PREDICTING BIODIVERSITY LOSS IN INSULAR NEOTROPICAL FOREST HABITAT PATCHES

Photo: Nina Attias

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CONTENTS

ABSTRACT

Neotropical forests have experienced high rates of biodiversity loss as a result of burgeoning land-use changes. Habitat conversion into cropland, pastures, and more recently hydroelectric lakes, are leading drivers of forest loss and fragmentation of pristine forests in the world's most biodiverse region. This thesis aims to improve our understanding of the impacts of habitat fragmentation on biodiversity loss in Neotropical forests by evaluating the patterns of floristic changes and vertebrate extinctions in forest patches. Two approaches at different scales were conducted. First, a systematic literature review was carried out on the effects of fragmentation on Neotropical primates at a continental-scale. Second, biodiversity inventories were conducted on medium and large-bodied vertebrates (including mammals, birds and tortoises) and trees ≥10 cm diameter at breast height at 37 islands and three continuous forest sites within the Balbina Hydroelectric Reservoir in Brazilian Amazonia. Patch area was a key driver of species persistence for all study taxa, yet other factors were also important. Hunting pressure exerted a strong influence on patterns of primate persistence within 760 fragments, and edge effects, including edge-related ground-fires, were the main predictors of floristic transitions using data from 87 quarter-hectare forest-plots at Balbina. Additionally, matrix composition and species life-history traits played a key role in explaining patterns of species persistence. This study therefore highlights the importance of considering anthropogenic stressors in assessing the effects of land-use change to explain patterns of species persistence in forest patches, aside from including parameters related to the matrix and ecological life-history traits of focal species. As conservation recommendations, prioritising large (>100 ha) patches, increasing their protection, and enhancing connectivity of surrounding habitats becomes clearly important. For future Amazonian dams, it is recommended that engineers should consider the overall topography of planned reservoirs to maximise landscape connectivity and/or reject plans targeting unfavourable river basins.

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CHAPTER 1

INTRODUCTION

Forest cover remaining within the Neotropical region, showing four distinct fragmented landscapes (Images: Google Earth and aerial photo from the Biological Dynamics of Forest Fragments Project).

1.1. Deforestation and habitat fragmentation in tropical forests

The world’s total tropical, temperate and boreal forest cover is over 4 billion hectares, one-quarter of which is found within the Neotropical realm (FAO 2010; Hansen *et al.* 2010). The importance of Neotropical forests for biodiversity is unquestionable, as the region harbour the largest number of species worldwide (IUCN 2014). However, these forests have been experiencing rapid rates of deforestation mainly driven by burgeoning human populations and an alarming pace of development. Every day, large tracts of pristine forests are converted into cattle pastures, agricultural lands, hydroelectric reservoirs among other infrastructural projects, aside of being continually logged, fragmented, burned and overhunted (Fearnside 2005; Laurance & Peres 2006; Ribeiro *et al.* 2009; Gibbs *et al*. 2010). The inevitable consequence of large-scale forest loss is the proliferation of forest patches, which are becoming increasingly isolated, more degraded and more vulnerable to further changes in forest structure. It is unsurprising, therefore, that the twin processes of habitat loss (*i.e*., the removal of habitat) and fragmentation (*i.e*., the subdivision of remaining habitat into isolated patches) are widely considered as major threats to terrestrial biodiversity (Foley 2005).

Disentangling the effects of habitat loss and habitat fragmentation and understanding their effects on biodiversity loss are central to the history of conservation ecology in Neotropical forests. In 1979, Thomas Lovejoy, Richard Bierregaard and colleagues initiated a large-scale experimental study of habitat fragmentation in the central Brazilian Amazonia at the BDFFP (Biological Dynamics of Forest Fragments Project) landscape, which to date has produced over than 500 publications on the topic (http://pdbff.inpa.gov.br). Although the responses to forest fragmentation vary greatly across different taxonomic groups, edge effects have been pinpointed as the dominant driver of community-wide forest dynamics, phytodemographics, and wildlife assemblage structure in forest fragments of this landscape, with the matrix (*i.e.,* the non-habitat surrounding the native habitat patches) also strongly influencing forest dynamics and faunal persistence in forest remnants (Laurance *et al.* 2000, 2006, 2011). In an intensely fragmented forest landscape in Mexico, investigators have showed that both area and isolation are strong predictors of patterns of species richness for plants and mammals (Estrada *et al*. 1994; Arroyo-Rodriguez & Mandujano 2006). Elsewhere, Carlos Peres and collaborators have been highlighting that different forms of anthropogenic disturbance interact with classic area effects in predicting the number of species of mammals, birds and trees in forest patches of a landscape in southern Amazonia (Michalski & Peres 2005; Lees & Peres 2006; Michalski *et al.* 2007). These results show that identifying the main drivers of biodiversity loss across Neotropical fragmented landscapes is difficult, mostly because they experienced varying histories of deforestation, anthropogenic perturbation, and external effects from the surrounding non-habitat matrix. Expanding the number of study landscapes in the region and performing reviews of existing fragmentation ecology studies are effective ways in which patterns of biodiversity loss in Neotropical forest remnants can be elucidated.

1.2. Species-area relationship in the 21st Century

The species-area relationship (SAR), *i.e*., the increase in the number of species recorded with increasing sampling area, is one of the few iron-clad laws in ecology, and one the most frequently studied relationships in conservation ecology (Rosenzweig 1995; Lomolino 2001). To explain this pattern, Robert H. MacArthur & Edward O. Wilson (1967) formulated the ageless Equilibrium Theory of Island Biogeography, in which large areas retain larger populations, are intrinsically less susceptible to local extinctions, and more prone to gain species through immigration events. Other hypotheses to explain higher species richness in increasingly larger habitat areas have been proposed thereafter, including that a large number of habitats types is sampled (Ricklefs & Lovette 1999); the rate of species proliferation is increased (Losos & Schluter 2000); the utilisation of niche space is enlarged (Lehman & Tilman 2000); among others. Notwithstanding the debate to explain species-area patterns, this relationship has been widely used to estimate local extinction rates in landscapes dominated by true or habitat islands (Jacquemyn *et al.* 2001; Harcourt & Doherty 2005; Jonsson *et al.* 2011; Mathew *et al.* 2014; Mendenhall *et al.* 2014) and discussions are often related to which are the most mathematically appropriate model fits (Lomolino 2000; Tjorve 2009). In addition to area, increasing island isolation is expected to reduce species colonisation events, thereby elevating species extinction rates (MacArthur & Wilson 1967). However, studies conducted within habitat islands on animal populations often detect a stronger effect of area than isolation (Watling & Donnelly 2006; Ferraz *et al*. 2007; Prugh *et al*. 2008), which reinforces for the extensive use of SARs in fragmentation ecology studies.

Over and above area and isolation effects, other variables have been considered important predictors of species richness within ‘real-world’ forest fragments. Habitat fragmentation is now recognised as a landscape-wide process, and patch, landscape and within-patch features have been frequently considered in studies examining the effects of fragmentation on biodiversity patterns (Fahrig 2003; Thornton *et al*. 2011a; Hu *et al*. 2012). Edge effects (Laurance *et al.* 2006; Banks-Leite *et al.* 2010), the suitability of the matrix surrounding fragments (Andrén 1994; Prugh *et al.* 2008) and anthropogenic disturbances within patches (Laurance & Peres 2006; Canale *et al*. 2012) are examples of robust predictors of species richness for plants and vertebrates across Neotropical fragmented forest landscapes. Indeed, fragmentation research has substantially advanced, transcending the simplistic area-effects (Laurance 2008). Multi-level studies, in which different local and regional scale metrics are related to focal surveyed patches, are becoming increasingly common, thereby further informing fragmentation ecology studies (Thornton *et al*. 2011a). Focusing only on area and isolation effects can therefore neglect other variables that can also explain patterns of species persistence in fragmented forest landscapes.

Another failure of a single-minded focus on area-effects is to overlook the role of species composition and functional attributes of those species. Firstly, species interactions can be highly affected by habitat fragmentation, leading to profound impacts on community composition and dynamics. For instance, large predators disappeared from forest fragments and favoured the density of large herbivores with profound changes on mammal composition and ecosystem structure (Terborgh *et al.* 2001). Secondly, species differ in their responses to habitat fragmentation, with some sensitive species decreasing in abundance and consequently showing higher vulnerability to extinction. For example, bats showing greater mobility and higher tolerance to habitat edges were less sensitivity to habitat fragmentation in islands within a reservoir in Panamá (Meyer *et al*. 2008). In northeastern Brazil, tree seed size, dispersal mode and regeneration strategy were important functional traits related to the rarity of species persisting in forest patches (Santos *et al.* 2008). Therefore, the life-history traits of species can be an additional factor to be considered in fragmentation studies, also contributing to our understanding of species loss in human-dominated forest landscapes (Davies *et al.* 2000; Thornton *et al*. 2011b).

1.3. Large vertebrates in fragmentation studies

Medium and large-bodied vertebrates (> 1kg) are key components of ecosystem dynamics and regeneration in tropical forests, playing direct roles as seed dispersers and predators, mega-herbivores and keystone predators (Wright *et al*. 1994; Galetti *et al.* 2006; Ahumada *et al*. 2011). They also comprise an important economic resource for local inhabitants through their use as food, pets and artefacts (Bodmer *et al.* 1994; Peres 2000). Additionally, some species including large felids and primates, are charismatic and therefore contribute for promoting conservation to the wider public (Terborgh 1988). Yet mammals have been greatly reduced due to direct exploitation, hunting, habitat loss and fragmentation (Morrison *et al*. 2007; Dirzo *et al.* 2014). Because they are essential elements of forest ecosystems and some organisms are sensitive to habitat disturbance, it becomes important to enhance our understanding on the effects of habitat fragmentation on patterns of large mammal and other mega-vertebrate persistence in fragmented forest landscapes, and subsequently propose conservation actions for their local persistence.

The number of studies examining the effects of habitat fragmentation on mid- and large-sized vertebrates has been increasing in the last decade in the Neotropics. Primates have been so far the most studied vertebrate order within forest patches, with the great advantage of having been extensively studied in pristine forests over several decades (Kinzey 1997; Janson *et al*. 1999). Hence, primates comprise a noteworthy group for revealing general patterns of responses to habitat fragmentation based on a large-scale review. Indeed, systematic reviews are an excellent approach in comparative analyses and conservation practice, as a large amount of evidence can provide a more efficient and less biased knowledge basis for decision making (Pullin & Stewart 2006). Both the experience working with primate behaviour and ecology in different landscapes and ability to find and read studies in Portuguese, Spanish and English, favoured the conduction of a robust review of the effects of habitat fragmentation on Neotropical primates. This thesis therefore includes two chapters that scrutinize the patterns of primate species persistence within a large number of landscape replicates from southern Mexico to northern Argentina.

More attention has been recently given to terrestrial mammals and large ground-dwelling bird species, as they are considered good indicators of ecosystem health and have therefore been targeted as prime bioindicators of large-scale monitoring programs throughout the Neotropics (Ahumada *et al.* 2011; Luzar *et al.* 2011; Nobre *et al*. 2013). By performing a detailed literature search of published studies investigating the effects of habitat fragmentation on terrestrial non-flying mammals and large birds in Neotropical forests, 12 distinct landscapes have been surveyed to date, considering a minimum of four forest sites surveyed (Figure 1.1; Table 1.1). Nearly 60% of these landscapes are within Brazil, which is unsurprising given the size of the country and long history of post-colonial forest habitat destruction (Dean 1995). The number of surveyed patches greatly varied across different landscapes, with those based on interviews of local residents on species presence/absence comprising a large number of sampling sites. Although interviews are considered a cost-effective approach to obtain terrestrial vertebrate species occupancy data (Uquiza-Haas *et al.* 2009), *in situ* field surveys provide more reliable data in addition to enabling density and abundance estimates. Yet they demand a labour-intensive, hard-own survey effort and due to differences in the ecology and behaviour of species, a combination of complementary sampling methods can provide highly reliable occupancy data (Munari *et al*. 2011).

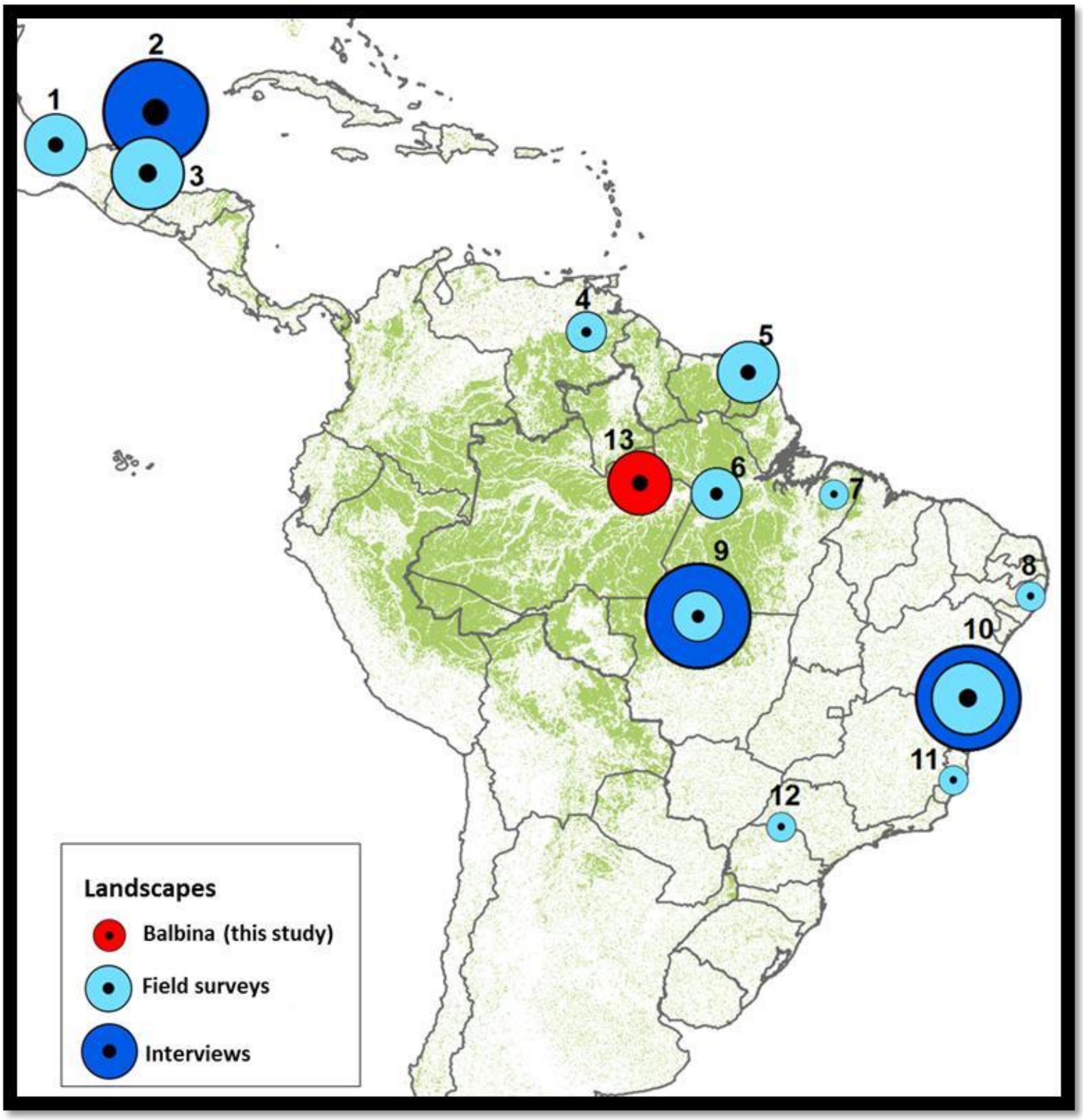

Figure 1.1. Geographic locations of the 12 fragmented forest landscapes that studied the effects of habitat fragmentation on terrestrial vertebrates across the Neotropics, through either field work surveys and/or interviews data, in addition to the study landscape reported in this thesis (Balbina). Circles are sized proportionally to the total number of forest sites surveyed within each landscape; and numbered according to Table 1.1, which provides further details on each landscape.

Table 1.1. Characteristics of the studies investigating the effects of habitat fragmentation on Neotropical large vertebrates.

							Sampling technique[5]						
ID[1]	**Landscape**	**Nº of Patches and (CF)[2]**	**Range of patch size (ha)**	**Time of isolation (years)**	**Matrix[3]**	**Group[4]**	**Diur**	**Noct**	**Sign**	**Arm**	**CT**	**Inter**	**Reference**
1	Guatemala	50 (12)	2.9-445	30	Past/agric	Mam	X	X			X		Thornton *et al.* 2011b
2	Yucatán	147 (0)	NA	NA	Secon	Mam/Bird						X	Urquiza-Haas *et al.* 2009
3	Los Tuxtlas	35 (0)	1-2000	20	Past/agric	Mam	X	X					Estrada *et al*. 1994
4	Guri	13 (1)	0.5-365	4	Water	Mam/Tort	X	X					Terborgh *et al*. 1997
5	Saint-Eugene	38 (1)	0.1-67	1-4	Water	Mam	X		X				Dalecky *et al*. 2002
6	Alter do Chão	16 (8)	8-361	150	Savana	Mam	X	X	X			X	Sampaio *et al*. 2010
7	East Amazonia	3 (1)	200-1809	NA	Past/agric/secon	Mam	X	X				X	Stone *et al.* 2009
8	Pernambuco	4 (0)	10-500	NA	Agric	Mam	X	X	X				Silva Jr & Mendes-Pontes 2008
9	Alta Floresta	17 (4)	2.4-1763.3	30	Past	Mam	X			X	X		Michalski & Peres (2007)
9	Alta Floresta	129 (15)	2.4-1763.3	30	Past	Mam						X	Michalski & Peres (2005)
10	South Bahia	46 (3)	0.2-194,341	NA	Past/agri	Mam	X		X	X	X		Canale *et al*. 2012
10	South Bahia	190 (6)	0.2-194,341	NA	Past/agri	Mam						X	Canale *et al*. 2012
11	Espírito Santo	4 (2)	210-2400	10-30	Past/agri	Mam	X	X	X			X	Chiarelo (1999)
12	Plateau SP	4 (1)	1700-2178	NA	Past	Mam	X						Cullen Jr *et al*. 2001
13	Balbina	37 (3)	0.83-1690	26	Water	Mam/Bird/Tor	X		X	X	X		This study

[1] Landscape identification according to Figure 1.1; [2] Number of forest patches and continuous forest sites (CF) surveyed; [3] Main surrounding habitat type (Past= pasture; agric = agriculture land; second= secondary forest; water = freshwater); [4] Vertebrate groups surveyed (Mam = mammals; bird = large ground-dwelling birds; Tort = tortoises); [5] Sampling technique used for surveys (Diur = diurnal line-transect census; Noct = nocturnal line-transect census; Sign = sign surveys; Arm = counts of armadillo burrows; CT = camera trapping; Inter = Interviews).

Five sampling techniques have been frequently used for surveying terrestrial medium and large vertebrates *in situ* in both pristine forests and forest patches in the Neotropics ─ diurnal line-transect census, nocturnal line-transect census, indirect sign surveys, armadillo burrows surveys and camera trapping. Diurnal line transect census is by far the most common methodology (Carrillo *et al.* 2000; Lopes & Ferrari 2000; Haugaseen & Peres 2005; de Thoisy *et al.* 2008; Table 1.1). Indeed, this method has been widely used in monitoring programs in Amazonia (Fonseca Jr *et al.* 2011; Nobre *et al.* 2013) due to its low starting financial costs and for being the only appropriate technique to survey arboreal species, such as primates (Peres 1999; de Thoisy *et al.* 2008; Munari *et al.* 2011). Nocturnal line transect census is used as a complementary technique to survey nocturnal species. However, it provided poor information for most night-time species in pristine Amazonian landscape, due to the visual limitation of the observers during data collection (Munari *et al.* 2011). Sign surveys, which can be conducted concomitantly to diurnal census surveys, are considered an efficient technique for presence/absence data. It involves low costs, but depends on a good substratum condition and trained personnel (Burnham 1980; Silveira *et al*. 2003). Armadillo surveys facilitate the identification of different species through the measurements of their burrows, which can be distinguished by their individual characteristics (Carter & Encarnação 1983). Lastly, camera trapping has been considered the most efficient technique among others in Neotropical forest landscapes due to its great number of advantages, including 24 hours operation, environment independent, no requirement of experienced field staff, well suited to standardization, and also favours the detection of elusive and rare species (Silveira *et al.* 2003; Tobler *et al.* 2009; Munari *et al.* 2011). Despite the high initial costs of equipment acquisition, the method is handled more easily with low costs in the long-term (Silveira *et al.* 2003). Additionally, the technique allows the obtainment of ecological and behaviour information, such as activity patterns, habitat use and reproductive habits of species (O'Connel *et al.* 2011). Yet just three of twelve fragmentation studies from the review (Table 1.1) adopted this efficient methodology for surveying terrestrial vertebrates in Neotropical forest patches, prior to the present study.

1.4. The Balbina Hydroelectric Reservoir: an experimental landscape in fragmentation ecology

1.4.1. History and geographic setting

The controversial Balbina Hydroelectric Dam, located 146 km northeast of Manaus in the central Brazilian Amazon (1^o 48'S; 59^o 29'W; Figure 1.2), was completed in October 1986, followed by the filling of the Uatumã River (Fearnside 1989). Expected to flood 2,360 km^2 of pristine forests to produce a modest amount of hydropower (112.2 MW average output from 250 MW installed capacity), Balbina was constructed to supply electricity to the 2 million strong capital city of Manaus. However, the dam is widely acknowledged as an economic, environmental and social disaster; only half of the estimated power-supply is now generated, the total flooded area is twice that foreseen at the time of construction, and 443,772 ha of primary forests were reduced to an archipelago of over 3,500 islands (Figure 1.3), displacing much of the local indigenous population (Fearnside 1989; Palmeirim *et al*. 2014). The vast majority of islands are forested, with their vegetation classified as sub-montane dense rain forest. The freshwater matrix surrounding the islands **still** contains relictial stands of dead canopy trees that rise above the water level (Figure 1.3). The mean annual temperature is 28^{o}C and mean annual rainfall is 2,376 mm (IBAMA 1997). To offset the forest habitat loss, part of the reservoir area and the adjacent mainland continuous forest became effectively protected from 1990 following the creation of the 940,000-ha Uatumã forest reserve, the largest Biological Reserve in Brazil (Figure 1.2). Subsequently, all areas on the left margin of the Uatumã river were classified as a strictly protected zone, enhancing the total protected area of the Reserve. Areas outside the Reserve (right margin of the river) are also considered of permanent preservation (*i.e.*, it is a protected area aiming to preserve the natural resources, but different to the strictly protected zone, people are allowed to visit and in the case of Balbina, to fish in this particular area of the lake) thereby greatly increasing the total protected area of the Balbina Reservoir.

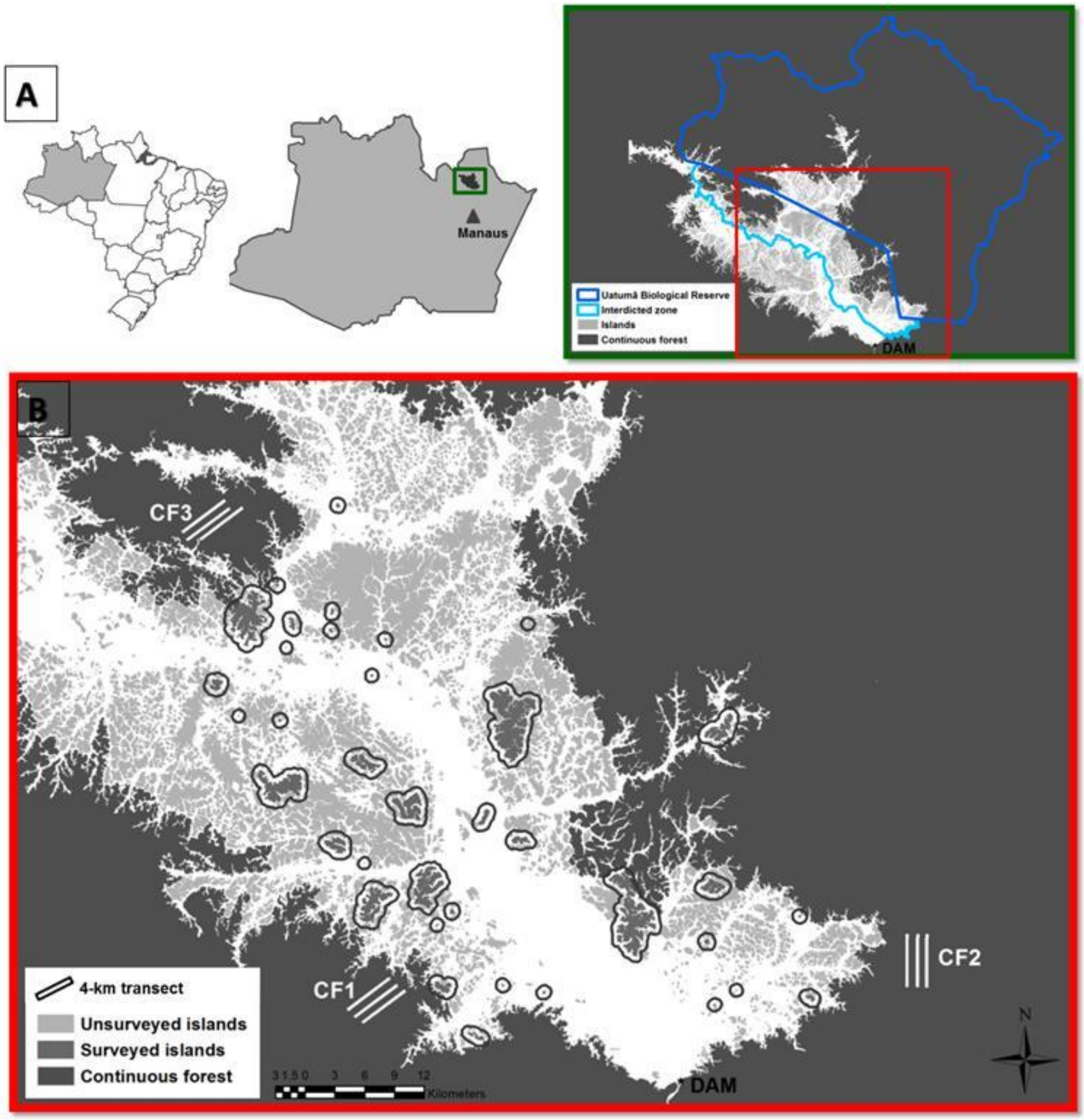

Figure 1.2. (A) Location of the Balbina Hydroelectric Dam in the state of Amazonas, Brazil, highlighting in dark blue the delimitations of the Uatumã Biological Reserve and in light blue the interdicted zone of the Reserve; (B) the study area within the reservoir, indicating the 37 islands and three continuous forest (CF) sites surveyed in this study. Each CF site is comprised by three parallel 4-km transect (white lines).

Figure 1.3. Aerial photographs (2005) showing (A) some of the islands within the Balbina reservoir and (B) the water matrix containing dead relict canopy trees. Photos by E. M. Venticinque.

1.4.2. Relevance

The experimental Balbina archipelagic landscape provides a unique opportunity to examine biotic responses to habitat fragmentation and isolation. In addition to long-term relaxation time, the Balbina Dam presents several advantages compared to other fragmented landscapes including a large number of replicates, a homogeneous habitat matrix, long-term effective protection from logging and hunting, and the logistical support from the Uatumã Biological Reserve. Additionally, the Balbina dam is located only ~70 km from the large-scale experimental study of the BDFFP, a landscape which shares a similar fauna and flora and comparable age of isolation, but contrasting in the matrix type (pasture and secondary forests), and number and range of forest patches (BFFPP consists of 9 1-, 10- and 100-ha patches). Hence, comparisons among both studies can also help ecologists to understand the effects of matrix type on forest biotas.

In fact, hydroelectric dams are considered excellent natural experimental settings for ecological studies from which invaluable lessons can be learned (Diamond *et al.* 2001; Wu *et al.* 2003). Several studies have also assessed the effects of fragmentation on terrestrial biotas in land-bridge forest archipelagos created by hydroelectric dams in Asia (Wang *et al.* 2010; Yong *et al.* 2011; Yu *et al.* 2012; Gibson *et al.* 2013). In Neotropical reservoirs, most studies are restricted to the immediate aftermath of water-level rise and isolation, when changes in faunal composition presumably occur more rapidly (Terborgh *et al.* 1997, 2001; Cosson *et al.* 1999; Dalecky *et al.* 2002; Table 1.1). Exceptions are the studies with bats after ~100 years of isolation in land-bridge islands of Lake Gatún in Panamá (Meyer & Kalko 2008; Mendenhall *et al*. 2014), with trees in the Tucuruí reservoir (Ferreira *et al*. 2012), and with ant-plant mutualistic networks (Emer *et al.* 2013), tapirs (Pinho *et al*. 2014) and primates in the Balbina reservoir (Benchimol & Venticinque 2014). Aside from ecological lessons, studies within Neotropical reservoirs can substantially contribute for conservation actions and policies ─ the Andes and lowland Amazon are facing escalating investments in hydropower projects, with 151 new dams larger than an installed capacity of 2 MW expected to be constructed within the next 20 years (Finer & Jenkins 2012; Castello *et al.* 2013). Therefore, understanding the impacts caused by mega-dams on forest biodiversity has become a high research priority in Amazonian conservation in order to avoid massive habitat loss of future hydropower projects and safeguard the remaining wildlife populations in these areas.

1.4.3. Target biota

Terrestrial vertebrates, as already discussed, are key components of forest communities. Yet no terrestrial mammal and large frugivorous bird study to date has been conducted in an Amazonian reservoir, and the few studies carried out in Neotropical hydroelectric dams were restricted to brief post-isolation periods (Table 1.1). Given these reasons, this thesis greatly stresses the patterns of vertebrate responses to habitat insularization induced by the construction of a major hydroelectric dam (2 chapters).

Tropical forest trees comprise another important bioindicator group. Tree assemblages have been well-studied across the Amazon (ter Steege 2013) and are also singled-out in a large-scale biodiversity monitoring program of the Brazilian Government (Nobre *et al*. 2013). Indeed, tree communities play important roles in tropical forest ecosystems in regulating microclimatic conditions (Laurance *et al.* 1998), storing carbon, and producing trophic resources for a wide variety of primary consumers (Richards 1998). To date, tree communities have only been examined at one Amazonian hydroelectric dam (Tucuruí Dam, in Pará state) and at that only in islands smaller than 100 ha (Ferreira *et al*. 2012). Given their ecological importance and key trophic and structural ecological roles for faunal assemblages, trees become a quintessential group to be examined within land-bridge islands (*i.e.*, terrestrial patch surrounded by an aquatic matrix that was previously connected to a more continuous “mainland” – see Watling & Donnelly 2006). In addition, trees constitute one, if not the best, taxonomic groups to be investigated in the BDFFP landscape providing both an excellent comparison among landscapes and information of species ecological traits (Laurance *et al*. 1998; 2006; 2011).

Hence, one of the chapters in this thesis is dedicated to understanding tree responses to forest fragmentation within the Balbina Hydroelectric Reservoir.

1.4.4. Sampling design

1.4.4.1. Vertebrates

Within the Balbina Hydroelectric Reservoir, 37 islands were carefully selected to be surveyed, on the basis of their size and degree of isolation, maintaining a minimum distance of 1 km from each other (Figure 1.2). Additionally, three continuous forest (CF) sites adjacent of the reservoir were also selected, and sampling stations (*i.e.*, transects) were established. These CF sites are expected to contain the full original complement of species (Terborgh 1974), and therefore serve as excellent 'pseudo-control' sites. Transects within islands were 0.5 to 3 km in length and 1 m wide (Figure 1.4), according to island size and shape so that a representative area of the island was covered, whereas on each CF sites, three 4-km linear transect in parallel, separated from each other by 1 km, were established (Figure 1.2). Although the total length of transects was greater in larger islands and CFs, the overall proportion of each island sampled decreased with island size. A total of 108.5 km of transects were opened by a team of four field assistants, over two months (June and July 2011) of an intense field campaign in the Balbina Lake. Each transect was measured and marked every 50 m, to facilitate accurate mapping of detection events (Peres 1999). Transects were "rested" for at least 20 days, to stabilize any possible disruptions created by transect preparation. Thereafter, a combination of four distinct sampling techniques were used to survey the vertebrate community along those transects: line-transect surveys, animal sign surveys, armadillo burrow counts, and camera trapping (Figure 1.4). Nocturnal surveys were not conducted since it was not considered a cost-effective technique in Amazonian forests (Munari *et al*. 2011). From August to December 2011, each transect was censused 4 times, comprising the first sampling session. Each time, one-way linear census surveys was conducted by two previously trained observers, with a robust amount of experience in surveying vertebrate assemblages in the Amazon, following the procedures recommended by Peres (1999). On return transect walks, sign surveys and armadillo burrow counts were conducted. Within continuous forest sites, all three transects were surveyed simultaneously by three different pairs of observers. Additionally, 2 to 15 camera traps (proportional to island area) were deployed for a continuous 30-day period in each forest site. From June to December of the following year, all sampling surveys were repeated (second sampling session), *i.e.*, transects were walked 4 times for linear transect, terrestrial animal sign, and armadillo surveys, and the same number of cameras were deployed exactly at the same locations of each forest site for another 30-day period. Only new armadillo burrows were counted during this second survey session.

1.4.4.2. Tree communities

For floristic surveys, 1 to 4 quarter-hectare forest plots were established on the same set of islands and CF sites in which vertebrates surveys were conducted, with the exception of three small islands that could not be sampled. Plots measured 250m x 10m at all forest sites, except for 10 small islands where rectangular plots were 125m x 20m. All live trees (including arborescent palms) ≥10 cm DBH (diameter at breast height) within each plot were measured, number-tagged and identified at the species level by A.E.S. Santos (Figure 1.5), an expert botanist with >20 years of fieldwork and herbarium experience in floristic inventories throughout Central Amazonia. Floristic surveys were carried out between September and December 2012, in which a total of 11,230 trees were identified within 87 plots, resulting in a total inventoried area of 21.75 ha.

Figure 1.4. Photographs taken during field work: (A) field team navigating in the Balbina lake; (B) A linear transect after it had been opened and cleared; (C) MB and a field assistant conducting linear-transect surveys; (D) a giant anteater carrying an offspring observed during a line-transect survey; (E) fresh faeces of lowland paca, recorded during a sign survey, and (F) MB deploying a camera trap in one of the islands.

Figure 1.5. Stepwise routine during floristic surveys - (A) each tree ≥10 cm DBH within each quarter-hectare plot was measured and identified by a botanist; (B, C) then number tagged using a metal plate; (D) information of tree number tag, DBH and species identification recorded. Photos by O. Ti.

1.5. Thesis aims and structure

This thesis aims to improve our understanding of the impacts of habitat fragmentation on biodiversity loss in Neotropical forests, by evaluating the patterns of large vertebrate extinctions and floristic changes in insular habitat forest patches. For this purpose, the thesis is structured into five data chapters (2 to 6) partitioned into two major parts, each of which comprises a distinct main goal as following:

Part I: Effects of forest fragmentation on platyrrhine primates

Chapters 2 aims to examine how both patch disturbance and landscape variables modulate species-area relationships (SARs) of Neotropical primates in fragmented forest landscapes, focusing on the community-level responses. It provides the first robust quantitative review of platyrrhine primate responses to habitat fragmentation throughout the Neotropics. The chapter has been published in *Diversity and Distributions* (2013; 19: 1339–1352).

Chapter 3 investigates the patterns of local extinctions of primates in Neotropical forest patches, attempting to disentangle the effects of landscape configuration, human-induced disturbance, and species life-history traits to examine how different primate functional groups respond to habitat fragmentation. The database used in this chapter is the same as Chapter 2, yet this one focuses on the species-specific responses of primates to habitat fragmentation. The chapter has been published in *American Journal of Primatology* (2014; 76: 289–302).

Part II: Effects of forest insularization induced by a mega hydroelectric dam on biodiversity

Chapter 4 examines how tree assemblages have responded to the 26-year post-isolation history of landscape alteration in land-bridge forest islands formed within one of the world's largest hydroelectric reservoirs ─ the Balbina Hydroelectric Dam. Aside from examining SARs, the chapter investigates the additional effects of patch and landscape scale metrics on patterns of tree assemblage heterogeneity, both in terms of taxonomic and functional diversity. The chapter is under review in *Journal of Ecology*.

Chapter 5 investigates the patterns of species extinctions for 35 mid- and large-sized vertebrate species within 40 forest sites across the Balbina Reservoir landscape, focusing on the species-specific responses to habitat fragmentation induced by a dam construction. Using a combination of four sampling techniques to survey 37 islands and three continuous forest sites, this chapter examines to what extent the local patch- and landscape scale contexts of islands and species life-history traits can explain pattern of local extinctions across all survey sites, and identifies the main predictors of species occupancy for each species. The chapter is under review in *Ecological Applications.*

Chapter 6 assesses how medium and large-bodied forest vertebrate assemblages (including mammals, large frugivorous birds and tortoises) responded to the process of insularization induced by the construction of the Balbina Dam. It is based on the same data set used in Chapter 5, but analyses the overall vertebrate community responses to habitat fragmentation. The chapter is expected to be submitted to *Nature Communications*.

Additionally, the thesis presents a set of broad concluding remarks (Chapter 7) and includes some appendices related to support the data chapters. With the exception of chapters 1 and 7, all others were written in the form of peer-reviewed papers.

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CHAPTER 2

ANTHROPOGENIC MODULATORS OF SPECIES-AREA RELATIONSHIPS IN NEOTROPICAL PRIMATES: A CONTINENTAL-SCALE ANALYSIS OF FRAGMENTED FOREST LANDSCAPES

The critically endangered woolly-spider monkey, *Brachyteles hypoxanthus.*
Courtesy of the artist Marco Bueno.

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2.1. Abstract

Aim

We conducted the first comprehensive quantitative review on the effects of habitat fragmentation on Neotropical primates to examine how both patch disturbance and landscape variables modulate species-area relationships (SARs) and species persistence in fragmented forest landscapes.

Location

Neotropical forests, from Mexico to Argentina.

Methods

We use species occupancy data from 705 forest fragments and 55 adjacent continuous forests nested within 61 landscapes, which we compiled from 96 studies reporting data on patch-scale species composition and patch size/location. Presence-absence data on 19 species functional groups and an index of hunting pressure and matrix type were assigned to each forest patch. We adopted a multi-level analysis, examining SARs and patterns of species retention coupled with the additive effects of hunting pressure and landscape connectivity both across all forest patches and 728 sites nested within 38 landscapes containing four or more sites.

Results

We uncovered a consistent effect of patch area in explaining primate species richness. Over and above area-effects, however, SARs were strongly modulated by levels of hunting pressure at the landscape-scale in predicting species occurrence and aggregate assemblage biomass. Matrix type was also a good predictor of both extant species richness and aggregate biomass when only non-hunted sites were considered, with patches in more permeable matrices containing more species. Likewise, the percentage of forest cover surrounding each patch was another important predictor of both richness and biomass when analyses could be performed including this variable.

Main Conclusions

Although the importance of patch area in predicting species persistence is undeniable, we found that SARs were clearly affected by within-patch human exploitation of increasingly isolated primate populations. Expanding the number of forest reserves, enforcing protection within nominal protected areas and re-

establish connectivity between forest patches are therefore required to ensure the long-term persistence of full primate assemblages. We highlight the importance of considering multiple anthropogenic effects in assessing the synergistic effects of land-use to explain patterns of species persistence in fragmented tropical forest landscapes.

2.2. Introduction

Tropical forests worldwide have been increasingly degraded by the relentless expansion of the twin processes of habitat loss and fragmentation (Heywood, 1995; Laurance & Peres 2006). As these processes proceed, large tracts of pristine forest habitat are converted into smaller and more isolated forest patches embedded within a largely inhospitable matrix, with long-term detrimental effects on biodiversity (Turner, 1996; Fahrig, 2003). Although habitat isolation exacerbates species loss in most fragmented ecosystems, area effects play a prevailing role, with larger patches sustaining larger populations of a larger set of species (Watling & Donnelly, 2006; Ferraz *et al.,* 2007). Species-area relationships (SARs) are therefore ubiquitous in most archipelagic landscapes, and have been widely used to estimate local extinction rates associated with declining habitat areas (Angermeier & Schlosser, 1989; Lomolino, 2001; Drakare *et al.,* 2006; He & Hubbell, 2011). In fact, SARs remain the most frequent approach in predicting biodiversity erosion in fragmented environments, despite outstanding uncertainties about the appropriateness of model fits (Lomolino, 2000; Tjorve, 2003, 2009; Triantis *et al.,* 2012). However, SARs typically overlook synergistic interactions between area-effects and external demographic stressors on (semi)isolated populations, which may accelerate local extinction rates. This includes anthropogenic forms of disturbance within fragmented landscapes such as edge-propagated wildfires and matrix mortality associated with hunting and roadkills (Woodroffe & Ginsberg, 1998; Peres, 2001; Cochrane & Laurance, 2002).

The landscape context may therefore be critical in determining the form of community disassembly within forest patches, yet these additive effects are rarely considered in empirical SARs. For instance, matrix permeability clearly affects patch occupancy, since species that can traverse the matrix or exploit its resources often occupy a larger number of patches (Gascon *et al.,* 1999; Antongiovanni & Metzger, 2005; Ewers & Didham, 2006; Lees & Peres, 2009). Human perturbation also affects species persistence in forest patches and amplifies the detrimental impacts of fragmentation (Ewers & Didham, 2006). In Amazonian forest patches, hunting interacts synergistically with habitat fragmentation vastly reducing the large vertebrate species retention capacity of small patches (Peres, 2001). Most SAR applications to real-world fragmented forest landscapes would therefore show reduced explanatory power without explicitly considering the patch- and landscape-scale history of anthropogenic disturbance.

Neotropical primates comprise a unique taxonomic group to test SAR models in fragmented tropical forest landscapes as they are strict forest dwellers, highly conspicuous group-living species, and highly variable in their tolerance to forest fragmentation (Harcourt & Doherty, 2005; Michalski & Peres, 2005). Forest primates play important roles in ecosystem structure and functioning because they account for a disproportionate share of the arboreal vertebrate biomass (Oates *et al.,* 1990), often operate as central trophic species in forest food webs (Terborgh, 1983; Marsh, 2003), and are key seed dispersers (Link & Di Fiore, 2006). Moreover, primates are widely hailed as regional conservation icons, represent the best studied terrestrial mammal order (Reed & Fleagle, 1995), have been widely investigated throughout the Neotropics, and account for much of the vertebrate data available from any tropical forest region. Neotropical forests contain the world's most diverse continental primate fauna (139 species in 19 genera: IUCN, 2008). Several studies have considered the detrimental effects of habitat fragmentation on primate species and assemblages (Estrada & Coates-Estrada, 1996; Marsh, 2003; Michalski & Peres, 2005). Yet no systematic review has attempted to examine the general continental-scale patterns of species persistence.

Here, we provide the first robust quantitative review of platyrrhine primate responses to habitat fragmentation throughout the Neotropics. In particular, we couple a patch- and landscape-level approach to variables describing the degree of anthropogenic disturbance to explain patterns of species persistence within forest isolates. We present the most comprehensive compilation on primate species occupancy of isolated forest patches from the northernmost (southern Mexico) to the southernmost (northern Argentina) Neotropical forest frontiers. These patches are embedded within a wide range of landscape contexts subjected to varying histories of human disturbance. We discuss the main drivers of primate local extinctions in fragmented forest landscapes, suggest how the fragmentation ecology research agenda could be enhanced, and recommend priority conservation actions.

2.3. Methods

2.3.1. The data set

We performed an exhaustive search of the formal and grey literature to identify all published and unpublished studies containing data on primate species composition within Neotropical forest fragments (defined as forest patches <10,000 ha). To identify these studies, we first conducted a Web of Science and a Google Scholar search using the following keywords: habitat fragmentation, primates, mammals, landscape, Neotropical, with and without '*Alouatta*' and '*Cebus*' or '*Sapajus*', the most widely distributed platyrrhine genera), the most widely distributed genera. We then Google-searched these same keywords translated into Spanish and Portuguese to find publications in non-indexed journals, and undergraduate and postgraduate dissertations, thesis and monographs archived in all Meso and South-American countries. We also searched and included the study bibliographies, unpublished studies we were aware of, and our own data from three fragmented landscapes (Michalski & Peres, 2005; Benchimol, 2009; Canale *et al.,* 2012). We used a strict set of criteria to select the studies compiled in our initial database (Roberts *et al.,* 2006). First, the study must have listed all primate species present within each patch, as obtained through field-verified interviews, linear-transect surveys, behavioural studies or any other documentation. Second, we selected only studies that explicitly provided either the size of fragments or exact geographic coordinates which enable us to measure patch size and assess the landscape context using *Google Earth Pro* tools. We set no restrictions on minimum numbers of sites surveyed and considered records of zero species-richness ($S = 0$) for previously occupied forest patches that no longer contained any species at the time of surveys.

Species data were tabulated following a functional classification of 24 platyrrhine primate ‘ecospecies’ (Peres & Janson, 1999). Ecospecies are considered discrete functional groups, corresponding to a single species, or subspecies, or a few ecologically equivalent congeners (see Peres & Janson, 1999 and Appendix 2.1). At each site, we assigned occupancy scores as either present [(1) for ecospecies that had been recorded at a patch] or absent [(0) when an ecospecies that was known to have occurred in the patch had been extirpated]. This enabled total primate species richness estimates (S) at any given patch. Post-fragmentation introductions of exotic and reintroductions of native species, as reported for a few sites, were excluded from our species richness estimates. Night monkeys (*Aotus* spp.), the only nocturnal platyrrhines, were added to our database for only those studies that explicitly documented nocturnal mammals using night surveys. At sites at which more than one independent data source describing the local species composition were available, we considered all species documented in at least one source.

We also compiled observed primate species composition data for large, unbroken forest areas adjacent to each fragment cluster (i.e. the best available continuous ‘pseudo-control’ sites), defined here as the nearest forest tracts >10,000 ha that shared the same primate source fauna of adjacent study patches. We coupled these data with published NatureServe (Patterson *et al.,* 2003) and IUCN (2008) range polygons, publications describing species ranges, and our own extensive joint personal knowledge (i.e. 42 years of fieldwork at >120 Amazonian and Atlantic Forest landscapes) to estimate the baseline (pre-fragmentation) composition of the primate fauna at each site. This allowed derivation of the historical maximum primate species richness that would have once occurred at each site (hereafter, S_{max}). Because local primate species richness is widely variable throughout the Neotropics (Peres & Janson, 1999), we also calculated the proportion of extant species (p_S) retained at each site as $p_S = S/S_{max}$. We also calculated the aggregate assemblage biomass for each patch (B) by summing the estimated body masses of all extant sympatric species occurring at that patch, and the estimated total biomass (B_{max}) of all extant and extinct species that once occurred at the same patch. This allowed us to calculate the proportional extant biomass retained at each site as $p_B = B/B_{max}$.

For each patch, we recorded the geographic coordinates, the matrix type (i.e. the predominant land-cover class within a 1-km external buffer from each patch), and the level of hunting pressure on primates. Because the history and landscape context of forest patches are rarely characterized, we were unable to obtain these variables from most studies. However, we characterized landscape connectivity using two complementary approaches. Firstly, by assigning a matrix type index to each fragment based on its predominant components: (1) water; (2) pasture or cropland; or (3) secondary forest; and secondly, using *Google Earth Pro* tools to estimate the percentage of available forest cover outside fragments within 1 km from their perimeter. Suitable habitat cover within the matrix is widely recognized as robust indicators of landscape connectivity (Tischendorf *et al*., 2003). Although we were able to assign a matrix type index to all forest patches, we could only estimate matrix forest cover for 384 of all 705 patches, either because some studies failed to provide exact geographic coordinates of their study patch(es) or due to poor quality of the relevant images and/or severe cloud cover. Information on levels of subsistence, recreational and commercial hunting pressure was either obtained from the studies or information provided by the authors, who were approached individually in each case. We thus assigned historical levels of post-fragmentation hunting pressure at each site into three classes: (1) non-hunted; (2) lightly or occasionally hunted; and (3) heavily or persistently hunted.

Patches were considered to be spatially nested within landscapes for all landscape-scale analyses. Using ArcGIS (ESRI, 2011), we further combined all sites in our database with pan-Neotropical land-cover and digital elevation, The

Shuttle Radar Topography Mission (SRTM) and distinguished landscapes within any given major region by overlaying spatial clusters of sites with layers of all significant geographic barriers including major rivers, montane areas, and large areas of historical deforestation. We deliberately avoided limiting the size threshold of a landscape as the number of patches they contained and their spatial configuration varied considerably.

From our comprehensive literature search, we included 96 publications in the final data base, providing information on 760 sites (705 forest patches and 55 continuous forests) embedded within 61 landscapes scattered across 11 Neotropical countries from Mexico to Argentina (Fig. 2.1). The number of study sites per landscape varied from 1 to 144 and fragment sizes ranged from 0.1 to 9,731 ha (see Appendix 2.2). Most sites examined here were exposed to light and heavy hunting pressure on primates (36.7% and 14.6%, respectively), and the predominant surrounding matrix was pasture and cropland (87.5%), compared to water (e.g. land-bridge islands within hydroelectric reservoirs) and secondary forests.

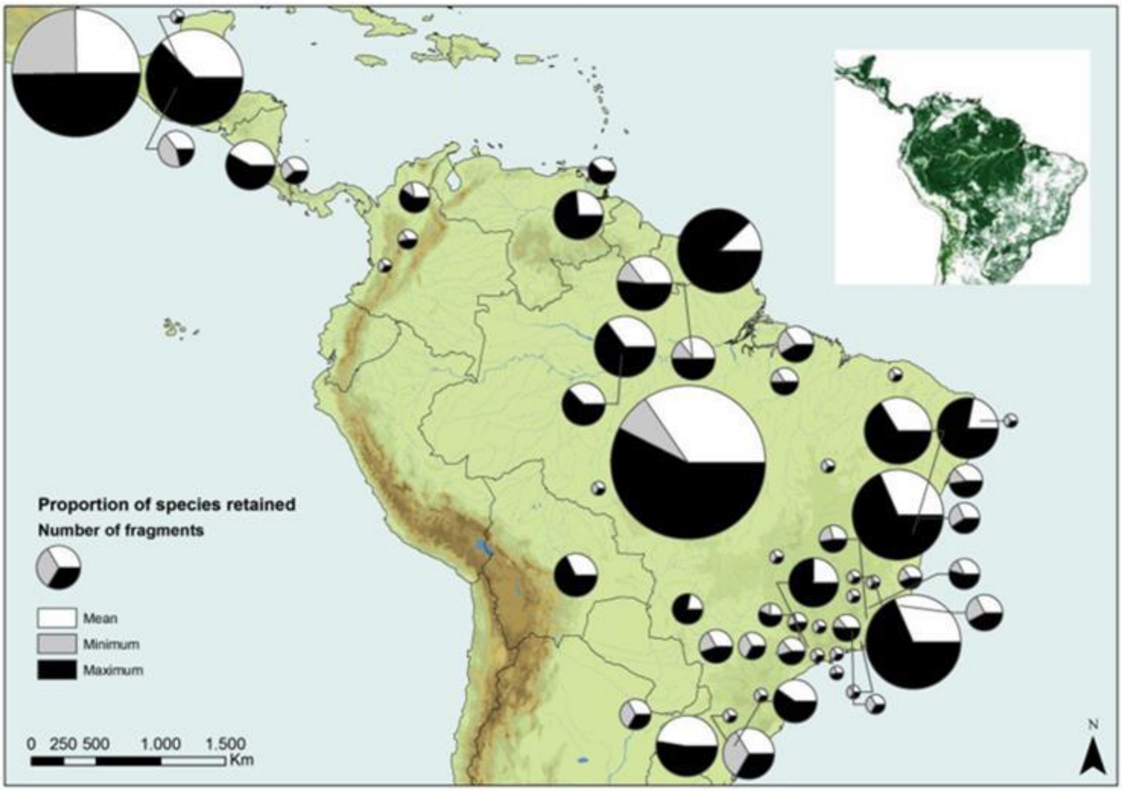

Figure 2.1. Geographic locations of the 61 fragmented forest landscapes examined in this study. The circles are sized proportionally to the total number of forest sites surveyed within each landscape. Pie-charts indicate the proportional number of fragments showing the mean, the minimum and the maximum of species retained (p_S) at each landscape.

2.3.2. Data analysis

To examine relationships between forest patch-area and primate species richness (S), we first considered all 760 study sites and performed linearized forms of SARs using semi-log models, which perform well in explaining SARs (Rosenzweig, 1995, Lomolino, 2001). Because baseline species richness (S_{max}) in local primate faunas within each landscape varied widely across the entire continent (range = 1 - 8 species), we repeated these models considering the within-patch proportion of extant species (p_S). We also assessed biomass-area relationships (BARs) between patch size and the total biomass (B) and the proportion of extant biomass retained in residual assemblages (p_B) to examine broad patterns of species deletion across the body size spectrum available in each landscape. We performed nonlinear multi-model SARs for 38 of the 61 study landscapes where ≥4 forest sites had been surveyed. This was implemented by fitting nonlinear relationships based on eight possible SAR models using 'mmSAR' (Guilhaumon *et al.,* 2010), including four convex (power, exponential, negative exponential, and Monod) and four sigmoidal models (rational function, logistic, Lomolino, and cumulative Weibull). A minimum of four sites per landscape was chosen because this is the smallest sample size required to run SARs using this R-package (Guilhaumon et al., 2010; http://mmsar.r-forge.r-project.org). We then used information theoretic analyses to evaluate model performance and parsimony using Akaike weights (Burnham & Anderson, 2002).

We further investigated the additive effects of external variables (hunting pressure and matrix-type) on SARs, using the proportion of species (p_S) and biomass (p_B) retained at all 760 sites. Next, we ran all possible SAR semi-log regression models considering only 38 landscapes containing ≥4 study sites, and examined how Z-values (a direct measure of initial and overall slopes), intercepts, and R^2-values of landscape-specific SAR models responded to our external variables. ANCOVA was used to investigate the effects of matrix type on p_S and p_B, with patch-area as a covariate. Finally, we used generalized linear mixed models (GLMMs) to relate variation in patch-area, matrix type, forest cover and hunting pressure to the proportion of extant species (p_S) and biomass (p_B) retained within patches. This approach was the most appropriate to account for potential spatial autocorrelation (Bolker *et al.,* 2009), with our global model incorporating a random term nesting 'patches' within 'landscapes', whereby same-landscape patches shared the same source primate fauna. We also included S_{max} or B_{max} values as offset variables in the proportion of species richness and biomass models, respectively, to account for patch-scale variation in the maximum species/biomass packing. We performed species richness and assemblage biomass GLMMs considering: (1) all 760 forest sites nested within 61 landscapes, with fixed effects available for each site - patch-area, matrix type and hunting pressure; (2) only those forest sites for which we were able to obtain forest cover estimates, added as a 4th-fixed effect (N=384 patches nested within 34 landscapes); and (3) only 728 forest sites nested within 38 landscapes containing ≥4 forest sites. Models were fitted using the 'lme4' package (Bates, 2007) within the R platform, and parameters were estimated using Laplace approximation as recommended by Bolker *et al.,* 2009. We selected the 'best' models using the 'MuMIn' package (Bartón, 2009); examined every possible first-order variable combination; ranked them based on the Akaike Information Criterion (AIC) (Burnham & Anderson, 2002); and determined the relative importance of each explanatory variable given their model frequency and cumulative Akaike weight.

2.4. Results

2.4.1. Species-area relationships

We found a clear positive patch-area effect on total primate species richness across all 760 sites considering all landscapes ($R^2_{adj} = 0.299$, $P < 0.001$). This was confirmed by a positive area effect on the proportion of local species pools persisting within forest sites ($R^2_{adj} = 0.229$, $P < 0.001$, Fig. 2.2). Furthermore, increasingly larger forest patches retained a greater aggregate assemblage biomass ($R^2_{adj} = 0.223$, $P < 0.001$) and a larger proportion of the total biomass in the original primate fauna ($R^2_{adj} = 0.162$, $P < 0.001$, Fig. 2.2).

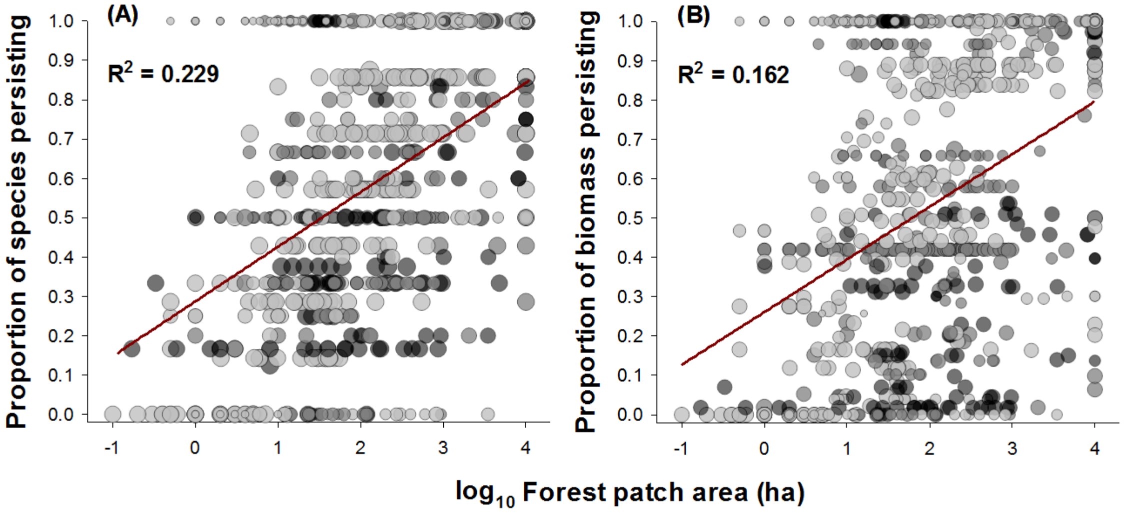

Figure 2.2. Overall relationship between forest patch area and the (A) proportion of primate species and (B) proportion of aggregate primate biomass persisting within 760 sites investigated in this study. Circles are coloured according to levels of hunting pressure, with darker circles indicating more heavily hunted sites. Circles sizes are proportional to the pre-fragmentation maximum number of species that should have occurred at each patch, given historical records and any other information on species distributions.

Forest patch size was also a significant predictor of primate species richness at the landscape-scale, explaining between 0% and 83.7% (mean R^2_{adj} = 30.2%) of the variation in semi-log SAR models for the 38 landscapes containing at least four surveyed sites (Table 2.1). This explanatory power was further substantially improved with a nonlinear multi-model framework using raw (untransformed) data, which explained up to 61% of the landscape-scale SARs (mean R^2_{adj} = 51.3%). The negative exponential model provided the most frequent ‘best-fit’ for SARs within those landscapes, followed by the power model. Nevertheless, we were unable to obtain proper convergence in nonlinear SAR models for 15 of the 38 landscapes, and this was independent of the number of patches investigated (r = –0.040, *N* = 38).

Table 2.1. Coefficients (c), slopes (z) and adjusted R^2-values of the ‘best’ non-linear and semi-log SAR model for 38 Neotropical forest landscape containing at least four study sites. Multi-model approach using ‘mmSAR’ were unable to run in landscapes containing only four or fewer sites.

Landscape	**Region**	**Geographic coordinates**	**N^{o} of sites**	**S_{max}**	**Hunting pressure**	**Matrix type**	**BEST MODEL**				**SEMI-LOG**[3]		
							NAME[2]	**c**	**z**	**R^2_{adj}**	**c_s**	**z_s**	**R^{2adj}**
Alta Floresta	Brazil (Amazon)	56° 05' W, 09° 54' S	144	7	None	Pasture-Cropland	Ratio	1.91	0.06	0.53	1.17	1.35	0.49
Los Tuxtlas	Mexico	90° 48' W, 16° 14' N	88	2	Moderate	Pasture-Cropland	Invalid	-	-	-	1.06	-0.02	0.01
Guatemala	Guatemala	89° 32' W, 16° 58' N	50	2	Moderate	Pasture-Cropland	Invalid	-	-	-	0.40	0.52	0.21
São João	Brazil (Atlantic Forest)	42° 01' W, 22° 27' S	49	3	Moderate	Pasture-Cropland	Invalid	-	-	-	0.68	0.35	0.07
Jequitinhonha	Brazil (Atlantic Forest)	40° 41' W, 16° 20' S	46	6	Heavy	Pasture-Cropland	Power	0.85	0.18	0.41	-0.10	1.05	0.39
Saint-Eugene	French Guiana	53° 04' W, 04° 51' N	39	6	None	Water	Power	0.59	0.26	0.55	-0.27	1.63	0.64
South Bahia	Brazil (Atlantic Forest)	39° 39' W, 14° 53' S	26	6	Heavy	Pasture-Cropland	Power	1.57	0.05	0.10	1.50	0.27	0.07
Balbina	Brazil (Amazon)	59° 38' W, 01° 49' S	21	7	None	Water	Logistic	6.22	0.02	0.87	-1.06	2.38	0.83
Pernambuco	Brazil (Atlantic Forest)	35° 50' W, 08° 43' S	20	3	None	Pasture-Cropland	Invalid	-	-	-	1.21	-0.19	0.00
Santa Maria	Brazil (Atlantic Forest)	53° 42' W, 29° 43' S	20	1	None	Pasture-Cropland	Invalid	-	-	-	0.85	0.05	0.00
South-central Amazon	Brazil (Amazon)	54° 53' W, 02° 50' S	17	7	Moderate	Pasture-Cropland	Negexpo	5.27	0.02	0.18	3.92	0.32	0.00
Alter do Chão	Brazil (Amazon)	54° 57' W, 02° 29' S	16	8	Heavy	Pasture-Cropland	Invalid	-	-	-	1.82	0.57	0.04
Guri	Venezuela	62° 52' W, 07° 21' N	14	4	None	Water	Power	0.67	0.18	0.54	0.17	0.88	0.61
Santa Rosa	Costa Rica	85° 39' W, 10° 50' N	13	3	Moderate	Pasture-Cropland	Exponential	-0.04	0.62	0.02	-0.12	1.48	0.00
Campinas	Brazil (Atlantic Forest)	46° 55' W, 22° 49' S	13	4	None	Pasture-Cropland	Exponential	-0.50	0.68	0.62	-0.69	1.66	0.58
Vale do Taquari	Brazil (Atlantic Forest)	52° 02' W, 29° 41' S	12	1	None	Pasture-Cropland	Invalid	-	-	-	0.47	0.16	0.09
BDFFP	Brazil (Amazon)	59° 52' W, 02° 24' S	11	6	None	Seconday forest	Weibull	5.49	0.17	0.90	1.60	1.29	0.61
Eastern Amazonia	Brazil (Amazon)	47° 47' W, 02° 33' S	11	7	Moderate	Pasture-Cropland	Negexpo	6.36	0.00	0.52	2.27	1.06	0.32
Bolívia	Bolívia	63° 03' W, 17° 47' S	10	6	Moderate	Pasture-Cropland	Negexpo	3.06	0.26	0.51	1.02	1.01	0.30
Chiapas	Mexico	90° 48' W, 16° 15' N	8	2	Moderate	Pasture-Cropland	Logistic	2.01	0.07	0.59	1.10	0.27	0.38
Michelin	Brazil (Atlantic Forest)	39° 19' W, 13° 46' S	8	4	Moderate	Pasture-Cropland	Logistic	2.74	0.00	0.55	0.89	0.46	0.36
Viçosa	Brazil (Atlantic forest)	42° 52' W, 20° 48' S	8	4	Moderate	Pasture-Cropland	Invalid	-	-	-	1.40	-0.09	0.00
Dois irmãos	Brazil (Atlantic Forest)	55° 18' W, 20° 30' S	7	2	None	Pasture-Cropland	Invalid	-	-	-	-1.00	0.47	0.79
Augusto	Brazil (Atlantic Forest)	40° 33' W, 19° 54' S	7	5	Moderate	Pasture-Cropland	Power	1.74	0.12	0.19	0.67	1.15	0.03
Upper Paraná	Brazil (Atlantic Forest)	53° 19' W, 22° 46' S	6	2	Heavy	Pasture-Cropland	Power	0.75	0.14	0.24	0.45	0.49	0.04
Sergipe	Brazil (Atlantic Forest)	37° 14' W, 11° 12' S	6	3	None	Pasture-Cropland	Negexpo	3.15	0.04	0.91	-0.72	1.89	0.84
North-eastern Colombia	Colombia	74° 16' W, 08° 35' N	6	5	Moderate	Pasture-Cropland	Power	1.04	0.17	0.70	0.49	1.02	0.57
Magdalena	Colombia	74° 44' W, 05° 39' N	6	5	Moderate	Pasture-Cropland	Invalid	-	-	-	4.03	-0.33	0.00
Rio Casca	Brazil (Atlantic Forest)	42° 44' W, 20° 04' S	5	5	Moderate	Pasture-Cropland	Negexpo	2.60	0.06	0.12	1.44	0.52	0.00
Maranhão	Brazil (Atlantic Forest)	48° 08' W, 05° 00’ S	5	5	None	Pasture-Cropland	Negexpo	4.35	0.04	0.92	0.55	1.34	0.54
Córrego	Brazil (Atlantic Forest)	39° 50' W, 18° 24' S	5	4	None	Pasture-Cropland	Negexpo	4.09	0.00	0.67	-4.97	2.27	0.48
Araras	Brazil (Atlantic Forest)	44° 15' W, 22° 25' S	5	5	Moderate	Pasture-Cropland	Exponential	-2.52	0.71	0.49	-2.53	1.64	0.32
Corrientes[1]	Argentina	58° 50' W, 27° 30' S	5	1	None	Pasture-Cropland	Invalid	-	-	-	-	-	-
La Suerte	Costa Rica	83° 46' W, 10° 26' N	4	3	None	Pasture-Cropland	Invalid	-	-	-	1.96	0.41	0.10

Trinidad	Trinidad & Tobago	61° 15' W, 10° 25' N	4	2	Moderate	Pasture-Cropland	Invalid	-	-	-	-4.75	1.80	0.18
Tucuruí	Brazil (Amazon)	49° 30' W, 04° 16' S	4	7	None	Water	Invalid	-	-	-	0.44	2.09	0.40
Barreiro Rico	Brazil (Atlantic Forest)	48° 05' W, 22° 41' S	4	5	None	Pasture-Cropland	Invalid	-	-	-	-5.00	3.33	0.41

[1] no variation across the data set.

[2] Formulae of each model:

Power – $S=cA^{z}$

Exponential – $S= c + z\log(A)$

Negative exponential (Negexpo) – $S=d(1-\exp(-zA))$

Monod – $S=d/(1-cA^{-1})$

Rational function (Ratio) – $S=(c+zA)/(1+dA)$

Logistic – $S=d/(1+\exp(-zA+f))$

Lomolino – $S=d/1+(z^{\log(f/A)})$

Cumulative Weibull (Weibull) – $S=d(1-\exp(-zA^{f}))$

Invalid – analysis was not run successfully

S= number of species; A= area; c, z, f, d are fitted parameters (Guilhamon *et al*., 2010).

[3] Formulae of the semi-log model: $S=c_s + z_s\log(A)$. Here, c_s= the intercept of the curve in arithmetic space and z_s= a direct measure of the initial and overall slope.

2.4.2. Are SARs modulated by hunting and connectivity?

Over and above patch-area effects, we detected a significant effect of hunting pressure reported for individual sites in predicting primate species occupancy and biomass. The slopes of the relationships between patch-area and the proportion of species (p_S) and total biomass (p_B) retained across all 760 forest sites were steeper in non-hunted sites than in lightly and heavily hunted sites (Fig. 2.3). In contrast, we failed to detect an effect of matrix type on the species-richness and biomass retained considering all forest sites. Considering each landscape separately, the level of hunting pressure also profoundly affected the R^2-values in semi-log SARs and BARs for the 38 landscapes containing at least four forest sites surveyed, whereas matrix type exerted minor influence (Fig. 2.4). Additionally, hunting pressure also affected the slopes of both SARs and BARs within patches sharing the same landscape (see Appendices 2.3 and 2.4). The Z-values and intercepts of these 38 SARs models did not show a clear trend in relation to hunting pressure and matrix type. However, when we considered only forest patches that had no history of hunting pressure, we detected a significant effect of matrix type on the relationship between patch-area and the proportion of species (ANCOVA, F=19.688, $p<0.001$) and proportion of extant biomass retained (ANCOVA, F=5.605, $p=0.018$, Fig. 2.5).

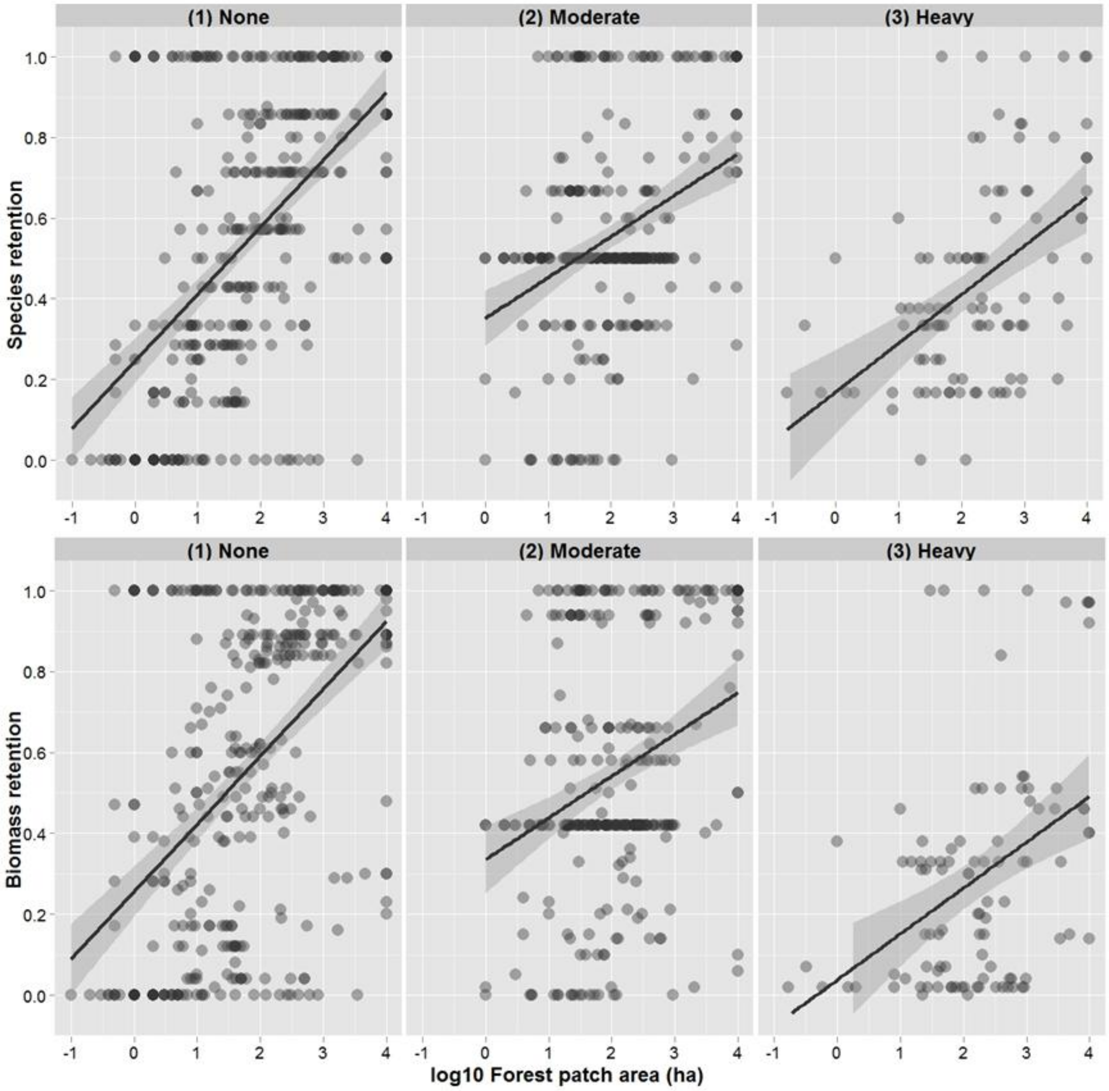

Figure 2.3. Relationship between forest patch size and the proportion of primate species (p_S) and total biomass (p_B) retained across 760 Neotropical forest sites, under varying levels of hunting pressure.

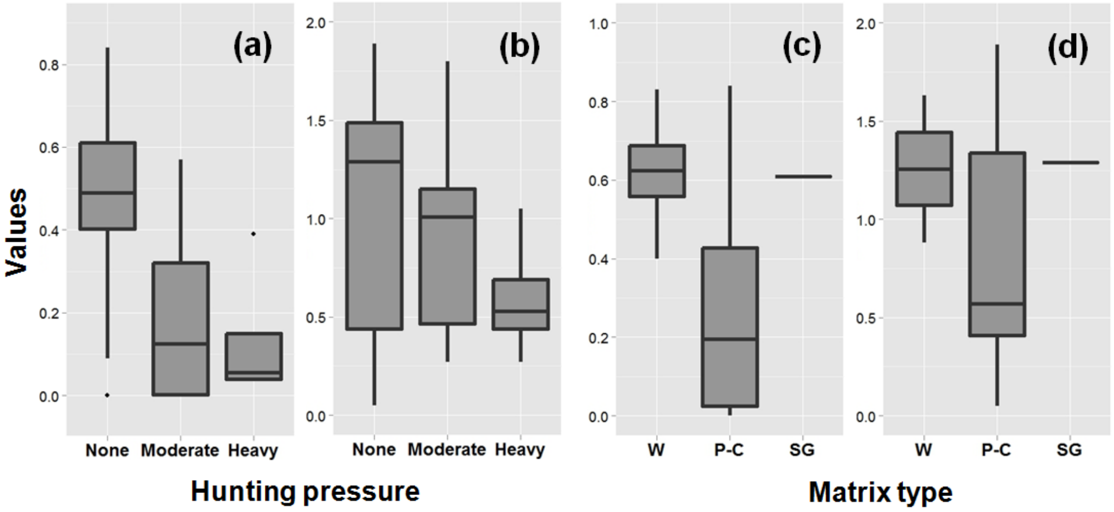

Figure 2.4. Variation in R^2-values, according to levels of hunting pressure and matrix type, in (a, c) semi-log species- and (b,d) biomass-area relationships for 38 landscapes containing a minimum of four forest fragments surveyed. Matrix types are coded as: (W) Water, (P-C) Pasture and cropland; (SG) Secondary growth.

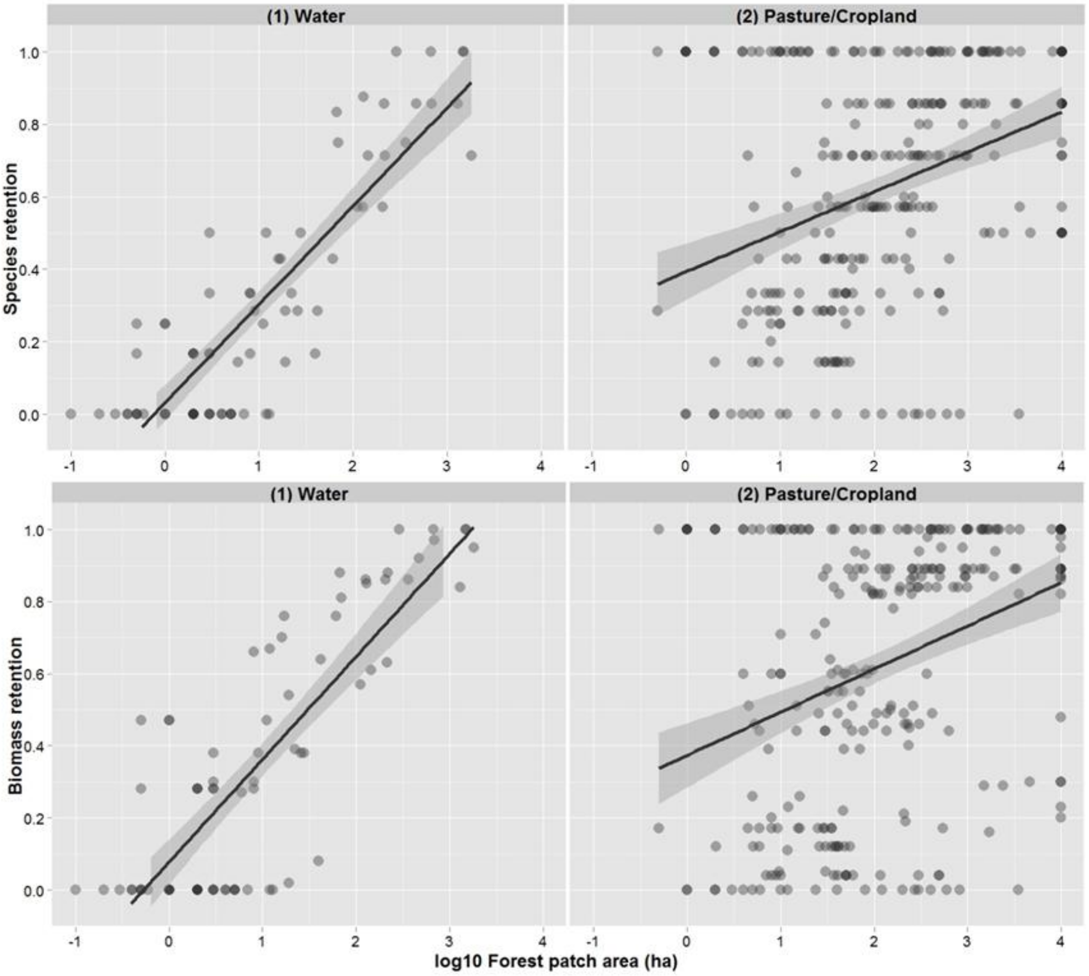

Figure 2.5. Relationship between forest patch size and the proportion of primate species (p_S) and aggregate biomass (p_B) retained within non-hunted forest isolates (*N* = 383) surrounded by either water (i.e. true islands) or a matrix of cattle pastures and cropland.

Considering all 760 forest sites nested within 61 study landscapes, GLMMs showed that forest area was a significant predictor of the proportion of extant species retained within patches, whereas forest area, level of hunting and matrix type were significant predictors of extant biomass (Table 2.2). The 'best' GLMM model explaining the proportion of species retained contained patch-area, followed by a model including patch-area and level of hunting pressure (ΔAIC=1.82, see Appendix 2.5). Considering the extant primate biomass, however, the top-ranking model included forest patch-area and level of hunting pressure, followed by a model containing only patch-area (ΔAIC=2.05). Given that pasture and cropland were the predominant matrix types surrounding forest patches across all studies, we ran all models again while excluding true islands and patches surrounded by secondary forest. However, this did not change the above pattern. We also found a similar pattern when performing GLMMs considering only the 728 forest sites nested within the 38 landscapes containing at least four forest sites. Patch-area was again the strongest predictor of species richness (β= 0.798, $p<0.001$), whereas forest area (β=1.169, $p<0.001$), level of hunting (β= –3.740, $p<0.001$) and matrix type (β= 4.285, $p<0.001$) were significant predictors of aggregate biomass. Likewise, we also detected the predominance of both area (β=1.081, $p<0.001$) and hunting pressure (β=–2.693, $p<0.05$) effects on the proportion of species retained when GLMMs considered the additional connectivity effect of matrix forest cover. The best model included both patch-area and level of hunting pressure, followed by a model containing patch-area, hunting pressure and matrix forest cover (ΔAIC=1.68). When we ran the GLMMs explaining extant primate biomass, however, matrix forest cover was also a good predictor in the best model (β=0.022, $p<0.05$), in addition to patch-area (β=2.764, $p<0.001$) and hunting pressure (β=–1.699, $p<0.01$).

Table 2.2. Summary of Generalized Linear Mixed Models (GLMMs) of the proportion of primate species (p_S) and extant biomass (p_B) retained within 760 forest sites nested in 61 fragmented forest landscapes across the Neotropics, with S_{max} and B_{max} as offsets. Model-averaged coefficients are presented.

Parameter	**Estimate**	**Unconditional SE**	**Confidence Interval**	**Relative Importance**
P_S				
(Intercept)	-1.137	0.345	(-1.812, -0.461)	_
Hunting2	-0.319	0.322	(-0.950, 0.311)	0.24
Hunting3	-0.574	0.409	(-1.375, 0.227)	_
Matrix2	0.954	1.028	(-1.060, 2.969)	0.16
Matrix3	0.475	0.445	(-0.398, 1.348)	
Area (log x)	0.723	0.097	(0.533, 0.914)	1.00
P_B				
(Intercept)	-1.165	0.376	(-1.902, -0.429)	
Hunting2	-0.708	0.411	(-1.514, 0.097)	0.74
Hunting3	-1.221	0.523	(-2.247, -0.195)	
Matrix2	0.025	0.261	(-0.490, 0.539)	
Matrix3	0.280	0.543	(-0.785, 1.344)	
Area (log x)	0.865	0.108	(0.653, 1.077)	1.00

2.5. Discussion

This is the most comprehensive systematic review of the effects of habitat fragmentation on an entire suborder of tropical forest vertebrates, and the first quantitative synthesis of community-wide Neotropical primate responses to anthropogenic forest fragmentation. A global-scale analysis on primate species-area relationships (Harcourt & Doherty, 2005) considered data from only 7.4% of the forest fragments and 34% of the landscapes that we examined here. Primate fragmentation studies tend to focus on species responses to habitat size and isolation within single landscapes (Onderdonk & Chapman 2000; Marsh, 2003, Marshall *et al.,* 2010). Here, we used an extensive dataset comprising 760 forest patches embedded within 61 landscapes to examine which patch and landscape variables best predict primate species richness throughout the Neotropics. We show that forest patch size is a robust predictor of primate species persistence, which is consistent with Harcourt and Doherty’s (2005) global scale analysis. We also show that patch-area is a good predictor of the proportion of primate assemblage biomass retained across all 760 forest sites. However, patch-area effects, rather than operating in isolation, interact synergistically with game population depletion by hunters, who are highly selective and preferentially target large-bodied species in most forest landscapes (Peres, 1990, 2000), thereby driving non-random local extinctions. Maintaining large patches of primary/secondary forest, or increasing their size and/or connectivity through forest restoration, are therefore central to any conservation initiative, but this alone does not ensure the persistence of full primate assemblages in overhunted fragmented forest landscapes.

Several studies have shown the importance of patch-area in retaining vertebrate species in tropical forest fragments (Ferraz *et al.,* 2007; Michalski & Peres, 2007; Stouffer *et al.,* 2009). This typically positive area-effect can be attributed to a greater habitat diversity; larger pools of trophic and/or structural resources; and larger populations, all of which can operate independently to reduce local extinction rates (Connor & McCoy, 2001). Yet a single-minded focus on habitat patch-area and isolation is not enough to maximise the biodiversity value of tropical forest remnants, since real-world ‘working’ landscapes are subjected to multifaceted natural and anthropogenic disturbances that interact synergistically with forest area (Laurance & Peres, 2006). These additive perturbation effects continue to be neglected in several fragmentation ecology studies, which largely focus on MacArthur & Wilson’s (1967) original island biogeography paradigm, which has single-mindedly stressed the effects of area and isolation while overlooking the influence of external stressors on species persistence within patches.

In addition to patch-area, hunting pressure also affected the pattern of primate species persistence across all sites. Large-bodied primates comprise the most preferred prey items for indigenous groups in Neotropical forests (Redford &

Robinson, 1987; Jerozolimski & Peres, 2003), and hunting is widely considered to be the most severe threat for many primate species (Milner-Gulland *et al.,* 2003), vastly surpassing the importance of habitat loss in the largest remaining tracts of tropical forests (Peres & Lake, 2003). Hunting interacts synergistically with forest fragmentation by facilitating physical access by hunters to prey populations, reducing local population sizes, and precluding immigrants from rescuing sink populations, all of which can accelerate local extinction rates in forest isolates (Peres, 2001). Accordingly, we found clear evidence that subsistence hunters had access to forest fragments within at least 27 landscapes. This aggravated the local extinction probability of midsized to large-bodied primate species, thereby reducing the explanatory power of species-area models in fragmented forest landscapes. Hunting also markedly inflated the minimum size of forest patches required to retain primate assemblages of any given size. For instance, forest fragments containing one half of the species in the original fauna were on average 233 ha in overhunted landscapes but only 34 ha in nonhunted landscapes. Conversely, retaining 90% of all species on average required a seven-fold increase in fragment size from 16,748 ha in nonhunted landscapes to 111,737 ha in landscapes where primates had been hunted.

Hunting pressure also strongly depressed the extant relative biomass persisting within forest patches, indicating that larger-bodied species had been disproportionately affected and driven to local extinction in overhunted fragments. This fits the broad patterns in Neotropical forests where primate species exceeding 3 kg are often considered fair game species, but smaller species are typically ignored by subsistence hunters (Redford & Robinson, 1987; Peres, 1990). Our body-mass weighed SAR models predicted that retaining 50% of the total biomass of the baseline primate assemblage at each fragment would require a patch size increase from 28 ha at nonhunted sites to 1,924 ha at heavily hunted sites. Primate surveys throughout lowland Amazonia indicate that hunting significantly reduces the crude primate biomass in otherwise undisturbed continuous forest sites, where large-bodied atelines (i.e. *Ateles, Lagothrix, Alouatta)* succumb to steep population declines (Peres & Palacios, 2007). This can be extended to fragmented forest landscapes where hunters had driven large-bodied species to local extirpation way before the longer-term effects of patch-area and/or isolation can operate (Peres, 2001). Likewise, our results clearly show that hunting pressure strongly affected both the proportion of species and the proportion of biomass retained within forest fragments, thereby flattening the slopes of both species-area and biomass-area relationships, and reducing their R-square values.

Although to a lesser extent, we also detected a discernible effect of landscape connectivity on overall species and biomass persistence. Matrix type exerted only a minor effect on species richness and aggregate assemblage biomass for all 760 forest sites examined here even though models containing ‘matrix type’ as a covariate appeared in the three top-ranking models explaining the proportion of extant primate species (see Appendix 2.5). However, we were able to detect a significant effect of matrix type on extant species richness and biomass when we restricted the analysis to non-hunted forest patches only. SAR slopes are good indicators of species persistence in island systems (Triantis *et al.,* 2012) and we detected a significantly higher z-value for both relationships considering fragments isolated within a matrix of pastures or cropland. Moreover, once we added an independently derived metric of matrix forest cover into our analysis, we found that patches surrounded by large amounts of forest habitat also retained a higher proportion of extant primate species richness and biomass. Several studies have shown the importance of neighbouring habitats on the occupancy rate of birds and mammals in tropical forest fragments (Andrén, 1994; Antongiovanni & Metzger, 2005; Prugh *et al.,* 2008; Lees & Peres, 2009), highlighting that enhancing matrix quality can facilitate movements across forest remnants (Franklin & Lindenmayer, 2009). The matrix plays a key role in both inter-patch travel and foraging of forest primates in a fragmented landscape in East Africa (Anderson *et al.,* 2007) and large-bodied species were able to colonize Amazonian forest fragments by traversing a benign second-growth matrix (Boyle & Smith, 2010). Indeed, the structure of the matrix influences the likelihood of movements across forest patches, depending on patterns of locomotion and dispersal. For primates, open-water seems to be more difficult to traverse than agropastoral and young secondary forest matrices, given that they can both serve as stepping stones or corridors for individual/group movements across forest patches. In the southern Amazonian landscape of Alta Floresta, for instance, a breeding group of spider monkeys occupying a ~7-ha forest fragment for several years has successfully overcome a gap distance greater than 1 km by traveling on the ground through scrubby cattle pastures to reach a neighbouring fragment (C.A. Peres, unpubl. data), underscoring the locomotion plasticity of even one of the most arboreal Neotropical mammals. However, once a landscape has been severely defaunated due to chronic overhunting, even relatively well-connected patches are likely to remain vacant as neighbouring source populations would remain unavailable for successful recolonization. Greater matrix permeability may therefore facilitate primate movements across forest patches, but this alone is not enough if hunting pressure continues to ravage populations unchecked.

2.6. Conclusions

2.6.1. Future directions

Most empirical applications of the species-area relationship fail to consider mechanisms of species loss other than the classic area and isolation effects that have been so heavily revisited under the traditional island biogeography paradigm. Using a meta-analytical approach, we detected decisive interactions between the effects of habitat area and human-induced wildlife depletion of local populations in determining patterns of primate species persistence and assemblage biomass right across the New World tropics. Further studies should therefore consider the historical land-use context contributing to the full mosaic of environmental perturbations in evaluating patterns of species persistence in fragmented landscapes. For tropical forest vertebrates in particular, future studies should consider the landscape structure in which fragments are embedded, rather than focusing entirely on patch-scale variables (Arroyo-Rodríguez & Mandujano, 2009). Improving the analytical power and policy utility of these studies will also require further details on the nature of historical anthropogenic disturbances affecting forest habitat isolates (e.g. wildfires, hunting, selective logging), larger spatial replication and sample sizes, and better measures of landscape connectivity between patches, all of which require better spatial data reported in individual studies. We also suggest that researchers should evaluate the interactions between landscape variables and species traits to enhance our understanding of species sensitivity to fragmentation and propose efficient mechanisms for species-specific conservation (Henle *et al.,* 2004).

2.6.2. Conservation Implications

Due to their universal charismatic appeal, nonhuman primates are widely recognized as conspicuous flagship species for biodiversity conservation (Mittermeier *et al.,* 2013). Conservation strategies designed to retain full complements of primate species can therefore ensure the persistence of much of the co-occurring tropical forest biota. Based on our continental wide analysis on patterns of primate persistence in fragmented forest landscapes, we propose the following recommendations to inform conservation policy and action.

(1) Allocate higher conservation and research priorities to fragmented landscapes under a restoration paradigm. Because even small, isolated forest patches can retain a significant fraction of the original forest biota, protection of forest fragments becomes an imperative, particularly in highly deforested and/or semi-defaunated landscapes (Turner & Corlett, 1996; Canale *et al.,* 2012). Expanding habitat area through forest restoration programs or enhancing protection of both forest structure and composition in existing forest fragments should therefore be encouraged in all Neotropical landscapes. However, we found that persistence of at least 60% of the local pool of primate species requires forest patches of 100 ha or larger, suggesting that conservation efforts should prioritize patches considerably larger than this minimum size threshold. Patches ≥100 ha comprise only 11.5% of the 245,173 remaining fragments across the Brazilian Atlantic forest (Ribeiro *et al.,* 2009) and approximately 25% of existing fragments (including over 1.12 million km^2 of forest) within four states of Brazilian Amazonia (Broadbent *et al.,* 2008). These two forest regions encompassed most South American forests and contain the largest number of sites in our dataset (Fig. 2.1).

(2) Depletion of primate populations within fragments by subsistence hunters should be curbed or precluded. Hunting pressure had a decisive detrimental effect on large-bodied primate persistence within the fragments we investigated. This is consistent with other studies showing that hunting pressure vastly accelerates species loss from tropical forest fragments (Peres, 2001; Thornton *et al.,* 2011). Enforcing hunting restrictions within forest fragments in both public protected areas and private landholdings, and implementing education programs designed for local communities near those fragments would mitigate the pervasive effects of hunting and other forms of patch scale disturbance on biodiversity.

(3) Re-establish connectivity between forest patches. In highly fragmented landscapes, enhancing the suitability of the surrounding habitats can facilitate matrix movements between fragments, thereby increasing patch occupancy in the long-term (Andrén, 1994; Prugh *et al.,* 2008). Setting aside or restoring riparian or upland forest corridors between remaining patches through land-use subsidies should also be considered in mitigating biodiversity erosion in fragmented landscapes.

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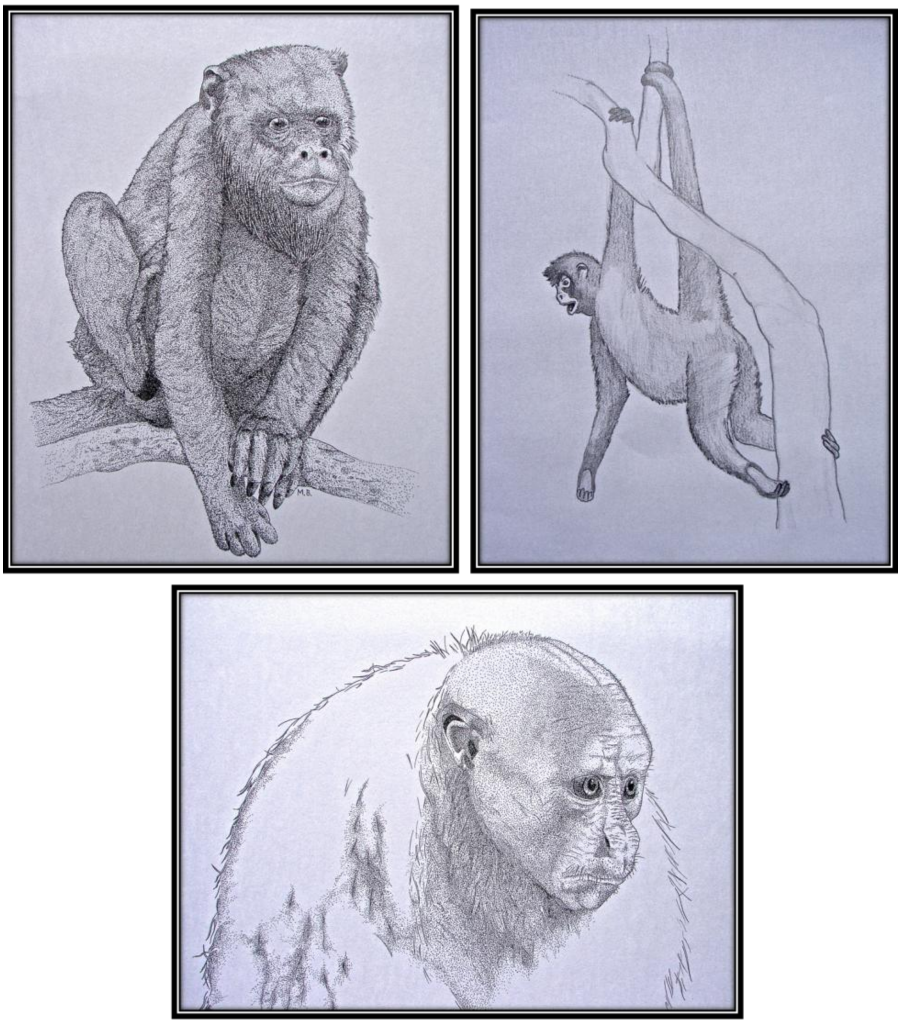
CHAPTER 3

PREDICTING PRIMATE LOCAL EXTINCTIONS WITHIN 'REAL-WORLD' FOREST FRAGMENTS: A PAN-NEOTROPICAL ANALYSIS



The howler monkey, *Alouatta nigerrima*, the spider monkey, *Ateles chamek,* and the bald uakari, *Cacajao calvus*. Courtesy of the artist Marco Bueno.

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3.1. Abstract

Understanding the main drivers of species extinction in human-modified landscapes has gained paramount importance in proposing sound conservation strategies. Primates play a crucial role in maintaining the integrity of forest ecosystem functions and represent the best studied order of tropical terrestrial vertebrates, yet primate species diverge widely in their responses to forest habitat disturbance and fragmentation. Here, we present a robust quantitative review on the effects of habitat fragmentation on Neotropical forest primates to pinpoint the drivers of species extinction across a wide range of forest patches from Mexico to Argentina. Presence-absence data on 19 primate functional groups were compiled from 755 forest patches and 55 adjacent continuous forest sites, which were nested within 61 landscapes investigated by 96 studies. Forest patches were defined in terms of their size, surrounding matrix and level of hunting pressure on primates, and each functional group was classified according to seven life-history traits. Generalized linear mixed models showed that patch size, forest cover, level of hunting pressure, home range size and trophic status were the main predictors of species persistence within forest isolates for all functional groups pooled together. However, patterns of local extinction varied greatly across taxa, with *Alouatta* and *Callicebus moloch* showing the highest occupancy rates even within tiny forest patches, whereas *Brachyteles* and *Leontopithecus* occupied fewer than 50% of sites, even in relatively large forest tracts. Our results uncover the main predictors of platyrrhine primate species extinction, highlighting the importance of considering the history of anthropogenic disturbances, the structure of landscapes, and species life-history attributes in predicting primate persistence in Neotropical forest patches. We suggest that large-scale conservation planning of fragmented forest landscapes should prioritize and set-aside large, well-connected and strictly protected forest reserves to maximise species persistence across the entire spectrum of primate life-history.

3.2. Introduction

Tropical forest remnants are undoubtedly proliferating in numbers but becoming smaller, more degraded, and increasingly isolated over time. Each year, 13 million hectares of tropical forests worldwide are lost due to forest conversion to agriculture and cattle pastures [FAO, 2010], leading to increasingly fragmented forest landscapes of highly questionable biodiversity value. As a result, forest-dwelling species experience wholesale changes in biotic and abiotic conditions, becoming highly vulnerable to extinction once populations become stranded in forest remnants [Fischer & Lindenmayer, 2007]. However, some species are at higher risk in fragmented landscapes, with rare, matrix-intolerant species, with limited mobility being most extinction-prone [Davies et al., 2000; Ewers & Didham, 2006; Henle et al., 2004] despite inconsistencies across studies in the key determinants of species vulnerability to habitat fragmentation and edge effects. This partly occurs because different fragmented landscapes have experienced varying histories of habitat perturbation and population depletion, resulting in marked differences in connectivity, habitat quality and population sizes, all of which affect within-patch species persistence. Pinpointing predictors of species extinction in forest fragmented landscapes has therefore become an important challenge for applied landscape ecologists.

Nonhuman primates comprise an excellent focal group to identify predictors of species extinction within forest patches experiencing different levels of anthropogenic disturbance [Isaac & Cowlishaw, 2004]. Neotropical primates are extremely forest-dependent, may be strongly affected by the twin processes of deforestation and forest fragmentation, and exhibit a wide spectrum of tolerance to forest habitat disturbance. Wild primate populations have also been extensively studied in relatively pristine forests over several decades, providing a reasonably good baseline knowledge of species life-history traits [Harcourt & Doherty, 2005; Marshall et al., 2010]. Moreover, primates account for a disproportionate share of the arboreal vertebrate biomass in tropical forests [Oates et al., 1990; Peres, 1999], are important seed dispersal vectors [e.g. Link & Di Fiore, 2006], and exert a key role in forest ecosystem functioning [Bourlière, 1985]. Conservation strategies designed to maintain full primate assemblages can therefore maximise the integrity of much of the co-occurring tropical forest biota.

Neotropical forests harbour the world's largest primate fauna (139 species in 19 genera, or 35.6% of species worldwide [IUCN, 2008]) but also experience higher rates of tropical deforestation. Some 4 Mha of forest were lost annually between 2000 and 2010 in South America alone [FAO, 2010], resulting in widespread collateral effects including forest fragmentation. Many studies have deliberately or unwittingly documented patterns of Neotropical primate species persistence in forest fragments within variable-sized study landscapes [Boyle & Smith, 2010a; Estrada & Coates-Estrada, 1996; Marsh, 2003], providing a unique dataset to understand primate responses to habitat loss and fragmentation. For instance, 72% of the studies included in the most comprehensive volume on primate responses to habitat fragmentation [Marsh, 2003] were conducted within the Neotropical realm. However, most of these studies are restricted to forest patches within single landscapes which operate within a particular historical setting of interacting anthropogenic threats. For instance, the degree of forest disturbance and hunting pressure within patches, the nature of the surrounding habitat matrix, and time since isolation are potentially major confounding effects that can undermine our understanding of the key drivers of species extinction within forest fragments.

Several species traits have been used to predict primate species retention within fragmented tropical forest landscapes sharing a particular set of attributes. Fragment size, degree of isolation and matrix type are among the most common patch and/or landscape-scale attributes used to explain patterns of species persistence, whereas species body size, group size, degree of frugivory and home range size comprise the most frequent morpho-ecological traits [e.g. Boyle & Smith, 2010a; Estrada & Coates-Estrada, 1996; Johns & Skorupa, 1987]. Nonetheless, primate responses to fragmentation can diverge widely even across conspecific populations. For instance, brown capuchins (*Cebus apella*) was the most ubiquitous species, occupying 98% of 129 forest fragments in a southern Amazonian landscape [Michalski & Peres, 2005], but were found in only 15% of nine forest patches in a central Amazonian landscape [Boyle & Smith, 2010a]. Because these landscapes have experienced idiosyncratic histories of structure, perturbation and primate depletion, extracting generalisations on degrees of species vulnerability to fragmentation becomes a challenge. Examining a wide range of landscape contexts can therefore provide a much better understanding of general patterns of species extinction risk to inform species-specific conservation planning.

Here, we address how different functional groups of Neotropical primates respond to anthropogenic habitat fragmentation from southern Mexico to northern Argentina, based on the most comprehensive systematic review of primate species occupancy of tropical forest fragments. Specifically, we examine (1) whether the landscape context of forest fragments affects patterns of species persistence in different functional groups; (2) how life-history traits can help us predict species survival within forest patches; and (3) which taxa are most susceptible to local extinctions across a wide range of landscape contexts. We then consider the current state of primate ecological studies in fragmented Neotropical forest landscapes, and propose conservation measures to maximise local persistence of regional species pools.

3.3. Methods

3.3.1. Quantitative literature review

We performed a literature search in March 2013 using the ISI Web of Science and Google Scholar with the following keywords: habitat fragmentation, primates, mammals, landscape, Neotropical (with and without ‘*Alouatta*’ and ‘*Cebus*’ or ‘*Sapajus*’, the most widely distributed platyrrhine genera) to identify all studies comprising primate species composition within forest patches (defined as patches smaller than 10,000 ha) throughout the Neotropics. In addition, we included the bibliography cited by these studies and undergraduate and postgraduate dissertations and theses either detected using Google search options based on keywords in Spanish, Portuguese or English or studies that we were aware of. Finally, we included our own field data based on four fragmented forest landscapes that we have studied in Brazil [Benchimol, 2009; Canale et al., 2012; Michalski & Peres, 2005; Sampaio et al., 2010]. To be included into our data set, the study must have listed all primate species detected within each site and provided either the size of fragments or exact geographic coordinates, which enabled us to measure the patch size and assess the landscape context using *Google Earth Pro* tools. We considered studies encompassing all types of primate surveys ─ including line-transect surveys, behavioural studies, and field-verified interviews ─ and any other type of documentation. We also compiled data for larger and more pristine forest tracts or 'pseudo-control' areas adjacent to each cluster of forest fragments, which are here defined as the best available continuous tract of neighbouring forest >10,000 ha that shared the same primate source fauna of adjacent study patches.

3.3.2. The dataset

Species data were tabulated following the functional classification of 24 groups of species (hereafter, 'ecospecies') proposed by Peres & Janson [1999] represented by different genera and a few ecologically divergent congeners. Some species are shown in Appendix 3.1 to exhibit the wide range of primate size structure. This classification enabled us to gather a greater amount of information for different taxa and consequently unveil their specific population responses. At each site, we assigned presence/absence scores as either one (1) for ecospecies that had been recorded at a patch; or zero (0) when an ecospecies that was known to have once occurred in a patch but was no longer observed. We therefore created a matrix composition describing the ecospecies occupancy across different forest sites. We derived the original species composition that would have once occurred at each site in historical times by coupling IUCN [2008] range polygons with information of baseline species composition provided by each study, georeferenced species range polygons, published by NatureServe [Patterson et al., 2003], and our own extensive personal knowledge (M.B. and C.A.P have conducted fieldwork at more than 120 forest landscapes within Amazonia and the Atlantic forest since 1980).

Introductions of exotic species and post-fragmentation reintroductions of native species, which were reported for a few sites, were not considered as valid occupancies in our database. Night monkeys (*Aotus* spp.), the only nocturnal platyrrhines, were added to our data set only in the case of those studies that had conducted night surveys. For those sites where more than one independent source describing the local species composition were available, we considered all species listed. We further compiled data on the morphological and ecological traits of each ecospecies based on previous studies conducted in a wide range of forest sites [Hawes & Peres, 2014; Lindenfors & Tullberg, 1998; Peres 1993, unpublished data; Smith & Jungers 1997] (Table 3.1). Although we are aware of the variation of species traits within different ecospecies, these studies performed a robust review or considered large sample sizes to enhance the accuracy of species ecological traits.

Table 3.1. Occupancy rates and ecological traits for 19 primate functional groups or 'ecospecies' within 760 forest sites examined in this study.

							Species Traits			
Ecospecies (codes)	**English name**	**Number of sites occupied**	**Number of sites expected to be occupied**	**Site occupancy (%)**	**Geographic range size (km^2) [1]**	**Critical fragment size (ha)[2]**	**Proportion of fruits in diet (%)[3]**	**Body mass (kg)[4]**	**Home-range size (ha)[5]**	**Trophic status[6]**
Alouatta (Al)	Howler monkeys	504	751	67.1	13,095,330	0.1	35.1	6.32	20	1
Aotus (Ao)	Night monkeys	91	189	48.1	7,711,498	170	76.5	0.93	40	3
Ateles (At)	Spider monkeys	169	437	38.7	6,784,000	210	78.3	8.56	230	2
Brachyteles (Br)	Woolly spider monkeys	22	103	21.4	267,800	8,420	42.6	8.84	120	2
Callicebus moloch (Cm)	Amazonian dusky titi monkeys	161	189	85.2	3,741,840	0.1	53.0	0.96	4	2
Callicebus personatus (Cp)	Atlantic Forest dusky titi monkeys	75	143	52.4	896,493	112	81.0	1.33	5	2
Callithrix (Cx)	Atlantic Forest/Cerrado marmosets	200	328	61.0	2,745,620	35	17.9	0.37	25	5
Cebus albifrons (Cf)	White-fronted capuchins	9	16	56.2	4,057,250	180	81.2	2.92	400	4
Cebus olivaceus (Co)	Wedge-capped capuchins	29	88	32.9	1,944,175	110	54.6	2.91	80	4
Cebus apella	Tufted	329	523	62.9	11,193,082	35	48.5	3.09	70	3

(Ca)†	capuchins									
Chiropotes (Ch)	Bearded saki monkeys	59	243	24.3	3,006,600	540	84.1	2.86	650	4
Lagothrix (La)	Woolly monkeys	2	6	33.3	3,351,007	480	73.4	8.46	350	2
Leontopithecus (Le)	Lion tamarins	20	107	18.7	85,208	2,500	76.1	0.58	40	6
Mico (Mi)	Amazonian marmosets	27	32	84.4	1,256,621	15	18.6	0.38	25	5
Pithecia (Pi)	Saki monkeys	22	86	25.6	3,677,870	125	85.0	2.31	100	4
Saguinus fuscicollis (Sf)	Saddle-back tamarins	2	2	100.0	2,436,081	80*	54.1	0.47	50	5
Saguinus niger (Sn)	Midas tamarins	37	90	41.1	1,574,740	80*	66.0	0.55	50	5
Saguinus oedipus (So)	Bare-faced tamarins	6	13	46.1	216,323	80*	61.5	0.44	35	5
Saimiri (Sa)	Squirrel monkeys	33	76	42.9	6,417,552	480	38.1	0.81	550	4

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[1] Based on Patterson *et al.* 2007 [2] Critical fragment size required to ensure a minimum occupancy probability of 50% based on our logistic regression models (see Fig. 3.3); [3] Hawes & Peres (2014); [4] Smith & Jungers (1997), Lindenfors & Tullberg (1998); [5] C.A. Peres (unpublished data), [6] (1) facultative folivore-frugivore; (2) frugivore-folivore; (3) frugivore-insectivore; (4) granivore-frugivore-insectivore; (5) insectivore-frugivore-grummivore; (6) faunivore-frugivore-insectivore (based on all published and unpublished studies of Neotropical primate diets (Hawes & Peres, 2014). * All *Saguinus* congeners were pooled together due to the small number of records. † Includes all brown capuchin taxa and allies within the newly renamed *Sapajus apella.*

For each forest patch, we recorded the total forest area, the most prevalent matrix type, the percentage of matrix forest cover, and the level of hunting pressure on primates. A categorical matrix type was assigned for each fragment based on its predominant (>50%) land-cover within a 1-km external buffer from each patch: (1) water; (2) pasture or cropland; and (3) secondary forest. This information was provided by most studies, but we used high-resolution images available in *Google Earth* whenever this information was missing. In addition, the percentage of available forest cover within a 1-km radius external buffer from each fragment was quantified using *Google Earth Pro* tools, which includes an historical time series of satellite images enabling us to select the relevant image at the approximate time of each study ─ typically 2-3 years and at most 5 years of time lag between the date of the image and the dates of field sampling. Information on levels of hunting pressure was obtained from either literature sources or direct personal communication with the authors, who were approached individually in each case. We thus considered historical trends to define levels of hunting pressure for each site or landscape as (1) non-hunted; (2) lightly / occasionally hunted; and (3) heavily or persistently hunted. Although we were able to assign a matrix type and level of hunting pressure to all forest patches, we could only quantify matrix forest cover for 384 of all 705 patches (54.5%), due to missing geographic coordinates of study patches, which were not provided by many studies; poor quality of the relevant images; or severe cloud cover. For 163 of those 384 (42.4%) forest patches investigated, we were able to obtain data on matrix forest cover directly from resources and figures contained in the original publication (i.e. papers, theses, reports, etc). We were also unable to obtain other landscape variables for each forest patch, such as year of isolation, shape of forest fragments, fire severity, and history of timber extraction, because most studies failed to properly characterize the history and landscape context in which forest patches were embedded.

Because the number of surveyed patches and their spatial configuration varied within landscapes, we did not define an invariant size threshold to limit a landscape. Instead, using ArcGIS [v. 10, ESRI, 2011], we plotted all sites in our data set on a final continental-scale map including the geographic distribution of all Neotropical primates based on range maps available from IUCN [2008] and

Patterson et al., [2003] and distinguished the landscapes within the same region by overlaying spatial clusters of sites with layers of all significant geographic barriers including major rivers, montane kniferidges, and historical deforestation boundaries [see Fig. 2.1 in Chapter 2].

A total of 96 studies were included in the final data set, mostly consisting of peer-reviewed articles (74.2%), followed by monographs, MSc and PhD dissertations and other unpublished ‘gray’ literature (20.6%), and book chapters (5.2%) [see Benchimol & Peres, 2013]. Most forest sites examined here were exposed to either light (36.7%) or heavy hunting pressure on primates (14.6%), and the predominant surrounding habitat matrix was pasture and cropland (87.5%) compared to open-water and young secondary forests. All fragments considered here consisted of closed-canopy unflooded forests, thereby minimising baseline differences in habitat quality.

This research work is based on empirical data obtained elsewhere, and otherwise adhered to the principles for the ethical treatment of primates honoured by the American Society of Primatologists.

3.3.3. Data analysis

We considered four patch/landscape features (forest patch size, hunting pressure, matrix type and matrix forest cover) and seven primate morphoecological traits [mean adult male and adult female body mass, level of frugivory (defined as the percentage of ripe and unripe fruits in the diet), home range size across all study populations, mean group size across all study populations, degree of primary forest habitat specialization, intrinsic rate of population increase and an ordinal classification of six major trophic modes (where facultative folivores scored lowest (1) and faunivore-frugivores scored highest (6)] as potential predictors of patterns of species-specific local extinctions within forest isolates. We controlled for high levels of variable inter-dependence by performing a Pearson correlation matrix, and excluded those variables that were intercorrelated by r > 0.70. Group size, degree of forest habitat specialisation and rate of population increase were highly correlated with other variables (*r* = 0.94 for group size and home range size; *r* = –0.97 for rate of population increase and body mass; and *r* = –0.74 for habitat specialisation and group size), so they were excluded from any subsequent model. To address the issue of potential spatial autocorrelation across landscapes, we first performed a Generalized Linear Model (GLM) to relate variation of forest patch area, matrix type, forest cover within the matrix and degree of hunting pressure to the proportion of extant species (i.e., the total primate species richness at any given patch divided by the maximum primate species richness that would have once occurred at that patch, see Benchimol and Peres 2013 for further explanation) retained within patches. We added an autocovariate term (i.e., a distance-weighted function of neighbouring response values; Dormann *et al*. 2007) as an extra parameter to our model using the 'autocov_dist' function in R (package spdep), weighted equally to all data points in the neighbourhood. We then performed the analysis twice: first considering all 760 forest patches (patch area, matrix type and hunting pressure as explanatory variables) and second considering only those 384 patches for which we were able to obtain reliable forest cover estimates within the matrix, added as a fourth explanatory variable. Our analyses showed that the autocovariate was never a significant variable ($P<0.05$) in our model in both cases (all and restrict dataset) lending support to the notion that this form of spatial autocorrelation was unimportant. We then performed Generalized Linear Mixed Models (GLMMs) considering all ecospecies, with a binomial error structure and logit-link function considering (1) all 760 forest sites nested within 61 landscapes; and (2) only those 384 forest patches nested within 34 landscapes in which we were able to obtain matrix cover estimates, added as another fixed effect in the model. This approach was the most appropriate to account for potential overall spatial autocorrelation (Bolker et al., 2009), with our global model incorporating a random term in which forest patches were nested within 'landscapes'. We also accounted for differential representation of species within the dataset by incorporating 'ecospecies' as an additional random factor. For each ecospecies individually, we also performed GLMMs to examine if landscape attributes could predict their occupancy rates within forest patches. Because we were unable to obtain matrix cover estimates for all patches, we opted to perform ecospecies-specific GLMMs considering only the fixed effects available for all patches: forest area, matrix type and hunting pressure. Models were fitted using the ‘lme4’ package [Bates, 2007] within the R platform, with parameters estimated using the Laplace approximation as recommend by Bolker et al., [2009]. We selected the most parsimonious ‘best’ models (ΔAIC <2.0) based on a multimodel approach and the Akaike Information Criterion (AIC), by examining every possible first-order combination of variables [Burnham & Anderson, 2002] using the ‘MuMIn’ package [Bartón, 2009].

3.4. Results

3.4.1. Data compilation

We compiled data from 760 forest sites (including 705 isolated forest patches and 55 continuous forest sites) within 61 landscapes distributed across 11 Neotropical countries, most of which were located in Brazil (70.0%), Mexico (12.8%), and Guatemala (6.6%; Fig. 3.1). The number of sites surveyed per landscape ranged from 1 to 144 (mean ± SD = 12.6 ± 23.0 sites) and forest fragment areas ranged between 0.1 ha to 9,731 ha (mean ± SD = 442.6 ± 1087.5 ha), more than half of which consisted of patches smaller than 100 ha (Fig. 3.1). For information on the distribution of study landscapes across the Neotropics see Benchimol & Peres [2013]. In the 384 forest fragments for which we were able to perform more detailed data analyses incorporating a measure of forest habitat cover within the matrix, 79.7% of patches were located in Brazil whereas others encompassed portions of Mexico, Venezuela, Guatemala, Bolivia and Panama. The number of sites per landscape varied from 1 to 127 (mean ± SD = 11.3 ± 22.6 sites) and forest fragment areas ranged between 1.2 ha to 9,731 ha (mean ± SD = 403.8 ± 978.7 ha).

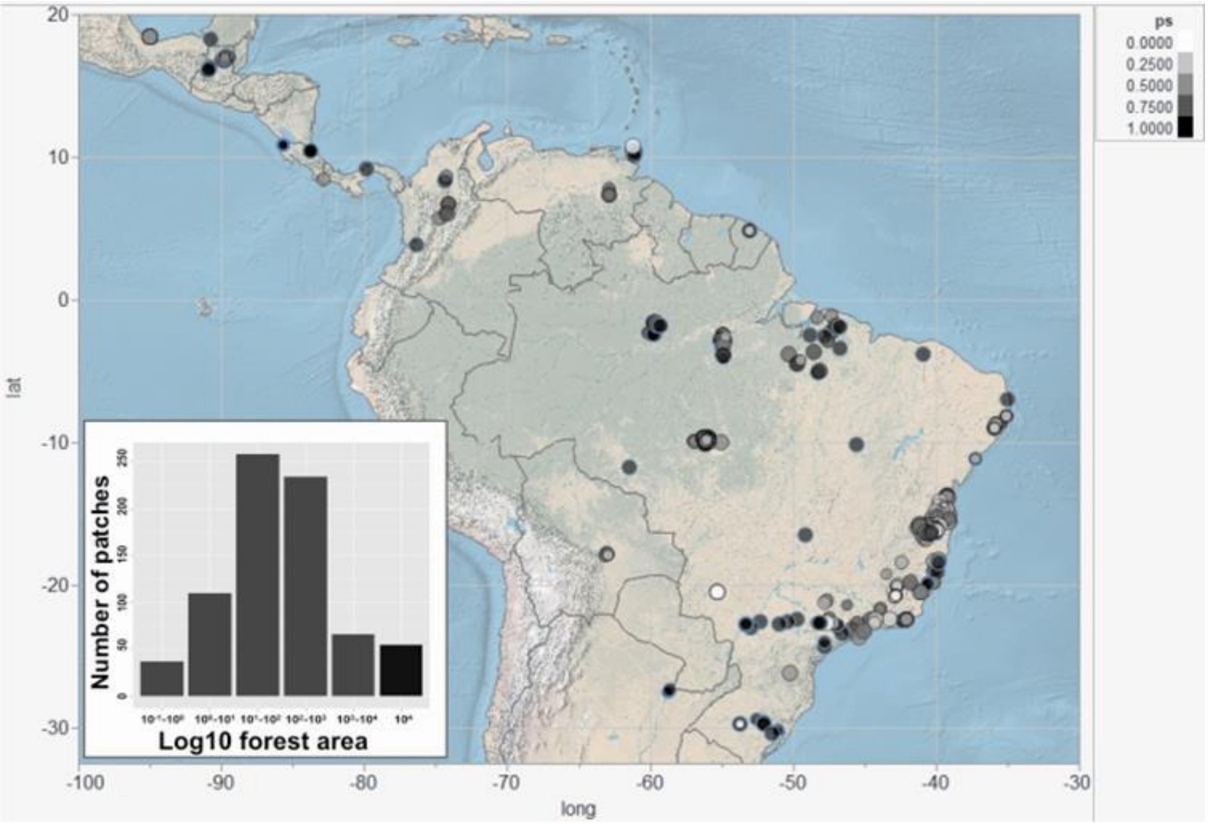

Figure 3.1. Geographic locations of the 760 forest patches examined in this study. Circles are sized proportionally to their patch size and colours represent the proportion of species extant within each patch at the time of studies (*i.e.* number of species recorded at a site divided by the number of species that once occurred at this site). The bottom left inset shows the size distribution of the 760 forest sites examined in this study. For details on the distribution and partition of landscapes, see Benchimol & Peres [2003].

3.4.2. Patterns of occupancy

Of the 24 functional groups or 'ecospecies' of Neotropical primates considered here, 19 occurred in at least a single forest patch (Table 3.1). This excluded records of *Cebuella*, *Callimico*, *Cacajao, Callicebus torquatus* and *Saguinus mystax*, which failed to occur within any of forest patches available within the fragmented landscapes examined here. As expected, ecospecies with the widest geographic ranges, such as *Alouatta* and *Cebus apella* (including all brown capuchin taxa and allies within the newly renamed *Sapajus apella*) appeared in a large number of forest sites and showed high occupancy rates. Conversely, ecospecies with narrow geographic distributions, such as the two Atlantic Forest endemics (*Leontopithecus* and *Brachyteles*), appeared in a small number of forest sites and showed low occupancy rates (Fig. 3.2; Table 3.1). *Saguinus fuscicollis* and *Mico* exhibited the greatest occupancy rates among all ecospecies within the landscapes where they could occur, despite the small number of forest sites in which they were recorded (2 and 27, respectively).

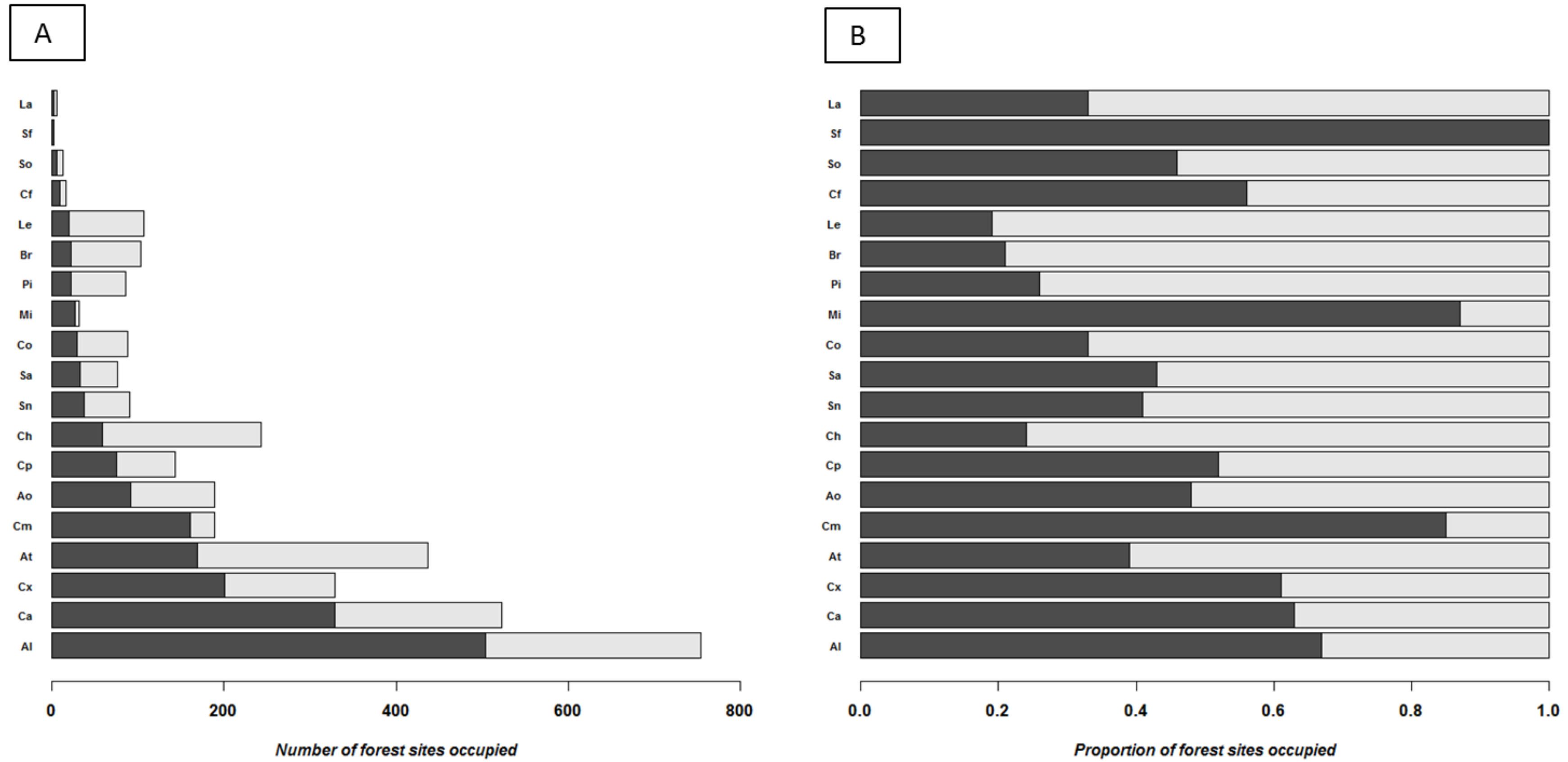

Figure 3.2. Patterns of forest occupancy for Neotropical primate species within the 760 forest sites examined in this study. (A) Gray bars represent the baseline (pre-fragmentation) occupancy for each species across the forest sites where they were expected to occur and solid bars represent the observed occupancy across those sites; (B) Proportion of forest sites in the data set that were actually occupied (see Table 3.1 for species codes).

3.4.3. Landscape and life-history predictors of patch occupancy

Considering all ecospecies within the 760 forest sites examined here, GLMMs showed that forest area, home range size and trophic status were significant predictors of the probability of species occupancy, showing the highest relative importance across all variables (Table 3.2). The ‘best’ GLMM model explaining local occupancy probability contained forest patch area, home-range size, trophic status, body mass and level of frugivory (model weight = 0.11). Other lower ranking but parsimonious models (ΔAIC <2.00) always included both forest patch area and trophic status but also body mass and level of frugivory (model weight = 0.09); body mass, home range size, degree of frugivory and degree of hunting pressure (model weight = 0.07); and body mass, degree of frugivory and degree of hunting pressure (model weight = 0.06). GLMMs considering the additional effect of matrix connectivity, defined as the proportional forest cover outside patches (for only 384 forest patches within 34 landscapes), detected that forest area (β= 1.243, $p<0.001$), degree of hunting pressure (β= –0.674, $p<0.001$), matrix forest cover (β= 0.006, $p<0.05$) and home range size (β= –0.003, $p<0.01$) were all strong predictors of species occupancy (Table 3.2). The ‘best’ fit model included these four significant predictors plus body mass and level of frugivory (model weight = 0.08), and other parsimonious models always included these four variables alone (model weight = 0.07); these four variables in addition to level of frugivory (model weight = 0.05); and these four variables in addition to level of frugivory and body mass (model weight = 0.04).

Table 3.2. Summary of Generalized linear mixed models (GLMMs) showing the predictors of overall patterns of primate occupancy and their relative importance within 760 Neotropical forest sites nested within 61 landscapes. This is repeated for 384 forest sites nested within 34 landscapes, for which data on forest cover within the matrix could be extracted. Model-averaged coefficients are presented.

Effect	Estimate	Unconditional Standard Error	Z-value	Confidence Interval (95%)	Relative Importance
N=760 patches					
Intercept	0.466	1.817	0.257	(-3.095; 4.027)	
Forest patch area (log$_{10}$)	1.060	0.059	18.091	(0.945; 1.175)	1.00
Surrounding matrix type	0.262	0.476	0.551	(-0.670; 1.194)	0.29
Level of hunting pressure	-0.232	0.221	1.051	(-0.665; 2.008)	0.38
Percentage of dietary fruit	-0.019	0.010	1.865	(-0.039; 0.691)	0.65
Body mass	-0.231	0.121	1.902	(-0.086; 0.037)	0.69
Home range size	-0.003	0.001	1.988	(-0.002; -0.000)	0.76
Trophic status	-0.473	0.236	2.001	(-0.936; 0.002)	0.73
N=384 patches					
Intercept	0.265	1.560	0.170	(-2.792; 3.321)	
Forest patch area (log$_{10}$)	1.243	0.082	15.066	(1.081; 1.404)	1.00
Surrounding matrix type	0.231	0.379	0.608	(-0.513; 0.975)	0.30
Matrix forest cover	0.007	0.003	1.865	(-0.000; 0.013)	0.68
Level of hunting pressure	-0.674	0.202	3.339	(-1.069; -0.278)	1.00
Percentage of dietary fruit	-0.018	0.012	1.578	(-0.041; 0.005)	0.58
Body mass	-0.191	0.125	1.526	(-0.435; 0.054)	0.59
Home range size	-0.003	0.001	2.445	(-0.006;-0.001)	0.85
Trophic status	-0.300	0.247	1.217	(-0.784; 0.183)	0.47

All 16 ecospecies with sufficient sample sizes to be examined in detail (which excluded *Lagothrix* but included all *Saguinus* pooled together) showed a positive occupancy-area relationship, but responses to forest patch area were highly variable (Fig. 3.3). *Alouatta* and *Callicebus moloch* were the least area-sensitive ecospecies, exhibiting high occupancy rates even in relatively small forest patches, and the smallest critical fragment sizes across all ecospecies, with a 50% occupancy probability in forest patches of only 0.1 ha (Table 3.3). Conversely, *Brachyteles, Leontopithecus, Chiropotes*, and *Saimiri* were only likely to occur in relatively large forest tracts, typically requiring areas larger than 100 ha. Forest patch area was therefore the strongest predictor of patch occupancy for 14 ecospecies (Table 3.3). However, human hunting within forest patches had a negative effect on the persistence of the largest Neotropical ecospecies (*Brachyteles*), whereas matrix type had a significant effect on the occupancy probability of *Saguinus* (consisting of three ecospecies pooled together due to small sample sizes). Three other functional groups — *Cebus albifrons*, *Lagothrix* and *Mico* — were not necessarily more likely to occur in increasingly larger forest sites. However, these taxa were restricted to a small number of sites, thereby weakening any indication that they could be less area-sensitive.

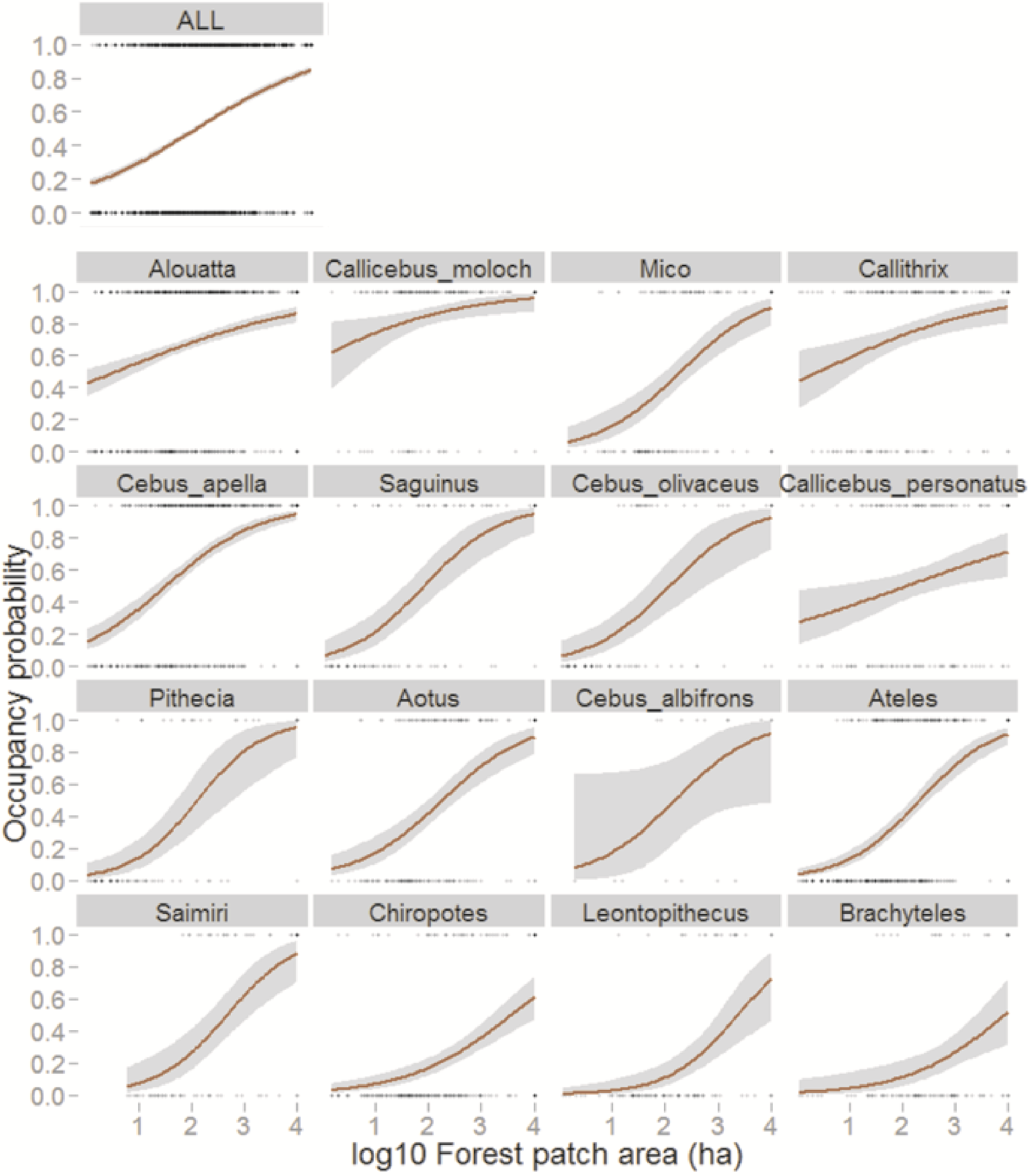

Figure 3.3. Occupancy probability of all 16 ecospecies of Neotropical primates pooled together (ALL) and each ecospecies individually, as a function of forest patch size, predicted using logistic regression models using the observed species occupancy data across all study landscapes. Solid lines and shaded areas indicate the mean and 95% confidence interval regions, respectively. *Lagothrix* was excluded from this figure due the small number of forest fragments at which this functional group occurred.

Table 3.3. Generalized linear mixed models (GLMMs) showing predictors of patch occupancy for each primate functional group across 760 Neotropical forest sites nested within 61 landscapes (see details in the text). Significant variables are indicated as: ****p* ≤ 0.001; ***p* ≤ 0.01; **p* ≤ 0.05.

Ecospecies	**Number of sites**	**Intercept**	**Predictors**		
			Patch area	**Hunting pressure**	**Matrix type**
Alouatta	751	0.85	1.07^{***}	–0.50	–0.70
Aotus	189	–1.15	1.22^{***}	–0.53	–0.47
Ateles	437	–2.57	1.93^{***}	–0.93	–0.06
Brachyteles	103	–1.93	2.63^{***}	-3.39^{*}	
Callicebus moloch	189	27.72	0.69^{**}	0.20	–13.82
Callicebus personatus	143	–0.08	0.56^{*}	–0.37	
Callithrix	328	-2.40^{**}	0.91^{***}	0.73	
Cebus albifrons	16	–3.20	1.39		
Cebus olivaceus	88	-11.55^{*}	2.66^{***}	–1.25	5.83
Cebus apella	523	–0.55	1.55^{***}	–0.79	–0.28
Chiropotes	243	–3.34	1.87^{***}	–1.66	0.80
Lagothrix	6	–2.51	0.93		
Leontopithecus	107	-3.48^{**}	1.22^{**}	–0.29	
Mico	32	–9.01	3.38	1.69	
Pithecia	86	-5.33^{***}	1.76^{***}		1.25
Saguinus†	105	-3.62^{***}	1.45^{***}	–0.64	1.08^{**}
Saimiri	13	-4.12^{**}	1.48^{***}	–0.13	0.24

Notes: † All *Saguinus* congeners were pooled together due to the small number of records.

Patterns of primate ecospecies incidence across Neotropical forest patches could also be predicted on the basis of their ecological traits. Those taxa exhibiting small home range sizes were consistently the most ubiquitous, persisting in a larger number of variable-sized patches of varying quality (Table 3.2). Conversely, wide-ranging, large-group-living taxa appeared to be most area-sensitive and were therefore missing from most forest patches. Additionally, the effect of body mass and level of frugivory appeared in some of top-ranking models, whereby highly frugivorous and large-bodied ecospecies were most likely to be driven to local extinction from forest remnants.

3.5. Discussion

This is the first quantitative and most comprehensive review of species-specific responses in Neotropical primates to forest habitat fragmentation across the entire continent. Of all 17 genera of extant platyrrhine primates, only howler monkeys have been comprehensively investigated to date in terms of their responses to landscape changes [Arroyo-Rodríguez & Dias, 2010]. Although primate responses to habitat fragmentation have been extensively examined [Marsh, 2003], most studies were carried out within a particular landscape context and/or focused on single species, rendering our understanding of species-specific responses to habitat disturbance too context-dependent. Here, we used a robust dataset consisting of a 3425-cell presence-absence matrix (*i.e.,* considering all species that would have once occurred at each site) describing species occupancy at 760 forest sites to uncover patterns of local extinction in forest remnants across all Neotropical primates. We attempted to disentangle the effects of landscape configuration, human-induced disturbance, and species life-history traits to examine how different ecospecies respond to habitat fragmentation, highlighting the relative importance of these factors in predicting primate persistence within fragmented forest landscapes.

3.5.1. Drivers of local primate extinction

Although individual ecospecies diverged markedly in their responses to habitat fragmentation, forest patch area was consistently the most important predictor of species occurrence across all sites. Shrinkage in available habitat area in itself has been widely considered as a major cause of extinctions [Fahrig, 2003]. Accordingly, we found that local extinctions were most likely to occur in small patches, and forest patch size figured prominently in all 'best' models predicting the probability of primate occupancy across the 760 forest sites we investigated. Forest patch area was also the strongest predictor of primate and carnivore [Boyle & Smith, 2010a ; Michalski & Peres, 2005] and bird occupancy [Ferraz et al., 2007; Lees & Peres, 2006] across forest remnants within two contrasting Amazonian landscapes. In a global review of species-area relationships, Harcourt & Doherty [2005] also emphasized the importance of forest fragment size in explaining patterns of local primate richness. However, forest fragments in 'real-world' working landscapes also frequently succumb to different forms of additional anthropogenic disturbances such as ground fires [Laurance & Cochrane, 2001], selective logging, and overhunting [Peres, 2001] that likely interact synergistically with habitat fragmentation. This is consistent with our results which indicate that human-induced perturbation other than area-effects cannot be overlooked in understanding patterns of local extinction in primates.

We also uncovered an effect of matrix connectivity and hunting pressure on patterns of primate persistence, indicating that the availability of surrounding habitat and chronic population depletion can interact additively with area effects in driving primate populations stranded in habitat isolates into a negative spiral. Large amounts of even young secondary forest surrounding old-growth patches clearly facilitate movements across forest remnants [Boyle & Smith, 2010a], not least because Neotropical primates are predominantly arboreal. As a net effect, this is expressed as higher rates of patch occupancy within fragments. Hunting is considered the greatest threat to primates in several African landscapes [e.g. Rovero et al., 2012] and can surpass the importance of habitat loss and fragmentation in most of lowland Amazonia [Peres & Lake, 2003]. Because physical access by hunters is facilitated in heavily settled fragmented landscapes, primate populations can be rapidly driven to local extinction in small fragments. For instance, two historically overhunted primate species (*Chiropotes albinasus* and *Ateles marginatus*) have been completely extirpated from all forest fragments in a central Amazonian landscape [Sampaio et al., 2010]. Likewise, the critically endangered *Brachyteles hypoxanthus* faces regional-scale extinction from forest remnants in the northern Atlantic Forest due to a history of heavy hunting pressure [Canale et al., 2012]. Howler monkeys (*Alouatta* sp.), which are one of the least area-sensitive primates worldwide, maintaining viable breeding populations in tiny islands of protected habitat for decades [Terborgh et al., 2001], have been wiped out from forest remnants in this protein-hungry part of Brazil [Canale et al., 2012]. In most cases, these primate populations have been repeatedly persecuted as a source of protein for local people, who consistently prefer large-bodied species [Peres, 1990]. However, many small-bodied primate species are also captured to fuel the pet trade, which can lead to severe declines in exploited populations. This can be illustrated by the endangered golden lion tamarin (*Leontopithecus rosalia*) which was extirpated from many municipal counties within its original coastal Atlantic Forest distribution [Kierulff & Rylands, 2003]. Therefore, rather than operating in isolation, overexploitation by hunters and live-trappers appears to interact synergistically with both area and isolation effects to vastly reduce the species retention capacity of contemporary forest patches [Peres, 2001].

In addition to habitat area, matrix connectivity and level of hunting pressure, patch-scale primate occupancy was also a function of individual species traits. Our results indicate that, all other things being equal, wide-ranging species consuming higher energy and nutrient-rich food items were most susceptible to local extinctions within fragmented landscapes. In terms of trophic status, facultative folivores, generalized frugivore/granivores, and faunivore/frugivores were increasingly more extinction-prone. Indeed, functional groups of Neotropical primates varied widely in their persistence probability within isolated forest patches which can be attributed to differences in ecological plasticity and overall spatial requirements of viable breeding groups, particularly in the often degraded habitat remaining in present-day forest fragments [Broadbent et al., 2008]. Several studies have shown the importance of life-history traits in predicting primate species sensitivity to fragmentation, yet there is little consensus over which traits are most important. Johns & Skorupa [1987] showed that body size and degree of frugivory explained most of the variation in species responses to moderate habitat disturbance, but these and other traits failed to predict which primate species survived in isolated forest patches in Uganda [Onderdonk & Chapman, 2000]. In a global review of primate persistence in small fragments, only dietary breadth provided a significant predictor of species occupancy on the basis of only 56 South American forest patches considered [Gibbons & Harcourt, 2009]. Our more robust data compilation is consistent with Boyle & Smith [2010a] in that home range size is an important predictor of patch occupancy of different species. Large-group-living species with large spatial requirements will be more susceptible to extinction in small fragments than species in small groups occupying small home ranges [Michalski & Peres, 2005]. We therefore further assess species traits, landscape structure and anthropogenic stressors in modulating patterns of species extinction.

3.5.2. Species-level responses

Neotropical primates ranged widely in their rates of patch-scale persistence and overall sensitivity to forest fragmentation. Considering our landscape metrics, patch area was consistently the most important predictor of local extinction for nearly all ecospecies. There was a generalized collapse in species assemblage composition in fragments smaller than 100 ha, in which most ecospecies showed an overall occupancy probability lower than 50%. However, we detected three main patterns of species occupancy as a function of patch size: (1) ecospecies such as *Alouatta*, *Callicebus moloch* and *Callithrix* exhibited high occupancy rates in large fragments and only a modest decline in occupancy probabilities in very small fragments; (2) ecospecies such as *Aotus*, *Ateles*, *Cebus apella*, *Cebus olivaceus*, *Mico*, *Pithecia*, *Saimiri* and *Saguinus* (all tamarins pooled together) exhibited high occupancy rates in large fragments, but these declined rapidly with fragment size; and (3) some ecospecies (e.g. *Leontopithecus*, *Chiropotes* and *Brachyteles*) failed to exhibit high occupancy rates even in large fragments. Home range size accounted for most of the response heterogeneity, with wide-ranging species showing the lowest occupancy rates.

Amazonian marmosets (genus *Mico*), which rely moderately on fruits, occupy relatively small home ranges and tolerate a fair amount of forest disturbance, showed an overall patch occupancy of ~85%. High levels of marmoset persistence is further facilitated by a strong preference for forest edges and secondary forests [Ferrari, 1993], which are ubiquitous in fragmented forest landscapes. Although roughly half of their diets consist of fruits, Amazonian dusky titis (*Callicebus moloch*) exhibit a wide dietary breadth, and can adopt an energetically conservative activity budget in forest fragments [Michalski & Peres, 2005]. They also occupy some of the smallest home ranges of all platyrrhines, and often thrive even in very small forest remnants [Ferrari et al., 2003]. Howler monkeys (*Alouatta*), brown capuchins (*Cebus or Sapajus apella*) and Atlantic Forest and Cerrado marmosets (*Callithrix*) also showed high levels of patch occupancy (>60%) across all forest sites and can also be defined as fragmentation-tolerant. As facultative folivores, howlers exhibit high levels of dietary plasticity, particularly whenever fruits become scarce, use small home ranges, and are ubiquitous in non-hunted forest patches, even where other species are unable to persist [Bicca-Marques, 2003; Estrada & Coates-Estrada, 1996; Lopez et al., 2005]. Brown capuchins are resourceful foragers that typically exhibit a wide dietary breadth, high levels of behavioural plasticity, and a fair degree of matrix tolerance in their ability to traverse cattle pastures between forest fragments, in addition to being highly adaptable to forest edges and degraded forest habitats [Michalski & Peres, 2005]. Atlantic Forest marmosets can often switch to plant exudates whenever alternative food sources are unavailable, have small home ranges and tolerate moderate levels of forest disturbance in many edge-dominated habitats [Ferrari, 2009].

On the other hand, lion tamarins (*Leontopithecus)*, woolly spider monkeys (*Brachyteles*) and bearded saki monkeys (*Chiropotes*) showed the lowest levels of patch occupancy across all ecospecies, occurring in less than one quarter of sites expected to be occupied. Lion tamarins populations were heavily persecuted in the past due to the pet trade [Kierulff & Rylands, 2003] and forage primarily in lowland forests with high densities of bromeliads [Dietz et al., 1997] but this forest type has been disproportionately targeted by agricultural conversion and is poorly represented in remaining forest fragments. Woolly spider monkeys have been decimated by subsistence hunting over historical times [Cunha et al., 2009] and no longer occur in much of their former geographic range. Indeed, hunting pressure significantly affected their patch occupancy and can be considered the leading driver of local extirpation of this ecospecies, a pattern consistent with overhunted regions in their distribution [Canale et al., 2012]. The large-group living bearded saki monkeys rely heavily on forest canopy ripe mesocarps and immature seeds, which comprise ~85% of their diet, and occupy some of the largest known home ranges of all Neotropical primates [Boyle & Smith, 2010b]. Indeed, this ecospecies succumbs to high local extinction rates in fragmented landscapes [e.g. Ferrari et al., 2003; Sampaio et al., 2010], providing clear evidence of its high sensitivity to area effects. It is important to note that matrix type and exposure to hunting pressure could not be evaluated for all ecospecies due to lack of sufficient variation, which may have affected other patterns of species-level responses.

3.6. Conclusions

3.6.1. Future primatological studies

A wide range of field studies that intentionally or serendipitously investigated the impacts of forest fragmentation on platyrrhines have mostly shown detrimental effects on arboreal primates [Chiarello & Melo, 2001; Estrada & Coates-Estrada, 1996; Marsh, 2003]. However, most studies have failed to properly characterize the landscape context and patch-scale history of forest disturbance [but see Boyle & Smith, 2010a; Canale et al., 2012; Michalski & Peres, 2005], which is crucial to assess species-specific responses to habitat modification. Moreover, many investigators fail to adequately appreciate that habitat fragmentation is a wider landscape process, often considering the forest patch as the single unit of analysis [Arroyo-Rodríguez & Mandujano, 2009]. We therefore suggest that future primatological studies should provide additional information on the landscape context of fragments (including age of isolation, and connectivity of isolates) and whenever possible, expand the number of sites within landscapes and/or study landscapes to better understand the effects of habitat fragmentation *sensu stricto* [Fahrig, 2003]. Finally, real-world landscapes are typically subjected to multiple, co-occurring forms of natural and anthropogenic disturbances that can interact additively or synergistically with the process of declining habitat area and increasing isolation [Laurance & Peres, 2006]. For example, we have shown that hunting pressure affects large-bodied primate persistence within forest isolates, thereby flattening species-area relationships and accelerating local extinction rates [see Benchimol & Peres, 2013]. Thus, different forms of human-induced disturbance — that either deplete isolated populations or affect habitat quality — should also be explicitly considered concomitantly with the effects of patch area and isolation.

We uncovered a severe imbalance in the degree to which different ecospecies have been studied across forest patches and landscapes in the New World tropics from Mexico to Argentina, which largely reflects the continental-scale geographic distribution of primate taxa within forest fragmentation frontiers. In our review, howler monkeys (*Alouatta*) were by far the best represented functional group (751 forest sites within 60 landscapes), whereas presence-absence data on woolly monkeys (*Lagothrix*) were available from only six fragments within a single landscape. Since habitat fragmentation will continue to expand across all major tropical forest regions [FAO, 2010], it becomes imperative to assess the extinction risk of all taxa, so that local extinctions can be prevented or mitigated. For instance, large-scale deforestation has severely impacted the southern and eastern flanks of Amazonia over the last four decades [de Espindola et al., 2012], directly affecting primate persistence in remaining forest isolates. We therefore suggest that future conservation studies on the effects of forest fragmentation on Neotropical primates should focus on the most poorly studied functional groups, including *Callimico, Cebuella, Lagothrix*, *Cebus albifrons, Mico, Saguinus, Saimiri* and *Pithecia*.

Although this is the most comprehensive review ever performed on Neotropical primate populations inhabiting forest fragments, it is important to emphasise some possible biases in our dataset. We included studies based on different sampling techniques and conducted at different temporal scales, which may contribute to false absences of cryptic or low-abundance species. Also, a single landscape (Alta Floresta) accounted for 19% of all forest sites examined here, and consequently the pattern of patch occupancy at this landscape may not be equivalent to that uncovered by the same number of fragments that may be widely spread across different landscapes. However, we have partly accounted for this imbalance by using a GLMM approach. Finally, we were unable to consider likely differences in habitat quality among forest fragments, which may also affect primate species persistence within forest fragments [Arroyo-Rodriguez & Mandujano, 2006]. We therefore recommend that future fragmentation ecology studies on primates include measures of habitat quality to enhance the predictive power of patch- and landscape-variables.

3.6.2. Conservation Implications

Primates play key roles in ecosystem functioning and arguably retain the strongest charismatic appeal of all tropical forest vertebrates in capturing hearts and minds in the wider public on behalf of tropical forest conservation [Mittermeier, 1988]. As such the relentless expansion of fragmented forest frontiers has a direct bearing on the fate of these flagship species, many of which have become severely threatened with regional to global scale extinction in human-modified landscapes [Chapman & Peres, 2001; Cowlishaw & Dunbar, 2000]. Therefore, identifying the environmental drivers of species depletion becomes vital to promote conservation action that can ensure ecosystem integrity.

Our results show that insufficiently large and increasingly isolated forest patches are the main drivers of primate species loss throughout the Neotropical realm, where forest remnants larger than 100 ha are typically required to retain even half of the original local primate fauna. However, most remaining forest patches in Neotropical landscapes are considerably smaller than 10 ha [Broadbent et al., 2008; Ribeiro et al., 2009; Canale et al. 2012] and more than half of all patches investigated here were <100 ha (Fig. 3.1). However, conservation actions should not focus on fragment area alone. Hunting pressure is also a threat to several primate species which vastly increases their local extinction probability in forest fragments [e.g. Peres, 2001]. Increasing the permeability of the surrounding habitat matrix would be a key option in ensuring matrix movements across forest fragments, thereby boosting the resource spectrum available for the most area-sensitive species and maximizing the local pool of primate species retained in fragmented landscapes.

In addition to forest patch size, the amount of tree cover remaining within the matrix and effective protection against hunting are most important determinants of primate persistence across Neotropical landscapes. Our results also show that species life history and ecological traits can also explain which species can persist and which are driven to extinction in forest isolates. Primates with large spatial requirements feeding higher up the trophic ladder were most susceptible to local extirpation. Landscape-scale conservation planning should therefore consider maintaining large, well-connected and strictly-protected forest reserves within fragmented landscapes, which would be most likely to retain the greatest number of primate species.

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CHAPTER 4

EDGE-MEDIATED FOREST DISTURBANCE DRIVES TREE ASSEMBLAGE COMPOSITION AND FUNCTIONAL DIVERSITY IN AMAZONIAN ISLANDS AFTER 26 YEARS OF ISOLATION

Floristic surveys. Photos by: M.Benchimol, O. Ti and N. Attias

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Benchimol, M.B & Peres, C.A. Edge-mediated forest disturbance drives tree assemblage composition and functional diversity in Amazonian islands after 26 years of isolation.

4.1. Abstract

1. Land-bridge islands formed upstream of mega hydroelectric dams are excellent experimental landscapes to assess the impacts of habitat fragmentation on biodiversity. We examined the effects of plot-, patch- and landscape-scale variables on the patterns of floristic diversity across 34 land-bridge forest islands that had experienced 26 years of isolation since the creation of the vast Balbina Hydroelectric Reservoir of central Brazilian Amazonia. In addition, three undisturbed continuous forest sites in neighbouring mainland areas were also sampled across a comparable elevational gradient.

2. We identified all live trees ≥10 cm DBH at species level within a total of 87 quarter-hectare forest plots and conducted a comprehensive compilation of functional attributes of each tree species. We then examined the species-area relationship (SAR) and the additional effects of patch and landscape scale metrics on patterns of tree assemblage heterogeneity, both in terms of taxonomic and functional diversity.

3. Despite a clearly positive SAR, edge-mediated forest disturbance was the most important driver of species composition and abundance within islands. Our results suggest that floristic transitions within island plots followed a predictable pattern, with different life-history traits either penalizing or rewarding local persistence of different functional groups. Distance to edges mediated the probability of tree mortality induced by episodic surface fires and windfalls, clearly resulting in faster species turnover and unidirectional changes in guild structure within small islands where light-wooded fast-growing pioneers largely replaced heavy-wooded old-growth species.

Synthesis – Following a simultaneous 26-year post-isolation history, we disentangle the effects of habitat loss and insularization on tree assemblages within a large set of variable-sized Amazonian land-bridge islands sharing a uniform water matrix. We show that forest edge effects can be a powerful driver of non-random floristic transitions across islands within the Balbina archipelago via a process of rapid pioneer hyper-proliferation, drastically affecting both the taxonomic and functional composition of insular tree communities. Edge-dominated small islands experienced stronger edge effects than comparable sized forest remnants surrounded by pasture and second-growth within

terrestrial fragmented landscapes. We therefore emphasise the perverse detrimental effects of hydropower infrastructure development on the persistence of tree diversity in lowland tropical forests, even if the resulting archipelagic landscape remains protected and excludes anthropogenic disturbance.

4.2. Introduction

Although vast, unbroken tracts of undisturbed tropical primary forests are essential to sustain tropical biodiversity (Barlow *et al.* 2007; Gibson *et al*. 2011), the fate of tropical forests has increasingly become inextricably linked to fragmented landscapes. Each year, 13 Mha of tropical forests worldwide are converted into agriculture and cattle pastures, reducing once continuous forests to many small isolated remnants (FAO 2010). Consequently, understanding how species diversity and ecological processes are shaped within newly isolated forest ecosystems is critical to identify the mechanisms governing the persistence of former tropical biotas in fragmented forest landscapes.

Tree communities play key roles in providing the structural architecture of forest ecosystems, regulating microclimatic conditions (Laurance *et al.* 1998), storing carbon, and producing essential trophic resources for a wide variety of consumers (Richards 1998). Although the ecological effects of forest fragmentation on tropical and subtropical trees assemblages have been examined by a growing number of studies (e.g. Tabarelli, Mantovani & Peres 1999; Michalski, Laurance *et al*. 2006; Nishi & Peres 2007; Yu *et al.* 2012), the key predictors of community composition following a history of isolation remain inconsistent across studies. For instance, edge effects are a dominant force controlling tree community dynamics in forest patches within the Biological Dynamics of Forest Fragments Project (BDFFP) of Central Amazonia (Laurance *et al*. 2011). In contrast, the interaction of habitat area and habitat disturbance best predicts the species composition of Atlantic Forest fragments in southeastern Brazil (Santos, Kinoshita & dos Santos 2007), whereas time since isolation, distance to edges and fire severity best explains patterns of tree composition in a fragmented forest landscape of southern Amazonia (Michalski, Nishi & Peres 2007). Furthermore, these studies did not find a positive and significant species-area relationship, which has often been mentioned to as the closest thing to a rule in ecology (Lomolino 2000). Tree community responses may diverge substantially among fragmented landscapes because of varying pre- and post-isolation histories of forest remnants, including differences in the structure of surrounding vegetation matrices and exposure to different forms of human perturbation that often aggravate the effects of forest fragmentation alone (Cochrane 2001; Peres, Barlow & Laurance 2006).

Land-bridge islands isolated in the aftermath of large hydroelectric projects are superb experimental settings for fragmentation ecology studies, providing several advantages over gradually fragmented terrestrial landscapes (Diamond 2001; Terborgh *et al.* 2001; Hu *et al*. 2011; Wu *et al*. 2003). First, hundreds to thousands of forest islands associated with varying landscape configurations are formed simultaneously, enabling the assessment of how biodiversity responds to habitat fragmentation in a large number of variable-sized patches isolated concurrently and subjected to the same history of anthropogenic disturbances. Second, these man-made archipelagos are embedded within a structurally uniform open-water matrix that is equally inhospitable to terrestrial organisms, thereby eliminating the confounding effects of varying degrees of matrix habitat use and permeability, which affect the functional connectivity of terrestrial landscapes (Cosson *et al.* 1999; Mendenhall *et al*. 2014). Third, mainland forest areas adjacent to hydropower reservoirs are often near-ideal control sites to test ecological hypotheses, as they contain the same biota that once occurred in all newly created islands (Terborgh 1974). Finally, land-bridge island systems consist of truly unplanned large-scale natural field experiments, with no previous financial and logistical costs to ecologists.

The Balbina Hydroelectric Dam of Central Brazilian Amazonia is an unrivalled experimental laboratory to examine tree responses to habitat fragmentation and isolation. This is the largest Amazonian dam, includes one of the most diverse tree floras worldwide, contains over 3,500 even-aged forest islands ranging in size from <1 ha to >4,500 ha, offering a long-term relaxation-time experiment for ecological studies (Fearnside 1989). Furthermore, similar tree floras sharing the same species functional attributes have been studied in the same biogeographic province (e.g. Guianan forest reserves: Steege & Hammond

2001 and BDFFP: Laurance *et al*. 2004a), providing an excellent comparative perspective. The history of human and natural disturbances rarely occurs homogeneously in space and cannot be easily reconstructed, thus differentially affecting the structure of insular tree assemblages, often aggravating the effects of forest fragmentation (Gascon, Williamson & da Fonseca, 2000). However, Balbina also has the critical advantage of spatial congruence with REBIO Uatumã, the largest strictly-protected Biological Reserve in Brazil, which has effectively suppressed spontaneous in-migration, small settlements, and timber and nontimber forest resource extraction throughout the vast archipelago and neighbouring areas. Yet islands at ~10 years of isolation were differently affected by understorey accidental fires. Although fire effects on tree assemblages have not been investigated in true islands within a Neotropical fragmented landscape, studies in habitat islands *(i.e.,* surrounded by a terrestrial matrix) indicate that fire can operate as a kind of edge effect (Cochrane & Laurance 2002; Alencar, Solórzano & Nepstad 2004; Broadbent *et al*. 2008). Given the inhospitality of the water-body matrix, which is likely to be subjected to greater wind effects, it is expected that fires had drastically propagated into forest islands leading to profound changes in floristic composition and functionality.

Here, we examine how tree assemblages have responded to the 26-year post-isolation history of landscape alteration in true forest islands within one of the world's largest hydroelectric reservoirs. We measured a set of local and landscape-scale variables to identify the main environmental predictors of species richness and composition within 34 variable-sized islands and three mainland continuous forest sites. We also selected a set of key tree functional traits to examine the degree to which forest insularization affects different tree functional groups, and used these traits to quantify functional diversity across all sites. We hypothesized that land-bridge islands will become heavily affected by habitat fragmentation effects due to high wind exposure, and that tree assemblage composition and functional diversity will be driven by non-random floristic transitions. Specifically we predict that (I) the number of species and diversity of tree assemblages will increase according to the increasing of island area; (II) fire intensity will interact synergistically with habitat fragmentation leading to severe compositional changes in tree composition; (III) edge will tend towards greater representation of pioneer species, severe decline in the abundance of emergent, large-seeded and biotically-dispersed species, and overall reduction in mean wood density.

4.3. Methods

4.3.1. Study site

We conducted this study in a large set of land-bridge islands created in 1986 following the permanent closure of the Balbina Hydroelectric Dam (1°01' – 1°55' S; 60°29' – 59°28' W), subsequently flooding a reservoir lake area of 4,437 km^2 along the Uatumã River, a first-order tributary of the Amazon. Consequently, an undisturbed upland (*terra firme*) primary forest area of 3,129 km^2 was converted into 3,525 forest islands surrounded by a large body of freshwater punctuated by dead trees rising above the maximum water-level. Sub-montane dense closed-canopy forests at Balbina are subjected to an average annual rainfall and temperature of ~2,376 mm [range = 2113.1 – 2716.3 mm] and 28°C [range = 21 – 35°C]. These forests are relatively diverse, averaging 143 tree species of ≥10 cm diameter-at-breast-height [DBH] ha^{-1} in continuous upland *terra firme* forests (range = 124 - 156 species ha^{-1}). The mean water column depth across the entire reservoir is 7.4m but as deep as 30m near the former river channel (Eletronorte 1997). The reservoir water-level has remained remarkably stable over the past 26 years (Melack & Wang 1998) due to a tight hydraulic system control at the dam site. Forest islands at Balbina, which range in size from 0.2 to 4,878 ha, have never been selectively logged, neither before nor after dam construction. To mitigate the environmental impact of the dam, the reservoir area and adjacent mainland continuous forests became strictly protected in 1990 with the creation of the ~940,000-ha Uatumã Biological Reserve, the largest forest reserve of this kind in Brazil. Following a severe El Niño drought from late 1997 to early 1998, ephemeral understorey fires accidentally affected much of the Balbina Reservoir region and adjacent areas, often penetrating into previously undisturbed primary forest islands.

4.3.2. Study design

In 2012, we conducted floristic inventories within 87 quarter-hectare forest plots distributed across 34 variable-sized forest islands and three continuous forest sites in undisturbed mainland areas adjacent to the reservoir (Fig. 4.1), spanning a study area of ~3,964 km^2. These plots measured 250m x 10m at all forest sites, except for ten small islands where rectangular plots were 125m x 20m. Floristic inventories were compiled considering the location of stems within 'subplots' of 50m x 10m (5 subplots per plot). The widely distributed forest islands and mainland sites were pre-selected using two cloudless georeferenced Landsat ETM+ scenes (230/061 and 231/061; year 2009) on the basis of their size and degree of isolation. Islands and continuous forest sites were spaced by at least 1 km from one another. On each island and mainland site, we inventoried one to four 0.25-ha forest plot according to island size as following: one plot per island <10 ha (mean ± SD island size = 4.0 ± 2.9 ha, range 0.8 – 9.5 ha, *N* = 12 islands); two plots per island of 10 – 90 ha (44.4 ± 30.1 ha, 13.4 – 78.4 ha, *N* = 9); three plots per island of 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 – 1,690 ha, *N* = 6) and mainland forest sites [to which, depending on the analysis, we assigned arbitrary area values of either infinity (∞) or one order of magnitude greater than our largest island] (Appendix 4.1). Island plots were always spaced by ≥50m from the nearest forest edge to preclude sampling areas subjected to the worst ravages of edge effects. Pairwise distances between midpoints of tree plots were on average 29.3 km ± 17.1 km (range = 0.3 – 86.6 km, *N* = 3741).

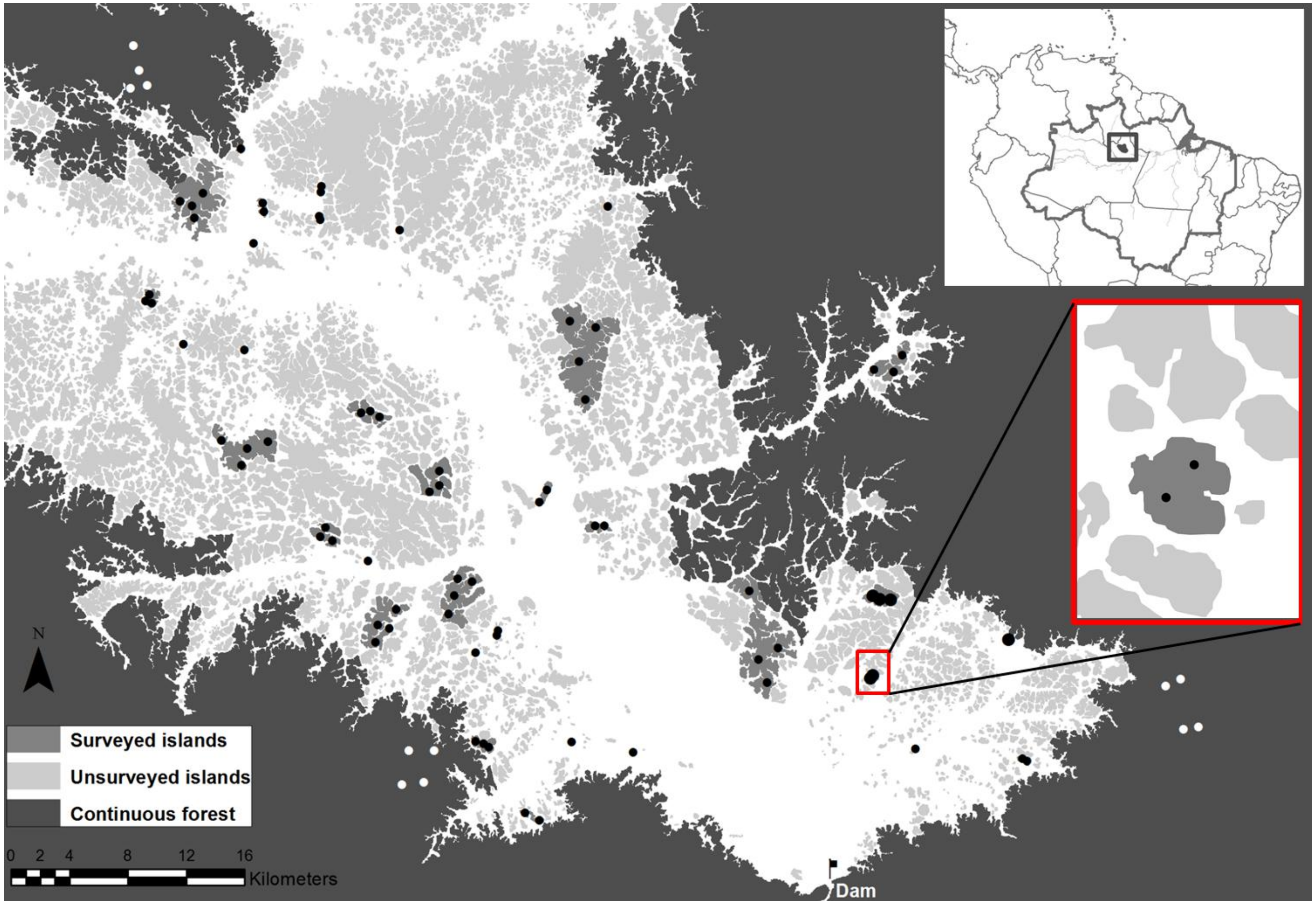

Figure 4.1. Spatial distribution of the 87 forest plots of 0.25 ha surveyed within 34 islands (black circles; N=75 plots) and three continuous forest sites (white circles; N=12 plots) within the Balbina Hydroelectric Reservoir of central Brazilian Amazonia. Inset rectangle is amplified to highlight the location of plots within a 26-ha island.

All live trees (including arborescent palms) ≥10 cm DBH within each plot were measured, tagged and identified at species level by A.E.S. Santos, an expert botanist with >20 years of fieldwork and herbarium experience in floristic inventories throughout Central Amazonia, including 8 years of tree identification work at BDFFP and the Ducke Reserve. These two landscapes are located ~60km and ~120km from the Balbina Reservoir, respectively, and share a similar tree flora (Ribeiro *et al.* 2002). Voucher specimens of all trees that could not be unambiguously identified *in situ* were collected and subsequently identified at the INPA (National Institute for Amazon Research) herbarium, which houses the largest voucher collection of the Amazonian tree flora (220,000 specimens), with a strong geographic bias toward the Manaus-Balbina region.

4.3.3. Functional attributes

We assigned five functional traits widely recognised as important determinants of tree recruitment, growth, and survival (see Hammond *et al.* 1996; Steege & Hammond 2001; Santos *et al*. 2008) to each tree species sampled across the Balbina landscape. These included regeneration strategy (short-lived pioneer, long-lived pioneer and old-growth species); vertical stratification (understorey, canopy, and emergent species); seed-dispersal mode (vertebrate-dispersed or abiotically dispersed); dry seed mass (eight classes on a log scale: 1 = 10^{-5} - 10^{-4} g, 2 = 10^{-4} - 10^{-3} g, ... 8 = >100 g); and wood density (g/cm^3), based on a comprehensive literature review encompassing data obtained across several Amazonian sites, but primarily the Guiana Shield which includes the regional scale tree flora of our study area (Guevara *et al.* 1986; Granville 1992; Hammond & Brown 1995; Hammond *et al.* 1996; Harms & Dalling 1997; Steege & Hammond 2001; Laurance *et al*. 2004a, 2004a,b; van Ulft 2004; Baraloto & Forget 2007; SID 2008; Amaral *et al*. 2009; Herault *et al.* 2010). Species-specific wood density (WD) measurements were obtained for 67.3% of the 368 tree species and 100% of the 189 genera included in the analysis. For those species for which species-level data were lacking we used the mean genus-level WD value from Guianan Shield sites or, if those were unavailable, from any lowland Amazonian site. We also calculated the total and proportional abundance of different functional groups within each plot — (a) emergent species, (b) pioneer species, (c) large-seeded species (seeds ≥1g), and (d) vertebrate-dispersed species — and the mean WD per stem.

4.3.4. Measures of diversity

Based on the species presence/absence and abundance data, we derived five robust metrics of tree taxonomic diversity (Magurran 2004) within each of the 87 plots to investigate patterns of species heterogeneity across islands and mainland sites: species richness (S), Simpson (D_S), Fisher's alpha, Dominance (D), and functional diversity (FD). To quantify FD, we used the five species attributes for each forest plot based on a dendrogram approach proposed by Petchey and Gaston (2002). This method encompasses five steps: (1) design of the trait matrix, which contains values ($x_{s,t}$) of trait t os species s; (2) design the community matrix, which describes which species are in each community; (3) conversion of the community matrix into a distance matrix; (4) hierarchical clustering of the distance matrix to produce a functional dendrogram; and (5) calculation of the total branch length of the dendrogram, providing a continuous FD measure. We used the Euclidean distance and the unweighted paired-group clustering method using arithmetic averages, and performed the analysis using Petchey's (2013) R code.

4.3.5. Explanatory variables

Following a two-stage unsupervised classification of the two georeferenced Landsat images, we used ArcView 10.1 (ESRI 2011) to extract seven plot-, forest patch- and surrounding landscape scale variables associated with each of our 87 forest plots. At the plot scale, we estimated the distance to forest edges (defined as the mean linear distance between the five midpoints of every 50-m section of each plot and the nearest points along the island perimeter; hereafter, 'EDGE DISTANCE'); the difference between maximum and minimum plot elevations based on the Shuttle Radar Topography Mission ─ SRTM ─ raster data (hereafter, 'SLOPE'); and the angular difference (0 - 90°) between the main axis of each rectangular plot and the median angular direction of prevailing strong winds recorded prior to and during convective windstorms (hereafter, 'WINDSTORM' angle). At the patch scale, we measured the total area in hectares ($\log_{10}$ x; 'AREA'); and obtained an index of fire severity (hereafter, 'FIRE'), measured according to a composite ordinal score (0-3) of both fire intensity (based on both the number of charred trees and height of char marks on each tree) and the extent to which each island had been affected by surface fires, which was estimated by three independent observers during detailed *in situ* surveys. At the wider landscape scale, we measured the shortest linear distance from the island to the nearest mainland ('D_{MAINLAND}'); and the percentage of FOREST COVER within a 500-m external buffer from the perimeter of each island and the survey area of mainland forests. We also modified the McGarigal *et al.* (2012) proximity index by considering both the aggregate area and distance to any land mass within 500 m of each island ('PROXIMITY'; see Table 5.1 in Chapter 5 for metric description).

4.3.6. Data analysis

We first performed a Mantel test with a Weighted Spearman rank correlation using the package '*ade4*' (Dray & Dufour 2007) to examine the spatial effect associated with plot location on species richness. We then fitted both semi-log linearized models and nonlinear multimodel tree species-area relationships (SARs) considering all 87 plots distributed across the 37 forest sites inventoried. We rarefied species richness to the minimum number of individuals recorded across all forest plots to account for differences in tree density, and then fitted SAR models considering both the rarefied estimates and raw data. We used the '*mmSAR*' R package (Guilhaumon *et al*. 2010) to evaluate model performance among eight possible nonlinear models — including four convex (power, exponential, negative exponential and Monod) and four sigmoidal models (rational function, logistic, Lomolino and cumulative Weibull) based on the Akaike Information Criterion (AIC; Burnham & Anderson 2002).

Second, we performed non-metric multidimensional scaling (NMDS) ordinations for all 87 plots using the Bray-Curtis dissimilarity matrix based on both qualitative (presence/absence) data and quantitative species composition (standardized and sqrt-transformed abundance data) to examine predictors of tree assemblage structure. Additionally, we investigated patterns of tree diversity according to island size, using Simpson (D_S), Fisher's alpha, Dominance (D) and functional diversity (FD) as response variables. We then performed BIOENV analysis (using 999 permutations) to compare two separate sample ordinations, one from species composition (using both the binary and abundance data) and the second from environmental data (our explanatory variables). This analysis selects the 'best' subset of environmental variables explaining the observed species ordination.

We further performed Generalized Linear Mixed Models (GLMMs) to examine the effects of plot-, patch (i.e. island or mainland site) and landscape-scale metrics on species richness. We initially used the Variance Inflation Factor (VIF) to test for multicollinearity among all variables for each GLMM (Dormann *et al.* 2013), and deleted those factors that were at least moderately redundant/collinear (VIF ≥ 6). In all GLMMs explaining plot-scale tree species richness, VIF analyses indicated high multicollinearity between our modified proximity index and landscape-scale forest cover (VIF>10.00). We therefore excluded forest cover, which consistently showed the highest VIF value, with the other seven plot- and patch-scale metrics subsequently showing low multicollinearity (VIF< 6.00). Also, pairwise Pearson correlations of fixed effects were consistently < 0.50. We therefore retained seven explanatory variables in the models (see Table 4.1). We then calculated pairwise Pearson correlation coefficients among all plot- , patch-and landscape-scale metrics within each GLMM, and considered any two variables as autocorrelated if r ≥ 0.70. Our global models incorporated a random term nesting 'plots' within island and mainland sites to account for potential spatial autocorrelation (Bolker *et al.* 2009), using a Poisson error structure. Models were fitted using the '*lme4*' package (Bates 2007) within the R platform. We ran all predictor subsets using the '*MuMIn*' package (Bartón 2009), retained all 'best' models that differed by ΔAIC ≤ 2.00 (Burnham & Anderson 2002), and obtained the relative importance of each variable. A model-averaging approach was further performed if at least five models were retained within the 'best' models. We further determined the unique and joint fractions of variation explained for each significant variable using variance partitioning (VP) within the '*vegan*' package (Oksanen *et al*.

2013) and used hierarchical partitioning (HP) to determine the relative importance of each significant variable within the '*hier.part*' package (Wash & Nally 2013).

We examined the effects of forest area on the abundance of functional groups using linear regression. These included the percentage of stems within plots defined as emergents, pioneers, large-seeded, and vertebrate-dispersed, as well as the mean wood density per live stem. We also performed a Mantel test to examine the effects of spatial structure on each functional response. Finally, we assessed the effects of plot, patch and local variables on the abundance of functional groups across all plots using GLMMs, considering both (1) 87 plots nested within the 37 forest sites; and (2) 435 'subplots' of 50m x 10m nested within the 87 plots, which were in turn nested within the 37 sites. For this second approach, we defined edge distances as the linear distances between the mid-point of each subplot and the nearest forest edge along island perimeters. We considered the number of live stems within each functional group but included the total number of stems as an offset variable using a Poisson error structure, to account for plot-scale variation in stem density. We performed GLMMs using the same steps described above, including multicollinearity and correlation tests, model selection, VP and HP. Finally, we used subplot-scale data to perform ANCOVAs to investigate the effects of burn severity on the relative abundance of different functional groups, with edge-distance as a covariate.

4.4. Results

4.4.1. Patterns of species diversity

We recorded a total of 11,230 live trees belonging to 368 species, 189 genera and 59 families within 21.75 ha of forest sampled across all 87 plots (Appendix 4.2). All trees were identified at the family-level, 99.2% at the genus-level, and 98.1% at the species-level. Surveyed islands ranged in size from 0.83 to 1,690 ha (mean ± SD = 228.8 ± 404.4 ha), and quarter-hectare plots contained between 14 and 78 tree species (mean ± SD = 58.9 ± 10.3; Appendix 4.1).

There was a positive semi-log linear relationship between island size and tree species richness per plot, whether we included ($R^2_{adj} = 0.286$, $N = 87$, $P < 0.001$) or excluded continuous forest plots ($R^2_{adj} = 0.250$, $N = 75$, $P < 0.001$; Fig. 4.2A). This explanatory power was further improved using eight nonlinear models, which explained up to 32.5% of the species-area relationships (mean $R^2_{adj} = 0.282$), with the cumulative Weibull providing the best-fit model, followed by the logistic model. This area effect was unlikely associated with island location within the Balbina Reservoir: a Mantel test failed to reveal any large-scale spatial effect on species richness across all 87 plots ($r = 0.002$, $P = 0.442$). Island size was also a significant predictor of functional diversity across all forest plots ($R^2_{adj} = 0.070$, $P = 0.013$; N=75, Fig. 4.2B), with small islands showing lower FD values compared to large islands and continuous forest sites. Indeed, islands smaller than 100 ha showed consistently low species diversity and dominance compared to islands larger than this threshold (Appendix 4.3). This pattern held true when we considered the plot-scale rarefied species richness to take into account any post-isolation variation in tree density due to differential tree mortality and recruitment across islands, whether we included ($R^2_{adj} = 0.172$, $N = 87$, $P < 0.001$) or excluded continuous forest plots ($R^2_{adj} = 0.157$, $N = 75$, $P < 0.001$).

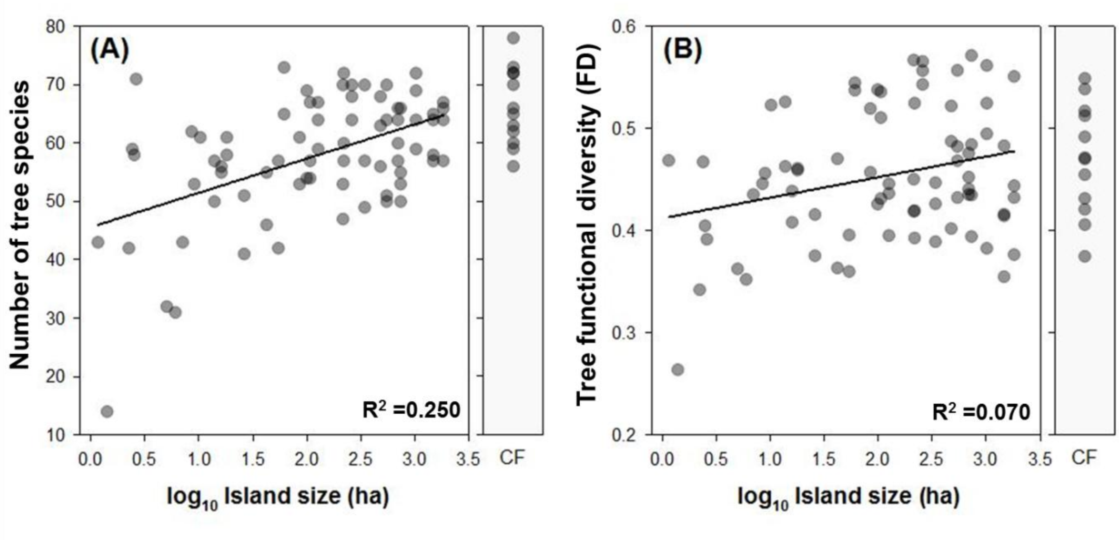

Figure 4.2. Relationship between forest island size and (A) the total number of tree species per plot; and (B) functional diversity of trees, considering all 87 inventoried forest plots. Values for plots embedded in continuous forest (CF) are shown in light-shaded panels, but are not included in linear fits.

GLMMs showed that island size was the only significant predictor of tree species richness across all 87 forest plots nested within the 37 sites (Table 4.1). Island size, topographic slope and the fire index were good predictors of functional diversity, whereas the Fisher-alpha of tree diversity was explained only by distance to the mainland (Table 4.1).

Table 4.1. Summary of best-fit Generalized Linear Mixed Models (GLMMs) examining tree assemblage structure and functionality in relation to explanatory variables considering all 87 plots nested within 37 forest sites. Coefficient estimates (β), their respective standard error values (SE), their relative importance, and both the hierarchical partition and the independent power based on variation partition of each significant variable are shown. Significant variables are indicated as: ****p* ≤ 0.001; ***p* ≤ 0.01; **p* ≤ 0.05.

Community attribute	**Explanatory variable**	**Estimate (± SE)**	**Relative Importance**	**Hierarchical partitioning (%)**	**R^2**
Species richness	Intercept***	3.888 (0.153)			
	AREA**	0.091 (0.034)	0.90		
	D_{MAINLAND}	0.001 (0.001)	0.37		
	FIRE	–0.025 (0.034)	0.28		
	PROXIMITY	0.024 (0.017)	0.49		
	EDGE DISTANCE	–0.106 (0.102)	0.32		
	SLOPE	–0.003 (0.003)	0.37		
	WINDSTORM	–0.001 (0.001)	0.34		
Functional diversity	Intercept***	3.497 (0.083)			
	AREA***	0.067 (0.018)	1.00	53.03	**0.165**
	D_{MAINLAND}	–			
	FIRE**	–0.057 (0.022)	1.00	24.32	0.099
	PROXIMITY	–			
	EDGE DISTANCE	–			
	SLOPE*	0.006 (0.003)	0.82	22.65	0.060
	WINDSTORM	–			
Fisher-alpha	Intercept***	2.675 (0.347)			
	AREA	0.123 (0.074)	0.70		
	D_{MAINLAND}*	0.162 (0.075)	0.77		
	PROXIMITY	0.078 (0.044)	0.45		
Pioneers stems(%)	Intercept	–0.605 (0.354)			
	AREA	–			
	D_{MAINLAND}**	–0.006 (0.002)	0.96	18.77	0.066
	FIRE***	0.332 (0.083)	1.00	63.83	**0.123**
	PROXIMITY	–			
	EDGE DISTANCE***	–0.420 (0.122)	0.99	17.40	0.014
	SLOPE	–			
	WINDSTORM	–			
Emergents stems(%)	Intercept***	–1.966 (0.486)			
	AREA***	0.261 (0.077)	0.97	60.35	0.081
	D_{MAINLAND}**	0.005 (0.002)	0.95	19.55	0.088
	FIRE*	–0.181 (0.076)	0.68	20.10	0.010
	PROXIMITY	–			
	EDGE DISTANCE*	–0.455 (0.228)	0.57		0.009
	SLOPE	–0.012 (0.006)	0.57		
	WINDSTORM	–			
Large-	Intercept***	–0.400 (0.107)			

seeded stems(%)	AREA	–			
	D_{MAINLAND}*	0.003 (0.001)	0.68	11.21	0.031
	FIRE***	–0.225 (0.062)	0.95	88.79	**0.171**
	PROXIMITY	–			
	EDGE DISTANCE	–			
	SLOPE	–			
	WINDSTORM	–			
Wood density (mean)	Intercept***	4.238 (0.027)			
	AREA	–			
	D_{MAINLAND}*	0.001 (0.001)	0.69	19.64	0.010
	FIRE***	–0.059 (0.018)	0.85	80.36	0.011
	PROXIMITY	–			
	EDGE DISTANCE	–			
	SLOPE	–			
	WINDSTORM	–			

4.4.2. Patterns of species composition

We also detected a significant effect of island area on species composition across all plots. Island size explained 22.7% of the variation in the species presence/absence data, with NMDS plots in small islands showing a lower overall similarity compared to plots in large islands and continuous forest sites. A similar pattern was found for abundance-weighted species composition ($R^2_{adj} = 0.177$, $P < 0.001$). The two-dimensional abundance-based NMDS ordination showed that live-stem species composition falls along a gradient of increasing fire severity (Kendall's $\tau = 0.524$, $P < 0.001$), decreasing proximity to other forest patches ($\tau = –0.456$, $P < 0.001$), decreasing island size ($\tau = –0.368$, $P < 0.001$), and decreasing distances to forest edges ($\tau = –0.331$, $P < 0.002$). Axis 2 was loaded by fire severity ($\tau = –0.335$, $P < 0.002$), distance to the mainland ($\tau = –0.293$, $P < 0.006$), island size ($\tau = 0.228$, $P < 0.040$), and distance to the nearest edge ($\tau = 0.221$, $P < 0.040$). Axis 1 was positively correlated with the proportion of pioneers stems ($\tau = 0.597$, $P <0.001$), but negatively correlated with the proportion of emergents stems ($\tau = –0.461$, $P <0.001$), the proportion of large-seeded stems ($\tau = –0.697$, $P <0.001$) and mean wood density per stem ($\tau = –0.513$, $P < 0.001$) across all 87 plots.

Considering our seven main explanatory variables, the highest correlation identified using BIOENV analysis on the abundance-based plot-by-species matrix was found for fire index and distance to nearest forest edges (Global r = 0.161, $P \approx 0.01$), and the presence/absence matrix yielded the same combination of 'best' variables (Global r = 0.142, $P \approx 0.01$; Fig. 4.3).

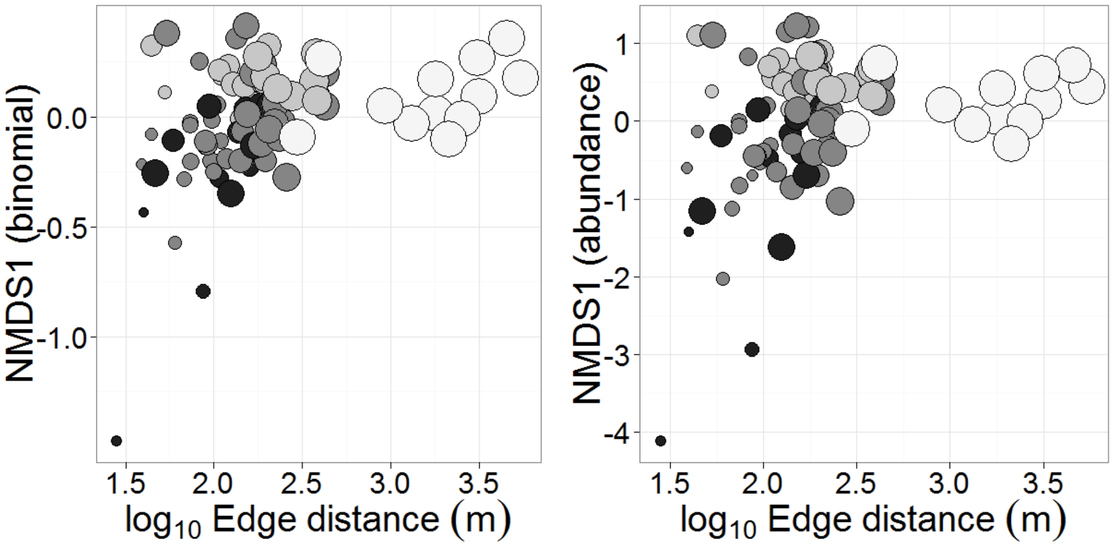

Figure 4.3. Relationships between ($\log_{10}$) mean edge distance of forest plots and the first non-metric multidimensional scaling axis representing the tree species assemblage structure considering both the presence/absence (left panel) and abundance (right panel) species composition data within 87 plots across 37 islands and three continuous forest sites. Sizes of circles are proportional to the log-transformed areas of forest sites and colours are according to fire intensity (increased fire intensity from light gray to black; white circles comprise unburnt continuous forest sites).

4.4.3. Predictors of functional drift

On the basis of 365 of the 368 species in our overall sample, we classified 27 species as emergents, 118 as pioneers, 167 as large-seeded species, and 327 exhibiting seed and fruit morphology traits typical of vertebrate dispersal. Wood density per species ranged from 0.24 to 1.03 g/cm^3. Island size was a strong predictor of the abundance of different tree functional groups across all 87 forest plots (Appendix 4.4). Forest plots in small forest islands contained a lower proportion of both emergent ($R^2_{adj} = 0.080$, $P = 0.005$) and large-seeded tree stems ($R^2_{adj} = 0.060$, $P = 0.013$), and a lower mean wood density per stem ($R^2_{adj} = 0.108$, $P = 0.001$). Conversely, pioneer species were more prevalent in small islands ($R^2_{adj} = 0.186$, $P < 0.001$), although the proportion of vertebrate-dispersed species was unrelated to patch area ($R^2_{adj} < 0.001$, $P = 0.998$).

We failed to detect spatial autocorrelation among the 87 plots in mean wood density ($r = 0.009$, $P = 0.399$) and the proportion of pioneer (Mantel test, $r = –0.061$, $P = 0.882$), emergent ($r = –0.060$, $P = 0.905$), large-seeded ($r = 0.015$, $P = 0.348$) and vertebrate-dispersed stems ($r = –0.093$, $P = 0.974$). GLMMs considering the relative abundance of different functional groups showed that fire index was the most important predictor of tree guild structure across islands, appearing in all ‘best’ models for each functional trait (Table 4.1). Distance to nearest edges and distance to the mainland were also significantly retained in the ‘best’ model explaining the proportion of pioneer stems across all plots nested within the 37 forest sites. Pioneer stems were more dominant in plots and subplots within 100 m from the nearest forest edge, and these rates stabilized at edge distances of ~300 m (Fig. 4.4). Moreover, burn severity also boosted the degree to which pioneers became dominant. Considering the same edge distance classes, we detected higher abundances of pioneer stems in severely burnt islands than in unburnt islands or those with low incidence of fire (Fig. 4.5). Indeed, higher dominance values due to high abundance of pioneer species were observed in heavily burnt islands (Appendix 4.5). Island size was closely related to the proportion of emergent stems, showing the highest relative importance among all variables retained in the ‘best’ model. Additionally, distance to the mainland and burn severity were also significant negative predictors of emergent prevalence, with severely burnt islands containing very few emergents (Appendix 4.5). Fire index and distance to the mainland were the only significant variables retained in the ‘best’ model explaining both the proportion of large-seeded stems and mean WD (Table 4.1). In contrast, our predictor variables failed to explain the proportion of vertebrate-dispersed stems.

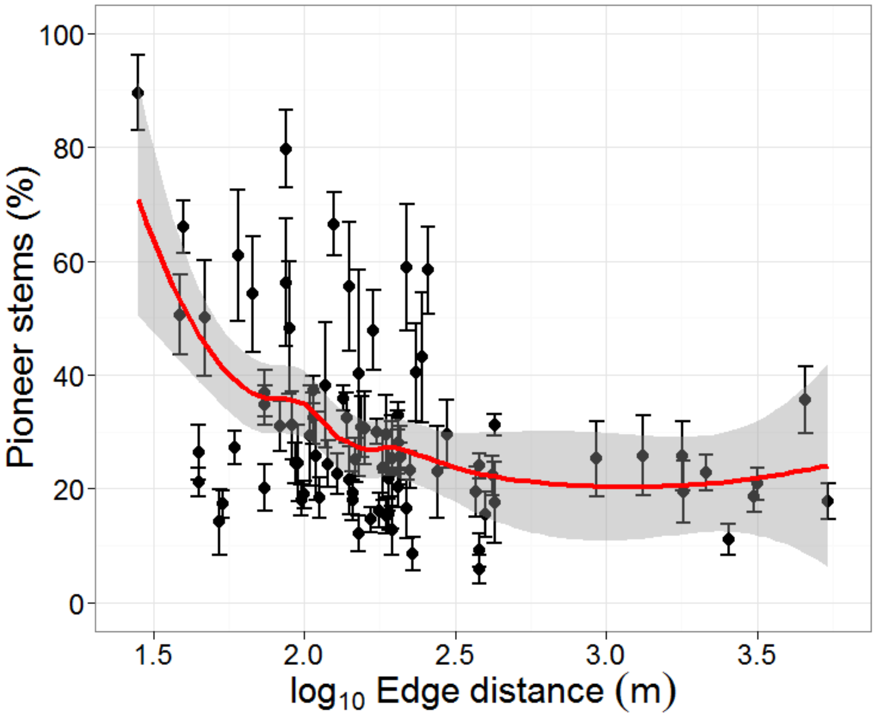

Figure 4.4. Relationship between ($\log_{10}$) mean edge distance of forest plots and the percentage of pioneer stems considering all 435 subplots of 10m x 50m nested within 87 plots across the 37 forest sites surveyed at the Balbina Reservoir. Error bars show the subplot scale variation for each plot. Shaded area represents the 95% confidence interval around a smoother fitted through the plot means.

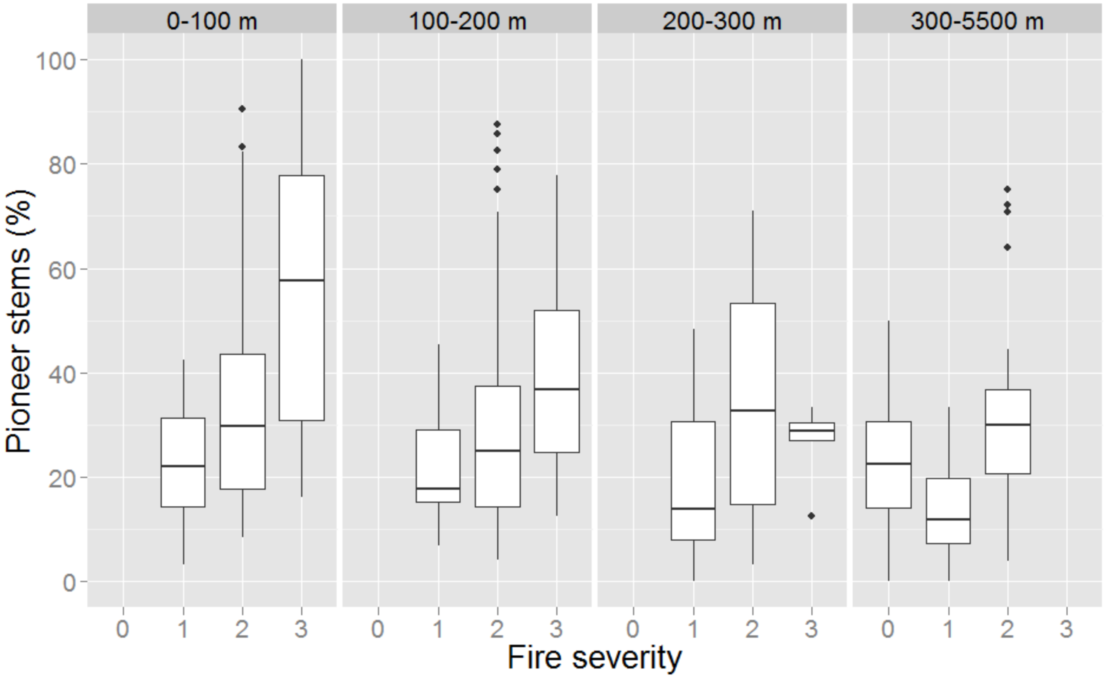

Figure 4.5. Box plot showing the effect of fire severity on the percentage of pioneer stems within four classes of edge distances, considering the variation across all 435 subplots nested within 87 plots inventoried at 37 forest sites within the Balbina Reservoir.

We also found similar patterns of guild structure when performing GLMMs considering all 435 'subplots' nested within 87 plots across the 37 forest sites, with fire index explaining most changes in tree guilds across forest plots. Fire index ($\beta = 0.299$, $P < 0.001$), island area ($\beta = –0.133$, $P < 0.05$) and distance to the mainland ($\beta = –0.005$, $P < 0.01$) were the strongest predictors retained in the 'best' model explaining the proportion of both pioneer and emergent stems. Fire index was the only significant variable retained in the 'best' model explaining the prevalence of both large-seeded ($\beta = –0.209$, $P < 0.001$) and vertebrate-dispersed stems ($\beta = –0.313$, $P < 0.05$), whereas f ($\beta = –0.058$, $P < 0.05$) in combination with distance to the mainland ($\beta = 0.002$, $P < 0.001$) were the strongest predictors of mean wood density.

Finally, we detected a significant effect of burn severity on the relationship between edge distance and mean wood density (ANCOVA, F = 8.454, P < 0.001), and the relative abundance of pioneer (ANCOVA, F = 29.387, P <

0.001), large-seeded (ANCOVA, F = 23.648, P < 0.001), and vertebrate-dispersed stems (ANCOVA, F = 6.668, P < 0.001). However, we failed to detect a significant effect of burn severity on the relationship between the proportion of emergent stems and edge distance (ANCOVA, F = 0.877, P = 0.453).

4.5. Discussion

This assessment of the ‘relaxation’ in post-isolation floristic guild structure within variable-sized land-bridge islands was based on the largest number of forest plots and the largest number of tropical forest patches ever sampled within the context of a major tropical hydroelectric reservoir. In such unique experimental landscape, we were able to assess how tree assemblages respond to forest habitat fragmentation *sensu stricto* (habitat fragmentation *per se*, see Fahrig 2003) following a 26-year history of isolation. Our results indicate that insular tree assemblages have been shaped by non-random floristic transitions that have occurred since the islands were isolated, rather than pre-existing differences in tree species composition and abundance. Although island size was a good predictor of both taxonomic and functional tree diversity, other forest patch and landscape scale variables exerted even more powerful forces on tree assemblage structure, driven primarily by edge-mediated fire effects.

4.5.1. Drivers of species diversity in land-bridge islands

Large islands contained the greatest number of tree species across the Balbina landscape at both plot and island scales. It has been widely accepted that area effects play a prevailing role in the erosion of species diversity within tropical forest fragments (Bell & Donnelly 2006; Ferraz *et al.* 2007), yet this pattern has not been widely observed in trees assemblages in forest remnants embedded within a matrix of pasture and cropland. For instance, studies in southern Mexico, southern Amazonia and the Brazilian Atlantic Forest have shown that tree species richness either declines or fails to respond to patch area (Metzger 2000; Arroyo-Rodríguez & Mandujano 2006; Laurance *et al.* 2006a; Michalski, Nishi & Peres 2007; Santos *et al.* 2007; Santos *et al.* 2008). In contrast, island area explained plant species richness within 154 sub-tropical land-bridge islands in China’s Thousand Island Lake, following ~50 years of isolation (Hu *et* *al*. 2011). Our positive species-area relationship at the Balbina archipelago suggests that forest islands experienced much higher extinction rates along transient "relaxation" stages than habitat patches surrounded by a terrestrial matrix. In particular, islands <100 ha often exhibited lower species diversity and higher dominance compared to larger forest areas, indicating that tree assemblages stranded in small islands have experienced a rapid loss of tree species after only 26 years of isolation.

Over and above the underlying effects of island size, tree species richness and composition was largely predicted by local burn severity and distance to the nearest forest edge. Species density was particularly low within 100 m of the nearest edges, but low species richness could also be detected in (sub)plots as far as 500 m from island margins. Forest patch boundaries are often exposed to a hostile microclimate including elevated temperatures, increased wind speed and greater desiccation compared to forest interiors (Kapos *et al.* 1997). Trees within nine BDFFP forest fragments north of Manaus experienced higher mortality within 60 m of edges, and this was aggravated in the smallest isolates (Laurance *et al.* 1998). However, post-isolation old-growth tree mortality in the Balbina islands was primarily driven by a greater susceptibility of edge-related forest disturbance including episodic surface fires coinciding with severe supra-annual droughts and windthrows. For instance, a single convective windstorm event led to the complete canopy implosion of a 6.1-ha island within the Balbina archipelago (M.B., *pers. obs.*). Moreover, matrix vegetation in terrestrial landscapes plays a strong role in the magnitude and penetration-distance of edge effects, with tree mortality being much higher in patches surrounded by pastures rather than young secondary forests (Mesquita, Delamônica & Laurance, 1999; Gascon, Williamson & da Fonseca, 2000). Given that Balbina islands were completely exposed to an open-water matrix, which tends to propagate rather than break-up the effects of peak wind turbulence, edges facing prevailing windstorms likely incurred higher rates of tree mortality (cf. Leigh *et al.* 1993). Indeed, plot slope had a strong effect on tree functional diversity, suggesting that trait loss in plots exhibiting a greater elevational range is associated with higher rates of tree turnover. In contrast, distance to nearest edges had no effect on forest structure in forest islands at the Tucuruí

Hydroelectric Dam of Eastern Amazonia (Ferreira *et al*. 2011), likely because the 17 islands sampled in that study had a much narrower size range (8 – 103 ha), were entirely edge-dominated, and effectively had no ‘core areas’.

4.5.2. Trait correlates of extinction risk

Forest habitat insularization at Balbina did not affect plant species uniformly, with life-history traits explaining varying degrees of vulnerability. In particular, emergent species associated with shade-tolerant seedlings, large seeds, dense wood and slow growth rates were more extinction prone. Island area predicted the abundance of emergents, but edge effects were again the strongest force driving changes in functional space of island tree assemblages. Indeed we can provide evidence that the non-random drift in species composition and abundance experienced by these tree assemblages was mediated by several species functional attributes (Laurance *et al*. 2006a,b; Tabarelli *et al*. 2010).

The proliferation of fast-growing successional trees in small patches has been shown to occur in several other Neotropical fragmented forest landscapes (Laurance *et al*. 2006a,b; Michalski, Nishi & Peres 2007; Tabarelli *et al*. 2010; Lôbo *et al*. 2011). Some disturbance-loving pioneers at the BDFFP landscape experienced a >1000% increase in density after only <20 years of fragmentation (Laurance *et al*. 2006b). Similarly, the number of both pioneer stems and pioneer species in the Atlantic Forest of northeastern Brazil increased more than fourfold in small fragments after a long post-isolation period (Santos *et al.* 2008). We uncovered a strong edge effect on the abundance of pioneer stems within our forest plots, with a significant decline of old-growth stems near forest edges. Additionally, fire severity apparently compounded edges effects, leading to a proliferation of disturbance-adapted pioneer species in plots that had burnt at least once. Pioneer abundance was significantly elevated in heavily burnt plots within 200 m of forest edges, compared to plots that had been moderately and lightly affected by fire. Indeed, fire interacts synergistically with forest habitat fragmentation effectively inflating edge effects, given that forests borders are disproportionately more susceptible to surface fires than forest interiors (Cochrane 2001; Cochrane & Laurance 2002).

We also detected that surface fires were more extensive in islands far from the mainland, suggesting that distance to the mainland is related to burn severity, thereby operating as a type of edge effect (Appendix 4.6). Fire history and distance to mainland were also good predictors of the abundance of large-seeded stems (larger than 1g), emergent stems, and mean wood density within forest plots. Large-seeded species are consistently affected in Amazonian forest fragments (Cramer, Mesquita & Williamson 2007) and more susceptible to forest fragmentation than small-seeded species, showing a one-third reduction in density in Atlantic Forest patches (Santos *et al*. 2008). Trees bearing large seeds are more specialised in their dispersal agents, primarily medium and large vertebrates, which are also more extinction-prone in forest remnants (Cordeiro & Howe 2001; Laurance *et al.* 2011). For instance, Silva & Tabarelli (2000) predicted that 34% of tree species bearing large fruits will become extinct in Atlantic forest fragments of northeast Brazil, due to dispersal bottlenecks. Frugivorous vertebrates in small and medium islands in hydroelectric reservoirs elsewhere were extirpated following a short period of isolation (Cosson *et al*. 1999, Terborgh *et al*. 2001), suggesting that several key dispersers of large-seeded plants also met a similar fate at the Balbina lake, aggravating dispersal limitation.

The overall mean wood density per stem was lower within severely burnt plots, which is consistent with the greater susceptibility of heavy-wooded species to desiccation (Borchert 1994). In Australian forest isolates, species showing lower average wood density were more prone to stem damage due to wind disturbance (Curran *et al*. 2008), yet this functional trait was considered a poor predictor of successional species’ responses to habitat fragmentation at the BDFFP landscape (Laurance *et al*. 2006b). Wood density can be a good measure of sensitivity to habitat disturbance (Steege & Hammond 2001), and provides another indication that thermal stress through unprecedented surface fires induced high levels of tree mortality within the Balbina islands. Finally, fire severity also depressed the abundance of emergent stems, although this was primarily mediated by area effects. Large trees are particularly vulnerable in isolated forest patches, given that they are susceptible to the detrimental effects of wind turbulence, desiccation and liana infestation (Laurance *et al.* 2000). Considering that lianas are increasing in abundance in forest patches at BDFFP (Laurance *et al.* 2014), it is possible that large trees within Balbina islands become even more susceptible to mortality in the long-term.

4.6. Conclusions

Land-bridge islands experience markedly high rates of species loss compared to oceanic islands (Terborgh 1974). Our unique experimental setting of thousands of forest islands within one of the largest South American hydroelectric reservoirs indicates that the detrimental effects of fragmentation in land-bridge islands are considerably stronger than in forest isolates embedded within a terrestrial landscape, confirming other Neotropical studies in analogous archipelagos (Cosson *et al.* 1999; Emer, Venticinque & Fonseca 2013). In contrast with other Neotropical fragmentation ecology studies on tree assemblages (Metzger 2000; Arroyo-Rodríguez & Mandujano 2006; Laurance *et al.* 2006a; Michalski, Nishi & Peres 2007; Santos *et al.* 2007; Santos *et al.* 2008; Magnago *et al*. 2014), we uncovered a significantly positive species-area relationship, indicating a rapid decay in tree diversity in most islands. Yet our results clearly show that edge effects, including edge-related fires and forest disturbance, were the main predictors of directional floristic transitions at Balbina. This suggests that area effects are expressed via a response to edge effects, given that trees in smaller islands were more susceptible to edge-related surface fires and windthrows, which is consistent with the biotic and abiotic changes occurring at forest patch boundaries (Murcia 1995; Laurance *et al.* 1998).

Secondly, the inhospitable open-water matrix seems to exert a key role in determining patterns of tree assemblage composition and functional space in our study landscape. Water is an unconditionally unsuitable habitat for tree species of the region and operates as a strong barrier for many vertebrate species, thus severing matrix movements of key seed dispersers. For example, primates and small mammals were unable to cross inundated areas only a few years after the flooding of the Sinnamary River in French Guiana (Cosson *et al*. 1999) and a decline of tree diversity in small Gatun Lake islands (Panama) was apparently induced by the absence of seed-burying agoutis (Leigh Jr *et al.* 1993). Large predators were extirpated in several islets within Lago Guri just after isolation, resulting in hyper-herbivory and a sharp decline in saplings (Terborgh *et al.* 2006). Furthermore, islands are likely strongly affected by edge effects, given that their boundaries are not buffered by the attenuating effect of second-growth vegetation, and therefore directly exposed to prevailing windstorms. In fact, edge-related tree mortality in Amazonian forest patches is partly a function of the structure of surrounding vegetation (Mesquita, Delamônica & Laurance, 1999). In other words, the dynamic of tree assemblages within islands created by hydroelectric impoundments appears to be more strongly sensitive to edge effects than most terrestrial fragmented forest landscapes. In light of the burgeoning hydropower engineering sector in several South American countries (Finer & Jenkins 2012; Kareiva 2012), our results highlight the drastic floristic erosion that new mega hydroelectric dams are expected to induce in similar archipelagic landscapes.

Finally, we uncovered the pervasive additive effect of fires within forest isolates, with surface fires more prevalent in islands far from the mainland and along the peripheral portions of all islands. These ground fires led to a near complete species turnover characterised by a proliferation of pioneer species, severe decline in the abundance of emergent and large-seeded species, and overall reduction in mean wood density. Fire disturbance operates as a large scale edge-effect, and represents a serious risk for fragmented tropical forest landscapes (Cochrane 2001; Cochrane & Laurance 2002). We suspect that fire causes a worst effect due to the large amounts of combustible fuel from dead trees that surround all islands. The Balbina archipelago has the unique advantage of being protected by the Uatumã Biological Reserve from panoply of human disturbances, such as logging and hunting activities, that may interact synergistically with forest fragmentation (Laurance & Peres 2006). Hence, long-term effects on plant guild structure would be expected to be far worse had these islands been left unprotected since the rise of floodwaters. Preventing or mitigating the compounding effects of anthropogenic forests disturbance in insular forest ecosystems in artificial archipelagos formed by mega hydroelectric dams will therefore slow down the process of forest composition decay and degradation of forest ecosystem services such as carbon retention.

4.7. References

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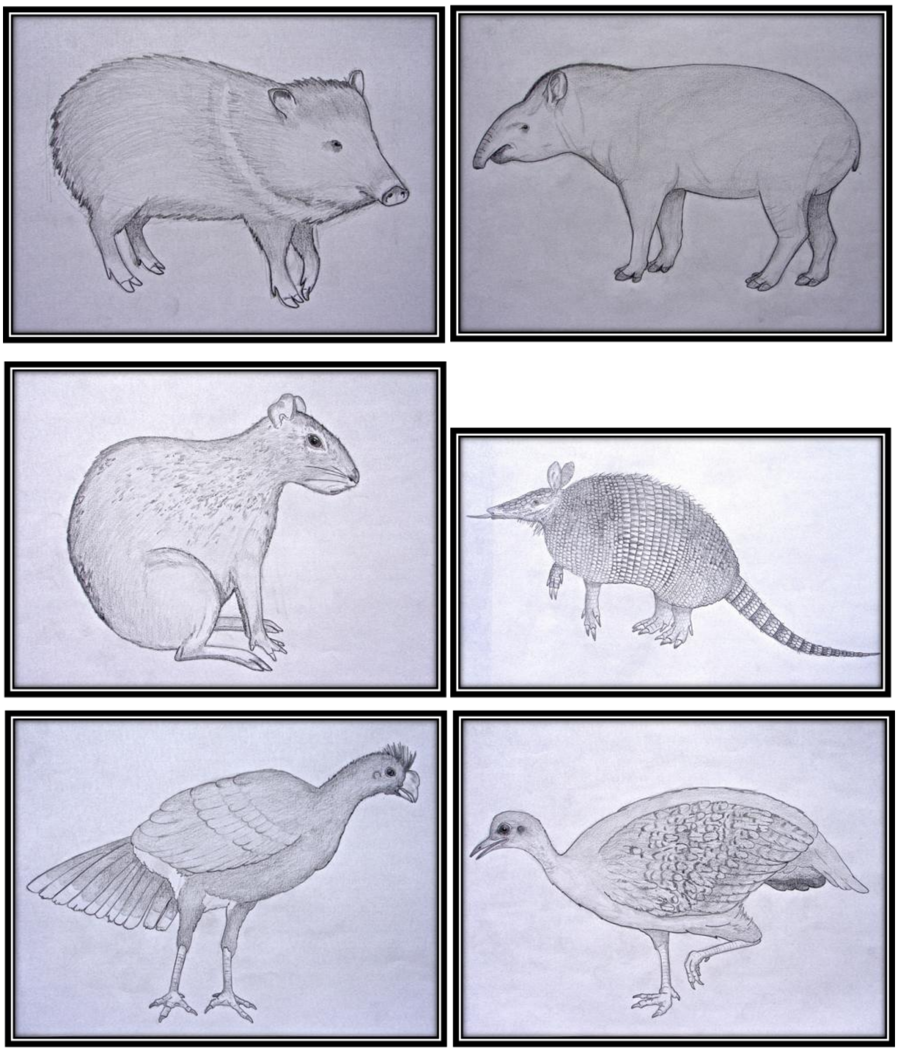
CHAPTER 5

PREDICTING LOCAL EXTINCTIONS OF FOREST VERTEBRATES IN AMAZONIAN LAND-BRIDGE ISLANDS



The collared peccary, *Pecari tajacu*; the tapir, *Tapirus terrestris;* the agouti, *Dasyprocta sp.*; the nine-banded armadillo (*Dasypus novemcinctus*), the currasow (Crax *sp.*) and the tinamous (*Tinamous sp.*). Courtesy of the artist Marco Bueno.

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5.1. Abstract

Hydropower projects are rapidly expanding across lowland Amazonia, driving the conversion of large tracts of once-continuous forests into archipelagos embedded within an open-water matrix. Forest vertebrate populations thus become stranded in habitat islands, with their survival prospects governed by a combination of species life-history traits, and island and landscape context. Here, we investigate the patterns of species extinction for 34 mid- and large-sized arboreal and terrestrial vertebrate species within 37 land-bridge islands and three continuous forest sites within a vast hydroelectric reservoir of Brazilian Amazonia, based on a combination of camera trapping, line-transect censuses, sign surveys and armadillo burrow counts. Forest area was the best predictor of species persistence, with occupancy rates varying greatly across taxa. Nine-banded armadillo was the most ubiquitous species, persisting in 97% of all surveyed sites, whereas white-lipped peccaries occupied only 8.1% of sites. In addition to forest area, home range size and an index of dispersal (swimming) capacity were the main predictors of local extinction rates within islands for all vertebrate species. Accounting for imperfect detection, species-specific models indicate that forest area was the best predictor of occupancy, appearing in the best model of 83% species. We then predicted species-specific occupancy rates across all 3,546 islands in the archipelago, suggesting that fewer than 2% of all islands are likely to harbour a minimum of 75% of all species. To minimize loss of vertebrate diversity, siting of future hydroelectric dam projects in lowland Amazonia should consider the landscape structure to maximise island size, landscape connectivity, and set aside strictly protected forest reserves within reservoirs.

5.2. Introduction

Mega hydroelectric dams have become a major driver of forest habitat loss and fragmentation across several Amazonian river basins, with dozens of new major hydropower projects either planned or currently under construction (Finer & Jenkins 2012; Fearnside 2014). Assessments of the social and environmental impacts of large dams have so far primarily focused on flooding of indigenous territories and displacements of local communities (Esselman & Oppermann

2010), alterations in fluvial hydrology (Nilsson *et al.* 2005), large emissions of greenhouse gases (Almeida *et al.* 2013), and losses in fisheries and aquatic biodiversity (Barthem *et al.* 1991; Alho 2011; Liermann *et al.* 2012, Palmeirim *et al*. 2014). In contrast, the performance of tropical terrestrial vertebrate populations in areas affected by dams has received comparatively little attention (but see Cosson *et al.* 1999; Benchimol & Venticinque 2014). Given hugely escalating investments in hydropower infrastructure worldwide, impact assessments of mega-dams on terrestrial biodiversity are conspicuously missing.

As mega-consumers and apex predators, large-bodied vertebrates are often considered as good bioindicators of intact tropical forests, as they provide key ecological services for ecosystem dynamics and are sensitive to forest disturbance and hunting (Dirzo *et al.* 2014). Local extinctions from forest patches can induce a series of trophic cascades, promoting unexpected shifts in forest composition and function. For instance, predator-free land-bridge islands in Venezuela are typically denuded by hyperabundant herbivores, decimating seedling recruitment in canopy trees (Terborgh *et al*. 2001). Also, rising floodwaters drastically reduced vertebrate species diversity only four years after French Guiana's Petiti Saut Dam was built (Cosson *et al.* 1999), suggesting that isolation effects in true islands are more severe than in habitat patches surrounded by a non-water matrix. Yet the long-term impacts of hydroelectric dams on terrestrial and arboreal vertebrates remains poorly understood, deterring effective large-scale conservation strategies on how to best prevent or mitigate biodiversity loss along dammed tropical river basins.

Newly isolated vertebrate assemblages could undergo nonrandom drifts in species composition within tropical land-bridge islands following a long relaxation time, but this is a function of species-specific responses to individual patches and the surrounding landscape. Vertebrate persistence in Neotropical fragmented landscapes is likely to be affected by landscape structure and the history of human disturbance (Michalski & Peres 2005; Canale *et al.* 2012), with a range of species responses to habitat fragmentation. Rare, matrix-intolerant species unable to disperse among patches are usually considered more extinction-prone in fragmented landscapes (Davies *et al*. 2000; Henle *et al.* 2004). Hence, some life-history traits can be excellent predictors of patch occupancy in forest remnants. For instance, home range size and trophic status were among the main predictors of primate local extinction within 760 Neotropical forest patches (Benchimol & Peres 2014), and large-bodied trophic generalist vertebrate species were most resilient to local extinction in recently isolated land-bridge islands (Cosson *et al*. 1999). Life-history traits, in addition to patch and landscape-scale site attributes, can help predict species survival within forest isolates, and inform species-specific conservation guidelines.

Here, we assess how 34 terrestrial and arboreal vertebrate species responded to the insularization process induced by a major hydroelectric dam in lowland Central Amazonia, based on intensive, well-replicated field surveys in a large number of islands and neighbouring continuous forest. Specifically, we examine (1) the patch occupancy of each species and estimate minimum critical island sizes required to ensure their persistence; (2) the relative importance of island landscape context and species traits in explaining pattern of local extinction across all sites; and (3) how different patch, landscape and habitat quality metrics affect patterns of occupancy for each species individually. Based on these results, we predict the aggregate vertebrate species richness and composition across over 3,500 islands within the reservoir, pinpointing priority islands for conservation and dissecting how large hydroelectric dams affect terrestrial vertebrate diversity in lowland Amazonia.

5.3. Methods

5.3.1. Study area

This study was conducted within the Balbina Hydroelectric Lake, a man-made reservoir within the Uatumã River basin of central Brazilian Amazonia ($1^{o}48'S$; $59^{o}29'W$). The Balbina Dam was completed in 1986 following to supply hydropower to Manaus, the capital of the state of Amazonas. The rising floodwaters inundated a 3,129-km^2 area, resulting in the formation of 3,546 land-bridge islands ranging in size from <1 to 4,878 ha. In 1990, the lake became largely protected by the creation of the ~940,000-ha Uatumã Biological Reserve, the largest protected area in this category in Brazil. Most islands consist of dense closed-canopy terra firme forest. There is no history of logging nor hunting in the reservoir (Benchimol & Venticinque 2014), but many islands experienced ephemeral understorey fires during the El Niño drought of late-1997 to early-1998.

We conducted our intensive vertebrate surveys within a subset of 37 islands and three widely spaced neighbouring continuous forest sites adjacent to the lake, which were spaced by at least 1 km from one another to maximise spatial independence, spanning a study area of ~3,964 km^2 (Figure 5.1). Islands were selected on the basis of their size, isolation and spatial distribution, to represent a wide range of island configurations within the reservoir. Surveyed islands ranged in forest area (0.55 – 1685.38 ha) and isolation distances from each focal island to the nearest mainland site ranged from 0.04 to 17.73 km (Table 5.1).

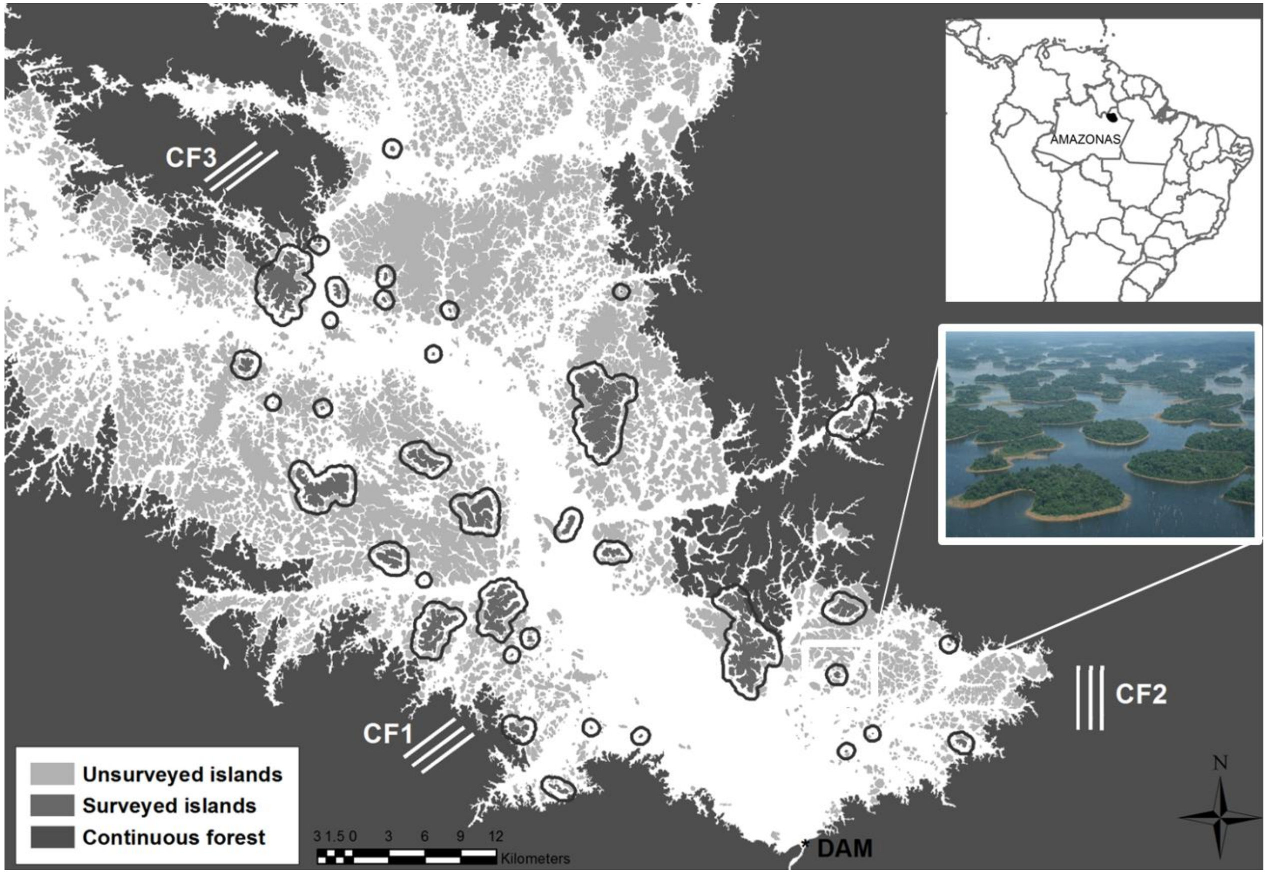

Figure 5.1. Distribution and size of the 37 land-bridge islands (dark grey) and three mainland undisturbed continuous forest (CF) sites (CF1, CF2 and CF3; each CF site is comprised by three parallel 4-km transect [white lines], in the very dark grey) surveyed using several methods within the Balbina Hydroelectric Reservoir landscape of Amazonas, Brazil. Black contours indicate 500-m buffer polygons around each island. All unsurveyed islands are shown in light grey. A group of small islands are shown in the inset photograph (credit: E. M. Venticinque).

Table 5.1. Patch, landscape and habitat quality variables considered in the analyses.

Variable name	Code names	Type	Description	Range (mean ± SD)
Area	AREA	Patch	Total forest area within each focal island	0.55 – 1685.38 ha (210.67 ± 392.08)
Isolation	ISOLATION	Patch	Euclidean distance from each island to the nearest neighbouring mainland forest site	0.04 – 17.43 km (4.87 ± 4.41)
Shape	SHAPE	Patch	Total perimeter length of each focal island divided by the total island area	0.004 – 0.106 (0.017 ± 0.019)
Proximity	PROXIMITY	Patch	Represents the sum of all island areas divided by the squared edge-to-edge distances to each focal island for all islands within a specified buffer. Instead of considering the area of each island that remains within the buffer (as in McGarigal *et al.* 2012), it is considered the total ("real") area of each island. Buffer considered in the final analysis: 500 m	0.0 – 9.65 (3.17 ± 1.97), (log x + 1)
Forest cover	COVER	Landscape	Percentage of forest cover within the buffer, defined as 500 m in the final analysis	0.0 – 56.1 % (30.55 ± 16.72)
Fire severity	BURN	Habitat quality	Fire severity within each focal island, scored on an ordinal scale based on the extent of each forest site affected by surface fires and the number of charred trees and height of char marks on each tree	0 – 3 (2.05 ± 0.70)
Closed-canopy	CC%	Habitat quality	Percentage of closed-canopy forest within the focal island	0 – 100 % (74.79 ± 20.93)
Basal area of fleshy fruits	BA_{ff}	Habitat quality	Basal area of trees bearing fleshy fruits, calculated from floristic surveys of trees > 10 cm diameter at breast height in 0.25 ha forest plots within each focal island	0.2 – 8.76 m^2/ha (5.03 ± 1.52)

5.3.2. Vertebrate sampling

We used a combination of four different sampling techniques to determine occupancy of the midsized to large-bodied vertebrate fauna at each island and mainland site between June 2011 and December 2012: camera trapping, line-transect censuses, sign surveys, and armadillo burrow counts. These methods were selected considering the wide range of ecological and behavioural characteristics of target species, with different activity times (diurnal, nocturnal and cathemeral), and use of vertical space (terrestrial, arboreal and scansorial), all of which are widely amenable to quantitative surveys (see Silveira *et al.* 2003; Michalski & Peres 2007; Munari *et al*. 2011; Thornton *et al*. 2011a). We restricted surveys to non-flying medium- and large-bodied terrestrial and arboreal mammals (except sloths), terrestrial birds and tortoises, which were widely distributed across the study landscape. Only tortoise congeners (*Chelonoidis carbonaria* and *C. denticulata*) were pooled under a single genus, given that they could not be usually identified to species and their strong ecological similarities. To facilitate surveys, we cut linear transects of 0.5 - 3 km in length at each island, according to island size and shape, so that a representative island area could be covered (Appendix 5.1). On each continuous forest site, three parallel 4-km linear transects were established, separated from each other by 1km (Figure 5.1; Appendix 5.1).

In 2011, we deployed two to ten Reconyx Hyperfire camera traps (hereafter, CTs) at each island according to their size for a continuous 30-day period in 2011, repeating the same procedure in 2012 using the same CT positions as in 2011 (Appendix 5.1). On continuous forest sites, 15 CTs were deployed (five on each transect), also during two exposure periods of 30 days each. We placed unbaited CTs 30 cm above ground along transects, spaced by at least 500 m (except for small islands). We configured each CT to obtain a sequence of five photographs for each animal or animal cluster recorded, using 15-sec intervals between records. However, we only considered CT records of as independent if conspecific individuals could be distinguished or if between-photo intervals exceeded 30 min. Additionally, we conducted eight visits of line-transect surveys per island, following guidelines proposed by Peres (1999). Two trained observers walked quietly at a constant speed (~ 1 km/h) on all transects established on each site. Surveys were conducted either in the morning (6:15h to 10:30h) or afternoon (14:00h to 17:30h), and we recorded all visual or acoustic encounters of individuals or groups of any target species. On return walks along each transect, we conducted sign surveys, intensively searching for any indirect evidence of any target terrestrial species, including tracks, superficial digging, burrows, fecal material, hair, and partly consumed fruits/seeds. Finally, we searched for armadillo burrows (≥ 50 cm depth) within a distance of 5m either side each transect, only once per transect, and measured them following Michalski & Peres (2007). This greatly enhanced our detection and identification of the four armadillo species occurring in the study area. In total, we obtained 12,420 CT-days (mean [SD] = 310.5 [251.83], range = 120-900 CT days/site) from 207 camera trap stations; 1,168 km of total line-transect census effort (including 592 km in islands and 576 km in continuous forest sites); 1,168 km of sign surveys; and 108.5 km of armadillo-burrow counts (Appendix 5.1).

5.3.3. Landscape structure and habitat quality variables

We used RapidEye© high-resolution (5-m pixel) imagery for the entire BHR landscape to quantify forest patch and landscape metrics, and forest habitat quality of all surveyed sites. We selected RapidEye tiles on the basis of low cloud cover (<10%) and months matching our field sampling. A total of 28 tiles covering an area of 6,980 km^2, available from March 2011 to September 2012, were used. At the patch scale, we measured island forest size (AREA, $\log_{10} x$); the distance between each focal island and the nearest continuous forest (ISOLATION); the perimeter length of focal islands divided by the total island area (SHAPE). At the landscape scale, we considered multiple buffers (250m, 500m and 1000m) outside the perimeter of each focal island and mainland forest sites and quantified both the percentage of total forest cover (COVER) and modified the proximity index of McGarigal *et al.* (2012) by considering the total size of any land mass within the buffer, rather than excluding land areas outside the buffer for patches contained within the buffer (PROXIMITY).

Finally, we considered three descriptors of forest habitat quality of each surveyed site: the understorey burn or fire severity (BURN), measured as a composite ordinal score (0-3) based on both the number of charred trees, the height of char marks on each burnt tree, and the extent to which each island had been affected by surface fires; the percentage of closed-forest canopy (CC%) within each island, following a semi-supervised classification using ArcMap (version 10.1) to obtain four land cover classes (closed-canopy forest, open-canopy forest, bare ground, and water); and the aggregate basal area of all trees ≥10 cm diameter at breast height bearing fleshy fruits (BA_{ff}), calculated from floristic surveys based on 87 quarter-hectare forest plots inventoried at all forest sites [see Chapter 4 for details and Appendix 5.1].

5.3.4. Species traits

We performed a literature search using Google Scholar with various combinations of traits and species as keywords, to obtain five morpho-ecological traits: body mass, group size, home range size, diet category and ranked trophic status for all vertebrate species considered in this study (Table 5.2). These species traits are commonly associated with susceptibility to habitat fragmentation in Neotropical mammals (Henle *et al*. 2004; Ewers & Didham 2006; Urquiza-Haas *et al.* 2009; Thornton *et al.* 2011b; Benchimol & Peres 2014). Values from studies conducted within Amazonian continuous forests were obtained for most species; mean values were calculated if two or more studies were available. However, values from extra-Amazonian Neotropical sites were used for species traits that were unavailable for any Amazonian landscape. In total, we obtained ecological attributes from 28 different studies (Appendix 5.2).

Table 5.2. Island occupancy rates based on all methodologies and species traits for 34 species within 37 islands at BHR.

					Species traits				
Species	**English vernacular name**	**Island occupancy (%)**	**Critical island size (ha)[1]**	**% of islands expected to be occupied[2]**	**Body mass (kg)[3]**	**Group size[3]**	**Home range[3]**	**Diet category[3]**	**Dispersal ability[4]**
Mammals									
Alouatta macconelli	Red howler monkey	75.7	4.46	73.38	6.15	8.2	53	1	77
Ateles paniscus	Black pider monkey	54.1	25.12	24.39	7.90	2.5	224	3	23
Cabassous unicinctus	Southern naked-tailed armadillo	37.8	151.36	3.24	4.80	1	101.6	5	0
Chiropotes sagulatus	Bearded saki	40.5	74.99	7.53	3.10	21.8	336	4	3
Cuniculus paca	Lowland paca	67.6	9.66	50.71	9.00	1	2.46	2	81
Dasyprocta leporina	Red-rumped agouti	59.5	19.72	30.91	3.50	1.5	5.66	3	39
Dasypus kappleri	Greater long-nosed armadillo	45.9	61.66	9.39	9.50	1	7	5	27
Dasypus novemcinctus	Nine-banded armadillo	97.3	0.20	97.43	3.50	1	3.4	5	51
Eira barbara	Tayra	21.6	363.08	0.85	3.91	1.2	1420	5	8
Guerlinguetus aestuans	Brazilian squirrel	24.3	446.68	0.73	0.19	1	1.5	3	0
Leopardus pardalis	Ocelot	59.5	20.01	31.39	11.90	1	162	6	37
Leopardus wiedii	Margay	16.2	912.00	0.34	3.25	1	2295	6	0
Mazama americana	Red brocket deer	48.6	37.15	16.89	22.80	1	100	1	130
Mazama nemorivaga	Amazonian brown brocket deer	32.4	141.25	3.47	16.30	1	100	1	45
Myoprocta acouchy	Red acouchi	73.0	5.49	67.32	0.95	1	1.5	3	15
Myrmecophaga tridactyla	Giant anteater	45.9	45.71	13.56	22.33	1	2500	5	116
Nasua nasua	South American coati	21.6	371.53	0.82	3.79	30	166	5	4
Panthera onca	Jaguar	37.8	131.82	3.72	80.00	1	20650	6	122
Pecari tajacu	Collared peccary	35.1	112.20	4.46	21.27	4.5	500	4	100
Pithecia chrysocephala	Golden-faced saki	32.4	181.97	2.48	1.38	3.4	103	3	10
Priodontes maximus	Giant armadillo	21.6	363.08	0.85	38.00	1	726.5	5	5
Puma concolor	Puma	43.2	95.50	5.61	51.60	1	3177	6	71
Puma yaguaroundi	Jaguarundi	10.8	1288.25	0.25	6.75	1	10000	6	6
Saguinus midas	Golden-handed tamarin	24.3	251.19	1.47	0.54	5.7	50	4	7
Saimiri sciureus	Squirrel monkey	24.3	398.11	0.76	0.90	22.5	500	4	1
Sapajus apella	Brown capuchin monkey	54.1	22.91	26.48	2.75	14.3	429	4	43
Tamandua tetradactyla	Southern tamandua	21.6	933.25	0.31	5.52	1	380	5	12

Tapirus terrestris	South American tapir	64.9	11.75	44.90	160.00	1	275	1	467
Tayassu pecari	White-lipped peccary	8.1	1202.26	0.28	32.23	500	2970	4	116
Birds									
Crax alector	Black curassow	67.6	9.44	51.41	3.40	2	20	4	198
Penelope marail	Marail guan	51.4	37.15	16.89	0.95	2.2	30	4	119
Psophia crepitans	Grey-winged trumpeter	37.8	107.15	4.77	1.50	8	120	4	52
Tinamus major	Great tinamou	70.3	7.94	56.54	1.20	1	20	3	30
Reptiles									
Chelonoidis spp.	Red and Yellow-footed tortoise	35.1	118.85	4.20	4.00	1	28.7	2	86

[1] Critical island size required to ensure a minimum occupancy probability of 60% based on our logistic regression models (see Fig. 5.3).

[2] Percentage of all islands within the reservoir (considering a total number of 3546 islands). Estimation based on the critical island size.

[3] See Appendix 5.2 for list of references used for life-history trait values.

[4] Based on interviews conducted in this study (see Methods).

We also derived an index of matrix dispersal (swimming) capacity for each species based on the number of times it had been observed swimming anywhere on the Balbina Lake. This was based on systematic interviews conducted with all boatmen, sports fishermen, and the Uatumã Reserve surveillance staff at Balbina village who had frequently navigated on the lake. As a precondition, the interviewee had previously navigated on the lake during at least 30 days per year. A total of 49 informants were interviewed from September to December 2012. We presented colour plates and photographs of each species individually, asking if they had ever seen that species traversing between islands or the mainland forest since the lake had been created. Despite observer differences in the number of days per year spent on the lake and the number of years they had been boat-drivers at Balbina, we assumed that all interviewees had the same probability of visually detecting a matrix dispersal event of any given species. Large-bodied species may have been more easily detected than small-bodied species (Pearson r = 0.542 between dispersal index and body mass) but correcting for true detectability is far from straight-forward here. We therefore summed all independently detected swimming events for each species to obtain an index of dispersal capacity over water (mean [SD] = 61.79 [87.06], range = 0-467; Table 5.2).

5.3.5. Data analysis

We adopted two approaches to assess island occupancy for the 34 vertebrate species considered here: [1] *observed site occupancy*, based on the species detected by any of the four sampling techniques during any of the sampling sessions; and [2] *estimated site occupancy*, accounting for imperfect detection predicted by a maximum likelihood hierarchical approach based on the presence/absence data obtained per visit per site. We first performed logistic regression models based on the observed site occupancy as a function of forest area, considering all species together and each species individually, to evaluate the effect of island size on species persistence. Based on these models, we determined a minimum critical threshold of occupancy probability of 0.6 as a function of island size, which enabled us to estimate the proportion of all islands within the reservoir likely to contain any given species.

We then examined the additive effects of other patch, landscape and habitat quality variables, as well as life-history traits on the observed island occupancy. We controlled for high levels of variable inter-dependence by performing a Pearson correlated matrix, retaining non-correlated variables ($r < 0.70$). Because some variables were highly related, we performed stepwise linear regression models to select the best predictors to be included in further analyses. Our full model therefore retained seven patch- and landscape-scale variables (area, isolation, shape, proximity defined as a 500-m buffer, fire severity, percentage of closed-canopy forest and tree basal area bearing fleshy fruits) and five species traits (body mass, group size, home range size, dietary status and dispersal capacity over water). Some of these variables were log-transformed to normalize the data. We then tested for multicollinearity among variables using the Variation Inflation Factor (VIF; Dormann *et al*. 2013) but none of those factors were moderately to highly redundant/collinear (VIF ≤ 3 for all variables). We then performed Generalized Linear Mixed Models (GLMMs) considering all 34 species within 37 islands, with a binomial error structure including the random factor ‘species’ to account for differential species representation within the dataset. Models were fitted using the ‘lme4’ package (Bates 2007) within the R platform, and selected based on a multimodel approach considering a ΔAIC < 2.00 (Burnham & Anderson 2002). Due to the large number of models below the ΔAIC threshold, we obtained model-averaged estimates.

We then used the most significant patch and landscape variables of island occupancy for 37 islands examined in this study to predict the completeness of vertebrate composition for all 3,546 islands across the Balbina reservoir. We assumed that each species is likely to either occupy or temporarily use an island if it meets a minimum local occupancy probability of 60%, based in logistic regression models. We therefore created a presence/absence matrix of islands *versus* 34 species, obtaining the estimate species richness per island by summing all potential presences of all species per forest island. We then performed non-metric multidimensional scaling (NMDS) ordinations for all 3,546 islands using the Bray-Curtis dissimilarity matrix based on qualitative (presence/absence) data, and related the NMDS axes to island area. Finally, we were able to pinpoint priority areas for vertebrate conservation for all islands within the Balbina Hydroelectric Reservoir based on the species richness estimates.

We used a maximum likelihood approach (MacKenzie *et al.* 2002) to obtain the estimated site occupancy and examine the detection probability for each species using the PRESENCE© software (Hines 2006), which computes the proportion of sites occupied accounting for detections probabilities < 1 (*i.e.*, accounting for false absences likely to occur during surveys). We constructed matrices of detections (1) and non-detections (0) for each species per visit per site, using data either combined from the three sampling techniques related to transects (line-transect, sign and armadillo surveys; hereafter, *transect data*) or only camera trapping surveys (hereafter, *CT data*). We opted to separate these two methodological approaches because they diverge markedly in the type of sampling visit. Visits were defined as a single day for transect data and 6 days for CT data, resulting in 8 and 10 visit-sessions, respectively. Each species was then examined using either the transect or CT data, given that some species were either exclusively or most efficiently detected by only one method (e.g. arboreal species during line-transect censuses). For species detected by more than one method, we selected the method providing the highest site occupancy estimates – CT and transect data were used for 18 and 16 species, respectively. Data from all transects and all CTs per island or continuous forest were pooled together per visit. We tested a set of simple models, considering only one landscape structure variable in each model (*i.e.*, the seven non-correlated patch, landscape and habitat quality variables individually) to model site occupancy (Ψ); and including sampling effort according to the method (number of km walked or CT-nights) to model the detection probability (*p*), accounting for potential biases in unequal sampling in different survey sites. We also tested the null model, which assumes constant species presence and detection probability across time and sites [Ψ(.); p(.)]. We used Akaike's Information Criterion (AIC) to rank models and to calculate Akaike weights (Burnham and Anderson 2002) to indicate the best model in the candidate set.

For those species exhibiting high dispersal capacity and large home range sizes, we interpret occupancy estimates as the probability of island use, rather than occupancy probability *per se* (MacKenzie *et al*. 2006; Thornton *et al*. 2011b).

5.4. Results

5.4.1. Forest island occupancy

A maximum of 34 species was recorded considering all 40 survey sites (Table 5.2), including 29 mammal, 4 large terrestrial bird, and two tortoise species (but considered one for the analyses). Appendix 5.3 presents CT photos of some of these species. We failed to record several species which almost certainly occurs in the study area (e.g. *Coendou prehensilis*, *Cyclops didactylus*, *Atelocynus microtis*, *Speothus venaticus*, *Galictis vittata* and *Potos flavus*), but these species are highly inconspicuous and have natural low densities. The 37 islands contained from 0 to 32 species (mean [SD] =14.6 [10.9]), whereas the three continuous forests harboured 33 species each, on the basis of 10,110 independent CT records (mean [SD] = 273.24 [264.6], range = 0-857), 5,765 visual and auditory records from line-transect censuses (mean [SD] = 155.8 [219.8], range = 0-1051); 1,850 sign records (mean [SD] = 50.0 [61.9], range = 0-251); and 427 armadillo burrows (mean [SD] = 14.72 [15.23], range = 0-47). Despite large overall sample sizes, site-specific occupancy rates were low for most species: the overall occupancy matrix for all 37 islands filled only 42.5% of the 1,258 cells, increasing to 46.6% when continuous forest sites were included (Figure 5.2). Species ranged widely in their island occupancy rates, from the most ubiquitous nine-banded armadillo, *Dasypus novemcinctus* (97.3% of islands) to the rare white-lipped peccary, *Tayassu pecari* (8.1% of islands; Fig. 5.2).

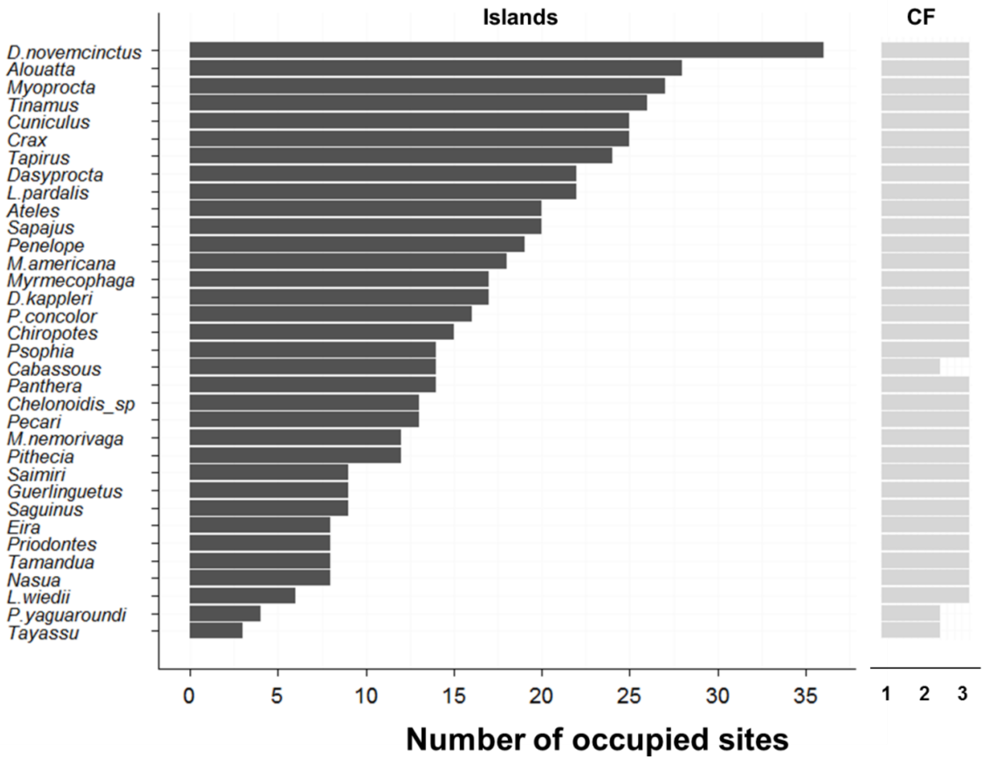

Figure 5.2. Patterns of occupancy for 34 vertebrate species within 37 surveyed islands and three mainland continuous forest (CF) sites surveyed at the Balbina Hydroelectric Reservoir landscape. Species/genus names match those in Table 5.2 and are ordered top to bottom from the most to the least ubiquitous across all forest islands.

Occupancy rates were highly variable but strongly responsive to forest patch area, with all species occupying gradually fewer smaller islands (Figure 5.3). The jaguarundi (*Puma yaguaroundi*) and the white-lipped peccary were the most area-sensitive species, exhibiting low occupancy even in large forest tracts ─ the smallest estimated insular forest patch required to capture a >60% occupancy probability for these species were 1288.2 and 1202.3 ha, respectively (Table 5.2). Conversely, nine-banded armadillos were least area-sensitive, showing a >60% occupancy probability in islands as small as 0.2 ha. Howler monkeys (*Alouatta macconelli*), red acouchi (*Myoprocta acouchy*), lowland paca (*Cuniculus paca*), great tinamou (*Tinamous major*) and black curassow (*Crax alector*) also exhibited high occupancy rates in small islands, with critical island sizes smaller than 10 ha. Considering the species-specific logistic regression models of all species, a minimum forest area of 95 ha would be required to ensure an aggregate 60% occupancy probability for the entire vertebrate assemblage.

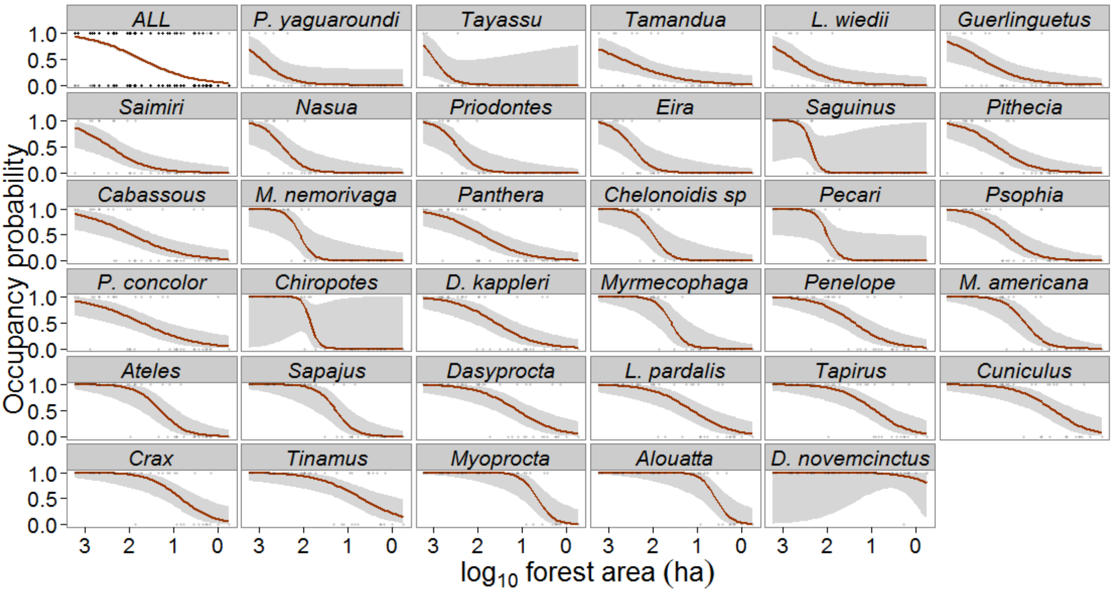

Figure 5.3. Occupancy probability of all 34 vertebrate pooled together ('ALL') and each species individually, as a function of insular forest area, predicted using logistic regression models. Species are ordered left to right and top to bottom according to empirical logistic curves from the most to the least sensitive to forest patch area.

5.4.2. Landscape and life-history predictors of island occupancy

Considering all 34 species within 37 surveyed islands, GLMMs showed that island size, home range size and dispersal capacity were the main predictors of the probability of species occupancy, with the highest relative importance across all variables (Table 5.3). Indeed, species that are adept swimmers with the highest dispersal capacity over open-water had high occupancy rates across islands ($R^2 = 0.255$, $P = 0.005$), but species using larger home ranges showing the most negative residuals in this relationship (Figure 5.4). Other significant variables identified in the averaged model included the patch SHAPE and PROXIMITY to other land masses.

Table 5.3. Summary of Generalized linear mixed models (GLMMs) showing the predictors of overall patterns of 34 vertebrate species occupancy within 37 forest islands at BHR and their relative importance. Model-averaged coefficients are presented. Significant variables are indicated as: ***$p \le 0.001$; **$p \le 0.01$; *$p \le 0.05$. See text for details of each variable.

Predictor	Estimate	Standard Error	z-value	Confidence Interval	Relative Importance
Intercept***	-5.820	1.423	4.091	(-8.609; -3.031)	
AREA***	2.816	0.240	11.744	(2.346; 3.286)	1.00
ISOLATION	0.292	0.152	1.916	(-0.007; 0.590)	0.70
SHAPE***	23.330	7.316	3.189	(8.991; 37.668)	0.99
PROXIMITY*	0.208	0.094	2.222	(0.024; 0.392)	0.85
BURN	-0.173	0.165	1.051	(-0.496; 0.150)	0.39
CC%	-0.004	0.007	0.586	(-0.0189; 0.010)	0.30
BA$_{ff}$	0.058	0.088	0.655	(-0.115; 0.231)	0.33
BODY MASS	0.320	0.618	0.518	(-0.891; 1.531)	0.29
GROUP SIZE	-0.540	0.416	1.297	(-1.356; 0.276)	0.45
HOME RANGE SIZE***	-1.204	0.298	4.043	(-1.788; -0.620)	1.00
DIET CATEGORY	0.202	0.199	1.014	(-0.188; 0.593)	0.37
DISPERSAL ABILITY***	1.466	0.398	3.683	(0.686; 2.246)	1.00

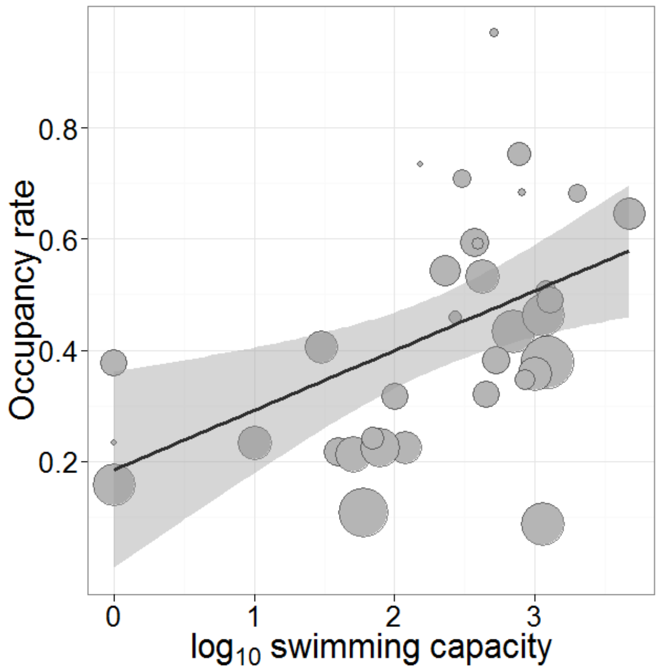

Figure 5.4. Relationship between dispersal (swimming) capacity over open-water and site occupancy rate for 34 forest vertebrate species recorded at 37 surveyed islands. Circles sizes are proportional to an estimate of home range of each species.

Given data from 37 islands, we were able to estimate species-specific vertebrate occupancy rates based on logistic regression models in relation to island area, since this was the most important predictor of species occupancy for most species. We therefore obtained the estimate species composition and richness, for the entire Balbina archipelago of 3,546 islands. This species occupancy data filled 19.42% of the overall presence-absence matrix (34 species • 3,546 islands), with a mean of ~7 species persisting in each island. The first axis of the NMDS shows the strong area effects on species composition (Fig. 5.5). We thus identified priority islands for conservation based on the species richness estimation, demonstrating that most of islands are likely to harbour a low number of vertebrate species (Fig. 5.6).

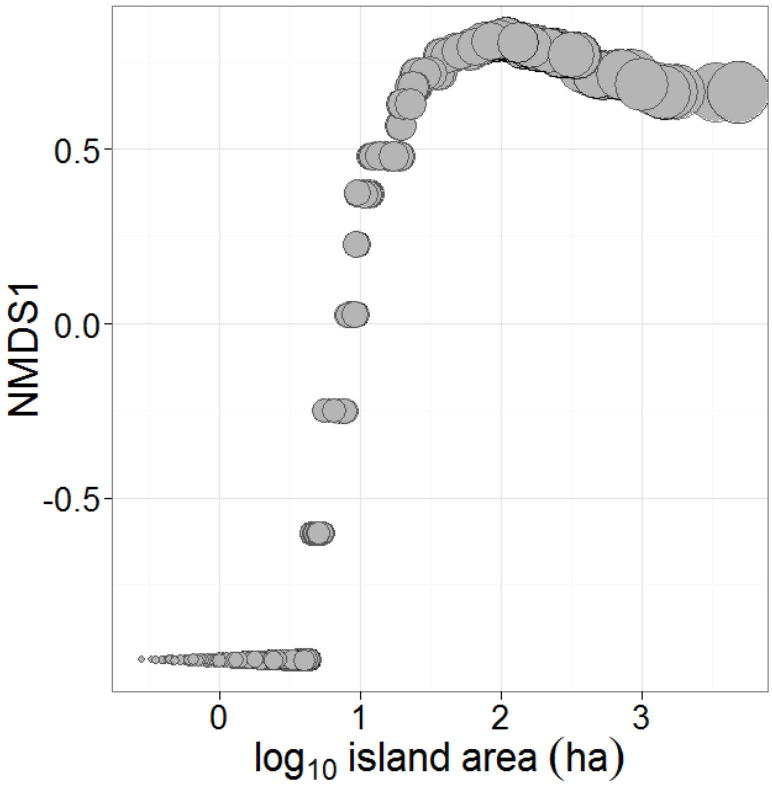

Figure 5.5. Nonmetric multidimensional scaling (NMDS) ordination of vertebrate species occupancy predicted for all 3,546 islands within the BHR landscape on the basis of logistic regression models in relation to island area.

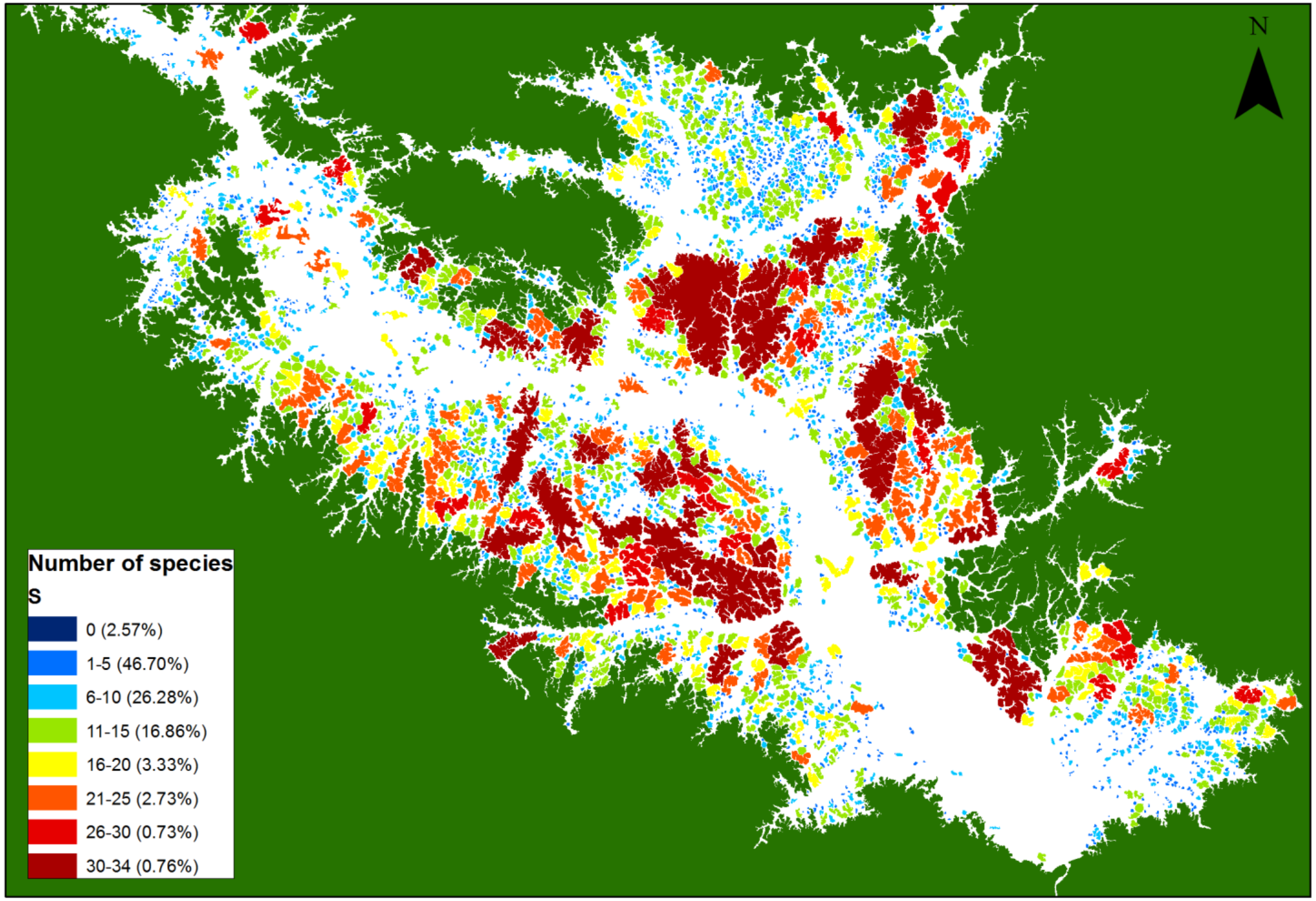

Figure 5.6. Priority areas for vertebrate conservation action based on the estimated species composition for all islands in the Balbina Hydroelectric Reservoir on the basis of species-specific logistic regression equations. All islands were assumed to be 'occupied' by any given species if their occupancy probability was equal to or exceeded 60% for that species.

When species were analysed individually accounting for imperfect detection, forest patch area was by far the best predictor of site occupancy for most of the species: 83% of 29 species for which the variance-covariance matrix could be adequately estimated included AREA in their best model (Table 5.4). PROXIMITY was the second best predictor among seven patch, landscape and habitat quality variables, appearing in the top model for lowland paca, great tinamou and jaguar (*Panthera onca*), and in the second best model for tapir (*Tapirus terrestris*). The percentage of closed-canopy forest was included in the best model for nine-banded armadillo, whereas the basal area of trees bearing fleshy fruits was included in the top ranking model explaining the occupancy of white-lipped peccary. Occupancy estimates from the maximum likelihood approach differed from those based on site-scale sampling surveys for 10 species. Detectability varied greatly among species, with red acouchi and grey-winged trumpeter (*Psophia crepitans*) showing the highest detection probability (p = 0.91) across all sites, whereas southern naked-tailed armadillo (*Cabassous unicinctus*) and jaguarundi showed the lowest detection probabilities (p = 0.07). Models for three armadillo species (southern naked-tailed; greater long-nosed, *Dasypus kappleri*; and giant armadillo, *Priodontes maximus*), and two anteaters (giant anteater, *Myrmecophaga tridactyla* and southern tamandua, *Tamandua tetradactyla*) yielded poor parameter estimates and the variance-covariance matrix could not be successfully calculated.

Table 5.4. The best models and parameter estimations of occupancy and detectability for 34 vertebrate species predicted by maximum likelihood hierarchical approach (accounted for imperfect detection) within 40 forest sites examined in this study.

				Best model(s)[1]			
Species	**Observed occupancy**	**Estimated occupancy (Ψ)[2]**	**Mean detection probability (*p*)[2]**	**Models**	**AIC**	**ΔAIC**	**Weight**
Mammals							
Alouatta macconelli	0.77	0.77	0.78	Ψ (area); *p* (effort)	232.72	0.00	0.99
Ateles paniscus	0.57	0.57	0.54	Ψ (area); *p* (effort)	247.27	0.00	1.00
*Cabassous unicinctus**	0.40	0.40	0.07	-			
Chiropotes sagulatus	0.45	0.45	0.50	Ψ (area); *p* (effort)	201.35	0.00	1.00
Cuniculus paca	0.70	0.70	0.54	Ψ (prox); *p* (effort)	364.30	0.00	0.79
Dasyprocta leporina	0.62	0.62	0.58	Ψ (area); *p* (effort)	248.61	0.00	0.96
*Dasypus kappleri**	0.50	0.50	0.21	-			
Dasypus novemcinctus	0.97	0.97	0.67	Ψ (closed-canopy); *p* (effort)	483.07	0.00	0.75
Eira barbara	0.27	0.30	0.21	Ψ (area); *p* (effort)	139.87	0.00	0.75
Guerlinguetus aestuans	0.30	0.37	0.18	Ψ (area); *p* (effort)	134.46	0.00	0.93
Leopardus pardalis	0.62	0.62	0.41	Ψ (area); *p* (effort)	329.51	0.00	0.74
Leopardus wiedii	0.22	0.26	0.17	Ψ (area); *p* (effort)	111.08	0.00	0.43
Mazama americana	0.52	0.52	0.53	Ψ (area); *p* (effort)	194.43	0.00	0.99
Mazama nemorivaga	0.37	0.37	0.46	Ψ (area); *p* (effort)	186.80	0.00	0.97
Myoprocta acouchy	0.75	0.75	0.91	Ψ (area); *p* (effort)	154.15	0.00	1.00
*Myrmecophaga tridactyla**	0.50	0.54	0.20	-			
Nasua nasua	0.22	0.25	0.20	Ψ (area); *p* (effort)	115.73	0.00	0.99
Panthera onca	0.42	0.52	0.11	Ψ (prox); *p* (effort)	139.08	0.00	0.80
Pecari tajacu	0.40	0.40	0.62	Ψ (area); *p* (effort)	171.02	0.00	1.00
Pithecia chrysocephala	0.37	0.42	0.25	Ψ (area); *p* (effort)	169.37	0.00	0.99
*Priodontes maximus**	0.27	0.27	0.19	-			
Puma concolor	0.47	0.47	0.28	Ψ (area); *p* (effort)	249.20	0.00	0.96
Puma yaguaroundi	0.15	0.30	0.07	Ψ (area); *p* (effort)	66.78	0.00	0.84

Saguinus midas	0.30	0.30	0.71	Ψ (area); *p* (effort)	124.65	0.00	1.00
Saimiri sciureus	0.30	0.30	0.45	Ψ (area); *p* (effort)	159.56	0.00	0.81
Sapajus apella	0.57	0.57	0.78	Ψ (area); *p* (effort)	194.50	0.00	1.00
Tamandua tetradactyla[*]	0.27	0.38	0.08	-			
Tapirus terrestris	0.65	0.65	0.44	Ψ (area); *p* (effort)	359.80	0.00	0.60
				Ψ (prox); *p* (effort)	360.65	0.85	0.39
Tayassu pecari	0.12	0.12	0.29	Ψ (basal area); *p* (effort)	52.99	0.00	0.37
				Ψ (area); *p* (effort)	54.52	1.53	0.17
				Ψ (closed canopy); *p* (effort)	54.93	1.94	0.14
Birds							
Crax alector	0.70	0.70	0.53	Ψ (area); *p* (effort)	367.73	0.00	0.94
Penelope marail	0.55	0.58	0.31	Ψ (area); *p* (effort)	225.61	0.00	0.95
Psophia crepitans	0.42	0.42	0.91	Ψ (area); *p* (effort)			
Tinamus major	0.72	0.72	0.46	Ψ (prox); *p* (effort)	372.59	0.00	0.74
Reptiles							
Chelonoidis spp.	0.40	0.40	0.41	Ψ (area); *p* (effort)	181.06	0.00	0.98

[1] AIC, Akaike Information Criteria; ΔAIC, difference between the model with the lowest AIC and the given model. Only models with ΔAIC ≤ 2.00 are shown.

[2] Estimated proportion of forest sites occupied and estimated probability of detection provided by the null model.

* The variance-covariance matrix could not be calculated successfully.

5.5. Discussion

A number of studies have addressed large-bodied terrestrial vertebrate populations in fragmented tropical forest landscapes (Michalski & Peres 2005; Urquiza-Haas *et al.* 2009; Sampaio *et al*. 2010; Thornton *et al.* 2011a,b; Canale *et al*. 2012). However, these study areas are dominated by a terrestrial vegetation matrix of varying degrees of permeability as there are few opportunities to examine faunal assemblages in truly archipelagic landscapes where insular forest remnants are isolated by a uniform matrix of open freshwater. Large hydroelectric dams may severely degrade both terrestrial and aquatic ecosystems of major river basins, but provide near ideal experimental landscapes that effectively control for the effects of matrix type and isolation history of habitat remnants (Cosson *et al.* 1999). Yet vertebrate studies in hydroelectric reservoirs usually document population outcomes within the first few years of inundation (e.g. Cosson et al. 1999; Terborgh *et al*. 2001; Daleck *et al*. 2002). To our knowledge, this is the first study examining how terrestrial and arboreal vertebrate populations have responded to a >25-year history of alteration in landscape structure and habitat quality by a major hydroelectric reservoir in a tropical forest region.

5.5.1. Drivers of local extinctions

Understanding the main drivers of species extinctions in human-modified landscapes has been a central pursuit of conservation biologists. Habitat area effects have been consistently identified as the main predictors of bird and mammal occupancy in tropical forest remnants (Ferraz *et al*. 2007; Gibson *et al*. 2013; Benchimol & Peres 2013; Benchimol & Venticinque 2014). However, other features of the patch and surrounding landscape — including the nature of neighbouring habitats (Andrén 1994, Prugh *et al*. 2008), patch habitat quality (Michalski & Peres 2005; Holland & Benett 2009; Wang *et al*. 2010) and human disturbances (Michalski & Peres 2005; Sampaio *et al.* 2010; Thornton *et al*. 2011b; Canale *et al.* 2012) — have been frequently indicated as strong predictors of species loss across multiple landscapes. Additionally, species life-history attributes have contributed to predict vertebrate species susceptibility to extinction in Neotropical forest remnants (Lees & Peres 2008; Meyer *et al.*

2008; Urquiza-Haas *et al*. 2009; Thornton *et al*. 2011a; Benchimol & Peres 2014). We therefore attempted to consider both intrinsic and extrinsic factors to elucidate the main drivers of local extinctions of midsized to large vertebrate species within forest islands embedded within an open-water matrix.

Considering all 12 explanatory variables, patch and life-history variables were the only significant predictors of local persistence of vertebrate populations across all 37 variable-sized islands. Specifically, island forest area, home range size and capability of matrix dispersal of vertebrate species were the strongest predictors, attaining the maximum relative importance among all variables. Indeed, the Balbina islands exhibit extremely powerful species-area relationships (SARs), a resounding endorsement of MacArthur & Wilson's (1967) island biogeography theory. Clearly positive SARs have been observed for small mammals, bats, primates and birds in artificial land-bridge island systems worldwide (Yu *et al*. 2012; Benchimol & Peres 2013; Gibson *et al*. 2013; Benchimol & Venticinque 2014; Mendenhall *et al*. 2014). Island occupancy was also a function of individual species traits, with wide-ranging species and poor swimmers showing evidence of high local extinction rates, low recolonization rates, or both (cf. Dale *et al*. 1994). In Amazonian fragmented forest landscapes, large mammals exhibiting large spatial requirements are highly vulnerable to extinction in small fragments (Timo 2003; Michalski & Peres 2005). Likewise, home range size has been singled-out as a key predictor of primate occupancy across 705 Neotropical forest fragments nested within 61 landscapes (Benchimol & Peres 2014). We also show that species that are more adept at matrix movements (through greater inherent swimming capacity) occupied more islands. Water is widely considered an effective barrier to terrestrial vertebrate dispersal (Cosson *et al*. 1999), but our results show that some species frequently could traverse great distances across this hostile matrix. For instance, tapirs (*Tapirus terrestris*) were observed swimming between islands more than 450 times, which corroborates genetic analyses showing high levels of gene flow within a single tapir population across the entire post-damming Balbina landscape (Pinho *et al*. 2014). At Lago Guri, Venezuela, even the most remote islands isolated by several kilometres were inhabited by capybaras (Terborgh et al. 1997) which are renowned for their long-distance swimming capability. In entirely terrestrial landscapes, species persistence in isolated forest patches is also strongly associated with their ability to traverse, if not exploit, the vegetation matrix (Gascon 1999; Michalski & Peres 2005; Lees & Peres 2009), which is consistent with our results in an archipelagic landscape.

5.5.2. Species-specific patterns of sensitivity

Although occupancy rates ranged widely across forest vertebrate species at Balbina, forest area was the most important predictor of local extinction, appearing in the best model of 24 of the 29 species for which it was possible to account for imperfect detection (Table 5.4). We can therefore distinguish three classes of species according to island size: (a) area-insensitive species, showing >60% occupancy probability even in islands smaller than 12 ha ─ nine-banded armadillo, howler monkey, red acouchi, great tinamou, black curassow, lowland paca and tapir; (b) moderately sensitive species, requiring islands larger than 20 ha but smaller than 80 ha to exhibit a 60% occupancy probability ─ ocelot, red-rumped agouti, brown capuchin monkey, spider monkey, marail guan, red brocket deer, giant anteater, greater long-nosed armadillo and bearded saki; and (c) area-sensitive species, which required more than 95 ha to show a >60% occupancy probability ─ puma, grey-winged trumpeter, collared peccary, tortoises, jaguar, brown brocket deer, southern naked-tailed armadillo, golden-faced saki, golden-handed tamarin, giant armadillo, tayra, South American coati, squirrel monkey, Brazilian squirrel, margay, southern tamandua, white-lipped peccary and jaguarundi. For five species, however, other variables were better predictors of persistence in islands: the importance of land mass proximity exceeded that of patch area for jaguar, lowland paca and great tinamou; whereas closed-canopy forest and basal area of trees bearing fleshy fruits were the best predictors for nine-banded armadillo and white-lipped peccary, respectively. Because jaguars have large spatial requirements, they typically occupy sufficiently accessible small islands as transients rather than as full-time residents. For instance, the species was absent from medium-sized islands at Lago Guri, following a short isolation time (Terborgh *et al*. 2001). Our interviews and field surveys show that jaguars are excellent swimmers and regularly trapline neighbouring islands, with large, poorly isolated islands most likely to be used by this threatened species. Additionally, other adept swimmer species, including tapir, puma, giant anteater and even large ground-dwelling birds, can be considered transients rather than true residents at Balbina (cf. Cosson *et al.* 1999).

The most ubiquitous species — nine-banded armadillo — occurred in all 40 surveyed sites, except for a single island consisting of scrub and lacking a tree canopy. Even tiny islands were large enough to retain this species, provided they remain forested, mirroring small forest patches in other landscapes (Michalski & Peres 2007; Urquiza-Haas *et al.* 2009; Thornton *et al.* 2011a). Although white-lipped peccary exhibited high dispersal capacity in the Balbina Lake, their large herds require vast forest areas that are sufficiently productive in terms of concentrations of large-seeded trees (Keuroghlian *et al.* 2004; Tobler *et al.* 2009). Unsurprisingly, basal area fleshy-fruiting trees was the most important predictor of white-lipped peccary occupancy.

In contrast to other Neotropical fragmentation ecology studies in terrestrial landscapes (Estrada *et al.* 1994; Michalski & Peres 2005; Sampaio *et al*. 2010; Thornton *et al.* 2011a; Canale *et al.* 2012), we detected an overall greater habitat area effect on local extinctions of mid- to large-sized vertebrate species. However, sufficiently large Balbina islands and mainland sites retained a larger proportion of species than that reported in those studies, which can be explained by the absence of some negative extrinsic factors, such as hunting pressure, at Balbina. Additive mortality induced by hunters accelerates local extinction rates of large-bodied vertebrates in tropical forest fragments (Peres 2001), often overriding the effects of fragment size on vertebrate species persistence (Thornton *et al.* 2011b; Canale *et al.* 2012). Comparing occupancy rates of forest ungulates, which are widely exploited by subsistence hunters, between Balbina and a set of 50 overhunted forest patches in northern Guatemala (Thornton *et al*. 2011a), reveals clear differences in estimated site occupancy of fragments of approximately the same age (30 years; see Appendix 5.4). In Guatemala, fragments were also well surveyed using both camera trapping and visual censuses surveys, and patch occupancy estimates also accounted for imperfect detectability; these differences are almost certainly related to hunting pressure and matrix type. Water is a much more hostile matrix movements of cursorial species compared to terrestrial landscapes embedded within a matrix of secondary forest, pasture and cropland. Likewise, other game species exhibited higher levels of island occupancy compared to forest patches intensively hunted elsewhere in the Neotropics. Large bodied-primates are often extirpated in hunted forest patches (Sampaio *et al.* 2010; Canale *et al.* 2012; Benchimol & Peres 2014) whereas the largest primates in Balbina (howler monkey, spider monkey, and brown capuchin monkey) showed the highest levels of occupancy (Benchimol & Venticinque 2014). Large game birds also showed high occupancy rates compared to their congeners in a densely settled forest landscape in southern Mexico (Urquiza-Haas *et al*. 2009), and in a fragmented landscape of northern Guatemala (Thornton *et al.* 2012). Tortoises, which are frequently consumed by local communities (Souza-Mazureck 2000), were detected in 13 of 37 islands.

Dasyproctids (agouties and acouchies) only occurred in islands larger than 10 ha at Balbina, a pattern observed in other land-bridge archipelagos (Asquith *et al*. 1997; Terborgh *et al*. 2001; Daleck *et al*. 2002). However, this is at odds with the Biological Dynamic Forest Fragment Project (BDFFP) where agoutis occur in ~1-ha forest fragments, which again is likely related to a matrix dominated by young second-growth (Jorge 2008). The three largest carnivore species ─ jaguar, puma and ocelot ─ also showed high island occupancy rates compared to forest patches at other Neotropical fragmented landscapes (Estrada *et al.* 1994; Michalski & Peres 2005; Thornton *et al*. 2011a), which is presumably related to their adept locomotion in water. We therefore surmise that — compared to hunted, terrestrial landscapes elsewhere — the absence of hunting pressure elevates the intercept, and the uniform aquatic matrix increases the slope, of the large vertebrate SAR at Balbina because of the twin processes of local extinction and recolonization of forest patches.

As a cautionary note, the high observed occupancy rates for most vertebrate species examined in this study masks a cryptic local extinction debt as many resident (meta)populations appear to be too small and will likely fail to persist in most islands in the long-term. Small populations combined with edge effects, stochastic disturbance events, and imbalances in trophic cascades render forest isolates extremely vulnerable to further biodiversity loss (Terborgh *et al*. 2001; Laurance *et al.* 2011), even if they remain effectively protected against human perturbation. Indeed, edge effects are a powerful driver of non-random floristic transitions in forest islands within the Balbina archipelago (Chapter 4) and a single convective windstorm event led to the complete canopy implosion of a 6.1-ha island, resulting in the extirpation of the only remaining howler monkey group (M.B., *pers. obs.*). We therefore encourage follow-up studies to better understand the long-term viability of vertebrate populations stranded on islands created by large dams.

5.6. Conservation Implications

The increasingly capitalized Brazilian government has been investing heavily in the hydropower infrastructure of the national grid to provide cheap energy for urban and industrial development. This sector is expected to increase in the near future – a total of 154 hydroelectric dams currently operate in the Amazon, 21 are under construction, and a further 277 are on the brink of approval (Castello *et al*. 2013). Understanding the long-term impacts of major dams on forest biodiversity and designing strategies to mitigate their detrimental impacts are a critical policy priority. Given data from 37 islands, we were able to estimate species-specific vertebrate occupancy rates, and therefore the species composition and richness, for the entire Balbina archipelago of 3,546 islands. This scaling-up scenario represents a gloomy outcome in that the species occupancy data filled less than one-fifth (19.42%) of the overall presence-absence matrix (34 species • 3,546 islands. Worse still, fewer than 2% of all islands are likely to harbour at least 26 vertebrate species (Fig. 5.6). This suggests that even in the context of a strictly-protected Biological Reserve, the vast majority of islands formed by the dam cannot ensure the local persistence of even a modest fraction of the original mid- and large-sized vertebrate fauna.

Simply put, Balbina and many other planned or under-construction major dams in lowland Amazonia still target relatively flat terrains with a moderately dissected topography, which apart from a highly undesirable inundated area to hydropower output ratio, creates vast shallow lakes favouring the formation of myriad small islands (Fearnside 1995, 2014). Likewise, the Tucuruí Hydroelectric Dam of eastern Amazonia also created a large shallow lake containing 2,200 variable-sized but increasingly degraded islands (Ferreira *et al.* 2012). Hence, pharaonic hydropower project blueprints appear to experience a similar fate: creation of vast archipelagos of small islands that are unlikely to retain a legacy of most of the biota from once continuous forests. Policy-makers and hydropower engineers should thus explicitly consider the overall topography of planned reservoirs to both maximise landscape connectivity resulting from legally approved dams or reject plans targeting unfavourable river basins ─ those ones located in lowland forests that will create shallow reservoirs and therefore large number of small islands.

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CHAPTER 6

WIDESPREAD FOREST VERTEBRATE EXTINCTIONS INDUCED BY A MEGA HYDROELECTRIC DAM IN LOWLAND AMAZONIA

Islands within the Balbina Hydroelectric Reservoir and some of the animals recorded in this study. Photo by E.M. Venticinque (aerial picture), M. Benchimol (anteater) and camera traps from this study (ocelot and collared peccary).

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6.1. Abstract

Mega hydropower projects in tropical forests pose a major emergent threat to both terrestrial and freshwater biodiversity worldwide. Despite the unprecedented number of existing, under-construction or planned hydroelectric dams in the Amazon, long-term effects on forest biodiversity have yet to be evaluated. Here, we examine how medium and large-bodied assemblages of terrestrial and arboreal vertebrates (including 35 mammal, bird and tortoise species) responded to the drastic 26-year post-isolation history of alteration in landscape structure and habitat quality in a major hydroelectric reservoir of lowland Central Brazilian Amazonia. The Balbina Dam inundated 3,129 km^2 of primary forests, subsequently converted into an archipelago of 3,546 land-bridge islands. We conducted intensive biodiversity surveys at 37 of those islands and three continuous forest sites using a combination of four sampling techniques, and detected strong forest habitat area effects in explaining patterns of vertebrate extinction. Over and above clear habitat-area effects, fire severity was the most important additional driver of species loss, particularly in islands smaller than 10 ha. Based on species-area models, we predict that only 0.7% of all islands are likely to harbour a species-rich vertebrate assemblage (≥80% of all species). We therefore highlight the colossal erosion in vertebrate diversity driven by a man-made dam and show that the biodiversity impacts of mega dams have been severely underestimated. The geopolitical strategy to deploy many large hydropower infrastructure projects in regions like lowland Amazonia should be urgently reassessed, and we strongly advise that long-term biodiversity impacts should be explicitly included in pre-approval environmental impact assessments.

6.2. Introduction

Hydroelectric dams are rapidly emerging as the new villain in the myriad of anthropogenic threats to tropical forest biotas. Dams displace indigenous communities (Esselman & Oppermann 2010), disrupt the natural flow of rivers (Bednarek 2001), critically affect fish populations (Ziv *et al.* 2012), release vast amounts of greenhouse gases (Fearnside & Pueyo 2012), and promote wholesale deforestation and fragmentation of pristine forests (Finer & Jenkins

2012). From China to Brazil, hydroelectric dams have been built at an unprecedented scale to supply burgeoning energy demands (Ansar *et al.* 2014). More than 945,000 dams higher than 15 m have been built worldwide, altering >50% of all large rivers (Nilsson *et al.* 2005). In South America alone, some 2,215 new hydropower projects are expected to be erected within the next few years (Kareiva 2012). Assessing the true impacts of hydropower infrastructure on natural ecosystems has therefore become an urgent priority for the policy agenda of many countries.

In Brazilian Amazonia, over 10 million ha of forests are expected to become permanently inundated following the planned construction of new dams (Fearnside 2006), potentially leading to a colossal impact on both terrestrial and aquatic biotas at regional scales. Hydroelectric dams in lowland forests typically resort to low-declivity river basins, thereby submerging vast upland areas per unit of megawatt output generated, which often creates enormous archipelagos of forest isolates. Land-bridge islands formed within these artificial lakes may experience stronger isolation effects than equivalent forest remnants embedded within a terrestrial landscape, largely because the open-water matrix is almost invariably less porous to terrestrial organisms than pastures and second-growth vegetation (e.g. Cosson *et al.* 1999; Emer *et al*. 2013; Mendenhall *et al*. 2014). However, despite an embryonic number of studies investigating the long-term impacts of major dams on biodiversity (Meyer & Kalko 2008; Yu *et al.* 2012; Gibson *et al*. 2013), the extinction dynamics of archipelagic landscapes created by hydroelectric reservoirs remains poorly understood in tropical forests.

Terrestrial vertebrates are pivotal components of tropical forest dynamics through their ecological roles as hyper-consumers, large predators, frugivores, seed dispersers, and structural habitat modification (Terborgh 1992). They are also widely hailed as pinnacle conservation icons, contributing with public charisma for tropical forest conservation. In Amazonia, hunting pressure is the strongest driver of local extinctions of medium and large mammals stranded in fragmented landscapes (Michalski & Peres 2005; Sampaio *et al*. 2010). With the exception of primates (Benchimol & Venticinque 2014), no study has assessed the long-term impacts of a hydroelectric reservoir on medium and large vertebrates in Amazonian land-bridge islands. Yet this is required to both elucidate the positive or negative effects of dams on biodiversity, and refine environmental impact assessments of future dams.

Here, we provide the first assessment of how medium- and large-bodied arboreal and terrestrial vertebrate assemblages (including mammals, birds and testudine reptiles) responded to the drastic 26-year post-isolation history of alteration in landscape and habitat quality by a mega hydroelectric dam in Central Brazilian Amazonia. The notorious Balbina Dam inundated 3,129 km^2 of primary forests, which were subsequently converted into an archipelago of 3,546 islands. Using a combination of four complementary sampling techniques, we conducted quantitative faunal surveys at 37 pre-selected islands and three mainland forest sites to examine how patterns of species persistence are related to habitat quality, forest patch and landscape metrics. We document the extent of local vertebrate extinctions within islands, build a model to predict extinction rates in unsurveyed islands, and identify priority areas for vertebrate conservation within the reservoir. This study serves a critical policy role at a time of greatly augmented investments in hydropower development in Amazonia in informing the scientific community and the wider public about the detrimental impacts of major dams on forest biodiversity.

6.3. Methods

6.3.1. Study sites

Following the completion of the Balbina Hydroelectric Dam in October 1986, a reservoir area of 4,437 km^2 was formed, comprising over 3,500 variable-sized land-bridge islands. To offset the forest habitat loss, the reservoir and adjacent mainland continuous forests was effectively protected from 1990 with the creation of the REBIO Uatumã, the largest Biological Reserve in Brazil. Due to the homogeneous habitat matrix and isolation time, major hydroelectric lakes are excellent island biogeography experimental landscapes with multiple land masses isolated simultaneously (Diamond 2001; Wu *et al.* 2003; Gibson *et al.* 2013). The Balbina Hydroeletric Reservoir (BHR) has several advantages compared to other archipelagic and terrestrial fragmented landscapes, including a long-term relaxation time, a large number of replicates, and effective protection from anthropogenic disturbance, including logging and hunting (Benchimol & Venticinque 2014). However, ephemeral understorey fires accidentally affected much of the BHR area during the severe drought of late 1997 to early 1998.

We used two cloudless georeferenced 30-m resolution Landsat ETM+ images (230/061 and 231/061; year 2009) to carefully pre-select 37 forest islands, which ranged in size from 0.83 to 1690 ha, to be surveyed on the basis of their size, degree of isolation and spatial distribution within the reservoir (Appendices 6.1 and 6.2). We also selected three widely distributed ‘pseudo-control’ continuous forest sites (CFs) in the adjacent mainland area. Surveyed islands and mainland sites, which spanned a study area of ~3,964 km^2, were spaced by at least 1 km from one another to maximise spatial independence.

5.3.2. Vertebrate surveys

Between June 2011 and December 2012, we surveyed midsized to large terrestrial and arboreal vertebrate species that are amenable to at least one of four sampling techniques (line-transect censuses, indirect sign surveys, armadillo surveys and camera trapping). We first listed all forest vertebrate species >100g expected to occur in the entire study landscape, based on field guides (e.g. Eisenberg & Redford 1989; Emmons & Feer 1990), IUCN range polygons (2008) and our own extensive personal knowledge, including previous studies at Balbina. These included 35 species: seven primate, seven carnivore, six xenarthran, five ungulate, four rodent, four large terrestrial bird, and two tortoise species (Appendix 6.3), excluding semi-aquatic species such as capybara (*Hydrochoerus hydrochaeris*) and Neotropical otter (*Lontra longicaudis*), and the highly elusive small-eared fox (*Atelocynus microtis*). One to five variable-length transects were thus cut within each island, according to their size and shape so that a representative island area could be covered (Appendix 6.1). On each CF, we established three parallel 4-km linear transects, separated from each other by 1 km (Appendix 6.2).

Line-transect surveys consisted of quiet walks conducted by two previously trained observers at a constant speed (~1.0 km/h) following a standardized protocol (Peres 1999). Surveys were carried out in the morning (06:15-10:30) and afternoon (14:00-17:30), and were discontinued during rainy periods. We conducted eight line-transect surveys on each sampling site at different hours, separated by at least 30-day intervals, minimising possible effects of time of day and seasonality. On return walks, we also conducted sign surveys. All signs of vertebrate activity (tracks, digging, feces, hair, burrows and partly consumed fruits) were searched along the transect, and species identification recorded. Whenever signs of the same species were encountered, we considered a minimum distance of 500-m for signs to be defined as spatially independent. Armadillo burrows deeper than 50 cm encountered within a distance of 5m from each transect were searched and recorded only once, and measured following Michalski & Peres (2007). We used Reconyx HC 500 Hyperfire digital camera traps (hereafter, CTs) to complement our vertebrate surveys. All CT stations at each forest site were sampled for a 30-day period during two consecutive years (2011 and 2012). We deployed two to ten CTs at each island (mean [SD] = 4.38 [3.21], according to island size, and 15 CTs at each continuous forest site ─ five on each transect (Appendix 6.1). CTs were unbaited, spaced by at least 500 m (except for small islands), and placed 30-40 cm above ground. We configured each CT to obtain a sequence of five photos for each animal record, using 15 sec intervals between records. However, we considered records of the same species to be independent if intervals between photos exceeded 30 min, or if different individuals could be recognized. During periods of CT surveys at any forest site, we did not conduct any other sampling technique. In total, 81 transects of lengths ranging from 0.5 to 4.0 km (mean [SD] = 2.71 km [3.32], total = 108.5 km) were implemented, amounting to a total effort of 1,168 km walked during line-transect surveys; 1,168 km during sign surveys; and 108.5 km during armadillo-burrow census. We obtained a total of 12,420 CT-days (mean [SD] = 310.5 [251.83], range = 120-900 CT days/site) from 207 CT stations (Appendix 6.1).

6.3.3. Forest patch, landscape, and habitat quality metrics

We adopted a patch-landscape approach (McGarigal & Cushman 2002), surveying focal patches but including variables at both patch and landscape scales in the analysis. We used high-resolution multi-spectral RapidEye$^{©}$ imagery to extract patch and landscape variables. RapidEye consists of a constellation of five identical satellites producing 5-m resolution with 5-band colour imagery. We selected tile images on the basis of low cloud cover (<10%) and from months matching our field sampling. A total of 28 different tiles from March 2011 to September 2012 were used, covering an area of 6,980 km^2. Using ArcMap (version 10.1), we then conducted a semi-supervised classification to obtain four land cover classes (closed-canopy forest, open-canopy forest, bare ground, and water). At the patch scale, we calculated island area, forest area (excluding bare ground), closed-canopy forest area, nearest distance to a continuous forest site, and island shape (perimeter:area ratio). These patch metrics were obtained for all 3,546 islands of the reservoir, including both surveyed and unsurveyed islands. At the landscape scale, we considered multiple buffers (250m, 500m and 1000m) outside the perimeter of each island and mainland forest sites and quantified the percentage of both total forest cover and closed-canopy forest within the buffer, and modified the proximity index of McGarigal *et al.* (2012) by considering the total size of any land mass within the buffer, rather than excluding land areas outside the buffer for patches contained within the buffer (see Table 5.1 in Chapter 5 for details). Within each forest site, we calculated the percentage of closed-forest canopy, a measure of fire severity (defined as a composite ordinal score based on the extent of each forest site affected by surface fires and the number of charred trees and char height marks on each tree), and the aggregate basal area of all trees ≥10 cm dbh [diameter at breast height] bearing fleshy fruits (based on 87 quarter-hectare forest plots inventoried at all forest sites [see Chapter 4 for details]).

5.3.4. Data analysis

We analysed all occupancy data in terms of species presence/absence (P/A). All four sampling techniques at the 40 sites surveyed recorded a total of 35 midsized and large vertebrate species (Appendix 6.3), on the basis of 5,765 visual and acoustic line-transect census records (mean [SD] = 155.8 [219.8], range = 0-1051); 1,850 sign records (mean [SD] = 50.0 [61.9], range = 0-251); 427 armadillo burrows (mean [SD] = 14.72 [15.23], range = 0-47); and 10,110 independent camera trapping records (mean [SD] = 273.24 [264.6], range = 0-857). Combining all four sampling methods, we then constructed three P/A matrices including all 35 species, initially considering all 40 forest sites, and then disaggregated the data at the scales of either 217 transect segments of 500m (in the case of line-transect censuses, sign surveys and armadillo surveys) or the 207 camera trapping stations.

We defined a species as ‘present’ at the scales of site, transect segment, or CT station if it appeared at least once during any of eight census repeats for both line-transect and sign surveys, or during either one of the two annual 30-day CT sessions per CT station. Because several species could be detected by more than one sampling technique, we then investigated which technique best detected each species, by comparing the species-specific proportions of occupied sites per technique. This allowed us to estimate the species richness and composition at the sub-patch scale, while considering only the most efficient census technique for each species. We then summed all means and standard deviations (SD) provided by each technique per forest site, to further obtain an aggregate mean (SD) species richness per forest site considering all four sampling techniques. We therefore obtained two species richness estimates: the total number of species, defined as the sum of all species recorded at each site regardless of sampling technique; and the summed mean (SD) number of species per technique, defined as the sum of the mean number of species, each of which assigned exclusively to its ‘best’ sampling technique. We then used a random resampling approach to examine species–area relationships on the basis of a standardized census effort at all sites in terms of species richness per either 500-m segments or individual CT stations. This was based on a jacknife procedure that resampled segments of census walks or CT stations at each of the 40 forest sites based on 1000 iterations. We then plotted both the total number of species and the resampled mean (SD) species richness against the forest-patch area ($\log_{10}$). This allowed us to account for potential biases in our sampling due to unavoidable between-site differences in sampling effort as a function of forest patch size, which could have biased our richness estimators.

Additionally, we performed nonmetric multidimensional scaling (NMDS) ordinations based on the Bray-Curtis similarity matrix of species composition using the combined occupancy data from all four sampling techniques. We also obtained a measure of aggregate biomass for each forest site, by summing the estimated body mass of all species occurring at each site (based on Smith *et al*. 2003 and a hunting study ~80 km from the study area where most game carcasses were weighed: Souza-Mazureck *et al.* 2000). We also used four species attributes (body mass, trophic status, locomotion habit and group size) to quantify the vertebrate functional diversity (FD) of each forest site based on a dendrogram approach (Petchey and Gaston 2002). This method encompasses four steps: (1) a design of the trait matrix; (2) a conversion of this matrix into a distance matrix; (3) a hierarchical clustering of the distance matrix to produce a functional dendrogram; and (4) a calculation of the total branch length of the dendrogram, providing a continuous FD metric. We used the Euclidean distance and the unweighted paired-group clustering method using arithmetic averages, and performed the analysis using Petchey's (2013) R code. We then investigated patterns of species composition, biomass and FD in relation to forest area through linear regression using semi-log models, considering the NMDS measure of species composition, aggregate biomass, and FD as response variables.

We further performed Generalized Linear Models (GLMs) to examine the vertebrate diversity responses to the explanatory variables. We firstly performed a Pearson's correlation analysis between patch-, landscape- and habitat quality variables across both all 40 forest sites and the 37 islands only, retaining weakly correlated variables ($r \leq 0.70$). Because some variables were highly related, we performed stepwise linear regression models to select the best patch- and landscape-scale predictors to be included in further analyses — forest area (hereafter, 'AREA'), patch SHAPE, distance to continuous forest site ('ISOLATION'), proximity index within 500-m buffers ('PROXIMITY'); percentage of closed-forest canopy within the patch (CC%), fire severity ('BURN'), and basal area of trees bearing fleshy fruits ('BA_{ff}'). We then tested for multicollinearity among these variables by deleting the Variation Inflation Factors (VIF; Dormann *et al*. 2013) that were at least moderately redundant or collinear (VIF ≥ 5). We performed species richness GLMs considering: (1) all 40 forest sites, with fixed effects available for CFs (AREA, BURN, CC% and BA_{ff}); (2) the 37 islands only, with all fixed effects retained (AREA, ISOLATION, SHAPE, PROXIMITY, BURN, CC% and BA_{ff}); and (3) only those 15 islands smaller than 10 ha, with all fixed effects retained but excluding forest AREA. Models were fitted using the '*lme4*' package (Bates 2007) within the R platform. We ran all predictor subsets using the '*MuMIn*' package (Bartón 2009) and obtained model-averaged estimates. We further determined both the relative importance of each variable using hierarchical partitioning (HP) and unique fractions of variation explained for each significant variable using variance partitioning (VP).

Finally, we used empirical models based on key patch and landscape variables that best explained patterns of species richness on surveyed islands to predict patterns of forest vertebrate species extinction across the entire BHR landscape.

6.4. Results

6.4.1. Determinants of species richness and diversity

Balbina forest islands harboured 0 to 33 of the 35 vertebrate species surveyed (mean [SD] = 14.81 [11.18] species), whereas all three CFs contained 34 species. All species detected in CFs were detected in at least one island. Forest area alone explained 91% of the overall patch-scale variation in species richness considering the combined occupancy data from all four sampling techniques, showing a steep slope (*i.e., Z*-value = 0.286; Fig. 6.1a). Likewise, forest area still explained 83% of the variation in effort-standardized resampled species richness (Fig. 6.1b). NMDS ordinations showed that vertebrate assemblage structure of large islands and CFs were more similar to one another than that of smaller islands, with islands <10 ha showing high levels of idiosyncratic dissimilarity depending on what small subset of species had been retained (Fig. 6.2a). Overall, forest patch area was a good predictor of species composition, with islands >100ha beginning to stabilize multivariate patterns of species similarity (Fig. 6.2b). Forest area was also a powerful predictor of the aggregate assemblage biomass ($R^2_{adj} = 0.769$, $P < 0.001$, Appendix 6.4.a) and functional diversity of all vertebrate species ($R^2_{adj} = 0.824$, $P < 0.001$, Appendix 6.4.b).

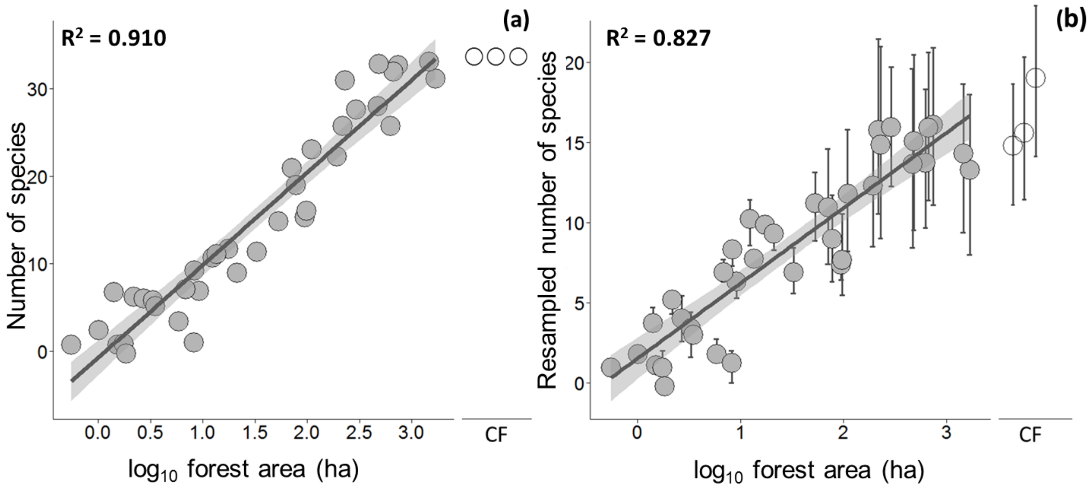

Figure 6.1. Relationships between forest patch area and species richness in 37 islands and three mainland forest sites at the Balbina Hydroelectric Reservoir landscape considering (a) the total number of vertebrate species; and (b) the resampled mean (± SD) number of species, based on a jacknife procedure that randomly resampled line-transect segments and CT stations at each of the 40 forest sites with 1000 iterations.

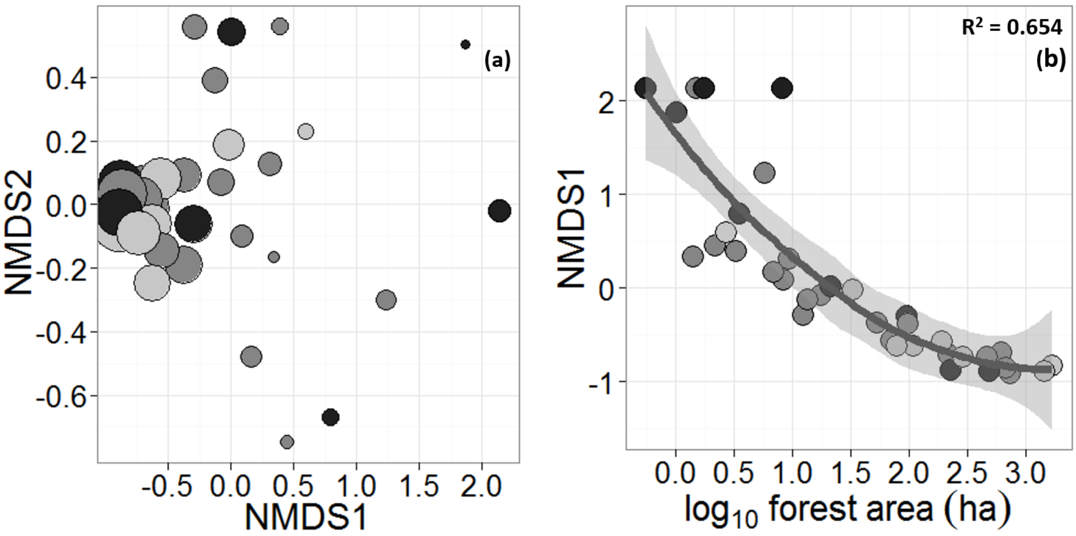

Figure 6.2. (a) Nonmetric multidimensional scaling (NMDS) ordination plot based on the Bray-Curtis similarity matrix of vertebrate species composition; (b) the relationship between the first NMDS axis and forest patch area. Circles are sized proportionally to ($\log_{10}$ x) forest area in (a), and colours are according to fire intensity (increased fire intensity from light-grey to black) in both graphs.

Incorporating all explanatory variables, GLMs showed that patch forest area, fire severity and within-patch percentage of closed-canopy forest were significant predictors of species richness considering all 40 forest sites. However, island area was the only significant predictor of species richness when we excluded mainland sites from the model (Table 6.1). In both cases, island area captured a higher power of hierarchical partitioning, accounting for 64.8% of relative importance among all significant variables considering all 40 forest sites. Considering only the 15 islands smaller than 10 ha and excluding island area from the analysis, only fire severity was a significant predictor of species richness (Table 6.1). For all GLMs, only models containing these variables could be defined as 'best' models (ΔAIC $\leq$ 2.00). Although levels of burn severity did not have a significant effect on the slopes of overall species-area relationships for all sites (SARs; Fig. 6.3a), the history of fire disturbance clearly modulated SARs in islands smaller than 10 ha, whereby intercepts predicted almost six species for unburnt small islands, but only one species for severely burnt islands (Fig. 6.3b).

Table 6.1. Summary of the full-model Generalized Linear Models (GLMs) of the vertebrate species richness at (1) all 37 forest islands and three continuous forest sites; (2) the 37 islands only; and (3) 15 islands smaller than 10 ha throughout the BHR landscape. Coefficient estimates (β), their unconditional standard errors (SE), the hierarchical partitioning (HP) of each variable, and the unique fractions of each significant variable based on variation partition (VP) are shown. Significant variables are indicated as: ***$p \le 0.001$; **$p \le 0.01$; *$p \le 0.05$. See text for details of each variable.

	Parameter	**β**	**SE**	**HP (%)**	**VP**
N=40	(Intercept)	0.100	0.452		
	AREA***	0.656	0.049	74.90	0.648
	BURN***	0.307	0.065	14.11	0.003
	CC%**	0.010	0.003	8.39	0.001
	BA_{ff}	-0.001	0.011	2.60	
N=37	(Intercept)	1.211	0.286		
	AREA***	0.752	0.067	48.56	
	ISOLATION	0.051	0.071	2.67	
	SHAPE	-1.451	5.846	22.42	
	PROXIMITY	0.039	0.034	17.77	
	BURN	0.000	0.074	3.04	
	CC%	0.001	0.003	3.44	
	BA_{ff}	-0.003	0.014	2.10	
N=15	(Intercept)	2.308	1.288		
	ISOLATION	0.037	0.225	1.45	
	SHAPE	0.298	5.430	1.29	
	PROXIMITY	0.128	0.132	22.61	
	BURN***	-0.684	0.247	43.00	
	CC%	0.012	0.010	27.94	
	BA_{ff}	-0.000	0.024	3.71	

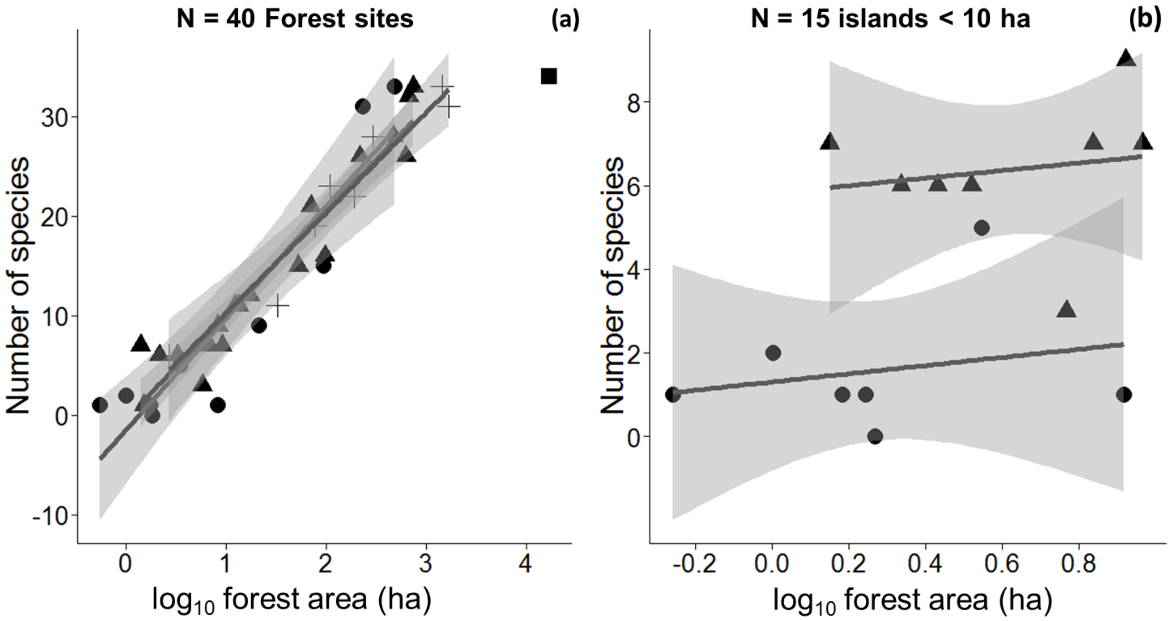

Figure 6.3. Relationships between forest patch area subjected to varying levels of fire severity and the total number of species persisting in (a) all 40 forest sites; and (b) only islands smaller than 10 ha. Symbols are coded according to fire severity (square = unburnt; solid triangles = low severity; cross = intermediate severity; solid circles = severely burnt).

6.4.2. Predicting local extinctions across the entire landscape

We modelled patterns of vertebrate extinction across all 3,546 surveyed and unsurveyed islands using the species-area relationship based on the 37 surveyed islands. Forest area alone was a powerful predictor of the number of species retained within islands (R^2 = 91%), so we used this SAR equation to predict the completeness of vertebrate assemblages for all 3,546 islands across the BHR. Our estimates show that 95% of these islands retained fewer than 60% of all 35 vertebrate species considered in this study. For better perception of this pattern, we included both forest area and island shape to predict the proportion of species extinction according to forest area (Fig. 6.4). Assuming that all landscape-wide species once occupied all islands prior to dam construction, we estimate an overall local extinction rate of 42.3% (548 of 1,295 populations) within the 37 islands surveyed. However, this rate increased to 70.3% (87,278 of 124,110 populations) for all 3,546 islands across the entire landscape. Only islands larger than 475 ha harboured a reasonably complete vertebrate community (≥80% of species), but these accounted for only 25 (0.7%) of all reservoir islands. We therefore identified the most species-rich islands across whole landscape (Fig. 6.5).

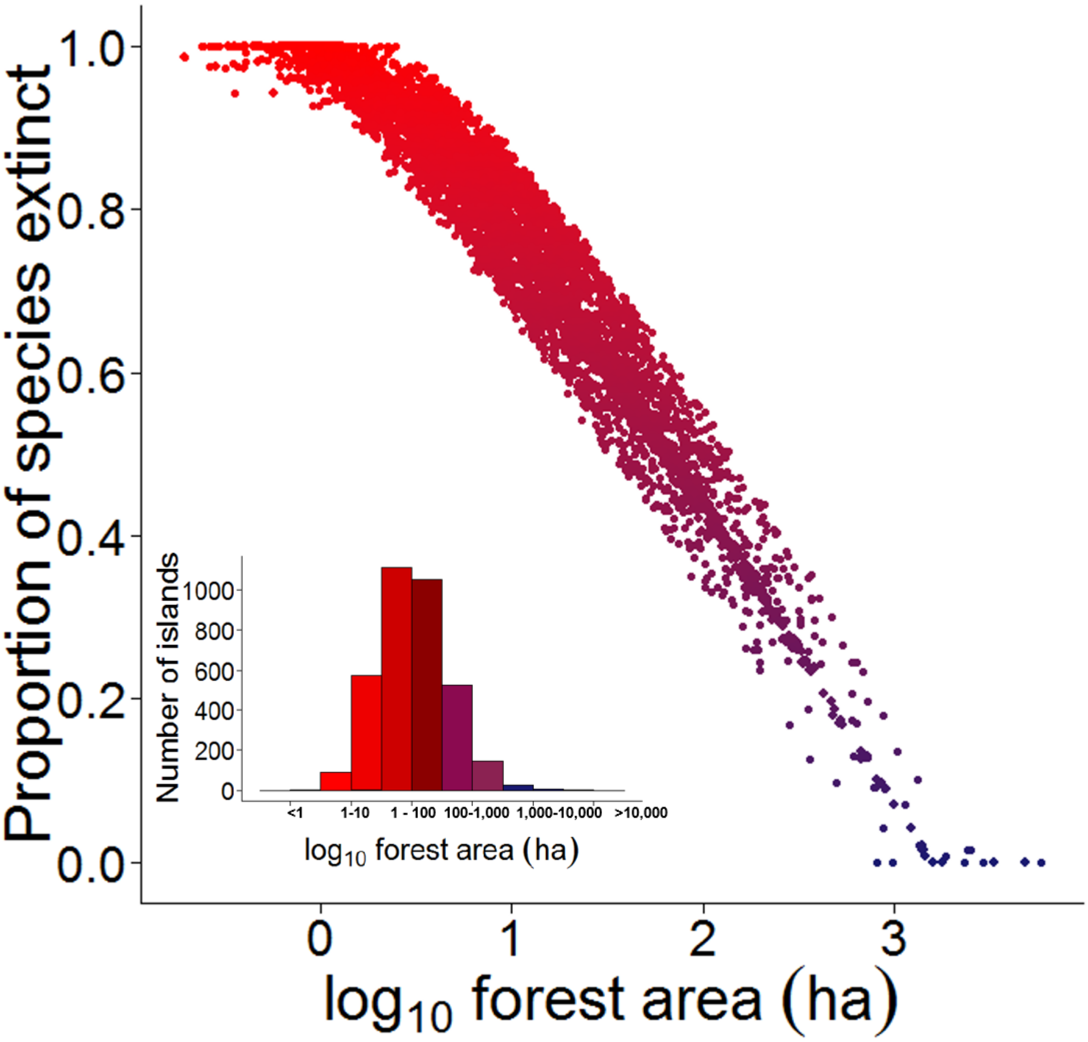

Figure 6.4. Proportion of forest vertebrate species predicted to be extinct according to forest patch area and island shape modelled for all 3,546 forest islands across the Balbina Hydroelectric Reservoir landscape. Colour gradient in histogram describing the overall distribution of island sizes match those of solid symbols in the scatterplot.

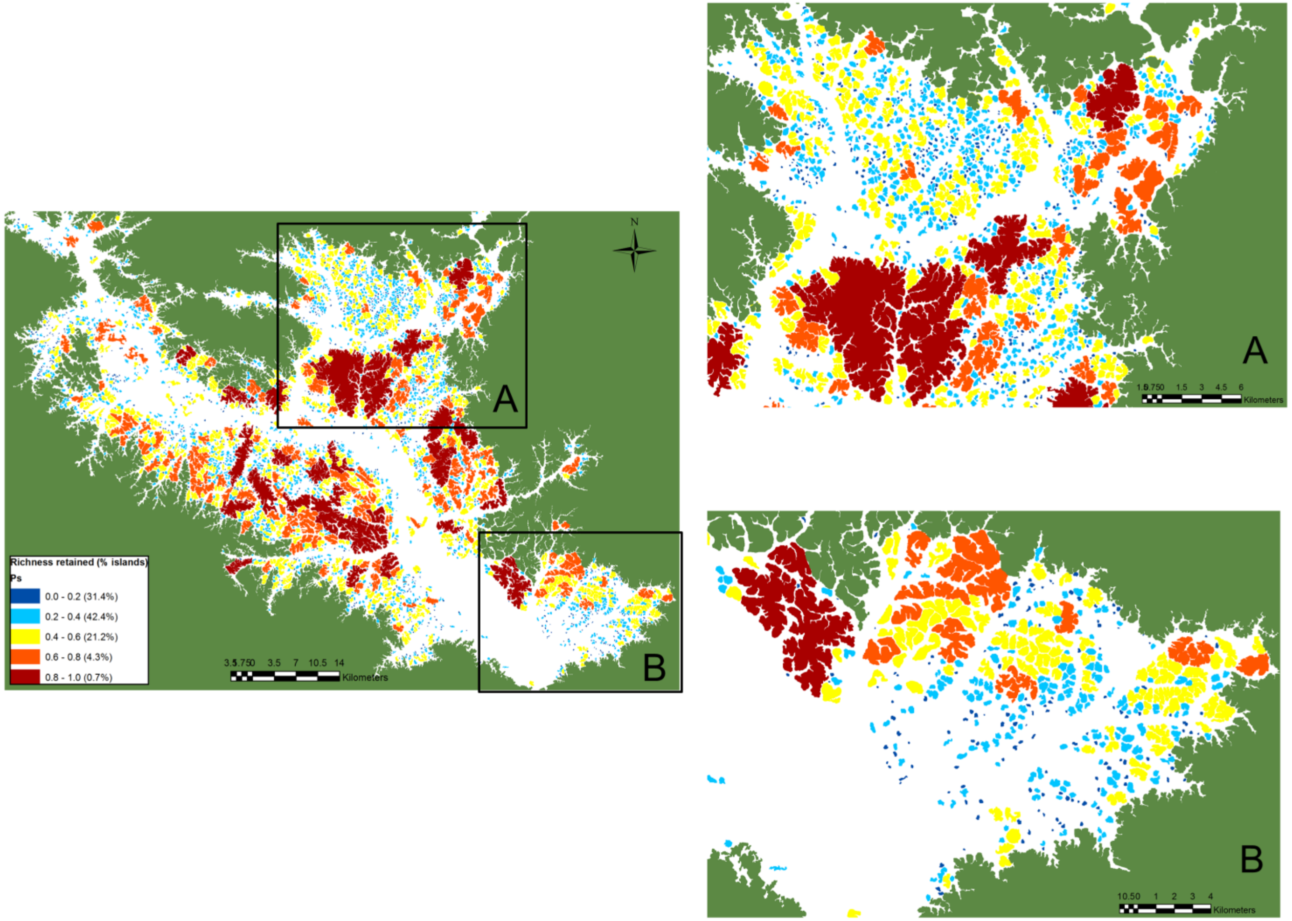

Figure 6.5. Heat map showing high, intermediate and low priority sites for forest vertebrate conservation across the 3,546 islands within the Balbina Hydroelectric Reservoir landscape, based on the empirical SAR (R^2 = 91%) derived from 37 surveyed islands. Islands are colour-coded according to levels of species persistence (see legend).

6.5. Discussion

Our study clearly demonstrates the colossal erosion in vertebrate diversity induced by a man-made tropical forest dam following a 26-yr relaxation history. Apart from the detrimental social and economic impacts induced by the Balbina dam, the long-term impacts on forest biodiversity in insular forest patches that are presumed to have remained intact are astounding. Approximately 70% of all local medium to large vertebrate populations were driven to local extinction within the reservoir, and only 0.7% of all 3,546 islands currently retains four fifths of a full complement of species. Even though large islands retained a species-rich vertebrate assemblage, the vast majority of islands failed to provide sufficiently large high-quality habitat for the terrestrial/arboreal vertebrate fauna. This is mirrored in the aquatic realm, where population estimates of the largest apex predator in the reservoir – the giant otter – failed to grow proportionally with the greatly expanded water-body at Balbina (Palmeirim *et al.* 2014), which also suggests that major hydroelectric reservoirs provide low-quality habitat for aquatic vertebrates. Moreover, many forest vertebrate populations stranded in small islands are too small and far from the thresholds of demographic or genetic viability, and will likely continue to pay an extinction debt (Terborgh *et al.* 2001; Kuussaari *et al.* 2009). We therefore surmise that the true multifaceted terrestrial biodiversity impact of mega hydroelectric dams have so far been severely underestimated given that long-term impacts on the terrestrial biota have been neglected by environmental impact assessments. At other major dammed tropical rivers worldwide, substantial declines in species diversity have been reported in the immediate aftermath of rising floodwaters and isolation (Cosson *et al.* 1999, Terborgh *et al.,* 2001), following a similar relaxation time as reported here (Gibson *et al*. 2014), and after a long isolation history (Wright *et* al. 1994; Wang *et al*. 2010; Mendenhal *et al.* 2014). Yet the even higher rate of species loss at the BHR landscape is inexorably associated with the undulating topography typical of most Amazonian lowland forest habitats which, once flooded, are prone to conversion into vast shallow lakes comprised by a large number of small islands (Palmeirim *et al.* 2014; Benchimol & Venticinque 2014). Given that management options for connecting forest islands, thereby enhancing dispersion rates among sites are unfeasible, insular biotas at Balbina will likely experience even higher species extinction rates in the long-term.

6.5.1. Main predictors of species loss

Several factors have been pinpointed to explain patterns of species extinction within tropical forest isolates. Since Island Biogeographic Theory was postulated (MacArthur & Wilson 1964), area and isolation effects have been consistently hailed as the prime predictors of species persistence in remaining habitat patches (Ferraz *et al.* 2007; Prugh *et al.* 2008). Other studies have emphasised the importance of considering the spatial arrangement of patches (Andrén 1994; Gascon *et al.* 1999), the additive effects of anthropogenic disturbances (including hunting, logging and forest fires; Michalski & Peres 2007; Canale *et al.* 2012*;* Benchimol & Peres 2013), and habitat quality (Urquiza-Haas *et al*. 2009). Additionally, matrix type has been recognised as a key driver of species loss, with true islands showing higher declines of species richness than equivalent-sized remnants in terrestrial landscapes (Mendenhall *et al*. 2014). Using a multi-level approach, we considered a number of factors, in addition to area- and isolation-effects, to understand the main drivers of local extinction at Balbina forest islands.

Unsurprisingly, area was by far the most important predictor, explaining as much as 91% and 82% of the overall variation in species richness and functional diversity, respectively, across all islands. In contrast, degree of isolation exerted no meaningful effect. Despite strong large mammal responses to landscape variables (Thornton *et al.* 2011), we did not find a significant effect of the proximity index on species richness. Moreover, the only human-induced threat that may affect BHR islands ─ fires through anthropogenic sources of ignition ─ exerted a significant effect, but only in fairly small islands (<10 ha). Hunting pressure is a strong predictor of medium and large mammal persistence across several fragmented tropical forest landscapes (Michalski & Peres 2005; Sampaio *et al*. 2010; Canale *et al.* 2012), and a prevalent modulator of SARs in Neotropical primates (Benchimol & Peres 2013), but all BHR islands were strictly protected from hunters by the Uatumã Reserve. This is consistent with the similarity in SAR slopes for different classes of vertebrate body mass (Appendix 6.5), which would be unlikely to occur given that hunters are highly selective to large-bodied species. Forest habitat quality, expressed via the proportion of closed-canopy forest, exerted a significant effect when all 40 forest sites were considered, but the relative importance of this variable was low compared to area effects. Finally, the inhospitable aquatic matrix appears to play a key role in explaining patterns of species persistence. The overall SAR Z-value (*i.e.,* the slope) at Balbina was considerably higher than those observed for both large vertebrate fragmentation ecology studies at Neotropical landscapes embedded within a terrestrial vegetation matrix (Michalski & Peres 2007; Canale *et al.* 2012) and other taxonomic groups within true islands (Yu *et al*. 2012; Mendenhall *et al*. 2014). Z-values can be considered as a strength metric of SARs, with steeper slopes consistently associated with low matrix permeability and immigration rates (Watling & Donnelly 2006). Our results thus reinforce the detrimental effects of the open-water matrix on the patterns of vertebrate retention within islands, which is likely related to the low capacity of vertebrate species to traverse the non-habitat matrix within a true archipelagic landscape (cf. Cosson *et al*. 1999).

Lowland tropical forest archipelagos created by major dams are therefore likely to succumb to higher rates of terrestrial biodiversity loss than most terrestrial fragmented landscapes, given that the ubiquitously predominant small islands are isolated by a uniform non-habitat matrix. Fortunately, the Balbina archipelago has been free from hunting pressure ─ or else the detrimental impacts would be even worse. Setting aside forest reserves, such as the REBIO Uatumã, is therefore a recommended mitigation measure in future reservoirs as they can both partly offset local biodiversity erosion and ensure a stable experimental landscape setting for long-term ecological studies.

6.5.2. Fire effects

As expected, vertebrate species composition was very similar among our three undisturbed continuous forest sites, but much less predictable particularly in islands <10 ha. These exhibited the most heterogeneous patterns of species composition, which were largely related to their recent history of fire disturbance (Fig. 5.3). Indeed, fire severity is an important driver of bird and mammal species loss in fragmented landscapes elsewhere (Lees & Peres 2006; Michalski & Peres 2007). Islands subjected to severe fire perturbation experienced rapid rates of tree turnover, favouring fast-growing pioneers at the expense of old-growth tree species (see Chapter 4). As faunal assemblages often change in response to compositional shifts in tree communities (Malcolm & Ray 2000), small island extinction rates for some species were undoubtedly accelerated by both structural and compositional degradation in tree assemblages. This was particularly the case of several primary forest specialists, such as the white-lipped peccary (*Tayassu pecari*) within the Balbina archipelago (see Chapter 5). Elsewhere in Amazonia, fire perturbation was a key driver of population declines and/or local extinctions of several vertebrate species in both fragmented (Michalski & Peres 2007) and continuous forest settings (Peres *et al*. 2003). Our results clearly show that small, severely burnt islands retained the lowest number of vertebrate species, indicating that fire disturbance operates synergistically with area effects. Preventing surface fires within increasingly flammable fragmented forest landscapes would therefore reduce the pace of vertebrate loss that plagues small forest remnants.

6.6. Policy implications

Major hydroelectric plants are widely purported to be ‘green’ energy sources. However, the decision-making process on whether or not to erect new major dams across lowland Amazonia urgently needs to be reassessed. For those dams that are already built, protection against hunting and fire disturbance should be key mitigation measures to safeguard insular faunal communities. Aside from the poorly quantified social, economic and environmental costs of large dams — including displacements of local communities, loss in fishery revenues (Ziv *et al*. 2012), alteration of aquatic wildlife (Alho 2011; Palmeirim *et al.* 2014), and significant greenhouse gas emissions (Fearnside & Pueyo 2012) — we now provide clear evidence on additional costs to terrestrial and arboreal biodiversity within typically vast forest areas. Apart from the 154 hydroelectric dams currently in operation across the Amazon, 277 additional planned dams are likely to be constructed over the next decades (Castello *et al*. 2013), with potential catastrophic effects to both aquatic and terrestrial biodiversity. Our study calls for decisive strategic rethinking by policy-makers of future scenarios of hydropower infrastructure deployment in regions like Amazonia. Nevertheless, if mega-dams will be in fact constructed, we suggest that the government should compensate both habitat and biodiversity losses by establishing of protected areas. Apart from the entire reservoir area, adjacent continuous forest sites should also be protected within nominal strictly forest reserves. The extension of those continuous forest sites needs to consider both the total flooding area (*i.e.,* forests that will be lost) and the sum of the area of all islands smaller than 475 ha (given that only islands larger than this threshold are expected to harbour at least 80% of all vertebrate species). Finally, we strongly encourage that previously ignored environmental costs, such as long-term terrestrial biodiversity loss, should be explicitly incorporated into the environmental impact assessments of new dams.

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CHAPTER 7

CONCLUSIONS & FUTURE DIRECTIONS

Mega hydroelectric dams: an emergent driver of forest loss and forest fragmentation in the Amazon (Images: upper – M. Benchimol; bottom – E.M. Venticinque).

7.1. Ecological and conservation lessons

Habitat fragmentation has been a central concern in conservation biology worldwide, mainly because it is considered a key driver of global species loss (Foley *et al.* 2005; Fisher & Lindenmayer 2007). At a global scale, a burgeoning number of 65,300 studies have so far investigated this process (Google Scholar, 16/7/2014, key-word “habitat fragmentation”), based on conceptual models, empirical field studies and quantitative syntheses. MacArthur & Wilson’s (1967) Theory of Island Biogeography provided a seminal model to be applied in conservation management towards species conservation, but empirical studies thereafter have been providing mounting evidence that focusing only on area and isolation effects is not enough to curb the rate of biodiversity loss in fragmented landscapes (Fisher & Lindernmayer 2007; Laurance 2008; Prugh *et al*. 2008). This thesis represents an effort to augment our understanding on the main predictors of biodiversity loss in insular forest habitat patches across the Neotropics, by conducting two complementary approaches — a continental-scale and a landscape-scale analysis — including different taxa. Three key ecological and conservation take-home messages from this work are hereafter summarised.

1) Anthropogenic disturbances cannot be overlooked

Patch area is indeed a strong driver of species persistence within Neotropical fragmented forest landscapes, emerging as the most important variable in predicting primate species richness at a continental-scale (Chapter 2). However, other factors are also key drivers of species persistence and should therefore be included in fragmentation ecology studies and considered in management actions for conservation. For instance, hunting pressure exerted a strong negative effect on patterns of large-bodied primate persistence within 760 forest fragments examined in a comprehensive literature review, greatly reducing the explanatory power of, and flattening, species-area relationships (SAR; Chapter 2). Surface fires also affected tree assemblage composition and diversity, leading to a hyper-proliferation of pioneer species, reducing the abundance of both emergent and large-seeded species, and reducing mean wood density of live stems (Chapter 4). Likewise, invasions of exotic mammals interacted synergistically with habitat fragmentation in driving local extinctions of native small mammals in islands within a reservoir in Thailand (Gibson *et al*. 2013). Hence, it becomes clear that anthropogenic disturbance can accelerate local extinction rates and decrease the diversity of species within fragmented forest landscapes. Future tropical fragmentation ecology studies cannot ignore these external stressors, so patch-scale environmental perturbations induced by humans need to be considered in evaluating patterns of species persistence in fragmented forest landscapes. Although undisturbed primary forests are irreplaceable in maintaining high diversity in the tropics (Gibson *et al*. 2011), forest fragments can retain a significant fraction of the original biota and deserve protection (Turner & Corlett 1996). Large islands, particularly > 100 ha, should be prioritised in conservation efforts, but enforcing protection against human perturbations is also imperative to maximise species persistence and maintain high levels of species/functional diversity within forest remnants.

2) The matrix really matters and differentiates true islands from habitat islands

Matrix composition and connectivity affected patterns of species persistence in fragmented landscapes. When the percentage of matrix forest cover was included in Generalized Linear Mixed Models investigating the patterns of primate species richness (Chapter 2) and occupancy (Chapter 3) in forest patches, this variable was a significant and strong predictor, appearing in the top models with area and hunting pressure. The results obtained for both trees and vertebrates in forest patches surrounded by vast expanses of water also suggest a strong influence of the matrix on patterns of species persistence. In the case of trees, edge-mediated forest disturbance was the most important driver of species composition within islands. It seems that in the absence of the buffer effect of surrounding vegetation, which can attenuate detrimental edge-effects (Mesquita *et al*. 1999), islands within the reservoir become highly exposed to strong winds, probably leading to higher rates of treefall and tree mortality. Long-term studies on floristic dynamics are therefore required, but results shown in Chapter 4 are consistent with other studies conducted in land-bridge island systems that demonstrate the more severe effects of fragmentation on true islands than in habitat isolates within a terrestrial matrix (Cosson *et al.* 1999; Emer *et al.* 2013). In the case of terrestrial vertebrates within the Balbina archipelago (Chapter 5), the high Z-value (slope) obtained in the SAR power model (Z = 0.286) suggests poor permeability and lower immigration rates due to a uniformly hostile matrix (see Watling & Donnelly 2006). Likewise, matrix type affected primates SARs when only non-hunted sites were considered, with patches surrounded by the freshwater matrix showing steeper slopes compared to patches embedded within a terrestrial matrix (Chapter 2). Results from these different chapters converge towards the importance of the matrix in modulating species persistence in tropical fragmented landscapes. Hence, integrating matrix composition into forest fragmentation studies and including parameters that describe the relative resistance of different matrix types may substantially improve our understanding of species persistence in fragmented landscapes (Rickets 2001; Anderson *et al.* 2007). Enhancing the suitability of matrix habitats is strongly recommended in terrestrial fragmented landscapes, in order to facilitate species movements between forest remnants, thereby rescuing patch occupancy and increasing gene flow.

3) Life-history traits of species also need to be considered

Forest fragmentation cannot be investigated by considering only landscape changes, but should also include species susceptibility as a function of their life-history traits. Species differ in their responses to habitat fragmentation, with some species showing greater risk than others (Henle *et al*. 2004). This thesis contributes to our understanding of the main traits that predict the sensitivity of primates, other arboreal and terrestrial vertebrates and tree species to fragmentation. Based on an extensive literature review, Chapter 3 finds that wide-ranging primate species consuming nutrient-rich food items were most prone to local extinctions within Neotropical fragmented landscapes. Considering 34 vertebrate species, including terrestrial and arboreal mammals, large frugivorous birds and tortoises, home range size, together with dispersal capacity over water, emerged as the most important traits in predicting species vulnerability to habitat insularization induced by a hydropower reservoir —

species with large area requirements but unable to cross wide open-water gaps were most adversely affected in forest patches (Chapter 6). Likewise, in an Amazonian landscape embedded within a terrestrial matrix, both traits were considered the most important predictors of species susceptibility to land-use change in several faunal groups pooled together (Dale *et al*. 1994). Surprisingly, interviews with professional boatmen who frequently navigated the Balbina Lake showed that a wide range of species is able to traverse the inhospitable water matrix (see Figure 7.1 for some examples), for whatever reasons. Therefore, species showing greater swimming capacity such as ungulates and large felids, exhibited a higher island occupancy probability (at least temporarily) and therefore coped better with habitat insularization. This information is important to enhance our understanding of the dispersal abilities of species within a hostile matrix, highlighting the importance of long-term effective protection of artificial archipelagos created by hydropower projects. Finally, Chapter 4 shows that canopy and emergent tree species presenting a shade-tolerant regeneration strategy, large seeds, and higher wood density were most negatively affected by habitat insularization. Therefore, we provide substantial evidence that habitat fragmentation leads not only to biodiversity loss but also to changes in species composition mostly driven by life-history traits. Including species life-history traits in studies investigating biological responses to habitat fragmentation is recommended, yet it is important to highlight that vulnerability of species may also be related to the properties of the wider landscape (see Thornton *et al.* 2011).

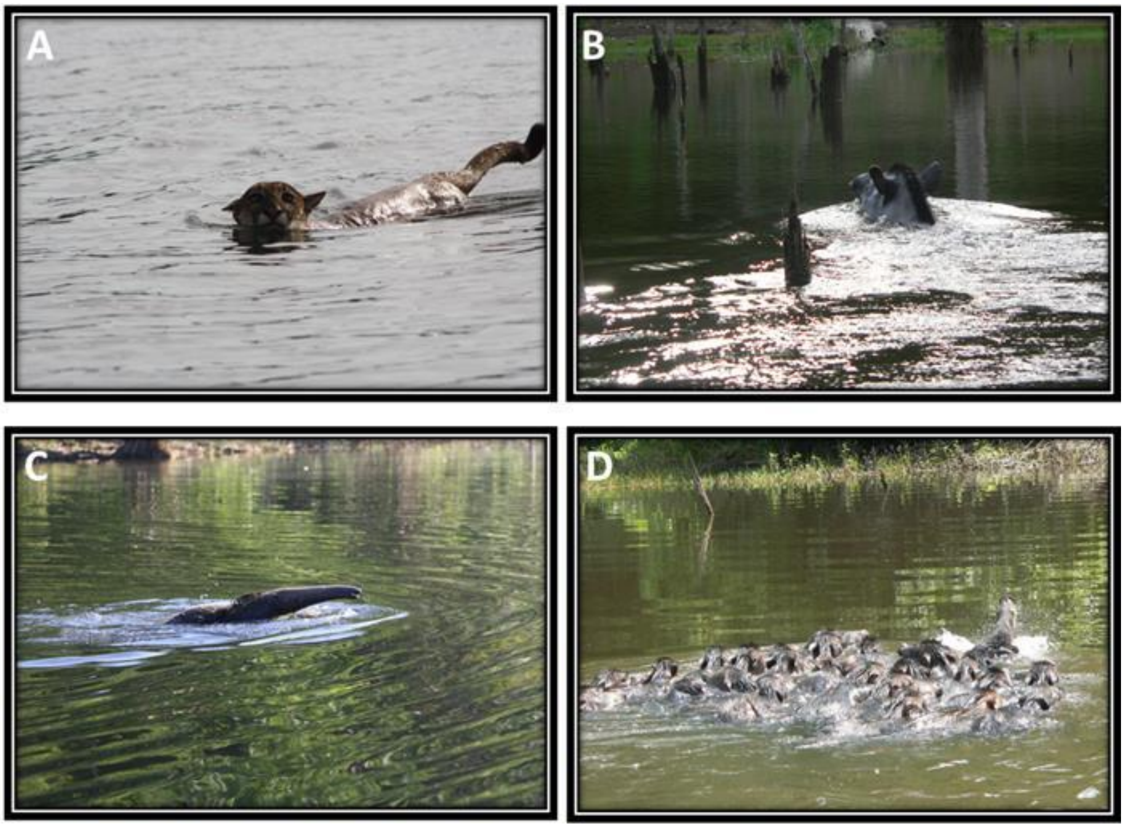

Figure 7.1. Terrestrial vertebrates swimming between islands within the Balbina reservoir: (A) puma, (B) tapir, (C) giant anteater and (D) a herd of white-lipped peccaries. Credit: Giant Otters Project/INPA (Projeto Ariranhas/INPA).

7.2. From theory to practice: assisting conservation in fragmented landscapes

Both small-scale and large hydroelectric dams are dramatically increasing across the Amazon ─ a total of 21 dams are currently under construction and 277 are planned to be erected within the next decade or so to boost energy supplies for urban center and attract energy-hungry industrial development including mining and metallurgic industries (Castello *et al.* 2013). In addition to destroying primary forests, dams require new roads and powerlines, all of which promote forest fragmentation (Finer & Jenkins 2012). Therefore, it becomes extremely important to understand the long-term impacts on forest biodiversity associated with large, capital-intensive dams and propose strategies to mitigate their myriad detrimental effects. Yet appropriate environmental impact assessments are yet to be carried out for any major Amazonian dam (Castello *et al.* 2013), and little knowledge of the long-term responses of terrestrial organisms to this type of fragmentation is available (Ferreira *et al.* 2012*;* Benchimol & Venticinque 2014). This thesis is to our knowledge the most comprehensive investigation of the long-term impacts of a major hydroelectric dam on patterns of terrestrial biodiversity loss in the tropics. It combines a wide-range of the robust sampling techniques to survey medium and large-bodied vertebrates in a large number of variable-sized replicate islands and three 'pseudo-control' continuous forest sites scattered across a study area polygon spanning 3,965 km^2. Also, more than 11,000 trees within forest plots on the same sampled islands were measured and identified at species level, elucidating the effects of insularization on another important bioindicator group. Based on the results, the following best- practice guidelines are recommended to be implemented both at the landscape (*i.e.*, Balbina reservoir) and regional scales (*i.e.*, future hydroelectric dams to be implemented in Amazonia). Additionally, some recommendations for other tropical fragmented forest landscapes are pinpointed.

(1) Landscape scale – It is unquestionable that the major effect of the Balbina dam construction was habitat loss. However, the islands that were subsequently created to serve as refuge for biodiversity should be protected to enhance population viability in the long-term. As quantified in this study, a minimum of 100 ha of forest is required to ensure at least 60% of all vertebrate species considered here. In Balbina, an area of 443,772 ha of pristine forests was flooded (Palmeirim *et al*. 2014) and transformed into an immense archipelago of 3,546 islands corresponding to 118,300 ha of forest cover encompassing former hilltops of the once continuous pre-inundation forest. Enforcing regulations across the entire lake is quite difficult, but conservation action should provide protection against anthropogenic perturbations such as hunting, selective logging and ground fires, to protect the remaining biodiversity in the landscape.

(2) Regional scale – Our findings show that terrestrial biodiversity succumbed to the negative effects experienced in a major dammed river basin, following 25-26 years of the rising floodwaters. This serves to alert the hydroelectric sector of

the potential consequences of major dams on biodiversity at other would-be Amazonian reservoirs. As the governments of many South America countries have decided to vastly expand their hydropower sectors regardless of social and environmental costs, it becomes important to propose ways to avoid or reduce the most harmful effects (see Kareiva 2012). We strongly suggest that the precautionary principle must be considered for future hydropower projects ─ because lowland Amazonia is predominantly flat, which favours the formation of small islands (Fearnside 1995; Benchimol & Venticinque 2014), hydropower engineers should consider the topography of these planned reservoirs in order to minimise the number of created islands, and enable the predominance of large islands that are well connected to each other. This can be done by controlling the water level of the reservoirs. For each mega-dam built in Amazonia, it is recommended that a strictly protected forest reserve be established to deter large-scale human disturbances associated with dam creation that may threaten local biodiversity. The entire reservoir and a considerable tract of adjacent continuous forest should be included in the reserve, as compensation for forest loss. Forest islands larger than 475ha are likely to harbour a high diversity of vertebrate assemblages (and probably the persistence of much of the co-occurring forest biota), but smaller islands are not. We therefore suggest that the adjacent protected continuous forest sites should cover an area at least equivalent to the total flooded area, plus the sum of the area of all islands smaller than 475ha. Finally, we strongly encourage that previously ignored environmental costs, such as long-term terrestrial biodiversity loss, should be explicitly incorporated into the environmental impact assessments of new dams.

(3) Global scale: As tropical deforestation has expanded in the past few decades (FAO 2010), the resulting large number of fragmented landscapes will require efficient conservation polices. Expanding the number of forest reserves in fragmented landscapes is strongly recommended, especially at regions containing few large tracts of forests, such as Southeast Asia (Achard *et al.* 2002) and the Brazilian Atlantic Forest (Ribeiro *et al*. 2009). Nevertheless, promoting mechanisms to facilitate individual movements across forest fragments is also vital. Our results have shown that matrix type and

heterogeneity consistently affect patterns of primate persistence in Neotropical fragmented landscapes (Chapter 2), an entirely arboreal faunal group that rarely comes to the ground. Even in the highly fragmented landscape of Balbina, comprised primarily of a hostile non-habitat matrix, some species like large predators exhibit transient stop-overs as they trap-line different islands, with the proximity to nearby forest sites affecting the probability of island occupancy (see Chapter 6). Hence, enhancing the suitability of surrounding habitats is recommended to assist large vertebrate movements across forest islands, and this is particularly important in landscapes elsewhere comprised of a terrestrial matrix such as pastures and croplands in which several species are able to cross gaps (Michalski & Peres 2005).

7.3. Future directions

This thesis work produced a massive amount of field data, much of which needs to be analysed in further detail to enhance our understanding of the effects of habitat insularization in Neotropical forest habitat patches. Part of this work has already been published in a conservational journal (Benchimol & Venticinque 2014) and chapters 4, 5 and 6 are expected to be published in high-impact ecology and conservation journals in 2014-2015. A list of several other publications are currently planned, encompassing both tree and vertebrate data, such as a study on biomass loss and committed forest carbon emissions, patterns of vertebrate abundance within surveyed islands, effects of fragmentation on group size, and large-scale predictions of vertebrate loss in planned hydroelectric dams that are yet to be formally approved in Brazilian Amazonia. Collaborations with other researchers are also planned, enabling animal-plant network investigations, the congruence of multi-taxa responses, and comparisons of impacts on biodiversity among different landscapes. The huge amount of camera trapping photos obtained (10,110 independent records) may contribute for a better comprehension of species behaviour and activity patterns, and comparisons among different techniques for surveying terrestrial vertebrates could provide information on the costs and benefits of alternative field techniques to be used in fragmentation studies. Additionally, the Balbina landscape deserves to be continuously investigated for our better knowledge of the main drivers of community dynamics and ecological processes within islands.

7.4. References

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APPENDICES

Appendices are included here in sequence, as referred to within the main text, as supplementary material relevant to each of the preceding chapters of this thesis.

Appendix 2.1. List of the 24 primate functional 'ecospecies' used in the database. Ecospecies recorded in at least one study are shown in bold.

Family	**Genus**	**Functional ecospecies**	**Vernarcular name**	**Taxonomic species included**
Cebidae	Cebus	**Cebus albifrons**	White-fronted capuchins	*C. albifrons*
		Cebus apella	Brown capuchins	*C. apella, S. apella, C. cay, C. flavius, C. libidinosus, C. macrocephalus, C. nigritus, C. robustus, C. xanthosternos*
		Cebus olivaceus	Wedge-capped capuchins	*C. kaapori, C. olivaceus*
	Saimiri	**Saimiri**	Squirrel monkeys	*Saimiri* spp.
	Callimico	Callimico	Goeldi's monkeys	*Callimico goeldi*
	Saguinus	**Saguinus fuscicollis**	Saddle-back tamarins	*S. fuscicollis, S. melanoleucus, S. nigricollis, S. tripartitus*
		Saguinus mystax	Moustached tamarins	*S. mystax, S. labiatus, S. imperator*
		Saguinus niger	Midas tamarins	*S. midas, S. niger*
		Saguinus oedipus	Bare-faced tamarins	*S. bicolor, S. geoffroyi, S. leucopus, S. martinsi, S. oedipus*
	Callithrix (inc. Mico)	**Callithrix**	Atlantic marmosets	*Callithrix* spp.
		Mico	Amazonian marmosets	*Mico* spp.
	Cebuella (inc. Callibella)	Cebuella (inc. Callibella)	Pygmy marmosets	*Cebuella pygmaea, Callibella humilis*
	Leontopithecus	**Leontopithecus**	Lion tamarins	*Leontopithecus* spp.
Atelidae	Ateles	**Ateles**	Spider monkeys	*Ateles* spp.
	Brachyteles	**Brachyteles**	Woolly spider monkeys	*Brachyteles* spp.
	Lagothrix (inc. Oreonax)	**Lagothrix (inc. Oreonax)**	Woolly monkeys	*Lagothrix* spp., *Oreonax flavicauda*
	Alouatta	**Alouatta**	Howler monkeys	*Alouatta* spp.
Pitheciidae	Pithecia	**Pithecia**	Saki monkeys	*Pithecia* spp.
	Chiropotes	**Chiropotes**	Bearded saki monkeys	*Chiropotes* spp.

	Cacajao	Cacajao	Uakaries	*Cacajao* spp.
	Aotus	**Aotus**	Owl monkeys	*Aotus* spp.
	Callicebus	**Callicebus moloch**	Dusky titi monkeys	*Callicebus moloch*
		Callicebus personatus	Atlantic forest dusky titi	*Callicebus personatus*
		Callicebus torquatus	Collared titi monkeys	*Callicebus torquatus*

Appendix 2.2. Summary of 61 fragmented forest landscapes used in this quantitative review of the effects of habitat fragmentation on Neotropical primate assemblages.

Landscape	**Geographic coordinates**	**Number of sites**	**Fragment size (ha)**	**Study**
Alta Floresta	56° 05' 30"W, 9° 54' 57"S	144	1 - 3536	Michalski & Peres, 2005
Alter do Chão	54°57' 55"W, 2° 29' 08"S	16	8 - 361	Sampaio *et al.,* 2010
Araras	44° 14' 58"W, 22° 25' 59"S	5	131 - 4000	Antonietto & Mendes, 1994 Oliveira & Manzatti, 1996; Alves & Andriolo, 2005; Loreto e Rajão, 2005; Alves & Zaú, 2007
Augusto	40° 33' 49"W, 19° 54' 20"S	7	210 - 3598	Chiarello, 1999, 2003; Passamani, 2008
Balbina	59° 37' 57"W, 1° 49' 46"S	21	5 - 1815	Benchimol, 2009; Brum, 2010
Barreiro Rico	48° 05' 09"W, 22° 41' 45"S	4	240 - 1450	Martins, 2005
BDFFP	59° 52' 33"W, 2° 24' 23"S	11	1 - 100	Gilbert, 2003; Boyle & Smith, 2010
Belo Monte	46°15'W, 21° 22'59"S	1	17	Martins & Setz, 2000
Bolivia	63°03' 47"W, 17° 46' 52"S	10	1 - 303	Pyritz *et al.,* 2010
Campinas	46° 55' 36"W, 22° 49' 45"S	13	2 - 250	Chiarello, 1994; Figueiredo & Longatti, 1997; Lima, 2008; Galetti *et al.,* 2009
Cantareira	46° 35' 27"W, 23° 23' 42"S	1	7917	Trevellin *et al.,* 2007
Caratinga	41° 49' 59"W, 19° 49' 59"S	1	890	Dias & Strier, 2000
Ceará	40°52' 00"W, 3° 48'S	1	563	Guedes, 2000
Chiapas	90° 48' 34"W, 16° 14' 52"N	8	1 - 1700	Estrada *et al.,* 2004; Chaves *et al.,* 2010
Cordillera	76° 19' 59"W, 3° 49' 59"N	1	559	Duque & Goméz-Posada, 2009
Córrego	39° 50' 40"W, 18° 24' 38"S	5	1504 - 2822	Chiarello, 1999; Chiarello & Melo, 2001
Corrientes	58° 49' 59"W, 27° 30'S	5	10 - 306	Zunino *et al.,* 1996; Oklander *et al.,* 2010
Cunha	45° 03'W, 23° 16' 59"S	3	1700	Galetti *et al.,* 2009
Dois Irmãos	55° 18'W, 20° 30'S	7	40 - 600	Caceres *et al.,* 2010
Eastern Amazonia	47° 46' 59"W, 2° 33'S	11	19 - 8000	Lopes & Ferrari, 1996, 2000;

				Pereira, 2002; Carvalho Jr, 2003; Ferrari *et al.,* 2007; Stone *et al.,* 2009
Goiás	49° 07' 00"W, 16° 30'S	1	3400	Villar, 2006
Guatemala	89° 32' 32"W, 16° 58' 07"N	50	3 - 446	Thornton *et al.,* 2011
Guri	62° 52' 00"W, 7° 21'N	14	0.5 - 365	Kinzey *et al.,* 1988, Terborgh *et al.,* 1997
Ibitipoca	43° 52' 59"W, 21° 42'S	2	32 - 80	Fontes *et al.,* 1996; Nogueira *et al.,* 2009
Jequitinhonha	40° 41' 16"W, 16° 20' 12"S	46	2 - 9731	Melo, 2004; Guidorizzi, 2008; Neves, 2008
La Suerte	83° 46' 15"W, 10 26' 30"N	4	15 - 10000	Pruetz & Leasor, 2002; Lucket *et al.,* 2004
Las Cruces	82° 52' 00"W, 8° 27'N	1	227	Daily *et al.,* 2003
Los Tuxtlas	95°W, 18° 25' 00"N	88	1 - 1000	Silva-López, 1993; Estrada & Coates-Estrada, 1996; Gómez-Marin *et al.,* 2001
Magdalena	74° 44' 14"W, 5° 38' 56"N	6	80 - 196	Vargas & Solano, 1996; Link *et al.,* 2010
Maranhão	48° 07' 59"W, 5° S	5	8 - 2000	Port-Carvalho, 2002
Michelin	39° 19' 06"W, 13° 46' 42"S	8	120 - 3000	Flesher, 2006; Moreira, 2009
NE Colombia	74° 16' 00"W, 8° 34' 59"N	6	1 - 200	Bernstein *et al.,* 1976
Panamá	79° 51'W, 9° 09'N	1	1500	Wright *et al.,* 1994
Paraíba	34° 57' 24"W, 7° 00' 44"S	1	1436	Fialho & Gonçalves, 2008
Peçanha	42° 25' 00"W, 18° 25' 59"S	1	60	Hirsch *et al.,* 2002
Pernambuco	35° 50' 27"W, 8° 43' 04"S	20	7 - 3478	Almeida *et al.,* 1995; Mendes-Pontes *et al.,* 2007; Silva-Jr & Mendes-Pontes, 2008
Piauí	45° 31' 59"W, 10° 10' 00"S	1	4000	Flesher, 2001
Plateau SP	51°W, 22° 43' 59"S	5	1700 - 2178	Cullen Jr *et al.,* 2001
Porto Alegre	51° 03'W, 30° 15'S	3	14 - 1535	Jardim, 2005
Rio Casca	42° 44' 22"W, 20° 04' 16"S	5	22 - 177	Melo *et al.,* 2005
Saint-Eugene	53° 04' 00"W, 4° 51'N	39	0.1 - 67	Dalecky *et al.,* 2002
Santa Catarina	50° 12'W, 26° 12'S	1	4600	Gonzáles-Solis *et al.,* 2001
Santa Maria	53° 42'W, 29° 43' 00"S	20	0.5 - 977	Fortes, 2008
Santa Rosa	85° 39'W, 10° 49' 59"N	13	22 - 56	Sorensen, 1998, Sorensen &

				Fedigan, 2000
São João	42° 01' 59"W, 22° 27'S	49	4.5 - 3215	Araújo *et al.,* 2008, Araújo, 2009
São José	47° 28' 41"W, 22° 21' 30"S	3	50 - 821	Gonzáles-Solis *et al.,* 2001; Bernardo & Galetti, 2004; Gheler-Costa *et al.,* 2002
Sergipe	37° 13' 59"W, 11° 12'S	6	5 - 118	Chagas, 2009
Serra	47° 40' 00"W, 21° 04' 59"S	2	150-154	Siemers, 2000; Galetti *et al.,* 2009
Serra do Cipó	43° 31' 01"W, 19° 15' 28"S	1	34	Oliveira *et al.,* 2003
South Mexico	90° 43' 55"W, 18° 16' 25"N	1	1400	Rath *et al.,* 2003
South-Central Amazon	54° 53' 14"W, 2° 50' 06"S	17	30 - 4500	Ferrari *et al.,* 2003, Gonçalves *et al.,* 2003, Sampaio *et al.,* 2010
Southwest Amazon	61° 29' 10"W, 11° 43' 39"S	1	1032	Ferrari *et al.,* 1996
SP Montane	45° 03'W, 23° 16' 59"S	2	400	Pianca, 2004, Galetti *et al.,* 2009
South Bahia	39° 39' 45"W, 14° 53' 11"S	26	0.33 - 4766	Rylands, 1988; Neves, 2008; Moreira, 2009; Canale *et al.,* 2012
Tijuca	43° 15' 16"W, 22° 25' 59"S	1	3466	Cunha & Vieira, 2004
Trinidad	61° 14' 57"W, 10° 25' 10"N	4	937 - 6483	Phillips & Abercrombie, 2003
Tucuruí	49° 30' 24"W, 4° 16' 25"S	4	16 - 1200	Vieira, 2005; Veiga, 2006; Silva & Ferrari, 2009
Unisc	52° 31' 59"W, 29° 22' 59"S	1	221	Abreu Júnior & Köhler, 2009
Upper Paraná	53° 18' 58"W, 22° 45' 59"S	6	30-1050	Aguiar *et al.,* 2007
Vale do Taquari	52° 02' 31"W, 29° 40' 51"S	12	1 - 20	Ribeiro & Bicca-Marques, 2005
Viçosa	42° 51' 51"W, 20° 48' 06"S	8	15 - 194	Pereira *et al.,* 1995

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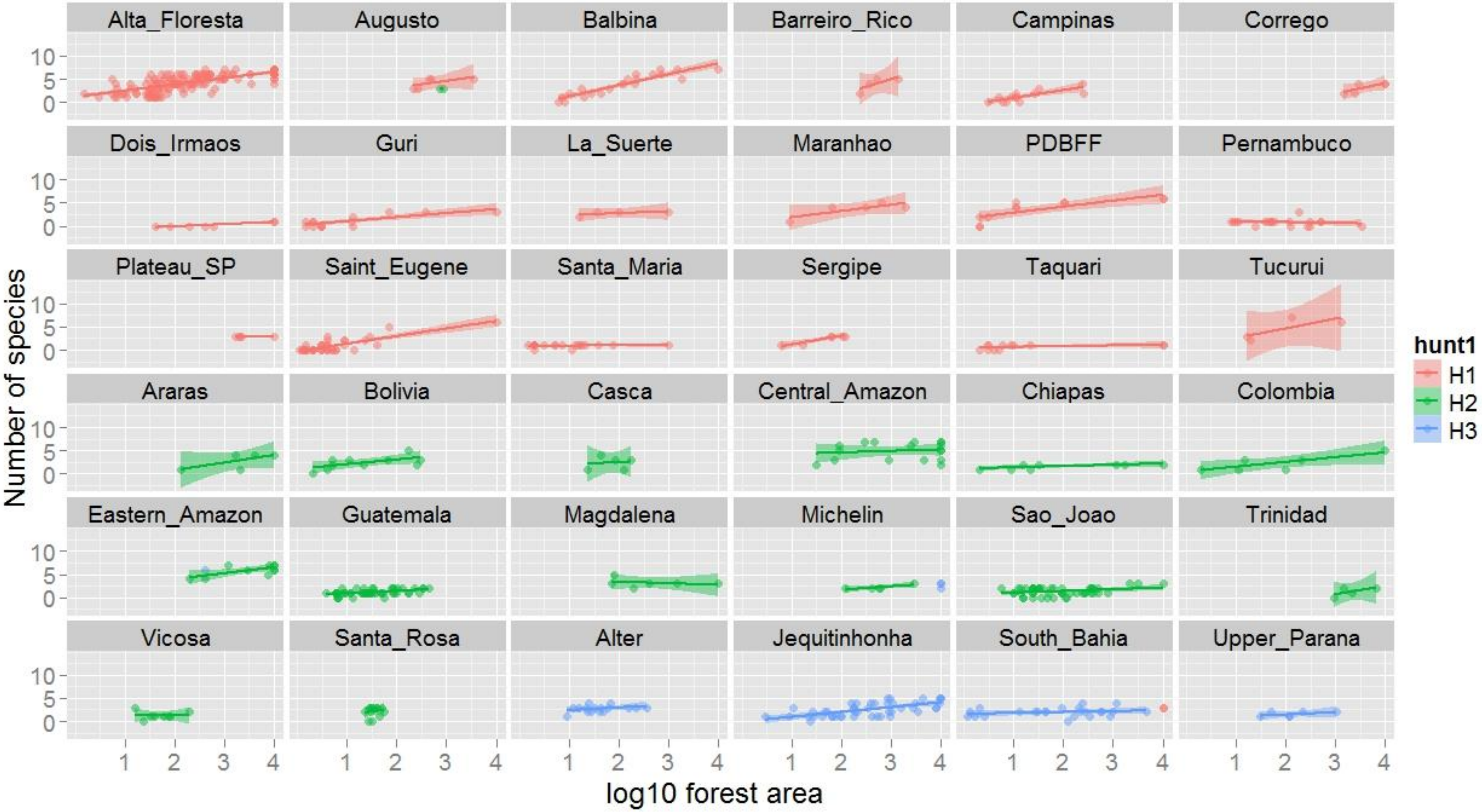
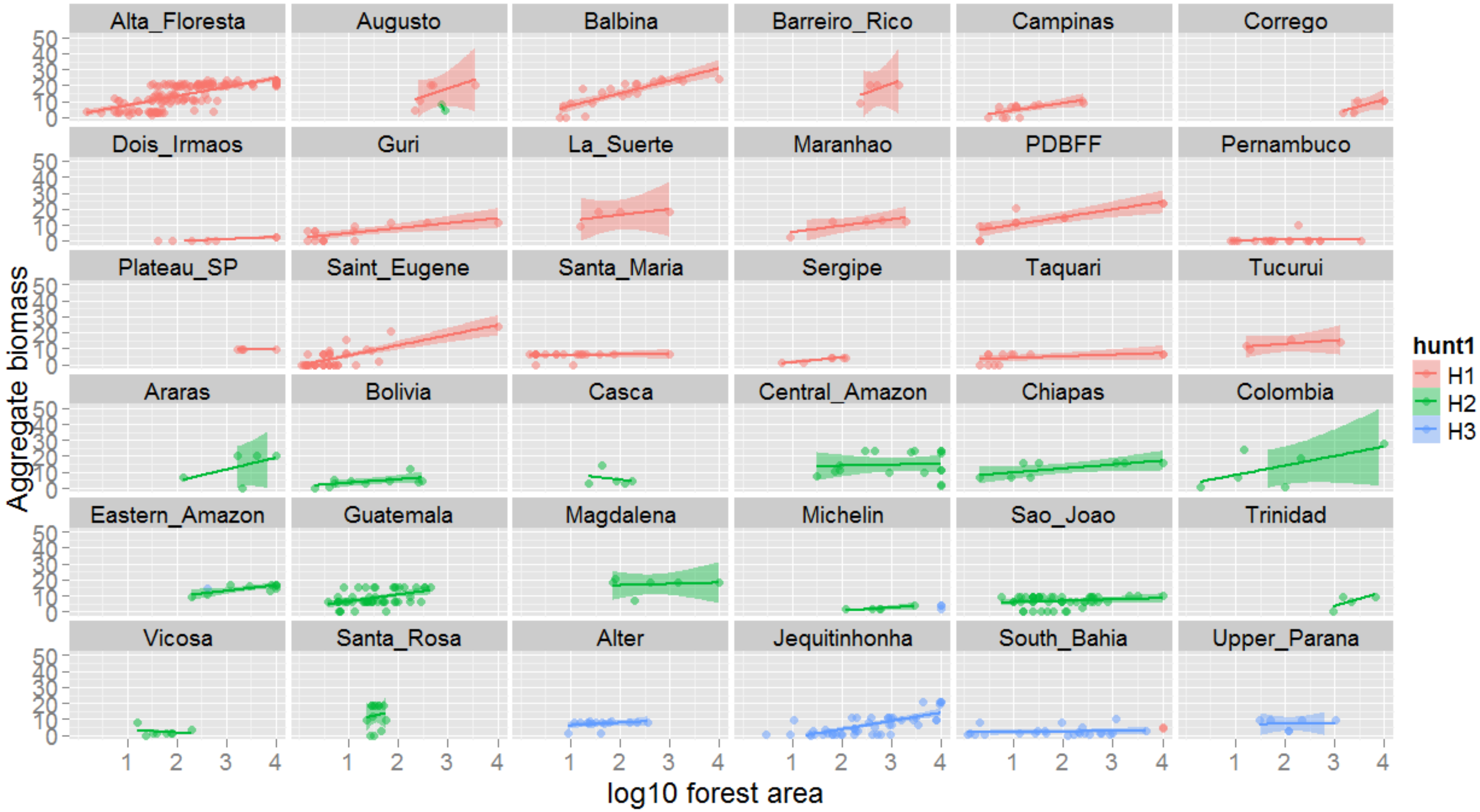
Appendix 2.3. Species-area relationships (SARs) for 36 landscapes containing a minimum of four forest sites, according to the level of hunting pressure (H1= non-hunted sites; H2= lightly hunted site; H3- heavily hunted site). Corrientes in northern Argentina and Los Tuxtlas, southern Mexico were excluded because all forest patches contained the same number of species.



Appendix 2.4. Biomass-area relationships (BARs) for 36 landscapes containing a minimum of four forest sites, according to the level of hunting pressure (H1= non-hunted sites; H2= lightly hunted site; H3- heavily hunted site). Corrientes in northern Argentina and Los Tuxtlas, southern Mexico were excluded because all forest patches contained the same number of species.

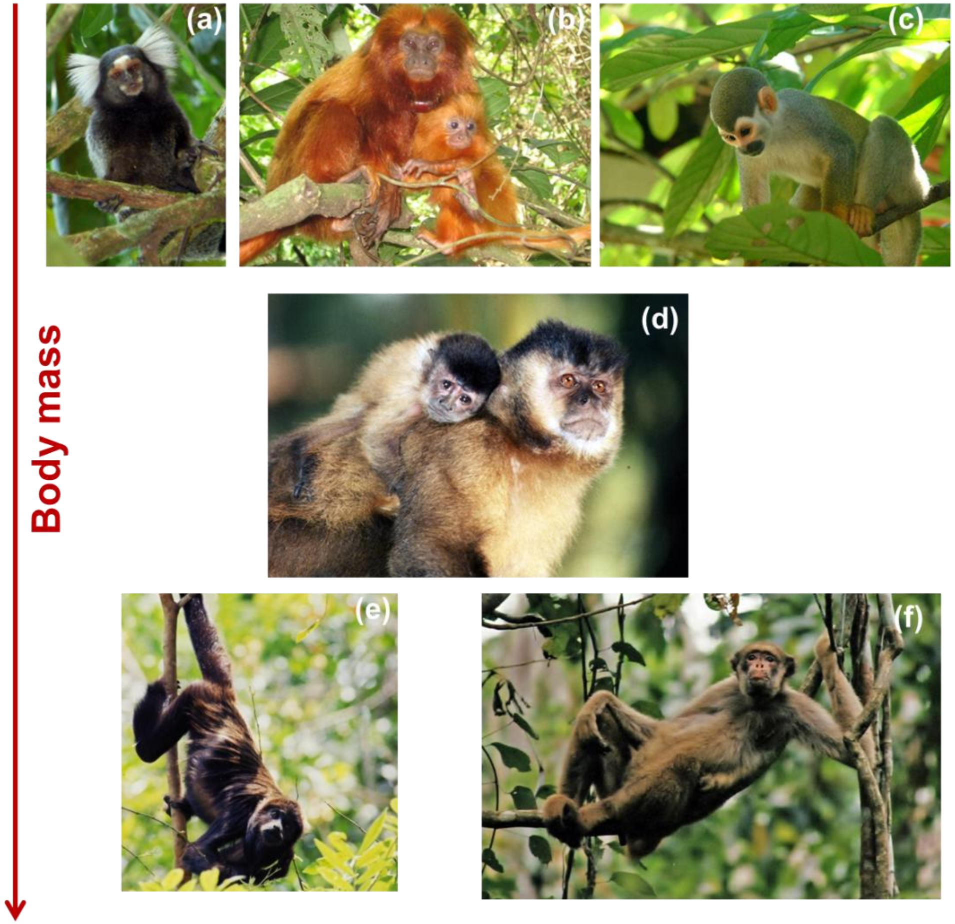


Appendix 2.5. Model selection table based on a candidate set of 'best' models predicting the proportion of primate species (p_S) and extant biomass (p_B) retained within 760 forest sites nested in 61 fragmented forest landscapes across the Neotropics, with S_{max} and B_{max} as offsets. The AIC score (AIC_c), the difference from the best model (ΔAIC) and Akaike weight (ω_i) are shown.

				Landscape variables				
	Model no.	**Intercept**	**Patch area**	**Hunting pressure**	**Matrix type**	**AIC_c**	**ΔAIC**	**ω_i**
P_S								
	1	-1.117	0.724			292.6	0.00	0.540
	2	-0.933	0.731	+		294.5	1.82	0.217
	3	-1.524	0.708		+	295.3	2.66	0.143
P_B								
	1	-1.058	0.865	+		357.0	0.00	0.645
	2	-1.464	0.864			359.1	2.05	0.232
	3	-1.210	0.859		+	361.0	3.96	0.089

Appendix 3.1. Size structure of some Neotropical primates, including (a) Atlantic forest marmoset; (b) golden-lion tamarin; (c) squirrel monkey; (d) capuchin monkey; (e) howler monkey; and (e) woolly-spider monkey. Photos by Marcio M. Morais Jr (a, d, e,f), Andressa S. Coelho (b) and Roberta M. Araujo (c).

Small	***Cebuella***
	Mico
	Saguinus
	Callimico
	Saimiri
	Callicebus
	Aotus
Medium	***Pithecia***
	Chiropotes
	Cacajao
	Cebus
Large	***Alouatta***
	Lagothrix
	Ateles



Appendix 4.1. Number of individuals and species of trees ≥ 10 cm DBH within each of all 87 plots studied across 37 forest sites in the Balbina dam.

Plot number	Island	Area (ha)	Number of individuals	Number of species
1	Toquinho	0.83	133	43
2	Joaninha	1.15	84	14
3	Formiga	1.52	95	42
4	Xibe	1.45	163	59
5	Andre	2.17	104	58
6	Cafundo	2.70	158	71
7	Panema	3.53	89	32
8	Torem	3.94	167	31
9	Pe Torto	5.85	132	43
10	Arrepiado	8.35	114	62
11	Jiquitaia	7.28	107	53
12	Garrafa	9.54	126	61
13	Abusado	13.41	101	55
14	Abusado	13.41	91	56
15	Coata	17.45	123	58
16	Coata	17.45	119	61
17	Palhal	21.21	123	41
18	Palhal	21.21	139	51
19	Piquia	13.59	109	50
20	Piquia	13.59	110	57
21	Neto	32.92	135	55
22	Neto	32.92	140	46
23	Bacaba	53.30	94	42
24	Bacaba	53.30	135	57
25	Adeus	97.62	114	65
26	Adeus	97.62	125	73

27	Relogio	72.10	100	53
28	Relogio	72.10	159	61
29	Sapupara	78.44	144	54
30	Sapupara	78.44	129	69
31	Moita	98.84	116	57
32	Moita	98.84	117	54
33	Moita	98.84	126	67
34	Pontal	110.43	118	59
35	Pontal	110.43	152	64
36	Pontal	110.43	164	67
37	Cipoal	218.74	157	70
38	Cipoal	218.74	139	53
39	Cipoal	218.74	118	47
40	Furo	193.00	119	60
41	Furo	193.00	124	57
42	Furo	193.00	124	72
43	Jabuti	231.39	129	64
44	Jabuti	231.39	122	68
45	Jabuti	231.39	122	70
46	Tucumari	292.41	132	70
47	Tucumari	292.41	107	57
48	Tucumari	292.41	125	49
49	Martelo	471.00	121	68
50	Martelo	471.00	137	63
51	Martelo	471.00	107	56
52	Tristeza	487.5	176	50
53	Tristeza	487.5	149	70
54	Tristeza	487.5	113	64
55	Tristeza	487.5	132	51
56	Beco Catitu	637.49	129	64
57	Beco Catitu	637.49	138	60
58	Beco Catitu	637.49	130	57

59	Beco Catitu	637.49	143	66
60	Mascote	673.35	96	50
61	Mascote	673.35	138	53
62	Mascote	673.35	116	66
63	Mascote	673.35	121	55
64	Fuzaca	761.02	126	59
65	Fuzaca	761.02	180	69
66	Fuzaca	761.02	109	64
67	Fuzaca	761.02	128	72
68	Porto Seguro	1466.00	139	58
69	Porto Seguro	1466.00	136	65
70	Porto Seguro	1466.00	151	64
71	Porto Seguro	1466.00	127	57
72	Gaviao-real	1690.04	140	66
73	Gaviao-real	1690.04	142	64
74	Gaviao-real	1690.04	148	67
75	Gaviao-real	1690.04	119	57
76	Mainland 1	∞	129	66
77	Mainland 1	∞	134	65
78	Mainland 1	∞	153	78
79	Mainland 1	∞	140	73
80	Mainland 2	∞	143	62
81	Mainland 2	∞	129	60
82	Mainland 2	∞	132	63
83	Mainland 2	∞	131	59
84	Mainland 3	∞	152	72
85	Mainland 3	∞	112	56
86	Mainland 3	∞	167	70
87	Mainland 3	∞	144	72

Appendix 4.2. List of 59 families, 368 tree species and their frequency (number of plots on which the species occurred) within 87 forest plots sampled within 37 forest sites in the Balbina dam. Species are listed by alphabetical order of family and species name.

Family	**Species**	**Frequency**
Anacardiaceae	*Anacardium giganteum*	9
	Anacardium parvifolium	2
	Tapirira guianensis	19
	Thyrsodium spruceanum	19
Anisophylleaceae	*Anisophyllea manausensis*	8
Annonaceae	*Bocageopsis multiflora*	24
	Duguetia flagellaris	8
	Duguetia stelechantha	13
	Duguetia surinamensis	20
	Fusaea longifolia	9
	Guatteria olivacea	59
	Guatteriopsis blepharophylla	23
	Rollinia insignis	4
	Unonopsis duckei	37
	Xylopia amazonica	9
	Xylopia benthamii	2
	Xylopia calophylla	18
	Xylopia cuspidata	1
Apocynaceae	*Aspidosperma aracanga*	4
	Aspidosperma nitidum	10
	Couma guianensis	6
	Geissospermum argenteum	13
	Himatanthus sucuuba	4
	Lacmellea aculeata	1
	Lacmellea gracilis	1
	Tabernaemontana angulata	2
	Tabernaemontana flavicans	1

	Aspidosperma aracanga	4
	Aspidosperma nitidum	10
	Couma guianensis	6
	Geissospermum argenteum	13
	Himatanthus sucuuba	4
	Lacmellea aculeata	1
	Lacmellea gracilis	1
	Tabernaemontana angulata	2
	Tabernaemontana flavicans	1
Araliaceae	*Schefflera morototoni*	13
Arecaceae	*Astrocaryum aculeatum*	2
	Astrocaryum murumuru	24
	Attalea maripa	3
	Euterpe precatoria	34
	Maximiliana maripa	1
	Oenocarpus bacaba	83
	Oenocarpus bataua	1
	Oenocarpus minor	2
	Orbignya phalerata	2
	Socrateae exorrhiza	1
	Syagrus inajai	1
Bignoniaceae	*Jacaranda copaia*	11
	Tabebuia incana	3
	Tabebuia serratifolia	22
Boraginaceae	*Cordia exaltata*	37
Burseraceae	*Protium altsonii*	55
	Protium apiculatum	37
	Protium aracouchini	3
	Protium decandrum	72
	Protium giganteum	2
	Protium hebetatum	83
	Protium opacum	13

	Protium pilosum	11
	Protium trifoliolatum	5
	Tetragastris altissima	2
	Tetragastris panamensis	43
Caryocaraceae	*Caryocar glabrum*	27
	Caryocar villosum	4
Celastraceae	*Maytenus guianensis*	3
Chrysobalanaceae	*Couepia canomensis*	2
	Couepia robusta	17
	Hirtella mymercophila	1
	Hirtella racemosa	5
	Licania adolphoduckei	3
	Licania bracteata	4
	Licania canescens	30
	Licania heteromorpha	29
	Licania impressa	73
	Licania micrantha	23
	Licania niloi	18
	Licania oblongifolia	9
	Licania rodriguesii	17
	Licania sothersiae	19
	Parinari excelsa	43
	Parinari montana	5
	Parinari parvifolia	25
	_	1
Clusiaceae	*Garcinia madruno*	1
	Moronobea coccinea	8
	Symphonia globulifera	10
	Tovomita obovata	17
Combretaceae	*Buchenavia grandis*	15
	Buchenavia guianensis	4
	Buchenavia parvifolia	9

Coricaceae	*Jacaratia spinosa*	1
Dichapetalaceae	*Tapura amazonica*	3
Ebenaceae	*Diospyros cavalcantei*	5
	Diospyros guianensis	25
Elaeocarpaceae	*Sloanea excelsa*	8
	Sloanea schomburgkii	1
	Sloanea synandra	28
Erythroxylaceae	*Erythroxylum citrifolium*	1
Euphorbiaceae	*Anomalocalyx uleanus*	20
	Aparisthmium cordatum	8
	Conceveiba guianensis	3
	Croton lanjouwensis	39
	Glycidendron amazonicum	4
	Hevea guianensis	17
	Mabea angularis	16
	Mabea piriri	1
	Mabea speciosa	18
	Maprounea guianensis	3
	Micrandra spruceana	2
	Micrandropsis scleroxylon	27
	Pausandra macropetala	2
	Pogonophora schomburgkiana	5
	Sapium glandulosum	11
Fabaceae	*Abarema jupunba*	4
	Andira micrantha	57
	Andira unifoliolata	3
	Bocoa viridiflora	56
	Dinizia excelsa	8
	Diplotropis martiusii	41
	Dipteryx magnifica	8
	Dipteryx odorata	14
	Eperua duckeana	2

Hymenaea intermedia	7
Hymenolobium modestum	7
Inga alba	42
Inga cayennensis	40
Inga cordatoalata	8
Inga gracilifolia	5
Inga grandiflora	15
Inga marginata	41
Inga obidensis	11
Inga paraensis	15
Inga splendens	1
Inga stipularis	1
Inga umbratica	2
Macrolobium limbatum	3
Macrolobium prancei	2
Paramachaerium ormosioides	19
Parkia multijuga	24
Parkia nitida	2
Parkia pendula	5
Peltogyne catingae	3
Peltogyne paniculata	5
Platymiscium duckei	14
Pseudopiptadenia psilostachya	5
Pterocarpus officinalis	42
Pterocarpus rohrii	9
Schizolobium amazonicum	7
Stryphnodendron guianense	11
Swartzia arborescens	2
Swartzia cuspidata	7
Swartzia oblanceolata	6
Swartzia panacoco	3
Swartzia polyphylla	2

	Swartzia reticulata	8
	Swartzia ulei	1
	Tachigali chrysophylla	8
	Tachigali glauca	33
	Tachigali micropetala	28
	Vatairea sericea	2
	Zygia juruana	4
	Zygia racemosa	39
	Zygia ramiflora	16
Flacourtiaceae	*Ryania speciosa*	5
Goupiaceae	*Goupia glabra*	30
Hugoniaceae	*Roucheria punctata*	4
Humiriaceae	*Endopleura uchi*	22
	Sacoglottis mattogrossensis	11
	Vantanea guianensis	2
	Vantanea parviflora	8
Hypericacaeae	*Vismia cayennensis*	13
	Vismia guianensis	24
	Vismia japurensis	4
	Vismia sandwithii	2
Icacinaceae	*Poraqueiba sericea*	2
Lacistemataceae	*Lacistema aggregatum*	4
Lauraceae	*Aniba canelilla*	2
	Aniba megaphylla	1
	Aniba rosaeodora	8
	Licaria guianensis	23
	Licaria martiniana	44
	Licaria rodriguesii	1
	Mezilaurus duckei	7
	Mezilaurus itauba	22
	Nectandra cuspidata	1
	Ocotea aciphylla	2

	Ocotea argyrophylla	1
	Ocotea cinerea	1
	Ocotea longifolia	1
	Ocotea myriantha	1
	Ocotea nigrescens	73
	Ocotea olivacea	6
	Rhodostemonodaphne grandis	9
	Sextonia rubra	13
Lecythidaceae	*Bertholletia excelsa*	7
	Cariniana micrantha	23
	Corythophora alta	13
	Corythophora rimosa	1
	Couratari stellata	5
	Eschweilera collina	32
	Eschweilera coriacea	49
	Eschweilera cyathiformis	5
	Eschweilera grandiflora	23
	Eschweilera pseudodecolorans	2
	Eschweilera romeucardosoi	68
	Eschweilera tessmannii	31
	Eschweilera truncata	80
	Eschweilera wachenheimii	43
	Gustavia elliptica	2
	Lecythis barnebeyii	1
	Lecythis prancei	8
	Lecythis zabucajo	12
Malpighiaceae	*Byrsonima chrysophylla*	22
	Byrsonima crispa	1
	_	1
Malvaceae	*Apeiba echinata*	31
	Catostemma albuquerquei	24
	Eriotheca globosa	8

	Lueheopsis rosea	4
	Quararibea ochrocalyx	49
	Scleronema micranthum	79
	Sterculia excelsa	10
	Theobroma grandiflorum	2
	Theobroma speciosum	2
	Theobroma subincanum	36
	Theobroma sylvestre	47
Melastomataceae	*Bellucia grossularioides*	1
	Bellucia imperialis	2
	Henriettella caudata	1
	Miconia argyrophylla	1
	Miconia dispar	4
	Miconia eriodonta	10
	Miconia martiniana	1
	Miconia poeppigii	4
	Miconia pyrifolia	2
	Miconia tetraspermoides	1
	Miconia tomentosa	1
Meliaceae	*Carapa guianensis*	5
	Guarea humaitensis	2
	Guarea pubescens	60
	Guarea silvatica	11
	Trichilia cipo	6
	Trichilia pleeana	29
	Trichilia schomburgkii	3
	Trichilia sp.	1
Memecylaceae	*Mouriri ficoides*	15
Moraceae	*Brosimum guianense*	2
	Brosimum parinarioides	31
	Brosimum rubescens	29
	Clarisia racemosa	11

	Ficus sp.	1
	Helianthostylis sprucei	2
	Helicostylis scabra	22
	Helicostylis tomentosa	5
	Maquira sclerophylla	39
	Naucleopsis caloneura	30
	Naucleopsis ulei	2
	Pseudolmedia laevigata	4
	Pseudolmedia laevis	44
	Sorocea guilleminiana	1
	Sorocea muriculata muriculata	38
Myristicaceae	*Iryanthera juruensis*	39
	Iryanthera laevis	1
	Iryanthera ulei	51
	Osteophloeum platyspermum	44
	Virola calophylla calophylla	20
	Virola juruensis	2
	Virola michelii	20
	Virola mollissima	16
	Virola pavonis	25
	Virola theiodora	24
Myrsinaceae	*Cybianthus guyanensis*	2
Myrtaceae	*Calycolpus goetheanus*	22
	Eugenia cupulata	6
	Eugenia florida	36
	Marlierea caudata	2
	Marlierea umbraticola	1
	Myrcia amazonica	8
	Myrcia fallax	1
	Myrcia fenestrata	2
	Myrcia huallagae	1
	Myrcia minutiflora	7

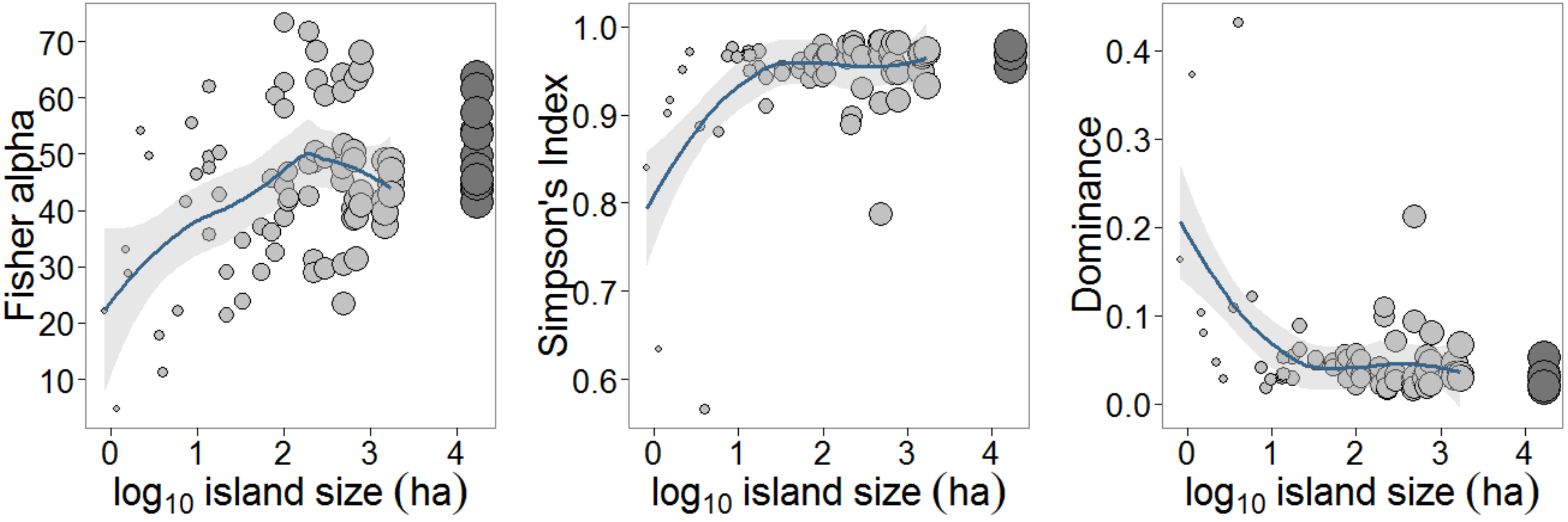
	Myrcia paivae	14
	Myrciaria floribunda	1
	Psidium guineense	1
Nyctaginaceae	*Guapira sp. 1*	3
	Neea oppositifolia	5
	Neea sp. 1	25
Ochnaceae	*Cespedezia spathulata*	1
	Ouratea discophora	4
	Ouratea odora	4
Olacaceae	*Dulacia candida*	5
	Heisteria barbata	9
	Minquartia guianensis	46
Polygalaceae	*Moutabea sp.*	14
Polygonaceae	*Coccoloba mollis*	1
Proteaceae	*Roupala montana*	3
Quiinaceae	*Lacunaria crenata*	1
	Lacunaria jenmanii	2
	Quiina amazonica	2
	Touroulia guianensis	1
Rhizophoraceae	*Sterigmapetalum obovatum*	5
Rubiaceae	*Borojoa claviflora*	1
	Chimarrhis barbata	9
	Duroia longiflora	12
	Duroia macrophylla	1
	Duroia saccifera	3
	Isertia hypoleuca	3
	Kutchubaea sericantha	2
Rutaceae	*Zanthoxylum djalma-batistae*	2
Salicaceae	*Casearia javitensis*	9
	Casearia manausensis	5
	Casearia pitumba	2
	Laetia procera	11

Sapindaceae	*Allophylus latifolius*	1
	Cupania scrobiculata	2
	Talisia mollis	30
	Toulicia cf. pulvinata	1
Sapotaceae	*Chromolucuma rubiflora*	1
	Chrysophyllum amazonicum	3
	Chrysophyllum sanguinolentum balata	8
	Chrysophyllum sanguinolentum sanguinolentum	1
	Ecclinusa guianensis	52
	Manilkara bidentata	4
	Manilkara cavalcantei	4
	Manilkara huberi	7
	Micropholis guyanensis	11
	Micropholis guyanensis duckeana	1
	Micropholis guyanensis guyanensis	8
	Micropholis splendens	5
	Micropholis venulosa	5
	Micropholis williamii	19
	Pouteria anomala	29
	Pouteria caimito	9
	Pouteria cuspidata	1
	Pouteria filipes	16
	Pouteria freitasii	24
	Pouteria guianensis	84
	Pouteria minima	28
	Pouteria oppositifolia	2
	Pouteria pallens	60
	Pouteria platyphylla	1
	Pouteria reticulata	41
	Pouteria rostrata	1
	Pouteria stipulifera	2
	Pouteria virescens	23

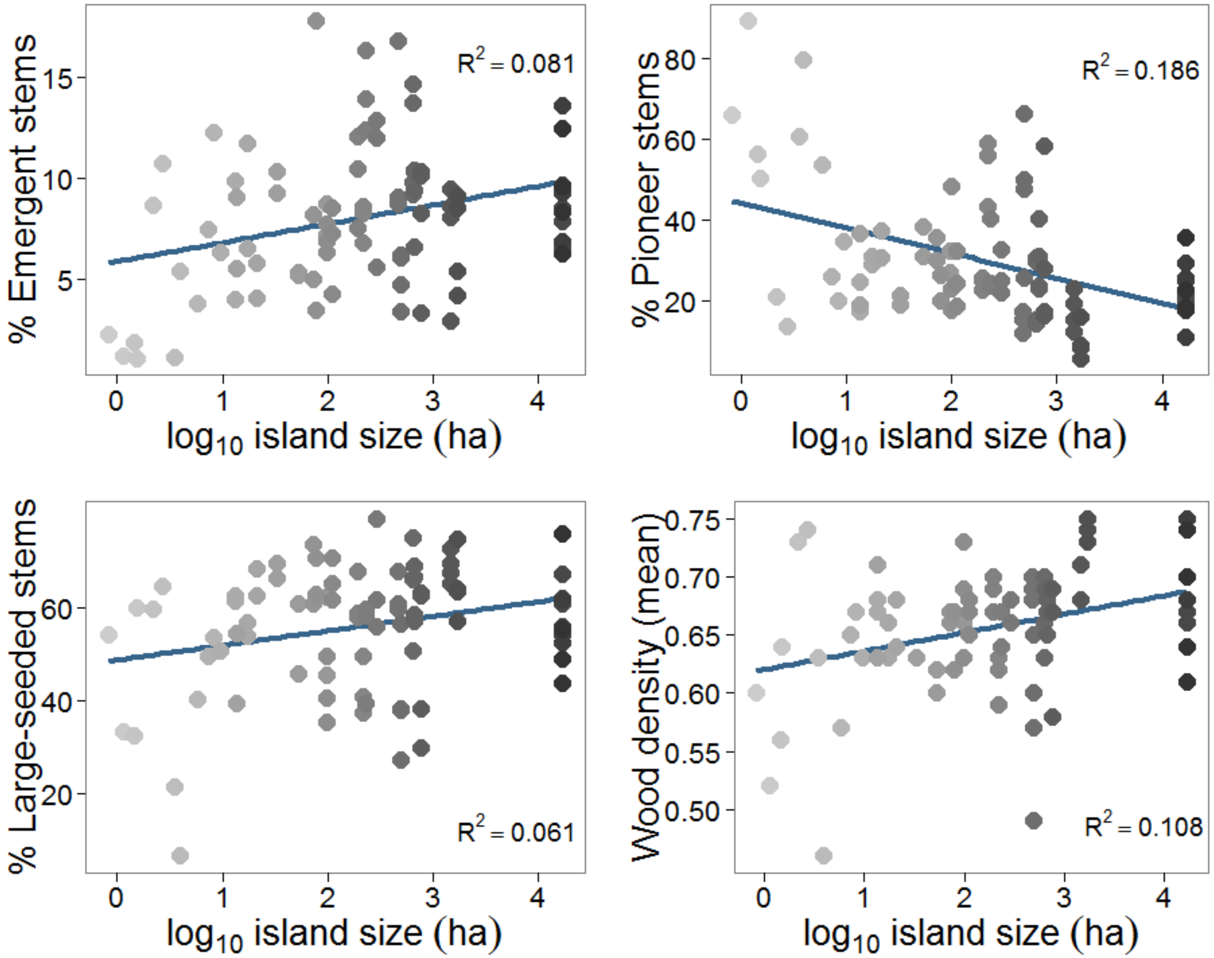
Pouteria williamii	1
Pradosia cochlearia praealta	1
Sarcaulus brasiliensis	9
Chromolucuma rubiflora	1
Chrysophyllum amazonicum	3
Chrysophyllum sanguinolentum balata	8
Chrysophyllum sanguinolentum sanguinolentum	1
Ecclinusa guianensis	52
Manilkara bidentata	4
Manilkara cavalcantei	4
Manilkara huberi	7
Micropholis guyanensis	11
Micropholis guyanensis duckeana	1
Micropholis guyanensis guyanensis	8
Micropholis splendens	5
Micropholis venulosa	5
Micropholis williamii	19
Pouteria anomala	29
Pouteria caimito	9
Pouteria cuspidata	1
Pouteria filipes	16
Pouteria freitasii	24
Pouteria guianensis	84
Pouteria minima	28
Pouteria oppositifolia	2
Pouteria pallens	60
Pouteria platyphylla	1
Pouteria reticulata	41
Pouteria rostrata	1
Pouteria stipulifera	2
Pouteria virescens	23
Pouteria williamii	1

	Pradosia cochlearia praealta	1
	Sarcaulus brasiliensis	9
Simaroubaceae	*Simaba cedron*	1
	Simaba polyphylla	2
	Simarouba amara	9
Siparunaceae	*Siparuna decipiens*	34
	Siparuna guianensis	2
Theaceae	*Ternstroemia urophora*	3
Ulmaceae	*Ampelocera edentula*	7
Urticaceae	*Cecropia purpurascens*	8
	Cecropia sciadophylla	39
	Coussapoa orthoneura	2
	Pourouma bicolor	26
	Pourouma cuspidata	26
	Pourouma guianensis	1
	Pourouma minor	31
	Pourouma ovata	15
	Pourouma tomentosa	14
	Pourouma villosa	10
Verbenaceae	-	1
Violaceae	*Amphirrhox longifolia*	14
	Leonia cymosa	1
	Leonia glycycarpa	1
	Paypayrola grandiflora	12
	Rinorea guianensis	36
	Rinorea macrocarpa	4
	Rinorea racemosa	51
Vochysiaceae	*Erisma bicolor*	7
	Erisma bracteosum	1
	Qualea paraensis	7

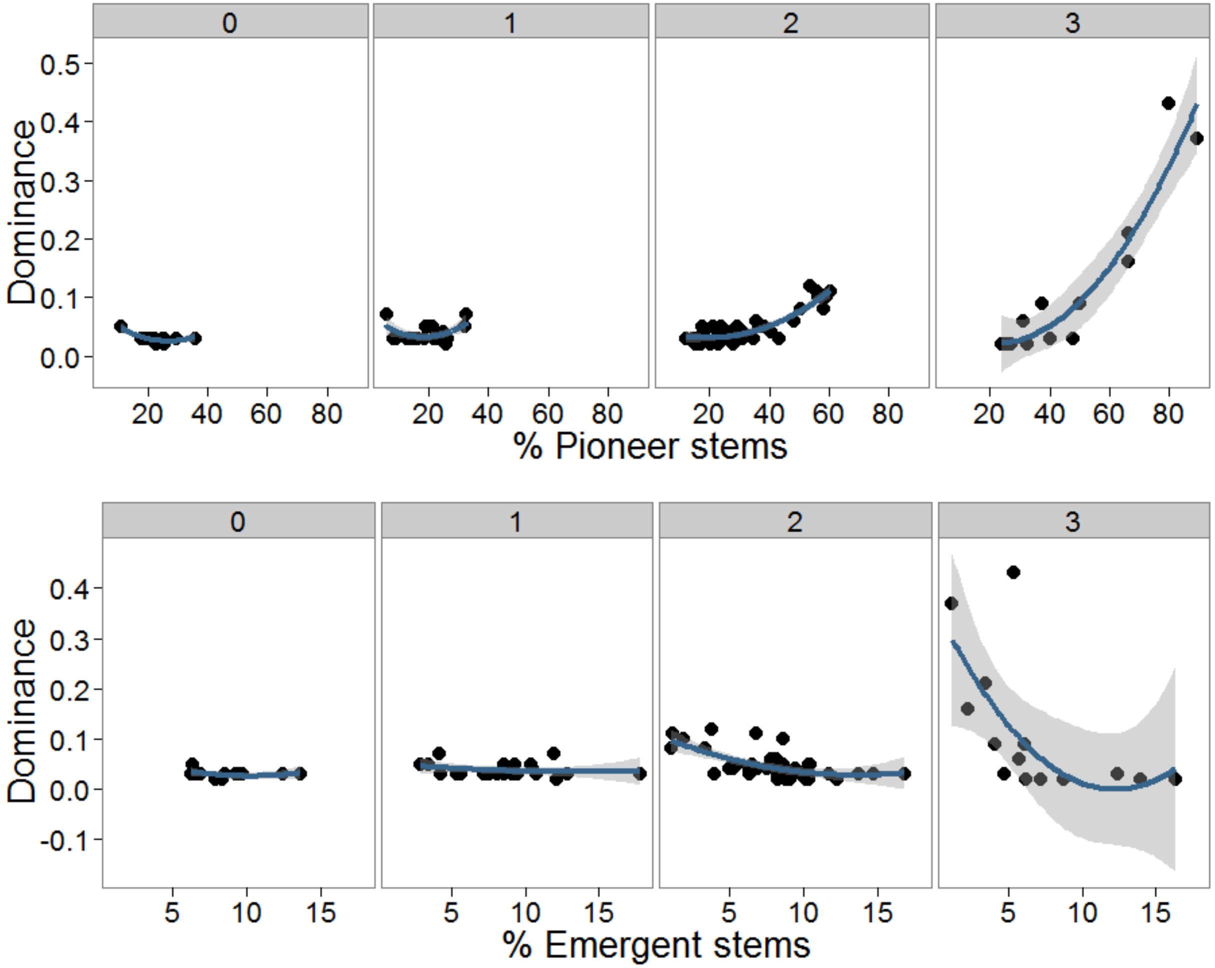
Appendix 4.3. Relationship between floristic diversity metrics and island area within 87 plots across 34 islands (light grey; N=75 plots) and three continuous (dark grey; N=12 plots) forest sites surveyed at the Balbina Reservoir. Sizes of circles are proportional to the log-transformed areas of forest sites.



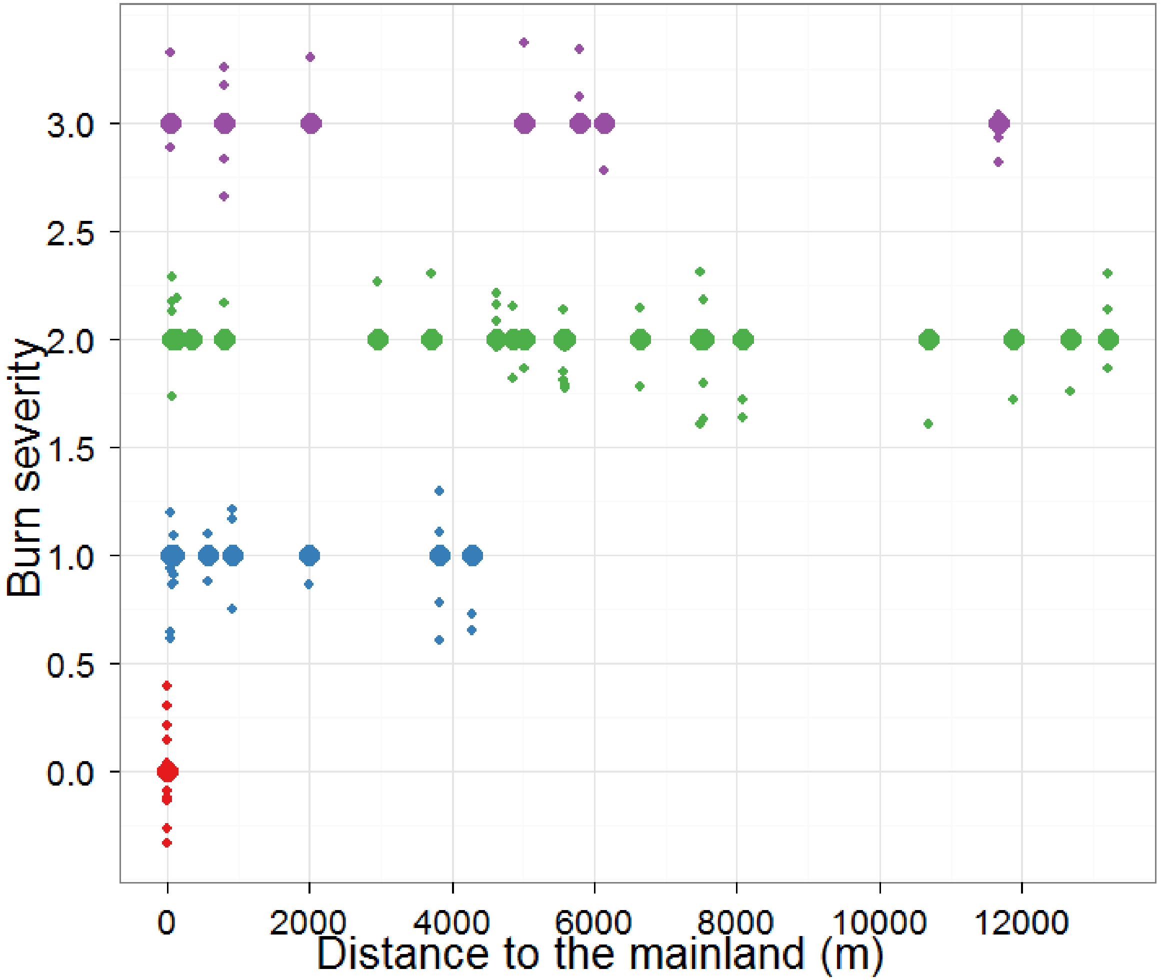
Appendix 4.4. Relationships between ($\log_{10}$) island area and functional attributes representing the tree species assemblage structure within 87 plots across 37 forest sites surveyed at the Balbina Reservoir. Circles are coloured according to the log-transformed areas of forest sites.



Appendix 4.5. Dominance of tree assemblages within 87 plots across 37 forest sites surveyed at the Balbina Reservoir in function of percentages of both pioneer and emergent stems, according to the level of fire severity [(0)= non-disturbed by fire; (1) = lightly disturbed; (2) moderately disturbed; and (3) heavily disturbed].



Appendix 4.6. Distribution of surface fires within 87 plots across 37 forest sites surveyed at the Balbina Reservoir according to the shortest linear distance from each island to the nearest mainland.



Appendix 5.1. Forest area and sampling effort allocated to the 40 forest sites surveyed across the Balbina Hydroelectric Reservoir landscape.

Site name	Forest area (ha)[1]	Number of transects	Length (km)	Camera-trapping [effort[4] / (no. CT stations[5])]	Line-transect censuses (km)	Sign surveys (km)	Armadillo-burrow counts (km)	Number of plots[7]
Toquinho	0.55	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Joaninha	1.01	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Xibe	1.41	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Formiga	1.52	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Louzivaldo	1.74	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Aline	1.86	1	0.5	120 (2)	4.0	4.0	0.5	1
Andre	2.17	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Cafundo	2.70	1	Sweep [0.5][2]	120 (2)	4.0	4.0	0.5	1
Panema	3.31	1	0.5	120 (2)	4.0	4.0	0.5	1
Torem	3.52	1	0.5	120 (2)	4.0	4.0	0.5	1
Pe Torto	5.85	1	0.5	120 (2)	4.0	4.0	0.5	1
Jiquitaia	6.85	1	0.5	120 (2)	4.0	4.0	0.5	1
Abandonada	8.23	1	Sweep [0.5][2,3]	120 (2)	4.0	4.0	0.5	1
Arrepiado	8.35	1	0.5	120 (2)	4.0	4.0	0.5	1
Garrafa	9.22	1	0.5	120 (2)	4.0	4.0	0.5	1
Abusado	12.37	1	0.5	120 (2)	4.0	4.0	0.5	2
Piquia	13.59	1	0.5	120 (2)	4.0	4.0	0.5	2
Coata	17.45	1	0.5	120 (2)	4.0	4.0	0.5	2
Palhal	21.21	1	0.5	120 (2)	4.0	4.0	0.5	2
Neto	32.82	1	1.0	120 (2)	8.0	8.0	1.0	2
Bacaba	53.20	1	1.0	120 (2)	8.0	8.0	1.0	2
Relogio	70.80	1	1.5	240 (4)	12.0	12.0	1.5	2
Sapupara	77.89	1	1.0	240 (4)	8.0	8.0	1.0	2
Adeus	95.05	2	0.5/0.5	240 (4)	8.0	8.0	1.0	2
Moita	97.42	2	1.0/1.0	240 (4)	16.0	16.0	2.0	3
Pontal	110.03	3	1.0/1.0/1.0	360 (6)	24.0	24.0	3.0	3
Furo	193.00	4	1.0/1.0/1.0/1.0	480 (8)	32.0	32.0	4.0	3
Cipoal	218.74	3	1.0/1.0/1.0	360 (6)	24.0	24.0	3.0	3
Jabuti	230.14	3	1.0/2.0/1.0	480 (8)	32.0	32.0	4.0	3
Tucumari	292.32	3	1.0/1.0/1.0	480 (8)	24.0	24.0	3.0	3

Martelo	469.76	4	1.0/1.0/1.0/1.0	480 (8)	32.0	32.0	4.0	3
Tristeza	484.03	4	0.5/1.5/2.0/1.0	600 (10)	40.0	40.0	5.0	4
Beco do Catitu	627.46	5	1.0/1.0/1.0/1.0/1.0	600 (10)	40.0	40.0	5.0	4
Mascote	669.88	2	2.0/3.0	600 (10)	40.0	40.0	5.0	4
Fuzaca	744.80	4	2.5/1.0/1.0/1.0	600 (10)	44.0	44.0	5.5	4
Porto Seguro	1459.70	5	1.5/2.0/1.5/1.0/1.0	600 (10)	56.0	56.0	7.0	4
Gaviao Real	1685.38	5	1.0/1.0/1.5/1.0/2.5	600 (10)	56.0	56.0	7.0	4
TF1	∞	3	4.0/4.0/4.0	900 (15)	192.0[6]	192.0[6]	12.0	4
TF2	∞	3	4.0/4.0/4.0	900 (15)	192.0[6]	192.0[6]	12.0	4
TF3	∞	3	4.0/4.0/4.0	900 (15)	192.0[6]	192.0[6]	12.0	4
TOTAL		81	108.5	12,420 (207)	1,168	1,168	108.5	90

[1] – Total area of island covered by vegetation including shrubs, second-growth and primary forests; [2] – Due to the small island size, sweep strip surveys were conducted by four independent observers operating simultaneously, until they each obtained a census distance of 0.5 km, with one line-transect set from the furthest edge to edge, established for camera traps deployment; [3] – Island dominated by shrubs, precluding the establishing of line transects; [4] – Total effort indicates the number of CT stations deployed, multiplied by the number of sampling days at each site; [5] – Number of CT stations deployed during each 30-day annual session; [6] – Two-way line-transect surveys were carried out within continuous forest sites; [7] – Each forest plot of 0.25 ha.

Appendix 5.2. Literature used for compilation of life-history data of vertebrate species examined in our study.

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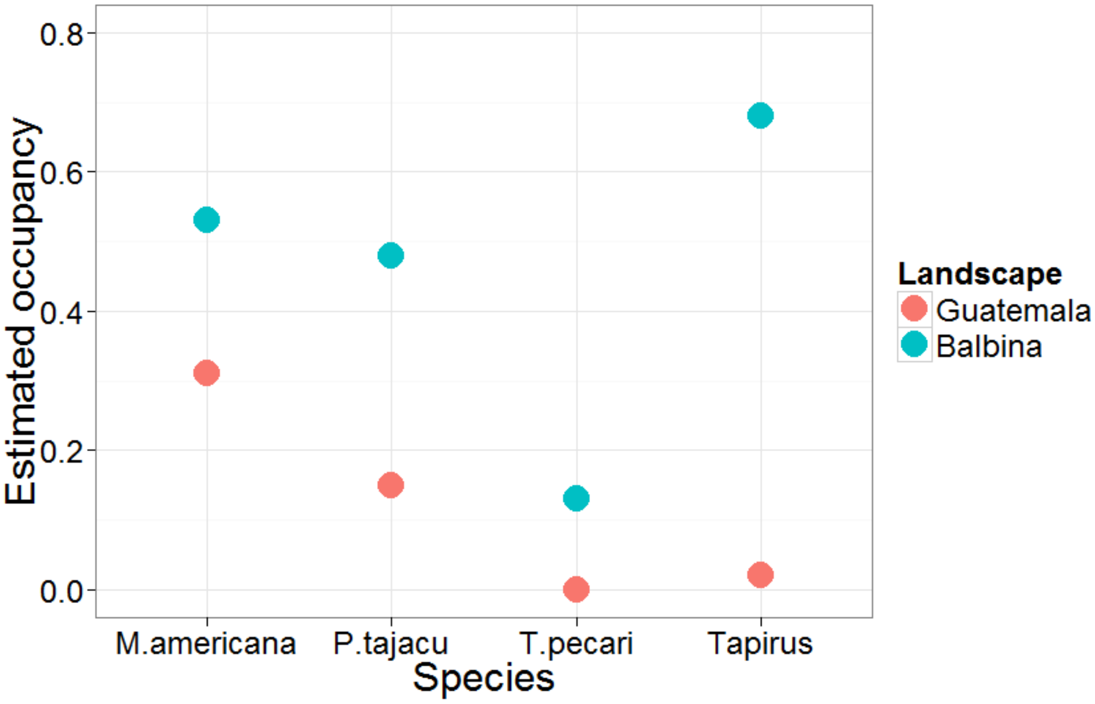
Appendix 5.3. Photographs of vertebrates recorded by camera traps within surveyed islands at the Balbina Hydroelectric Reservoir landscape (from the left to the right, side by side: Amazonian brown brocket deer, tapir, red-rumped agouti, black currasow, giant anteater, giant armadillo, tayra and puma).

Appendix 5.4. Estimated site occupancy obtained for four ungulate species among the Balbina (N=40) and Guatemala landscapes (N=50). Tapirus constitutes *Tapirus terrestris* at Balbina and *Tapirus bairdii* at Guatemala landscapes.



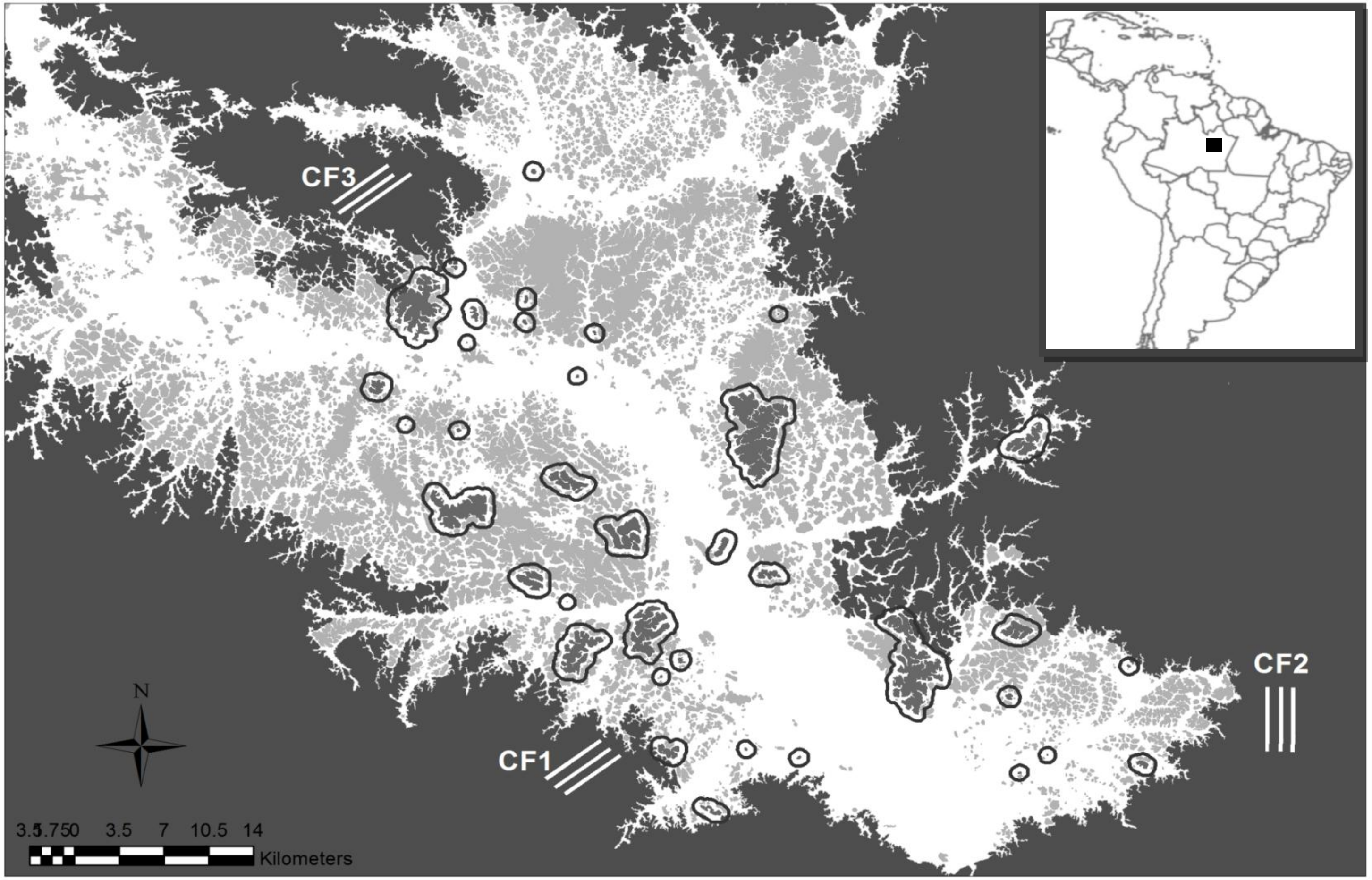
Appendix 6.1. Geographic information, patch/landscape metrics, and sampling effort allocated to the 40 forest sites surveyed across the Balbina Hydroelectric Reservoir landscape.

Site name	Site characteristics							Sampling effort			
	UTM (X)	UTM (Y)	Forest area (ha)[1]	Isolation (km)[2]	Number of plots[3]	Number of transects	Length (km)	Line-transect censuses (km)	Sign surveys (km)	Armadillo-burrow counts (km)	Camera-trapping [effort[7] / (no. CT stations[8])]
Toquinho	193046	9809792	0.55	5.01	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Joaninha	185184	9831524	1.01	6.12	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Xibe	184359	9837426	1.41	0.34	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Formiga	230702	9797149	1.52	5.02	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Louzivaldo	228576	9795661	1.74	3.62	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Aline	193794	9828616	1.86	17.43	1	1	0.5	4.0	4.0	0.5	120 (2)
Andre	180451	9824638	2.17	10.68	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Cafundo	209613	9833955	2.70	2.00	1	1	Sweep [0.5][4]	4.0	4.0	0.5	120 (2)
Panema	200419	9803597	3.31	2.96	1	1	0.5	4.0	4.0	0.5	120 (2)
Torem	207096	9797589	3.52	2.02	1	1	0.5	4.0	4.0	0.5	120 (2)
Pe Torto	237118	9804515	5.85	0.15	1	1	0.5	4.0	4.0	0.5	120 (2)
Jiquitaia	211331	9796843	6.85	0.80	1	1	0.5	4.0	4.0	0.5	120 (2)
Abandonada	190366	9845914	8.23	3.92	1	1	Sweep [0.5][4,5]	4.0	4.0	0.5	120 (2)
Arrepiado	195111	9832440	8.35	12.67	1	1	0.5	4.0	4.0	0.5	120 (2)
Garrafa	184620	9824267	9.22	11.82	1	1	0.5	4.0	4.0	0.5	120 (2)
Abusado	201895	9804887	12.37	4.82	2	1	0.5	4.0	4.0	0.5	120 (2)
Piquia	189588	9833341	13.59	7.44	2	1	0.5	4.0	4.0	0.5	120 (2)
Coata	189721	9834874	17.45	6.67	2	1	0.5	4.0	4.0	0.5	120 (2)
Palhal	227620	9802094	21.21	5.80	2	1	0.5	4.0	4.0	0.5	120 (2)
Neto	238378	9796254	32.82	0.58	2	1	1.0	8.0	8.0	1.0	120 (2)
Bacaba	185791	9834066	53.20	3.71	2	1	1.0	8.0	8.0	1.0	120 (2)
Relogio	205429	9815025	70.80	8.09	2	1	1.5	12.0	12.0	1.5	240 (4)
Sapupara	209362	9812209	77.89	4.28	2	1	1.0	8.0	8.0	1.0	240 (4)
Adeus	205064	9792225	95.05	0.05	2	2	0.5/0.5	8.0	8.0	1.0	240 (4)
Moita	177596	9827596	97.42	7.53	3	2	1.0/1.0	16.0	16.0	2.0	240 (4)
Pontal	200258	9797872	110.03	0.07	3	3	1.0/1.0/1.0	24.0	24.0	3.0	360 (6)
Furo	228359	9808020	193.00	0.91	3	4	1.0/1.0/1.0/1.0	32.0	32.0	4.0	480 (8)
Cipoal	190502	9811122	218.74	5.58	3	3	1.0/1.0/1.0	24.0	24.0	3.0	360 (6)
Jabuti	192651	9820569	230.14	11.67	3	3	1.0/2.0/1.0	32.0	32.0	4.0	480 (8)
Tucumari	229622	9824006	292.32	0.09	3	3	1.0/1.0/1.0	24.0	24.0	3.0	480 (8)

Martelo	196973	9814617	469.76	13.22	3	4	1.0/1.0/1.0/1.0	32.0	32.0	4.0	480 (8)
Tristeza	194478	9805095	484.03	0.79	4	4	0.5/1.5/2.0/1.0	40.0	40.0	5.0	600 (10)
Beco do Catitu	198737	9806219	627.46	5.56	4	5	1.0/1.0/1.0/1.0/1.0	40.0	40.0	5.0	600 (10)
Mascote	182883	9818284	669.88	4.62	4	2	2.0/3.0	40.0	40.0	5.0	600 (10)
Fuzaca	182475	9834117	744.80	0.06	4	4	2.5/1.0/1.0/1.0	44.0	44.0	5.5	600 (10)
Porto Seguro	220417	9800867	1459.70	0.04	4	5	1.5/2.0/1.5/1.0/1.0	56.0	56.0	7.0	600 (10)
Gaviao Real	208080	9820719	1685.38	3.82	4	5	1.0/1.0/1.5/1.0/2.5	56.0	56.0	7.0	600 (10)
TF1	194892	9795365	∞	0.00	4	3	4.0/4.0/4.0	192.0[6]	192.0[6]	12.0	900 (15)
TF2	249932	9801631	∞	0.00	4	3	4.0/4.0/4.0	192.0[6]	192.0[6]	12.0	900 (15)
TF3	179365	9844218	∞	0.00	4	3	4.0/4.0/4.0	192.0[6]	192.0[6]	12.0	900 (15)
TOTAL					90	81	108.5	1,168	1,168	108.5	12,420 (207)

[1] – Total area of island covered by vegetation including shrubs, second-growth and primary forests; [2] – Linear distance to the nearest continuous forest; [3] – Each forest plot of 0.25 ha; [4] – Due to the small island size, sweep strip surveys were conducted by four independent observers operating simultaneously, until they each obtained a census distance of 0.5 km, with one line-transect set from the furthest edge to edge, established for camera traps deployment; [5] – Island dominated by shrubs, precluding the establishing of line transects; [6] – Two-way line-transect surveys were carried out within continuous forest sites; [7] – Total effort indicates the number of CT stations deployed, multiplied by the number of sampling days at each site; [8] – Number of CT stations deployed during each 30-day annual session.

Appendix 6.2. Location of the Balbina Hydroelectric Reservoir (BHR) landscape in the state of Amazonas, Brazil, showing the 37 surveyed land-bridge islands (dark grey) and three undisturbed continuous forest (CF) sites in the mainland (CF1, CF2 and CF3; very dark gray). Black contours indicate 500-m buffer polygons around each island. All unsurveyed islands are shown in light gray.

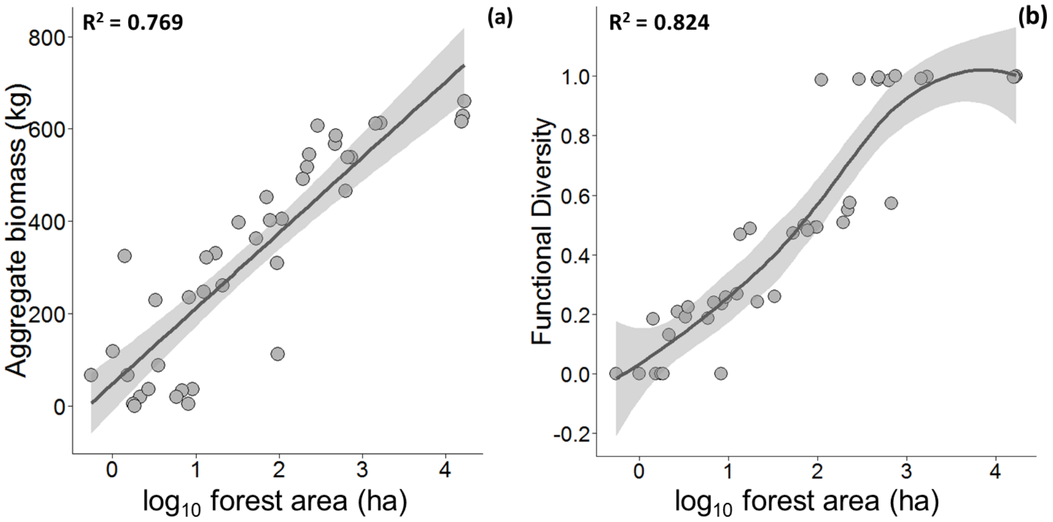


Appendix 6.3. Checklist of 35 vertebrate species surveyed within 40 forest sites at the Balbina archipelagic landscape and neighbouring mainland areas, and the sampling techniques associated with each species. Solid circles (●) denote the most efficient survey technique, for those species that could be detected by more than one method.

Order/Family	**Species**	**English vernacular name**	**Survey method**			
			Line-transect censuses	**Sign surveys**	**Armadillo burrows counts**	**Camera trapping**
Mammals						
Artiodactyla/Cetartiodactyla	*Mazama americana*	Red brocket deer	X	●		X
Artiodactyla/Cetartiodactyla	*Mazama nemorivaga*	Amazonian brown brocket deer	X	X		●
Artiodacytla/Tayassuidae	*Pecari tajacu*	Collared peccary	X	X		●
Artiodacytla/Tayassuidae	*Tayassu pecari*	White-lipped peccary	X	●		X
Carnivora/Mustelidae	*Eira barbara*	Tayra	X			●
Carnivora/Felidae	*Leopardus pardalis*	Ocelot	X	X		●
Carnivora/ Felidae	*Leopardus wiedii*	Margay				●
Carnivora/ Felidae	*Panthera onca*	Jaguar	X	X		●
Carnivora/ Felidae	*Puma concolor*	Puma	X	X		●
Carnivora/ Felidae	*Puma yaguaroundi*	Jaguarundi	X			●
Carnivora/Procyonidae	*Nasua nasua*	South American coati	X	X		●
Cingulata/Dasypodidae	*Cabassous unicinctus*	Southern naked-tailed armadillo	X	X	●	
Cingulata/Dasypodidae	*Dasypus kappleri*	Greater long-nosed armadillo		X	●	X
Cingulata/Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo		X	X	●
Cingulata/Dasypodidae	*Priodontes maximus*	Giant armadillo		X	X	●
Perissodactyla/Tapiridae	*Tapirus terrestris*	South American tapir	X	●		X
Pilosa/Myrmecophagidae	*Myrmecophaga tridactyla*	Giant anteater	X	X		●
Pilosa/Myrmecophagidae	*Tamandua tetradactyla*	Southern tamandua	●			X
Primates/Atelidae	*Alouatta macconnelli*	Red howler monkey	●	X		
Primates/Atelidae	*Ateles paniscus*	Black spider monkey	●	X		
Primates/Pitheciidae	*Chiropotes sagulatus*	Northern bearded saki	X			
Primates/Pitheciidae	*Pithecia chrysocephala*	Golden-faced saki	X			
Primates/Callithrichidae	*Saguinus midas*	Golden-handed tamarin	X			
Primates/Cebidae	*Saimiri sciureus*	Squirrel monkey	X			
Primates/Cebidae	*Sapajus apella*	Brown capuchin monkey	X			
Rodentia/Cuniculidae	*Cuniculus paca*	Lowland paca		X		●
Rodentia/Dasyproctidae	*Dasyprocta leporina*	Red-rumped agouti	X	X		●
Rodentia/Dasyproctidae	*Myoprocta acouchy*	Red acouchi	●	X		X
Rodentia/Sciuridae	*Guerlinguetus aestuans*	Brazilian squirrel	●	X		X

Birds						
Galliformes/Cracidae	*Penelope marail*	Marail guan	●			
Galliformes/Cracidae	*Crax alector*	Black curassow	X			●
Gruiformes/Psophiidae	*Psophia crepitans*	Grey-winged trumpeter	X			●
Tinamiformes/Tinamidae	*Tinamus major*	Great tinamou	●	X		X
Reptiles						
Testudines/Testudinidae	*Chelonoidis carbonaria*	Red-footed tortoise	●			
Testudines/Testudinidae	*Chelonoidis denticulata*	Yellow-footed tortoise	●			

Appendix 6.4. Relationships between insular and continuous forest areas and (a) a measure of aggregate vertebrate assemblage biomass, and (b) the vertebrate functional diversity persisting in 40 forest sites surveyed using four complementary sampling techniques across the Balbina Hydroelectric Reservoir landscape.



Appendix 6.5. Species-area relationships as a function of body size classes of vertebrate species (Small: ≤ 3.00 kg; Medium: 3-9 kg; Large: ≥ 9 kg) surveyed within 37 islands and three continuous forest sites at the Balbina Hydroelectric Reservoir landscape.