, 1663–1680

Asquith, N.M., Mejía-Chang, M., 2005. Mammals , Edge Effects , and the Loss of Tropical Forest Diversity. Ecology 86, 379–390

Asquith, N.M., Terborgh, J., Arnold, A.E., Riveros, C.M., 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. J. Trop. Ecol. 15, 229–235

Asquith, N.M., Wright, S.J., Clauss, M.J., 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78, 941–946

Badano, E.I., Regidor, H.A., Nunez, H.A., Acosta, R., Gianoli, E., 2005. Species richness and structure of ant communities in a dynamic archipelago: effects of island area and age. J. Biogeogr. 32, 221–227

Bastos, H.B., Gonçalves, E.C., Ferrari, S.F., Silva, A., Schneider, M.P.C., 2010. Genetic structure of red-handed howler monkey populations in the fragmented landscape of Eastern Brazilian Amazonia. Genet. Mol. Biol. 33, 774–80

Bégin, Y., Sirois, L., Meunier, C., 2010. The effects of hydroelectric flooding on a reservoir's peripheral forests and newly created forest islands, in: Stoffel, M., Bollschweiler, M., Butler, D.R., Luckman, B.H. (Eds.), Tree Rings and Natural Hazards: A State-of-the-Art, Advances in Global Change Research. Springer Netherlands, Dordrecht, pp. 241–256. doi:10.1007/978-90-481-8736-2

Benchimol, M., Peres, C. A, 2015a. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. J. Ecol. 103, 408–420. doi:10.1111/1365-2745.12371

Benchimol, M., Peres, C. A, 2015b. Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. Biol. Conserv. 187, 61–72. doi:10.1016/j.biocon.2015.04.005

Benchimol, M., Peres, C.A., 2015c. Widespread Forest Vertebrate Extinctions Induced by a Mega Hydroelectric Dam in Lowland Amazonia. PLoS One 1–15. doi:10.5061/dryad.c301h

Benchimol, M., Venticinque, E.M., 2014. Responses of Primates to Landscape Change in Amazonian Land-bridge islands-a Multi-scale Analysis. Biotropica 0, 1–9. doi:10.1111/btp.12122

Benchimol, M., Venticinque, E.M., 2010. Harpy Eagle (*Harpia harpyja*) predation on an Infant brown Capuchin Monkey (*Cebus apella*) in the Brazilian Amazon. Rev. Bras. Ornitol. 18, 352–354

Boyett, W.D., Endries, M.J., Adler, G.H., 2000. Colonization-extinction dynamics of oppossums on small islands in Panama. Can. J. Zool. 78, 1972–1979

Brandão, R., Araújo, A., 2008. Changes in Anuran Species Richness and Abundance Resulting from Hydroelectric Dam Flooding in Central Brazil. Biotropica 40, 263–266

Carvalho, L.S., Gomes, J.O., Neckel-Oliveira, S., Lo-Man-Hung, N.F., 2012. Microhabitat use and intraspecific associations in the whip spider *Heterophrynus longicornis* (Arachnida: Amblypygi) in forest fragments formed by the Tucuruí Dam lake , Pará , Brazil 46, 1263–1272

Cosson, J., Pons, J.-M., Masson, D., 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. J. Trop. Ecol. 15, 515–534

Cosson, J.F., Ringuet, S., Claessens, O., de Massary, J.C., Dalecky, A., Villiers, J.F., Granjon, L., Pons, J.M., 1999. Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. Biol. Conserv. 91, 213–222. doi:10.1016/S0006-3207(99)00091-9

Crete, M., Huot, J., Fortin, M.-J., Doucet, G., 1997. Comparison of plant and animal diversity on new reservoir islands and established lake islands in Northern Boreal Forest of Quebec. Can. field-naturalist 111, 407–416

Daleky, A., Chauvet, S., Ringuet, S., Claessens, O., Juda, J., Larue, M., Cosson, J.F., 2002. Large mammals on small islands: short-term effects of forest fragmentation on the large mammal fauna in French Guiana. Rev. d'ecologie 57, 145–164

Davies, R., 2002. Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation. Oecologia 133, 233–242. doi:10.1007/s00442-002-1011-8

Davies, R.G., Hernández, L.M., Eggleton, P., Didham, R.K., Fagan, L.L., Winchester, N.N., 2003. Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. J. Trop. Ecol. 19, 509–524. doi:10.1017/S0266467403003560

Ding, Z., Feeley, K.J., Wang, Y., Pakeman, R.J., Ding, P., 2013. Patterns of bird functional diversity on land-bridge island fragments. J. Anim. Ecol. 781–790. doi:10.1111/1365-2656.12046

Emer, C., Venticinque, E.M., Fonseca, C.R., 2013. Effects of dam-induced landscape fragmentation on amazonian ant-plant mutualistic networks. Conserv. Biol. 27, 763–73. doi:10.1111/cobi.12045

Ennen, J.R., Birkhead, R.D., Kreiser, B.R., Gaillard, D.L., Qualls, C.P., Lovich, J.E., 2011. The effects of isolation on the demography and genetic diversity of long-lived species: implications for conservation and management of the gopher tortoise (*Gopherus polyphemus*). Herpetol. Conserv. Biol. 6, 202–214.

Estrada-Villegas, S., Meyer, C.F.J., Kalko, E.K.V., 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. Biol. Conserv. 143, 597–608. doi:10.1016/j.biocon.2009.11.009

Feeley, K., 2003. Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. Oecologia 137, 104–13. doi:10.1007/s00442-003-1321-5

Feeley, K.J., Gillespie, T.W., Lebbin, D.J., Walter, H.S., 2007. Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. Anim. Conserv. 10, 493–501. doi:10.1111/j.1469-1795.2007.00140.x

Feeley, K.J., Terborgh, J.W., 2008. Direct versus indirect effects of habitat reduction on the loss of avian species from tropical forest fragments. Anim. Conserv. 11, 353–360. doi:10.1111/j.1469-1795.2008.00182.x

Feeley, K.J., Terborgh, J.W., 2006. Habitat Fragmentation and Effects of Herbivore (Howler Monkey) Abundances on Bird Species Richness. Ecology 87, 144–150

Feeley, K.J., Terborgh, J.W., 2005. The Effects of Herbivore Density on Soil Nutrients and Tree Growth in Tropical Forest Fragments. Ecology 86, 116–124

Feer, F., Hingrat, Y., 2005. Effects of Forest Fragmentation on a Dung Beetle Community in French Guiana. Conserv. Biol. 19, 1103–1112. doi:10.1111/j.1523-1739.2005.00087.x

Ferreira, L. V, Neckel-Oliveira, S., Galatti, U., Fáveri, S.B., Parolin, P., 2012. Forest structure of artificial islands in the Tucuruí dam reservoir in northern Brazil: a test core-area model. Acta Amaz. 42, 221–226.

Gibson, L., Lynam, A.J., Bradshaw, C.J. A, He, F., Bickford, D.P., Woodruff, D.S., Bumrungsri, S., Laurance, W.F., 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. Science 341, 1508–10. doi:10.1126/science.1240495

Granjon, L., Cosson, J., Judas, J., Ringlet, S., 1996. Influence of tropical rainforest fragmentation on mammal communities in French Guiana: short-term effects. Acta Oecologica 17, 673–672

Granjon, L., Ringuet, S., Cheylan, G., 2002. Evolution of small terrestrial mammal species richness on newly formed islands in primary tropical forest of French Guiana: a 6 year study. Rev. d’ecologie 8, 131–144.

Henry, M., Cosson, J.F., Pons, J.M., 2010. Modelling multi-scale spatial variation in species richness from abundance data in a complex neotropical bat assemblage. Ecol. Modell. 221, 2018–2027. doi:10.1016/j.ecolmodel.2010.05.011

Henry, M., Cosson, J.-F., Pons, J.-M., 2007a. Abundance may be a misleading indicator of fragmentation-sensitivity: The case of fig-eating bats. Biol. Conserv. 139, 462–467. doi:10.1016/j.biocon.2007.06.024

Henry, M., Pons, J.-M., Cosson, J.-F., 2007b. Foraging behaviour of a frugivorous bat helps bridge landscape connectivity and ecological processes in a fragmented rainforest. J. Anim. Ecol. 76, 801–13. doi:10.1111/j.1365-2656.2007.01258.x

Hu, G., Feeley, K.J., Wu, J., Xu, G., Yu, M., 2011. Determinants of plant species richness and patterns of nestedness in fragmented landscapes: evidence from land-bridge islands. Landsc. Ecol. 26, 1405–1417. doi:10.1007/s10980-011-9662-7

Hu, G., Wu, J., Feeley, K.J., Xu, G., Yu, M., 2012. The effects of landscape variables on the species-area relationship during late-stage habitat fragmentation. PLoS One 7, e43894. doi:10.1371/journal.pone.0043894

Karr, J.R., 1990. Avian Survival Rates and the Extinction Process on Barro Colorado Island, Panama Island. Conserv. Biol. 4, 391–397

Karr, J.R., 1982a. Population Variability and Extinction in the Avifauna of a Tropical Land Bridge Island. Ecology 63, 1975–1978

Karr, J.R., 1982b. Avian Extinction on Barro Colorado Island, Panama: A Reassessment. Am. Nat. 119, 220–239

Lambert, T.D., Adler, G.H., Riveros, C.M., Lopez, L., Ascanio, R., Terborgh, J., 2003. Rodents on tropical land-bridge islands. J. Zool. 260, 179–187. doi:10.1017/S0952836903003637

Larsen, T.H., Lopera, A., Forsyth, A., 2008. Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. Conserv. Biol. 22, 1288–98. doi:10.1111/j.1523-1739.2008.00969.x

Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8, 538–47. doi:10.1111/j.1461-0248.2005.00749.x

Leigh, E.G., Wright, S.J., Herre, E.A., Putz, F.E., 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. Evol. Ecol. 7, 76–99.

Lima, J., Galatti, U., Lima, C., Faveri, S., Vasconcelos, H., Neckel-Oliveira, S., 2015. Amphibians on Amazonian Land-Bridge Islands are Affected More by Area Than Isolation. Biotropica 47, 369–376

Lopez, G.O., Terborgh, J., Ceballos, N., 2005. Food selection by a hyperdense population of red howler monkeys (*Alouatta seniculus*). J. Trop. Ecol. 21, 445–450. doi:10.1017/S0266467405002415

Lopez, L., Terborgh, J., 2007. Seed predation and seedling herbivory as factors in tree recruitment failure on predator-free forested islands. J. Trop. Ecol. 23, 129. doi:10.1017/S0266467406003828

Lu, J., Jiang, L., Yu, L., Sun, Q., 2011. Local factors determine plant community structure on closely neighbored islands. PLoS One 6, e19762. doi:10.1371/journal.pone.0019762

Lynam, A.J., 1997. Rapid decline of small mammal diversity in Monsoon evergreen fragments in Thailand, in: Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. pp. 222–240

Lynam, A.J., Billick, I., 1999. Differential responses of small mammals to fragmentation in a Thailand tropical forest. Biol. Conserv. 91, 191–200

Mangan, S.A., Eom, A.-H., Adler, G.H., Yavitt, J.B., Herre, E.A., 2004. Diversity of arbuscular mycorrhizal fungi across a fragmented forest in Panama: insular spore communities differ from mainland communities. Oecologia 141, 687–700. doi:10.1007/s00442-004-1684-2

Meyer, C.F.J., Kalko, E.K. V., 2008a. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. J. Biogeogr. 35, 1711–1726. doi:10.1111/j.1365-2699.2008.01916.x

Meyer, C.F.J., Kalko, E.K. V., 2008b. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. Divers. Distrib. 14, 644–654. doi:10.1111/j.1472-4642.2007.00462.x

Meyer, C.F.J., Kalko, E.K. V., Kerth, G., 2009. Small-Scale Fragmentation Effects on Local Genetic Diversity in Two Phyllostomid Bats with Different Dispersal Abilities in Panama. Biotropica 41, 95–102. doi:10.1111/j.1744-7429.2008.00443.x

Milton, K., Lozier, J.D., Lacey, E. A., 2008. Genetic structure of an isolated population of mantled howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. Conserv. Genet. 10, 347–358. doi:10.1007/s10592-008-9584-3

Norconk, M.A., Grafton, B.W., 2003. Changes in forest composition and potential feeding tree availability on a small land-bridge island in Lago Guri, Venezuela , in: Marsh, L.K. (Ed.), Primates in Fragments. Springer US, pp. 211–227

Peetz, A., Norconk, M.A., Kinzey, W.G., 1992. Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. Am. J. Primatol. 28, 223–228

Pons, J.-M., Cosson, J.-F., 2002. Use of forest fragments by animalivorous bats in French Guiana. Rev. d'ecologie 57, 117–130

Qie, L., Lee, T.M., Sodhi, N.S., Lim, S.L.-H., 2011. Dung beetle assemblages on tropical land-bridge islands: small island effect and vulnerable species. J. Biogeogr. 38, 792–804. doi:10.1111/j.1365-2699.2010.02439.x

Rao, M., 2000. Variation in leaf-cutter ant (Atta sp.) densities in forest isolates: the potential role of predation. J. Trop. Ecol. 16, 209–225.

Rao, M., Terborgh, J., Nunez, P., 2001. Increased Plant Herbivory in Forest Isolates: Implications for Plant Community Structure and Composition. Conserv. Biol. 15, 624–633.

Rebelo, H., Rainho, A., 2009. Bat conservation and large dams: spatial changes in habitat use caused by Europe's largest reservoir. Endanger. Species Res. 8, 61–68. doi:10.3354/esr00100

Ringuet, S., 2000. An assessment of the potential influence of rainforest fragmentation on small terrestrial mammal predation in French Guiana. Rev. d'ecologie 55, 101–116

Robinson, W.D., 1999. Long-Term Changes in the Avifauna of Barro Colorado Island, Panama, a Tropical Forest Isolate. Conserv. Biol. 13, 85–97. doi:10.1046/j.1523-1739.1999.97492.x

Shahabuddin, G., Herzner, G.A., Aponte, C., Gomez, M. del C., 2000. Persistence of a frugivorous butterfly species in Venezuelan forest fragments: the role of movement and habitat quality. Biodivers. Conserv. 9, 1623–1641

Shahabuddin, G., Ponte, C. A., 2005. Frugivorous butterfly species in tropical forest fragments: correlates of vulnerability to extinction. Biodivers. Conserv. 14, 1137–1152. doi:10.1007/s10531-004-7842-3

Shahabuddin, G., Terborgh, J.W., 2000. Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and the effects of isolation. J. Trop. Ecol. 15, 703–722

Silva, S.S.B., Ferrari, S.F., 2009. Behavior patterns of southern bearded sakis (*Chiropotes satanas*) in the fragmented landscape of eastern Brazilian Amazonia. Am. J. Primatol. 71, 1–7. doi:10.1002/ajp.20624

Terborgh, J., Feeley, K., Silman, M., Nunez, P., Balukjian, B., 2006. Vegetation dynamics of predator-free land-bridge islands. J. Ecol. 94, 253–263. doi:10.1111/j.1365-2745.2006.01106.x

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923–6. doi:10.1126/science.1064397

Terborgh, J., Lopez, L., S, J.T., 1997a. Bird Communities in Transition: The Lago Guri Islands. Ecology 78, 1494–1501

Terborgh, J., Lopez, L., Tello, J., Yu, D., Bruni, A.R., 1997b. Transitory states in Relaxing Ecosystems of Land Bridge Islands, in: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, London, pp. 256–274

Tremblay, A., Begin, Y., 2005. The effects of snow packing on tree growth forms on an island in a recently created reservoir in northern Quebec. Ecoscience 12, 530–539

Tremblay, A., Begin, Y., 2000. The response of black spruce to the climatic influence of Robert-Bourassa Reservoir, in northern Quebec. Ecoscience 7, 228–236

Veiga, L.M., Ferrari, S.F., 2006. Predation of Arthropods by Southern Bearded Sakis (*Chiropotes satanas*) in Eastern Brazilian Amazonia. Am. J. Primatol. 68, 209–215. doi:10.1002/ajp

Wang, Y., Zhang, J., Feeley, K.J., Jiang, P., Ding, P., 2009. Life-history traits associated with fragmentation vulnerability of lizards in the Thousand Island Lake, China. Anim. Conserv. 12, 329–337. doi:10.1111/j.1469-1795.2009.00257.x

Wang, Y., Bao, Y., Yu, M., Xu, G., Ding, P., 2010. Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. Divers. Distrib. 16, 862–873. doi:10.1111/j.1472-4642.2010.00682.x

Wang, Y., Chen, S., Ding, P., 2011. Testing multiple assembly rule models in avian communities on islands of an inundated lake, Zhejiang Province, China. J. Biogeogr. 38, 1330–1344. doi:10.1111/j.1365-2699.2011.02502.x

Wang, Y., Zhang, M., Wang, S., Ding, Z., Zhang, J., Sun, J., Li, P., Ding, P., 2012a. No evidence for the small-island effect in avian communities on islands of an inundated lake. Oikos 121, 1945–1952. doi:10.1111/j.1600-0706.2012.20322.x

Wang, Y., Wang, X., Ding, P., 2012b. Nestedness of snake assemblages on islands of an inundated lake. Curr. Zool. 58, 828–836

Wang, Y., Zhu, Y., Wang, Y., 2012c. Differences in spatial genetic structure and diversity in two mosses with different dispersal strategies in a fragmented landscape. J. Bryol. 34, 9–16. doi:10.1179/1743282011Y.0000000035

Wang, Y., Lane, A., Ding, P., 2012d. Sex-biased dispersal of a frog (*Odorrana schmackeri*) is affected by patch isolation and resource limitation in a fragmented landscape. PLoS One 7, e47683. doi:10.1371/journal.pone.0047683

Weerakoon, W.M.S.K., 2001. Comparative richness of amphibians inhabiting the islands at Randenigala reservoir with mainland of the Victoriya Randenigala Ranambe (VRR) sanctuary. Lyriocephalus 44, 124–129

Willis, E.O., 1974. Populations and Local Extinctions of Birds on Barro Colorado Island, Panama. Ecol. Monogr. 44, 153–169

Wright, S.J., Gompper, M.E., DeLeon, B., 1994. Are large predators keystone species in Neotropical forestsThe evidence from Barro Colorado Island. Oikos 71, 279–294

Yong, D.L., Lohman, D.J., Gan, C.W., Qie, L., Lim, S.L.-H., 2012. Tropical butterfly communities on land-bridge islands in Peninsular Malaysia. Raffles Bull. Zool. 25, 161–172

Yong, D.L., Qie, L., Sodhi, N.S., Koh, L.P., Peh, K.S.-H., Lee, T.M., Lim, H.C., Lim, S.L.-H., 2010. Do insectivorous bird communities decline on land-bridge forest islands in Peninsular Malaysia? J. Trop. Ecol. 27, 1–14. doi:10.1017/S0266467410000520

Yu, L., Lu, J., 2011. Does landscape fragmentation influence sex ratio of dioecious plants? A case study of Pistacia chinensis in the Thousand-Island Lake region of China. PLoS One 6, e22903. doi:10.1371/journal.pone.0022903

Yu, M., Hu, G., Feeley, K.J., Wu, J., Ding, P., 2012. Richness and composition of plants and birds on land-bridge islands: effects of island attributes and differential responses of species groups. J. Biogeogr. 39, 1124–1133. doi:10.1111/j.1365-2699.2011.02676.x

Yuan, N., Comes, H.P., Mao, Y.-R., Qi, X.-S., Qiu, Y.-X., 2012. Genetic effects of recent habitat fragmentation in the Thousand-Island Lake region of southeast China on the distylous herb Hedyotis chrysotricha (Rubiaceae). Am. J. Bot. 99, 1715–25. doi:10.3732/ajb.1200054

Zhang, X., Xu, G., Shen, D., Gu, Y., Gao, H., Luo, X., Chen, X., 2007. Maintenance and natural regeneration of Castanopsis sclerophylla populations on islands of Qiandao Lake Region, China. Acta Ecol. Sin. 27, 424–430. doi:10.1016/S1872-2032(07)60014-6

S2.2: Coefficients of fixed effects in linear mixed effects models. Coefficients for the fixed effects of models that treat study identity, dam, and taxonomic group as random effects. The Chi-square (x^2) value and p-value from model comparison by ANOVA is given. The final model used in analysis only included significant fixed effects: AREA and T_{ISO}. Values presented in this table are from model comparisons using a reduced dataset (n islands = 148) to account for missing values. Following model comparison, the final model was used on the full dataset (n islands = 249) which did not have missing values for the variables included in the model.

Fixed effects	Estimate	SE	*t*-value	df	x^2	*P*-value
Intercept	-0.514	0.237	-2.168			
AREA	0.237	0.02	11.958	1	94.744	<0.001
T_{ISO}	-0.328	0.069	-4.720	1	16.136	<0.001
D_{MAIN}	-0.037	0.039	-0.951	1	0.894	0.344
D_{ISLAND}	-0.062	0.043	-1.434	1	1.991	0.158

S2.3: Best linear unbiased predictors. Intercepts for the best unbiased linear predictors (BLUPs) for each dam generated using the 'ranef' function in lme4 (Bates et al., 2014). Negative BLUPs indicate lower species richness values than predicted by the model; positive BLUPs indicate higher species richness values than predicted.

Dam	**Intercept (Dam)**
Balbina	0.0367
Cabra Corral	-0.131
Chiew Larn	-0.071
Gatun Lake	0.361
Lago Guri	-0.059
Lake Kenyir	-0.247
Petit Saut	-0.079
Randenigala	-0.007
Thousand Island Lake	0.196

CHAPTER 3

Directional change in tree communities on islands created by an Amazonian mega-dam

The research ideas were conceived by Isabel Jones, Carlos Peres and Daisy Dent. IJ collected tree sapling data. Adult tree data were collected by Maíra Benchimol. Trees were identified by A.E.S. Santos, and field assistance provided by E. Damasceno. IJ performed all analyses and wrote the Chapter. Peter Morely gave technical advice on the calculation of the NDVI fire metric using LandSat imagery. Drafts of this Chapter were commented on by DD, Lynsey Bunnefeld, and Alistair Jump.

3.1 ABSTRACT

Fragmentation of tropical forests can lead to long-term changes in tree community composition, loss of carbon storage, and elevated carbon emissions. Edge effects associated with fragmentation can induce high levels of tree turnover and mortality, shifting tree community composition away from that of continuous forests towards a more unstable state, leading to a loss of ecosystem functioning such as carbon storage. Undisturbed Amazonian forests are mega-diverse, and are vital for global carbon cycling, yet these forests are increasingly fragmented. Of particular concern is the extent and impacts of forest fragmentation induced by dam development. Recent studies have shown that following reservoir creation and isolation on land-bridge islands comprised of former hilltops, remnant tree communities rapidly degrade i.e. lose biomass and species. However, to elucidate the potential long-term impacts of inundation on tree communities, sapling tree communities recruited post-inundation must be investigated. We examine the differences in structure and composition of sapling and adult tree communities on islands and in surrounding mainland continuous forests of the Balbina hydroelectric mega-dam system, Brazilian Amazon. We find that for both sapling and adult tree communities, islands consistently sustain lower tree density, richness and diversity than nearby continuous forest. Furthermore, the community composition of saplings and adults on islands show a directional shift away from mainland forest assemblages, which is related to island area, degree of isolation, amount of surrounding forest cover and fire disturbance. Finally, we show that species-level recruitment of saplings per adults ($\log_{10}$ (number of saplings : number of adults); S:A) is significantly lower on islands compared to mainland continuous forest. Across islands, the significant decline in mean sapling : adult recruitment is driven by the degree of fire disturbance, and communities with higher mean abundance-weighted wood density values exhibited the largest declines in mean S:A. Our results suggest that island tree communities are increasingly unstable, likely leading to a loss of ecosystem functioning including carbon storage. We recommend that any future dam development requires the aggregate area of reservoir islands be explicity included in impact assessments of biodiversity loss. Moreover, we propose that the long-term loss of carbon associated with ongoing tree community degradation be considered in carbon cost/benefit analyses of tropical dams.

3.2 INTRODUCTION

Forests of the Amazon Basin constitute the largest remaining intact tract of tropical forest, representing ~40% of global tropical forest cover (Laurance 2001; Peres 2005). Over the past 50 years land-use change has driven large-scale deforestation and forest fragmentation in the Amazon (Laurance 2001). Over 20 % of tree species have been predicted to be extirpated from Amazonian forests under projected levels of forest loss and changing climate scenarios within the next decade (Laurance 2001; Peres 2001a; Hubbell *et al.* 2008; Malhi *et al.* 2008). Fragmentation of Amazonian forests is driven by development of infrastructure, which penetrates into frontier lands. For example, the proliferation of roads in rural Amazonia increases local population densities, hunting, agricultural expansion and resource extraction, which drives forest loss and fragmentation (Peres 2001a; Laurance *et al.* 2002b, 2009, 2014b; Peres & Lake 2003; Simon & Garagorry 2006; Kirby *et al.* 2006; Asner *et al.* 2010; Peres *et al.* 2010; Ahmed *et al.* 2013). Construction of hydroelectric dams is a novel threat contributing to the loss and fragmentation of both terrestrial and aquatic environments. Across the Amazon watershed, 191 dams are already in operation and a further 246 dams are planned or under construction. These dams cause wholesale changes in the functioning of riverine systems (Finer & Jenkins 2012; Lees *et al.* 2016), as well as extensive loss of tropical forest cover and landscape-scale fragmentation of forests remaining above the water level (Fearnside 1989; Benchimol & Peres 2015a).

Tropical forest tree communities are highly vulnerable to fragmentation, and once fragmented, undergo rapid species loss and changes in community composition. The turnover of tree species in fragmented forest communities is temporally variable rendering these communities compositionally unstable, and resulting in loss of ecosystem functioning (Laurance *et al.* 2006b; Santo-Silva *et al.* 2016). Desiccation and wind damage at fragment edges causes substantial tree mortality within 100 m of the forest edge, and fast-growing pioneer tree species can exploit these high light conditions, resulting in a shift towards more homogenous low wood density tree communities (Laurance *et al.* 2006a; Lôbo *et al.* 2011). Fires that penetrate into fragment interiors can cause pervasive loss of old growth species since tropical forest species are not historically adapted for fire disturbance (Michalski, Nishi & Peres 2007). Repeated fire disturbance can lead to divergence of post-fire tree communities from the initial adult tree community in favour of fast-growing pioneer communities able to exploit fire-disturbed conditions (Barlow & Peres 2008; Balch *et al.* 2013).

The quality of the surrounding habitat matrix modifies both the present and future composition of insular tree communities. Open or deforested matrices reduce movement of animals and seed dispersal among fragments, and exacerbate edge effects compared to other matrices such as partially forested pasture or young secondary forest (Nascimento *et al.* 2006a; Tabarelli *et al.* 2008; Ewers *et al.* 2017). Fragments surrounded by a water matrix are subject to extreme fragmentation effects, with impeded species immigration, and no buffer to edge effects (Ewers & Didham 2006; Mendenhall *et al.* 2011, 2014; Jones *et al.* 2016). Tree communities isolated on land-bridge islands created by river impoundment in Amazonia have undergone rapid change, with tree species becoming locally extinct and shifts towards remnant forest communities dominated by pioneer tree species and lianas (Leigh *et al.* 1993; Terborgh *et al.* 2001; Benchimol & Peres 2015a). Thus, erosion of remnant tree communities and a concomitant reduction in community-level carbon storage on reservoir islands, could represent a significant loss of carbon not yet accounted for in the decision-making processes surrounding construction of new dams in Amazonia (Zarfl, Lumsdon & Tockner 2015; Fearnside 2016a; b; Lees *et al.* 2016; Winemiller *et al.* 2016).

Habitat fragmentation fundamentally alters tree communities: fragmented tree communities have increased mortality rates and are dominated by small-diameter (<20 cm) low wood density pioneer species. Such shifts increase forest carbon cycling and reduce carbon storage in the long term (Nascimento & Laurance 2004; Laurance *et al.* 2006b, 2014a; Santos *et al.* 2008). Forest fragmentation leads to a net production of carbon at the fragment edge (~12-15 Mg C produced for every 100 m of forest edge created; Nascimento & Laurance 2004), and reduced carbon storage within fragments compared to forest interiors (25 % reduction in carbon storage <500 m from the fragment edge, and 10 % reduction at 500-1500 m; Chaplin-Kramer *et al.* 2015). Processes that fragment forests therefore not only cause direct loss of carbon through deforestation, but also result in long-term carbon emissions from forest fragments.

Tropical forests are of unparalleled importance for biodiversity and the global carbon cycle (Malhi & Grace 2000; Barlow *et al.* 2007; Gibson *et al.* 2011; Pan *et al.* 2011). Amazonian forests are estimated to store a total of ~93 ± 23 Pg C within above-ground living biomass, 80 % of which is held in large trees >10 cm diameter, which is driven by high net primary productivity rates estimated at ~10-14 Mg C ha^{-1} $year^{-1}$ (Nascimento & Laurance 2002; Baker *et al.* 2004a; Malhi *et al.* 2009; Malhi *et al.* 2006). The amount of carbon held within the aboveground woody biomass of a forest depends on the tree species present, due to species-specific differences in allocation of carbon to woody tissue (Muller-Landau 2004; Chave *et al.* 2009). Hence, wood density is broadly related to successional status; fast-growing light-demanding pioneer species typically have lower wood densities than slow-growing shade-tolerant species due to trade-offs in life-history strategies (Muller-Landau 2004; Chao *et al.* 2008; Chave *et al.* 2009). At the community level, abundance-weighted mean wood density (i.e. community-weighted mean wood density) therefore provides an indication of both the carbon storage capacity, and the dynamism of the tree community as a whole, with low community-weighted mean wood density indicative of low carbon pioneer-dominated assemblages (Chao *et al.* 2008; Chave *et al.* 2009; Baker *et al.* 2004b).

Given the importance of Amazonian forests for global carbon storage (Baker *et al.* 2004a; Malhi *et al.* 2006; Pan *et al.* 2011), maintaining forest cover in this region is imperative for mitigating the impacts of anthropogenic greenhouse gas emissions and reducing levels of atmospheric CO_2 (IPCC 2014). Inundation of tropical forests after river impoundment can result in significant carbon emissions (CO_2 and CH_4) from the decomposition of submerged biomass, and the seasonal exposure of the reservoir bottom during periods of low rainfall (Fearnside 2002a; Demarty & Bastien 2011; Fearnside & Pueyo 2012). Emissions can persist throughout the lifetime of the reservoir, and given the extensive dam construction outlined for the Amazon Basin, better consideration of the full carbon costs of hydropower development are needed (Abril *et al.* 2005; Fearnside & Pueyo 2012; Lees *et al.* 2016). Given the evidence for long-term carbon loss caused by forest fragmentation (Asner *et al.* 2010; Chaplin-Kramer *et al.* 2015) the carbon costs of ongoing degradation of insular tree communities within hydropower reservoirs requires attention.

In order to understand the long-term impact of dam-induced forest fragmentation on remnant insular tree communities, the tree sapling community recruited post-inundation must be described. Tree sapling communities will provide us with improved insight into the long-term impacts of fragmentation, as adult tree communities tend to represent degraded relics of the formerly continuous forest. Describing sapling and adult trees in concert may therefore shed light on potential trajectories of floristic change within insular tree communities (Tabarelli *et al.* 2008; Santo-Silva *et al.* 2016; Ewers *et al.* 2017). In this study we investigate tree sapling communities recruited after the isolation of islands within the Balbina hydroelectric reservoir, Brazilian Amazon, to investigate the cross-generational impact of dam-induced habitat fragmentation on tree assemblages. We answer the following questions:

1) How do sapling communities and adult tree communities respond to environmental variables associated with habitat fragmentation across islands in terms of density, richness, diversity, and community-weighted mean wood density? And how do these metrics compare to mainland continuous forest?

2) How do patterns of abundance- and incidence-based dissimilarity between sapling and adult communities vary across islands and mainland continuous forest?

3) How do patterns in the ratio of saplings : adults differ across islands in relation to environmental variables and wood density, and in comparison to mainland continuous forest?

3.3 METHODS

3.3.1 Study area

We conducted this study in the Balbina hydroelectric mega-dam system, central Brazilian Amazon (1°010 – 1°550 S; 60°290 – 59°280 W). Balbina was created when the Uatumã River was dammed in 1986, flooding 312,900 ha of continuous lowland old-growth wet tropical forest, transforming the landscape into an archipelago of >3500 islands within the reservoir (Fig. 3.1). The landscape was not logged prior to inundation, and thousands of dead trees remain standing within the reservoir. In an attempt to offset the area of forest inundated, all islands and mainland *terra firme* forest to the east of the former Uatumã River bank became strictly protected within the ~940,000 ha Reserva Biológica do Uatumã. The reserve has largely prevented the establishment of small-scale slash-and-burn agriculture and hunting in the protected portion of Balbina. However, islands and mainland to the west of the former Uatumã River bank are accessible by road and boat, and there is some small-scale agriculture and resource extraction. In 1997 a fire was accidentally started in the unprotected portion of Balbina, and spread through exposed and standing deadwood within the reservoir, penetrating into many islands to differing extents.

Fig. 3.1: Islands within the Balbina reservoir, Brazil. >3500 islands were created from formerly continuous old-growth tropical forest when the Balbina dam was constructed in 1986.

We used a network of 89 permanent survey plots (0.25 ha; 10 x 250 m), which have been established on 36 islands, and in three widely spaced areas of nearby mainland continuous forest, over a comparable elevational gradient (Fig. 3.2). The 36 islands were carefully selected for permanent plot establishment by M. Benchimol and C.A. Peres (Benchimol & Peres 2015a), using cloudless georeferenced Landsat ETM+ scenes from 2009 (230/061 and 231/061). Islands were selected to ensure spatial independence, and have a minimum distance of 1 km between one another. Survey islands were also selected to span a range of island sizes found within the reservoir (0.83-1690 ha; mean ± SD = 210.7 ± 392.1), to be located at varying distances from the mainland (0.04-17.7 km; mean ± SD = 4.9 ± 4.4), and to cover the fire disturbance gradient. All permanent plots are situated ≥50 m from island edges. Depending on the size of the survey island, there are between one and four permanent plots per island: one plot on islands <10 ha (mean ± SD island size = 4.0 ± 2.9 ha, range 0.8–9.5 ha, n = 14 islands); two plots per island 10-90 ha (44.4 ± 30.1 ha, 13.4–78.4 ha, n = 9); three plots per island 91–450 ha (230.8 ± 116.5 ha, 98.8–471 ha, n = 7); and four plots per island >450 ha (952.6 ± 454.2 ha, 487.5–1690 ha, n = 6).

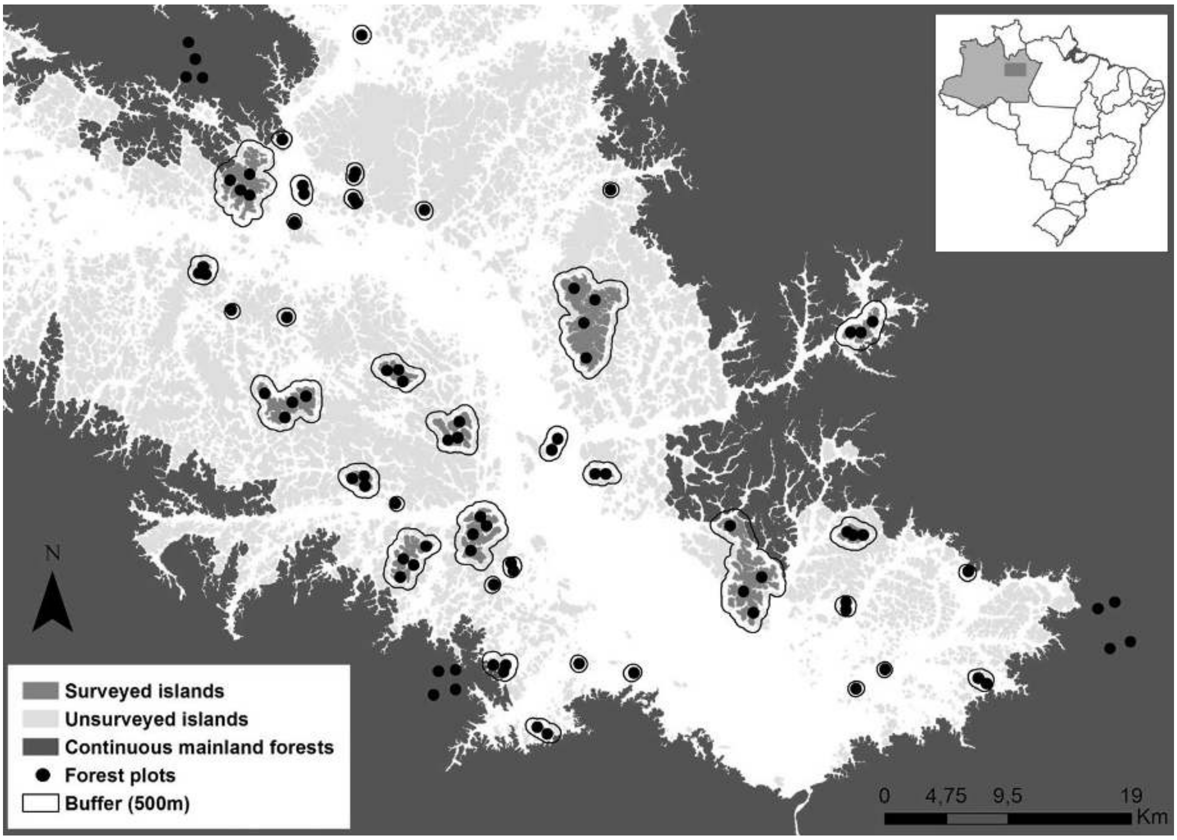


Fig. 3.2: Geography of the 89 permanent plots within the Balbina landscape. 77 plots are located on 36 islands, and 12 plots are located within three separate areas of continuous mainland forest. The 500 m buffer marked is the buffer used to calculate the percentage of forest cover surrounding islands (the 'COVER' metric). Map modified from Fig. 4.1.

3.3.2 Sapling and adult tree surveys

Sapling and adult tree surveys were conducted in each of the 89 permanent plots. All live adult trees and arborescent palms ≥10cm diameter at breast height (DBH) were surveyed in 87 plots in 2012 (Benchimol & Peres 2015a), and in two additional plots in 2014. One 0.025 ha subplot (1 x 250 m running along the central axis of permanent plots) was surveyed for sapling trees and arborescent palms in each of the 89 permanent plots in 2014. In 11 of the 89 plots a reduced area was surveyed for saplings (0.015-0.02 ha) rather than the full 0.025 ha. We chose a subplot area of 0.025 ha for sapling surveys because we identified that this area contained the same species richness for tree saplings as for adult trees.

All adult and sapling trees were identified to species level by A.E.S. Santos, an expert botanist with extensive experience of the Amazonian flora and >20 years' experience of field and herbarium work in Central Amazonia. This includes eight years of tree identification work in the BDFFP landscape and the Ducke Reserve, both of which harbour a similar flora to that found in the Balbina landscape (Benchimol & Peres 2015a). Only saplings of tree and palm species that could potentially reach reproductive maturity at a size ≥10 cm DBH were surveyed, to ensure comparability between sapling and adult tree census data. Tree saplings were defined as those reaching ≥1 m height, with a diameter of ≤2 cm at 1 m height. Unlike trees, arborescent palms grow thickly and incrementally from their base, and thus arborescent palm saplings were defined as those without woody tissue at 1 m height but with fronds reaching ≥1 m height. The species lists produced from both the sapling and adult surveys were screened for any changes in nomenclature occurring between the two surveys (2012 and 2014), and updated where necessary.

3.3.3 Tree community attributes

Four plot-level attributes of both the sapling and adult tree communities were investigated: (1) density, calculated as the number of individuals per 100 m^2. Density, rather than abundance was used because saplings and adults were surveyed over different areas. (2) Rarefied species richness, whereby species richness is rarefied to the minimum number of individuals present within a size class (n = 16, saplings; n = 40, adults). When using rarefied richness values of saplings and adults within the same analysis e.g. ANOVA, we rarefied all species richness values to the minimum number of individuals observed (n = 16, saplings). (3) Fisher's α diversity, which is a measure of diversity robust to low and varying numbers of individuals within assemblages (Beck & Schwanghart 2010); and (4) community-weighted mean wood density. To calculate the community-weighted mean wood density, we compiled species-specific wood density data from the Global Wood Density database (GWD; Chave et al. 2009; Zanne et al. 2009). Wood density values from Central Amazonia were used when possible, followed by the next most geographically proximate source e.g. the Guiana Shield. Where species-level data were unavailable in the GWD, genus level data were used as wood density tends to be a well-conserved trait at the genus-level (Chave *et al.* 2006).

3.3.4 Environmental variables

Five variables of ecological importance at plot- patch- (i.e. island or mainland site) and landscape-scales were included in analyses. These included at the plot-scale: (1) distance to the nearest edge ('D_{EDGE}', metres), which was calculated as the mean shortest linear distance between each permanent plot and the forest edge, providing information on proximity to the forest-water boundary where edge-effects are most severe. At the patch-scale, we included: (2) island area ('AREA', in hectares), based on the number of 5 m pixels in a seamless Rapid-Eye© composite image assembled for the entire study area; (3) the shortest linear distance from the perimeter of a survey island to continuous mainland forest ('ISOLATION', metres); and because of ephemeral surface fires in December 1997 (4) a measure of the gradient of fire disturbance ('FIRE'). 'FIRE' was based on the difference in NDVI between pre- (June 1997) and post-fire (July 1998) Landsat 5 TM scenes. Images from June 1997 and July 1998 were used to reduce the potential for phenological differences in vegetation. Orthorectified surface reflectance data, corrected for atmospheric differences, were downloaded and image pairs mosaicked using histogram matching and the result visually inspected (R package "RStoolbox"; Leutner & Horning, 2017). The NDVI vegetation index was calculated from each mosaicked image (pre- and post-fire) and the difference between the pre- and post-fire values was calculated. The mean change in NDVI was then calculated for each focal island, and this value was used as the metric to indicate the severity of fire penetration into each focal island. All mainland continuous forest was unaffected by fire, while all islands showed evidence of partial to extreme levels of fire disturbance.

Finally, at the landscape-scale, we used (5) the percentage of forest cover ('COVER', %) within a 500 m buffer extending from the perimeter of each survey island and the mainland sites. COVER provides a measure of landscape connectivity, encompassing both the degree of isolation from, and extent of, surrounding forested habitat (Fahrig 2013).

3.3.5 Statistical analyses

Community attributes

All analyses were conducted using 'R' (version 3.3.2; R Core Team 2016). Two-way ANOVA was used to test for overall differences in community attributes (density, rarefied species richness, Fisher's α diversity, and community-weighted wood density) between saplings and adults, on islands and in mainland sites.

We conducted analyses of the tree community attributes across islands, separately for sapling and adult trees. Using linear mixed effects models (LMMs with Gaussian error structure) we regressed each community attribute (density, rarefied species richness, Fisher's α diversity, and community-weighted wood density) with the five environmental variables encompassing the gradient of disturbance across Balbina (COVER, AREA, ISOLATION, FIRE, D_{EDGE}). We did not include data from mainland sites in regression analyses to avoid assigning arbitrary values for AREA and ISOLATION to mainland sites, which may have influenced the regression artificially, and because any mainland/island effect is confounded with the FIRE effect (all mainland sites are unburned, while all islands have been burned).

In order to directly compare the effect sizes of explanatory variables on the community attributes, all explanatory variables were rescaled (centred and divided by two standard deviations; (Schielzeth 2010)) prior to modelling, using ‘rescale’ within the ‘arm’ R package (Gelman & Su 2016). For each model, a pair-wise Pearson’s correlation matrix was inspected, and if a pair of environmental variables was highly correlated (r >0.7) the variable explaining the least variation when modelled alone was removed. Variance inflation factors (VIFs) for each explanatory variable were also inspected for each model, with variables with a VIF >4 excluded. The distribution of each response variable was inspected and was required to be approximately normally distributed; if variables did not show a normal distribution, they were transformed appropriately prior to modelling (Zuur, Ieno & Elphick 2010).

Our nested sampling design, and any potential pseudo-replication arising from multiple plots being situated on a single island, was accounted for in LMMs by fitting “island” as a random effect. We also fitted “survey area” as a random effect, to account for saplings being surveyed over a different area in 11 of the 77 island plots. We did not fit “survey area” as a random effect when modelling sapling density 100 m^{-2} as survey area is already controlled for in this metric. Models were simplified through stepwise deletion of non-significant terms (t-values <-2 or >2 were deemed significant) and inspection of AIC values, whereby a difference of <2 between the AIC values of two models indicated that models were not significantly different and the most parsimonious model could be retained (Burnham & Anderson 2002). Model fit was assessed by visually inspecting the distribution of model residuals, which were required to be approximately normally distributed. Model residuals were plotted on a map of the study area and coloured according to whether residuals were over- or under-predicted, to visually inspect for spatial autocorrelation: no spatial autocorrelation was observed. We calculated 95 % confidence intervals around the coefficient estimates of each explanatory variable by multiplying the standard error by 1.96. LMMs were run using ‘lmer’ within the ‘lme4’ R package (Bates *et al.* 2015)).

Community composition

We visually examined the plot-level similarity between sapling and adult communities using non-metric multi-dimensional scaling (NMDS) ordination. NMDS ordination collapses community-wide variation in species composition into two to three dimensions, to enable visualisation and interpretation of important patterns in community composition across multiple surveyed sites. The proximity of points plotted within ordination space indicates the degree of similarity among the compositions of communities, whereby points plotted closer to one another have more similar community compositions (Anderson *et al.* 2011).

In order to visualise the similarity between sapling and adult communities simultaneously in ordination space, we constructed a 'species abundance × plot matrix' considering saplings and adults per plot for all species. Abundance-based dissimilarity values were produced using the Bray-Curtis dissimilarity index. An assumption of the Bray-Curtis index is that the same area is surveyed across plots. Although, we surveyed a smaller area for saplings than for adults in each plot, species richness of saplings and adults is comparable (S3.1) and thus our use of the Bray-Curtis index is justified. The Morisita-Horn index would also have been suitable because of its applicability to communities sampled over different areas (Chao *et al.* 2006). However even with three dimensions, an accurate visual representation of plots within ordination space could not be found using values generated by the Morisita-Horn index. We generated incidence-based dissimilarity values using the Jaccard index, which converts abundances into binary presence/absence data. Distance values were produced using 'vegdist,' and unconstrained NMDS ordination was performed using 'metaMDS' both within the 'vegan' R package (Anderson *et al.* 2011; Oksanen *et al.* 2016). Patch and landscape environmental variables were fitted to ordinations using 'envfit' and their significance ascertained ($P < 0.05$) using 999 permutations ('vegan' R package; Oksanen *et al.* 2016).

We extracted plot-level abundance-based and incidence-based dissimilarity values for sapling and adult communities, generated from the Bray-Curtis and Jaccard dissimilarity indices. We used one-way ANOVA to test for overall differences in dissimilarity values between island and mainland plots. To investigate the potential drivers of plot-level dissimilarity between saplings and adults across islands, we regressed the dissimilarity values and the five environmental variables following the procedure previously described for LMM modelling. Both abundance- and incidence-based dissimilarity values were log-transformed (ln x) prior to modelling.

The proportion of species present in each plot that were i) present only in the sapling layer, ii) present only in the adult layer, and iii) present in both layers simultaneously were calculated. We used two-way ANOVA to test for overall differences in these proportions between island and mainland plots. In order to investigate variation in species-level sapling and adult populations across islands and mainland continuous forest, we calculated the $\log_{10}$ ratio of saplings : adults (S:A) for each species in each plot. We added one to all sapling and adult populations to remove zero values, to allow calculation of S:A. We then generated plot-level mean values of S:A ($S{:}A_m$) and modelled $S{:}A_m$ with environmental variables and sapling community-weighted mean wood density using LMMs.

3.4 RESULTS

3.4.1 Sapling and adult tree surveys

The 89 permanent plots harboured a total of 484 species, across 11,046 saplings (396 species) and 11,330 adult trees (376 species), with 288 species (60 %) common to sapling and adult layers. Tree saplings were surveyed over a total area of 2.145 ha, and adult trees over 22.25 ha, distributed over 36 islands (n plots = 77) and mainland continuous forest sites (n plots = 12). Between 16 and 240 tree saplings (mean ± standard deviation; 124 ± 46) of 10 to 89 species (56 ± 17) were recorded per 0.025 ha plot, and between 40 and 180 adult trees (127 ± 23) of 14 to 78 species (58 ± 12) were recorded per 0.2 5ha plot. We obtained species-level wood density data for 465 species, representing 99.1 % of saplings and 99.8 % of adult trees. Wood density ranged from 0.24 to 1.08 g cm^{-3} (0.65 ± 0.15).

3.4.2 Structural differences between saplings and adults on islands and in continuous forest

Density ranged from 8 to 96 (mean ± standard deviation; 51 ± 17) for saplings, and from 2 to 7 (5 ± 1) for adult trees. Densities of both saplings and adults were significantly higher in mainland plots compared to island plots ($P < 0.001$; Fig. 3.3a; S3.2). Rarefied species richness and diversity was also significantly higher in mainland plots compared to islands (S3.2; Figs. 3.3b, c). Sapling and adult assemblages had comparable levels of richness and diversity (S3.2). Unlike density, richness and diversity metrics, there was no pattern in community-weighted wood density related to plot location (island vs. mainland, $P = 0.37$, S3.2; Fig. 3.3d) nor between ontogenetic layers (sapling vs. adult, $P = 0.13$, S3.2; Fig. 3.3d). Community weighted mean wood densities of plots ranged from 0.59 to 0.74 (0.65 ± 0.03) for saplings, and 0.51 to 0.76 (0.66 ± 0.04) for adult trees.

3.4.3 Sapling and adult tree communities on islands

Sapling and adult tree communities on islands show similar patterns regarding environmental variables associated with habitat fragmentation

The density of stems in both sapling and adult tree assemblages increased when the percentage of forest cover surrounding islands was higher, however sapling stem density was strongly negatively affected by the degree of fire disturbance (Figs. 3.4a, e; S3.3). Species richness and diversity of sapling and adult tree assemblages was also higher when surrounding forest cover was greater (Figs. 3.4b, c, f, g; S3.3). In addition, sapling species diversity was significantly lower on islands further from the mainland and when levels of fire disturbance were higher (Fig. 3.4c; Table S3.3). Community-weighted mean wood density of adult trees significantly decreased with fire disturbance (Fig. 3.4h; S3.3whereas tree sapling communities slightly increased in mean wood density when further from the mainland (Fig. 3.4d; S3.3).

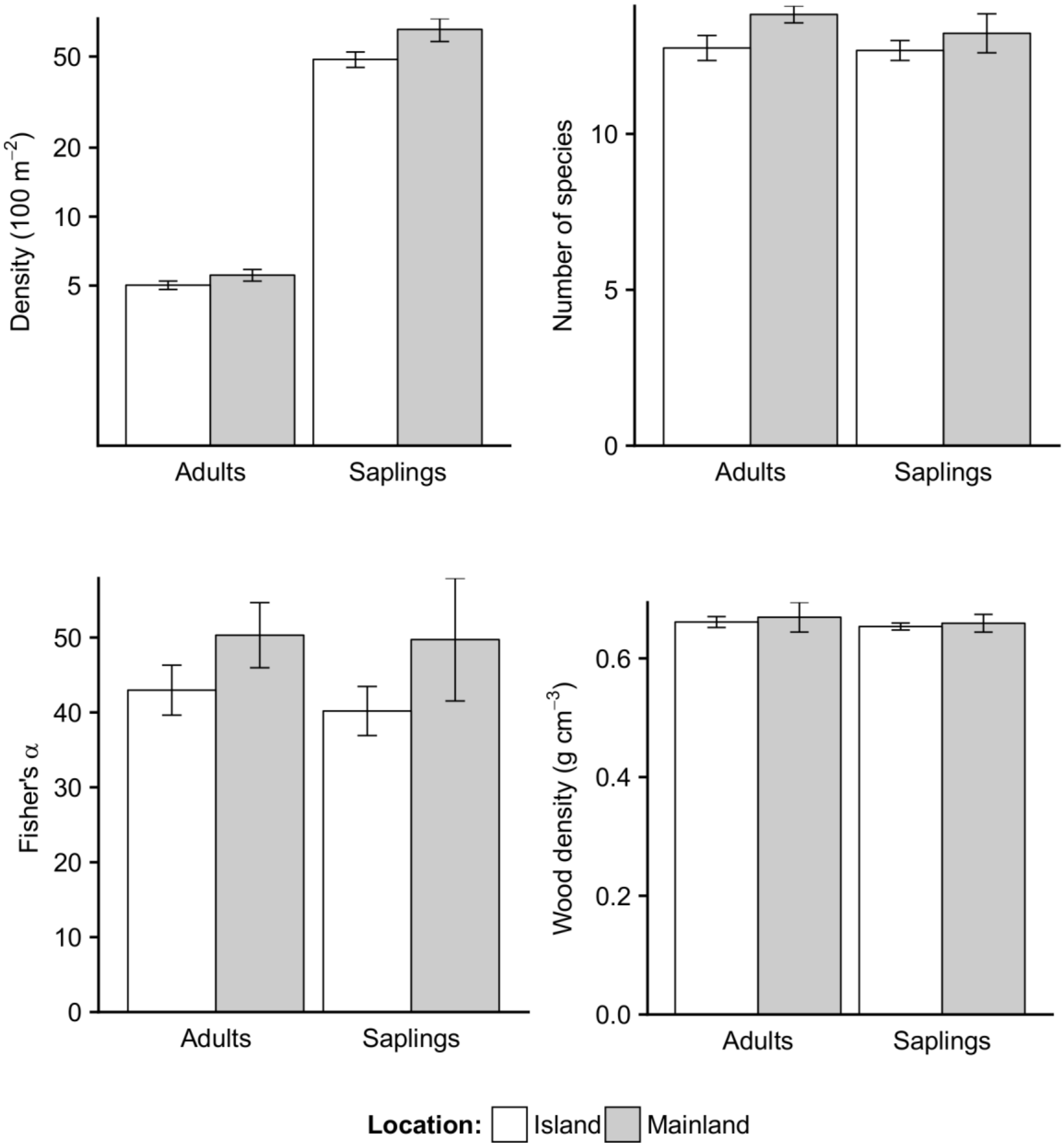


Fig. 3.3: Sapling and adult tree community attributes across islands and mainland continuous forest plots. Mean values with 95 % confidence intervals are shown. Two-way ANOVAs testing differences between saplings and adults, on islands and in mainland continuous forest, revealed that mainland forests had significantly higher tree density, richness and diversity than islands; apart from stem density, there was no significant difference between saplings and adult tree communities (S3.1). No significant patterns relating to community-weighted mean wood density were found (S3.1).

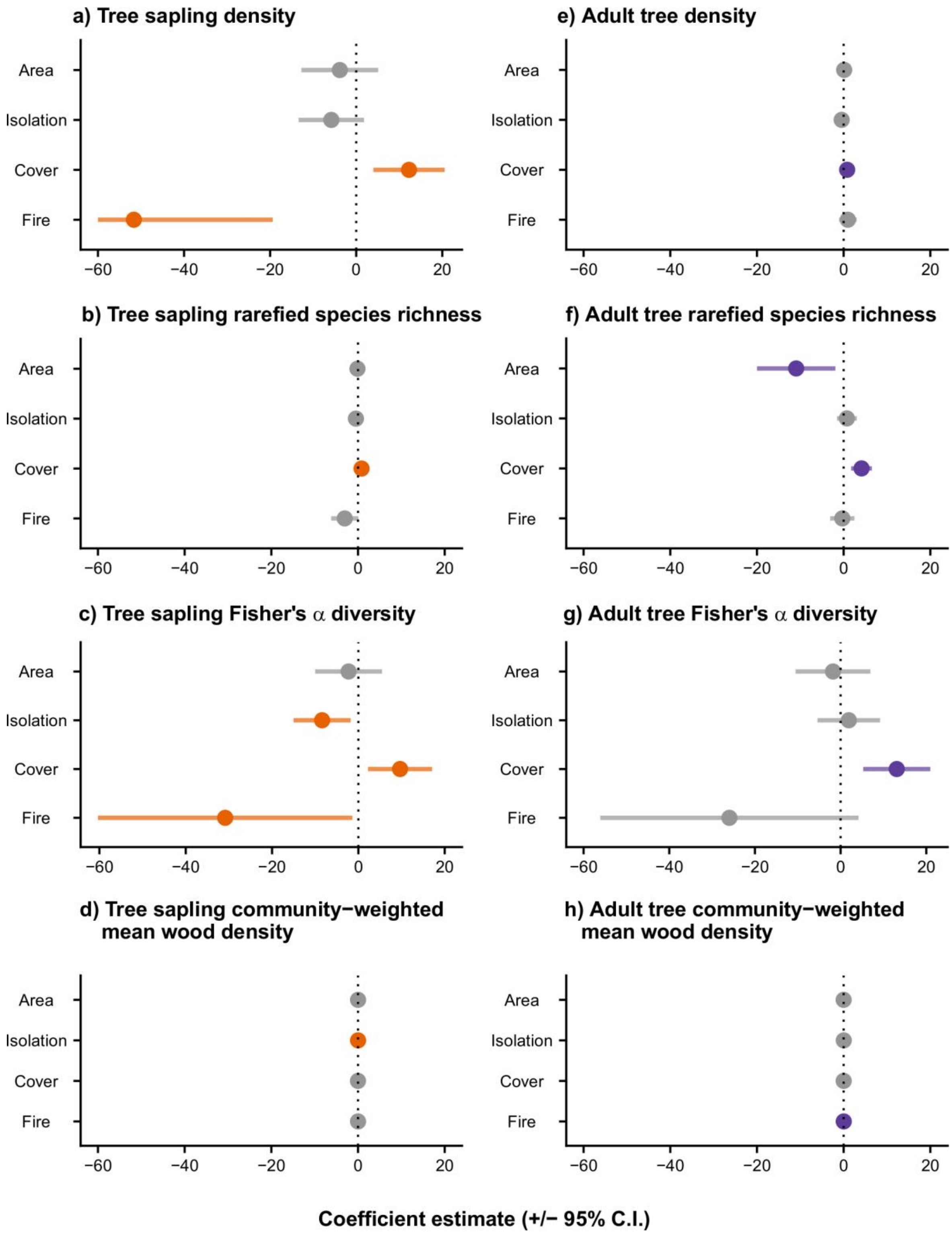


Fig. 3.4: Standardised effect sizes of plot- patch- and landscape-scale variables on sapling and adult tree community attributes on islands. Coefficient estimates from maximal models are plotted with 95 % confidence intervals. Points in colour indicate that coefficient estimates and confidence intervals do not overlap zero, and the variables have a significant effect on the response variable. Points < 0 indicate a negative effect and > 0 indicate a positive effect of the explanatory variable on the response variable. The most parsimonious models are summarised in S3.3.

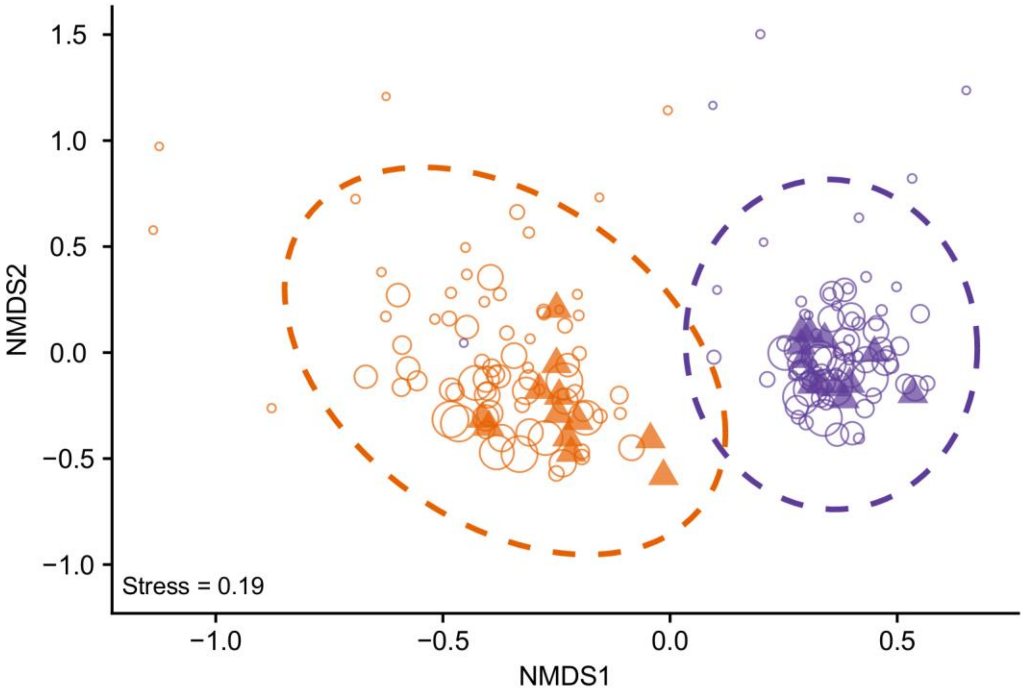
3.4.4 Tree community composition

Compositions of sapling and adult tree communities are more similar in mainland continuous forest and show a directional shift on islands

There was strong differentiation between sapling and adult community compositions across the landscape, for both abundance- and incidence-based metrics as revealed by NMDS ordination (Fig. 3.5). Such a pattern indicates that the presence/absence of species, rather than the relative abundance of individuals, largely determines the species composition of sapling and adult communities. In both ordinations, axis NMDS1 was significantly correlated with area, degree of isolation, and the percentage of surrounding forest cover ($P < 0.05$).

For both sapling and adult assemblages, mainland plots were tightly clustered in ordination space indicating that they were more similar to one another. Sapling assemblages showed a greater degree of difference among plots than adult assemblages, indicating that sapling community composition was more variable than adult tree community composition. The smallest islands appeared to have the most variable compositions of both saplings and adult trees, and were located at the extreme fringes of ordination space. However, these points were positioned non-randomly towards higher values of NMDS1, and so tend to have smaller areas, lower surrounding forest cover, and higher isolation and greater fire disturbance history. Larger islands appeared to be more similar to mainland plots as they were positioned in the same ordination space, and this was particularly pronounced for adult tree assemblages. In contrast, sapling assemblages showed a greater degree of variance even on larger islands.

a) Abundance−based dissimilarity



b) Incidence−based dissimilarity

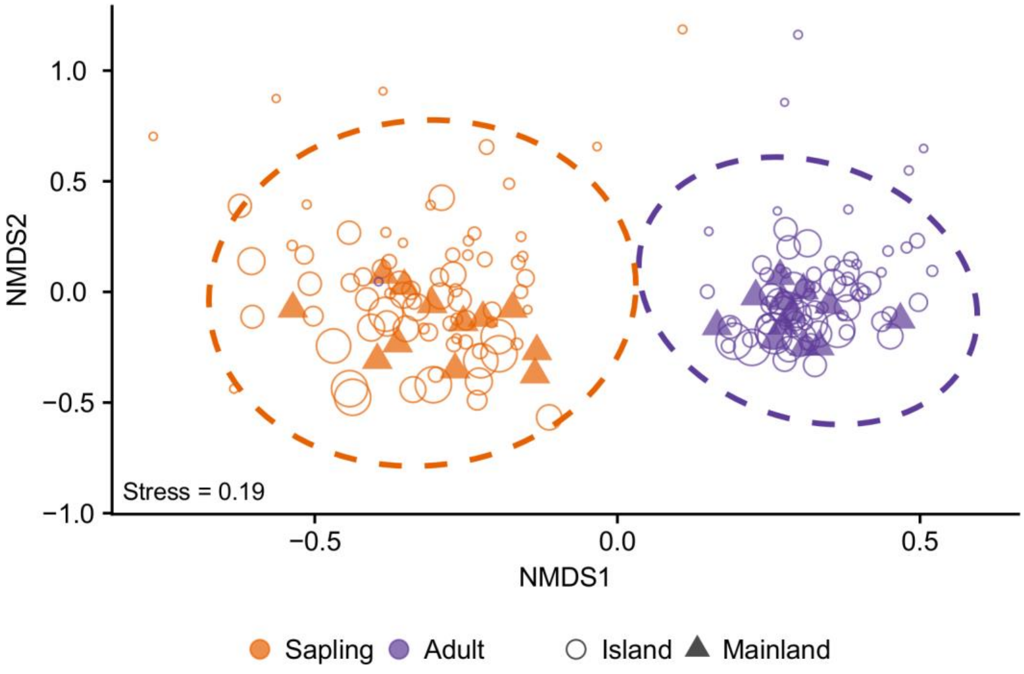


Fig. 3.5: NMDS ordinations of abundance-based (Bray-Curtis) and incidence-based (Jaccard) plot-level dissimilarities for sapling and adult assemblages. Circles are scaled by island size (0.83-1690 ha; mean ± SD = 210.7 ± 392.1). Dashed lines represent 95 % confidence intervals. NMDS1 was significantly correlated with area, degree of isolation, and the percentage of surrounding forest cover (*P* < 0.05). Axes are not equally spaced to maximise visual clarity. We present only the first two of three dimensions needed to position points accurately in ordination space.

The composition of sapling and adult layers were less similar to one another on islands compared to the mainland, considering both abundance-based dissimilarity (*F*[1,87] = 4.45, *P* = 0.04) and incidence-based dissimilarity (*F*[1,87] = 8.25, *P* = 0.005). For island plots, abundance-based dissimilarity between saplings and adults was lower when plots were further from island edges (Fig. 3.6a; S3.3). However, the incidence-based dissimilarity btween saplings and adults was not significantly related to any environmental variables (Fig. 3.6b; S3.3).

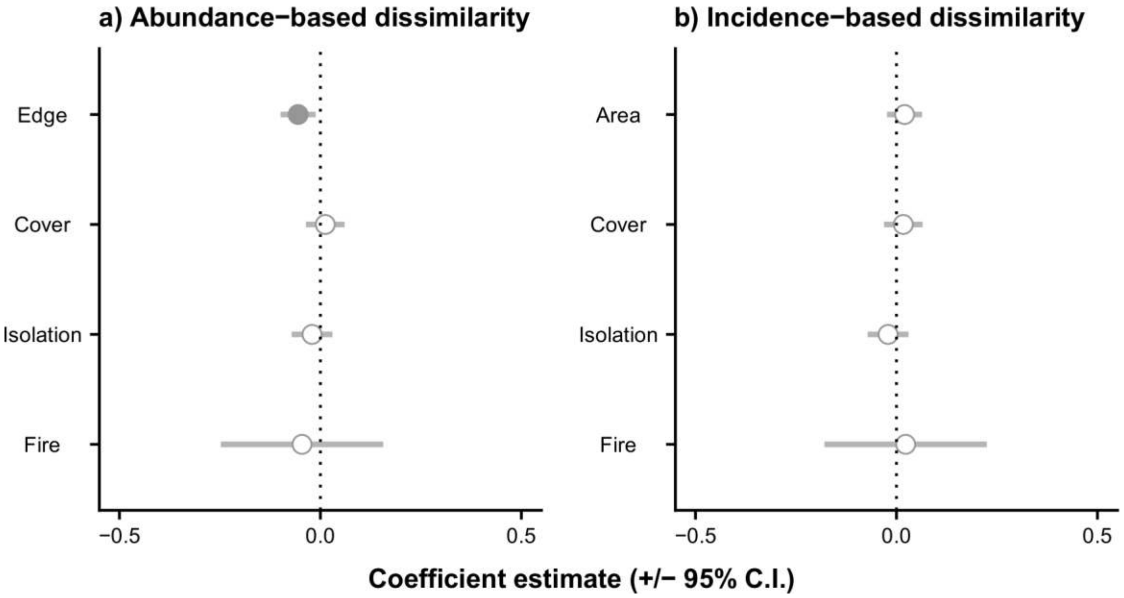


Fig. 3.6: Standardised effect sizes of plot- patch- and landscape-scale variables on plot-level dissimilarity between sapling and adult tree communities on islands. Abundance-based dissimilarity was calculated using the Bray-Curtis index, and incidence-based dissimilarity was calculated using the Jaccard index. In these graphics a negative coefficient estimate indicates a reduction in dissimilarity i.e. sapling and adult communities become more similar. Therefore, in this instance, abundance-based similarity increases with increasing distance from island edges. Filled points indicate that the corresponding variable has a significant effect on dissimilarity, summarised in Table S3.2.

3.4.5 Sapling : adult ratio

The sapling : adult ratio is lower on islands compared to mainland continuous forest

When we compared the proportions of species within each plot that occur only in the sapling layer, only in the adult layer, or in both layers simultaneously, we found that there were significantly fewer species occurring as both saplings and adults simultaneously, than in either class independently (*F*[2,263] = 381.4, *P* < 0.001; Fig. 3.6). This suggests that species within adult tree assemblages are not being readily recruited into the sapling layer, which is further highlighted by the fact that a significantly greater proportion of species occurred only as adults compared to saplings (*F*[2,263] = 381.4, *P* < 0.001).

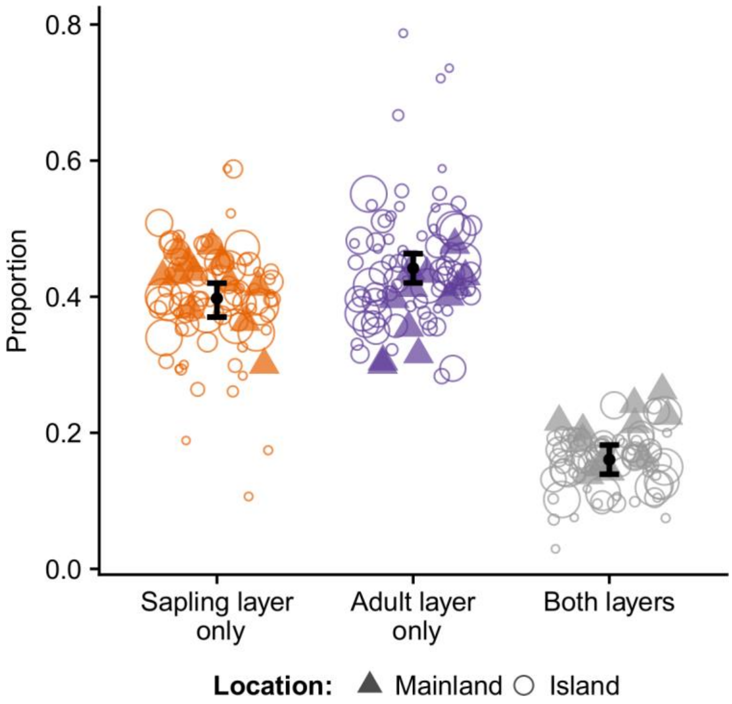


Fig. 3.7: Proportion of species within each plot that are represented i) only in the sapling layer, ii) only in the adult layer, or iii) in both sapling and adult layers simultaneously. Significantly fewer species occurred as both saplings and adults simultaneously, than in either class independently (*F*[2,263] = 381.4, *P* < 0.001). There was no significant difference between island and mainland plots (*F*[1,263] = 0.0, *P* = 1).

Furthermore, the $\log_{10}$ ratio of saplings : adults (S:A) was significantly different lower on islands than in mainland continuous forest (F[1,8697] = 7.5, $P = 0.006$). Tree communities on islands had significantly fewer saplings per adult than did communities in mainland continuous forest (Fig. 3.8). Across islands, the degree of fire disturbance was the strongest driver of declines in plot-level mean $\log_{10}$ sapling : adult ratios (S:A_m; Fig. 3.9; S3.2). Tree communities with higher community-weighted mean wood density displayed the greatest declines in S:A_m (Fig. 3.10; S3.2).

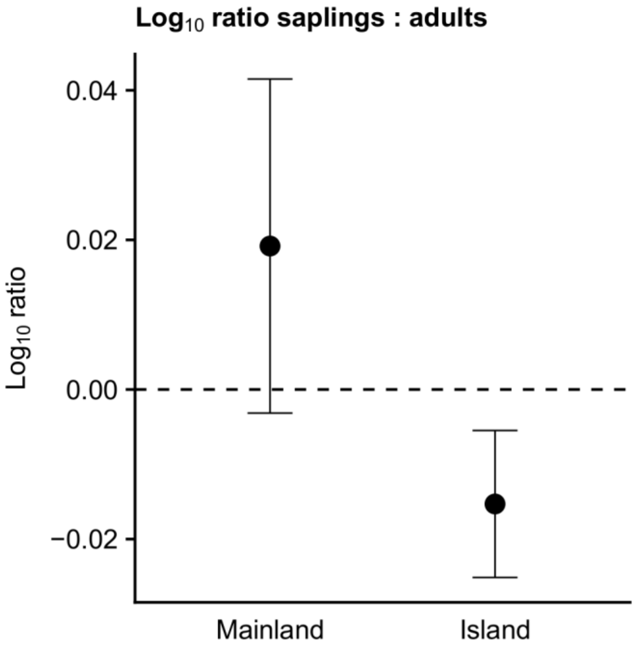


Fig. 3.8: Species-level $\log_{10}$ of sapling : adult communites in mainland continuous forest and on islands. Islands had significantly lower S:A ratios compared to the mainland (F[1,8697] = 7.5, $P = 0.006$).

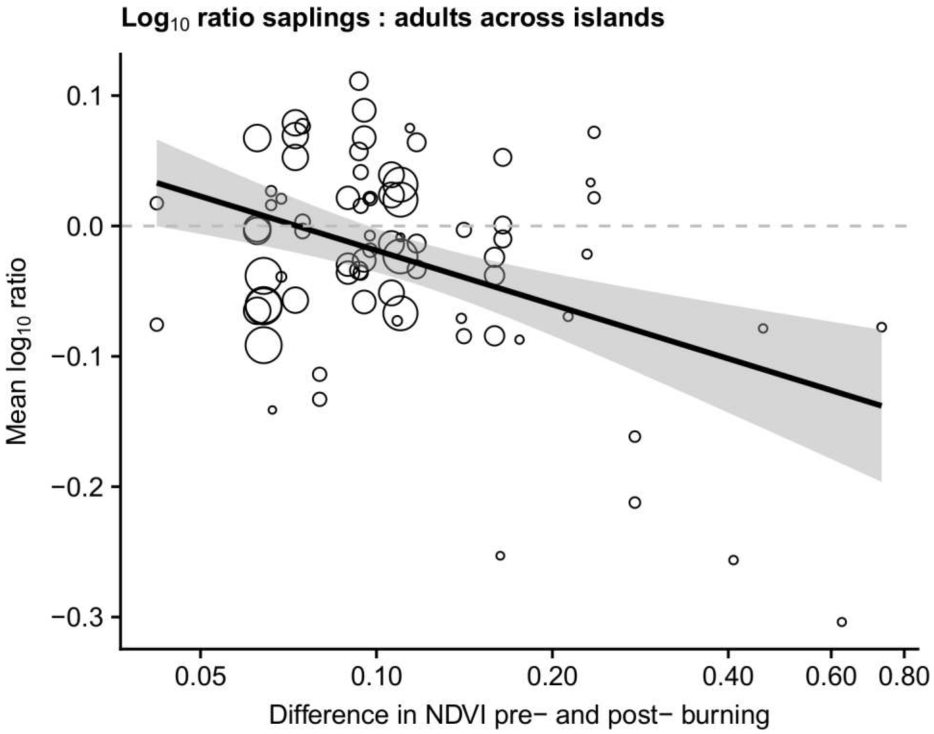


Fig. 3.9: Plot-level mean $\log_{10}$ ratio of sapling : adult communites across islands is significantly negatively affected by the degree of fire disturbance. Points are scaled by island size, and the 95% C.I. is shown as grey shading around the model prediction. The x axis is on a $\log_{10}$ scale.

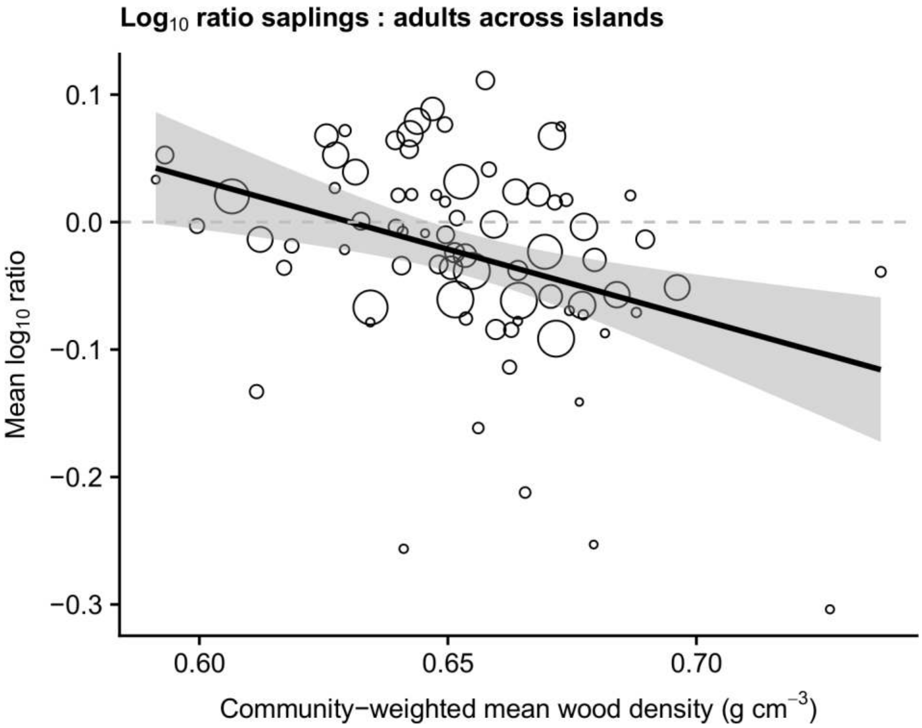


Fig. 3.10: Plot-level mean $\log_{10}$ ratio of sapling : adult communites across islands is significantly reduced when the community-weighted mean wood density of sapling communities is higher. Points are scaled by island size, and the 95% C.I. is shown as grey shading around the model prediction.

3.5 DISCUSSION

We investigated the cross-generational impact of dam-induced habitat fragmentation on Amazonian tropical forest tree assemblages. We consistently found that mainland continuous forest supported a significantly greater density, richness and diversity of both sapling and adult trees compared to remnant forest isolated on islands post-inundation. Mainland continuous forest also supported more stable tree communities in terms of the balance of recruitment and replacement of adult individuals. The per-adult abundance of saplings (S:A) was significantly lower on islands compared to mainland sites. Declines in mean plot-level sapling : adult ratios were driven by fire disturbance, with communities with higher community-weighted mean wood density exhibiting the largest declines in mean sapling : adult ratios (Figs 3.8, 3.9, 3.10). The amount of surrounding forest cover was consistently an important factor leading to higher tree densities, richness and diversity, whereas the effect of fire disturbance was the strongest driver of declines in these tree community characteristics (Fig. 3.4). Across all plots, saplings and adults had significantly different species community compositions (Fig. 3.5). Both sapling and adult assemblages on islands showed a directional shift away from mainland assemblages as island area and surrounding forest cover decreased, and as isolation distance and fire disturbance increased.

Islands support lower tree densities, richness and diversity than continuous forest

In line with previous findings from fragmented Amazonian forest systems, we found that mainland continuous forest supported consistently higher densities of sapling and adult trees, with significantly more species-rich and diverse assemblages compared to islands. In the nearby BDFFP, tree density was reduced and floristic composition was much altered within fragments, following high rates of mortality and species turnover caused by fragmentation-related disturbance (Laurance *et al.* 2006b). Similarly in fragments of Atlantic Forest, tree density and species richness were also lower than in undisturbed forests, particularly in small fragments and forest edges (Santos *et al.* 2008). Such findings reiterate the general consensus that forests lose integrity and degrade over time following fragmentation (Gibson *et al.* 2011; Haddad *et al.* 2015).

Small, isolated and highly disturbed islands show greater degrees of tree community degradation

Islands surrounded by more forest sustained a greater diversity of trees and a greater number of individuals, although still significantly less than in continuous forest. Similarly, levels of forest cover have been important in determining sapling and adult tree communities in Atlantic Forest fragments, where forest cover loss resulted in reductions in richness and diversity of both adults and saplings (Benchimol *et al.* 2017). We also found sapling and adult tree communities to be negatively affected by isolation and reduced habitat area, however, the degree of fire disturbance had the greatest impact on island tree communities. Fire disturbance led to significant declines in sapling richness and diversity, and significant reduction in the mean plot-level sapling : adult ratio ($S{:}A_m$) across islands. The smallest islands displayed some of the greatest declines in sapling : adult ratios, and declines were pronounced for communities with higher wood densities, indicating that hard-wooded species are particularly sensitive to disturbance (Tabarelli, Peres & Melo, 2012). The stressful environmental conditions experienced on small, edge-dominated islands may select for low wood density species with fast growth that enable individuals to exploit the disturbed, high-light conditions and grow rapidly to escape vulnerable early life stages (Muller-Landau 2004, 2010; Larjavaara & Muller-Landau 2010a; Visser *et al.* 2016). Thus, islands, particularly those most heavily impacted by fragmentation effects, may be on a trajectory towards future tree communities dominated by low-wood density species (Tabarelli *et al.* 2008; Lôbo *et al.* 2011).

Island tree communities show increased variance in community composition

Across all plots the composition of sapling assemblages was significantly different from that of adults, which was likely due to the low proportion of species shared between sapling and adult layers within plots (Fig. 3.7). Both sapling and adult communities on islands showed a directional shift in composition away from mainland plots related to reduced island size, lower surrounding forest cover, and increasing degree of isolation and fire disturbance (Fig. 3.5). The most heavily impacted islands showed the greatest degree of divergence from mainland assemblages, for example small, isolated islands that had experienced a history of severe fire disturbance. Sapling and adult assemblages were more similar when plots were situated further from forest edges, and when the percentage forest cover surrounding islands was higher. Such findings again highlight that edge effects lead to a general shift in sapling communities away from the initial adult assemblage, and that the quality of the surrounding matrix can mediate the impacts of edge effects on remnant forest patches (Ewers & Didham 2006; Nascimento *et al.* 2006b; Laurance *et al.* 2011). Similar directional shifts in community composition in relation to fragmentation effects have also been found in the BDFFP fragments, where edge-dominated plots exhibited a non-random shift in composition away from interior forest plots, which was largely driven by elevated levels of tree mortality (Laurance *et al.* 2006b, 2011).

Sapling communities showed a greater degree of plot-level variation in composition than did adult communities, indicating that fragmentation has potentially led to compositionally-unstable sapling communities (Laurance *et al.* 2006b). On the smallest islands there is low species overlap between saplings and adults, and a high proportion of species are restricted to the adult layer (Fig. 3.7). This is particularly apparent in analyses of sapling : adult ratios where the smallest islands show the greatest declines in saplings : adults with increasing fire disturbance (Fig. 3.9). Small islands also have high values of community-weighted mean wood density, yet show the greatest magnitudes of decline in saplings : adults (Fig. 3.10). Such a pattern indicates that recruitment of saplings (of both high and low wood density species) is generally low on these small and highly disturbed islands. Singleton or doubleton recruits of high wood density species may therefore increase the community-weighted mean wood density of the island because low wood density species are also not readily recruiting, compared to the number of adult pioneer trees present. Pioneer trees dominate adult tree communities on small and highly disturbed and edge-dominated islands (Benchimol & Peres, 2015), and thus may have created too much shade for new pionners to recruit. If, due to a lack of dispersal ability or disturbance regime, recruitment of shade-tolerant species is low on such islands, then these islands could effectively become stalled in an early successional state, leading to instability and a reduction of ecosystem service provision including carbon storage (Tabarelli *et al.* 2008; Lôbo *et al.* 2011; Ewers *et al.* 2017).

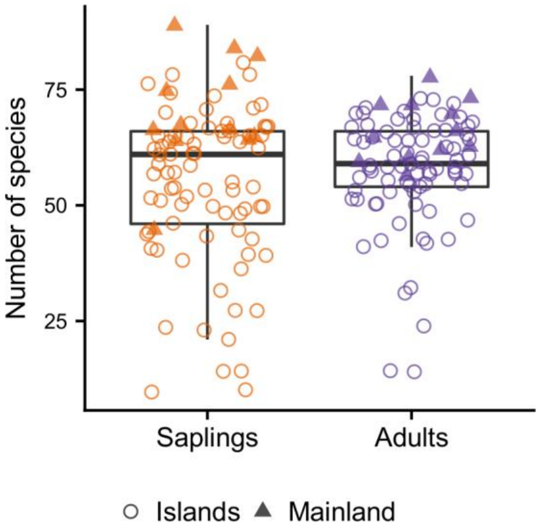
3.5.1 Caveats and future directions

Ours is a snapshot study of sapling and adult tree assemblages ~30 years after island isolation. Given the high turnover of both sapling and adult tree communities in fragmented systems, repeated inventories of both saplings and adults are needed to fully understand the dynamics of remnant forest fragments isolated within a water matrix (Laurance *et al.* 2006b, 2007, 2011). Furthermore, saplings can remain in the sapling layer for considerable periods of time (e.g. 12-126 years in Guyana; Zagt 1997), and thus we may have inadvertently sampled saplings which had been recruited before inundation; we may therefore not yet be seeing the full effects of habitat fragmentation on tree communities (Tilman *et al.* 1994; Metzger *et al.* 2009; Jones *et al.* 2016; Rosa *et al.* 2016). However even in ~30 years of island isolation, we find significant decay in sapling assemblage structure and diversity on islands compared to mainland continuous forest, and shifts in community composition correlated with island area, degree of isolation, quality of the surrounding non-water matrix, and fire disturbance. Though sapling community composition is a strong predictor of the future tree assemblage (Ewers *et al.* 2017), significant degrees of habitat filtering determining survival can occur at other life stages such as the seedling stage. Therefore, investigating other life stages of trees would be valuable to fully tease-apart tree community change in response to habitat fragmentation. Furthermore, other environmental variables, such as soil type and fertility, could be integrated into analyses as these may also play a significant role in determining establishment success and survival (Fortunel *et al.* 2014).

3.5.2 Conclusion

The fragmentation of Amazonian tropical forest, and subsequent isolation of remnant forest patches within a water matrix following dam construction, leads to a directional shift in tree community assemblages away from those seen in mainland continuous forest. The degree of mismatch in tree communities, between islands and the mainland, and between saplings and adults is driven by synergies between island area, degree of isolation, amount of surrounding forest cover, and level of fire disturbance. The smallest islands (<10 ha) are consistently the most heavily impacted by environmental variables associated with fragmentation, and show the greatest degree of floristic breakdown in comparison to continuous forests. Island tree communities with higher abundance-weighted mean wood density are particularly affected, suggesting that remnant forests on islands are on a trajectory towards a future tree community typical of forests in an earlier successional state. Such a trajectory would likely be characterised by high carbon turnover and emissions, representing a significant source of additional emissions associated with tropical dams (Nascimento & Laurance 2004; Larjavaara & Muller-Landau 2010a; Chaplin-Kramer *et al.* 2015). Dam-induced fragmentation has been clearly shown to be detrimental to relict tree communities (Benchimol & Peres 2015a). We now show that the effects of dam-induced fragmentation persist, and shift sapling communities away from those found in continuous forest: this represents a further, and hitherto undocumented long-term ecological impact associated with tropical dams. Ongoing degradation of tree communities on reservoir islands will lead to a pervasive loss of biodiversity and carbon throughout the lifetime of the dam.

S3 SUPPLEMENTARY INFORMATION



S3.1: The number of species recorded for sapling and adult trees across islands and mainland continuous forest in Balbina.

S3.2: Summary of two-way ANOVA results of differences between sapling and adult trees on islands and in mainland continuous forest.

Community characteristic		**SS**	**Mean SS**	**df**	***F***	***P***	**% variance explained**
Density (100 m^{-2})	Saplings vs Adults	93253	93253	1	654.6	<0.001	77.8
	Island vs Mainland	1615	1615	1	11.3	<0.001	1.34
Rarefied species richness	Saplings vs Adults	1.02	1.02	1	0.42	0.52	0.24
	Island vs Mainland	13.7	13.7	1	5.75	0.02	3.17
Fisher's α	Saplings vs Adults	274	274.3	1	1.32	0.25	0.72
	Island vs Mainland	1478	1477.9	1	7.14	0.008	3.89
Community-weighted mean wood density (g cm^{-3})	Saplings	0.003	0.003	1	2.33	0.13	1.31
	Adults	0.001	0.001	1	0.8	0.37	0.04

S3.3: Summary of most parsimonious models of adult and sapling regressions. Marginal R^2 (R^2_m) values represent the proportion of variance explained by the fixed effects within the models, and conditional R^2 (R^2_c) represents the proportion of variance explained considering both fixed and random effects. *T*-values <-2 and >2 indicate that the explanatory variable is a significant predictor of the response variable

Community characteristic		**Fixed effects**	**Estimate**	**Standard error**	***t*-value**	**R^2_m**	**R^2_c**
Density (100 m^{-2})	Saplings	Intercept	26.7	7.4	3.6	0.29	0.4
		COVER	10.5	3.9	2.7		
		FIRE	-48	16.1	-3		
	Adults	Intercept	5.4	0.5	11.4	0.2	0.39
		COVER	0.8	0.3	3		
Rarefied species richness	Saplings	Intercept	12.6	0.19	65.1	0.13	0.42
		COVER	1.1	0.4	3.03		
	Adults	Intercept	21.3	2	10.7	0.36	0.56
		COVER	4	1.1	3.7		
		FIRE	-11.2	4.4	-2.6		
Fisher's α	Saplings	Intercept	24.7	7	3.5	0.24	0.42
		COVER	8.9	3.5	2.5		
		ISOLATION	-7.9	3.2	-2.4		
		FIRE	-29.8	14.8	-2.009		
	Adults	Intercept	42.69	1.8	23.76	0.25	0.45
		COVER	15.5	3.33	4.65		
Community-weighted mean wood density (g cm^{-3})	Saplings	Intercept	0.7	0.02	41.9	0.06	0.37
		ISOLATION	0.01	0.006	2.05		
	Adults	Intercept	0.66	0.006	110	0.19	0.69
		COVER	0.03	0.01	3.56		
$_{log}$(Abundance-based dissimilarity)	-	Intercept	-0.2	0.04	-5.7	0.09	0.64
		D_{EDGE}	-0.06	0.02	-2.8		
$_{log}$(Incidence-based dissimilarity)	-	-	-	-	-	-	-

CHAPTER 4

Woody lianas increase in dominance and maintain compositional integrity across an Amazonian dam-induced fragmented landscape

A version of this chapter has been published as:

> *Jones, I.L., Peres, C.A., Benchimol, M., Bunnefeld, L., Dent, D.H. (2017) Woody lianas increase in dominance and maintain compositional integrity across an Amazonian dam-induced landscape. PLoS ONE 12(10): e0185527.*

Isabel Jones, Daisy Dent and Carlos Peres formulated the research ideas. IJ collected the data and performed analyses with advice from Lynsey Bunnefeld. Additional data were collected and contributed by Maíra Benchimol. All authors commented on draft versions of this manuscript, and the re-submitted version formatted for the thesis is presented here.

4.1 ABSTRACT

Tropical forest fragmentation creates insular biological communities that undergo species loss and changes in community composition over time, due to area- and edge-effects. Woody lianas thrive in degraded and secondary forests, due to their competitive advantage over trees in these habitats. Lianas compete both directly and indirectly with trees, increasing tree mortality and turnover. Despite our growing understanding of liana-tree dynamics, we lack detailed knowledge of the assemblage-level responses of lianas themselves to fragmentation, particularly in evergreen tropical forests. We examine the responses of both sapling and mature liana communities to landscape-scale forest insularization induced by a mega hydroelectric dam in the Brazilian Amazon. Detailed field inventories were conducted on islands created during reservoir filling, and in nearby mainland continuous forest. We assess the relative importance of variables associated with habitat fragmentation such as area, isolation, surrounding forest cover, fire and wind disturbance, on liana community attributes including abundance, basal area, diversity, and composition. We also explore patterns of liana dominance relative to tree saplings and adults ≥10 cm diameter at breast height. We find that 1) liana community composition remains remarkably similar across mainland continuous forest and islands, regardless of extreme area- and edge- effects and the loss of vertebrate dispersers in the latter; and 2) lianas are increasing in dominance relative to trees in the sapling layer in the most degraded islands, with both the amount of forest cover surrounding islands and fire disturbance history predicting liana dominance. Our data suggest that liana communities persist intact in isolated forests, regardless of extreme area- and edge-effects, while simultaneously, tree communities show evidence of increased turnover and supressed recruitment. These processes may lead to lianas becoming a dominant component of this dam-induced fragmented landscape in the future, due to their competitive advantage over trees in degraded forest habitats. Additional loss of tree biomass and diversity brought about through competition with lianas, and the concurrent loss of carbon storage, should be accounted for in impact assessments of future dam development.

4.2 INTRODUCTION

Fragmentation of primary tropical forests results in the loss of integrity of biological communities isolated in remnant forest fragments (Laurance *et al.* 2011; Benchimol & Peres 2015a; Haddad *et al.* 2015). Synergistic area- and edge-effects can lead to biodiversity loss, changes in community composition, and declines in ecosystem functioning of forest fragments (Haddad *et al.* 2015). Tropical forests are a global sink of atmospheric carbon (Pan *et al.* 2011). Yet once fragmented, remnant tree communities experience rapid turnover, significantly reducing the carbon storage potential of forest fragments (Laurance *et al.* 2006b). Lianas (woody vines) are well-adapted to the harsh environmental conditions associated with fragmented landscapes, and compete with trees at all life stages (Wright *et al.* 2015). Thus, through competition for resources with trees, lianas may intensify the loss of tree diversity and reduce carbon storage across fragmented landscapes (Schnitzer *et al.* 2014; van der Heijden *et al.* 2015). Few studies, however, have assessed the assemblage-level effects of forest fragmentation on lianas. Improving our understanding of liana assemblage responses to insularization is therefore essential to assess the long-term impacts of tropical forest fragmentation on forest composition and carbon storage (Laurance *et al.* 2001).

Lianas are ubiquitous in tropical forests, contributing to species diversity, ecosystem functioning and dynamics, forest architecture and arboreal connectivity (Putz 1984; Schnitzer & Bongers 2002). Lianas can comprise up to 44 % of woody species (Pérez-Salicrup, Sork & Putz 2001) and 10-45 % of woody stems present within tropical forest communities (Schnitzer 2005). Lianas compete with trees for light, water and nutrients (Wright *et al.* 2015), reducing tree reproduction, recruitment and diversity (Wright *et al.* 2005; Schnitzer & Carson 2010), growth and survival (Phillips *et al.* 2005; Ingwell *et al.* 2010). Studies from Panama have shown that the competitive strength of liana-tree interactions may be greater than that between trees (Tobin *et al.* 2012). Although all tree species may be affected by competition with lianas (Alvarez-Cansino *et al.* 2015), the effects are more detrimental to slow-growing shade-tolerant trees than fast-growing pioneer species, due to higher rates of crown infestation and physical damage (Ingwell *et al.* 2010; Schnitzer & Carson 2010). Lianas have a competitive advantage over trees in high light and low moisture conditions (Schnitzer & Bongers 2011), making them a common feature of degraded and secondary tropical forest habitats (DeWalt *et al.* 2000). Lianas have been found to arrest successional processes in forest gaps by stalling tree recruitment (Schnitzer *et al.* 2000), highlighting the profound effect lianas may have in determining future tree assemblages as tree communities respond to fragmentation through time.

Unlike trees, lianas do not channel resources into trunk diametric growth to reach forest canopies. Instead, they use trees as trellises and invest resources into rapid vertical growth and leaf production (Schnitzer & Bongers 2002; van der Heijden *et al.* 2013). Liana biomass is therefore lower than that of trees, and represents an estimated 4 % to 14 % of total forest above-ground biomass (Gerwing & Farias 2000; DeWalt & Chave 2004). Across the Neotropics, studies have shown that the abundance and biomass of lianas is increasing (Laurance *et al.* 2001; Phillips *et al.* 2002; Wright *et al.* 2004; Schnitzer & Bongers 2011). If slow-growing high-carbon-storing tree species are particularly impacted by liana proliferation, this may lead to a reduction in tropical forest carbon storage (Schnitzer, Bongers & Wright 2011; van der Heijden *et al.* 2013, 2015). Furthermore, because lianas allocate more carbon to leaf production than trunk growth, increasing liana abundance and biomass could shift the carbon balance in tropical forests from long-term carbon sequestration in woody biomass, towards more rapid turnover in leaves (van der Heijden *et al.* 2015). An increase in litterfall from lianas may also accelerate below-ground carbon cycling through priming effects, further reducing total carbon storage within tropical forests (Sayer *et al.* 2011).

Primary tropical forests are becoming increasingly fragmented and degraded due to deforestation and land-use change (FAO 2016). The flooding of tropical forests for hydropower is an emerging driver of tropical forest fragmentation and degradation (Zarfl *et al.* 2015; Lees *et al.* 2016). Tropical dams are controversial in terms of the area of land flooded and significant greenhouse gas emissions from reservoirs (Fearnside & Pueyo 2012), pervasive loss of species from reservoir islands (Jones *et al.* 2016), and inadequate carbon cost/benefit analyses (Zarfl *et al.* 2015). During reservoir filling, tropical forest habitat becomes isolated on land-bridge islands within an open-water matrix, leading to the most extreme scenario in terms of fragmentation effects (Terborgh *et al.* 2001; Gibson *et al.* 2013; Mendenhall *et al.* 2014; Benchimol & Peres 2015a; b). All reservoir land-bridge islands, regardless of their area, exhibit long-term species loss, but rates are higher on small islands which pay their extinction debts faster (Jones *et al.* 2016). Tropical forest tree communities isolated on reservoir land-bridge islands undergo rapid compositional change, with functional shifts, declines in abundance of many species, and local extinctions (Leigh *et al.* 1993; Terborgh *et al.* 2001; Yu *et al.* 2012; Benchimol & Peres 2015a). Loss of biotic seed dispersal due to diminished vertebrate communities may further alter future floristic composition and carbon storage potential of insular tree assemblages (Cramer *et al.* 2007; Markl *et al.* 2012).

In this study, we explore community-wide liana responses to landscape-scale fragmentation induced by the Balbina mega-dam in Central Brazilian Amazonia. We consider both sapling and mature lianas, and investigate a number of metrics including liana abundance, basal area, dominance relative to trees, and seed dispersal mode, as well as diversity and community composition. We relate these community attributes to environmental variables widely associated with fragmented systems at plot-, site-, and landscape-scales including island area, isolation, surrounding forest cover, and degree of fire and wind disturbance.

Given the propensity for lianas to establish in degraded habitats, we hypothesise that 1) both sapling and mature lianas will increase in abundance, basal area, and dominance relative to trees in the most disturbed island habitats, where synergistic area- and edge-effects are most pronounced. This is in contrast to tree communities on islands, which have rapidly eroded across the Balbina archipelago (Benchimol & Peres 2015a). When considering the sapling layer we also expect that 2) the abundance of vertebrate-dispersed lianas will be lower in disturbed habitats due to the loss of biotic seed dispersal capacity caused by widespread local extinctions of animal seed dispersers (Benchimol & Peres 2015b). As edge-and area-effects become less pronounced, such as when island area is greater and fire disturbance lower, forest communities appear to more closely resemble those found in mainland continuous forest (Benchimol & Peres 2015a; b). Thus, we expect that 3) the diversity and community composition of lianas will converge with those of mainland continuous forest as area- and edge-effects diminish.

4.3 METHODS

4.3.1 Study site

The Balbina Hydroelectric Dam in Central Amazonia (1°010 – 1°550 S; 60°290 – 59°280 W) was closed in 1986, flooding ~3129 km^2 of lowland primary wet tropical forest, creating 3546 forest islands within the reservoir, ranging in size between 0.2 and 4878 ha (Benchimol & Peres 2015a; b). These forest islands have never been logged, and both the islands and the mainland extending east of the former Uatumã River bank are strictly protected as part of the Reserva Biológica do Uatumã, the largest biological reserve in Brazil. Such measures have largely prevented subsequent anthropogenic disturbance. However, in 1997 a fire was accidentally started in the unprotected portion of the Balbina reservoir, which spread between some islands; mainland continuous forest areas were unaffected.

We selected 36 spatially-independent focal islands, and three widely-spaced mainland continuous forest sites adjacent to the archipelago (Fig 1) using two cloudless georeferenced Landsat ETM+ scenes from 2009 (230/061 and 231/061). Islands were selected on the basis of their size (0.83-1690 ha; mean ± SD = 210.7 ± 392.1), isolation, i.e., distance to the nearest mainland (0.04-17.73 km; mean ± SD = 4.9 ± 4.4), spatial distribution (keeping a minimum distance of 1 km from one another), and to span the gradient of fire severity. In 2011, one to four 0.25 ha (10 m x 250 m) rectangular permanent plots were established on 34 forest islands and in all three mainland continuous forest sites, creating a preliminary network of 87 forest plots. In 2014, one additional 0.25 ha plot was established on each of two small islands (< 10 ha) bringing the total number of permanent plots to 89: 77 plots are nested within 36 islands, and 12 plots are nested within three mainland continuous forest sites surrounding the reservoir (Fig. 4.1).

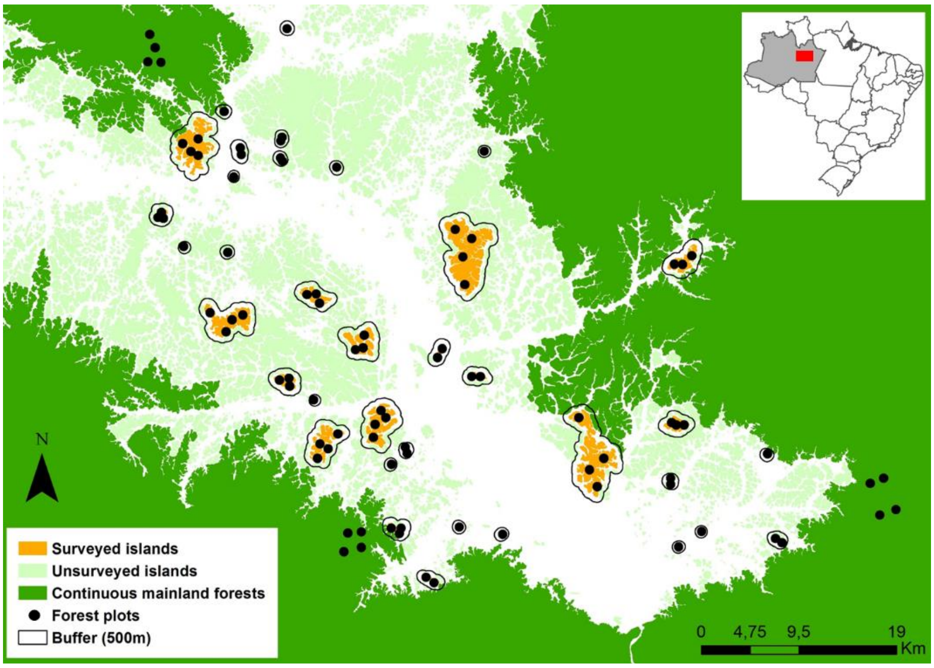


Fig. 4.1. Location of permanent census plots within the Balbina Hydroelectric Dam (Amazonas, Brazil). The 89 permanent plots are nested within 36 spatially-independent islands and in three continuous mainland forest sites. The percentage of forest cover ('COVER') within each 500 m buffer was used as one of seven ecologically-relevant variables used within analyses of liana assemblages. [Map created by M. Benchimol].

4.3.2 Liana and tree inventories

We performed surveys to record both saplings and mature woody lianas, and sapling and adult trees ≥10 cm diameter at breast height (DBH, ~130 cm). In 2014, woody liana saplings ≤2 cm diameter and ≥1 m height were recorded within 0.025 ha (1 m × 250 m) subplots, which followed the central axis of each of the 89 permanent plots. In 11 of the 89 plots, a reduced area was sampled for saplings (0.015-0.02 ha) compared to the standard 0.025 ha. No saplings had reached the forest canopy. Saplings were identified to genus level by A.E.S. Santos, an expert botanist with >20 years of herbarium and field experience working in Central Amazonia, and extensive experience of the Balbina woody flora (Benchimol & Peres 2015a). We broadly classified liana genera by dispersal mode (either biotically- or abiotically-dispersed) by assessing morphological characteristics of fruits and seeds associated with dispersal, from the literature and personal observation of A.E.S Santos and the co-authors. For example brightly coloured fleshy fruits tend to be biotically-dispersed, whereas dry capsules or winged seeds tend to be abiotically-dispersed (Gentry 1993; Cornejo & Janovec 2010). Tree sapling abundances were also obtained for each of the 89 0.025 ha sapling subplots in 2014, using the same survey method employed for liana saplings. Sapling surveys were carried out under permit No. 45849 issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA).

In 2012, lianas ≥2.5 cm DBH were recorded within 87 of the 89 0.25 ha plots, following the measurement protocols of (Gerwing *et al.* 2006). As 80% of lianas ≥2.5cm diameter are likely to have reached the forest canopy, we refer to these as 'mature lianas' (Kurzel, Schnitzer & Carson 2006). Mature lianas were not identified. During the same 2012 survey period, all live adult trees ≥10cm DBH were inventoried within the 0.25 ha plots. Adult trees ≥10cm DBH were identified to species-level by A.E.S. Santos, and by identification of voucher specimens at the National Institute for Amazon Research (INPA). Full details of adult tree inventories are presented in (Benchimol & Peres 2015a).

4.3.3 Liana community attributes

We investigated six ecological attributes related to liana communities at the plot-scale: 1) abundance, 2) basal area, 3) proportion of biotically- vs. abiotically-dispersed individuals, 4) dominance relative to trees, i.e. abundance of lianas : abundance of trees (e.g. Phillips *et al.* 2002), 5) liana genera diversity and 6) community composition. Diameter measurements were used to calculate the basal area of mature lianas ($Ba(m^2) = pi \times \frac{DBH(cm)^2}{4000}$) which were summed to give plot-level estimates. Taxonomic information was only available for liana saplings, therefore analyses of seed dispersal mode, diversity and community composition were conducted only for this size class. To compare liana community diversity among plots, we calculated Fisher's α diversity values, as Fisher's α is a robust metric of assemblages with varying numbers of individuals (DeWalt *et al.* 2000).

4.3.4 Environmental variables

We used and processed 28 tiles of Rapid-Eye© high-resolution (5 m pixel) imagery covering an area of 698,000 ha of the Balbina landscape to quantify seven ecologically important environmental variables at the scale of whole landscapes, sites and individual plots that were identified as potentially important drivers of observed patterns of sapling and mature liana communities (see Benchimol & Peres (2015a) for more details). Following a semi-supervised image classification using ArcMap (ESRI 2011), we obtained four land cover classes (closed-canopy forest, open-canopy forest, bare ground, and water) across the landscape. Thus, at the landscape-scale, we derived estimates of the percentage of forest cover ('COVER', %) within a 500 m buffer extending from the perimeter of each island and mainland sites, considering the sum of both closed-canopy and open-canopy forests. COVER provides a measure of landscape connectivity, encompassing both the degree of isolation from, and extent of, surrounding forested habitat.

At the site-scale, we used island area ('AREA', in hectares), obtained by calculating the total area of each island (i.e. ArcGIS polygon). We also calculated site isolation as the shortest linear distance from the perimeter of a focal island to continuous mainland forest ('ISOLATION', metres), which together with area is central to the island biogeography paradigm (MacArthur & Wilson 1967; Lomolino 2000). The extent to which fires have penetrated the forest understorey of each site ('FIRE') was defined as an ordinal factor with scores of 0-3. No mainland continuous forest sites had been burned (score 0), but all islands had been burned to different extents (scores 1-3).

Finally, at the plot-scale, we obtained the distance to the nearest edge ('D_{EDGE}', metres), which was calculated as the mean shortest linear distance between each census plot and the forest edge, and provides information on how close plots are to the forest-water boundary where the impacts from edge-effects are most severe. Balbina experiences powerful convective windstorms, which have a known prevailing direction. We therefore used the angular difference (0-90°) between the main axis of each rectangular plot and the median prevailing windstorm direction ('WIND'), where higher WIND values indicate that the prevailing wind direction is increasingly perpendicular to plots. Windstorms that hit plots along their entire length are thought to cause more structural disturbance across a greater area of the plot, potentially driving patterns of liana abundance and diversity. As terrain steepness can influence rates of species turnover and the variety of edaphic niches present (DeWalt & Chave 2004), we obtained a measure of plot-scale topographic heterogeneity by calculating the difference in maximum and minimum elevation using Shuttle Radar Topography Mission - SRTM - raster data ('SLOPE', metres).

4.3.5 Data analysis

Liana community attributes

All analyses were conducted using 'R' (version 3.3.2 (R Core Team 2016)). We initially tested for overall differences in liana community attributes (abundance, basal area, seed dispersal mode, dominance relative to trees, and diversity) between islands and mainland sites using one-way ANOVAs.

The effects of environmental drivers on liana community attributes across the Balbina archipelago were explored using both linear mixed models (LMMs) and generalised linear mixed models (GLMMs) to account for a nested sampling design ('lmer' and 'glmer' within the 'lme4' R package; Bates *et al.* 2015). Prior to analysis, all continuous environmental variables were rescaled (centred and divided by two standard deviations (Schielzeth 2010)), using the 'rescale' function within the 'arm' R package (Gelman & Su 2016), to enable comparison of the relative effect sizes of each environmental variable on response variables.

Abundance data were modelled using a GLMM with Poisson error structure (link = "log"). Relative dominance and the proportion of biotically- vs. abiotically-dispersed stems were modelled using binomial GLMMs (link = "logit"), to enable the data to be modelled while accounting for sample size. Basal area and Fisher's α values were log-transformed and modelled using a LMM with a Gaussian error structure. All regression analyses included only island plots, both because any potential mainland/island effect is confounded with FIRE (all islands had been burned to some degree while none of the mainland sites had been burned), and to avoid assigning arbitrary values for AREA and ISOLATION for mainland continuous forest sites, which may have artificially influenced model fits.

Before fitting each model, a pair-wise correlation matrix was inspected. If any pair of environmental variables showed high co-linearity (r >0.7; Pearson's correlation coefficient) then one variable from the pair was removed from the model. Additionally, variance inflation factors (VIFs) for each variable were inspected for each model, with variables retained if VIF <4 (Zuur *et al.* 2010). D_{EDGE} was consistently highly correlated with AREA, and failed to enhance the amount of variance explained, so was excluded from all linear regressions. All full models included AREA, ISOLATION, COVER, WIND, SLOPE, and FIRE as fixed effects. SLOPE was not included in models investigating seed dispersal mode, as it was deemed negligibly biologically meaningful in determining the proportion of biotically- vs. abiotically-dispersed stems within plots.

The 77 island plots were nested within 36 islands, thus, 'island' was fitted as a random effect to account for potential pseudo-replication of plots on the same island. 'Sampling area' was also fitted as a random effect to account for potential variation arising from the different areas sampled in a small number of plots. If there was no difference in effect between two levels of burn severity, the two levels in question were collapsed creating a binary FIRE variable. If there was no difference in effect among all three levels of FIRE, all islands were effectively equal in terms of the burn severity effect, and FIRE was removed from the model. Full models were simplified through stepwise deletion of non-significant terms (t-value >2 or <-2) and inspection of AIC values (Burnham & Anderson 2002), and the best model confirmed by inspecting both AIC and AIC weight after model selection performed in the 'MuMin' R package (Barton 2016). To ascertain the relative importance of each environmental variable on response variables, coefficient estimates for each environmental variable were extracted from full models, and 95 % confidence intervals were calculated.

Community composition

To determine if island and mainland sites were spatially auto-correlated, a Mantel test was performed on two dissimilarity matrices of pair-wise distances between islands and mainland sites, using Euclidean geographic distance and Hellinger-transformed species composition (Legendre, Fortin & Borcard 2015; Oksanen *et al.* 2016).

The degree of community composition similarity between island and mainland plots was visually inspected using non-metric multidimensional scaling (NMDS) ordination (Anderson *et al.* 2011). We performed unconstrained NMDS ordinations of liana genera within plots using two indices: the abundance-based Morisita-Horn dissimilarity index, which is particularly suited to communities that may have been insufficiently sampled (Chao *et al.* 2006), and the incidence-based Jaccard dissimilarity index. We then performed further abundance- and incidence-based ordinations excluding mainland plots, to explore potential patterns in community dissimilarity among island plots. We fitted the rescaled environmental variables used in the regression analyses to ordinations of island plots, and retained variables that were significant (P <0.05) in explaining plot positions within ordination space. All NMDS was performed using 'metaMDS' within the 'vegan' R package (Oksanen *et al.* 2016).

We used permutational multivariate analysis of variance (perMANOVA) to statistically test for differences in abundance- and incidence-based community composition across all island and mainland plots, while accounting for our nested sampling design. perMANOVA was also used to assess the relative importance of site- and landscape-scale environmental variables in driving differences in abundance- and incidence-based community composition among island plots. To obtain significance values for individual environmental variables, variables were added sequentially to different models, and the significance reported is the value generated when the corresponding variable was added last. perMANOVA was performed using 'adonis' within the 'vegan' R package (Oksanen *et al.* 2016).

4.4 RESULTS

4.4.1 Liana inventories

A total of 2,688 liana saplings belonging to 31 genera were recorded across the 89 0.025-ha subplots (S4.1). Of the 31 genera, 16 were biotically-dispersed (1,016 stems), and 15 abiotically-dispersed (1,850 stems; S4.2). The number of stems per genus ranged from 1 to 553 (mean = 93); five genera were represented by singletons. Between 9 and 78 liana saplings representing 3 to19 genera were recorded in each subplot. Some 40 % of liana saplings (*N* = 1,105) belonged to two abiotically-dispersed genera, *Macherium* (Fabaceae) and *Memora* (Bignoniaceae). A total of 2,261 mature lianas were recorded, with between 0 and 69 individuals recorded per 0.25 ha plot (S4.1). Mature lianas were not present in two plots located on small (< 10 ha) islands. The majority of mature lianas (78 %, *N* = 1,766) ranged between 2.5 and 10 cm DBH.

4.4.2 Liana community attributes

There was no overall difference between liana sapling abundance in island vs. mainland plots (S4.3), and among island plots, abundance was not significantly related to any environmental variables (Fig. 4.2a). The abundance of mature lianas was, however, significantly lower on islands compared to the mainland (Fig. 4.3; S4.3). On islands, the abundance of mature lianas was significantly reduced in severely burned areas and when terrain was steeper, but increased with higher levels of COVER (Fig. 4.2b and Fig. 4.4a; Table 4.1). The total basal area of mature lianas did not significantly differ between islands and the mainland (S4.3), nor did it vary among island plots (Fig. 4.2c). There was also no overall difference in the proportion of biotically- vs. abiotically-dispersed stems between islands and the mainland (S4.3), or among islands (Fig. 4.2d).

There was no significant difference in the dominance of liana saplings relative to tree saplings in islands vs. mainland plots (S4.3). However, liana saplings were significantly more dominant than tree saplings in severely burned island plots, and significantly less dominant where neighbouring forest cover was greater (Fig. 4.2e and Fig. 4.4b; Table 4.1). The dominance of mature lianas relative to trees ≥10 cm DBH was significantly lower on islands compared to mainland plots (S4.3). On islands, mature lianas became increasingly dominant relative to trees in more forested landscapes (Fig. 4.4c; Table 4.1), and significantly less dominant in plots with steeper slopes that experienced a history of severe fires (Fig. 4.2f; Table 4.1). Liana diversity (Fisher's α) at the genus level was not significantly different between island and mainland plots (S4.3), but liana diversity significantly declined in more isolated islands (Fig. 4.2g; Table 4.1).

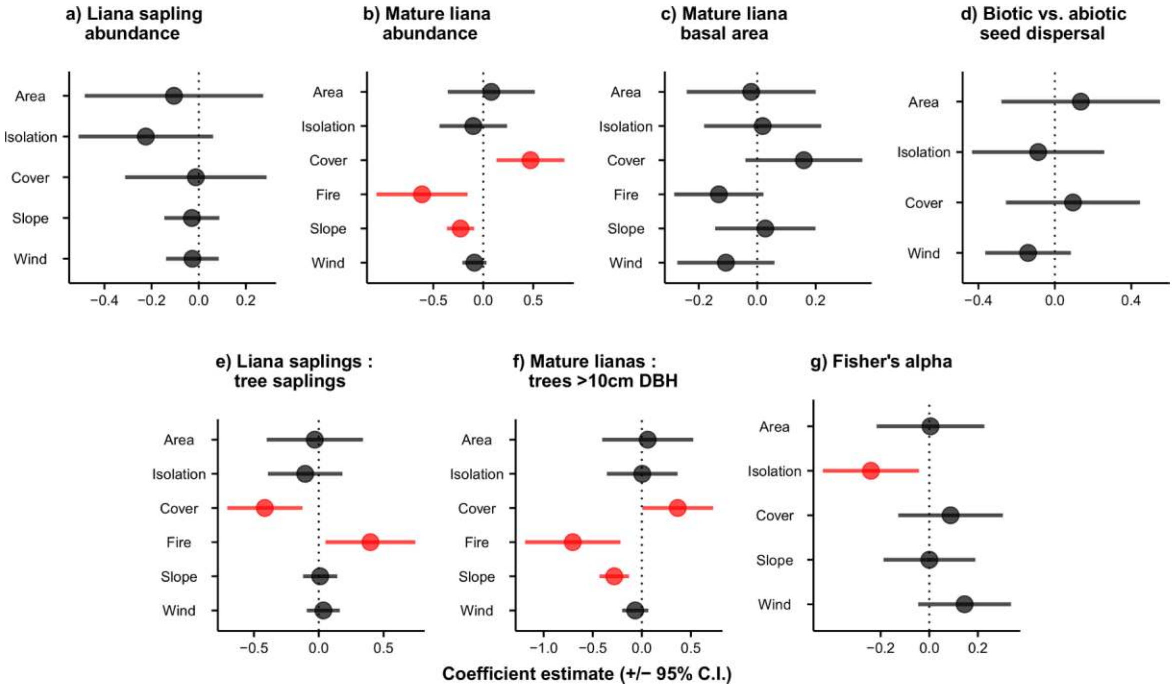


Fig. 4.2: Standardised effect sizes of environmental variables associated with sapling and mature liana communities on forest islands. Coefficient estimates from maximal models are plotted with 95 % confidence intervals. Points in red indicate that coefficient estimates and confidence intervals do not overlap zero.

Table 4.1. Model selection table of the most parsimonious model for different attributes of woody liana communities across 77 island plots, based on LMMs or GLMMs. Coefficient estimates for significant fixed effects within 'best models', with 'site' and 'sampling area' as random effects, are presented; *t*-values >2 or <-2 were treated as significant. AICc values and AICc weights of final models are presented. Dashes indicate a lack of any significant predictors.

Community characteristic	**Fixed effects**	**Estimate**	**Standard error**	***t*-value**	**AIC$_c$**	**AIC$_c$ weight**
Abundance of liana saplings	-	-	-	-	-	-
Abundance of mature lianas	Intercept	3.16	0.08	32.45	651.3	0.43
	COVER	0.49	0.16	3.01		
	SLOPE	-0.23	0.07	-3.28		
	FIRE	-0.65	0.24	-2.7		
Total basal area of mature lianas	-	-	-	-	-	-
Proportion of biotic vs. abiotically dispersed stems	-	-	-	-	-	-
Relative dominance of liana saplings	Intercept	-1.38	0.08	-16.97	583.0	0.64
	COVER	-0.44	0.13	-3.32		
	FIRE	0.4	0.17	2.22		
Relative dominance of mature lianas	Intercept	-1.67	0.1	-16.34	641.7	0.59
	COVER	0.38	0.17	2.28		
	SLOPE	-0.28	0.08	-3.65		
	FIRE	-0.6	0.22	-2.89		
Fisher's α	Intercept	1.58	0.05	33.01	97.0	0.82
	ISOLATION	-0.23	0.09	-2.49		

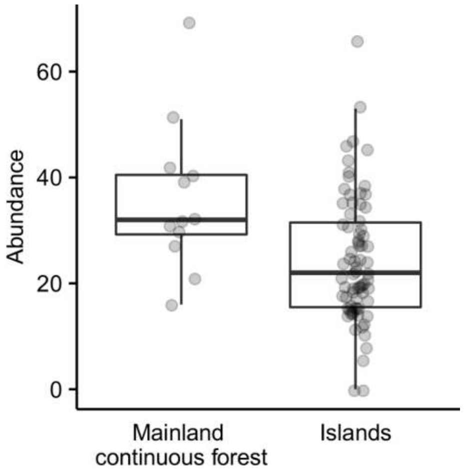


Fig. 4.3: Abundance of mature lianas within island and mainland forest plots. Circles represent total numbers of mature lianas within each surveyed plot.

4.4.2 Community composition

Mantel tests showed that island and mainland sites were not spatially auto-correlated, as dissimilarities in liana community composition were not significantly related to geographic distances among island and mainland sites (r = 0.07, *P* = 0.18). Both abundance- and incidence-based NMDS ordinations indicated that there was no obvious pattern of convergence in community composition between larger islands (where area- and edge-effects are thought to be weakest) and mainland sites (Fig. 4.5a, b). When environmental descriptors of island plots were considered, AREA and FIRE were the only significant predictors ($P<0.05$) in abundance-based ordinations, and AREA and ISOLATION were significant ($P<0.05$) in incidence-based ordinations. However perMANOVA analyses, accounting for our nested sapling design, revealed that there was no significant difference between the community composition of island and mainland plots for both abundance- and incidence-data (S4.4). Similarly, when exploring community composition among island plots, perMANOVA analyses did not reveal any significant environmental predictors for either abundance- or incidence-based compositions (S4.4).

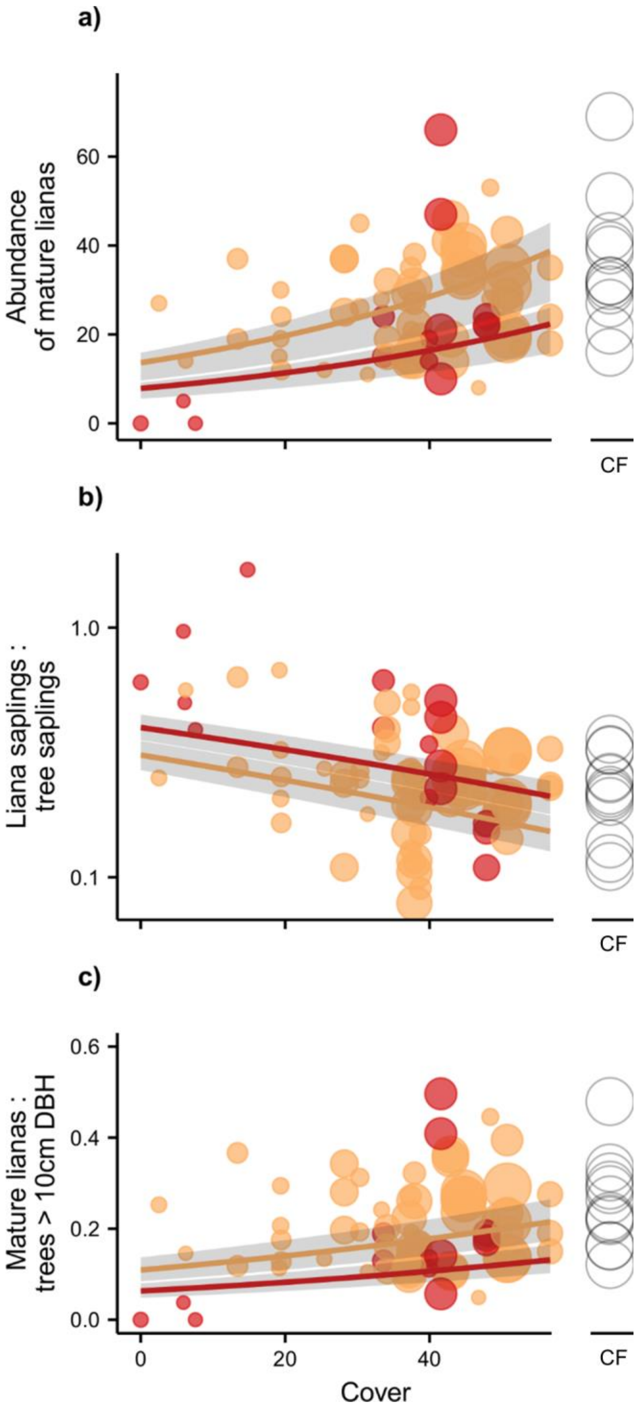


Fig. 4.4: Abundance and relative dominance of lianas. The (a) abundance, (b) relative dominance of liana saplings to tree saplings, and (c) relative dominance of mature lianas to trees ≥10 cm DBH, as a function of the amount of neighbouring forest cover. Plot-level data are plotted as circles, scaled in size by island area. In each case a binary FIRE variable was used, where low-moderate burn severity (scores 1 and 2; orange circles) were collapsed into a single level and compared to severe burning (score 3; red circles). Lines are predicted values, with grey shading indicating 95 % confidence intervals. Data for mainland continuous forest plots (CF; open circles) were not included in model fits but are shown here for comparison.

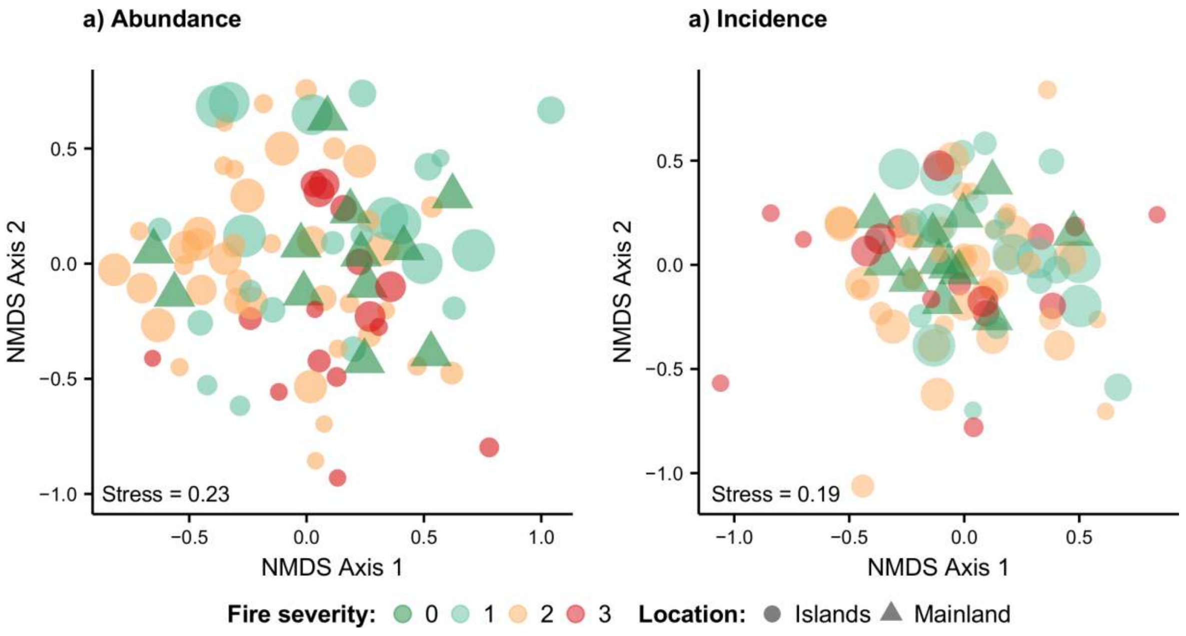


Fig 4.5: NMDS ordination of liana sapling communities. NMDS ordination of all island and mainland continuous forest plots using (a) the abundance-based Morisita-Horn dissimilarity index, and (b) the incidence-based Jaccard dissimilarity index. Plotted circles are scaled by island area. Points are colour-coded by burn severity: 0 = no burn, 1 = light burn, 2 = moderate burn, and 3 = severe burn. The proximity of plotted points indicates the degree of similarity between communities.

4.5 DISCUSSION

We investigated community-wide liana responses to landscape-scale forest fragmentation induced by a mega-dam, and our results demonstrate that liana communities remain remarkably intact despite insularization caused by reservoir filling. Our results also suggest that because there are more lianas than trees in the sapling layer on small, severely burned islands with little surrounding forest cover, lianas may be able to recruit more readily than trees in the most degraded habitats. Therefore as pervasive area- and edge-effects continue to act upon remnant forest isolates, future forest communities are likely to be increasingly dominated by lianas, with negative implications for tree community diversity and function. We propose that our findings provide further evidence of negative long-term biodiversity and carbon storage impacts of forest fragmentation induced by an Amazonian mega-dam.

Increased dominance of young lianas in degraded forest sites

We found that recruitment of lianas into the sapling community appeared higher than recruitment of tree saplings in the most degraded insular forest habitats, and that lianas did not exhibit any evidence of community collapse across the Balbina archipelago. Liana compositional profiles remained remarkably consistent across both insular and continuous forest sites, in contrast to a rapidly eroding tree community (Benchimol & Peres 2015a). Such a pattern suggests that lianas will likely become a dominant feature of reservoir land-bridge islands in the long term, and that liana communities appear to be robust to many of the negative impacts associated with landscape-scale habitat fragmentation (Murcia 1995; Ries *et al.* 2004). A compositionally intact liana community could potentially exacerbate the erosion of remnant tree communities through direct and indirect competition (Schnitzer, Kuzee & Bongers 2005; Tobin *et al.* 2012; van der Heijden *et al.* 2015). Even in forest fragments embedded within a terrestrial habitat matrix, liana proliferation severely impacts tree communities and reduces carbon storage (Magnago *et al.* 2016). Given that reservoir land-bridge islands are the worst-case scenario in terms of fragmentation effects on remnant taxa (Jones *et al.* 2016), liana-induced reductions in tree diversity and carbon storage will likely be even more severe on islands than observed for forest fragments in a terrestrial landscape.

The dominance of liana saplings relative to tree saplings was elevated on small (< 10 ha) islands with low surrounding forest cover, particularly when fire disturbance was high, where lianas could apparently recruit more successfully than trees. Our findings are in line with previous studies where liana recruitment increased markedly in degraded forest fragments, edges and gaps, compared to tree recruitment (Schnitzer *et al.* 2000; Laurance *et al.* 2001; Benítez-Malvido & Martínez-Ramos 2003). However, the apparent increase in liana saplings relative to tree saplings appears to be the product of a decline in tree sapling recruitment, as liana sapling abundances remained largely consistent across island and mainland sites, indicating that tree saplings rely on higher quality forest in order to recruit successfully (Benítez-Malvido & Martínez-Ramos 2003). Nevertheless, successful recruitment of lianas in highly degraded islands will likely continue due to their competitive ability to establish in, for instance, the high light regimes associated with low-stature forests and higher density of canopy gaps as remnant forests continue to degrade (Gerwing &

Farias 2000; Schnitzer *et al.* 2000; Benítez-Malvido & Martínez-Ramos 2003). Tree communities on small Balbina islands are structurally degraded and have reduced diversity (Benchimol & Peres 2015a). Thus, liana recruitment will doubtless continue to increase relative to tree recruitment as island time increases, leading to highly liana-dominated forest communities in the future. Repeated surveys of the sapling layer would be needed to thoroughly investigate recruitment rates, as our study provides a snapshot of floristic communities ~30 years after island creation.

Influence of forest cover and fire severity on mature lianas

In contrast to the sapling layer, we found that there were significantly fewer mature lianas on islands compared to the mainland, yet their total basal area did not significantly differ. The abundance of mature lianas also declined with fire severity, and increased with the amount of forest habitat surrounding islands. Such patterns indicate that low mature liana abundances on islands have been induced by a rapid turnover, and even loss, of canopy trees (Benchimol & Peres 2015a). Lianas rely on large trees for structural support, and thus the abundance of mature lianas is lower in insular tree communities that have been most impacted by area- and edge-effects, and no-longer support tall closed-canopy forests (Benchimol & Peres 2015a; Poulsen *et al.* 2016). As forest quality and vertical structure continues to decline across islands, we may therefore see concurrent degradation of the mature liana community in the long-term. However, lianas often circumvent the problem of loss of structural support through their ability to grow horizontally or along the ground (Schnitzer & Bongers 2002). Even high-climbing lianas can form low-lying tangles after their host trees fall, which continue to expand without the need for structural support from trees. Mature lianas will therefore likely persist across even the most degraded islands, further suppressing tree regeneration through competition (Schnitzer *et al.* 2000; Schnitzer & Carson 2010).

The lower abundances of mature lianas on islands may also result from potential under-sampling of the mature liana community, as our sampling methodology only considered lianas growing vertically. On islands, where lianas lack sufficient trees for vertical growth, we may have under-estimated the abundance of mature lianas forced to grow horizontally or along the ground. This limitation also extends to under-sampling of non-vertical liana saplings. Yet even considering this potential under-sampling of liana saplings, we find strong evidence for increased recruitment of lianas into the sapling layer compared to trees on small and highly disturbed islands. We suggest that our evidence for heightened liana sapling recruitment and persistence of mature lianas, will continue to impact recruitment of both pioneer and shade-tolerant tree species on highly disturbed islands (Tobin *et al.* 2012; de Campos Franci *et al.* 2016).

Long-term persistence of lianas on semi-defaunated islands

The long-term persistence of lianas across this fragmented landscape may be further enhanced by the ability of vertebrate-dispersed lianas to persist, even in small semi-defaunated islands (Benchimol & Venticinque 2014; Benchimol & Peres 2015b; c; Aurélio-Silva *et al.* 2016). There was no significant difference in the proportion of biotically- vs. abiotically-dispersed stems found on islands compared to mainland sites, but most lianas surveyed were represented by two wind-dispersed genera. Liana communities may therefore shift towards being dominated by abiotically-dispersed genera over time, but the ability for biotically-dispersed lianas to reproduce vegetatively may temper this shift (Gerwing 2004). In contrast, studies have demonstrated that biotically-dispersed trees show significant declines through habitat fragmentation and loss of vertebrate dispersers (Cramer *et al.* 2007), and in Balbina, biotically-dispersed trees have been strongly affected by fire disturbance across the archipelago (Benchimol & Peres 2015a). The persistence of liana assemblages in the aftermath of landscape-scale fragmentation, and loss of vertebrate dispersers, is echoed by similarities in liana diversity between island and mainland sites. Although liana diversity declined in increasingly isolated islands, the most distant islands exhibited patterns of diversity within the range of mainland sites.

Similarity of liana community composition among islands and mainland continuous forest

Despite diverse disturbance regimes, island and mainland plots have remarkably consistent liana community compositions. Again, this is in stark contrast to, for example, the adult tree community within Balbina, which has undergone drastic compositional shifts due to area- and edge-effects (Benchimol & Peres 2015a). The absence of any clear patterns of liana community composition related to area, isolation and fire disturbance could be due to low taxonomic resolution, as we only identified lianas to the level of genus (Henle *et al.* 2004; Ewers & Didham 2006). However when genus-level information for tree saplings was used in comparable analyses, we found that tree saplings displayed strikingly different responses, such as significant increases in diversity with island area, and clear separation of community composition between the most highly disturbed islands and mainland continuous forest sites, following similar patterns seen at species-level (Benchimol & Peres 2015a). We therefore conclude that the observed similarities of liana community compositions are 'true' patterns, rather than artefacts of low taxonomic resolution.

Drivers of liana assemblage responses to insularization

Given that the species richness and functional diversity of adult tree assemblages in Balbina significantly increased with island area (Benchimol & Peres 2015a), we expected that area would be similarly influential in predicting the community attributes and composition of lianas across this fragmented landscape, through species-area effects (Triantis, Guilhaumon & Whittaker 2012). Instead, the amount of forest habitat surrounding isolates, and historical fire disturbance, acted synergistically as the strongest drivers determining the abundance and dominance of lianas relative to trees (Gerwing 2002; Barlow & Peres 2008; Fahrig 2013). In studies of liana communities in forest fragments embedded within a terrestrial matrix, historical forest disturbance was also an important driver of liana abundance and diversity, as was distance to forest edges and soil properties (Laurance *et al.* 2001, 2014a).

4.5.1 Conclusions

We show that liana communities persist across a man-made archipelagic landscape, and increase in abundance and dominance relative to trees in both sapling and mature size classes. Diversity and community composition of lianas were apparently relatively unaffected by insularization, and there were no compositional differences between island and mainland forest sites. We stress that given the continuing decline of tree communities on hydroelectric reservoir land-bridge islands (Benchimol & Peres 2015a; Jones *et al.* 2016), a persistent liana community will likely exacerbate the degradation of remnant tree communities through direct and indirect competition in the long term (Tobin *et al.* 2012; Pasquini *et al.* 2015; Wright *et al.* 2015). Declines in remnant tree communities not only impact faunal populations (Benchimol & Peres 2015c), but also the carbon cost/benefit calculations of dams (Kareiva 2012). Dams in lowland tropical forest regions are controversial in terms of their net carbon budget, in which losses are not always offset by their 'green energy' production (Fearnside 2002a; Scherer & Pfister 2016). Reservoir islands are not currently accounted for in environmental impact assessments of new dam proposals (Trussart *et al.* 2002; International Energy Agency 2006), and declines in both the biodiversity value and carbon storage capacity of reservoir islands could be exacerbated by elevated liana abundance and dominance relative to trees (Schnitzer & Bongers 2011).

4.6 ACKNOWLEDGEMENTS

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S4 SUPPLEMENTATARY INFORMATION

S4.1: Overview of lianas and trees inventoried. Number of sapling and mature lianas, number of liana genera, and number of tree saplings and adults within all 89 plots inventoried across 36 islands and three mainland continuous forest sites across the Balbina Hydroelectric Dam landscape (Brazilian Amazon). NS = not surveyed.

Island	Area (ha)	Plot number	Number of liana saplings	Number of liana sapling genera	Number of mature lianas	Number of tree saplings	Number of adult trees
Abandonada	0.65	1	14	8	NS	27	14
Toquinho	0.83	1	29	5	5	30	14
Joaninha	1.15	1	16	7	0	41	21
Xibé	1.45	1	27	13	8	130	57
Formiga	1.52	1	9	3	14	16	10
Andre	2.17	1	12	6	11	67	38
Lozivaldo	2.39	1	70	17	NS	41	10
Cafundó	2.7	1	10	6	23	44	24
Panema	3.53	1	30	10	12	110	40
Torem	3.94	1	26	10	0	43	27
Pé Torto	5.85	1	50	11	15	74	36
Jiquitaia	7.28	1	23	8	27	92	50
Arrepiado	8.35	1	30	8	28	95	43
Garrafa	9.54	1	28	5	17	96	48
Abusado	13.41	1	24	10	30	116	57
Abusado	13.41	2	34	12	19	105	50
Piquiá	13.59	1	64	15	16	133	39
Piquiá	13.59	2	76	14	21	138	57
Coatá	17.45	1	25	10	28	138	62
Coatá	17.45	2	36	9	53	128	67
Palhal	21.21	1	15	6	14	44	27
Palhal	21.21	2	11	7	19	53	23
Neto	32.92	1	49	12	26	184	71
Neto	32.92	2	31	10	45	125	61
Bacaba	53.3	1	25	10	12	99	48
Bacaba	53.3	2	19	10	24	115	43

Relógio	72.1	1	45	7	37	71	32
Relógio	72.1	2	21	8	19	76	39
Sapupara	78.44	1	15	7	18	117	54
Sapupara	78.44	2	39	12	35	143	71
Adeus	97.62	1	51	9	15	83	44
Adeus	97.62	2	54	14	24	136	72
Moita	98.84	1	18	9	20	87	50
Moita	98.84	2	23	8	17	154	64
Moita	98.84	3	15	4	15	166	61
Pontal	110.43	1	41	12	38	158	81
Pontal	110.43	2	34	11	18	163	66
Pontal	110.43	3	18	7	27	156	70
Furo de Santa Luzia	193	1	36	9	18	110	62
Furo de Santa Luzia	193	2	39	9	35	171	68
Furo de Santa Luzia	193	3	35	10	24	149	65
Cipoal	218.74	1	56	9	32	143	61
Cipoal	218.74	2	68	14	15	136	67
Cipoal	218.74	3	56	9	19	162	78
Jabuti	231.39	1	21	6	22	128	53
Jabuti	231.39	2	21	9	22	137	61
Jabuti	231.39	3	21	7	24	192	76
Tucumari	292.41	1	9	4	37	82	52
Tucumari	292.41	2	20	7	37	84	53
Tucumari	292.41	3	27	13	25	105	46
Martelo	471	1	30	9	29	155	64
Martelo	471	2	16	5	27	112	65
Martelo	471	3	21	10	43	108	45
Tristeza	487.5	1	42	10	10	96	41
Tristeza	487.5	2	64	14	21	125	65
Tristeza	487.5	3	49	15	47	216	74
Tristeza	487.5	4	45	11	66	161	63
Beco Catitu	637.49	1	31	12	29	158	65
Beco Catitu	637.49	2	44	16	15	175	54
Beco Catitu	637.49	3	22	8	15	92	54
Beco Catitu	637.49	4	29	10	14	192	74
Mascote	673.35	1	23	9	14	122	67
Mascote	673.35	2	10	5	22	95	50
Mascote	673.35	3	28	10	31	240	67
Mascote	673.35	4	13	7	17	165	66

Fuzaca	761.02	1	37	15	46	151	78
Fuzaca	761.02	2	35	11	19	92	59
Fuzaca	761.02	3	23	14	41	111	65
Fuzaca	761.02	4	37	11	14	139	68
Porto Seguro	1466	1	42	14	33	146	65
Porto Seguro	1466	2	30	7	38	131	59
Porto Seguro	1466	3	27	10	40	114	51
Porto Seguro	1466	4	35	10	34	131	63
Gavião-Real	1690.04	1	23	7	19	119	49
Gavião-Real	1690.04	2	44	11	31	138	44
Gavião-Real	1690.04	3	23	7	20	115	55
Gavião-Real	1690.04	4	27	11	35	85	52
Mainland 1	NA	1	39	9	21	185	65
Mainland 1	NA	2	37	11	42	147	67
Mainland 1	NA	3	34	9	51	137	66
Mainland 1	NA	4	20	9	31	147	75
Mainland 2	NA	1	30	8	40	149	82
Mainland 2	NA	2	20	10	32	168	45
Mainland 2	NA	3	78	13	27	240	89
Mainland 2	NA	4	41	11	69	189	64
Mainland 3	NA	1	29	13	32	130	66
Mainland 3	NA	2	38	13	30	118	64
Mainland 3	NA	3	64	19	39	179	84
Mainland 3	NA	4	20	9	16	181	76

S4.2: Overview of liana seed dispersal modes. Liana sapling genera with total abundances and seed dispersal mode classification.

Genus	Seed dispersal mode	Number of liana saplings
Abuta	Biotically	73
Ampelozizyphus	Abiotically	17
Bauhinia	Abiotically	107
Cheiloclinium	Biotically	84
Cissus	Biotically	1
Coccoloba	Biotically	1
Connarus	Abiotically	1
Cupania	Biotically	11
Davilla	Biotically	126
Derris	Abiotically	215
Dioclea	Abiotically	61
Doliocarpus	Biotically	73
Ficus	Biotically	1
Gurania	Biotically	6
Machaerium	Abiotically	553
Mansoa	Abiotically	207
Memora	Abiotically	552
Mimosa	Abiotically	8
Moutabea	Biotically	315
Mucuna	Abiotically	62
Odontadenia	Abiotically	23
Passiflora	Biotically	34
Paullinia	Biotically	9
Salacia	Biotically	242
Senna	Abiotically	27
Serjania	Abiotically	9
Smilax	Biotically	12
Stigmaphyllon	Abiotically	4
Strychnos	Biotically	27
Uncaria	Abiotically	4
Vitis	Biotically	1

S4.3: Summary of ANOVA results. ANOVA testing overall differences between island and mainland plots.

Variable	SS	df	Mean Square	F	*P*
Abundance of sapling lianas	389.3	1	389.28	1.59	0.21
Abundance of mature lianas	1352	1	1352.3	8.97	0.004
Total basal area of mature lianas	0.006	1	0.006	0.57	0.45
Ratio biotic : abiotically dispersed stems	0.65	1	0.65	3.58	0.06
Relative dominance of liana saplings : tree saplings	0.06	1	0.064	1.43	0.23
Relative dominance of mature lianas : trees >10cm DBH	0.05	1	0.05	4.66	0.03
Fisher's α	4.85	1	4.85	1.02	0.31

S4.4: Overview of perMANOVA analysis. perMANOVA tests of abundance- and incidence-based community compositions, which were carried out between island and mainland plots, and among island plots with environmental variables. perMANOVA for abundance-based compositional data was carried out using dissimilarities derived from the Morisita-Horn dissimilarity index, and for incidence-based composition using Jaccard dissimilarities.

Explanatory variable	Dissimilarity	df	SS	F	R^2	*P*
Island vs. mainland	Abundance	1	0.29	3.35	0.04	>0.05
	Incidence	1	0.4	1.68	0.02	>0.05
AREA	Abundance	1	0.19	2.21	0.02	>0.05
	Incidence	1	0.44	1.84	0.02	>0.05
ISOLATION	Abundance	1	0.41	4.91	0.06	>0.05
	Incidence	1	0.64	2.68	0.03	>0.05
COVER	Abundance	1	0.08	0.95	0.011	>0.05
	Incidence	1	0.28	1.19	0.015	>0.05
FIRE	Abundance	2	0.28	0.82	0.02	>0.05
	Incidence	2	0.66	0.32	1.37	>0.05

CHAPTER 5

Carbon storage in soils and necromass across an 80 year tropical secondary forest chronosequence

The research ideas were conceived by Isabel Jones and Daisy Dent. IJ collected the data and performed analyses with input from Lynsey Bunnefeld. H. Muller-Landau, M. Larjavaara, B. Turner and H. Elsenbeer contributed additional data and provided advice on analyses. DD and LB commented on versions on this Chapter.

5.1 ABSTRACT

Reducing levels of atmospheric CO_2 is an international priority to mitigate the detrimental impacts of a changing climate. Recent research has shown that tropical forests regenerating after land abandonment can rapidly uptake carbon into above-ground biomass. Alongside reducing deforestation of intact old growth forest, increasing the cover of secondary tropical forests presents a natural and cost-effective means of lowering atmospheric CO_2. However, global estimates of the value of secondary forests for carbon sequestration solely investigate above-ground living biomass and do not include other important carbon pools such as soil carbon and deadwood (necromass).

We are therefore likely be underestimating the value of secondary tropical forests for long-term carbon storage. Furthermore, important relationships between soil nutrients and both above- and below-ground carbon stocks remain largely unexplored. Here, we use a chronosequence of regenerating secondary forest stands in Panama, ranging from 40 to 120 years, to investigate how soil and necromass carbon pools alter with secondary forest age. Soil carbon stocks ranged from 128 to 205 Mg C ha^{-1} considering soils 0-100 cm. Soil C stocks showed no relationship with forest age; only soil nutrient status (specifically % N) was a significant predictor of soil C stocks. We therefore demonstrate the role of soil fertility in driving observed patterns in soil carbon stocks across the chronosequence, and highlight the need to fully consider soil nutrient status when modelling the carbon storage potential of secondary tropical forests. Necromass C stocks exhibited a small but significant decline with forest age, and ranged from 1.7 to 3.6 Mg C ha^{-1} across the chronosequence. Necromass carbon stocks were increasingly held in necromass $\geq$20 cm diameter in secondary forests >90 years. Necromass in older secondary forests may therefore provide long-term carbon storage even after above-ground biomass has approached the levels of old growth forest. We emphasise that integration of detailed plot-level estimates of both above- and below-ground carbon storage pools, and inclusion of specific variables such as soil nutrient status, are essential for accurately modelling the value of secondary forests for carbon storage.

5.2 INTRODUCTION

Tropical forests are a persistent sink of atmospheric CO_2 and the largest terrestrial store of carbon; tropical forest carbon stocks have been estimated at 471 ± 93 Pg, equivalent to 55% of global carbon stocks (Pan *et al.* 2011). In an era of unprecedented anthropogenic greenhouse gas emissions, resulting in pervasive changes in global climatic patterns, maintaining the tropical forest carbon sink and stocks is central to preserving the global carbon balance (Dixon *et al.* 1994; Malhi & Grace 2000; Grace *et al.* 2014).

Within tropical forests, over half of the total carbon stock is stored in living above-ground biomass, ~80 % of which is held in large trees (>10 cm diameter at breast height; Nascimento & Laurance 2002; Pan *et al.* 2011). Intact primary tropical forests typically hold between 120 and 220 Mg C ha^{-1} in above-ground biomass, with forests in Amazonia containing an average of 150 Mg C ha^{-1} (Baker *et al.* 2004a) and African forests 220 Mg C ha-1 (Lewis *et al.* 2009). The second largest carbon pool in tropical forests is soil carbon, which typically contains ~30 % of total stocks (Jobbagy & Jackson 2000; Pan *et al.* 2011). Roots are also a considerable carbon store and contain approximately a third of the amount of carbon found in living above-ground biomass (Saatchi *et al.* 2011). Finally, dead above-ground biomass or necromass, such as dead trees and fallen branches, typically hold 7-25 % of above-ground carbon stocks (Clark *et al.* 2002; Baker *et al.* 2007; Palace *et al.* 2012). Fallen deadwood contributes the greatest portion of the necromass carbon stock (Nascimento & Laurance 2002; Palace et al. 2007).

The amount of carbon stored within tropical forests is determined by feedbacks between primary production (whereby carbon is fixed from atmospheric CO_2 into plant biomass), soil fertility, and climate. At regional scales, primary production of undisturbed tropical forests, and hence carbon stocks, increases with precipitation and soil fertility (Jobbagy & Jackson 2000; Malhi *et al.* 2004, 2009), while the spatial heterogeneity of available specific nutrients (such as nitrogen, phosphorus and potassium; Wright et al. 2011), topography (Grimm *et al.* 2008), and plant composition (Jobbagy & Jackson 2000; Batterman *et al.* 2013;) are important determinants of forest carbon stocks at finer spatial scales. Deforestation and land-use change drastically alter the carbon balance of tropical forests through shifts in plant composition and function, soil nutrients and local precipitation (Hughes, Kauffman & Cummings 2002; Grace *et al.* 2014; Durigan *et al.* 2017), leading to increased carbon turnover and emissions estimated at 1-2 Pg C year^{-1} (Pan *et al.* 2011; Houghton, Byers & Nassikas 2015).

Approximately 50 % of global tropical forest cover is now degraded or regenerating secondary forest rather than primary forest (FAO 2016). Secondary forests are therefore increasingly important for the provision of tropical forest ecosystem services, such as active uptake of atmospheric CO_2 and long-term carbon storage (Silver, Ostertag & Lugo 2000; Wright 2005; Pan *et al.* 2011; Chazdon *et al.* 2016). Recent pan-tropical studies have shown that above-ground biomass and carbon stocks of regenerating secondary tropical forests rapidly accumulate during the first 20 years of growth to 34.53 ± 1.84 Mg C ha^{-1}, followed by a more steady increase to 133.89 ± 4.67 Mg C ha^{-1} at 100 years (Anderson-Teixeira *et al.* 2016). This rapid accumulation of carbon represents an estimated net carbon sink of ~1-3 Pg C $year^{-1}$ (Pan *et al.* 2011; Houghton *et al.* 2015). In the Neotropics, regenerating secondary forests (1-100 years old) actively take up atmospheric carbon into above-ground biomass at 11 times the rate of primary tropical forests, and during the first 20 years of secondary forest regeneration the rate of uptake is 3.05 Mg C ha^{-1} $year^{-1}$ (Poorter *et al.* 2016). Regrowth of secondary tropical forests, alongside preservation of intact old growth tropical forests, could therefore constitute a powerful tool in climate change mitigation policies such as REDD+ (Berenguer *et al.* 2014; Chazdon *et al.* 2016).

Evidence suggests that the capacity of secondary forests to uptake atmospheric carbon and accumulate above-ground biomass increases with water availability and soil fertility (Anderson-Teixeira *et al.* 2016; Poorter *et al.* 2016). However present estimates of the importance of soil fertility in determining above-ground carbon stock accumulation are based on a coarse metric of soil cation exchange capacity, which lacks site-specific and nutrient-specific detail (Poorter *et al.* 2016). Thus, we may currently be underestimating the importance of soil nutrients in determining secondary forest carbon stocks (Neumann-Cosel *et al.* 2011; Batterman *et al.* 2013; Chazdon *et al.* 2016; Paz *et al.* 2016). In addition, current broad-scale estimates of carbon in secondary forests are incomplete, considering only above-ground biomass (Poorter *et al.* 2016) and soil carbon (Don *et al.* 2011) and do not yet include other important carbon pools such as root biomass and necromass (Martin et al. 2013; but see Sierra *et al.* 2007, Fonseca *et al.* 2011 and Batterman *et al.* 2013). Initial estimates of secondary forest soil carbon dynamics suggest that >80 % of total secondary forest carbon storage may be within soils (Sierra *et al.* 2007), and that soil carbon can recover to ~17-50 % of primary forest levels after ~30 years of secondary forest regeneration (Don *et al.* 2011). Soil carbon stocks also vary with depth, carbon stocks are typically highest in the first 30 cm of soil, yet we lack detailed understanding of the relationship between soil fertility and carbon stocks with soil depth (Jobbagy & Jackson 2000; Batterman *et al.* 2013; Ngo *et al.* 2013). The relationship between above-ground biomass accumulation and accumulation of other forest carbon pools varies: below-ground root biomass is thought to track patterns in biomass accumulation above-ground, while necromass lags behind above-ground biomass accumulation (Carey *et al.* 1994; Anderson-Teixeira *et al.* 2016).

To better understand how regenerating secondary forests contribute to reducing levels of atmospheric CO_2 through carbon uptake and long-term sequestration, we urgently need more detailed information on patterns of carbon accumulation, and the relative importance of different carbon pools as secondary forests develop (Chazdon *et al.* 2016). Specifically we need to couple above- and below-ground biomass estimates with plot-level data for specific soil nutrients such as nitrogen (Hungate *et al.* 2003; van Groenigen *et al.* 2006; Paz *et al.* 2016; Poorter *et al.* 2016), and integrate estimates of understudied secondary forest carbon pools such as necromass (Sierra *et al.* 2007; Fonseca *et al.* 2011; Martin *et al.* 2013). Additionally, our knowledge of carbon stock dynamics in intermediate (~60-90 years) and older (>100 years) secondary forests is lacking (Neumann-Cosel *et al.* 2011; Martin *et al.* 2013; Marín-Spiotta & Sharma 2013; Anderson-Teixeira *et al.* 2016). Such information is vital to enhance our predictive power regarding the value of secondary forests in climate change mitigation strategies (Gibbs *et al.* 2007; Pan *et al.* 2011; Anderson-Teixeira *et al.* 2016), whilst contextualising the exceptional value of maintaining intact primary tropical forests and their existing carbon stocks (Lewis *et al.* 2009; Pan *et al.* 2011; Grace *et al.* 2014).

In the present study we measure necromass, soil carbon stocks and soil fertility across a chronosequence of secondary forest plots in Panama, to understand how stand age and soil nutrient status affect patterns of carbon storage. Specifically we ask:

(1) How do patterns in soil carbon stocks relate to soil depth and soil nutrient status across different forest ages?

(2) How do necromass carbon stocks relate to necromass abundance, size and volume across different forest ages?

5.3 METHODS

5.3.1 Study area

This study was conducted in a chronosequence of secondary forest plots located in central Panama within the Barro Colorado Nature Monument (BCNM), on Barro Colorado Island (BCI; 9°9′ N, 79°51′ W) and nearby mainland peninsulas (Denslow & Guzman 2000). The BCNM comprises a mosaic of old growth and secondary tropical forests of different ages, which are the product of forest regrowth following successive episodes of agricultural land abandonment between the 1880s and 1979 (Leigh, Rand & Windsor 1982; Denslow & Guzman 2000; DeWalt, Maliakal & Denslow 2003). The region receives ~2600 mm of rainfall annually, predominantly during a 7-month wet season from May to December, followed by a dry season during which many trees are leafless (Denslow 2000; DeWalt 2003; Yavitt 2000). Geologically, the BCNM is a patchwork of volcanic and sedimentary parent material which has weathered to form clay-rich oxisols and silty-clay alfisols, which are relatively rich in nitrogen and potassium (Yavitt 2000; Baillie *et al.* 2007).

Chronosequence plots

All data were collected within a network of permanent secondary forest plots, with two independent replicate 1-ha plots (50 x 200 m) in each of 40, 60, 90 and 120 year old secondary forest stands within the BCNM (Denslow & Guzman 2000; Dent, DeWalt & Denslow 2013). Stands selected for chronosequence plot establishment have a similar land-use history (fruit production and/or pasture), and have not been subject to further disturbance since land abandonment. Plots are located on different geological substrates, but have similar values for soil pH and bulk density (Denslow 2000).

5.3.2 Field data collection

All field data collection was conducted during the dry season between February and May 2015. Both soil and necromass sampling broadly follow protocols established for the 50 ha CTFS plot on BCI (Larjavaara & Muller-Landau 2009; Turner 2010).

Soil

Within each chronosequence plot, soil samples were collected along two parallel 200 m transects, 30 m apart. Five sampling points were located at 40 m intervals along each transect, giving 10 sampling points per plot. Soils from 0-10 cm and 10-20 cm were collected at each of the 10 sampling points, while at alternate sampling points (five in total per plot) deeper soils from 20-50 cm and 50-100 cm were collected. Sampling generated 30 samples per plot (0-10 cm, n = 10; 10-20 cm, n = 10; 20-50 cm, n = 5; and 50-100 cm, n = 5).

If the sampling point was disturbed by animals, such as by tracks or burrows, sampling was carried out at an undisturbed area as close to the original sampling point as possible. Obvious surface litter including decaying but recognisable leaves and twigs was removed at the sampling point, with care taken not to disturb the soil surface; any surface roots were left intact.

Soil cores from depths 0-10 cm and 10-20 cm were taken using a 2” (~5cm) diameter fixed volume auger. If stones or roots interrupted coring, then either the roots were cut or sampling was started again within 1.5 m of the original sampling point. If roots and stones repeatedly prevented sampling to the desired depth, then the depth achieved was measured using a ruler. All roots and stones were retained with the sample.

Soils from 20-50 cm and 50-100 cm depths were sampled using a Dutch auger. If coring was interrupted by stones and the depth achieved was <80 % of the required depth, sampling was started again within 1.5 m of the original sampling point. If the depth achieved was >80 % of the required depth, a measuring tape was used to measure the exact depth achieved. All soil from the core was collected in a bucket and homogenised in the field and a subsample of the entire core was taken back to the lab.

For all soil samples, roots and stones were exhaustively removed by hand, and were separated and dried at 60 degrees for a minimum of 24 hours and weighed. All soils were air-dried in air-conditioned laboratory conditions for a minimum of five days. Once dry the 0-10 cm and 10-20 cm cores were weighed to obtain the dry weight of soil for bulk density calculation. Due to the coring technique used and the quantity of soil obtained from the deeper cores (20-50 cm and 50-100 cm), bulk density values could not be obtained for these samples. Instead, we used bulk density values produced using the compliant cavity method from soil pits located as close to the sampling location as possible, and estimated percentage stone fraction (Ben Turner pers. comm; Helmut Elsenbeer pers. comm.).

Only soil cores that reached ≥ 80 % of the required depth were used for soil carbon analyses so as not to bias the carbon concentration (% C) data for each depth interval. A subsample of each soil sample reaching the threshold depth was transported to the University of Stirling where it was ground and analysed for carbon (% C) and nitrogen concentration (% N) using a CN analyser (Elementar Vario III EL).

Necromass

Fallen dead wood (≥10 cm diameter) was inventoried along 1000 m of transects located within each chronosequence plot (5 x 200 m transects, 10 m apart) using the line intercept method (Larjavaara & Muller-Landau 2009). The diameter of all deadwood bisecting a transect was recorded, along with the orientation of the deadwood, because transect-level summed mass and volume calculations depend on the angle between the central axis of deadwood and the transect

(Larjavaara & Muller-landau 2011). All standing deadwood ≥ 10 cm diameter (diameter at 1.3 m if >1.3 m high, or, diameter at the mid-point of the stump if <1.3 m high) was inventoried throughout the entire 1-ha plots, with diameter and height recorded.

For fallen and standing deadwood ≥20 cm diameter, wood density was estimated non-destructively using a penetrometer (which uses a 1-kg weight to penetrate deadwood). Wood density was then calculated from deadwood diameter and depth of penetration using a relationship developed using deadwood within the BCNM (Larjavaara & Muller-landau 2010b). For deadwood <20 cm diameter it is not possible to use the penetrometer to estimate wood density, as the relationship developed only relates to deadwood ≥20 cm diameter. Thus, to estimate density for deadwood <20 cm diameter, a plot-level mean wood density derived from deadwood ≥20 cm diameter was used.

5.3.3 Calculations

Soil

For soil samples from 0-10 cm and 10-20 cm depths, bulk density values (*Bd*; g cm^{-3}) were calculated using the following equation:

Equation (1)

$$Bd = \frac{Soil_m - Stone_m}{V - \left(\frac{Stone_m}{Stone_d}\right)}$$

where $Soil_m$ is the dry mass of soil (g), $Stone_m$ is the dry mass of stones (g), $Stone_d$ is rock particle density (2.65 g cm^{-3}) and V is the volume of the soil core (cm^3).

Carbon and nitrogen concentration (% C and % N) values for each sample were corrected for the percentage stone fraction by volume for each sample, by:

Equation (2)

$$C_{conc}.Adj = C_{conc} - \left(C_{conc} \times Stone_{prop}\right)$$

where $Stone_{prop}$ is the percentage stone fraction expressed as a proportion, and C_{conc} is expressed as a percentage.

Carbon stocks per depth interval were then calculated using the equation:

Equation (3)

$$C_{stock} = D \times Bd \times C_{conc}.\text{Adj}$$

where C_{stock} is the stock of carbon (Mg ha^{-1}) and D is the depth of sample (cm).

Carbon stock values for each soil sample were generated using equations 1-3. These values were pooled by soil depth and forest stand age, and followed an approximately normal distribution across plots. Mean carbon stocks were calculated for each depth, with 95 % confidence intervals generated by multiplying the standard error by 1.96. To produce an overall mean carbon stock value for each forest stand age, mean carbon stock values for each depth were summed, and the overall 95 % confidence intervals calculated by multiplying the overall standard error (SE_{grand}) by 1.96. The overall standard error was calculated by:

Equation (4)

$$SE_{grand} = \frac{\sqrt{sd1^2 + sd2^2 + sd3^2 + sd4^2}}{\sqrt{nD \times nS}}$$

where for each depth interval within the *i*th forest stand age *sd1, sd2* etc. are the standard deviations of each depth interval. *nD* is the number of soil depths (n = 4) and *nS* is the total number of individual samples in the *i*th forest stand age.

Soils within the chronosequence stands and on BCI have relatively low pH, therefore we did not expect carbonates to be present and assume that the carbon concentration values are equivalent to soil organic carbon (Denslow & Guzman 2000; Grimm *et al.* 2008).

Necromass

To calculate the volume and mass (and hence carbon stock) of fallen necromass inventoried using the line intercept method, we used the following equations from Larjavaara and Muller-Landau (2011), and assume that 47 % of the deadwood mass is carbon (IPCC 2006). The volume of fallen deadwood (V_f; m^3 m^{-2}) is calculated by:

Equation (5)

$$V_f = \frac{1}{L}\sum \frac{A_i}{sin\theta_i}$$

where L is the length of the transect (m). A_i is the cross section area (m^2) of the ith piece of fallen deadwood, calculated as for the area of a circle: this method assumes that deadwood is circular, and does not account for void space. The sine of the angular difference between the ith piece of deadwood and the transect is denoted by $sin\Theta_i$. V_f was converted to m^3 ha^{-1} for integration with standing deadwood volume which is summed at the plot-level.

To obtain carbon stock estimates, the total mass of fallen deadwood per transect must be calculated, whereby M is the total mass (kg m^{-2}) of deadwood along a transect. The cross section mass (C_i) of the ith piece of fallen deadwood is calculated by multiplying the cross section area (A_i) by wood density (kg m^{-3}) so that:

Equation (6)

$$M = \frac{1}{L}\sum \frac{C_i}{sin\theta_i}$$

Volume (V_s; m^3 ha^{-1}) and mass of standing deadwood were summed at the plot level. V_s is calculated from diameter and height by assuming the volume of the ith standing deadwood is equivalent to the volume of a cylinder (m^3).The mass of standing deadwood was calculated by multiplying the volume of the ith piece of standing deadwood by its wood density, and summed for each 1-ha plot.

For each stand age mean necromass carbon stocks and volumes were calculated for fallen deadwood by using transect-level values obtained from the equations above. These data did not follow a normal distribution and were log-transformed, and thus, 95 % confidence intervals around the mean were generated using the distribution of log-transformed data from each stand age with the following equation:

Equation (8)

$$95\ \%\ C.I\ = tX \times \frac{sdX}{\sqrt{nX}}$$

where *tX* is the critical value derived from the t-distribution of *X*, *sdX* is the standard deviation of *X* and *nX* is the number of samples of *X*. Values for standing deadwood are at the plot-level, and therefore mean values for each forest stand age are calculated as in equation (4), substituting *nD* for the number of replicate stands for each forest age (i.e. 2). Overall mean carbon stock and volume values for each stand age, combining data from fallen and standing deadwood, were calculated following equation (4).

5.3.4 Data analysis

We used a combination of ANCOVA and linear mixed effects models (LMMs) to investigate how soil carbon stocks were partitioned between different soil depths, as well as patterns relating to % C and % N across different forest ages. We also used LMMs to investigate how necromass carbon stocks and the size and volume of necromass changed with forest age. We modelled the abundance of necromass using a generalised linear mixed effects model (GLMM) with Poisson error distribution. Mixed effects models enabled us to account for pseudo-replication of samples within a plot, and for any potential variation arising from differences in land-use history and/or soil type between plots within the same forest stand age by fitting “plot” as a random effect. Continuous predictor variables were rescaled (centred and standardised by two standard deviations; Schielzeth 2010) prior to analysis to enable direct comparison of effect sizes between categorical and continuous predictor variables.

Prior to model fitting, the distribution of response variables was visually inspected and variables transformed if necessary to achieve a Gaussian distribution (S5.1). A Pearson's correlation matrix of each response variable and its predictor variables was constructed to allow assessment of correlation between predictor variables (significant correlation was indicated by r >0.7; no predictor variables showed significant correlation). LMM models were simplified through step-wise deletion of non-significant terms (t-value <-2 or >2 were classed as significant) and comparison of AIC values (Burnham & Anderson 2002). Interactions between predictor variables were tested for and removed if non-significant. All analyses were performed using R (version 3.3.2; R Core Team 2016).

5.4 RESULTS

5.4.1 Variation in soil carbon stocks with soil depth and nutrient status across secondary forest ages

Mean total soil carbon stocks across the chronosequence ranged from ~176 – 206 Mg C ha^{-1} (Table 5.1). Forest age was not a significant predictor of soil carbon stocks or the concentration of carbon (% C) within soils (Table 5.1). Soil carbon stocks and % C significantly declined with increasing soil depth (F[3, 217] = 31.5, P <0.001; F[3, 213] = 72.6, P <0.001 respectively; Table 5.2) but soil depth was not a significant predictor of soil carbon stocks when modelled using LMMs (Fig. 5.1; S5.1).

Table 5.1: Mean total soil and necromass carbon stocks, and necromass volume, across secondary tropical forest stands of 40-120 years. There were two replicate 1-ha plots per stand age. Overall mean soil carbon stocks (0-100 cm depth) were obtained from summing mean carbon stocks from each soil depth surveyed (0-10 cm, 10-20 cm, 20-50 cm, 50-100 cm); soil carbon stock data were obtained for a total of 242 soil samples. Mean necromass (woody debris) carbon stocks were, for fallen deadwood, derived from 1000 m of replicate 200 m transects in each 1-ha plot; all standing deadwood was inventoried within a 1-ha plot. 95 % confidence intervals are presented in brackets.

Forest age (years)		**40**	**60**	**90**	**120**
Mean carbon stocks (Mg ha^{-1})	Soil (0-100 cm)	176.22 (172.2-180.3)	205.7 (200.4-211)	128.04 (118.2-123.9)	175.6 (172.4-178.8)
	Necromass (standing + fallen)	1.72 (1.51-1.93)	2.42 (1.99-2.85)	3.63 (2.46-4.53)	3.34 (2.62-4.06)
Necromass volume (m^3 ha^{-1})		18.2 (16-20.5)	21.4 (17.6-25.1)	34.9 (24.1-45.8)	31.4 (24.6-38.2)

Table 5.2: Mean soil carbon stocks across soil depths 0-100 cm. Mean carbon stocks (Mg C ha^{-1}; ± 95 % confidence intervals, in brackets) were obtained from 222 soil samples from four depths. Soil samples were collected in eight 1-ha secondary forest plots, with two replicate plots per forest stand age. Soil carbon data from each depth were pooled for each forest stand age. The number of individual soil samples per depth used to generate mean carbon stock values (± 95 % confidence intervals) are italicised.

Forest age (years)		**40**	**60**	**90**	**120**
Soil depth (cm)	0-10	62.19 (56.2-68.2) *20*	73.11 (63.8-82.4) *20*	46 (41.3-50.7) *20*	54 (48.5-59.6) *20*
	10-20	47.7 (41.1-43.3) *14*	50.2 (39.5-61) *17*	32 (24.1-39.9) *17*	36.7 (32.2-41.1) *13*
	20-50	33.5 (26.3-40.7) *10*	45.7 (37.3-54.2) *10*	27.8 (24.4-31.2) *10*	47.1 (38.6-55.6) *10*
	50-100	32.8 (19.6-46) *10*	36.6 (22.7-50.5) *10*	15.3 (11.1-19.5) *9*	37.9 (30.4-45.4) *9*

The effect of soil nutrient status on soil carbon stocks

Soil carbon stocks were significantly predicted by the concentration of N (% N) in soils, with higher levels of % N leading to higher carbon stocks (Fig. 5.2; S5.1); forest stand age did not predict % N in soils (S5.1). % N significantly decreased with soil depth as did the C:N ratio (Fig. 5.3; S5.1). There was a high degree of variation in % C and % N between sites within the same forest stand age (Fig. 5.4), and fitting "site" as a random effect when modelling carbon stocks accounted for 33 % of the variation observed in the data. Such intra-age variation may be explained by plot-level differences in topography and concentrations of other soil nutrients such as phosphorus.

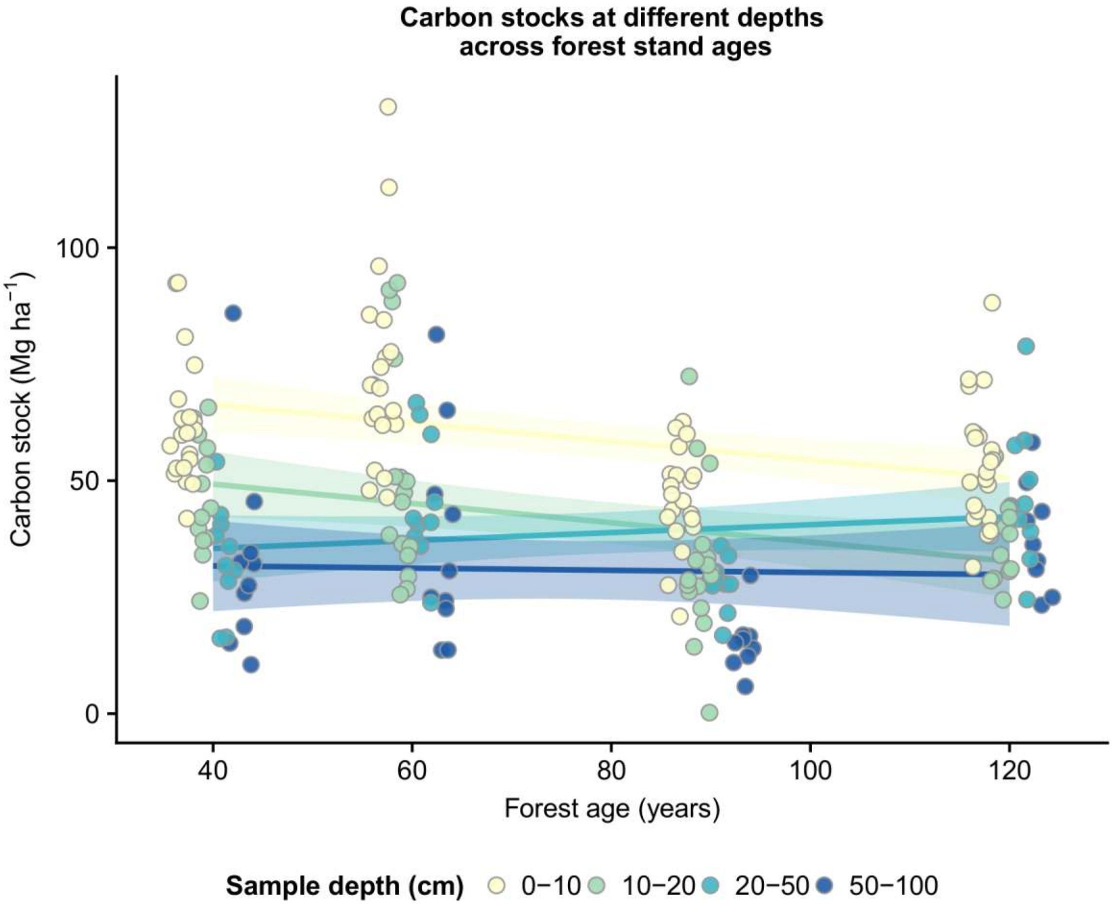

Fig 5.1: Relationship between soil carbon stocks, soil depth, and forest age. Soil depth was not a significant predictor of soil carbon stocks across the chronosequence. Lines represent predicted values of soil carbon stocks between 0-100cm depths, with 95 % confidence intervals.

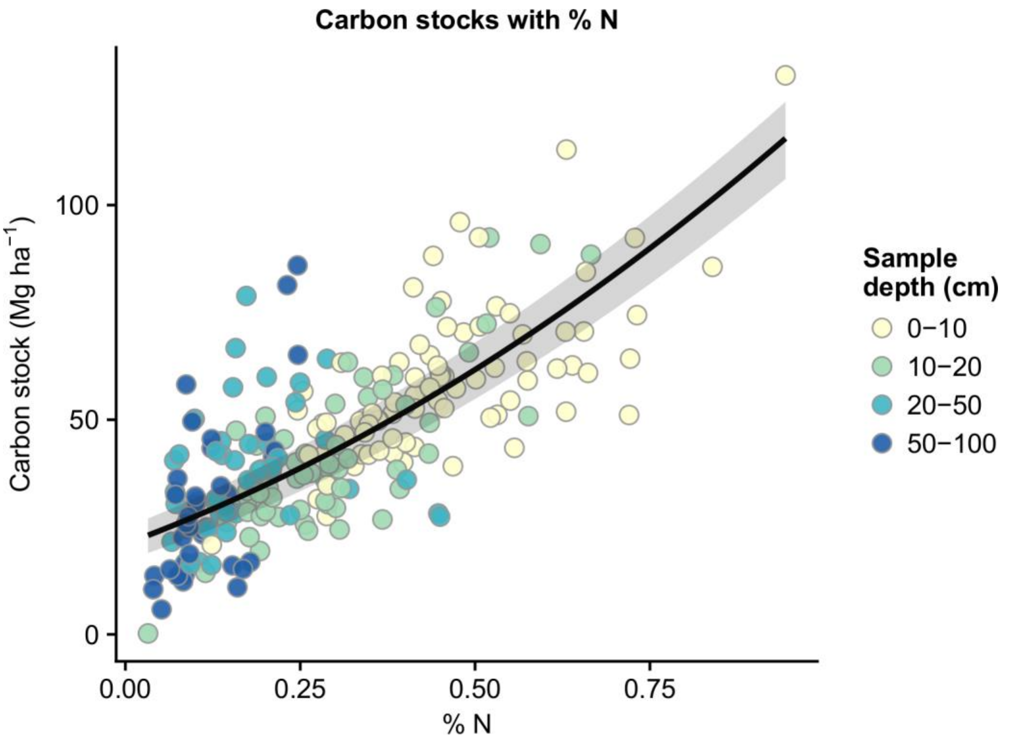

Fig. 5.2: Relationship between soil carbon stocks and soil N concentration within soils 0-100 cms. Plotted points correspond to individual soil samples (n = 222) collected across eight independent replicate 1-ha forest plots of 40-120 years (n = 2 plots per forest stand age). Lines correspond to predicted values generated from linear regression, with 95 % confidence intervals indicated by grey shading. There was no significant interaction between % N and soil depth and stand age was not a significant predictor of soil carbon stocks (S5.1).

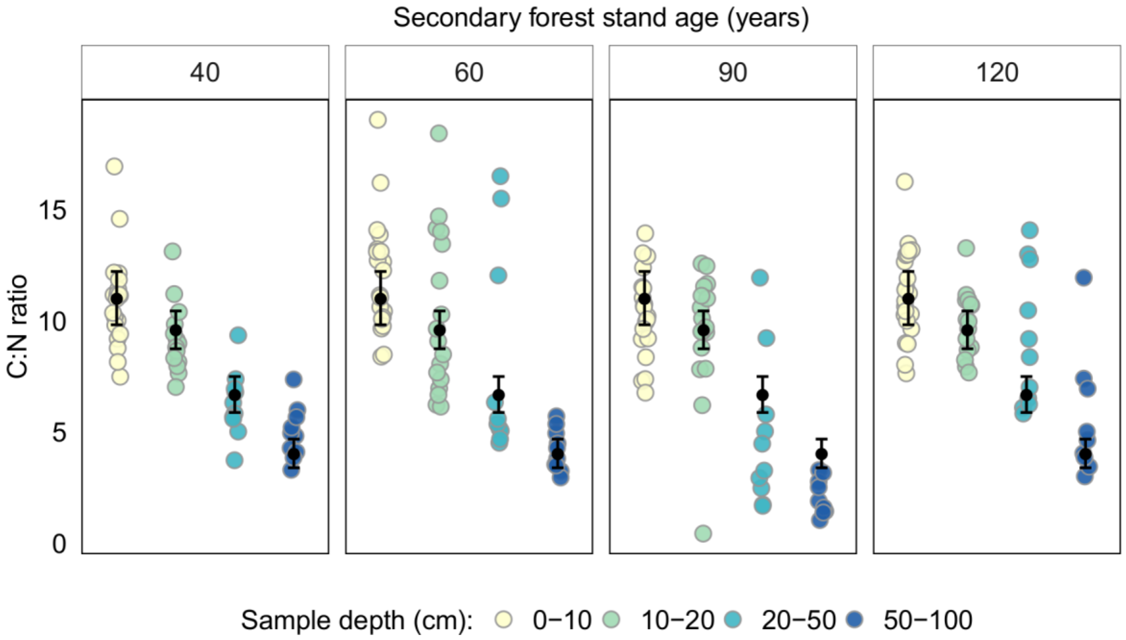

Fig. 5.3: Soil C:N ratios between 0-100 cm soil depth across 40-120 year secondary tropical forest stands. Points correspond to 222 individual soil samples pooled by forest stand age, collected within eight 1-ha forest plots, with two replicate plots per forest stand age. Soil C:N ratios significantly decline with soil depth, but patterns in C:N ratios are consistent across forest stand ages (S5.1). Coefficient estimates (± 95 % confidence intervals) are plotted in black and are derived from linear regression (S5.1).

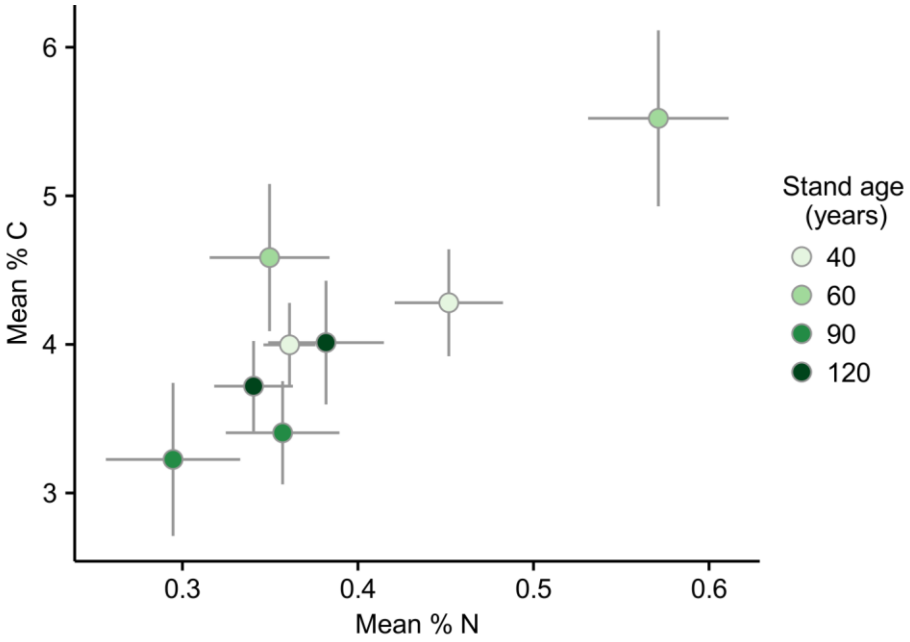

Fig. 5.4: Mean soil C and N concentrations at 0-20 cm depth, across eight replicate 1-ha plots of 40-120 year secondary forest stands. Mean values (± 95 % confidence intervals) are derived from 145 soil samples.

5.4.2 Variation in necromass carbon stocks across secondary forest ages

Across the chronosequence, total necromass carbon stocks ranged from 1.72 – 3.63 Mg ha^{-1} and exhibited a small but significant decline with increasing forest age, as did necromass abundance and volume (S5.1). However stand age interacted with necromass diameter such that carbon stocks were increasingly held in larger (≥20 cm) deadwood in older secondary forests >90 years (Fig. 5.5; S5.1). The diameter of necromass significantly increased with forest stand age, and to a higher degree for standing compared to fallen necromass (S5.1). Necromass carbon stocks also significantly increased with the total volume of necromass, abundance of deadwood, and wood density (S5.1). Larger deadwood (≥20 cm diameter) became more abundant in older forest stands, and made a greater contribution to the total necromass volume in these stand ages (S5.1). Overall necromass carbon stocks were predominantly contained within fallen deadwood (~80-95%) compared to standing deadwood.

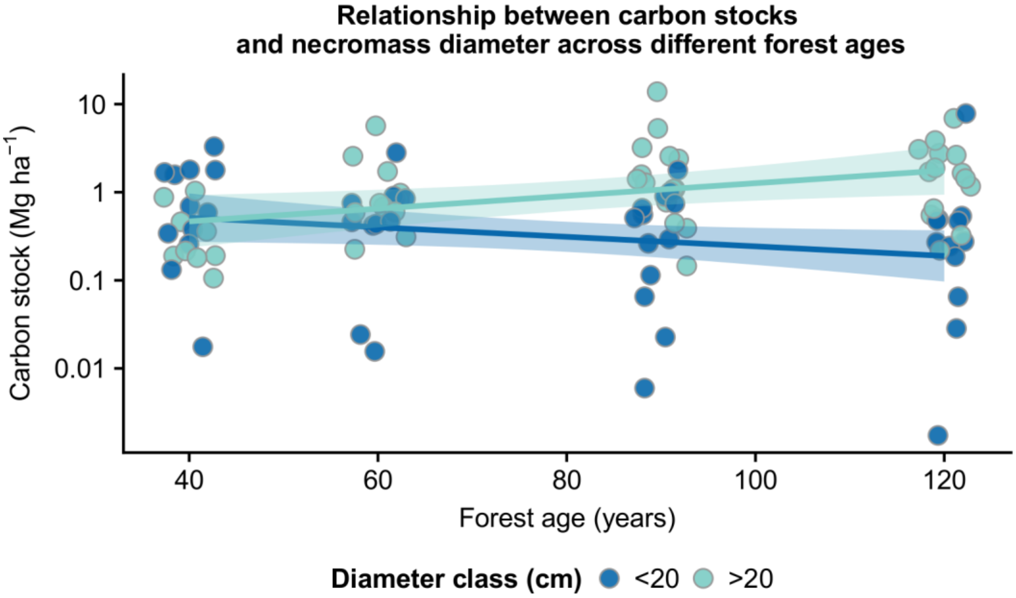

Fig. 5.5: Necromass carbon stocks contained in different size classes over secondary forest stands of 40-120 years. Data for necromass ≥10 cm diameter were obtained from eight 1-ha forest plots, with two replicate plots per forest age. Data were pooled by forest age, and plotted points relate to carbon stocks summed across replicate 200 m transects for fallen deadwood (5 x 200 m transects surveyed per 1-ha plot). Carbon stocks for standing deadwood are also plotted as a single point per 1-ha plot, as standing deadwood carbon is summed at the plot level. Predicted mean values and 95 % confidence intervals are plotted in black.

5.5 DISCUSSION

We find that soil nitrogen concentration (% N), not forest stand age, exhibits the strongest positive correlation with soil carbon stocks during secondary forest stand development. Our findings highlight that soil fertility, and specific soil nutrients such as nitrogen, are important predictors of soil carbon stocks. Thus, detailed soil nutrient information should be incorporated when modelling the below-ground carbon storage potential of secondary tropical forests. Within necromass, we find that older secondary forests hold a greater proportion of carbon stocks in larger dead and fallen trees (≥20cm diameter), suggesting that the necromass carbon pool, while slightly reduced, becomes more stable with greater carbon retention in secondary forests over approximately 70 years of age.

Soil carbon stocks in 40-120 year secondary forest stands are similar to young secondary and old-growth forests

Mean total soil carbon stocks for the secondary forest stands studied range from 176 to 206 Mg C ha^{-1} (40-120 years; 0-100 cm soil depth; Table 5.1). Other studies of soil carbon stocks within the BCNM have considered soils to 50 cm depth from a mixture of old growth and secondary forests on BCI, and found them to contain 90 Mg C ha^{-1} on average (Grimm et al. 2008). If we use comparable data from this study (i.e. mean carbon stocks from 0-50 cm rather than 0-100 cm depth), we find that our mean carbon stock estimate across the secondary forest stands is broadly comparable, but significantly higher at ~139 (135 – 143.1; 95 % C.I.) Mg C ha^{-1}. Carbon stocks have also been estimated in nearby younger secondary forests (5-15 years), where soils 0-20 cm deep contained ~49 Mg C ha^{-1} on average (Neumann-Cosel *et al.* 2011). If we consider our 0-20 cm soils, we find that the mean carbon stock is significantly higher at ~100.5 (95.6 – 105.4; 95 % C.I.) Mg C ha^{-1} and thus reflects the rapid accumulation of carbon within 0-40 years of secondary forest regeneration (Poorter *et al.* 2016). Differences in land-use history may also be a contributing factor in the different levels of soil carbon between sites within the same geographic region (Berenguer *et al.* 2014). However, land-use history and soil type has previously been found to be a poor predictor of soil carbon stocks in the area, and thus this difference may be due to other factors such as topography and levels of soil nutrients (Grimm *et al.* 2008; Batterman *et al.* 2013).

Soil nitrogen is the strongest correlate of soil carbon stocks

Carbon and nitrogen are tightly coupled in tropical forest soils and we find that soil nitrogen concentration (% N) is the strongest correlate of soil carbon stocks (Mg C ha^{-1}) across the chronosequence (Yang & Luo 2011; Li, Niu & Luo 2012). We find that both % C and % N significantly decline with soil depth, however when integrated with soil bulk density data, this pattern does not translate to a reduction in soil carbon stocks with increasing soil depth when modelled using LMMs. A similar pattern of significant reductions in % C with depth, not necessarily resulting in a reduction in carbon stocks, has previously been observed for soils on BCI (Grimm *et al.* 2008). This highlights the necessity of correcting % C data for soil bulk density when inferring soil carbon stocks, as basing carbon stock estimates solely on % C could generate spurious results (Li *et al.* 2012). Generally, soil carbon stocks decline with soil depth, but this decline is less pronounced in tropical soils compared with other biomes (Jobbagy & Jackson 2000). Our findings that depth is not a significant predictor of carbon stocks support previous studies that highlight the importance of deeper tropical soils for carbon storage, and that estimates of the contribution of soil carbon to total forest carbon are greatly improved by the addition of data from deeper soils. For example, soil carbon stocks between 1-3 m depth have been found to contain ~56 % of the carbon contained within the first 0-1 m (Jobbagy & Jackson 2000; Ngo *et al.* 2013).

Secondary forest stand age does not determine soil carbon stocks

Secondary forest stand age did not predict soil carbon stocks in our study. A similar lack of forest age effect has been found in early secondary forests in the nearby Agua Salud chronosequence (Neumann-Cosel *et al.* 2011), and more widely in the Neotropics (De Camargo *et al.* 1999; Hughes, Kauffman & Jaramillo 1999; Schedlbauer & Kavanagh 2008; Marin-Spiotta *et al.* 2009), as well as pan-tropically (Martin *et al.* 2013; Marín-Spiotta & Sharma 2013). The absence of an age effect across our chronosequence may be explained by the steady pattern in the ratio of soil

C:N across the secondary forest stands: while C:N ratios declined with soil depth, there were no differences in patterns related to stand-age. Findings from a global meta-analysis revealed that soil C:N ratios remained constant, and were independent of above-ground changes in C:N inputs with secondary forest stand development, which may explain why no clear effect of forest stand age was found in our study (Powers 2004; Yang & Luo 2011). The stoichiometry and cycling of soil carbon and nitrogen, independent of patterns in above-ground biomass, has been further demonstrated in Amazonian secondary forests, where secondary forests were found to have almost identical below-ground carbon cycling as primary forests, even though above-ground biomass was only 17 % that of primary forests (De Camargo *et al.* 1999).

Where increases in soil carbon stocks with tropical forest stand development have been reported, the predictive power of stand age on soil carbon stocks was weak, or only influenced carbon stocks at certain soil depths (Silver *et al.* 2000; Feldpausch *et al.* 2004; Fonseca *et al.* 2011). Evidence suggests that stand age may be more influential on soil carbon stocks during the first 10-30 years of forest stand establishment, but this is dependent on the land-use history of the area, climate, and composition of the regenerating forest (Paul *et al.* 2000; Silver *et al.* 2000; Li *et al.* 2012; Batterman *et al.* 2013; Marín-Spiotta & Sharma 2013; Berenguer *et al.* 2014; Durigan *et al.* 2017). Our 40-120 year secondary forest stands may already have undergone rapid soil carbon accumulation during earlier stages of stand development, especially considering that soil carbon stocks in nearby secondary forests <15 years are lower than in our stands (Neumann-Cosel *et al.* 2011).

Importance of soil nutrients in future predictions of secondary forest carbon storage potential

Given our findings that soil nutrient status, rather than secondary forest age, correlates with below-ground carbon storage in secondary forests, we suggest that soil nutrients must be considered when attempting to predict the carbon storage potential of secondary forests (Batterman *et al.* 2013; Chazdon *et al.* 2016; Paz *et al.* 2016; Poorter *et al.* 2016). The inherent link between soil nutrients and above-ground biomass accumulation means that both above- and below-ground carbon storage will likely be constrained by soil nutrient availability in secondary forests (Hungate *et al.* 2003; Luo *et al.* 2004; van Groenigen *et al.* 2006; Batterman *et al.* 2013). Furthermore, gradients of climate and soil weathering also influence biomass accumulation and biogeochemical cycling, and hence above- and below-ground carbon stocks in secondary forests (Powers & Schlesinger 2002). Plot-specific information on soil nutrients coupled with other significant carbon pools, such as above-ground biomass, is therefore essential for calibrating predictive models of total forest carbon stocks, especially considering that we find relatively large variation in % C and % N between forest plots of the same age.

Necromass carbon is increasingly held in larger deadwood as forests age

Inventories of fallen and standing necromass across the chronosequence revealed that the necromass carbon pool holds between 1.7 - 3.6 Mg C ha^{-1}. Similar necromass carbon stocks have been estimated for Colombian secondary forests (~3 Mg C ha^{-1}; Sierra et al. 2007), Costa Rican secondary forests (~4 Mg C ha^{-1}; Fonseca et al. 2011) and for 20-100 year secondary forests pan-tropically (~5 Mg C ha^{-1}; Anderson-Teixeira et al. 2016). Our values are also similar to those calculated for fallen deadwood in old growth forests within the BCI CTFS 50 ha plot at 4.6 (3.1-6.39) Mg C ha^{-1} (H. Muller-Landau, pers. comm.). However, the necromass carbon stock estimates from our 120 year stands and the BCI 50 ha plot are lower than for other old growth tropical forests pan-tropically (~17 Mg C ha^{-1}; Anderson-Teixeira et al. 2016). In line with previous necromass inventories, we find that the majority of the necromass carbon stock is within fallen rather than standing deadwood (Nascimento & Laurance 2002; Baker *et al.* 2007; Palace *et al.* 2012).

Across the chronosequence stands, necromass volume for both fallen and standing deadwood ranges from 18-35 m^3 ha^{-1}. In a survey of necromass volume within the chronosequence plots 20 years prior to our study, the volume of fallen necromass ranged from ~6.5 m^3 ha^{-1} in 20 year old stands (now 40 year old), to 35 m^3 ha^{-1} in old growth forest stands (DeWalt *et al.* 2003). Necromass volumes in the younger forest stands have clearly increased over 20 years of stand development, and we now find a small but significant reduction in necromass volume, abundance and carbon stocks with increasing stand age, in contrast to the significant positive effect of age found in the earlier survey by DeWalt et al. (2003), reflecting the reduced turnover of trees in older secondary forests and a more stable necromass carbon stock.

Increased stability and stocks of the necromass carbon pool in older secondary forests

Both the volume and carbon stocks of necromass are increasingly held within larger (≥20 cm diameter deadwood) in older forest stands >70 years. A similar pattern was found previously across the chronosequence stands, with the volume of medium (10-15 cm diameter) and large deadwood (>15 cm diameter) highest in older secondary (>70 years) and old-growth forest stands (DeWalt *et al.* 2003). We found that the diameter of standing deadwood was generally greater than for fallen deadwood, and that both fallen and standing deadwood achieved the greatest mean diameter in the oldest forest stands reflecting the structural development of above-ground biomass over succession.

The decomposition rate for larger diameter necromass is lower than for small necromass. Deadwood of ~20 cm diameter takes an estimated 18 years to lose 95 % of its mass at a rate of 0.19 year^{-1} (Chambers *et al.* 2000). Thus the increasing abundance of large necromass in older secondary forests suggests that the necromass carbon pool in secondary forests >70 years will be more stable and retain carbon for longer than in younger forests. Mature secondary forests could therefore accumulate additional carbon stocks in deadwood after above-ground biomass has reached that of old growth forests (Carey *et al.* 1994).

5.5.1 Limitations and future directions

Several studies of soil carbon stocks have found topographic attributes such as slope to be important determinants of soil carbon stocks (Grimm *et al.* 2008; Mascaro *et al.* 2011; Berenguer *et al*. 2014). We do not include information on slope or elevation within our study, and therefore may be missing important variables explaining within- and between-plot variation in soil carbon stocks and nutrient levels. However we account for plot-level differences in topography by fitting “plot” as a random effect in LMM regression, this method also accounts for any differences in land-use history and soil type, although previous studies on BCI have found that soil type has little effect on soil nutrient status and carbon content (Yavitt 2000; Grimm *et al.* 2008). Future work should also consider correlations between other soil nutrients, such as phosphorus, which are important drivers of above- and below-ground carbon allocation and stocks, and include additional plots to explore variability in soil nutrients within forests of the same age (Hungate *et al.* 2003; van Groenigen *et al.* 2006; Wright *et al.* 2011; Yang & Luo 2011). Recent studies in Panama have found a seasonal effect on soil carbon content in old growth forests, whereby soil carbon was 16 % lower and nitrogen 9 % lower in the dry season compared to the wet season (Turner *et al.* 2015). As our soil samples were collected in the dry season, it would be beneficial to compare them with soil carbon data from the wet season, to better understand the effect season may have on plot-level carbon cycling as secondary forest stands develop.

Necromass is highly variable and episodic within tropical forests, with rare large tree falls (Palace *et al.* 2012). Confidence intervals surrounding mean necromass carbon stocks and volumes are typically large, and sampling should be carried out over the greatest area possible. While we survey 1000 m of transects within each secondary forest plot (i.e. 2000 m per forest stand age), surveying a greater area could improve the chances of encountering rare large deadwood. However our 2000 m of transects is a comparable survey effort to another recent study of tropical forest necromass using the line intercept method (Ngo *et al.* 2013). Ours is a snapshot of necromass production across a secondary forest chronosequence, and further inventories would be required to more fully understand long-term necromass dynamics through stand development. However our comparisons of necromass volume with the survey conducted when stands were 20 years younger, show that the necromass carbon pool is developing with secondary forest stand age in terms of volume, total carbon stocks, and structure (DeWalt *et al.* 2003).

Integration of above- and below-ground living biomass data is crucial to gain a complete understanding of carbon cycling through secondary forest regeneration (Poorter *et al.* 2016). Thus, the next phase of research across the study chronosequence needs to focus on combining soil and necromass carbon stocks with above- and below-ground living biomass and carbon stock estimates at the plot-level. By investigating above-ground biomass and plant functional type at fine spatial scales, we can begin to explain mechanisms driving patterns in carbon accumulation (Batterman, *et al.* 2013). For example, plant functional types allocate carbon differently to above- and below-ground components, which may influence the distribution of carbon in soils driving high within-plot variability of soil carbon (Jobbagy & Jackson 2000; Malhi *et al.* 2009). Similarly, information on above-ground biomass and plant functional type will assist in understanding necromass dynamics across secondary forest stands, since necromass is strongly related to above-ground living biomass, mortality rates, and wood density (Chao *et al.* 2009).

5.5.2 Concluding remarks

We show that plot-level data (i.e. soil nutrient status) not broad-scale attributes (secondary forest stand age) are the strongest correlates of soil carbon stocks, suggesting that detailed plot-level information is necessary when attempting to identify broad spatial and temporal patterns in secondary forest carbon storage (Martin *et al.* 2013; Paz *et al.* 2016; Poorter *et al.* 2016). We also find that the necromass carbon pool becomes more stable in secondary forests >70 years, highlighting the potential value of secondary forests for long-term carbon storage (Carey *et al.* 1994). Finally, we emphasise that while plot-level estimates of above-ground biomass are typically available, estimates of below-ground biomass, soil nutrients, and detailed site information are not, hampering our ability to accurately predict large-scale carbon stock accumulation in secondary tropical forests. Thus, while increasing the global area of secondary forests, alongside the cessation of old growth forest loss, doubtless provides an effective means for climate change mitigation, we now need better integration of plot-level detail into large-scale models of secondary forest carbon accumulation (Chazdon *et al.* 2016).

5.6 ACKNOWLEDGEMENTS

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S5 SUPPLEMENTARY INFORMATION

S5.1: Summary of effect sizes for fixed effects within ‘best’ models (linear mixed effects; LMM). T-values <-2 or >2 were treated as significant. Marginal R^2 (R^2_m) represents the degree of model fit contributed by the fixed effects alone, while the conditional R^2 shows the degree of model fit considering both random and fixed effects included within models (computed using ‘r.squaredGLMM’ in the ‘MuMin’ R package; Barton 2016). “Plot” (corresponding to the identity of individual 1-ha forest plots) was fitted as a random term to account for pseudo-replication arising from multiple samples originating from the same plot.

	Variable	**Fixed effects**	**Estimate**	**Std. error**	***t*-value**	**R^2_m**	**R^2_c**
Soil	√(C stock)	Intercept	6.58	0.21	25.2	0.53	0.66
		% N	2.3	0.13	17.73		
	ln(% C)	Intercept	1.13	0.09	12	0.81	0.85
		% N	0.97	0.09	10.87		
		Depth 10-20 cm	-0.19	0.08	-2.42		
		20-50 cm	-0.79	0.1	-7.67		
		50-100 cm	-1.50	0.11	-13.08		
	√(% N)	Intercept	0.67	0.02	35.63	0.58	0.65
		Soil depth: 10-20 cm	-0.14	0.02	-8.36		
		20-50 cm	-0.25	0.02	-13.6		
		50-100 cm	-0.33	0.02	-17.3		
	√(C:N)	Intercept	3.31	0.09	35.98	0.50	0.62
		Soil depth: 10-20 cm	-0.22	0.07	-3.10		
		20-50 cm	-0.73	0.08	-9.13		
		50-100 cm	-1.31	0.08	-15.91		
Necromass	ln(C stock) (standing + fallen cwd combined)	Intercept	-0.53	0.078	-6.85	0.82	0.82
		Forest age (years)	-0.42	0.15	-2.8		
		Volume	1.30	0.12	10.97		
		Wood density	0.29	0.14	2.61		
		Abundance	0.58	0.14	4.30		
		Forest age : diameter >20 cm	0.6	0.21	2.72		

ln(Volume)	Intercept	1.47	0.11	12.75	0.54	0.54
	Forest age (years)	-1.19	0.34	-3.42		
	Diamter class	0.84	0.24	3.47		
	Forest age (years): >20 cm	2.3	0.49	4.66		
	Abundance	-1.45	0.24	-5.87		
ln(Diameter)	Intercept	2.88	0.04	68.14	0.1	0.14
	Forest age (years)	0.26	0.08	3.11		
	Standing/Fallen	0.17	0.05	3.26		
Abundance	Intercept	1.45	0.08	18.67	0.34	0.34
	Forest age (years)	-0.43	0.15	-2.79		
	Diameter class	0.56	0.13	-4.28		
	Forest age : > 20 cm	0.95	0.26	3.66		

CHAPTER 6

General discussion

6.1 BACKGROUND

Tropical forests are globally important for biodiversity and provision of ecosystem services such as carbon storage (Malhi & Grace 2000; Foley *et al.* 2007; Gibson *et al.* 2011; Pan *et al.* 2011). Following extensive development of tropical forest regions, around 50 % of remaining tropical forest cover is now degraded or regenerating secondary forest, rather than intact old-growth forest (FAO 2010; Mitchard *et al.* 2013; Achard *et al.* 2014). Thus, secondary tropical forests are becoming increasingly important for tropical biodiversity and ecosystem service provision such as carbon sequestration (Dent & Wright 2009; Chazdon *et al.* 2016). Due to the immense value of tropical forest systems for the global carbon cycle (Malhi & Grace 2000) and climate change mitigation policies such as REDD+ (Gullison *et al.* 2007; Gibbs *et al.* 2007), there is pressing need to understand the role secondary tropical forests play in atmospheric carbon sequestration. Recent broad-scale studies of atmospheric carbon uptake by secondary tropical forests have found that within 20 years of forest regeneration, secondary forests can accumulate ~35 Mg C ha^{-1} (Poorter *et al.* 2016). However there is still much to be learnt about how carbon storage changes with secondary forest stand development, and the importance of site-specific variables such as soil nutrients (Paz *et al.* 2016; Poorter *et al.* 2016).

Habitat fragmentation is a pervasive threat to our remaining tropical forest cover, leading to species loss, community composition change, and loss of ecosystem functioning of remnant biological communities (Asner *et al.* 2010; Chaplin-Kramer *et al.* 2015; Haddad *et al.* 2015). Dam construction creates possibly the most extreme form of fragmentation by isolating terrestrial habitat on land-bridge islands within a water matrix. Understanding of how remnant terrestrial communities isolated on islands within a reservoir respond to habitat fragmentation in the long-term is growing, but is far from complete (Mendenhall *et al.* 2014). We specifically lack understanding of the long-term biodiversity and carbon storage impacts of dam-induced fragmentation on mega-diverse tropical tree communities remaining on reservoir islands, and the trajectories of tree community composition change following post-isolation recruitment dynamics (Benchimol & Peres 2015a). We also lack understanding of the role that other forest groups such as lianas may play in shaping future insular forest communities (Schnitzer & Bongers 2002). The findings presented within this thesis contribute to our knowledge of these issues and provide greater understanding of the factors influencing the long-term impacts of habitat fragmentation on remnant terrestrial communities, and their ability to perform ecosystem services such as carbon storage.

6.2 LONG-TERM IMPACTS OF DAM-INDUCED HABITAT FRAGMENTATION

6.2.1 Summary of results

Habitats isolated within a water matrix are subject to an extinction debt

Findings presented in Chapter 2 reveal that biological communities isolated on reservoir land-bridge islands are strongly negatively impacted. Islands isolated within reservoirs cannot maintain species richness at similar levels to mainland habitat in the long-term. Reservoir islands are subject to an extinction debt, whereby all islands lose species with increasing island isolation time, regardless of island size or proximity to other terrestrial habitat. The smallest islands lose species most rapidly, and while larger islands can maintain species for longer, ultimately, all islands regardless of their size undergo significant species loss in <100 years of isolation. An extinction debt was found for all taxonomic groups, across all habitat types, and all dams studied. We propose that as a general rule applicable to all dams, reservoir islands cannot maintain species indefinitely, and thus cannot be used as part of dam impact mitigation strategies. Reservoir islands should be explicitly counted as part of the total area of land impacted by dam creation.

Loss of integrity of insular tree communities and proliferation of lianas

In Chapter 3 we demonstrate that islands within the Balbina mega-dam, Brazil, maintain significantly lower density, richness and diversity in sapling and adult tree communities compared to nearby continuous forest. Sapling and adult tree communities on small islands (particularly those <10 ha) show clear and directional divergence from tree assemblages found in nearby continuous forests. Tree communities on islands have significantly lower $\log_{10}$ ratios of saplings : adults compared to mainland continuous forest, and tree communities with higher abundance-weighted mean wood density values have show the greatest declines in sapling : adult ratios. Differences in tree communities across the Balbina archipelago are related to island area, degree of island isolation, the amount of forest cover surrounding islands, and fire disturbance history. The fragmentation-mediated shifts in tree communities observed suggest that there may be ongoing, and currently unaccounted-for, additional biodiversity and carbon losses associated with tropical dams.

Furthermore, results presented in Chapter 4 reveal that across the Balbina archipelago, even in the most disturbed island habitats, liana communities remain remarkably similar to those found in mainland continuous forest. Lianas were found to increase in dominance relative to trees on small and highly disturbed islands. In contrast to trees, liana assemblages therefore appear to be robust to many of the detrimental impacts associated with fragmentation within a water matrix. Our findings suggest that as tree communities continue to degrade, lianas may become a key feature of the Balbina archipelagic landscape.

6.2.2 Synthesis and implications

Findings presented in Chapter 2 indicate that dam-induced fragmentation leads to an extinction debt for reservoir islands, which is supported by other studies reporting extinction debts in fragmented systems (Kuussaari *et al.* 2009; Metzger *et al.* 2009). In a recent study of vertebrate extinctions across the Balbina archipelago, it was found that a relatively large island size of 475 ha was needed to sustain >80 % of vertebrate species, but that only 0.7 % of the >3500 islands created by the Balbina dam met this size criterion (Benchimol & Peres 2015b). The fact that the vast majority of islands could not support a species-rich vertebrate community characteristic of mainland environments lends further support for the globally applicable findings presented in Chapter 2: reservoir islands cannot support a full complement of species post-isolation. Moreover, we show that all islands are effectively too isolated for species populations to be buffered by the 'rescue effect' and metapopulation dynamics (Hanski & Ovaskainen 2000). In our analysis, island isolation distance did not explain patterns in island species richness. We therefore demonstrate that principles of the Island Biogeography Theory (IBT; MacArthur and Wilson, 1967) do not necessarily apply to dam-induced fragmented landscapes, since the water matrix unconditionally isolates terrestrial habitats fragmented within these reservoirs (Lomolino 2000; Ewers & Didham 2006). Instead our findings support the concept that habitat fragmentation within a water matrix presents the worst-case scenario in terms of impacts for remnant biological communities (Ewers & Didham, 2006; Mendenhall *et al.* 2014).

The results presented in Chapters 2, 3 and 4, are in agreement with many other studies that highlight that small, edge-dominated habitat fragments, are the most susceptible to severe erosion of remnant biological communities (Laurance *et al.* 2006a; Santo-Silva *et al.* 2016). For example in Chapter 2, small islands are subject to the most rapid species loss, and in Chapter 3, small islands display the greatest divergence in tree community composition away from those found in continuous forest, and the greatest declines in sapling : adult ratios. In Chapter 4, we show that lianas are increasingly dominant compared to trees on small islands. In artificial archipelagic systems, larger islands may be able to sustain species compositions more similar to those found in mainland continuous habitats for longer, and pay their extinction debts more slowly, as described in

Chapter 2. However in detailed analyses of tree and liana communities across the Balbina archipelago (Chapters 3 and 4), island area was not a strong predictor of differences in community attributes, such as species richness and diversity. Also contrary to the general pattern found in Chapter 2 - that the proximity of islands to nearby habitat had little effect on island species richness - island isolation distance was an important factor in determining some patterns of tree and liana community attributes, such as diversity (Chapters 3 and 4). Chapter 2 is limited to analysis of species richness data. Therefore if data were available to conduct broad-scale analyses on other ecological metrics such as diversity, additional variables such as island isolation distance may come to the fore in terms of explaining general patterns in remnant biological communities on reservoir islands.

Advances in our understanding of the long-term impacts of tropical forest fragmentation on remnant tree communities have been made through long-term study systems such as the BDFFP (Laurance *et al.* 2011). Such studies have provided clear evidence that tropical forest fragmentation and associated area- and edge-effects cause remnant tree communities to undergo increased mortality, rapid species turnover, and directional shifts away from their initial composition towards communities dominated by low wood density pioneers (Laurance *et al.* 2006a). However, given previous comparative studies of fragmentation effects contingent on the surrounding matrix type, evidence of an extinction debt (Chapter 2) and previous studies of tree communities isolated on reservoir land-bridge islands, impacts to insular tree communities within tropical reservoirs are likely to be even more severe (Leigh *et al.* 1993; Terborgh *et al.* 2001; Yu *et al.* 2012; Mendenhall *et al.* 2014; Benchimol & Peres 2015a).

In line with other studies, results in Chapter 3 suggest that tree communities on reservoir islands within Balbina are on a trajectory towards lower wood-density state, more closely resembling early successional tree communities rather than those associated with intact old-growth forest (Laurance *et al.* 2006a; Tabarelli *et al.* 2008; Lôbo *et al.* 2011; Santo-Silva *et al.* 2016). However, due to different life history strategies, habitat fragmentation *per se* may not always have detrimental impacts on a particular species or taxonomic group, as highlighted in Chapter 2 where ~10 % of studies reported positive or no effect of fragmentation on the study taxon. In Chapter 4 we show that lianas do not appear to be subject to the island extinction debt (Chapter 2), nor directional shifts in composition, in contrast to trees (Chapter 3). Liana communities, ubiquitous in fragmented and degraded forests, therefore appear to be robust to many of the negative impacts associated with dam-induced inundation (DeWalt *et al.* 2000; Schnitzer & Bongers 2002; Letcher & Chazdon 2012). This may be because lianas have a competitive advantage in the high-light and low moisture conditions associated with fragment edges and low stature forest (Schnitzer & Bongers 2011). Lianas can also persist without the structural support provided by canopy trees, by growing laterally and forming large ground-level liana tangles (Schnitzer & Bongers 2002). Finally, lianas are able to reproduce vegetatively, and may be better able to withstand physical damage from, for example, strong winds associated with fragment edges (Gerwing 2004).

Analyses conducted in Chapters 3 and 4 revealed that patterns in liana and tree communities broadly mirrored each other in terms of their responses to dam-induced fragmentation. Higher percentages of surrounding forest cover decreased the relative dominance of lianas, while simultaneously increasing the density and diversity of trees. Across analyses of both trees and lianas, the percentage of forest cover within 500 m of islands, along with fire disturbance intensity, were the strongest drivers of differences in forest communities among islands. Such findings have broad application to the conservation of forest fragments, and suggest that some of the detrimental effects of habitat fragmentation may be mediated if the quality of the surrounding landscape is improved (Nascimento *et al.* 2006b; Mendenhall *et al.* 2011; Fahrig 2013; Ruffell *et al.* 2016). While global patterns, such as those regarding species richness loss and extinction debt presented in Chapter 2 are useful for broad-scale generalisations, they may mask nuanced and site-specific patterns as described in Chapters 3 and 4, which are essential for predicting the full consequences of landscape-scale habitat fragmentation.

Shifts in tree and liana community composition and dynamics have been found to lead to a reduction in ecosystem functioning and significant carbon emissions at fragment edges and within degraded forest (Asner *et al.* 2010; Chaplin-Kramer *et al.* 2015; Magnago *et al.* 2016). Thus, as tree communities continue to disassemble on reservoir islands (Chapter 3), there will likely be a future carbon cost to pay - an ecosystem function debt, as well as an extinction debt - associated with insular tropical forest communities on reservoir islands (Rosa *et al.* 2016). Furthermore, evidence suggests that lianas, through competition for light, water and nutrients, can inhibit tree recruitment and effectively stall forests in an early-successional state (Schnitzer *et al.* 2000), and lower the carbon storage potential of forests (van der Heijden *et al.* 2013, 2015). The increasing dominance of lianas across the Balbina landscape (Chapter 4) could therefore result in additional long-term impacts on tree communities and carbon storage (Wright *et al.* 2004).

Dam construction is surging across the Amazon watershed (Finer & Jenkins 2012; Zarfl *et al.* 2015; Lees *et al.* 2016) and will flood vast areas – estimated at 10 million ha - of mega-diverse tropical forests, which account for 40 % of our remaining intact tropical forest globally (Gentry 1988; Laurance 2001; Pitman *et al.* 2001; Fearnside 2006). The impact assessments for proposed dams are inadequate, and do not currently consider the aggregate area of habitat isolated on islands as being subject to environmental impact; instead, developers propose that reservoir islands can act as wildlife refuges (Trussart *et al.* 2002; International Energy Agency 2006; Ritter *et al.* 2017). Given that islands within reservoirs are unable to support remnant terrestrial communities indefinitely (Chapter 2), the isolation of tropical forest communities on islands within reservoirs is a serious concern in terms of loss of biodiversity and loss of ecosystem services, such as carbon storage.

To account for the additional biodiversity and carbon losses we present in Chapters 2, 3, and 4, we call for the aggregate area of reservoir islands, and mainland edges, to be included in future dam impact assessments. Emissions calculations for tropical dams have been estimated, but do not yet include emissions associated with long term tree community degradation as a result of forest insularization within the reservoir matrix (Demarty & Bastien 2011; Fearnside & Pueyo 2012; Deemer *et al.* 2016; Scherer & Pfister 2016).The potential long-term source of carbon emissions from degradation of remnant tree communities should therefore be included in carbon cost/benefit analyses of proposed dams (Kareiva 2012). Our findings consistently show that flooding tropical forests for reservoir creation leads to severe long-term biodiversity and carbon impacts, and bolster the strong arguments against further hydropower development in tropical forest regions (Fearnside 2013, 2016a; Lees *et al.* 2016; Prado *et al.* 2016).

6.3 SECONDARY TROPICAL FORESTS AND CARBON STORAGE

6.3.1 Summary of results

In Chapter 5 we present details of soil and necromass carbon storage across a chronosequence of 40-120 year secondary forest stands. We show that soil and necromass carbon stocks remain constant between 40-120 years of secondary forest stand development, and are comparable to soil carbon stocks in nearby younger secondary forests and old-growth forests (Grimm *et al.* 2008; Neumann-Cosel *et al.* 2011). We highlight the strong role of soil nutrients in influencing soil carbon stocks, nitrogen in particular (Yang & Luo 2011; Li *et al.* 2012). Necromass carbon stocks across the 40-120 year stands were consistently higher than in younger secondary forest stand ages (DeWalt *et al.* 2003) and had carbon stocks comparable to old-growth forest (Muller-Landau, pers. comm.). We also show that carbon stocks are increasingly held in larger necromass as secondary forest stands develop.

6.3.2 Synthesis and implications

Tropical secondary forests have the potential to play a key role in mitigating carbon emissions and biodiversity loss due to deforestation (Barlow *et al.* 2007; Chazdon *et al.* 2009, 2016; Poorter *et al.* 2016). Increasing the cover of secondary forests around remnant forest fragments could help mitigate some of the species and carbon storage losses associated with fragmentation as described in Chapters 2,3, and 4. Given that secondary forests can harbour a significant proportion of forest species, increasing the cover of secondary forests surrounding manmade reservoirs may help to mitigate some of the detrimental effects of the water matrix on remnant taxa (Nascimento *et al.* 2006b; Fahrig, 2013; Haddad *et al.* 2016; Ruffell *et al.* 2016). Furthermore, developing secondary forest cover may also help to mitigate carbon emissions associated with tropical dams (Fearnside & Pueyo 2012).

Assessing total carbon stocks within secondary forests is essential if we are to fully understand the value of secondary tropical forests for ecosystem service provision such as carbon storage as stand age increases (Pan *et al.* 2011; Anderson-Teixeira *et al.* 2016). Previous studies of total carbon storage within secondary tropical forests have indicated the importance of carbon pools such as soil and necromass (Sierra *et al.* 2007; Fonseca *et al.* 2011). Our results support this and suggest that these additional carbon pools should be included in broad-scale analyses of secondary forest carbon stocks (Chazdon *et al.* 2016). We also call for broad-scale models to include site-specific nutrient information as an important parameter explaining carbon stocks. Currently only coarse metrics of soil fertility are included in models such as cation exchange capacity, and thus our broad-scale understanding of the potential factors influencing secondary forest carbon uptake is incomplete (Chazdon *et al.* 2016). In addition, necromass data across the chronosequence show that while carbon stocks slightly decrease with stand age, the structure of necromass changes with increasing stand age~~,~~ such that necromass in older secondary forests contains carbon in larger deadwood which has a longer residence time (Chambers *et al.* 2000). Therefore, the necromass carbon pool will likely become increasingly in important for more long-term carbon storage as secondary forest stands develop in stature, which may be an additional consideration when parameterising predictive models of carbon storage (Carey *et al.* 1994).

In support of broad-scale analyses that report rapid carbon accumulation in secondary forests <20 years of age (Poorter *et al.* 2016), results in Chapter 5 suggest that soil and necromass carbon stocks rapidly accumulate in <40 years of secondary forest stand development. With international pressure mounting for countries to reduce carbon emissions, increasing the cover of secondary tropical forest stands may provide a cheap and relatively quick method of reducing atmospheric carbon (Gibbs *et al.* 2007; Chazdon *et al.* 2016). Furthermore, developing secondary forest stands around remnant tropical forest fragments may provide some mitigation of the negative area- and edge-effects associated with habitat fragmentation discussed in Chapters 2, 3 and 4 (Nascimento *et* *al.* 2006b; Mendenhall *et al.* 2011; Ruffell *et al.* 2016). For example in the Atlantic Forest of Brazil it has been shown that a three-year investment of 6.5 % of the current Brazilian Government agricultural subsidies would be needed to increase forest cover by 30 % in agricultural matrices surrounding forest fragments. This 30 % increase in secondary forest cover may increase the species richness and composition of forest-specialist vertebrates within the landscape to levels similar to those in protected areas, and rural inhabitats losing productive land to forestry could be directly compensated using payments for ecosystem services (Banks-Leite *et al.* 2014). Thus, secondary forests could be used as an effective tool to help buffer the edges of fragments, and protected areas, and help to reduce species and ecosystem function loss for minimal financial investment (Gardner *et al.* 2009).

Many landscapes surrounding tropical reservoirs are not under strict protection, and are heavily developed for agriculture. The old-growth forest landscape east of the former Uatumã River adjacent to Balbina (the study system described in Chapters 3 and 4) is strictly protected. Thus, Balbina presents the best-case scenario for remnant tropical forest species impacted by dam creation, as there is an intact species source pool surrounding the reservoir. The fact that isolation distance was in some instances an important driver of tree and liana community attributes on islands (Chapters 3 and 4), indicates that this high-quality species source pool may mitigate, or at least decelerate, some of the species losses associated with reservoir islands (Ewers & Didham 2006; Mendenhall *et al.* 2014). Thus, developing secondary forest cover surrounding manmade reservoirs where forests have been lost may bolster some populations of remnant species on islands. Furthermore increasing secondary forest cover may help balance the carbon losses associated with tropical dams through rapid uptake of atmospheric carbon (Poorter *et al.* 2016), and also help to increase precipitation and regulate sediment and water flows necessary for efficient hydropower generation (Stickler *et al.* 2013).

However, it may prove challenging to instigate such additional reforestation programmes as landownders in Brazil for example, are already required to set aside 80 % of their land for forest cover under the Brazilian Forest Code (Soares-Filho *et al*. 2014). Thus, only land which has been abandoned may be available for reforestation in this manner. A spatial analysis of land abandonment in Amazonia revealed that land near large rivers is significantly more likely to be abandoned (Laue & Arima 2014). Given the necessity of maintaining river flow and reducing sediment transportation into reservoirs from upstream erosion (Stickler *et al.* 2013), such land may provide am ideal opportunity for dam developers to invest in REDD+ programmes to reforest degraded areas, as part of a measurable long-term offset for forest and carbon loss associated with dam construction without creating an economic cost to society (Laue & Arima 2014). In addition, dam developers could be required to contribute to funds to bolster the enforcement of the Brazilian Forest Code, as the lack of compliance of landowners has led to, for example, 32% of deforestation in the Brazilian Amazonian state of Pará occurring on private properties, with half of this deforestation occurring illegally in designated set-asides (Gibbs *et al.* 2015). Given the complexities surrounding the Brazilian Forest code, difficulties in enforcement across the ~5 million rural properties, political pressure from the agricultural sector, and availability of abandoned land, arguably, using investment from dam developers to maintain intact forest cover surrounding new dams by creating strictly protected areas could be the most straightforward option.

All options for lessening the ecological and social impacts of large dams in Amazonia, and to avoid ‘greenwashing’ of proposed projects, requires a thorough assessment of impacts at a range of scales (Gibson et al. 2017; Latrubesse *et al.* 2017). There remains no signatory agreement for dam developers to undertake, or comply with, adequate impact assessments (Ritter *et al.* 2017). Impact assessments conducted are currently inadequate, and alongside the long-term impacts of forest fragmentation and isolation discussed within this thesis, also do not consider the basin-scale consequences of disruption to river flows (Latrubesse et al. 2017). Even with the potential means to offset some of the ecological and carbon losses incurred due to dam development discussed here, such as increasing the quality of the habitat surrounding reservoirs, the ecological damage from dam-induced tropical forest inundation is unlikely to be fully offset (Barlow *et al.* 2007; Gibson *et al.* 2011; Barlow *et al.* 2017; Gibson *et al.* 2017; Latrubesse et al. 2017).

6.4 LIMITATIONS AND FUTURE WORK

The value of long-term studies of tropical fragmented systems is highlighted by the BDFFP for example, which provide detailed insight into species turnover in fragments (Laurance *et al.* 2011). The studies within Chapters 3 and 4 are snapshots of tree and liana communities ~30 years post island isolation within the Balbina reservoir, and therefore we can only speculate what the long-term trajectory of tree and liana communities may be. Long-term studies from the BDFFP have highlighted how temporally variable the responses of trees and lianas are to edge-effects (Laurance *et al.* 2011). In addition, other studies have highlighted how sporadic events such as drought and fire often have delayed impacts on community dynamics (Barlow & Peres 2008; Phillips *et al.* 2009). Repeat surveys of trees and lianas across the Balbina landscape would allow us to make inferences about the projected future forest communities within Balbina, and the turnover rates of species.

Extrapolation of findings to the >3500 islands that have not been surveyed would allow us to produce a ‘heat map’ of island size classes that are undergoing the greatest shifts in forest composition. Production of a visual aid such as this would be extremely useful to highlight to policy-makers the long-term impacts of reservoir creation on remnant tropical forest communities, and to explain additional sources of carbon emissions associated with tropical dams. Such information could feed into the wider planning and decision-making process of whether, and where, to construct new dams in tropical regions (Fearnside, 2016; Prado *et al.*, 2016; Winemiller *et al.*, 2016).

To improve projected emissions estimates of tropical dams, we need to extend the work conducted in Chapter 3 to estimate the carbon emissions associated with tree community degradation on reservoir islands, and the mainland edge. A useful extension of the work presented in Chapters 2, 3 and 4, would be to incorporate findings from Chapter 5 and broad-scale models of secondary forest carbon uptake (Chazdon *et al.* 2016; Poorter *et al.* 2016), to design a carbon emissions offset template for tropical hydroelectric dams. Ongoing establishment of secondary forest regrowth stands throughout a dam's lifetime in allignment with existing environmental laws could potentially offset carbon emissions associated with 1) carbon emissions from the reservoir, and 2) pervasive loss of carbon storage due to degradation of insular tree communities. Nevertheless, it would likely prove impossible to offset the extreme ecological costs of dam development for aquatic systems and loss of endemic terrestrial and aquatic species, let alone the far-reaching social impacts (Peres *et al.* 2010; Kareiva 2012; Lees *et al.* 2016; Winemiller *et al.* 2016).

The work presented in Chapter 5 should be extended to include estimates of both above-ground biomass and below-ground biomass across the chronosequence stands, to generate complete carbon storage estimates for each stand age. Incorporating all carbon pools into carbon storage estimates would shed light on the relative importance of each carbon pool for carbon storage. If above- and below-ground biomass also remain constant between 40 and 120 years of stand development, this would indicate that the period of most rapid carbon uptake by secondary forests is the first ~40 years. Tropical forest conservation and climate change mitigation policies could therefore focus efforts on increasing the cover of regenerating secondary tropical forests, which may provide rapid sequestration of atmospheric carbon for ~40 years, followed by long-term storage (Chazdon *et al.* 2016) as well as providing habitat for forest species and bolster species recovery in degraded landscape (Gardner *et al.* 2009; Chazdon *et al.* 2009).

6.5 GENERAL SYNTHESIS AND CONCLUDING REMARKS

The work presented in this thesis demonstrates that the impacts of habitat fragmentation are severe when fragments are surrounded by a wholly different matrix type, such as water. All insular biological communities within manmade reservoirs are subject to an extinction debt, regardless of taxonomic group or habitat. Our results indicate that there are serious ramifications for biodiversity and carbon emissions caused by the insularization of tropical forest communities by dam development. Thus, all habitat impacted by dam creation, including reservoir islands and mainland edges, must be accounted for in environmental impact assessments when considering the viability of new dams in tropical regions. As national and international markets continue to drive the demand for resources, secondary tropical forests will likely contribute an ever increasing percentage of our global tropical forest cover. Future broad-scale models of the value of secondary forests for atmospheric carbon uptake and climate change mitigation need to now fully consider all forest carbon pools, and incorporate detailed site-specific information on soil nutrients.

This thesis highlights that intact old-growth forests are irreplaceable for biodiversity and ecosystem service provision, and landscape-scale habitat fragmentation, particularly fragmentation associated with tropical dams, leads to considerable loss of both biodiversity and carbon. Findings also highlight that through developing mechanisms to increase secondary tropical forest cover, in concert with halting deforestation of old-growth forests, there is scope for compromise between the global needs of both development and tropical forest cover.

REFERENCES

Abril, G., Guérin, F., Richard, S., Delmas, R., Galy-Lacaux, C., Gosse, P., Tremblay, A., Varfalvy, L., Dos Santos, M.A. & Matvienko, B. (2005) Carbon dioxide and methane emissions and the carbon budget of a 10-year old tropical reservoir (Petit Saut, French Guiana). *Global Biogeochemical Cycles*, **19**, 1-16.

Abril, G., Parize, M., Perez, M.A.P. & Filizola, N. (2013). Wood decomposition in Amazonian hydropower reservoirs: and additional source of greenhouse gases. Journal of South American Earth Sciences, **44**, 104-107.

Achard, F., Beuchle, R., Mayaux, P., Stibig, H.-J., Bodart, C., Brink, A., Carboni, S., Desclee, B., Donnay, F., Eva, H.D., Lupi, A., Rasi, R., Seliger, R. & Simonetti, D. (2014) Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology*, **20**, 2540–2554.

Adler, G.H. (1996) The Island Syndrome in Isolated Populations of a Tropical Forest Rodent. *Oecologica*, **108**, 694–700.

Agostinho, A., Pelicice, F. & Gomes, L. (2008) Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology*, **64**, 1119–1132.

Ahmed, S.E., Souza, C.M., Riberio, J. & Ewers, R.M. (2013) Temporal patterns of road network development in the Brazilian Amazon. *Regional Environmental Change*, **13**, 927–937.

Alvarez-Cansino, L., Schnitzer, S.A., Reid, J.P. & Powers, J.S. (2015) Liana competition with tropical trees varies seasonally but not with tree species identity. *Ecology*, **96**, 39–45.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H. V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of beta diversity: A roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.

Anderson-Teixeira, K.J., Wang, M.M.H., McGarvey, J.C. & LeBauer, D.S. (2016) Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Global change biology*, **22**, 1690–1709.

Asner, G.P., Powell, G.V.N., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., Kennedy-Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M. & Hughes, R.F. (2010) High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 16738–16742.

Aurélio-Silva, M., Anciães, M., Henriques, L.M.P., Benchimol, M. & Peres, C.A. (2016) Patterns of local extinction in an Amazonian archipelagic avifauna following 25 years of insularization. *Biological Conservation*, **199**, 101–109.

Baillie, I., Elsenbeer, H., Barthold, F., Grimm, R. & Stallard, R. (2007) Semi-detailed soil survey of Barro Colorado Island, Panama. Smithsonian Tropical Research Institute, Panama.

Baker, T., Phillips, O., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurence, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D. A., Patiño, S., Pitman, N.C., Silva, J.N.M. & Martínez, R.V. (2004b) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Nunez Vargas, P., Pitman, N.C.A., Silva, J.N.M. & Vasquez Martinez, R. (2004a) Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 353–365.

Baker, T.R., Honorio Coronado, E.N., Phillips, O.L., Martin, J., Van Der Heijden, G.M.F., Garcia, M. & Silva Espejo, J. (2007) Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia*, **152**, 495–504.

Balch, J.K., Massad, T.J., Brando, P.M., Nepstad, D.C., Curran, L.M., B, P.T.R.S., Balch, J.K., Massad, T.J., Brando, P.M., Nepstad, D.C. & Curran, L.M. (2013) Effects of high-frequency understorey fires on woody plant regeneration in southeastern Amazonian forests Effects of high-frequency understorey fires on woody plant regeneration in southeastern Amazonian forests. *Philosophical Transactions of the Royal Scoiety of London. Series B, Biological Sciences,* **386**, 1-10

Banks-Leite, C., Pardini, R., Tambosi, L., Pearse, W., Bueno, A., Bruscagin, R., Condez, T., Dixo, M., Igari, A., Martensen, A. & Metzger, J.P. (2014) Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science*, **345**, 1041–1045.

Barlow, J., Lagan, B.O. & Peres, C.A. (2003a) Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*, **19**, 291–299.

Barlow, J., Peres, C., Lagan, B.O. & Haugaasen, T. (2003b) Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, **6**, 6–8.

Barlow, J., Gardner, T. A, Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L. V, Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C. & Peres, C. A. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18555–18560.

Barlow, J. & Peres, C.A. (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1787–1794.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., Thomson, J.R., Frosini de Barros Ferraz, S., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragao, L.E.O.C., Begotti, R.A., Braga, R.F., Moreira Cardoso, T., Cosme de Oliveira Jr., R., Souza Jr., C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Melo, F.Z., Veiga, R.C.S., Venturieri, A. & Gardner, T.A. (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, **535**, 144-147.

Barreto, P. (2014). O risco de desmatamento associado a doze hidreletricas na Amazonia. Tapajos Hidreletricas Infraestrutura e Caos (de Sousa, W.C., ed.), 149-175, Instituto Aeronautica.

Barreto, P., Brandao, J.A., Martins, H., Silva, D., Souza Jr., C., Sales, M. & Feitosa, T. (2011) Risco de Desmatamento Associado a Hidreletrica de Belo Monte. *Imazon*.

Barton, K. (2016) MuMIn: Multi-Model Inference.

Basset, Y., Barrios, H., Segar, S., Srygley, R.B., Aiello, A., Warren, A.D., Delgado, F., Coronado, J., Lezcano, J., Arizala, S., Rivera, M., Perez, F., Bobadilla, R., Lopez, Y. & Ramirez, J.A. (2015) The Butterflies of Barro Colorado Island, Panama: Local Extinction since the 1930s. *Plos One*, **10**, e0136623.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1–48.

Batterman, S.A., Hedin, L.O., van Breugel, M., Ransijn, J., Craven, D.J. & Hall, J.S. (2013) Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature, **502**, 224-227.

Beck, J. & Schwanghart, W. (2010) Comparing measures of species diversity from incomplete inventories: an update. *Methods in Ecology and Evolution*, **1**, 38–44.

Benchimol, M., Mariano-Neto, E., Faria, D., Rocha-Santos, L., de Souza Pessoa, M., Gomes, F.S., Talora, D.C., Cazetta, E. (2017) Translating plant community responses to habitat loss into conservation practices: Forest cover matters. *Biological Conservation*, **209**, 499-507.

Benchimol, M. & Peres, C.A. (2015a) Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*, **103**, 408–420.

Benchimol, M. & Peres, C.A. (2015b) Widespread Forest Vertebrate Extinctions Induced by a Mega Hydroelectric Dam in Lowland Amazonia. *PloS one*, **10**, 1–15.

Benchimol, M. & Peres, C.A. (2015c) Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. *Biological Conservation*, **187**, 61–72.

Benchimol, M. & Venticinque, E.M. (2010) Harpy Eagle (*Harpia harpyja*) predation on an Infant brown Capuchin Monkey (*Cebus apella*) in the Brazilian Amazon. *Revista Brasileira de Ornitologia*, **18**, 352–354.

Benchimol, M. & Venticinque, E.M. (2014) Responses of Primates to Landscape Change in Amazonian Land-bridge islands - a Multi-scale Analysis. *Biotropica*, **46**, 470–478.

Bender, D.J., Contreras, T.A. & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, **79**, 517–533.

Benítez-Malvido, J. & Martínez-Ramos, M. (2003) Impact of Forest Fragmentation on Understory Plant Species Richness in Amazonia. *Conservation Biology*, **17**, 389–400.

Berenguer, E., Ferreira, J., Gardner, T.A., Oliveira Cruz Aragao, L.E., Barbosa de Camargo, P., Cerri, C.E., Durigan, M., de Oliveira Junior, R.C., Vieira, I.C.G. & Barlow, J. (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, (**20**)12, 3713-3726.

Bierregaard, R.O., Lovejoy, T.E., Kapos, V., Augusto dos Santos, A. & Hutchings, R.W. (1992) The Biological Dynamics of Tropical Rainforest Fragments. *BioScience*, **42**, 859–866.

Boudou, A., Maury-Brachet, R., Coquery, M., Durrieu, G. & Cossa, D. (2005) Synergic effect of gold mining and damming on mercury contamination in fish. *Environmantal Science & Technology*, **39**, 2448–2454.

Briant, G., Gond, V. & Laurance, S.G.W. (2010) Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation*, **143**, 2763–2769.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*, **58**, 445–449.

Bunnefeld, N. & Phillimore, A.B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature’s experiments. *Ecography*, **35**, 15–22.

Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd Ed).

De Camargo, P.B., Trumbore, S.E., Martinelli, L.A., Davidson, E.A., Nepstad, D.C. & Victoria, R.L. (1999) Soil carbon dynamics in regrowing forest of eastern Amazonia. *Global Change Biology*, **5**, 693–702.

Carey, E. V, Brown, S., Gillespie, J. & Lugo, A. (1994) Tree Mortality in Mature Lowland Tropical Moist and Tropical Lower Montane Moist Forests of Venezuela. *Biotropica*, **26**, 255–265.

Castello, L., McGrath, D.G., Hess, L.L., Coe, M.T., Lefebvre, P.A., Petry, P., Macedo, M.N., Renó, V.F. & Arantes, C.C. (2013) The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, **6**, 217–229.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L. V. & Melack, J.M. (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2006) Abundance-Based Similarity Indices and Their Estimation When There Are Unseen Species in Samples. *Biometrics*, **62**, 361–371.

Chao, K.J., Phillips, O.L., Gloor, E., Monteagudo, A., Torres-Lezama, A. & Martínez, R.V. (2008) Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology*, **96**, 281–292.

Chao, K.-J., Phillips, O.L., Baker, T.R., Peacock, J., Lopez-Gonzalez, G., Vásquez Martínez, R., Monteagudo, A. & Torres-Lezama, A. (2009) After trees die: quantities and determinants of necromass across Amazonia. *Biogeosciences*, **6**, 1615–1626.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., Mandle, L., Engstrom, P., Baccini, A., Sim, S., Mueller, C. & King, H. (2015) Degradation in carbon stocks near tropical forest edges. *Nature communications*, **6**, 10158.

Chauvet, S. & Forget, P.-M. (2005) Edge effects on post-dispersal seed removal in a fragmented rain forest in French Guiana. *Journal of Tropical Ecology*, **21**, 113–116.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H. & Webb, C. (2006) Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecological Applications*, **16**, 2356–2367.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E. & Miller, S.E. (2009) The potential for species conservation in tropical secondary forests. *Conservation biology*, **23**, 1406–1417.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Duran, S.M., Espirito-Santo, M.M., Fandino, M.C., Cesar, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Martinez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Munoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Orihuela-Belmonte, E., Pena-Claros, M., Perez-Garcia, E.A., Piotto, D., Powers, J.S., Rodriguez-Velazquez, J., Romero-Perez, I.E., Ruiz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B. & Poorter, L. (2016) Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances*, **2**, e1501639–e1501639.

Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F. & Veldkamp, E. (2002) Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *Forest Ecology and Management*, **164**, 237–248.

Cochrane, M.A. & Laurance, W.F. (2002) Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology*, **18**, 311–325.

Cochrane, M.A. & Laurance, W.F. (2008) Synergisms among fire, land use, and climate change in the Amazon. *Ambio*, **37**, 522–7.

Collins, C.D., Banks-Leite, C., Brudvig, L.A., Foster, B.L., Cook, W.M., Damschen, E.I., Andrade, A., Austin, M., Camargo, J.L., Driscoll, D.A., Holt, R.D., Laurance, W.F., Nicholls, A.O. & Orrock, J.L. (2017) Fragmentation affects plant community composition over time. *Ecography*, **40**, 119–130.

Connor, E.F. & McCoy, E.D. (1979) The Statistics and Biology of the Species-Area Relationship. *The American Naturalist*, **113**, 791–833.

Cook, W.M., Lane, K.T., Foster, B.L. & Holt, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619–623.

Cornejo, F. & Janovec, J. (2010) *Seeds of Amazonian Plants*. Princeton University Press, Princeton.

Cosson, J., Pons, J.-M. & Masson, D. (1999a) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology*, **15**, 515–534.

Cosson, J.F., Ringuet, S., Claessens, O., de Massary, J.C., Dalecky, A., Villiers, J.F., Granjon, L. & Pons, J.M. (1999b) Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. *Biological Conservation*, **91**, 213–222.

Costanza et al. (1997) The value of the world’s ecosystem services and natural capital. *Nature*, **387**, 253–260.

Cramer, J.M., Mesquita, R.C.G. & Williamson, G.B. (2007) Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, **137**, 415–423.

Crawley, M.J. (2005) Statistics: An Introduction Using R. John Wiley & Sons Ltd, Chichester.

Crawley, M.J. & Harral, J.E. (2001) Scale dependence in plant biodiversity. *Science*, **291**, 864–868.

de Campos Franci, L., Svenning, J.-C., Balslev, H., Martins, F.R. & Nabe-Nielsen, J. (2016). The demography of a dominant Amazon liana species exhibits little environmental sensitivity. *Journal of Tropical Ecology*, **32**, 79-82.

Deemer, B., Harrison, J., Li, S., Beaulieu, J., Delsontro, T., Barros, N., Bezerra-Neto, J., Powers, S., Dos Santos, M. & Vonk, J. (2016) Greenhouse Gas Emissions from Reservoir Water Surfaces: A New Global Synthesis. *BioScience*, **66**, 949–964.

DeFries, R.S., Rudel, T., Uriarte, M. & Hansen, M. (2010) Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geosciences*, **3**, 178–181.

Demarty, M. & Bastien, J. (2011) GHG emissions from hydroelectric reservoirs in tropical and equatorial regions - review of 20 years of CH4 emission measurements. *Energy Policy*, **39**, 4197–4206.

Denslow, J.S. & Guzman, S.G. (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science*, **11**, 201–212.

Dent, D.H. (2010) Defining the conservation value of secondary tropical forests. *Animal Conservation*, **13**, 14–15.

Dent, D.H. & Wright, S.J. (2009) The future of tropical species in secondary forests: A quantitative review. *Biological Conservation*, **142**, 2833–2843.

Dent, D.H., DeWalt, S.J. & Denslow, J.S. (2013) Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. *Journal of Vegetation Science*, **24**, 530–542.

Develey, P.F. & Stouffer, P.C. (2001) Effects of Roads on Movements by Understory Birds in Mixed-Species Flocks in Central Amazonian Brazil. *Conservation biology*, **15**, 1416–1422.

DeWalt, S.J., Schnitzer, S.A. & Denslow, J.S. (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology*, **16**, 1–19.

DeWalt, S.J., Maliakal, S.K. & Denslow, J.S. (2003) Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management*, **182**, 139–151.

DeWalt, S.J. & Chave, J. (2004) Structure and Biomass of Four Lowland Neotropical Forest. *Biotropica*, **36**, 7–19.

Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest pacific islands. *Proceedings of the National Academy of Sciences of the United States of America*, **69**, 3199–3203.

Diamond, J. (2001) Dammed Experiments! *Science*, **294**, 1847–1848.

Dixon, R.K., Solomon, A., Brown, S., Houghton, R.A., Trexier, M.C. & Wisniewski, J. (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.

Don, A., Schumacher, J. & Freibauer, A. (2011) Impact of tropical land-use change on soil organic carbon stocks - a meta-analysis. *Global Change Biology*, **17**, 1658–1670.

Durigan, M.R., Cherubin, M.R., Barbosa de Camargo, P., Nunes Ferreira, J., Berenguer, E., Gardner, T.A., Barlow, J., Tadeu dos Santos Dias, C., Signor, D., de Oliveira Junior, R., Cerri, C.E.P.C. (2017) Soil organic matter responses to anthropogenic forest disturbance and land use change in the Eastern Brazilian Amazon. *Sustainability*, **9**(3), 1-16.

EIA. (2013) International Energy Outlook 2013. U.S. Energy Information Administration, Washington, DC, USA.

Emer, C., Venticinque, E.M. & Fonseca, C.R. (2013) Effects of dam-induced landscape fragmentation on amazonian ant-plant mutualistic networks. *Conservation Biology*, **27**, 763–773.

ESRI. (2011) ArcGIS Desktop. Release 10. Environmental Systems Research Institute. Redlands, CA, USA.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological reviews*, **81**, 117–142.

Ewers, R.M., Thorpe, S. & Didham, R.K. (2007) Synergistic Interactions between Edge and Area Effects in a Heavily Fragmented Landscape. *Ecology*, **88**, 96–106.

Ewers, R.M., Andrade, A., Laurance, S.G., Camargo, J.L., Lovejoy, T.E. & Laurance, W.F. (2017) Predicted trajectories of tree community change in Amazonian rainforest fragments. *Ecography*, **40**, 26-35.

FAO. (2010) Global Forest Resources Assessment 2010. Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO. (2016) Global Forest Resources Assessment 2015. How Are the World's Forests Changing? 2nd Edition. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology and Systematics*, **34**, 487–515.

Fahrig, L. (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.

de Faria, F.A.M., Jaramillo, P., Sawakuchi, H.O., Richey, J.E. & Barros, N. (2015) Estimating greenhouse gas emissions from future Amazonian hydroelectric reservoirs. *Environmental Research Letters*, **10**, 1-13.

Fearnside, P.M. (1989) Brazil's Balbina Dam: Environment versus the Legacy of the Pharaohs in Amazonia. *Environmental Management*, **13**, 401–423.

Fearnside, P.M. (1999) Social Impacts of Brazil's Tucurui Dam. *Environmental Management*, **24**, 483–495.

Fearnside, P.M. (2001) Environmental Impacts of Brazil's Tucurui Dam: Unlearned Lessons for Hydroelectric Development in Amazonia. *Environmental Management*, **27**, 377–396.

Fearnside, P.M. (2002a) Greenhouse Gas Emissions from a Hydroelectric Reservoir (Brazil's Tucurui Dam) and the Energy Policy Implications. *Water, Air, and Soil Pollution*, **133**, 69–96.

Fearnside, P.M. (2002b) Soybean cultivation as a threat to the environment in Brazil. *Environmental Conservation*, **28**, 23–38.

Fearnside, P.M. (2002c) Avança Brasil: environmental and social consequences of Brazil's planned infrastructure in Amazonia. *Environmental management*, **30**, 735–747.

Fearnside, P.M. (2006) Dams in the Amazon: Belo Monte and Brazil's hydroelectric development of the Xingu River Basin. *Environmental management*, **38**, 16–27.

Fearnside, P.M. (2008) The roles and movements of actors in the deforestation of Brazilian Amazonia. *Ecology and Society*, **13**, 1-22.

Fearnside, P.M. (2009) Hydroelectric Dams in the Brazilian Amazon as Sources of "Greenhouse" Gases. *Environmental Conservation*, **22**, 7-19.

Fearnside, P.M. (2013) Carbon credit for hydroelectric dams as a source of greenhouse-gas emissions: the example of Brazil's Teles Pires Dam. *Mitigation and Adaptation Strategies for Global Change*, **18**, 691–699.

Fearnside, P.M. (2016a) Environmental and Social Impacts of Hydroelectric Dams in Brazilian Amazonia: Implications for the Aluminum Industry. *World Development*, **77**, 48–65.

Fearnside, P.M. (2016b) Tropical dams: to build or not to build? *Science*, **329**, 1466–1468.

Fearnside, P.M. & Pueyo, S. (2012) Greenhouse-gas emissions from tropical dams. *Nature Climate Change*, **2**, 382–384.

Feeley, K.J. & Terborgh, J.W. (2006) Habitat Fragmentation and Effects of Herbivore (Howler Monkey) Abundances on Bird Species Richness. *Ecology*, **87**, 144–150.

Feeley, K.J., Gillespie, T.W., Lebbin, D.J. & Walter, H.S. (2007) Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. *Animal Conservation*, **10**, 493–501.

Feer, F. & Hingrat, Y. (2005) Effects of Forest Fragmentation on a Dung Beetle Community in French Guiana. *Conservation Biology*, **19**, 1103–1112.

Feldpausch, T.R., Rondon, M.A., Fernandes, E.C.M. & Riha, S.J. (2004) Carbon and Nutrient Accumulation in Secondary Forests Regenerating on Pastures in Central Amazonia. *Ecological Applications*, **14**, 164–176.

Ferreira, L. V, Neckel-Oliveira, S., Galatti, U., Fáveri, S.B. & Parolin, P. (2012) Forest structure of artificial islands in the Tucuruí dam reservoir in northern Brazil: a test core-area model. *Acta Amazonica*, **42**, 221–226.

Finer, M. & Jenkins, C.N. (2012) Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PloS one*, **7**, e35126.

Finer, M., Jenkins, C.N., Pimm, S.L., Keane, B. & Ross, C. (2008) Oil and gas projects in the Western Amazon - threats to wilderness, biodiversity and indigenous peoples. *PloS one*, **3**. e2932.

Foley, J.A. (2005) Global Consequences of Land Use. *Science*, **309**, 570–574.

Foley, J.A., Asner, G.P., Costa, M.H., Coe, M.T., Defries, R., Gibbs, H.K., Howard, E.A., Olson, S., Patz, J., Ramankutty, N. & Snyder, P. (2007) Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment*, **5**, 25–32.

Fonseca, W., Benayas, J.M.R. & Alice, F.E. (2011) Carbon accumulation in the biomass and soil of different aged secondary forests in the humid tropics of Costa Rica. *Forest Ecology and Management*, **262**, 1400–1408.

Ford, H.A., Walters, J.R., Cooper, C.B., Debus, S.J.S. & Doerr, V.A.J. (2009) Extinction debt or habitat change? - Ongoing losses of woodland birds in north-eastern New South Wales, Australia. *Biological Conservation*, **142**, 3182–3190.

Forman, R.T.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology, Evolution, and Systematics*, **29**, 207–31.

Fortunel, C., Paine, C.E.T., Fine, P.V.A., Kraft, N.J.B. & Baraloto, C. (2014) Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*, **102**, 145–155.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A. & Sodhi, N.S. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, **12**, 561–582.

Gelman, A. & Su, Y.-S. (2016) arm: Data Analysis Using Regression and Multilevel/Hierarchical Models.

Gentry, A.H. (1988) Tree species richness of upper Amazonian forests. *Ecology*, **85**, 156–159.

Gentry, A.H. (1993) A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru). The University of Chicago Press, Chicago.

Gerwing, J.J. (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management*, **157**, 131-141.

Gerwing, J.J. (2004) Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. *Forest Ecology and Management*, **190**, 57–72.

Gerwing, J.J. & Farias, D.L. (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology*, **16**, 327–335.

Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R.B., Kenfack, D., Martinez-Ramos, M., Parren, M., Parthasarathy, N., Perez-Salicrup, D.R., Putz, F.E. & Thomas, D.W. (2006) A Standard Protocol for Liana Censuses. *Biotropica*, **38**, 256–261.

Gibbs, H.K., Brown, S., Niles, J.O. & Foley, J.A. (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, **2**, 045023.

Gibbs, H.K., Rausch, L., Munger, J., Schelly, I., Morton, D.C., Noojipady, P., Soares-Filho, B., Barreto, P., Micol, L. & Walker, N.F. (2015) Brazil's Soy Moratorium. *Science*, **347**, 377-378.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T. A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378–381.

Gibson, L., Lynam, A.J., Bradshaw, C.J.A., He, F., Bickford, D.P., Woodruff, D.S., Bumrungsri, S. & Laurance, W.F. (2013) Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, **341**, 1508–1510.

Gibson, L., Wilman, E. & Laurance, W. (2017). How green is green? Trends in Ecology and Evolution, **2306**, 1-14.

Gilani H.R. & Innes, J. (2017). Environmental and social aspects of underwater logging. Geoforum, **86**, 188-191.

Gonzalez, A. (2000) Community relaxation in fragmented landscapes: The relation between species richness, area and age. *Ecology Letters*, **3**, 441–448.

Google. (2015) Google Earth Pro.

Grace, J., Mitchard, E. & Gloor, E. (2014) Perturbations in the carbon budget of the tropics. *Global Change Biology*, **20**, 3238–3255.

Grimm, R., Behrens, T., Märker, M. & Elsenbeer, H. (2008) Soil organic carbon concentrations and stocks on Barro Colorado Island - Digital soil mapping using Random Forests analysis. *Geoderma*, **146**, 102–113.

van Groenigen, K.-J., Six, J., Hungate, B.A., de Graaff, M.-A., van Breemen, N. & van Kessel, C. (2006) Element interactions limit soil carbon storage. *Proceedings of the National Academy of Sciences*, **103**, 6571–6574.

Grubb, P.J. (1977) the Maintenance of Species-Richness in Plant Communities: the Importance of the Regeneration Niche. *Biological Reviews*, **52**, 107–145.

Gullison, R.E., Frumhoff, P.C., Canadell, J.G., Field, C.B., Nepstad, D.C., Hayhoe, K., Avissar, R., Curran, L.M., Friedlingstein, P., Jones, C.D. & Nobre, C. (2007) Tropical Forests and Climate Policy. *Science*, **316**, 1136163–1136986.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X. & Townshend, J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, **1**, 1–9.

Halley, J.M., Sgardeli, V. & Triantis, K.A. (2014) Extinction debt and the species-area relationship: a neutral perspective. *Global Ecology and Biogeography*, **23**, 113–123.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, **42**, 3–16.

Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.

Hanski, I. & Ovaskainen, O. (2002) Extinction Debt at Extinction Threshold. *Conservation Biology*, **16**, 666–673.

Hanski, I., Zurita, G.A, Bellocq, M.I. & Rybicki, J. (2013) Species-fragmented area relationship. *Proceedings of the National Academy of Sciences*, **110**, 12715–20.

Haya, B., McCully, P. & Pearson, B. (2002) Damming The CDM: Why Big Hydro Is Ruining the Clean Development Mechanism. International Rivers/CDM Watch, Berkeley, CA, US.

van der Heijden, G.M., Schnitzer, S.A., Powers, J.S. & Phillips, O.L. (2013) Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica*, **45**, 682–692.

van der Heijden, G.M.F., Powers, J.S. & Schnitzer, S.A. (2015) Lianas reduce carbon accumulation and storage in tropical forests. *Proceedings of the National Academy of Sciences*, **112**, 13267–13271.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.

Houghton, R.A. (2012) Carbon emissions and the drivers of deforestation and forest degradation in the tropics. *Current Opinion in Environmental Sustainability*, **4**, 597–603.

Houghton, R.A., Byers, B. & Nassikas, A.A. (2015) A role for tropical forests in stabilizing atmospheric CO2. *Nature Climate Change*, **5**, 1022–1023.

Hubbell, S.P., He, F., Condit, R., Borda-de-Agua, L., Kellner, J. & ter Steege, H. (2008) How many tree species are there in the Amazon and how many of them will go extinct? *Proceedings of the National Academy of Sciences*, **105**, 11498–11504.

Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, Carbon, and Nutrient Dynamics of Secondary Forests in a Humid Tropical Region of México. *Ecology*, **80**, 1892–1907.

Hughes, R.F., Kauffman, J.B. & Cummings, D.L. (2002) Dynamics of Aboveground and Soil Carbon and Nitrogen Stocks and Cycling of Available Nitrogen along a Land-use Gradient in Rondônia, Brazil. *Ecosystems*, **5**, 244–259.

Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y. & Field, C.B. (2003) Nitrogen and Climate Change. *Science*, **302**, 1512–1513.

ICOLD. (2016) International Commission on Large Dams. http://www.icold-cigb.org

Ingwell, L.L., Joseph Wright, S., Becklund, K.K., Hubbell, S.P. & Schnitzer, S.A. (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology*, **98**, 879–887.

International Energy Agency. (2000) Hydropower and the Environment: Effectiveness of Mitigation Measures. Paris, France.

International Energy Agency. (2006) Hydropower Good Practices: Environmental Mitigation Measures and Benefits. Paris, France.

International Rivers. (2012) *Belo Monte: Massive Dam Project Strikes at the Heart of the Amazon*. Berkeley, CA, USA.

IPCC. (2006) Forest land. 2006 IPCC Guidelines for National Greenhouse Gas Inventories, pp. 4.1-4.83. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

IPCC. (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds RK Pachauri and LA Meyer). Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Jobbagy, E.G. & Jackson, R.B. (2000) The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation. *Ecological Applications*, **10**, 423–436.

Jones, I.L., Bunnefeld, N., Jump, A.S., Peres, C.A. & Dent, D.H. (2016) Extinction debt on reservoir land-bridge islands. *Biological Conservation*, **199**, 75–83.

Kareiva, P.M. (2012) Dam choices: Analyses for multiple needs. *Proceedings of the National Academy of Sciences*, **109**, 5553–5554.

Kareiva, P. & Wennergren, U. (1995) Connecting landscape patterns to ecosystem and population processes. *Nature*, **373**, 299–302.

Kemenes, A., Forsberg, B.R. & Melack, J.M. (2007) Methane release below a tropical hydroelectric dam. *Geophysical Research Letters*, **34**, 1-5.

Kirby, K.R., Laurance, W.F., Albernaz, A.K., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M. & da Costa, C. (2006) The future of deforestation in the Brazilian Amazon. *Futures*, **38**, 432–453.

Kitzes, J. & Harte, J. (2015) Predicting extinction debt from community patterns. *Ecology*, **96**, 2127–2136.

Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, **15**, 8–20.

Kurzel, B.P., Schnitzer, S.A. & Carson, W.P. (2006) Predicting liana crown location from stem diameter in three Panamanian lowland forests. *Biotropica*, **38**, 262–266.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, **24**, 564–571.

Lambert, T.D., Adler, G.H., Riveros, C.M., Lopez, L., Ascanio, R. & Terborgh, J. (2003) Rodents on tropical land-bridge islands. *Journal of Zoology*, **260**, 179–187.

Larjavaara, M. & Muller-Landau, H.C. (2009) Woody debris research protocol: Long transects. CTFS Global Forest Carbon Initiative.

Larjavaara, M. & Muller-Landau, H.C. (2010a) Rethinking the value of high wood density. *Functional Ecology*, **24**, 701–705.

Larjavaara, M. & Muller-landau, H.C. (2010b) Comparison of decay classification, knife test, and two penetrometers for estimating wood density of coarse woody debris. *Canadian Journal of Forest Research*, **40**, 2313–2321.

Larjavaara, M. & Muller-landau, H.C. (2011) Cross-Section Mass : An Improved Basis for Woody Debris Necromass Inventory. *Silva Fennica*, **45**, 291–298.

Lasky, J.R., Sun, I.F., Su, S.H., Chen, Z.S. & Keitt, T.H. (2013) Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology*, **101**, 722–733.

Latrubesse, E.M., Arima, E.Y., Dunne, T., Park, E. Baker, V.R., d'Horta, F.M., Wight, C., Wittmann, F., Zuanon, J., Baker, P.A., Ribas, C.C., Norgaard, R.B., Filizola, N., Ansar, A., Flyvbjerg, B. & Stevaux, J.C. (2017) Damming the rivers of the Amazon basin. *Nature*, **546**, 363-369.

Laue, J. & Arima, E. (2014) Spatially explicit models of land abandonment in the Amazon. *Journal of Land Use Science*, **11**(1), 48-75.

Laurance, W.F. (1998) A crisis in the making: responses of Amazonian forests to land use and climate change. *Trends in Ecology & Evolution*, **13**, 411–415.

Laurance, W.F. (2001) The future of the Brazilian Amazon. *Science*, **291**, 438–439.

Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. & Lovejoy, T.E. (2001) Rain Forest Fragmentation and the Structure of Amazonian Liana Communities. *Ecology*, **82**, 105–116.

Laurance, W.F., Albernaz, A.K.M. & da Costa, C. (2002a) Is deforestation accelerating in the Brazilian Amazon? *Environmental Conservation*, **28**, 305-311.

Laurance, W.F., Albernaz, A.K.M., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M. & da Costa, C. (2002b) Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography*, **29**, 737–748.

Laurance, S.G.W., Stouffer, P.C. & Laurance, W.F. (2004) Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology*, **18**, 1099–1109.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L. & Capretz, R.L. (2006a) Rain Forest Fragmentation and the Proliferation of Successional Trees. *Ecology*, **87**, 469–482.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J., Harms, K.E. & D'Angelo, S. (2006b) Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences*, **103**, 19010–19014.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizão, R.C.C. & Ribeiro, J.E. (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*, **2**, e1017.

Laurance, W. (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*, **141**, 1731–1744.

Laurance, W.F. & Curran, T.J. (2008) Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology*, **33**, 399–408.

Laurance, W.F., Goosem, M. & Laurance, S.G.W. (2009) Impacts of roads and linear clearings on tropical forests. *Trends in ecology & evolution*, **24**, 659–69.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Bruce Williamson, G., Benítez-Malvido, J. & Vasconcelos, H.L. (2011) The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, **144**, 56–67.

Laurance, W., Andrade, A., Magrach, A., Camargo, J., Campbell, M., Fearnside, P., Edwards, W., Valsko, J., Lovejoy, T. & Laurance, S. (2014a) Apparent environmental synergism drives the dynamics of Amazonian forest fragments. *Ecology*, **95**, 3018–3026.

Laurance, W.F., Sayer, J. & Cassman, K.G. (2014b) Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution*, **29**, 107–116.

Lees, A.C., Peres, C.A., Fearnside, P.M., Schneider, M. & Zuanon, J.A.S. (2016) Hydropower and the future of Amazonian biodiversity. *Biological Conservation*, **25**, 451-466.

Legendre, P., Fortin, M.-J. & Borcard, D. (2015) Should the Mantel test be used in spatial analysis? *Methods in Ecology and Evolution*, **6**, 1239–1247.

Leigh, E.G.J., Rand, A.S. & Windsor, D.M. (1982) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (eds. EGJ Leigh, AS Rand, and DM Windsor). Smithsonian Institution Press, Washington, DC, USA.

Leigh, E.G., Wright, S.J., Herre, E.A. & Putz, F.E. (1993) The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology*, **7**, 76–99.

Letcher, S.G. & Chazdon, R.L. (2012) Life History Traits of Lianas During Tropical Forest Succession. *Biotropica*, **44**, 720–727.

Leutner, B. & Horning, N. (2017) Tools for remote sensing data analysis. RStoolbox (version 0.1.9)

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, K.M., Ewango, C.E., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R. & Woll, H. (2009) Increasing carbon storage in intact African tropical forests. *Nature*, **457**, 1003–1006.

Li, D., Niu, S. & Luo, Y. (2012) Global patterns of the dynamics of soil carbon and nitrogen stocks following afforestation: A meta-analysis. *New Phytologist*, **195**, 172–181.

Lôbo, D., Leão, T., Melo, F.P.L., Santos, A.M.M. & Tabarelli, M. (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions*, **17**, 287–296.

Lomolino, M. V. (2000) A call for a new paradigm of island biogeography. *Global Ecology and Biogeography*, **9**, 1–6.

Lopez, L. & Terborgh, J. (2007) Seed predation and seedling herbivory as factors in tree recruitment failure on predator-free forested islands. *Journal of Tropical Ecology*, **23**, 129-137.

St. Louis, V., Kelly, C.A., Duchemin, É., Rudd, J.W.M. & Rosenberg, D.M. (2013) Reservoir Surfaces as Sources of Greenhouse Gases to the Atmosphere: A Global Estimate. *BioScience*, **50**, 766–775.

Luo, Y., Su, S., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R. & Field, C.B. (2004) Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide. *BioScience*, **54**, 731–739.

MacArthur, R. & Wilson, E. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) The Theory of Island Biogeography. Princeton University Press, Princeton.

Mace, G., Masundire, H. & Baillie, J. (2005) Biodiversity. Ecosystems and Human Well-being: Current State and Trends (eds G. Ceballos, S. Lavorel, G. Orians & S. Pacala). Millenium Ecosystem Assessment.

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V. & Edwards, D.P. (2016) Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? *Functional Ecology*, **31**, 542–552.

Magurran, A.E. & McGill, B. (2011) Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press.

Mahasenan, N., Smith, S. & Humphreys, K. (2003). Greenhouse Gas Control Technologies – 6th International Conference. Processdings of the 6th International Conference on Greenhouse Gas Control Technologies. Volume II, 995-1000.

Malhi, Y. & Grace, J. (2000) Tropical forests and atmospheric carbon dioxide. *Trends in Ecology & Evolution*, **15**, 332–337.

Malhi, Y., Baker, T., Phillips, O., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C., Fiore, A., Higuchi, N., Killeen, T., Laurance, S., Laurance, W., Lewis, S., Montoya, L., Monteagudo, A., Neill, D., Vargas, P., Patino, S., Pitman, N., Quesada, C., Salomao, R., Silva, J., Lezama, A., Martinez, R., Terborgh, J., Vincenti, B. & Lloyd, J. (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 563–591.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martínez, R.V. & Vinceti, B. (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107–1138.

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W. & Nobre, C.A. (2008) the Fate of the Amazon. *Science*, **319**, 169–172.

Malhi, Y., Aragão, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., da Costa, A.C.L., Hutyra, L.R., Oliveira, P., Patiño, S., Pyle, E.H., Robertson, A.L. & Teixeira, L.M. (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, **15**, 1255–1274.

Marín-Spiotta, E. & Sharma, S. (2013) Carbon storage in successional and plantation forest soils: a tropical analysis. *Global Ecology and Biogeography*, **22**, 105–117.

Marin-Spiotta, E., Silver, W.L., Swanston, C.W. & Ostertag, R. (2009) Soil organic matter dynamics during 80 years of reforestation of tropical pastures. *Global Change Biology*, **15**, 1584–1597.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J. & Böhning-Gaese, K. (2012) Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. *Conservation Biology*, **26**, 1072–1081.

Martensen, A.C., Ribeiro, M.C., Banks-Leite, C., Prado, P.I. & Metzger, J.P. (2012) Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. *Conservation Biology*, **26**, 1100–1111.

Martin, P.A., Newton, A.C., Bullock, J.M. & B, P.R.S. (2013) Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the National Academy of Sciences*, **280**, 1–8.

Mascaro, J., Asner, G.P., Muller-Landau, H.C., Van Breugel, M., Hall, J. & Dahlin, K. (2011) Controls over aboveground forest carbon density on Barro Colorado Island, Panama. *Biogeosciences*, **8**, 1615–1629.

Mendenhall, C.D., Sekercioglu, C.H., Brenes, F.O., Ehrlich, P.R. & Daily, G.C. (2011) Predictive model for sustaining biodiversity in tropical countryside. *Proceedings of the National Academy of Sciences*, **108**, 16313–16316.

Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A. & Daily, G.C. (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, **509**, 213–217.

Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira, A.M.G. & Pardini, R. (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biological Conservation*, **142**, 1166–1177.

Michalski, F., Nishi, I. & Peres, C.A. (2007) Disturbance-Mediated Drift in Tree Functional Groups in Amazonian Forest Fragments. *Biotropica*, **39**, 691–701.

Mitchard, E.T., Saatchi, S.S., Baccini, A., Asner, G.P., Goetz, S.J., Harris, N.L. & Brown, S. (2013) Uncertainty in the spatial distribution of tropical forest biomass: a comparison of pan-tropical maps. *Carbon Balance and Management*, **8**, 1-13.

Moore, R.P., Robinson, W.D., Lovette, I.J. & Robinson, T.R. (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecol Lett*, **11**, 960–968.

Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20–32.

Muller-Landau, H.C. (2010) The tolerance-fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences*, **107**, 4242–4247.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, **10**, 58–62.

Muscarella, R. & Uriarte, M. (2016) Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society of London, Seris B, Biological Sciences*, **283**, 20152434.

Nakhasathien, S. (2009) Chiew Larn Dam Wildlife Rescue Operation. *Oryx*, **23**, 146-154.

Nascimento, H.E.M. & Laurance, W.F. (2002) Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecology and Management*, **168**, 311–321.

Nascimento, H.E.M. & Laurance, W.F. (2004) Biomass dynamics in amazonian forest fragments. *Ecological Applications*, **14**, 127–138.

Nascimento, H.E.M., Andrade, A.C.S., Camargo, J.L.C., Laurance, W.F., Laurance, S.G. & Ribeiro, J.E.L. (2006a) Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology*, **20**, 853–860.

Nascimento, H.E.M., Andrade, A.N.A.C.S., Camargo, J., Laurance, W.F., Laurance, S.G. & Ribeiro, J. (2006b) Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments. *Conservation Biology*, **20**, 853–860.

Nepstad, D.C., Verissimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M. & Brooks, V. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.

Neumann-Cosel, L., Zimmermann, B., Hall, J.S., van Breugel, M. & Elsenbeer, H. (2011) Soil carbon dynamics under young tropical secondary forests on former pastures—A case study from Panama. *Forest Ecology and Management*, **261**, 1625–1633.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R. a, Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Dıáz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha Pinto Correia, D., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P. & Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, **520**, 45-50.

Ngo, K.M., Turner, B.L., Muller-Landau, H.C., Davies, S.J., Larjavaara, M., Nik Hassan, N.F. Bin & Lum, S. (2013) Carbon stocks in primary and secondary tropical forests in Singapore. *Forest Ecology and Management*, **296**, 81–89.

Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science*, **308**, 405–408.

Oki, T. & Kanae, S. (2006) Global Hydrological Cycles and World Water Resources. *Science*, **313**, 1068–1072.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2016) vegan: Community Ecology Package.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience*, **51**, 933-938.

Paine, C.E.T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., de Gouvenain, R.C., Doucet, J.L., Doust, S., Fine, P.V.A., Fortunel, C., Haase, J., Holl, K.D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., Mart??nez-Garza, C., Messier, C., Paquette, A., Philipson, C., Piotto, D., Poorter, L., Posada, J.M., Potvin, C., Rainio, K., Russo, S.E., Ruiz-Jaen, M., Scherer-Lorenzen, M., Webb, C.O., Wright, S.J., Zahawi, R.A. & Hector, A. (2015) Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology*, **103**, 978–989.

Palace, M., Keller, M., Asner, G.P., Silva, J.N.M. & Passos, C. (2007) Necromass in undisturbed and logged forests in the Brazilian Amazon. *Forest Ecology and Management*, **238**, 309–318.

Palace, M., Keller, M., Hurtt, G. & Frolking, S. (2012) A Review of Above Ground Necromass in Tropical Forests. Tropical Forests (eds P. Sudarshana, M. Nageswara-Rao & J.R. Soneji), pp. 215–252. Intech (online publisher).

Palmeirim, A.F., Peres, C.A. & Rosas, F.C.W. (2014) Giant otter population responses to habitat expansion and degradation induced by a mega hydroelectric dam. *Biological Conservation*, **174**, 30–38.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–93.

Pasquini, S.C., Wright, S.J., Santiago, L.S. & Uriarte, M. (2015) Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. *Ecology*, **96**, 1866–1876.

Paul, K.I., Polglase, P.J., Nyakuengama, J.G. & Khanna, P.K. (2000) Change in Soil Carbon Following Afforestation or Reforestation. *Forest Ecology and Management*, **168**, 241–257.

Paz, C.P., Goosem, M., Bird, M., Preece, N., Goosem, S., Fensham, R. & Laurance, S. (2016) Soil types influence predictions of soil carbon stock recovery in tropical secondary forests. *Forest Ecology and Management*, **376**, 74–83.

Pearson. T.R.H., Brown, S., Murray, L. & Sidman, G. (2017). Greenhouse gas emission from tropical forest degradation: and underestimated source. Carbon Balance and Management, **12**(3), 1-11.

Pereira, D., Santos, D., Vedoveto M., Guimaraes, J. Verissimo, A. (2010) Fatos Florestais da Amazonia 2010. Imazon, Belem.

Peres, C.A. (2001a) Paving the way to the future of Amazonia. *Trends in Ecology & Evolution*, **16**, 217–219.

Peres, C.A. (2001b) Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. *Conservation Biology*, **15**, 1490–1505.

Peres, C.A. (2005) Why We Need Megareserves in Amazonia. *Conservation Biology*, **19**, 728–733.

Peres, C.A. & Lake, I.R. (2003) Extent of Nontimber Resource Extraction in Tropical Forests: Accessibility to Game Vertebrates by Hunters in the Amazon Basin. *Conservation Biology*, **17**, 521–535.

Peres, C.A., Gardner, T.A., Barlow, J., Zuanon, J., Michalski, F., Lees, A.C., Vieira, I.C.G., Moreira, F.M.S. & Feeley, K.J. (2010) Biodiversity conservation in human-modified Amazonian forest landscapes. *Biological Conservation*, **143**, 2314–2327.

Pérez-Salicrup, D.R., Sork, V.L. & Putz, F.E. (2001) Lianas and Trees in a Liana Forest of Amazonian Bolivia. *Biotropica*, **33**, 34–47.

Phillips, O.L., Martínez, R.V., Mendoza, A.M., Baker, T.R. & Vargas, P.N. (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, **86**, 1250–1258.

Phillips, O.L., Vásquez Martínez, R., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Núñez Vargas, P., Alexiades, M., Cerón, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vinceti, B. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*, **418**, 770–774.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., Alves de Oliveira, A.C., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. Ter, Stropp, J., Vásquez, R., Zelazowski, P., Alvarez Dávila, E., Andelman, S., Andrade, A., Chao, K., Erwin, T., Di Fiore, A., Honorio C, E., Keeling, H., Killeen, T.J., Laurance, W.F., Peña Cruz, A., Pitman, N.C.A., Núñez Vargas, P., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J. & Torres-Lezama, A. (2009) Drought sensitivity of the Amazon Rainforest. *Science*, **323**, 1344–1347.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., V, P.N., Neill, A., Cerón, C.E., Palacios, W.A. & Aulestia, M. (2001) Dominance and Distribution of Tree Species in Upper Amazonian *Terra Firme* Forests. *Ecology*, **82**, 2101–2117.

Poorter, L. (2007) Are species adapted to their regeneration niche, adult niche, or both? *The American naturalist*, **169**, 433–442.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O. & Wright, I.J. (2008) Are Functional Traits Good Predictors of Demographic Rates? Evidence From Five Neotropical Forests. *Ecology*, **89**, 1908–1920.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J. a., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B. & Rozendaal, D.M.A. (2016) Biomass resilience of Neotropical secondary forests. *Nature*, **530**, 211-214.

Poulsen, J.R., Koerner, S.E., Miao, Z., Medjibe, V.P., Ngok Banak, L. & White, L.J.T. (2016) Forest structure determines the distribution of large lianas in Gabon. *Global Ecology and Biogeography*, **26**, 472-485.

Powers, J.S. (2004) Changes in Soil Carbon and Nitrogen after Contrasting Land-use Transitions in Northeastern Costa Rica. *Ecosystems*, **7**, 134–146.

Powers, J.S. & Schlesinger, W.H. (2002) Relationships among soil carbon distributions and biophysical factors at nested spatial scales in rain forests of northeastern Costa Rica. *Geoderma*, **109**, 165–190.

Prado, F.A., Athayde, S., Mossa, J., Bohlman, S., Leite, F. & Oliver-Smith, A. (2016) How much is enough? An integrated examination of energy security, economic growth and climate change related to hydropower expansion in Brazil. *Renewable and Sustainable Energy Reviews*, **53**, 1132–1136.

Putz, F.E. (1984) The Natural History of Lianas on Barro Colorado Island, Panama. *Ecology*, **65**, 1713–1724.

R Core Team. (2016) R: A language and environment for statistical computing.

Ries, L., Fletcher, R.J., Battin, J. & Sisk, T.D. (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and Systematics*, **35**, 491–522.

Ritter, C.D., McCrate, G., Nilsson, R.H., Fearnside, P.M., Palme, U. & Antonelli, A. (2017) Environmental impact assessment in Brazilian Amazonia: Challenges and prospects to assess biodiversity. *Biological Conservation*, **206**, 161–168.

Robinson, W.D. (1999) Long-Term Changes in the Avifauna of Barro Colorado Island, Panama, a Tropical Forest Isolate. *Conservation Biology*, **13**, 85–97.

Rosa, L.P., Aurelio, M., Santos, D.O.S., Matvienko, B., Oliveira, E. & Sikar, E. (2004) Greenhouse gas emissions from hydroelectric reservoirs in tropical regions. *Climate Change*, **66**, 9–21.

Rosa, I.M.D., Smith, M.J., Wearn, O.R., Purves, D. & Ewers, R.M. (2016) The Environmental Legacy of Modern Tropical Deforestation. *Current Biology*, **26**, 2161–2166.

Ruffell, J., Clout, M.N. & Didham, R.K. (2016) The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. *Ecography*, **40**, 171–178.

Sá-Oliveira, J.C., Hawes, J.E., Isaac-Nahum, V.J. & Peres, C.A. (2015) Upstream and downstream responses of fish assemblages to an eastern Amazonian hydroelectric dam. *Freshwater Biology*, **60**, 2037–2050.

Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salaas, W., Zutta, B., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, **108**, 9899–9904.

Sala, O.E., Iii, F.S.C., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Poff, N.L., Sykes, M.T., Walker, B.H. & Walker, M. (2000) Global Biodiversity Scenarios for the Year 2100. *Science*, **287**, 1770–1775.

Santo-Silva, E.E., Almeida, W.R., Tabarelli, M. & Peres, C.A. (2016) Habitat fragmentation and the future structure of tree assemblages in a fragmented Atlantic forest landscape. *Plant Ecology*, **217**, 1129–1140.

Santos, B.A., Peres, C.A., Oliveira, M.A., Grillo, A., Alves-Costa, C.P. & Tabarelli, M. (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation*, **141**, 249–260.

Sayer, E.J., Heard, M.S., Grant, H.K., Marthews, T.R. & Tanner, E.V.J. (2011) Soil carbon release enhanced by increased tropical forest litterfall. *Nature Climate Change*, **1**, 304–307.

Schedlbauer, J.L. & Kavanagh, K.L. (2008) Soil carbon dynamics in a chronosequence of secondary forests in northeastern Costa Rica. *Forest Ecology and Management*, **255**, 1326–1335.

Scherer, L. & Pfister, S. (2016) Hydropower's Biogenic Carbon Footprint. *Plos One*, **11**, e0161947.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.

Schnitzer, S.A. (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *The American naturalist*, **166**, 262–276.

Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*, **17**, 223–230.

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecology Letters*, **14**, 397–406.

Schnitzer, S.A., Bongers, F. & Wright, S.J. (2011) Community and ecosystem ramifications of increasing lianas in Neotropical forests. *Plant signaling & behavior*, **6**, 598–600.

Schnitzer, S.A. & Carson, W.P. (2010) Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters*, **13**, 849–857.

Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, **88**, 655–666.

Schnitzer, S.A., Kuzee, M.E. & Bongers, F. (2005) Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, **93**, 1115–1125.

Schnitzer, S.A., van der Heijden, G.M.F., Mascaro, J. & Carson, W.P. (2014) Lianas in Gaps Reduce Carbon Accumulation in a Tropical Forest. *Ecology*, **95**, 3008–3017.

Seabloom, E.W., Dobson, A.P. & Stoms, D.M. (2002) Extinction rates under nonrandom patterns of habitat loss. *Proceedings of the National Academy of Sciences*, **99**, 11229–11234.

Sierra, C.A., del Valle, J.I., Orrego, S.A., Moreno, F.H., Harmon, M.E., Zapata, M., Colorado, G.J., Herrera, M.A., Lara, W., Restrepo, D.E., Berrouet, L.M., Loaiza, L.M. & Benjumea, J.F. (2007) Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. *Forest Ecology and Management*, **243**, 299–309.

Silver, W.L., Ostertag, R. & Lugo, A.E. (2000) The Potential for Carbon Sequestration Through Reforestation of Abandoned Tropical Agricultural and Pasture Lands. *Restoration Ecology*, **8**, 394–407.

Simon, M.F. & Garagorry, F.L. (2006) The expansion of agriculture in the Brazilian Amazon. *Environmental Conservation*, **32**, 203–212.

Soares-Filho, B., Rajão R., Macedo, M., Carneiro, A., Costa, W., Coe, M., Rodrigues, H. & Alencar, A. (2014) Cracking Brazil's Forest Code. *Science*, **344**, 363-364.

Stickler, C.M., Coe, M.T., Costa, M.H., Nepstad, D.C., McGrath, D.G., Dias, L.C.P., Rodrigues, H.O. & Soares-Filho, B.S. (2013) Dependence of hydropower energy generation on forests in the Amazon Basin at local and regional scales. *Proceedings of the National Academy of Sciences*, **110**, 9601–9606.

Tabarelli, M., Lopes, A. V. & Peres, C.A. (2008) Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica*, **40**, 657–661.

Tabarelli, M., Mantovani, W. & Peres, C.A. (1999) Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation*, **91**, 119–127.

Terborgh, J., Lopez, L., Tello, J., Yu, D. & Bruni, A.R. (1997) Transitory states in Relaxing Ecosystems of Land Bridge Islands. Tropical forest remnants: Ecology, management, and conservation of fragmented communities (eds W.F. Laurance & R.O. Bierregaard), pp. 256–274. University of Chicago Press, London.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.

Terborgh, J., Feeley, K., Silman, M., Nunez, P. & Balukjian, B. (2006) Vegetation dynamics of predator-free land-bridge islands. *Journal of Ecology*, **94**, 253–263.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

Tobin, M.F., Wright, A.J., Mangan, S.A. & Schnitzer, S.A. (2012) Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere*, **3**, 1-11.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London, Series B, Biological sciences*, **270**, 467–73.

Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species-area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.

Trussart, S., Messier, D., Roquet, V. & Aki, S. (2002) Hydropower projects: A review of most effective mitigation measures. *Energy Policy*, **30**, 1251–1259.

Turner, A.I.M. (1996) Species Loss in Fragments of Tropical Rain Forest : A Review of the Evidence. *Journal of Applied Ecology*, **33**, 200–209.

Turner, B.L. (2010) Protocol for Soil Carbon Sampling in CTFS Census Plots.

Turner, B.L., Yavitt, J.B., Harms, K.E., Garcia, M.N. & Wright, S.J. (2015) Seasonal changes in soil organic matter after a decade of nutrient addition in a lowland tropical forest. *Biogeochemistry*, **123**, 221–235.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Calster, H. Van, Peterken, G. & Hermy, M. (2006) Extinction Debt of Forest Plants Persists for More Than a Century Following Habitat Fragmentation. *Reports Ecology*, **87**, 542–548.

Visser, M.D., Bruijning, M., Wright, S.J., Muller-Landau, H.C., Jongejans, E., Comita, L.S. & de Kroon, H. (2016) Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology*, **30**, 168–180.

Vitousek, P.M., Mooney, H. a, Lubchenco, J. & Melillo, J.M. (1997) Human Domination of Earth's Ecosystems. *Science*, **277**, 494–499.

Wang, Y., Zhang, J., Feeley, K.J., Jiang, P. & Ding, P. (2009) Life-history traits associated with fragmentation vulnerability of lizards in the Thousand Island Lake, China. *Animal Conservation*, **12**, 329–337.

Watling, J.I. & Donnelly, M. a. (2006) Review: Fragments as Islands: a Synthesis of Faunal Responses to Habitat Patchiness. *Conservation Biology*, **20**, 1016–1025.

Watson, D.M. (2002) A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems. *Journal of Biogeography*, **29**, 823–834.

WCD. (2000) Dams and Development: A New Framework for Decision-Making. World Commission on Dams. International Rivers, Berkeley, CA, USA.

Wearn, O.R., Reuman, D.C. & Ewers, R.M. (2012) Extinction Debt and Windows of Conservation Opportunity in the Brazilian Amazon. *Science*, **337**, 228–232.

van der Werf, G., Morton, D.C., DeFries, R.S., Olivier, J.G.J., Kasibhatla, P.S., Jackson, R.B., Collatz, G.J. & Randerson, J.T. (2009) CO_2 emissions from forest loss. *Nature Geoscience*, **2**, 737–738.

Whittaker, R.H. (1972) Evolution and the measurement of species diversity. *Taxon*, **21**, 213–251.

Williams, J.C., ReVelle, C.S. & Levin, S.A. (2005) Spatial attributes and reserve design models: A review. *Environmental Modeling and Assessment*, **10**, 163–181.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwall, W., Lujan, N.K., Harrison, I., Stiassny, M.L.J., Silvano, R.A.M., Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Baran, E., Jr, M.P., Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C.C., Sousa, L.M., Koning, A.A., Hoeinghaus, D.J., Sabaj, M., Lundberg, J.G., Armbruster, J., Thieme, M.L., Petry, P., Zuanon, J., Vilara, G.T., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C.S., Akama, A., van Soesbergen, A. & Sáenz, L. (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, **351**, 128–129.

With, K.A. & King, A.W. (2001) Analysis of landscape sources and sinks: The effect of spatial pattern on avian demography. *Biological Conservation*, **100**, 75–88.

Wright, S.J. (2005) Tropical forests in a changing environment. *Trends in ecology & evolution*, **20**, 553–60.

Wright, S.J. & Muller-landau, H.C. (2006) The Uncertain Future of Tropical Forest Species. *Biotropica*, **38**, 443–445.

Wright, S.J., Calderon, O., Hernandez, A. & Paton, S. (2004) Are Lianas Increasing in Importance in Tropical Forests? A 17-Year Record from Panama. *Ecology*, **85**, 484–489.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P. & Foster, R.B. (2005) Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology*, **21**, 307–315.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C.A., Poorter, L., Silman, M.R., Vriesendorp, C.F., Webb, C.O., Westoby, M. & Wright, S.J. (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, **99**, 1003–1015.

Wright, S.J., Yavitt, J.B., Wurzburger, N., Turner, B.I., Tanner, E.V.J., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E., Garcia, M.N. & Corre, M.D. (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, **92**, 1616–1625.

Wright, A., Tobin, M., Mangan, S. & Schnitzer, S.A. (2015) Unique competitive effects of lianas and trees in a tropical forest understory. *Oecologia*, **177**, 561–569.

Yang, Y. & Luo, Y. (2011) Carbon:nitrogen stoichiometry in forest ecosystems during stand development. *Global Ecology and Biogeography*, **20**, 354–361.

Yavitt, J.B. (2000) Nutrient dynamics of soil derived from different parent material on Barro Colorado Island, Panama. *Biotropica*, **32**, 198–207.

Yu, M., Hu, G., Feeley, K.J., Wu, J. & Ding, P. (2012) Richness and composition of plants and birds on land-bridge islands: effects of island attributes and differential responses of species groups. *Journal of Biogeography*, **39**, 1124–1133.

Zagt, R.J. (1997) Tree Demography in the Tropical Rain Forest in Guyana. Tropenbos International. Georgetown, Guyana.

Zanne, A., Lopez-Gonzalez, G., Coomes, D., Ilic, J., Jansen, S., Lewis, S.L., Miller, R., Swenson, N., Wiemann, M. & Chave, J. (2009) Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository.

Zarfl, C., Lumsdon, A.E. & Tockner, K. (2015) A global boom in hydropower dam construction. *Aquatic Sciences*, 161–170.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.