How ecosystem functioning in tropical forests varies with anthropogenic land use and environmental change

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DECLARATION

I confirm that all the work presented in this thesis is my own unless otherwise stated. References are given for all data sources and software usage. The use of the term 'we' is to acknowledge the contribution of collaborators and my supervisor Dr Cristina Banks-Leite, who provided advice and guidance throughout. Feedback on all chapters was received from members of my peer review panel, Professor Guy Woodward and Professor Jon Lloyd.

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Michelle Lisa Kiri Harrison, February 2019

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ABSTRACT

The combined effect of habitat degradation and shifts in climate are pushing many species towards local and global extinctions. Often, the most sensitive species to disturbance are the most important for the maintenance of healthy ecosystems. With conservation efforts focussing on biodiversity, can we assume that ecosystem functions will also be preserved? We aimed to test these assumptions by disrupting trophic interactions along natural and anthropogenic gradients of diversity with vertebrate exclusions. In chapter two, we focus on shifts in biotic distribution that occur naturally with elevation. Vertebrate exclusion caused strong trophic cascades on herbivory in pristine tropical forests, but only at high altitudes. In contrast, at lower elevations, forests showed little response to predator exclusion, with no effect on herbivore density or subsequent plant damage. We hypothesis that habitat in the warmer and wetter lowlands harbours higher levels of diversity within mid and low trophic levels and this may confer some resilience to disturbance. In chapters three and four, we investigate how distance to edge and habitat loss effects the above processes. Edge effects significantly mediated trophic cascades, which occurred only within the forest interior. Changes in vertebrate community composition along interior to edge gradients are likely to be responsible for these findings. The effect of exclusion on both arthropod densities was mediated by habitat loss, although the proportion of plant damage was not. The generality of plant-herbivore interactions may make them robust to perturbation, hence the neutral response of herbivory to habitat loss. Our findings provide insight into how the provision of ecosystem function is mediated by biodiversity loss. This information can be vital in identifying which areas of habitat might lose functionality in the wake of disturbance. We

suggest that conservation efforts are refocussed to target ecosystems in which functions are reliant on vulnerable specialist species.

CONTENTS

1. Introduction **14**

1.1 Gradients of tropical biodiversity 16

1.1.1 Natural elevational gradients 16

1.1.2 Anthropogenic gradients of habitat loss 18

1.2 Trophic cascades in terrestrial ecosystems 20

1.3 Functional roles of vertebrates 22

1.4 Processes that determine the provision of ecosystem function 24

1.5 Thesis aims and outline 27

2. Are trophic cascades in tropical rainforests mediated by altitude? **31**

2.1 ABSTRACT 32

2.2 INTRODUCTION 33

2.3 METHODOLOGY 36

2.3.1 Site selection 36

2.3.2 Experimental plots 36

2.3.3 Herbivory measurements 38

2.3.4 Understory fauna 40

2.3.5 Belowground fauna 41

2.3.6 Decomposition rate 41

2.3.7 Soil nutrients 42

2.3.8 Climatic data 42

2.3.9 Avifaunal data 42

2.3.10 Data analysis 43
2.4 RESULTS 44
2.4.1 Climatic variation with altitude 44
2.4.2 General trends in aboveground arthropod community 45
2.4.3 Aboveground variation with altitude 46
2.4.4 Changes in aboveground ecosystem functioning with altitude 48
2.4.5 General trends in belowground arthropod community 48
2.4.6 Belowground variation with altitude 50
2.4.7 Changes in belowground ecosystem functioning with altitude 50
2.4.8 Changes in avifaunal community with altitude 52
2.5 DISCUSSION 53

3. Are there edge effects on trophic cascades in tropical rainforests? 59

3.1 ABSTRACT 60
3.2 INTRODUCTION 61
3.3 METHODOLOGY 63
3.3.1 Site selection 63
3.3.2 Experimental plots 64
3.3.3 Herbivory measurements 66
3.3.4 Understory fauna 68
3.3.5 Avifaunal data 68
3.3.6 Data analysis 69
3.4 RESULTS 71

3.4.1 Do edge effects alter abundance in avian functional groups? 71

3.4.2 General trends in arthropod community 72

3.4.2 Are there edge effects on arthropods and herbivory levels? 72

3.4.3 Do edge effects alter the outcome of vertebrate exclusion? 74

3.4.4 Do edge effects alter trophic cascades? 75

3.5 DISCUSSION 78

4. Does ecosystem function in tropical rainforests vary with habitat loss? 83

4.1 ABSTRACT 84

4.2 INTRODUCTION 85

4.3 METHODOLOGY 88

4.3.1 Site selection 88

4.3.2 Experimental plots 89

4.3.3 Herbivory measurements 91

4.3.4 Understory fauna 92

4.3.5 Data analysis 93

4.4 RESULTS 94

4.4.1 General trends in arthropod community 94

4.4.2 Effects of forest cover and distance to edge on arthropods 94

4.4.3 Trophic cascades along a gradient of forest cover 96

4.5 DISCUSSION 98

5. Discussion 105

5.1 How does biodiversity influence trophic cascades? 107

5.1.1 Occurrence of trophic cascades varies with gradient type 107

5.1.2 Commonalities of vertebrate insectivory 108

5.2 When is ecosystem function resilient to change? 109

5.3 Caveats and limitations 111

5.3.1 The validity of exclusion experiments 112

5.3.2 Experimental design and sampling 113

5.3.3 Additional measures 114

5.4 Implications for conservation strategies 115

5.4.1 A focus on less biodiverse habitats 115

5.4.2 Mitigation of edge effects 116

5.4.3 Resilience of belowground systems 117

5.5 Future directions 118

5.5.1 Edge, area and matrix effects 118

5.5.2 Relative impact of top-down and bottom-up effects 119

5.6 Conclusions 119

Bibliography **121**

APPENDICES

A. Arthropod orders and categorisation into broad functional guilds 145

B. Percentage forest cover of sites and GPS locations 148

C. Variation in arthropod abundance between procedural and control plots 149

LIST OF FIGURES

2.1. Experimental plot schematic 38

2.2. Climatic conditions at low and high altitude 44

2.3. Aboveground arthropod abundance and herbivory at varying altitude 46

2.4. Effect of exclusion on aboveground arthropods and herbivory 47

2.5. Belowground arthropods, decomposition and soil nitrogen with altitude 49

2.6. Effect of exclusion on belowground arthropods, decomposition and soil nitrogen at varying altitude 51

2.7 Changes in within-guild avifaunal abundance and total biomass with altitude 52

3.1. Experimental plot schematic 65

3.2. Changes in within-guild avifaunal abundance and total biomasswith location 71

3.3. Response of arthropod orders to forest location 73

3.4. Variation in arthropod abundance and leaf damage with location 74

3.5. Effect of exclusion on arthropods and herbivory at edge and interior sites 76

3.6. Path models for trophic cascades at edge and interior sites 77

4.1. Experimental plot schematic 90

4.2. Relationships between forest cover, arthropod density and herbivory 95

4.3. Relationships between forest cover and difference in arthropod density 97

C.1. Paired plots of aboveground arthropod abundance at high and low altitude 150

C.2. Paired plots of belowground arthropod abundance at high and low altitude 152

C.3. Paired plots of arthropod abundance in edge and interior habitat 154

C.4. Variation in arthropod abundance with forest cover at edge and interior 156

LIST OF TABLES

3.1. Effects of exclusion on arthropod abundance at interior and edge sites 74

A.1. Aboveground functional arthropod groups 146

A.2. Belowground functional arthropod groups 147

B.1. Percentage forest cover and GPS location of sites 148

C.1. Variation in mean abundance of aboveground arthropods with altitude 149

C.2. Variation in mean abundance of belowground arthropods with altitude 151

C.3. Variation in mean abundance of arthropods between edge and interior 153

C.4. Variation in the density of arthropod functional groups with forest cover 155

CHAPTER 1

Introduction

Despite covering only 7% of the earth's terrestrial surface, tropical forests are home to roughly 60% of land species, a large proportion of which are endemic (Laurance, 1999). This highly diverse and ecologically complex biome is subject to multiple anthropogenic pressures, which often act in synergy to have devastating impacts on biota (Bradshaw, Sodhi and Brook, 2009). Changes in climate can push vulnerable species, such as those in tropical mountains, to the limits of their range (Şekercioğlu, Primack and Wormworth, 2012). In combination with habitat loss, climate change could be responsible for the extinction of hundreds of tropical species (Sekercioglu *et al.*, 2008; Stork, 2010). Few areas of pristine forest remain, with most habitat degraded or modified in some or multiple ways (Kareiva *et al.*, 2007). Deforestation continues to accelerate, with an increase in net forest loss of 2101 km^2/year (Hansen *et al.*, 2013), and is thought to have the most pervasive impact on biodiversity (Laurance and Peres, 2006). Vertebrate communities are becoming increasingly more impoverished, resulting in 'empty forests' (Peres and Palacios, 2007). In combination with other more insidious threats such as poaching, invasive species, exotic pathogens and climate change, habitat loss is driving the alteration of forest ecosystems (Laurance and Peres, 2006). With only 9.8% of tropical forests being afforded protection (Schmitt *et al.*, 2008), degradation is set to continue, leading to the extinction of ever more tropical species. Often the most vulnerable species to local extirpation are important functionally and their disappearance can alter biotic interactions and cause disruption to ecosystem functioning (Schmitz, 2006; Şekercioğlu, 2006; Kurten, 2013). In this chapter we review the processes, habitat characteristics and species interactions that influence biodiversity and ecosystem functioning in tropical landscapes. How the diversity of different taxa fluctuate along

natural and anthropogenic gradients is examined in more detail within specific chapters.

1.1 Gradients of tropical biodiversity

1.1.1 Natural elevational gradients

Biodiversity patterns along naturally-occurring environmental and habitat gradients are caused by multiple interacting factors, which are not easy to disentangle. This is certainly the case with species distributions along elevational gradients, which do provide an ideal setting in which to test theories on how biota respond to climatic variation. However, there are pitfalls for researchers seeking direct relationships between biodiversity and altitude. Land area, atmospheric pressure and temperature vary as a function of elevation showing declining trends globally (Körner, 2007). There also exists an array of climatic factors that vary regionally and inconsistently with altitude, including precipitation, wind velocity and seasonality. The dynamic interaction of environmental variables is one of the primary determinants of biotic diversity and distribution along elevational gradients (Rahbek, 1995). Patterns that seem to vary as a direct function of altitude should be viewed with caution, as climatic conditions that are not altitude-specific could drive these trends (Körner, 2007).

Another key factor that influences the observed patterns of biodiversity along elevational gradients is the choice of scale. As demonstrated by Rahbek (2005), if one extreme of a gradient is neglected in the sampling regime, an apparent monotonic relationship may actually be masking an underlying mid-elevation peak. The natural structure of mountains also means that often altitude is intrinsically

linked to landscape area (Körner, 2007), thus associated gradients of diversity are particularly susceptible to area effects. Many of the biotic trends reported in the literature have not been standardised to account for this (Bachman *et al.*, 2004; Rahbek, 2005). Such discrepancies between studies means comparisons that have been drawn may be inaccurate and that generalisations may not reflect true trends.

Despite these issues, two dominant patterns have emerged relating elevation to biotic variation. The 'mid-domain effect' (Colwell and Lees, 2000), where species richness shows a hump-shaped distribution along an altitudinal gradient, is the most typical, occurring in roughly 50% of cases (Rahbek, 2005). Several hypotheses have been posited for this pattern, centring around the convergence of optimal biotic and abiotic factors (Olson, 1994). A greater degree of overlap in species ranges at mid-elevations (Colwell and Lees, 2000), as well as climatic constraints at either end of the range (Smiley and Rank, 1986; Fu *et al.*, 2014), may also explain this commonly-observed trend. The occurrence of mid-domain effect has been reported for floristic community composition (Lieberman *et al.*, 1996), arthropods (Olson, 1994) and vertebrate communities (Rahbek, 1997; McCain, 2007)

Less typical is a monotonic decrease in diversity with increasing elevation, which occurs in approximately 25% of cases (Rahbek, 2005). This inverse relationship with altitude is thought to mirror a similar declining pattern of primary productivity (Rahbek, 1997; Kaspari, O'Donnell and Kercher, 2000), which is closely coupled with species richness (Srivastava and Lawton, 1998). Plant growth is constrained by availability of moisture and soil nutrients, particularly nitrogen, which tend to be reduced in montane regions (Vitousek, 1984; Gentry, 1988; Tanner and Vitousek,

1998; Givnish, 1999; DeWalt *et al.*, 2006). This gives rise to monotonic declines in plant diversity with altitude (Vazquez and Givnish, 1998; Kitayama and Aiba, 2002; Moser, Hertel and Leuschner, 2007; Alves *et al.*, 2012). Such linear patterns are also reported for bat and bird diversity (Kessler *et al.*, 2001; McCain, 2005; Sanchez-Cordero, 2008) and arthropod communities (Brehm, Süssenbach and Fiedler, 2003; Richardson, Richardson and Soto-Adames, 2005).

1.1.2 Anthropogenic gradients of habitat loss

Deforestation involves a reduction in habitat area and an increase in artificial borders, which leaves forest dwelling fauna exposed to a hostile surrounding matrix. How edge effects directly and indirectly impact biotic diversity has received a large amount of research attention (Ewers and Didham, 2007; Banks-Leite, Ewers and Metzger, 2010; Pfeifer *et al.*, 2017). Recent analyses suggest that 85% of species globally respond to edge effects, either in a negative or positive manner (Pfeifer *et al.*, 2017). As 20% of tropical forests now occur within 100m of an ecotone zone (Haddad *et al.*, 2015), this means the impact on tropical forest assemblages is immense. However, not all edge effects are equal. These degraded zones show high variability, much of which is due to adjacent matrix type, making predictions on how species will respond difficult (Laurance and Peres, 2006).

Edge effects can be abiotic or biological (Murcia, 1995) with processes interacting to determine biotic distribution. The exposure of natural habitats to anthropogenic matrices causes significant changes in microclimatic conditions. Temperatures in forest areas at 50-100m from the edge can be altered (Cadenasso, Traynor and Pickett, 1997; Chen *et al.*, 1999). Light penetrates much deeper into forest interiors

and humidity is reduced towards the forest/matrix border. Some edge effects are known to extend up to 1km into the forest (Ewers and Banks-Leite, 2013). How strong these environmental edge effects are is greatly influenced by matrix type (Prevedello and Vieira, 2010). The greater the contrast in structure between the natural habitat and the matrix, the stronger the edge effects on forest species (Hatfield, 2018). Belowground systems, however, tend to be buffered against the microclimate change that occurs with edge creation, with reduced effects on biota and processes (Ewers and Banks-Leite, 2013)

Edge and area effects that occur with tropical forest habitat loss are typically confounded. Edge effects are responsible for the majority of fragmentation effects, with area effects all but disappearing once edge influences are controlled for (Banks-Leite, Ewers and Metzger, 2010). Species that have strong edge intolerances will have similar intolerances for high levels of fragmentation. Many forest-dwelling animals have physiological responses towards the warmer, lighter ecotone areas and actively avoid them (Banks-Leite, Ewers and Metzger, 2010; Pfeifer *et al.*, 2017). Thus when edge-to-interior ratios are high, as is the case in small patches, the entire fragment becomes unsuitable for forest-dwelling species with high habitat specificity (Ewers and Didham, 2007).

Biotic changes due to edge effects exhibit general negative trends, which apply to many forests ecosystems (Pfeifer *et al.*, 2017), but these patterns are by no means universal. Plant communities show major shifts in community composition, towards assemblages dominated by pioneer and successional species (Tabarelli, Lopes and Peres, 2008). Invertebrate densities are increased in ecotone areas, but assemblage

richness tends to decline with distance to edge (Didham *et al.*, 1998). Both the abundance and occurrence of specialist insectivorous species decreases in more intensively-modified habitats (Newbold *et al.*, 2013). The presence of these guilds is also strongly affected by proximity to edge in tropical forest habitats. Mammal diversity and abundance are correlated with fragment size, with small to medium sized forest area supporting more impoverished communities (Pardini *et al.*, 2005). Amphibian and reptile species richness has a positive relationship with forest patch size (Cabrera-Guzmán and Reynoso, 2012). Combining the responses of three vertebrate groups to fragmentation: mammals, birds and amphibians, Banks-Leite et al (2014) discovered that community integrity is preserved until the area reaches a threshold of between 24 and 33% forest cover. Their results also suggest that below this threshold, forest specialist species are replaced by generalist, disturbance-adapted species.

1.2 Trophic cascades in terrestrial ecosystems

Perturbation within top trophic levels can lead to direct and indirect changes to communities and interspecies interactions in lower trophic tiers, and in some cases can lead to the occurrence of a trophic cascade. A single, all-encompassing definition for the wide range of trophic cascades has yet to be found. In general terms, a trophic cascade can be described as the indirect effects of top trophic tiers on lower tiers, acting through intermediate trophic levels.

Trophic cascades have been reported in a wide range of biomes and ecosystems. Originally, trophic cascades were thought to be almost unique to aquatic systems and rare or absent from terrestrial biomes (Strong, 1992). High uniform palatability of

phytoplankton and the simple nature of inter-level relationships in aquatic environments were thought to increase their susceptibility to trophic cascades (Strong, 1992). In comparison, the reticulate nature of terrestrial food webs, which exhibit greater complexity and higher rates of omnivory, was thought to buffer such systems against such occurrences (Strong, 1992). Indeed, research shows that trophic cascades are more frequent and pronounced in water than those on land, but that the reasons for this may be more convoluted than previously thought (Shurin *et al.*, 2002). Furthermore, a suite of studies have shown that trophic cascades do occur on land and in differing types of habitat and environments (Schmitz, Hambäck and Beckerman, 2000; Halaj and Wise, 2001; Van Bael *et al.*, 2008; Beck, Snodgrass and Thebpanya, 2013; Pejchar *et al.*, 2018).

Trophic cascades have been found to be particularly strong in agroforests (Koh, 2008; Van Bael *et al.*, 2008; Maas *et al.*, 2015). As diversity is significantly reduced in such modified habitats (Gardner *et al.*, 2010), this reflects the theory that ecosystem dynamics are more susceptible to perturbation in simpler systems. In diverse systems, such as undisturbed tropical forests, food webs tend to be complex with multiple interspecies linkages and interactions (Shurin *et al.*, 2002; Lewis, 2009). Diversity within predator groups contributes significantly to food web complexity as individuals prey on each other, as well as acting as competitors (Polis and Holt, 1992; Holt and Polis, 1997). High species richness in this top trophic level has been found to significantly dampen the occurrence of trophic cascades in some terrestrial systems (Finke and Denno, 2004). Equally, high diversity in lower trophic levels is thought to have a buffering effect against perturbation at high levels, mitigating cascading effects on ecosystem dynamics (Schmitz, Hambäck and

Beckerman, 2000; Halaj and Wise, 2001; Ewers *et al.*, 2015). However, despite these findings, there is an ever-growing body of research proving that cascades are in evidence within tropical forests (Kalka and Kalko, 2006; Dunham, 2008; Kalka, Smith and Kalko, 2008; Morrison and Lindell, 2012; Karp and Daily, 2014; Maas *et al.*, 2015). This is discussed further in the next section.

1.3 Functional roles of vertebrates

As habitat loss and climate change push vertebrate species to their limits, we are likely to see increased extirpation of species from tropical forests (Laurance and Peres, 2006). A worrying trend is that the most vulnerable species tend to be the ones that are important for ecosystem function (Mouillot *et al.*, 2013). In particular, birds and mammals, which occupy top trophic levels, are known to play an array of important functional services within a variety of ecosystems (Sekercioglu 2006; Andresen, 2000). Here we discuss three of the more vital roles vertebrates play in the functioning of tropical forest ecosystems.

As seed dispersers, vertebrates can mitigate density-dependent mortality and lessen the risk from predators or pathogens (Packer and Clay, 2000). Frugivores are often attracted to different sources of food, with large mammals such as monkeys providing dispersal functions for large-seeded species, and birds taking fruits with smaller seeds (Pizo, 2002). This has implications for the dispersal distance, and plant community composition and abundance (Cain, Milligan and Strand, 2000).

In tropical forests, 98-99% of pollination is animal-mediated, with insects, particularly Hymenoptera, playing the dominant role in this function (Bawa, 1990). A substantial

proportion, however, is carried out by highly motile vertebrate taxa such bats and birds (Fleming and Muchhala, 2008). In Costa Rican rainforests, almost 25% of understory plants rely on vertebrates for pollination (Kress and Beach, 1994). Hummingbirds are perhaps the most influential nectarivores, with many showing specificity towards certain food plants (Johnson and Nicolson, 2007). These mutualisms may be more vulnerable to perturbation, because of the specialised connection between species (Magrach *et al.*, 2014). Through such mutualistic functions, such as seed dispersal and pollination, vertebrates can act as genetic linkers, helping to connect isolated plant populations and maintain high genetic diversity (Şekercioğlu, 2006).

The top-down control of arthropod populations by insectivorous vertebrates regulates herbivory levels in both natural and anthropogenic systems (Koh, 2008; Mooney *et al.,* 2010; Newbold *et al.* 2013). In particular, birds and bats are providers of this pest control function, limiting arthropod populations in pristine and modified systems alike (Kalka and Kalko, 2006; Dunham, 2008; Kalka, Smith and Kalko, 2008; Koh, 2008; Morrison and Lindell, 2012; Karp and Daily, 2014; Maas *et al.*, 2015). In tropical forests, where arthropod diversity and activity levels are high, the exclusion of insectivores elicits a 200% increase in herbivory (Kalka, Smith and Kalko, 2008). Bats alone have a substantial impact on arthropod populations reducing them by as much as 84% (Williams-Guillén, Perfecto and Vandermeer, 2008).

Halaj and Wise (2001) found that in a review of vertebrate exclusion experiments, most produced an increased density of herbivorous arthropods and greater amounts of plant damage. These aboveground trophic cascades can trickle down to impact

below-ground processes (Wardle *et al.* 2005). Evidence suggests that the loss of specialist insectivores can produce a ripple effect through trophic levels, even causing fluctuations in nutrient cycling (Dunham 2008). As yet, few comparable studies exist to confirm such findings. Very little is known about how these cascading effects are influenced by climatic variations or the degree of human habitat modification. In tropical forests, however, some top predator exclusion experiments show divergent effects. Indeed, the exclusion of birds indirectly caused an increase in leaf damage within the canopy of a tropical forest, but not within the less productive understory (Van Bael, Brawn and Robinson, 2003). This supports food web theory, which suggests that the likelihood of a trophic cascade occurring is positively related to primary productivity (Okansen *et al.*, 1981). However, other studies support the idea that ecosystem processes in tropical forests remain resilient to perturbation (Ewers *et al.*, 2015) due to high levels of diversity and functional similarity between species.

The functional roles fulfilled by vertebrates are well-described. How the provision of ecosystem services is mediated by changes in biodiversity along anthropogenic and environmental gradients, is less well-known. Given that species that occupy top trophic levels tend to become extinct faster than those in lower levels (Holt, 1996), the need to understand how top-down effects are altered by disturbance is pressing.

1.4 Processes that determine the provision of ecosystem function

Biodiversity and ecosystem functioning (BEF) theory posits that biodiversity declines lead to parallel losses in ecosystem function (Hooper *et al.*, 2005). Research into ecosystem processes has boomed in recent years but compared to the large volume of literature on biodiversity, functioning studies lag behind. There are also strong biases to be aware of. Much of the BEF literature centres around temperate regions, with only 13% of data originating in the tropics (Clarke *et al.*, 2017). Experiments have been focused on plant-based functions, including carbon storage and soil nutrient cycling (Tilman *et al.*, 2001). A recent review by Hatfield et al (2018) found that real-world examples linking functional diversity metrics and ecosystem services were in short supply. With the biodiversity crisis set to worsen (Hansen *et al.*, 2013), this gap in knowledge needs to be redressed urgently if we are to truly understand how biodiversity loss affects functioning. This is particularly important for diverse and highly endangered biomes like tropical forests.

Ecological interactions can be classified as either mutual or antagonistic (Magrach *et al.*, 2014). The former category includes processes which are beneficial to both parties, like seed dispersal and pollination. Many of these interactions show a degree of specialisation, which can make them vulnerable to disturbances like habitat loss (Aguilar *et al.*, 2006). In contrast, antagonistic interspecific relationships, like those between plants and herbivores, tend to be much more generalised (Poisot, Mouquet and Gravel, 2013). This may provide them with a degree of resilience to perturbation as neither species is entirely dependent on the other. Herbivory is a good example of how antagonistic processes, with low specialisation, can show varying responses to disturbance. Four recent reviews reported opposing trends: decreased herbivory with habitat loss (Martinson and Fagan, 2014), the inverse relationship (De Carvalho

Guimarães, Viana and Cornelissen, 2014) and neutral responses (Magrach *et al.*, 2014; Rossetti *et al.*, 2017).

These broad classifications are useful, but within this category, different mutualisms and antagonisms show varying levels of response to disruption. Seed size, for example, is a key determinant of how resilient dispersal mechanisms are to fragmentation (Cramer, Mesquita and Williamson, 2007). Large-seeded plant species rely on fewer, larger frugivores for dispersal. As size is a predictor of extinction in mammals (Hamann and Curio, 1999), the dispersal functions for these plants are as vulnerable as their carriers to habitat loss, as well as other pressures like hunting. Smaller seeded species are less tied to certain frugivore groups, and thus are dispersed more frequently over a greater area. Fragmentation, therefore, has differential effects on seed dispersal that is dependent on seed size, with dispersal of large seeds being dramatically reduced (Cramer, Mesquita and Williamson, 2007). These processes, and how they are modulated, have significant effects on plant communities, with large-seeded species being rare in forest fragments (Fortuna and Bascompte, 2006).

These examples highlight the variability of interspecific interactions, particularly in degraded areas of forests (Ewers and Didham, 2006). Categorising processes as mutualistic or antagonistic can be beneficial in helping researchers predict how ecosystem functioning will be altered with various pressures. However, broad groupings like these sometimes mask interaction-specific variation, which can better determine the resilience of functions.

1.5 Thesis outline and aims

Patterns of biodiversity along land-use and environmental gradients have been the focus of much research, with some general trends having emerged and being widely accepted. Although the positive BEF relationship is generally accepted, there is still a paucity of tangible examples from megadiverse terrestrial systems such as tropical rainforest (Clarke *et al.*, 2017; Hatfield, Harrison and Banks-Leite, 2018). There are even fewer studies assessing how the provision of ecosystem function in tropical forests is mediated by the changes in biodiversity associated with climatic variation and habitat loss.

With known diversity trends in mind, we can assess whether ecosystem function fluctuates in a similar manner or whether some systems are resilient despite loss of biodiversity. Specifically, our aim is to establish how loss of vertebrate predators permeates through the trophic chain to indirectly impact herbivory rate. We study leaf damage for several reasons. The effects of herbivory can be far-reaching, impacting aboveground plant community composition (Halpern and Underwood, 2006). Effects can also cascade to influence processes within the belowground subsystem (Wardle *et al.*, 2004; Dunham, 2008) including carbon storage and nitrogen cycling (Metcalfe *et al.*, 2014). This subject was also selected for logistical reasons as, in the field, herbivorous damage is easy to identify.

We investigate how the strength of trophic cascades fluctuates along anthropogenic gradients of land-use change and natural-occurring environmental gradients. The role of vertebrates as the primary predators and mediators of trophic cascades may become more or less important along such gradients. The greater the reliance on

vertebrates to provide such services, the more vulnerable the ecosystem to diversity loss within the top trophic tier. In contrast, a system in which birds and mammals play a lesser role, may be able to buffer against perturbation and mediate the occurrence of trophic cascades. Such information could be vital in informing conservation decisions, highlighting habitat that requires an intact top trophic tier to maintain ecosystem function.

Our work takes place in the Atlantic forest of Brazil, a region which has been the focus of much tropical forest research (Chiarello, 1999; Faria *et al.*, 2007; Tabarelli *et al.*, 2010; Banks-Leite *et al.*, 2014; Joly *et al.*, 2014). This highly diverse biome is home to approximately 8% of the world's species (da Silva and Casteleti, 2003), including the most threatened avifaunal community in the Americas (Manne, Brooks and Pimm, 1999). Originally covering 150 million hectares, the Atlantic Forest has suffered large-scale deforestation and is now one of the most endangered ecosystems in the world (Ribeiro *et al.*, 2009). In Brazil, only 11 to 16% of the original forest remains. Most of this habitat is highly fragmented with 73% occurring less than 250m from surrounding matrix and 45% located within 100m of the forest edge (Ribeiro *et al.*, 2009). This mosaic landscape is the ideal setting to test how anthropogenic pressures such as habitat modification and loss, impact ecosystem functioning. The Atlantic forest of Brazil also exhibits highly complex geology and topography, which causes microclimatic and edaphic variation along short altitudinal gradients. Such environmental heterogeneity gives rise to significant variation in the distribution of plant and faunal diversity (Carnaval and Moritz, 2008). These natural biotic gradients provide opportunities to determine how elevation, and associated variation in diversity, mediate the occurrence of trophic cascades.

In chapter two, we assess how elevation mediates trophic cascade strength in areas of pristine topical forest. We select twenty interior forest sites, ten at altitudes above 1000 m asl and ten below 100 m asl. By constructing vertebrate exclusion plots, we determine how the absence of the top trophic tier directly affects arthropod populations and has cascading effects on ecosystem functioning. As aboveground and belowground systems are subject to different microclimatic conditions (Ewers and Banks-Leite, 2013) we analyse the effects of exclusion on them separately. We assess trophic cascades: on herbivory rate in the aboveground system; and decomposition rate and soil nitrogen concentration in the belowground subsystem.

The focus in chapters three and four turns to the impact of anthropogenic habitat modification on trophic cascades. As human land use encroaches further on forested habitat (FAO and JRC, 2014), forest habitats will have increased edge-to-interior ratios (Tabarelli, Mantovani and Peres, 1999) and be situated within anthropogenic matrices, which are hostile for many forest species (Tabarelli, da Silva and Gascon, 2004). We aim to assess how the unique vertebrate community in the Atlantic Forest provides ecosystem services and how this varies with habitat loss and artificial edge formation. In chapter three we determine how the occurrence of trophic cascades is mediated by distance to edge. As belowground subsystems are often slow to respond, here we focus solely on aboveground ecosystem function. In chapter four, we assess how trophic cascades are mediated by habitat loss within forest interiors and edges. We achieve this by measuring how exclusion affects the arthropod populations and herbivory rate along a gradient of forest cover and whether these responses differ with distance to edge. Collectively, these studies will create a broad

overview of how the provision of top-down arthropod control varies with biodiversity loss (both natural and human-driven) and how this mediates trophic cascade strength on herbivory. We hope this information will help inform conservation strategies, refocussing them to preserve healthy ecosystems as well as biodiversity.

CHAPTER 2

Are trophic cascades in tropical rainforests mediated by altitude?

2.1 ABSTRACT

Vertebrate communities fulfil a wide-ranging array of ecosystem functions within tropical forests. Specialist insectivores are particularly important in the top-down control of arthropods and in the mediation of herbivory rates. How the provision of such functions is mediated by environmental change, and the associated natural variation in biodiversity, is not well-established. We aimed to investigate how aboveground and belowground arthropod populations respond to vertebrate exclusion along an elevation gradient in the Atlantic Forest of Brazil. We assessed how changes in the invertebrate community cascade to affect: a) herbivory rates on plants in the understory aboveground system and b) decomposition rates and soil nitrogen concentration in the belowground subsystem. At high altitudes, herbivorous and predaceous arthropod groups showed concurrent increases in abundance in the absence of vertebrates. Changes in invertebrate density elicited a significant rise in the proportion of herbivorous plant damage. In contrast, at low altitudes, only the predatory guild responded to exclusion, increasing significantly in abundance. Changes in herbivore density were minimal and therefore there was no cascading effect on plant damage. Tropical forests at low altitude are warmer, wetter and typically more speciose. Such high diversity may confer greater resilience to biodiversity loss than a less diverse ecosystem, like that at high altitudes. The belowground subsystem was more resilient to changes in vertebrate biodiversity, with little evidence of trophic cascades on decomposition or soil nutrients at either altitude. Detritivore species are numerous, but there is a high degree of overlap in the functions they provide. This functional complementarity is thought to make the entire subsystem more robust to perturbation.

2.2 INTRODUCTION

It is widely acknowledged that biodiversity–ecosystem functioning (BEF) relationships are positive (Hooper et al. 2005; Mace et al. 2012) and that species extinction has consequences for ecosystem dynamics. This idea is founded primarily on studies of plant-based functions such as carbon sequestration, nutrient cycling and aboveground biomass (Tilman et al. 2001), with fewer assessing how animal-mediated processes are affected by biodiversity loss (Ferger et al. 2016). Even though the tropics support some of the highest levels of biodiversity, this megadiverse biome has received little attention for BEF research, constituting only 13% of studies (Clarke et al. 2017). Furthermore, only a few tangible examples exist linking functional diversity with the provision of ecosystem services (Jack H. Hatfield et al. 2018) and there has been little assessment of how loss in function is mediated by the environment. Altitudinal gradients, in particular, provide a perfect setting for testing these questions given the natural variation in levels of biodiversity. In theory, stronger trophic cascades should be observed in poorer communities (Halaj & Wise 2001; Schmitz et al. 2000), which raises the question do trophic cascades vary along gradients of diversity associated with elevation?

Within the tropics, species richness of understory shrubs, vines and herbs (Vazquez & Givnish 1998), liana biomass and abundance (Alves et al. 2012) and aboveground biomass (Moser et al. 2007; Kitayama & Aiba 2002) are negatively correlated with altitude. However, for plant communities, the occurrence of mid-domain effect – where diversity peaks in the middle of the altitudinal range – is commonly observed (Lieberman et al. 1996, Bachman 2004, da Silva 2015). Invertebrate community composition can be directly associated with climatic conditions, as well as being

strongly influenced by vegetation patterns along elevational gradients (Hodkinson 2005). The harsher climate above 2,000 m above sea level (asl) causes a ubiquitous decline in ectothermic arthropod numbers (Brehm et al. 2003). Below this threshold, peaks in arthropod diversity at intermediate elevations (Olson 1994) and monotonic declines with altitude have been observed (Richardson et al. 2005; Morris et al. 2015). Similar divergent elevational trends have been reported for vertebrate communities. Declines in tropical vertebrate density and diversity with increasing altitude are frequently observed (Mallet-Rodrigues et al. 2015; Kessler et al. 2001; Young et al. 1998; Patterson et al. 1996; Sanchez-Cordero 2008; McCain 2005). However, mid-domain effects are a common occurrence (Rahbek 1997; Kessler et al. 2001; McCain 2005), whilst some studies suggest the effect of altitude on vertebrates is negligible (Raman et al. 2005; Blake & Loiselle 2000). Functionally-important, large, avian insectivores – with a body mass above 100g – are less common at higher elevations (Janes 1994), as are ant swarms and associated antbirds (Blake & Loiselle 2000; Olson 1994), likely due to the scarcity of large invertebrates.

There is a paucity of research on how tropical ecosystem processes covary with biodiversity along elevational gradients, with none addressing the relative strength of trophic cascades. Initial findings suggest that declining faunal diversity with altitude leads to a parallel reduction in the provision of ecosystem services. Belowground invertebrates have a strong, significant impact on litter decomposition rates and nitrogen release in wet lowland tropical forest, but were found not to be as important in dry sub-alpine forests (Gonzalez & Seastedt 2001). The role of parasitoids in controlling herbivorous moths attenuates with elevation (Hodkinson 2005), as does

vertebrate frugivory rate, reflecting declines in avian diversity (Ferger et al. 2016). However, elevation was found to have little predictive power in determining bird predatory effect on arthropods in tropical agroforests (Philpott et al. 2009). Few conclusions can be drawn due to the limited sample size and further research is required to elucidate patterns.

The Atlantic Forest of Brazil exhibits highly complex geology and topography, which gives rise to microclimatic and habitat variation along short altitudinal gradients. This has implications for the distribution of plant and faunal diversity, which also varies along these gradients (Carnaval & Moritz 2008). Such significant abiotic and biotic heterogeneity is likely to have important consequences for the occurrence and strength of trophic cascades. We aim to assess how ecosystem functions are altered in the absence of vertebrates along a gradient of altitude within the Brazilian Atlantic forest. Using an exclusion experiment, we simulated the absence of vertebrates within old-growth forest at two altitudes: above 1000 m asl and below 100 m asl. Our goals were to: 1) assess how the exclusion of vertebrates impacts arthropod abundance and subsequent trophic cascades affecting herbivory, 2) determine the magnitude of any variation and how this may fluctuate with altitude, and 3) determine the level of mediation provided by predaceous arthropods on non-predaceous groups.

2.3 METHODOLOGY

2.3.1 Site selection

The study took place in the Atlantic Forest of Brazil; specifically, within the administrative areas of Santa Virginia and Picinguaba in the Parque Estadual da Serra do Mar (PESM). Study sites were situated in interior forest and close to the permanent experimental plots of project Biota Gradiente within the National Park. These 1-hectare plots have been established for previous ecological projects and occur along an altitudinal gradient from 10 to 1000 m asl. Forest type varies along this gradient from sandbank vegetation and lowland forest between 0 to 100 m asl, to montane forest at 1000 m asl (Joly et al. 2012). We selected ten experimental sites below 100 m asl and ten above 1000 m asl, providing a total of 20 for the study. Sampling sites at the same altitude were positioned at least 200m apart to ensure spatial independence. Unfortunately, by the second month of the experimental period, at two of the low altitude sites, the exclusion equipment was stolen. As such, results are based on eight replicates at lower altitude.

2.3.2 Experimental plots

At each site, we constructed three experimental plots: exclosure, procedural and control. Thus, across all altitudes and sites there were 54 experimental plots (excluding the plots that were destroyed). Each type of plot was randomly assigned to 2 m x 2 m areas, which were at least three metres apart from each other. Effort was made throughout the construction process to minimise the cutting of plants and removal of roots to ensure continuity of the forest understory structure.

Exclosure plots were constructed of plastic poles and wire mesh and measured 2 m x 2 m in area, with a height of 1.5 m. The mesh had openings of 20 mm x 18 mm allowing the passage of all but the largest insects, whilst excluding the majority of vertebrates. Lengths of nylon thread were sown through the overlapping parts of the mesh walls and top to ensure the structure was mammal and bird-proof. The bottom of the mesh was buried into the ground and secured with metal pins to stop animals burrowing underneath. Access to the exclosure was via a mesh door, which was closed securely on departure with reusable plastic ties.

Procedural plots (e.g. Koh 2008) were composed of the basic framework of poles, a mesh top and an additional four sections of mesh fitted lengthwise to form corners (Fig 2.1). The purpose of this structure was twofold. Firstly, the mesh top collects leaves in the same manner as the exclosure and controls for the effect of reduced litter fall expected under exclusion. Secondly, spiders were likely to use the structure of the exclosure to build webs. The mesh corners of the procedural plot also provide this foundation, controlling for microclimatic effects on spider density, whilst still allowing access by mammals and birds. Control plots were simply four short lengths of pole placed into the ground to demarcate the 2 m x 2 m area. Previous analyses revealed little difference between the control and the procedural control (see Appendix C), so here we report only comparisons between the control and exclosure.

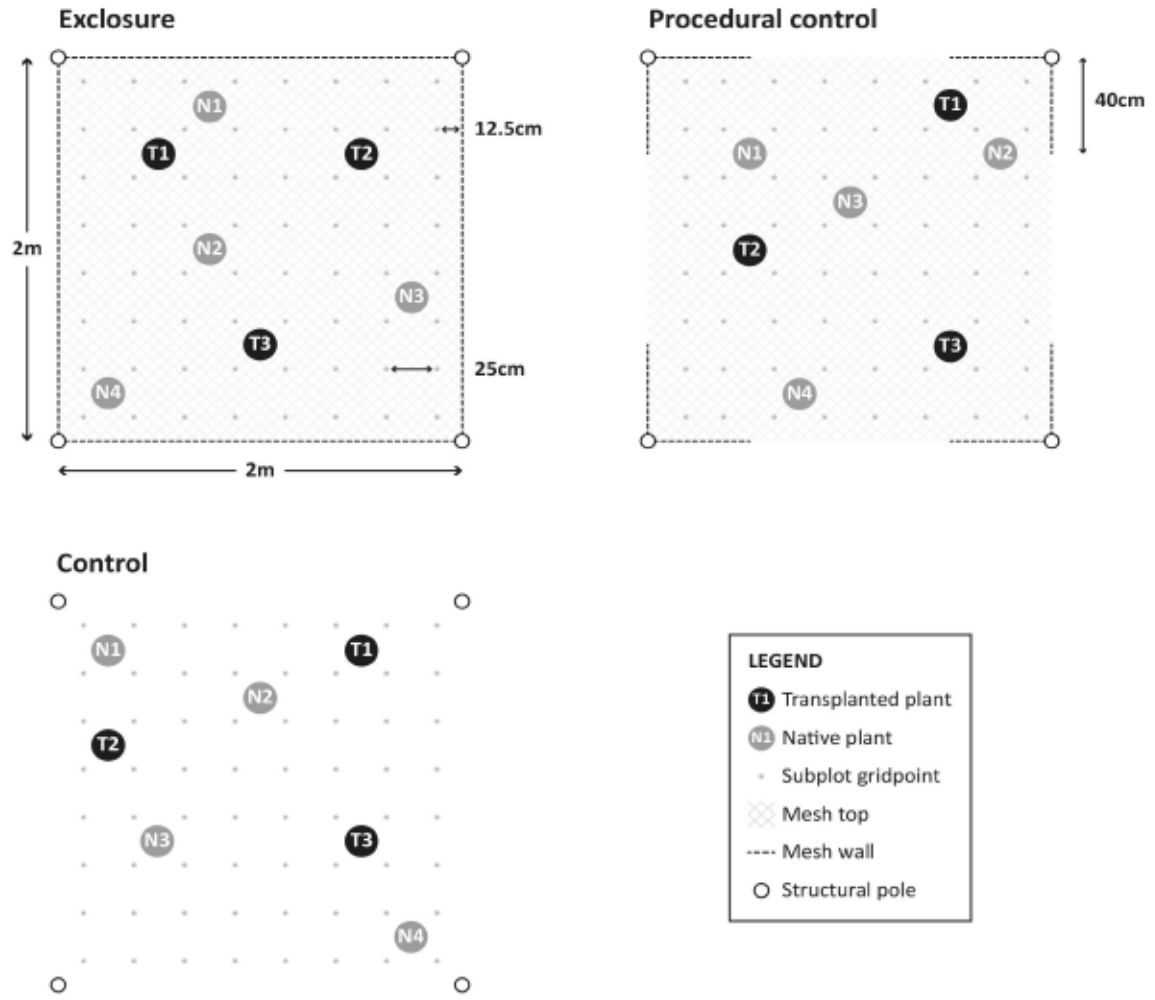


Figure 2.1. Schematic diagram of the plots at each site. In the field, each plot is positioned at least three metres from the others.

2.3.3 Herbivory measurements

To provide a consistent measure of herbivory across all plots, sites and altitudes, three plants of species native to Serra do Mar were translocated to each of the plots. The selected species were *Erythrina speciosa*, *Inga vera* and *Ocotea puberula,* which are known to experience a moderate degree of insect herbivory and naturally occur across the altitudinal range of the study area. Within each plot, the three translocated individuals were positioned one metre apart, each forming the point of a

rough triangle. Seedlings were chosen as younger plants undergo a period of rapid growth and are known to experience a higher degree of herbivory than more mature plants (Coley & Barone 1996).

To supplement measurements of herbivory taken from three translocated plants, a further four in-situ seedlings were randomly selected from the community within each plot. These individuals measured between 5 and 100 cm (Benítez-Malvido & Martínez-Ramos 2003) and also displayed a moderate level of historical herbivory. Thus, seven plants were sampled per plot, totalling 315 plants across all altitudes. All sampled plants were marked with inconspicuous, blue, plastic tags, each of which had a coded number.

Due to an uncharacteristic dry period in 2014, very few new leaves emerged during the first few months and sampling was restricted to four of the mature leaves already present. With the onset of the wet season in November, there was a corresponding surge in leaf emergence. At this time, four new leaves were marked per plant and followed for three months or until other new leaves appeared. They were then replaced in the sampling scheme by the younger leaves. This replacement process continued for the duration of the experiment. Employing this method ensured that throughout the year, monthly measurements of herbivory were taken from young leaves at similar life stages. This is important, as the leaves of shade-tolerant tropical species experience almost 70% of their lifetime herbivory in the 1–3 week expansion period following emergence (Coley & Barone 1996). We followed the suggestion of Coley & Barone (1996), to include both mature and expanding leaves in our sampling, as well as to take measurements at intervals over time.

The sampled leaves were photographed every four weeks. Image J software was used to calculate initial leaf area (ILA), new growth, desiccation, pathogen and fungal damage, as well as insect and mammalian herbivory. This method provides a greater degree of accuracy than relying on visual estimates of proportion in the field. Only herbivory caused by chewing insects was assessed from holes in the leaves. The impact of other insects such as phloem feeders is much harder to ascertain (Coley & Barone 1996) and beyond the limits of this study. Insect herbivory can generally be distinguished from mammalian, as mammals tend to clip the leaf close to the stem (Dunham 2008). Areas of desiccation, pathogen or fungal damage were measured and subtracted from the leaf area available for herbivory. Leaf damage measurements were taken from all plants including those already in-situ and transplanted plants. However, due to the drought, in the dry, high altitude forest very few new leaves emerged on the established forest plants, so this study focuses on herbivory of only transplanted individuals.

2.3.4 Understory fauna

Every month, the leaves and stems of all plants within each plot were visually inspected for arthropods. Individuals were identified to order and their body length, from the most anterior part of the head to the tip of the abdomen, was estimated. Formicidae were recorded as a separate group from other Hymenoptera. Lepidoptera were catalogued as adult or larval forms due to the significant impact the larvae have on herbivory rates. All recorded orders and functional categories are presented in Appendix A.

2.3.5 Belowground fauna

On a monthly basis, three leaf litter samples of 30 cm x 30 cm were selected using the subplot grid. Leaf litter is described here as decaying leaves and loose detritus that can easily be separated from the denser, more compressed soil (Brühl et al. 2003). Each sample was placed in a white tray and shaken vigorously for 20 seconds to dislodge insects from the leaves. Leaf litter was carefully inspected and living invertebrates were identified to order and categorised based on broad function (see Appendix A).

Samples of soil arthropods were made every third month of the experiment to minimise the destructive impact of digging on the ecosystem. Soil samples were taken from the same sections as leaf litter to ensure that a full horizon through the leaf litter, detritus and soil was sampled. Each section of soil was 15 cm x 15 cm and 10 cm deep – smaller than the typical 25 cm x 25 cm area usually employed to assess soil meso-fauna (Coleman et al. 1999). However, three smaller samples were taken per each plot, equating to a greater soil volume than one larger typical sample. By using smaller samples, damage caused by soil extraction was distributed across the plot, instead of being concentrated in one region. Soil was manually sifted in a similar fashion to the leaf litter and annelids were counted and measured. In-situ methods were employed instead of laboratory analyses, so as not to influence ecosystem interactions by removing material and biota.

2.3.6 Decomposition rate

In the final three months of the experiment, litterbags were placed in control and exclusion plots at four of the sites at each altitude. Bags were 25 cm x 25 cm and

constructed of 5 mm mesh allowing entry of macro- and meso-fauna. Each bag was filled with 15 g of oven-dried mixed leaves from species native to the area, as per (Anderson & Ingram 1993). At the end of the experiment, litterbags were taken to the Laboratory of Isotope Ecology CENA, USP, where the litter was dried and weighed to determine the rate of decomposition.

2.3.7 Soil nutrients

Soil ammonium and nitrate concentrations were measured in the first and final weeks of the experiment. Within each plot, a core of soil was taken and placed within a chilled container for transport from the field. To a subsample of 10 g from each core, 50 ml of 2 M KCl was added. After 24 hours, samples were filtered and frozen, to be later analysed at the laboratory. The extraction of ammonium and nitrate was done using automatic continuous flow injection in the laboratories of Laboratory of Isotope Ecology of CENA / USP. The concentration of soil nitrogen, extracted as ammonium and nitrate, at baseline and after 10 months exclusion was calculated.

2.3.8 Climatic data

Hourly data on temperature and rainfall for both sites over the ten-month experimental period was provided by Laboratório de Clima e Biosfera at the University of São Paulo (LCB-IAG-USP). We then calculated monthly average temperature (ºC) and cumulative monthly precipitation (mm) from this data set.

2.3.9 Avifaunal data

Bird point counts were undertaken in October, November and December, providing three temporal replicates per site. Individuals were identified to species. Counts

lasted 15 minutes with a survey range of 25m radius. Data from the temporal replicates was aggregated to provide a cumulative abundance for each site. Trait data on prey choice and adult biomass for each species was taken from Wilman et al. (2014) and original references therein. Species were categorised based on their preferred prey choice, forming the following groups: invertebrate, fruit/nectar, plant/seed, vertebrate and omnivore. Abundance for each species was multiplied by body mass to produce a total biomass for each functional guild per site.

2.3.10 Data analysis

Analysis focused on the cumulative abundance of macro-arthropod (body length ≥ 0.4 mm) groups, summed over the ten-month experimental period of repeated sampling. Formicidae were excluded from the analysis as they were too numerous to count accurately, and their high abundance has potential to skew results. To determine the effect of altitude alone on aboveground ecosystem functioning, we performed two-sample t-tests on the mean cumulative abundance of two functional groups of arthropods: predaceous and herbivorous; as well as cumulative proportion of leaf damage. For the belowground system, we focussed analyses on predaceous and detritivorous invertebrate groups, annelid body length, decomposition rate and soil nitrogen concentration. Paired t-tests were used to assess the impact of exclusion at high and low altitude on these above and belowground variables. We used Cohen's D to determine effect size of treatment between control and exclusion plots. Following thresholds described in Cohen (1992), the magnitude of effect was deemed to be: 'negligible' if $d < 0.2$, 'small' if $d < 0.5$, medium if $d < 0.8$, and 'large' if $d \geq 0.8$. For the avifaunal data, t-tests were performed to test within-guild differences

in abundance and total biomass between sites at high and low altitude. To account for multiple comparisons and control for false discovery rates, t-tests were corrected following the methods of Benjamini, Hochberg, and Yekutieli (1995).

2.4 RESULTS

2.4.1 Climatic variation with altitude

Mean monthly temperature at high and low altitude showed correlated temporal trends, with temperatures consistently between and 4 and 5ºC higher at lower elevations (Fig. 2.2). Below 100 m asl, temperatures ranged from 20 to 28ºC,

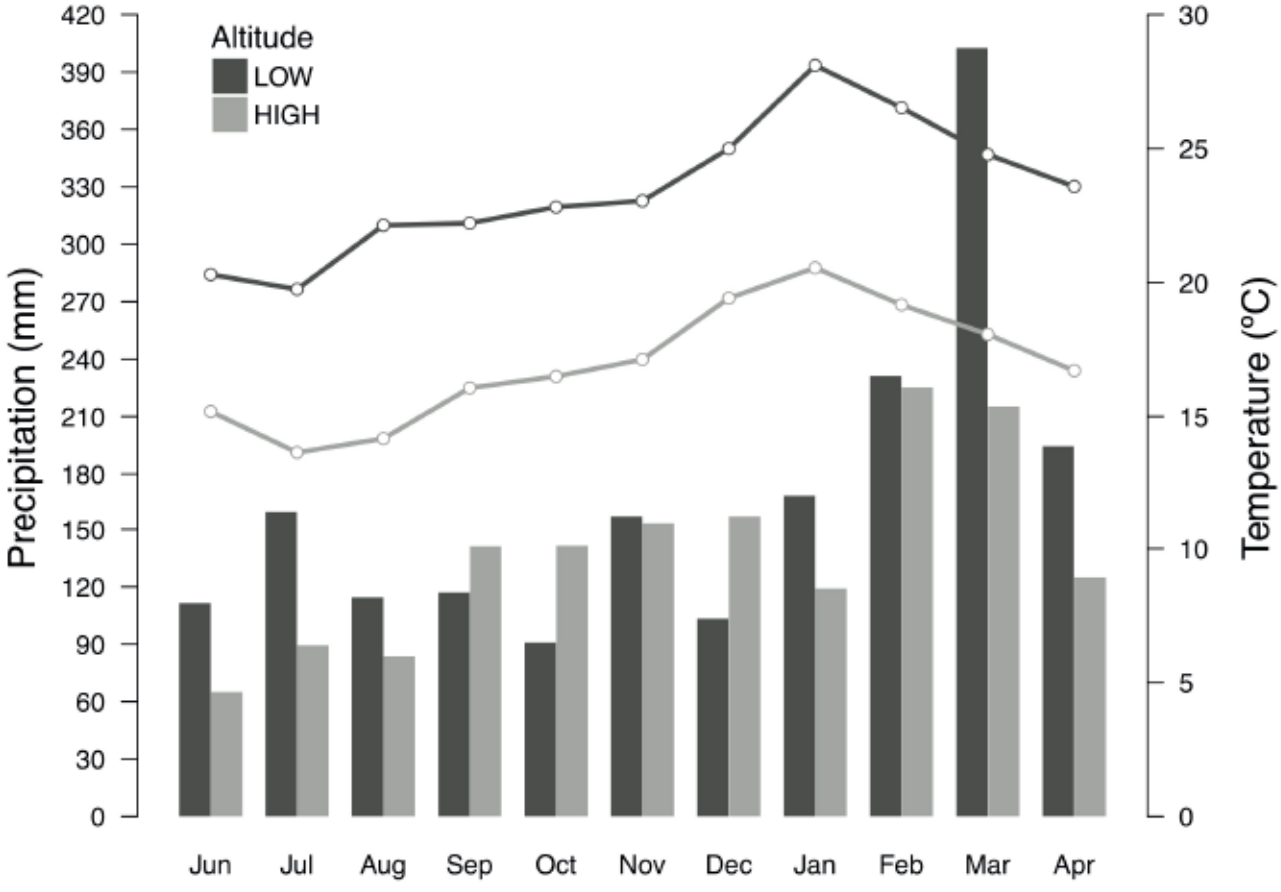


Figure 2.2. Mean monthly temperature (lines) and precipitation (bars) for sites at low and high altitudes. Low altitude is depicted by dark grey lines and bars; high altitude by light grey.

peaking in January and reaching lowest levels in July. At higher altitudes, the climate was cooler with lows of 14ºC in July and August and peaking at only 20ºC in January. Fluctuations in temperature were of a similar magnitude, with both sites displaying a degree of seasonality with a warmer period from December to March. Sites at low altitude received an annual total of 1853 mm of rainfall, 22% greater than the annual precipitation of 1517 mm above 1000 m asl. Monthly rainfall at higher altitude ranged from 65 mm in June to a high of 225 mm in February. In contrast, monthly rainfall at sites below 100 m asl did not drop below 90 mm and peaked at a maximum of 403 mm in March (Fig. 2.2).

2.4.2 General trends in aboveground arthropod community

Across all sites and plots, 1335 arthropods were sampled and identified. Arachnids formed the largest proportion of the understory arthropod community, constituting 33.4%, followed by Hemiptera at 19.9%, Orthoptera at 12.8% and Coleoptera 8.2%. The ratio of functional guilds was weighted towards herbivorous groups, which comprised 42.4% of the community compared to 37.2% by predaceous taxa.

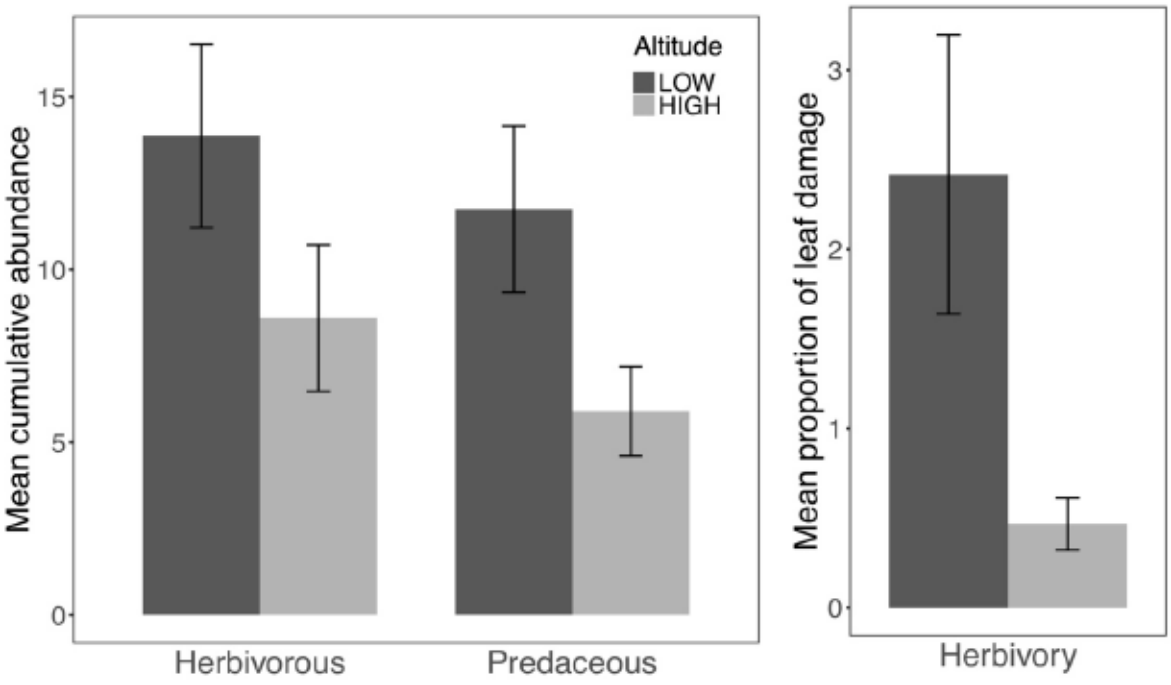


Figure 2.3. Variation in mean cumulative abundance of aboveground arthropod and proportion leaf damage in control plots at high and low altitudes. Error bars represent standard error of the mean (SEM). Asterisks represent p-values with * p < 0.05; ** p < 0.01; *** p < 0.001

2.4.3 Aboveground variation with altitude

The mean cumulative abundance of both predaceous and herbivorous arthropods was greater at lower elevations compared to high. Predaceous group abundance was 99% higher at low altitudes (t=2.14, p=0.080, Fig. 2.3), whilst herbivorous invertebrate abundance was only 61% higher at lower altitudes – an effect size that was not significant (Fig. 2.3). Variation in the density of herbivores between sites was primarily driven by a nine-fold increase in the number of Orthoptera at low altitude compared to high (t=2.52, p=0.038). Leaf damage was greater at low elevation (t = 2.46, p = 0.080, Fig. 2.3), showing a significant increase of 419%.

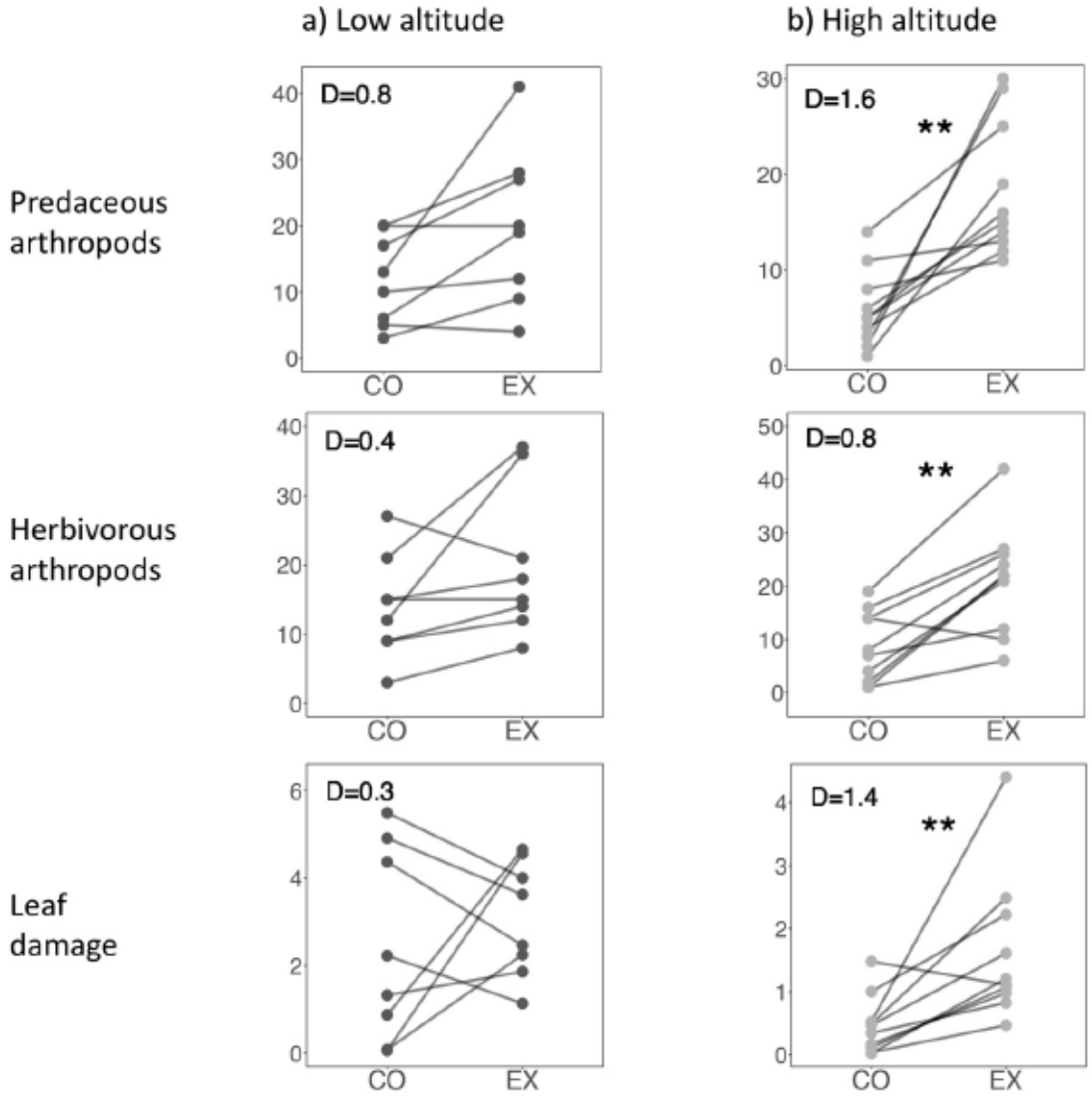


Figure 2.4. The effect of vertebrate exclusion at varying altitude on cumulative aboveground arthropod abundance and proportional area of invertebrate leaf damage. All data are scaled to allow comparison. Asterisks represent p-values from a paired t-test with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Effect size of treatment is represented as Cohen's d, with magnitude defined as: 'negligible' < 0.2, 'small' < 0.5, medium < 0.8, and 'large' ≥ 0.8.

2.4.4 Changes in aboveground ecosystem functioning with altitude

We observed a parallel increase in predatory arthropod abundance with vertebrate exclusion at both altitudinal levels. Closer to sea level, density increased from a mean of 11.8 in control plots to 20.0 under exclusion (t= 2.49, p=0.120) with a large effect size (d=0.8, Fig. 2.4). However, the effect of vertebrate removal was two times greater at high altitudes (d=1.6, Fig. 2.4), with predaceous invertebrate numbers rising by 212% from a mean in the control of 5.9 to 18.4 with treatment (t= 4.47, p=0.002). The absence of vertebrates had little impact on herbivorous arthropods at low altitudes, causing only a small rise in numbers of 45% (t=1.87, p=0.154, Fig. 2.4). In contrast, at high elevations, the mean abundance of herbivorous arthropods increased by a much greater magnitude of 147% from 8.6 to 21.2 with exclusion (t=4.66, p=0.002, Fig. 2.4). The mean proportion of leaf damage rose by 251% in exclusion plots compared to controls at high altitude (t=2.99, p=0.009, Fig. 2.4), whereas a difference of only 27% occurred between plots at lowland sites – an effect that was not significant.

2.4.5 General trends in belowground arthropod community

A total of 1210 arthropods were sampled within the leaf litter. The belowground community was dominated by Isopoda, a predominantly detritivorous order, comprising 26.5% of individuals. The contribution of other commonly-encountered orders to the community was more balanced, with Coleoptera making up 11.2%, Blatteria 10.2%, Diplopoda 8.5% and Araneae 8.4%. Detritivorous taxa were predominant within the assemblage, constituting 55.8% of individuals, whilst predaceous groups amounted to only 23.5%.

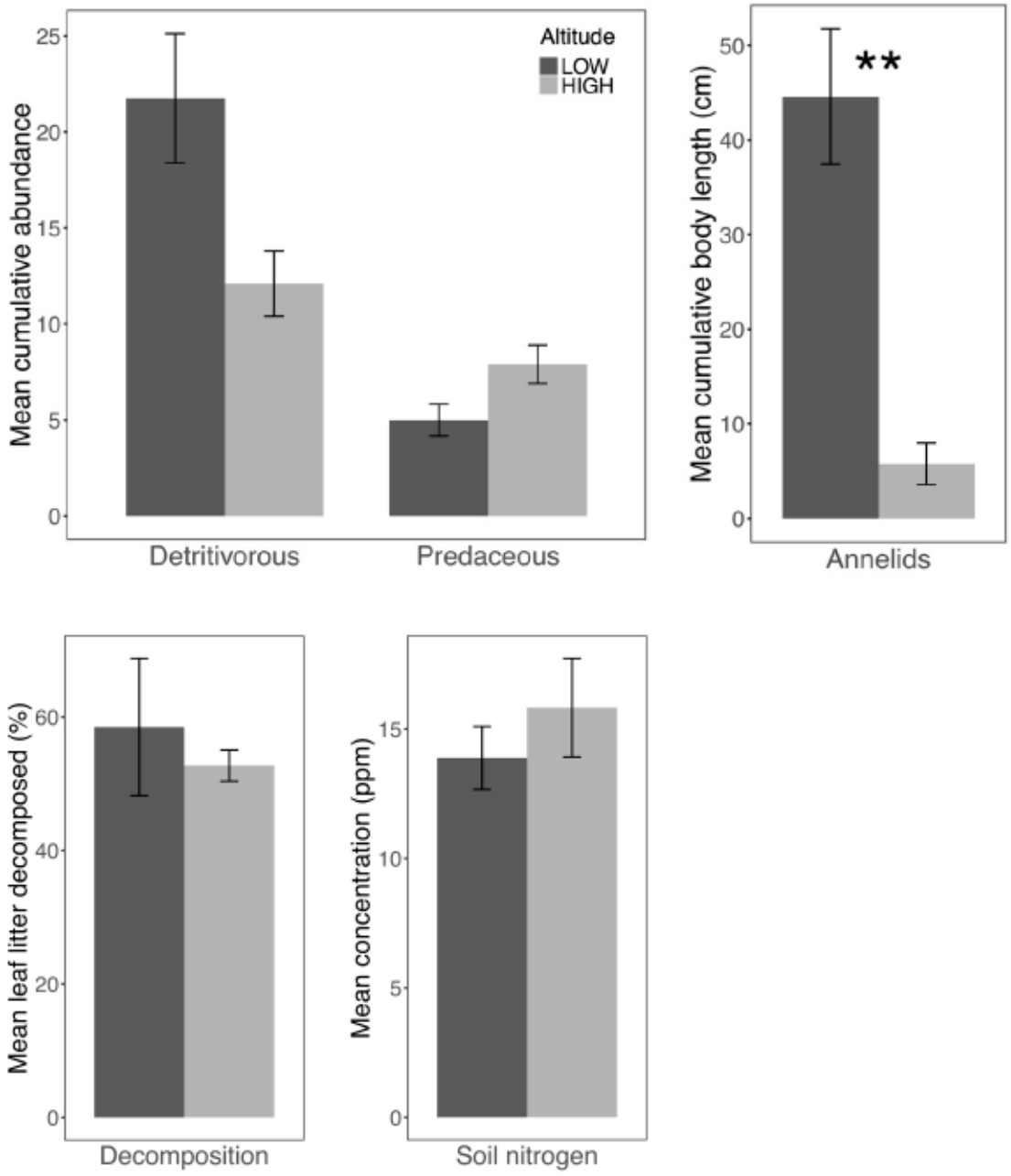


Figure 2.5. Variation in belowground arthropod abundance (predaceous and non-predaceous groups), annelid body length, leaf litter decomposition rate and extractable soil nitrogen with altitude. Error bars represent standard error of the mean (SEM). Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

2.4.6 Belowground variation with altitude

The mean cumulative abundance of leaf litter arthropods varied between sites, but functional groups showed opposing trends. Predaceous arthropods were found in greater numbers at higher elevations with a mean of 7.9 individuals compared to 5 in lowland forest ($t=2.24$, $p=0.060$, Fig. 2.5). In contrast, detritivorous groups occurred at higher densities in the wetter forests nearer sea level (mean= 21.8) than in drier habitat above 1000 m asl (mean =12.1, $t=-2.55$, $p=0.060$, Fig. 2.5). Mean annelid body length, summed over the ten-month experimental period, was significantly greater at lower altitudes with an average cumulative length of 44.6 cm compared to a mean of 5.8 in soil at higher altitude ($t=-5.18$, $p=0.003$). However, there was no significant variation in leaf litter decomposition and extractable soil nitrogen along the altitudinal gradient (Fig. 2.5).

2.4.7 Changes in belowground ecosystem functioning with altitude

Both predaceous and detritivorous leaf litter invertebrate guilds exhibited increases in density under exclusion at higher altitudes but not at lower elevations (Fig. 2.6). Numbers of predaceous individuals rose significantly by 43% in the exclosure compared to the control ($t=2.15$, $p=0.046$, Fig. 2.6) whilst a larger increase of 72% occurred within the detritivorous group ($t=2.32$, $p=0.050$, Fig. 2.6). Effect size was the same for both groups ($d=0.7$), classified as medium (Cohen 1992). Closer to sea level, the effect of exclusion on arthropod numbers was minimal, regardless of functional guild. Litter decomposition or concentration of soil nitrogen did not change with vertebrate exclusion.

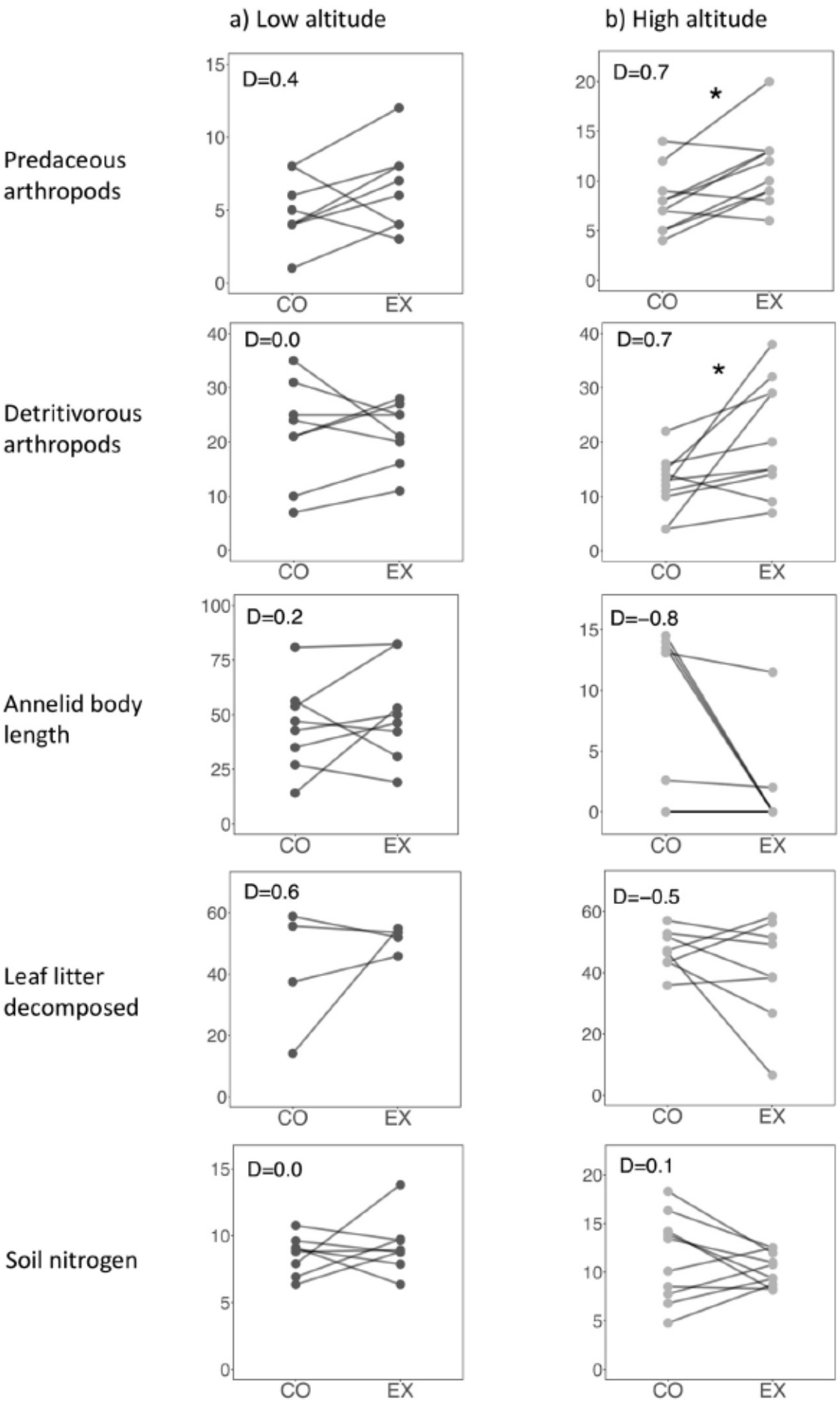

a) Low altitude
b) High altitude
Predaceous arthropods
Detritivorous arthropods
Annelid body length
Leaf litter decomposed
Soil nitrogen
D=0.4
D=0.7
D=0.0
D=0.7
D=0.2
D=−0.8
D=0.6
D=−0.5
D=0.0
D=0.1
CO
EX
*

Figure 2.6. The effect of the exclusion of vertebrates at varying altitude on cumulative leaf litter arthropod abundance, annelid body length, leaf litter decomposition and soil nitrogen. All data are scaled. Asterisks represent p-values with * p < 0.05; ** p < 0.01; *** p < 0.001.

2.4.8 Changes avifaunal community with altitude

Analysis revealed no significant within-guild differences in abundance and total biomass between low and high altitudes (Fig. 2.7).

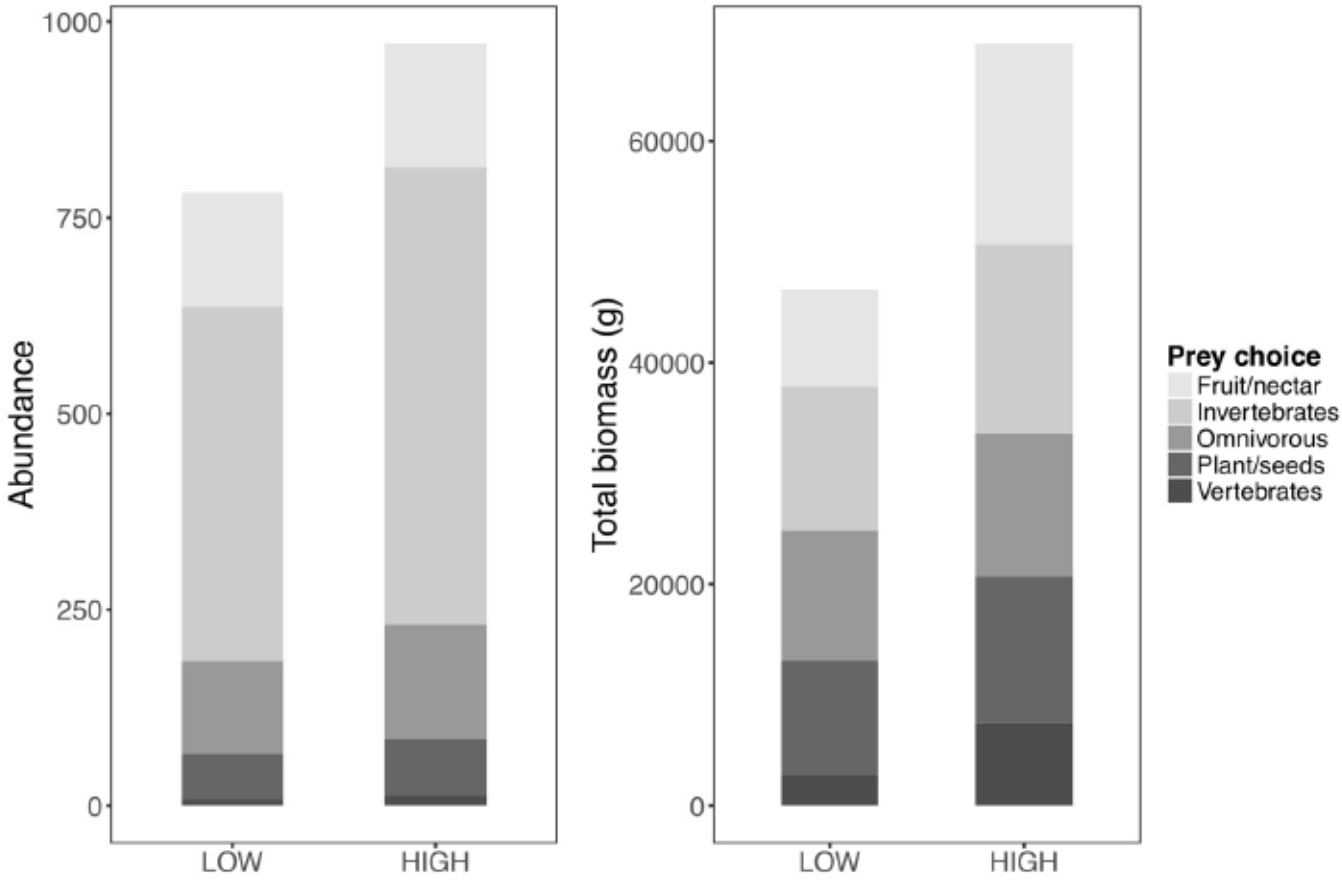


Figure 2.7. The effect of altitude on the abundance and total biomass of different avian functional groups. Asterisks represent p-values with * p < 0.05; ** p < 0.01; *** p < 0.001.

2.5 DISCUSSION

Our results give new insight into how gradients of altitude, and associated variation in biodiversity and changes in plant-animal interactions, have significant consequences for ecosystem functioning. Aboveground tropical systems at low attitude, which typically support more species and individuals, exhibit greater resilience to perturbation than those at high elevations. Only the predaceous arthropod guild responded to the absence of vertebrates at low altitude, but herbivorous populations and herbivory rate remained unaffected in lowland habitat. Releasing arthropods from vertebrate predation pressure at high altitude catalyses a trophic cascade, which results in increased leaf damage, despite a concurrent rise in intermediate predator density.

Interestingly, top-down vertebrate control appears less important for ecosystem functioning belowground. Leaf litter arthropods only responded to exclusion at high altitudes, but fluctuations in their density did not cascade to affect decomposition rates or soil nitrogen concentration. The consequences of biodiversity loss in the top trophic level may not become apparent within the subsystem until years after the initial disturbance event. Our experiment shows that changes in climate and resultant biotic variation have potential implications for ecosystem processes. These findings support the notion that diversity within lower trophic tiers, and the multifunctional ability of some organisms, may confer a degree of resilience to disturbance (Halaj & Wise 2001; Schmitz et al. 2000; Ewers et al. 2015).

In highland forest, vertebrates fulfil a role as the primary predatory and regulatory force controlling understory arthropod populations. Acting as intraguild predators,

they feed on predaceous invertebrates, whilst simultaneously competing with them for prey species in the form of herbivorous arthropods (Polis & Myers 1989; Polis & Holt 1992). When released from vertebrate top down pressure, an increase in abundance occurs in both invertebrate functional groups (Fig. 2.4). This correlates with findings across various habitat types that suppression of arthropods by vertebrates is ubiquitous, without preference towards a particular guild (Mooney et al. 2010). A classic trophic cascade exists at this altitude, whereby the absence of vertebrates elicits a rise in herbivore density, which translates into a corresponding increase in leaf damage.

Top down control of arthropods by mammals and birds is still of importance in lowland forest but may be less deterministic of population size. Theory suggests that when vertebrates act as intra-guild predators, they negate the effect of predaceous arthropods on herbivorous assemblages (Polis & Myers 1989; Polis & Holt 1992; Rosenheim et al. 1993). Thus, in the absence of insectivorous mammals and birds, intermediate predators can flourish and adopt the role of primary predators, inhibiting a rise in herbivore density. Our results show that release from predation pressure does elicit a significant rise in predaceous arthropod density, although the effect size is half that at high altitude (Fig. 2.4). The increased abundance of meso-predators may have counteracted the release in predation pressure from vertebrates to mitigate a corresponding increase in herbivore density, preventing the occurrence of a trophic cascade to affect levels of plant damage. In this way, predaceous arthropods may take on the functional role originally provided by vertebrates in controlling herbivore populations.

Cascade strength has been found to attenuate with increasing diversity within intermediate and low trophic levels (Halaj & Wise 2001; Schmitz et al. 2000), suggesting that species-rich ecosystems could be more resilient to perturbation. Complex interactions within highly diverse systems and between and within trophic levels can diffuse the effect of top-down forces and limit cascades (Holt & Polis 1997; Pace et al. 1999; Polis et al. 2000; Strong 1992). Thus, where altitudinal gradients of biodiversity exist, it is likely that ecosystem functioning will vary in a corresponding manner.

Even over short elevational gradients, sufficient environmental heterogeneity can cause vegetation zonation to be concentrated in a phenomenon called the 'Massenerhebung' effect (Richards 1996). This is in evidence along the Serra do Mar, Brazil, where steep topography and local variation in water regime and edaphic conditions lead to a spatially heterogeneous plant community. Studies specific to this region show that the diversity of legumes peaks in sub-montane forests between 100 to 200 m asl (da Silva et al. 2015), whilst tree species richness shows a similar hump-shaped distribution (Sanchez et al. 2013; Joly et al. 2012; Eisenlohr et al. 2013). With increasing elevation into montane forests above 1000 m asl, declines in floristic diversity are consistently reported (Sanchez et al. 2013; Joly et al. 2012; Eisenlohr et al. 2013; Rezende et al. 2015).

A habitat rich in plant species at low elevations is likely to support a greater diversity and density of arthropods. The high degree of host plant specificity exhibited by a large proportion of herbivorous arthropods (Colwell & Coddington 1994; Novotny et al. 2010) means that floristic diversity models can be extrapolated to predict patterns

within this invertebrate guild (Hamilton et al. 2010). And despite lower levels of host specialism, predaceous groups may also be directly and indirectly influenced by vegetation patterns (Basset et al. 2012; Siemann et al. 1998). As such, the greater abundance of understory predatory and herbivorous invertebrates at low altitudes in this study may be closely coupled with plant diversity (Fig. 2.3). These findings are corroborated by previous studies in the Serra do Mar, which suggest arthropod species richness fluctuates significantly with altitude, peaking in lowland forests (Almeida-Neto et al. 2006; Lazzarotto & Lázzari 1998). Higher diversity within the bottom and intermediate trophic tiers may buffer against indirect top-down effects on herbivory rate (Strong 1992; Polis et al. 2000; Halaj & Wise 2001; Schmitz et al. 2000) preventing the occurrence of trophic cascades at low elevations (Fig. 2.4). A less speciose habitat at higher elevations, may not be able to diffuse the cascading effect of perturbation within the top trophic level, with consequences for increased herbivory rates (Fig. 2.4). In species-rich lowland systems, the top-down control exerted by vertebrates may not be as important, and this may account for the weaker effect of exclusion on both invertebrate functional guilds (Roslin et al. 2017). Insectivorous arthropods may play the primary role in controlling their herbivorous counterparts. Interestingly, predation risk for herbivorous invertebrates has been found to increase towards sea level, with arthropod predators responsible for the greater number of attacks. Thus, the observed meso-predator release at low altitude, although weaker than at in montane forests, inhibits a concurrent rise in herbivore abundance, with no cascading effect on leaf damage.

The belowground ecosystem along the altitudinal gradient appears to be more robust to disturbance at higher trophic levels. Vertebrate exclusion did elicit a rise in the

density of both predaceous and detritivorous arthropod populations above 1000 m asl, suggesting an intact top trophic tier is important in controlling numbers. Fluctuations in the saprophagous guild, however, did not cascade to affect decomposition rates or soil nitrogen concentration. Birds and mammals at low altitude exert little control over belowground arthropod density and the entire system seems resilient to the absence of the top trophic level. These results correspond with findings that belowground taxa take longer to respond to biodiversity loss compared with their aboveground counterparts (Scherber et al. 2010). The experimental removal of key taxa in the belowground food webs has been shown to have little effect on processes such as net primary production and rates of soil respiration (Liiri et al. 2002). Detritivores are a diverse group but tend to fulfil functionally similar roles, exhibiting a low degree of specialization (Bradford 2002). Thus, a large proportion of the belowground community provide the same ecosystem service, conferring a high degree of resilience to disturbance aboveground. Functional compensation in this manner buffers against tropic cascades, until multiple stresses combine to place pressure on entire trophic levels (Lawton & Brown 1994). Longer-term studies are required to determine how the continued absence of top predators may affect trophic cascade strength.

Conclusions regarding fluctuations in soil nitrogen in this study should be made with caution. In situ methods of measuring soil nitrogen concentration and mineralisation rate have inherent problems, with extraction conditions such as soil water dynamics, having implications for nutrient recovery (Hanselman, Graetz and Obreza, 2004). The choice of chemical used to extract nitrogen, in the form of ammonium and nitrate, may also influence outcome. A comparison of results revealed significant

variation in soil nitrogen concentration when using KCl, $CaCl_2$ or electro-ultrafiltration, with the degree of dissimilarity largely influenced by soil type (Dou, Alva and Appel, 2000).

Due to resource and time pressure, single plot samples were taken at baseline and in the final week of the 10-month experimental period. Given the high variability associated with soil nitrogen measurements (Kolberg *et al.*, 1997), a greater number of temporal and spatial replicates is required in future studies to corroborate the outcomes described here.

Vertebrate communities, particularly avian insectivores, are vital for the provision of ecosystem services (Andresen 2000; Şekercioğlu 2006), specifically in the control of arthropod herbivorous activity. The value of these ecosystem services may decrease with increasing ecosystem diversity within lower and intermediate trophic levels. If this is the case, it is essential to preserve vertebrate communities at high altitude as they fulfil a role that cannot easily be replicated by other groups.

CHAPTER 3

Are there edge effects on trophic cascades in tropical rainforests?

3.1 ABSTRACT

The cascading effects of biodiversity loss on ecosystem functioning within forested systems have recently become more apparent. However, how edge effects shape these processes has yet to be established. Here we assessed how edge effects alter arthropod populations and the strength of any resultant trophic cascade on herbivory rate in tropical forests of Brazil. We experimentally excluded vertebrates from seven paired edge and interior sites in habitat with a high percentage of forest cover. Understory arthropods and percentage leaf damage were sampled every four weeks to give cumulative data summed over a ten-month experimental period. Path analysis was used to determine the strength of trophic cascades within the interior and close to the forest/matrix border. Within the forest interior, vertebrate exclusion had a positive impact both predaceous and herbivorous arthropods, with significant cascading effects on herbivory. Edge-dwelling invertebrates responded weakly to exclusion and there was no evidence of trophic cascade. Our results suggest that the vertebrate community at forest edges controls invertebrate densities to a lesser extent than that within the interior. Ecotone habitat is known to support vertebrate communities with a smaller contingent of specialist insectivores. This allows arthropods to flourish and indirectly accounts for higher levels of plant damage at these sites. Increased herbivory rates may have important consequences for floristic community composition and primary productivity, as well as cascading effects on nutrient cycling. As forests become more dominated by edge habitat, we need to understand how ecosystem functioning will be fundamentally altered in these changed environments.

3.2 INTRODUCTION

Tropical forests are becoming progressively more dominated by edge habitat (Ribeiro et al. 2009; Haddad et al. 2015). As edge effects can pervade deep into the forest, they have a profound effect on the ability of some species to persist in ecotone areas. Indeed, the vertebrate community within close proximity to tropical forest edges is known to be significantly changed compared with that of the interior (Şekercioğlu et al. 2002; Banks-Leite et al. 2010; Pfeifer et al. 2017). Within avian communities in particular, species which exhibit habitat and dietary specificity are sensitive to habitat modification and fragmentation (Newbold et al. 2013; Barbaro & Van Halder 2009; Restrepo & Gomez 1998). These specialist groups fulfil varied and vital roles for the functioning of ecosystems (Şekercioğlu 2006). Within forest interiors, insectivores control arthropod populations, mediating the occurrence of trophic cascades on herbivory rate (Dunham 2008; Schmitz et al. 2000). If these functionally-important groups, and the predation pressure they exert, are absent from edge habitat, will this translate into altered ecosystem functioning?

The top-down control of arthropod populations by insectivorous vertebrates helps to regulate herbivory levels in both natural and anthropogenic systems (Koh 2008; Mooney et al. 2010; Newbold et al. 2013). In tropical forests this control function is of particular importance given the high density and diversity of the arthropod community. In the absence of insectivorous vertebrates, arthropod abundance can increase by 150% with a corresponding rise in herbivory of 200% (Kalka et al. 2008). As folivorous species are known to consume a large proportion of plant carbon, increased herbivory can have important consequences for carbon sequestration and soil fertility (Metcalfe et al. 2014). Other studies, however, support the theory that

ecosystem processes in tropical forests remain resilient to perturbation due to high levels of diversity and functional similarity between species (Ewers et al. 2015). Despite growing interest in this area, it is still unclear whether ecosystem functioning is altered in edge habitats as a result of changes in the predator community.

Forest edges tends to be warmer, lighter and drier than the interior (Murcia 1995; Foggo et al. 2001; Jose et al. 1996), affecting floristic diversity and community composition (Benítez-Malvido & Lemus-Albor 2005; Harper et al. 2005). Many forest vertebrates react adversely to these changed environments, preferring to remain in the cooler, damper forest interior (Stevens & Husband 1998; Dale et al. 2007; Banks-Leite et al. 2010). Species that show high habitat specificity are sensitive to edge creation, decreasing in occurrence and abundance in modified forest areas (Newbold et al. 2013). Some small mammal species favour forest interiors and occur rarely in border areas, whilst others with low habitat specificity benefit from edge creation, exploiting both matrix and forest habitats (Stevens & Husband 1998). Bird communities in particular are significantly affected by edge creation, which has diverging effects on different functional guilds (Dale et al. 2007). The diversity of specialist avian insectivores declines significantly at forest edges, whilst the richness of other functional guilds remains comparable with that found within the interior (Banks-Leite et al. 2010). Insectivorous understory birds avoid dense undergrowth at edges and show a preference for foraging in dark interior areas with damp leaf litter (Canaday 1997).

A depauperate insectivore community in ecotone areas is likely to control arthropod numbers to a lesser extent than within the interior. Released from this predation

pressure, and benefitting from resources in adjacent matrix habitat, arthropod populations are known to increase in density at forest edges (De Carvalho Guimarães et al. 2014). This reflects findings that herbivory patterns, which are also higher in edge areas with crop or pastureland (Didham et al. 1998; Coley & Barone 1996). Thus, if top-down pressure from the bird and mammal community is weak at edges, will there be any cascading effects with vertebrate exclusion? This study aimed to determine whether edge effects impact trophic cascades in the Brazilian Atlantic forest. Using an exclusion experiment, we simulated the absence of vertebrates at paired edge and interior sites in habitat with a high percentage of forest cover. We investigated the impact of treatment on arthropod abundance and community composition, and the cascading effects on herbivory rate. We posed the following questions: 1) Are there edge effects on the arthropod community and herbivory rates? 2) Does vertebrate exclusion have differing effects on arthropods, and subsequent leaf damage, depending on proximity to forest edges? 3) Do edge effects alter trophic cascade strength? We use path analysis to address these questions.

3.3 METHODOLOGY

3.3.1 Site selection

The study took place in the Atlantic Forest of Brazil, specifically, within the administrative area of Santa Virginia in the Parque Estadual da Serra do Mar (PESM). With only 11 to 16% of the original forest remaining, the Atlantic Forest ecosystem is considered to be one of the most endangered in the world (Ribeiro et al. 2009). Most of this habitat is highly fragmented with 73% occurring less than 250m from surrounding matrix and 45% located within 100m of the forest edge

(Ribeiro et al. 2009). Potential sites were identified based on maps provided by Instituto Florestal do Estado de São Paulo (Instituto Florestal do Estado de São Paulo 2010) and SOS Mata Atlântica (SOS Mata Atlântica & Instituto Nacional de Pesquisas Especiais 2014). Seven paired interior and edge sites with forest cover greater than 40% were randomly selected for the experiment. This threshold of cover was chosen because vertebrate communities in the interior of such areas have similar levels of integrity to those found in areas with 100% forest cover (Banks-Leite et al. 2014).The seven edge sites were situated no further than 5 m into the forest, whilst the seven interior sites were positioned at least 100m from the border. The minimum distance to ensure spatial independence between replicates was 200 m. The surrounding matrix for all sites was pastureland.

3.3.2 Experimental plots

At each site, we constructed three experimental plots: exclosure, procedural and control. Thus, in total, across 14 edge and interior sites, there were 42 experimental plots. Each type of plot was randomly assigned to 2 m x 2 m areas, which were at least three metres apart from each other. Effort was made throughout the construction process to minimise the cutting of plants and removal of roots to ensure continuity of the forest understory structure.

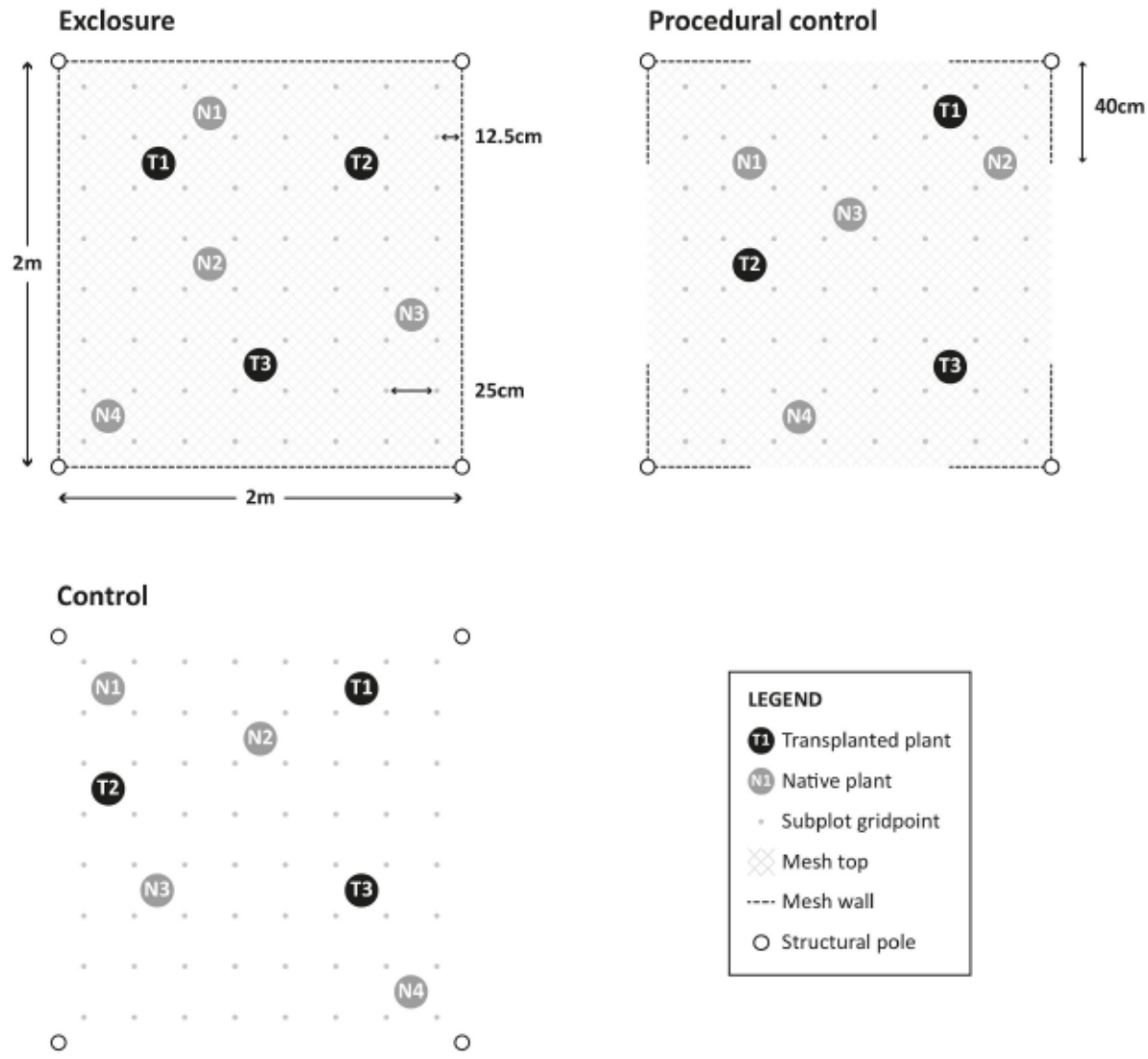


Figure 3.1. Schematic diagram of the plots at each site. In the field, each plot is positioned at least three metres from the others.

Exclosure plots were constructed of plastic poles and wire mesh and measured 2 m x 2 m in area, with a height of 1.5 m. The mesh had openings of 20 mm x 18 mm allowing the passage of all but the largest insects, whilst excluding the majority of vertebrates. Lengths of nylon thread were sown through the overlapping parts of the mesh walls and top to ensure the structure was mammal and bird-proof. The bottom of the mesh was buried into the ground and secured with metal pins to stop animals

burrowing underneath. Access to the exclosure was via a mesh door, which was closed securely on departure with reusable plastic ties.

Procedural plots (Koh 2008) were composed of the basic framework of poles, a mesh top and an additional four sections of mesh fitted lengthwise to form corners (see Fig. 3.1). The purpose of this structure was twofold. Firstly, the mesh top collects leaves in the same manner as the exclosure and controls for the effect of reduced litter fall expected under exclusion. Secondly, spiders were likely to use the structure of the exclosure to build webs. The mesh corners of the procedural plot also provide this foundation, controlling for microclimatic effects on spider density, whilst still allowing access by mammals and birds.

Control plots were simply four short lengths of pole placed into the ground to demarcate the 2 m x 2 m area. Previous analyses revealed little difference between the control and the procedural control (see Appendix C), so here we report only comparisons between the control and exclosure.

3.3.3 Herbivory measurements

To provide a consistent measure of herbivory across all plots, sites and altitudes, three plants of species native to Serra do Mar were translocated to each of the plots. The selected species were *Erythrina speciosa*, *Inga vera* and *Ocotea puberula,* which are known to experience a moderate degree of insect herbivory and naturally occur across the altitudinal range of the study area. Within each plot, the three translocated individuals were positioned one metre apart, each forming the point of a rough triangle. Seedlings were chosen as younger plants undergo a period of rapid

growth and are known to experience a higher degree of herbivory than more mature plants (Coley & Barone 1996).

To supplement measurements of herbivory taken from the three translocated plants, we also were randomly selected and measured four in-situ seedlings from the community within each plot. These individuals measured between 5 and 100 cm (Benítez-Malvido & Martínez-Ramos 2003) and also displayed a moderate level of historical herbivory. Thus, seven plants were sampled per plot, totalling 315 plants across all altitudes. All sampled plants were marked with inconspicuous, blue, plastic tags, each of which had a coded number.

Due to an uncharacteristic dry period in 2014, very few new leaves emerged during the first few months and sampling was restricted to four of the mature leaves already present. With the onset of the wet season in November, there was a corresponding surge in leaf emergence. At this time, four new leaves were marked per plant and followed for three months or until other new leaves appeared. They were then replaced in the sampling scheme by the younger leaves. This replacement process continued for the duration of the experiment. Employing this method ensured that throughout the year, monthly measurements of herbivory were taken from young leaves at similar life stages. This is important, as the leaves of shade-tolerant tropical species experience almost 70% of their lifetime herbivory in the 1–3 week expansion period following emergence (Coley & Barone 1996). We followed the suggestion of Coley & Barone (1996), to include both mature and expanding leaves in our sampling, as well as to take measurements at intervals over time.

The sampled leaves were photographed every four weeks. Image J software was used to calculate initial leaf area (ILA), new growth, desiccation, pathogen and fungal damage, as well as insect and mammalian herbivory. This method provides a greater degree of accuracy than relying on visual estimates of proportion in the field. Only herbivory caused by chewing insects was assessed from holes in the leaves. The impact of other insects such as phloem feeders is much harder to ascertain (Coley & Barone 1996) and beyond the limits of this study. Insect herbivory can generally be distinguished from mammalian, as mammals tend to clip the leaf close to the stem (Dunham 2008). Areas of desiccation, pathogen or fungal damage were measured and subtracted from the leaf area available for herbivory. Leaf damage measurements were taken from all plants, including those already in-situ and transplanted plants.

3.3.4 Understory fauna

Every month, the leaves and stems of all plants within each plot were visually inspected for arthropods. Individuals were identified to order and their body length, from the most anterior part of the head to the tip of the abdomen, was estimated. Formicidae were recorded as a separate group from other Hymenoptera. Orders were assigned to broad categories based on the dominant dietary habits of species within the taxon. A list of sampled orders and broad functional categories can be found in Appendix A.

3.3.5 Avifaunal data

Bird point counts were undertaken in October, November and December, providing three temporal replicates per site. Individuals were identified to species. Counts

lasted 15 minutes with a survey range of 25m radius. Data from the temporal replicates was aggregated to provide a cumulative abundance for each site. Trait data on prey choice and adult biomass for each species was taken from Wilman et al. (2014) and original references therein. Species were categorised based on their preferred prey choice, forming the following groups: invertebrate, fruit/nectar, plant/seed, vertebrate and omnivore. Abundance for each species was multiplied by body mass to produce a total biomass for each functional guild per site.

3.3.6 Data analysis

Analysis focused on the cumulative abundance of macro-arthropod groups, summed over the ten-month experimental period of repeated sampling. Macro-arthropods are defined here as individuals with body length greater than 0.4 cm. To determine the effect of plot location alone on arthropod community composition, I performed two-sample t-tests on the mean cumulative abundance of the most common arthropod orders from control plots. I also analysed the degree of herbivory in control plots using paired t-tests. For the avifaunal data, paired t-tests were performed to test within-guild differences in abundance and total biomass between edge and interior sites. To account for multiple comparisons and control for false discovery rates, t-tests were corrected following the methods of Benjamini, Hochberg, and Yekutieli (1995).

Path analysis was employed to test the hypothesis that the exclusion of vertebrates would affect the degree of herbivory through changes in insect populations and that this effect would vary depending on site location. I tested the direct top down effect of exclusion on predatory and phytophagous arthropods, the effect of predatory groups on herbivorous

groups, as well as the impact of phytophagous arthropods on herbivory. I used confirmatory path analysis in a generalised multilevel context as proposed by Shipley (2009). This approach allows for mixed categorical, count and continuous data as well as non-linear paths and interactions. In this way a hypothesized causal model can be deconstructed into subsets of generalised linear mixed models. A sub-model was created for each of the endogenous variables found within the hypothesized causal model. Each endogenous variable was fitted as the response variable, with any causal variables, both direct and indirect, fitted as explanatory variables. Location and treatment were fitted as separate variables and as an interaction. Site was included as a random factor to account for variation between replicates. I used the nlme package (Pinheiro et al. 2017) and the lme4 package (Bates et al. 2014) in R (R Core Team, 2016) to undertake these analyses. In all cases, residual plots were inspected to highlight any deviations from normality or homoscedasticity and all models were produced using restricted maximum likelihood (REML). If any non-normality was observed, the data were fitted using a more suitable error structure. Where possible, sub-models were reduced using backwards stepwise selection based on the Akaike Information Criteria (AIC) with smaller AIC values representing a better fit (Zuur et al. 2009). The delta AIC was calculated for all models and only those producing values of less than two were considered as candidate models (Burnham & Anderson 2004). The final hypothesized causal models were reconstructed with these sub-models and tested with Shipley's d-separation test (Shipley 2009). D-separation tests whether pairs of variables that should be uncorrelated when other related variables are held constant, are truly independent. If all the independence claims within a path model are true, then the path model can be accepted as a viable hypothesis. The path coefficients of the final model correspond to the slopes of the partial regressions of the variables in the LMM

and GLMM sub-models. All variables were scaled so that the path coefficients were comparable.

3.4 RESULTS

3.4.1 Do edge effects alter abundance within avian functional groups?

Paired t-tests revealed differences in within-guild avian abundance and total biomass between edge and interior sites (Fig. 3.2). There was a 25% increase in insectivorous bird abundance within the interior, rising from a mean of 86 at edge sites to 108 within the forest (t=0.34, p=0.05). In contrast, omnivore and granivore abundance increased at edge habitat by 14% (t=0.16, p=0.05) and 53% (t=0.56, p=0.05) respectively.

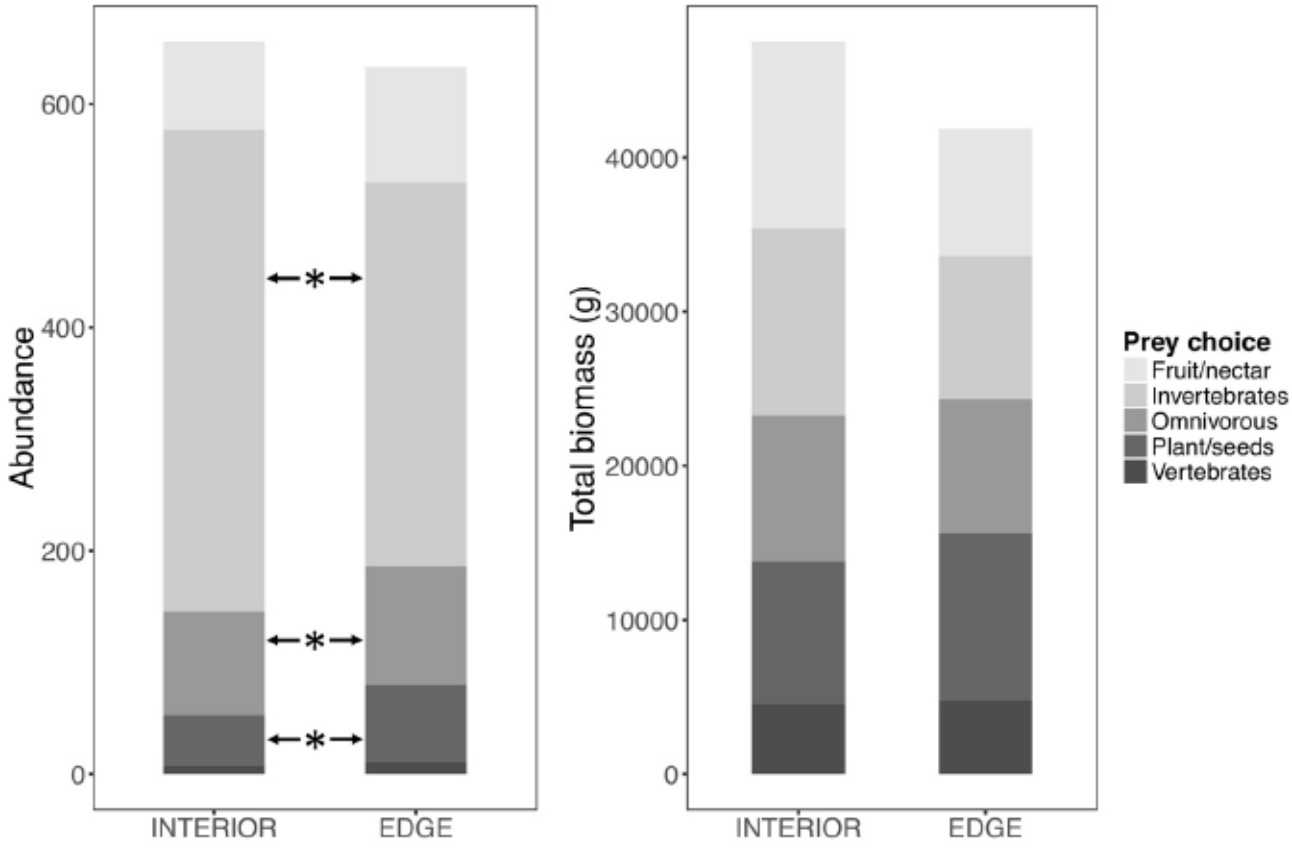


Figure 3.2. Edge effects on the abundance and total biomass of different avian functional groups. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

3.4.2 General trends in arthropod community

Over ten months of sampling, 643 arthropods, belonging to 17 arthropod taxa, were recorded on the leaves and stems of plants within control and exclusion plots at seven paired interior and edge sites. The two most abundant orders were Araneae and Hemiptera, which comprised 30% and 19% of arthropod counts respectively. Combined with Coleoptera, Diptera, Lepidoptera and Orthoptera, which were also encountered frequently, these taxa accounted for 90% of the data.

3.4.2 Are there edge effects on arthropods and herbivory levels?

In control subplots, total arthropod density was significantly greater at edge sites (mean = 25.3) compared with interior sites (mean= 11.8), showing an increase of 113% ($t=4.00$, $p=0.030$). This variation is primarily due to the abundance of Coleoptera, Hemiptera, Lepidoptera and Orthoptera increasing significantly at forest edges (Fig. 3.3). Herbivorous arthropods, but not predaceous, exhibited significantly greater densities at edge sites (mean=12.4) compared with interior sites (mean=4.3, $p=0.001$, Fig. 3.4). Leaf damage showed a corresponding rise of 81% at edge sites, but this effect was not significant ($t=1.75$, $p=0.17$, Fig. 3.4).

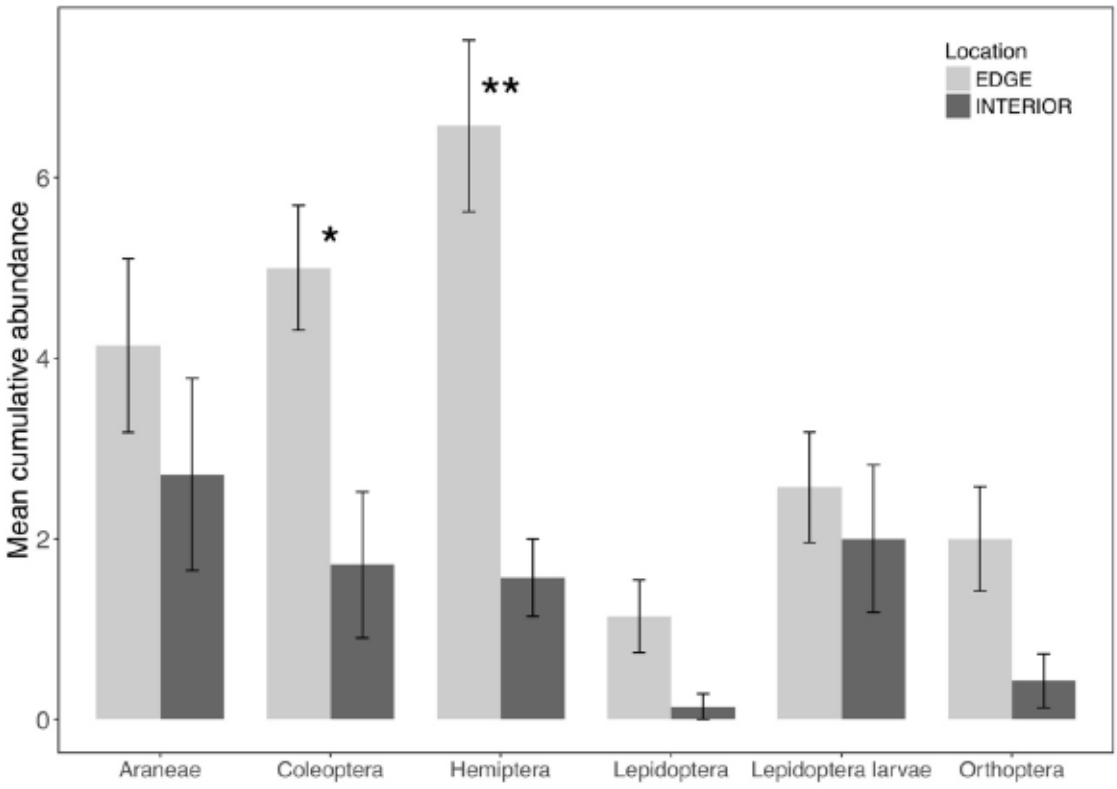


Figure 3.3. Effects of forest location on the abundance of arthropods orders. The graph shows mean cumulative abundance of arthropods in control plots across seven paired edge and interior sites. Error bars represent standard error of the mean (SEM). Asterisks represent p-values with * p < 0.05; ** p < 0.01; *** p < 0.001.

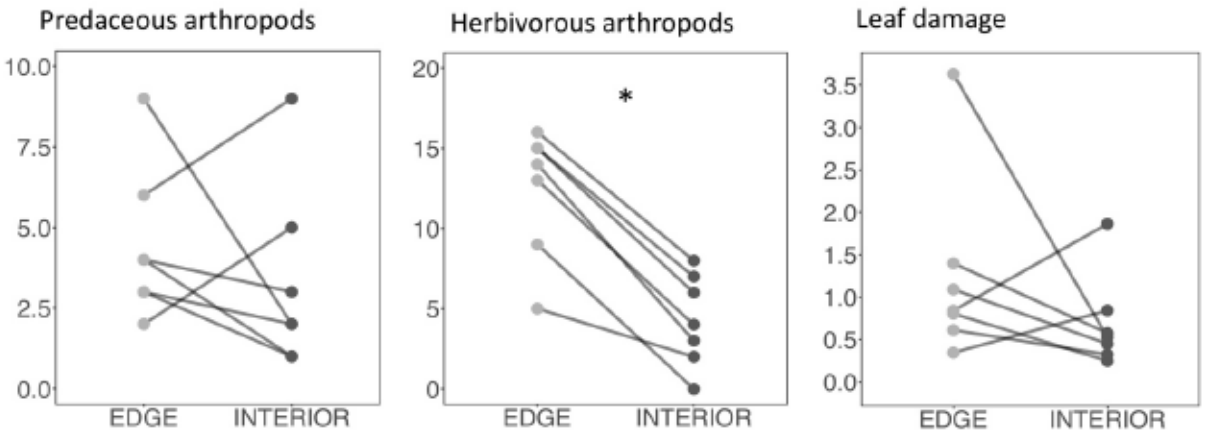


Figure 3.4. Paired plots depicting the variation in cumulative abundance of predaceous and herbivorous arthropods and percentage of leaf damage with forest location. Asterisks represent p-values with * p < 0.05; ** p < 0.01; *** p < 0.001.

3.4.3 Do edge effects alter the outcome of vertebrate exclusions?

At interior forest sites, there was an increase of 155% in total arthropod density in exclosures (mean = 30.2) compared with control plots (mean = 11.9, t=3.71, p=0.03, Table 3.1). This increase was primarily due to a significant five-fold rise in the

Taxa	Interior				Edge			
	CO	EX	t	p	CO	EX	t	p
TOTAL	**11.9**	**30.2**	**3.71**	**0.03**	25.3	24.4	-0.24	0.93
Araneae	**2.7**	**13.4**	**3.42**	**0.03**	4.1	7.3	1.87	0.72
Coleoptera	1.7	1.6	-0.16	0.88	5.0	3.6	-1.05	0.80
Diptera	1.1	0.9	-0.54	0.67	1.4	0.9	-0.86	0.91
Hemiptera	1.6	2.1	0.90	0.48	6.6	6.7	0.12	0.90
Lepidoptera	0.1	1.0	1.55	0.25	1.1	1.0	-0.26	0.90
Lepidoptera larvae	2.0	4.9	1.71	0.21	2.6	2.3	-0.30	0.82
Orthoptera	**0.4**	**3.7**	**3.40**	**0.03**	2.0	1.4	-0.70	0.80
Leaf damage	**0.7**	**1.8**	**2.39**	**0.05**	1.2	0.8	-0.83	0.83

Table 3.1. Effects of exclusion of vertebrates on arthropod abundance at interior and edge sites. The table shows mean cumulative abundance across seven paired control (CO) and exclosure (EX) plots situated at the interior and edge of the forest. The last row shows percentage of leaf damage. Values in bold indicate results at a significance level of p < 0.05.

numbers of Araneae (t=3.42, p=0.03) and a nine-fold increase in Orthoptera (t=3.40, p=0.03, Table 3.1). Other arthropod groups, such as Lepidoptera, Lepidoptera larvae and Hemiptera also exhibited increased abundance under exclusion at forest interior sites; however, these differences were not found to be significant (Table 3.1). The predatory arthropod guild also increased by 326% (p=0.01) under exclusion, whilst herbivorous arthropods invertebrates rose by 180% (p=0.01). The proportion of leaf damage increased three-fold in exclosure subplots (p=0.05, Fig. 3.5a).

At edge sites, arthropod numbers varied little between control (mean=25.3) and exclosure (mean=24.4, Table 3.1) plots. In fact, these results are more comparable with the mean density of arthropods under exclusion within the forest interior (mean=30.2) than to interior control plots (mean = 11.9). None of the common arthropod orders (Table 3.1), or functional guilds (Fig. 3.5b), showed significant increases in density with exclusion. The absence of vertebrates also had little effect the proportion of leaf damage at edge sites, which was actually 48% higher within control plots (t=0.83, p=0.80, Fig. 3.5b).

3.4.4 Do edge effects alter trophic cascades?

The interior forest path model suggests that the exclusion of vertebrates had a significant direct and positive impact on the abundance of both predaceous (1.58, p=0.00) and herbivorous arthropods (0.70, p=0.03, Fig. 3.6a). The increase in the density of herbivorous arthropods was not directly caused by changes in the predaceous guild. The positive effect of vertebrate exclusion on herbivorous damage was mediated indirectly by variation in herbivorous arthropods (0.09, p=0.002). At edge sites, however, the effect of vertebrate exclusion was noticeably weaker than at

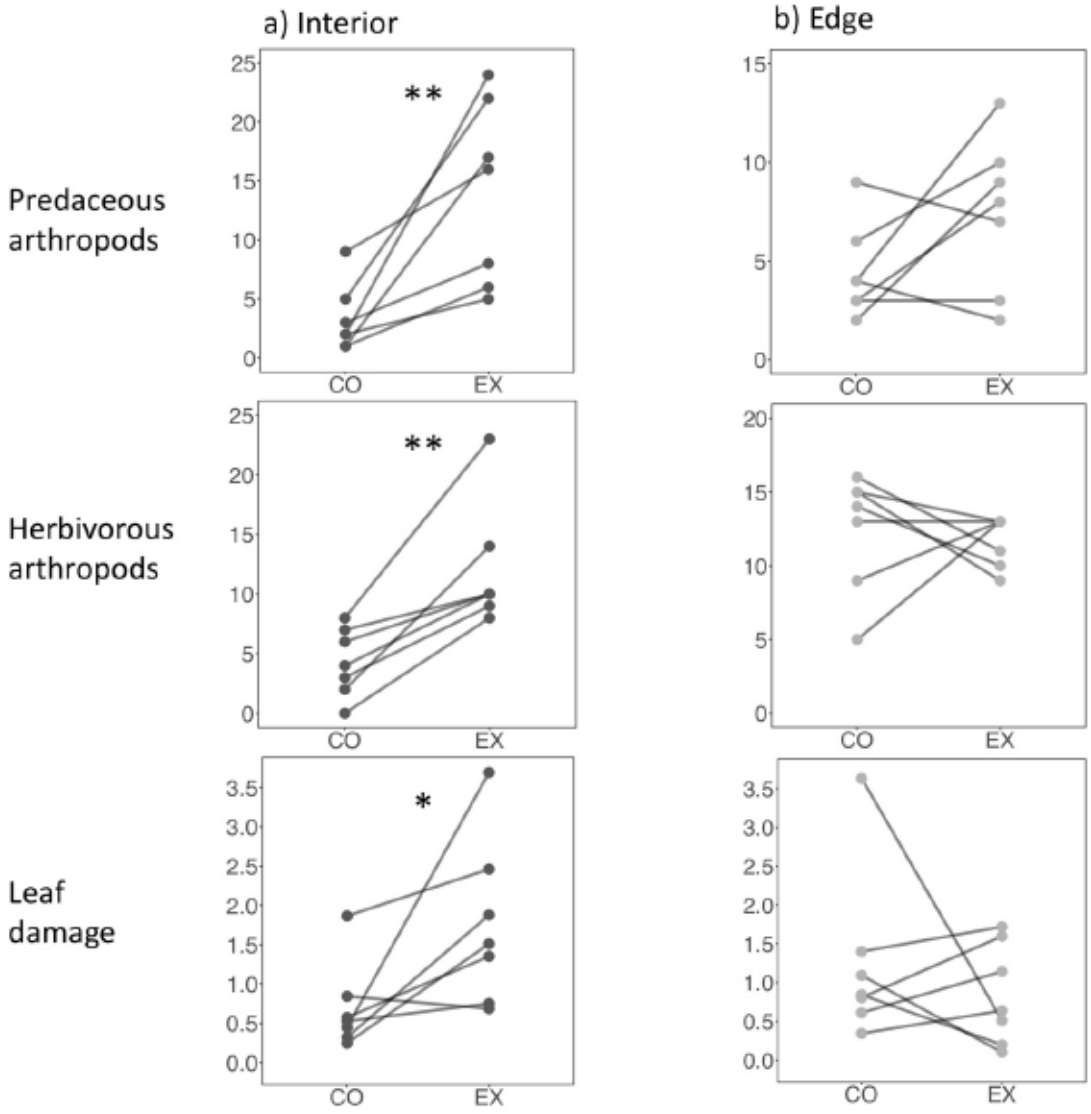


Figure 3.5a and b. Paired plots depicting the variation in cumulative abundance of predaceous and herbivorous invertebrates and percentage of leaf damage between control and exclusion plots at a) forest interiors and b) forest edges. Asterisks represent p-values with * p < 0.05; ** p < 0.01; *** p < 0.001.

interior sites and there was little evidence for any significant direct or indirect interaction between vertebrate exclusion, arthropod density and herbivorous damage (Fig. 3.6b).

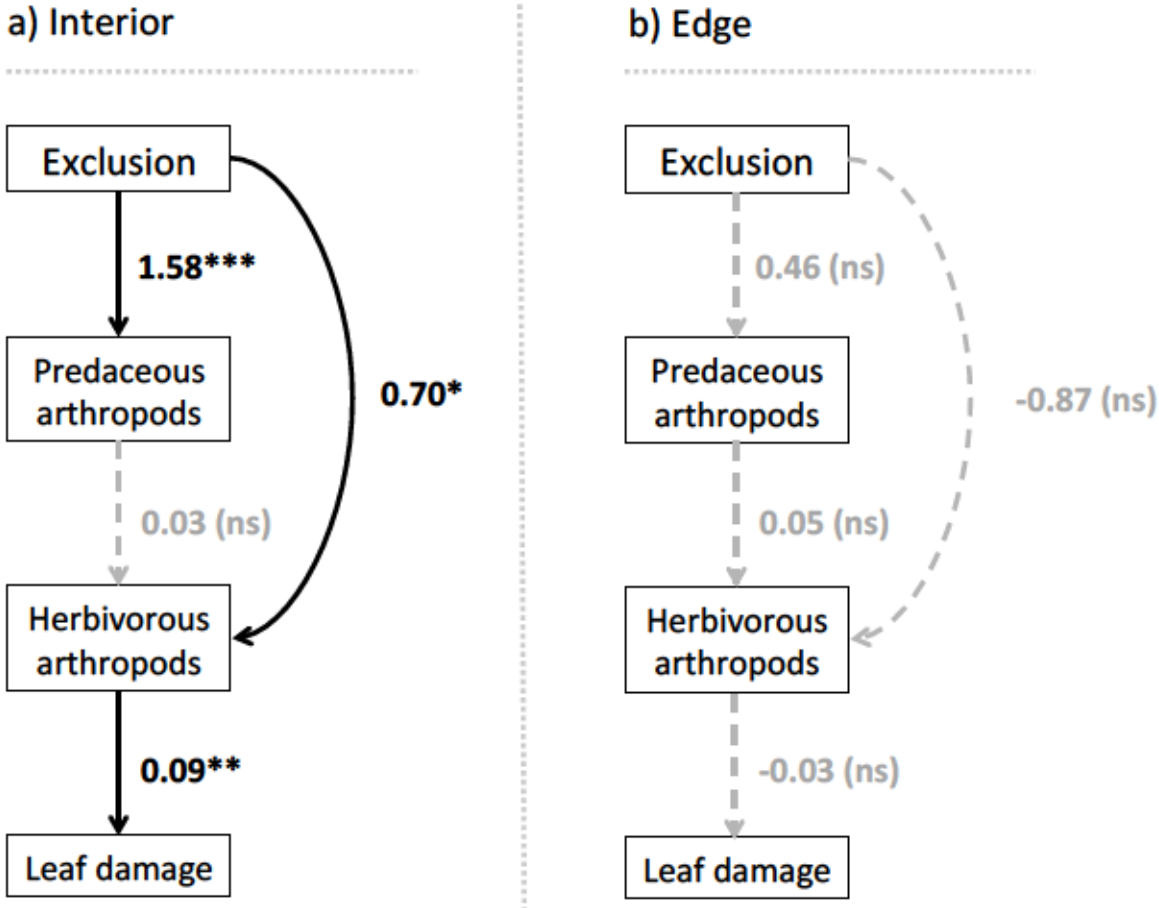


Figure 3.6a and b. Final reduced path model depicting relationships between predaceous arthropods, herbivorous arthropods and leaf damage between control and exclusion plots within a) forest interiors and b) forest edges. Path coefficients are described with associated asterisks indicating significance of each path: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant. Solid arrows indicate significant pathways and dashed arrows non-significant. Models described here conform to Shipley's d-separation test and were supported by the data judging by delta AIC.

3.5 DISCUSSION

Our study provides a new understanding of how edge effects impact ecosystem functioning through the changes in vertebrate community. The exclusion of vertebrates at edges had little effect on arthropods and herbivory, suggesting top down pressure from birds and mammals on invertebrates is weak at the forest border. A depauperate insectivore community allows herbivorous arthropods to flourish in edge habitat, causing higher rates of plant damage. In stark contrast, exclusion of birds and mammals within the forest interior had a direct impact on predaceous and herbivorous arthropods and indirectly caused cascading effects on herbivory rate. This highlights the important regulatory service provided by the forest vertebrate community in controlling arthropod populations and indirectly suppressing leaf damage. In a changing landscape, with increasing ratios of edge to forest interior habitat, this study shows that the prevalence of arthropods is likely to increase in disturbed habitat and with it, the rate of herbivory.

Within the forest interior, the exclusion of vertebrates released arthropod populations from top-down predation pressure, causing arthropod numbers to rise to levels comparable with edge plots. Groups that particularly benefitted from exclusion included predaceous Araneae and a predominantly herbivorous taxon – Orthoptera. This suggests that the forest-dwelling vertebrate insectivores are clearly acting as intra-guild predators (Polis & Myers 1989; Mooney et al. 2010), whereby they compete with predaceous arthropods, eating the same prey species, whilst simultaneously preying on their arthropod competitors. In this way, understory mammals and birds suppress populations of predaceous arthropods as well as herbivorous. Trophic cascade theory suggests that this type of intra-guild predation

by vertebrates would offset the negative impact of predaceous arthropods on herbivorous groups (Polis & Myers 1989; Polis & Holt 1992; Rosenheim et al. 1993). As such, it might be expected that in the absence of the top trophic level, intermediate arthropod predators could act as mediators of trophic cascades, akin to a meso-predator release (Ritchie & Johnson 2009). However, despite the rise in predaceous arthropod density under exclusion, our study shows that herbivorous invertebrates exhibited a parallel increase in numbers, leading to a corresponding rise in herbivory rate. The endogenous pathway between predaceous and herbivorous groups was not significant and increases in the latter occurred as a direct result of exclusion, independent of changes in the former. The rise in leaf damage within the forest interior was therefore directly dependent on changes within the herbivorous group. This suggests that vertebrate insectivores have a much stronger functional role than predatory arthropods. Indeed, in a comprehensive meta-analysis of terrestrial exclusion experiments, top predators reduced invertebrates of both functional groups by 38% and 39% and led to a corresponding decrease in plant damage of 40% (Mooney et al. 2010).

If insectivorous vertebrates are non-discriminatory in their feeding habits (Mooney et al. 2010; Gunnarsson 2007), we would expect functional arthropod groups to respond similarly to exclusion, with numbers increasing by similar magnitudes. However, within the forest interior, the effect size of exclusion on herbivorous arthropods was smaller than that on predaceous species. The absence of vertebrate insectivores not only releases predaceous arthropods from top-down predation pressure, but also removes competition for prey resources. Dual release in this manner could explain the larger effect size of exclusion on predatory arthropods

compared with phytophagous. A second explanation for this discrepancy between functional arthropod guilds could be that predaceous invertebrates do exert predation pressure on prey species, but this is not sufficient to suppress a growth in population. Thirdly, differences in effect size may simply be an artefact of sampling methods. Results may be conservative with regards to herbivorous arthropod abundance as counts were undertaken only during the day and therefore do not account for nocturnal individuals. Indeed, many tropical phytophagous arthropods are more active at night (Lowman 1982; Kalka & Kalko 2006). A dietary analysis of bats in the forests of Panama, revealed that herbivorous arthropods comprised almost 70% of the arthropod prey biomass (Kalka & Kalko 2006).

Forest edges are known to be mostly devoid of specialist understory insectivore species, which actively avoid border areas (Banks-Leite et al. 2010; Pfeifer et al. 2017). This is reflected in our findings that there is a 25% increase in the abundance of avian arthropod predators at interior sites when compared to edge. Indeed, arthropods are thought to benefit from lower predation rates in tropical forest ecotone or edge areas (Peh et al. 2006) as well as having a fitness advantage by exploiting resources available in adjacent habitats. This pattern was corroborated by our findings (Fig. 3.3 and 3.4), with a greater abundance of Coleoptera, Hemiptera, Lepidoptera and Orthoptera occurring in ecotone areas. Surprisingly, leaf damage was not significantly affected by forest location alone (Fig. 3.4). Although this contrasts with findings that herbivory rate is higher at the forest/matrix boundary (Coley & Barone 1996), it is possible that we simply did not have the statistical power to detect a significant difference. The rise in plant damage at edges is thought to be

directly related to the increased abundance and richness of the arthropod community (Didham 1998).

Exclusion of vertebrates at the forest edge had little effect on the most common arthropod orders (Table 3.1), nor on invertebrate functional groupings (Fig. 3.5b and 3.6b). As a result, herbivory rate remained unchanged in both control and exclusion plots. This corroborates findings that the understory avian community at forest borders is composed of fewer specialist insectivores than that within the interior (Banks-Leite et al. 2010). Vertebrate assemblages in disturbed forest margins exert weak predation pressure and play a lesser role in the top-down control of invertebrate populations. In the absence of a top tier of predators, food webs are simpler at edges compared to forest interiors and the likelihood of trophic cascades diminishes. This is in contrast to a more complex system within the interior, consisting of vertebrate top predators, invertebrate meso-predators, invertebrate consumers and plants. At forest borders, predatory arthropods are the main top-down force controlling of herbivore populations and only exclusion of this group could result in changes to the proportion of plant damage. However, as both functional arthropod groups persist in much greater abundance in ecotone areas, the control of herbivorous populations, by their predatory counterparts, must be weak within this disturbed habitat. This supports food web theory that top trophic tiers are more prone to local extinction in disturbed habitat than those lower in the chain (Kruess & Tscharntke 1994; Kareiva 1987)

The introduction of human-modified edge habitats has changed ecosystem functioning irrevocably. Invertebrates, particularly herbivorous, dominate in these

areas given the weaker predation pressure from vertebrates. Without this level of top down control, the risk of pest outbreaks, which may spill over into adjacent farmland, is much greater (Roland 1993). Increased herbivore density and leaf damage at forest borders has important consequences for plant biomass, plant community composition and mortality (Allan & Crawley 2011; Carson & Root 2000). Herbivorous invertebrates may attack dominant species, allowing for greater plant diversity, whilst simultaneously reducing primary productivity (Allan & Crawley 2011; Coupe & Cahill 2003). The evolution of functional traits can also be shaped by pressure from herbivores, with plants evolving and investing more in defence (Agrawal et al. 2012). Although the long-term impact of increased herbivory rate could take many years to materialise (Allan & Crawley 2011), the ecosystem in edge habitat and associated functions will be fundamentally changed compared to that of forest interiors. As almost 20% of the world's forests are situated within 100m of a matrix border (Haddad et al. 2015), the need to understand how edge effects determine numerous ecosystem processes is becoming ever more important. If the pervasive impacts of edge creation can reach as far as 1 km into the forest interior (Ewers & Didham 2006), the loss of ecosystem function could be just as far-reaching.

CHAPTER 4

Does ecosystem function in tropical rainforests vary with habitat loss?

4.1 ABSTRACT

The continuing defaunation of tropical biomes has intensified research on how ecosystem function will be altered in their absence. Habitat loss, in particular, is responsible for high levels of biodiversity loss, with specialist groups being the most sensitive to disturbance. It is often these specialist taxa that fulfil important functional roles. Surprisingly, there is still a paucity of research on how ecosystem function is mediated by habitat loss. We aim to redress this gap in knowledge and determine how trophic cascades on herbivory rate are mediated by habitat loss. By using exclusion plots, we assessed how the absence of vertebrates affected arthropod populations and levels of plant damage along a gradient of forest cover. Within forest interiors, the effect of exclusion on both predaceous and herbivorous arthropod guilds increased in magnitude with forest cover. This indicates that the top-down pressure exerted by forest-dwelling vertebrates varies in a corresponding manner to changes in their community composition. However, despite significant variation in herbivore density, the proportion of leaf damage with exclusion showed no relationship to habitat loss. Although contrary to expectations, these findings are not surprising given the inconsistent patterns of herbivory with fragmentation reported in the literature. It has been suggested that the generality of antagonistic plant-animal interactions such as herbivory confers them some degree of resilience to perturbation. Edges were unaffected by exclusion, regardless of the forest cover of local surrounding habitat. This corroborates findings that edges tend to be devoid of specialist insectivores and the functional services they provide. Our results highlight the need for further research to elucidate how top-down processes are mediated by habitat loss.

4.2 INTRODUCTION

The widespread loss and fragmentation of natural habitats is one of the primary drivers of biodiversity decline (Turner 1996; Newbold et al. 2015). Nowhere is this more apparent than in the tropics (Sala et al. 2000), where intense land-use modification has left much of the forest highly fragmented (Haddad et al. 2015). Degraded habitat is unsuitable for many forest-dwelling vertebrates, with highly sensitive specialist species often becoming locally extirpated from small forest remnants (Banks-Leite et al. 2010; Martensen et al. 2012). This loss of diversity within these functionally important groups that occurs with habitat loss alters biotic interactions (Didham et al. 1996; Benitez-Maldivo 1998) and modifies ecosystem dynamics (Didham 1998; Magrach et al. 2014). Previous studies have shown strong top down pressure from birds and mammals on insect populations and indirect effects on herbivory (Van Bael et al. 2008; Mooney et al. 2010; Dunham 2008). However, how such trophic cascades vary with habitat loss has yet to be determined. Will trophic cascade strength vary along a gradient of forest cover, reflecting changes in vertebrate community composition?

Food quality and quantity, dispersal ability and habitat specificity are all contributing factors in this general decline of biodiversity (Zanette et al. 2000; Şekercioğlu et al. 2002; Jack H Hatfield et al. 2018). Mammal diversity and abundance, for instance, correlate with fragment size, with small to medium sized patches supporting impoverished communities (Pardini et al. 2005; Chiarello 1999). Avian communities are significantly impacted by the loss of habitat and associated increases in edge habitat (Şekercioğlu et al. 2002; Sodhi et al. 2004; Bregman et al. 2014; Barbaro et al. 2012; Banks-Leite et al. 2010). Although most animal assemblages are negatively

affected (Turner 1996; Haddad et al. 2015), species show varied responses to habitat loss (Banks-Leite et al. 2012). Previous studies have shown that in the Atlantic Forest of Brazil, community integrity (i.e. the similarity in community composition between disturbed and pristine forest) of these vertebrate groups is maintained until forest cover falls below a threshold of 30%, after which forest specialists become replaced by generalist, disturbance-adapted species (Banks-Leite et al. 2014; De Coster et al. 2015). This is because areas with a low proportion of forest cover have high edge to interior ratios, to the point where edge effects permeate the entire patch (Laurance & Ferreira 1998). For interior-dwelling species, intolerant of edge habitat, the whole fragment becomes uninhabitable. Thus, specialist avian groups are often entirely absent from small fragments (Martensen et al. 2012; Banks-Leite et al. 2010).

Other taxa also show similar changes in composition and diversity. For plants, losses in biodiversity are accompanied by a long-term qualitative shift in community composition, with secondary, successional species replacing mature forest trees (Benitez-Maldivo 1998; Sizer & Tanner 1999; Harper et al. 2005). These modified ecosystems harbour different arthropod assemblages compared to pristine habitat, with many groups being adversely affected by habitat loss (Didham et al. 1998). Herbivorous species tend to benefit from changes in forest cover, taking advantage of thick plant growth in the greater proportion of edge habitat and exploiting resources from the surrounding matrix (Ricketts et al. 2001; De Carvalho Guimarães et al. 2014). Surprisingly, increases in herbivore richness and density do not always elicit a corresponding rise in plant damage. Four recent reviews show highly contrasting results: lower herbivory in fragments compared to continuous forest

(Martinson & Fagan 2014); higher herbivory with increased edge formation in fragments (De Carvalho Guimarães et al. 2014) and a neutral response to habitat fragmentation (Magrach et al. 2014; Rossetti et al. 2017). The disparity of these findings shows the great variability in plant–animal interactions and highlights the need to investigate mechanisms that influence herbivory along such gradients.

The role of vertebrates, particularly avian insectivores and bats, in regulating herbivory rates by directly suppressing arthropod populations is now well recognised (Şekercioğlu 2006; Kalka et al. 2008; Karp & Daily 2014; Maas et al. 2015). The experimental removal of this top trophic tier has cascading effects on plant damage (Mooney et al. 2010) in multiple forest systems, as well as on decomposition rate and nutrient cycling (Dunham 2008). However, the question remains as to whether this top down control diminishes as functionally-important insectivores disappear along gradients of fragmentation.

Few studies have investigated trophic cascades on herbivory along gradients of habitat loss. One short-term experiment found that despite variation in bird community composition, herbivorous arthropod density did not fluctuate with forest fragmentation or exclusion (Peter et al. 2015). Percentage of leaf damage was higher in exclosures but was uncorrelated with fragmentation (Peter et al. 2015). These outcomes, however, were based on a single sample at the end of a three-month exclusion experiment. We aimed to undertake an extensive exclusion study, with cumulative data summed from multiple monthly measures over a 10-month period. In this study, we aimed to answer the following questions: 1) does the arthropod community respond to changes in forest cover and distance to edge? 2)

do trophic cascades vary along a gradient of forest cover? and 3) does this differ in edge and interior habitats?

4.3 METHODOLOGY

4.3.1 Site selection

The study took place in the Atlantic Forest of Brazil; specifically, within the administrative area of Santa Virginia in the Parque Estadual da Serra do Mar (PESM). Potential sites were identified based on maps provided by Instituto Florestal do Estado de São Paulo (Instituto Florestal do Estado de São Paulo 2010) and SOS Mata Atlântica (SOS Mata Atlântica & Instituto Nacional de Pesquisas Especiais 2014). Patch centroid values for all sites within the vicinity of Santa Virginia were taken using ESRI ArcGIS 10 and the program Fragstats was used to calculate percentage forest cover at 800m following (McGarigal et al. 2012). Forest cover at a scale of 200 hectares (800m radius) was used as the selection criterion based on previous findings by (Banks-Leite et al. 2012). Data were compiled for fragments and continuous forest sites within and adjacent to the national park. The surrounding matrix for potential sites was pastureland. Eleven paired interior and edge sites that ranged from 7% to 70% forest cover were randomly selected (See Appendix B). Edge sites were situated no further than 5 m into the forest, whilst interior sites were positioned at least 100 m from the border. The minimum distance to ensure spatial independence between replicates was 200 m.

4.3.2 Experimental plots

At each site, we constructed three experimental plots: exclosure, procedural and control. In total, there were 66 experimental plots. Plot type was randomly assigned to 2 m x 2 m areas, which were at least three metres apart from each other. Effort was made throughout the construction process to minimise the cutting of plants and removal of roots to ensure continuity of the forest understory structure.

Exclosure plots were constructed of plastic poles and wire mesh and measured 2 m x 2 m in area, with a height of 1.5 m. The mesh had openings of 20 mm x 18 mm allowing the passage of all but the largest insects, whilst excluding the majority of vertebrates. Lengths of nylon thread were sown through the overlapping parts of the mesh walls and top to ensure the structure was mammal and bird-proof. The bottom of the mesh was buried into the ground and secured with metal pins to stop animals burrowing underneath. Access to the exclosure was via a mesh door, which was closed securely on departure with reusable plastic ties.

Procedural plots (e.g. Koh 2008) were composed of the basic framework of poles, a mesh top and an additional four sections of mesh fitted lengthwise to form corners (Fig. 4.1). The purpose of this structure was twofold. Firstly, the mesh top collects leaves in the same manner as the exclosure and controls for the effect of reduced litter fall expected under exclusion. Secondly, spiders were likely to use the structure of the exclosure to build webs. The mesh corners of the procedural plot also provide this foundation, controlling for microclimatic effects on spider density, whilst still allowing access by mammals and birds.

Control plots were simply four short lengths of pole placed into the ground to demarcate the 2 m x 2 m area. Previous analyses revealed little difference between the control and the procedural control along the gradient of forest cover, so here we report only comparisons between the control and exclosure (See Appendix C).

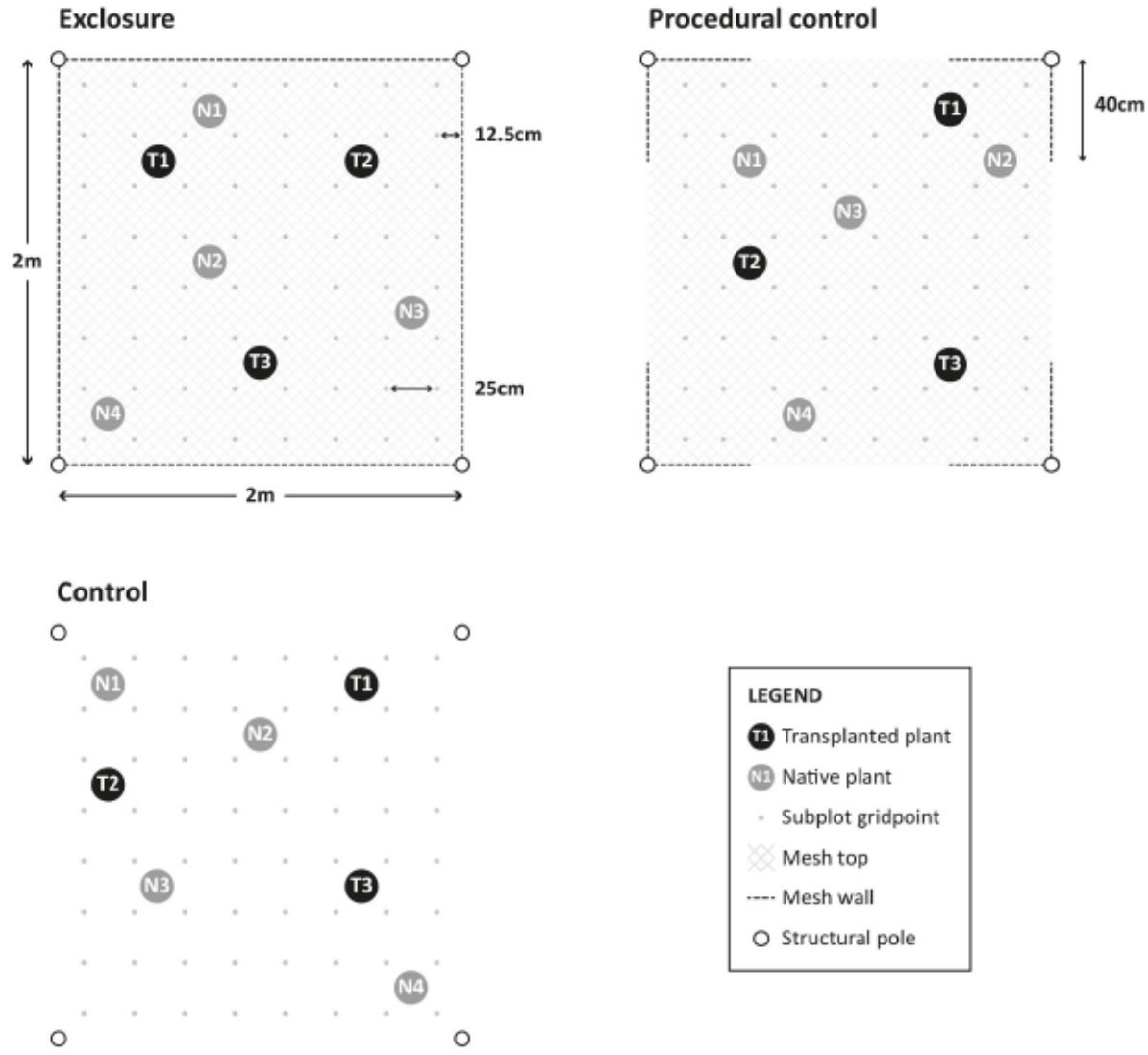


Figure 4.1. Schematic diagram of the plots at each site. In the field, each plot is positioned at least three metres from the others.

4.3.3 Herbivory measurements

To provide a consistent measure of herbivory across all plots, sites and altitudes, three plants of species native to Serra do Mar were translocated to each of the plots. The selected species were *Erythrina speciosa*, *Inga vera* and *Ocotea puberula,* which are known to experience a moderate degree of insect herbivory and naturally occur across the altitudinal range of the study area. Within each plot, the three translocated individuals were positioned one metre apart, each forming the point of a rough triangle. Seedlings were chosen as younger plants undergo a period of rapid growth and are known to experience a higher degree of herbivory than more mature plants (Coley & Barone 1996).

To supplement measurements of herbivory taken from three translocated plants, a further four in-situ seedlings were randomly selected from the community within each plot. These individuals measured between 5 and 100 cm (Benítez-Malvido & Martínez-Ramos 2003) and also displayed a moderate level of historical herbivory. Thus, seven plants were sampled per plot, totalling 315 plants across all altitudes. All sampled plants were marked with inconspicuous, blue, plastic tags, each of which had a coded number.

Due to an uncharacteristic dry period in 2014, very few new leaves emerged during the first few months and sampling was restricted to four of the mature leaves already present. With the onset of the wet season in November, there was a corresponding surge in leaf emergence. At this time, four new leaves were marked per plant and followed for three months or until other new leaves appeared. They were then replaced in the sampling scheme by the younger leaves. This replacement process

continued for the duration of the experiment. Employing this method ensured that throughout the year, monthly measurements of herbivory were taken from young leaves at similar life stages. This is important, as the leaves of shade-tolerant tropical species experience almost 70% of their lifetime herbivory in the 1–3 week expansion period following emergence (Coley & Barone 1996). We followed the suggestion of Coley and Barone (1996), to include both mature and expanding leaves in our sampling, as well as to take measurements at intervals over time.

The sampled leaves were photographed every four weeks. Image J software was used to calculate initial leaf area (ILA), new growth, desiccation, pathogen and fungal damage, as well as insect and mammalian herbivory. This method provides a greater degree of accuracy than relying on visual estimates of proportion in the field. Only herbivory caused by chewing insects was assessed from holes in the leaves. The impact of other insects such as phloem feeders is much harder to ascertain (Coley & Barone 1996) and beyond the limits of this study. Insect herbivory can be distinguished from mammalian, as mammals tend to clip the leaf close to the stem (Dunham 2008). Areas of desiccation, pathogen or fungal damage were measured and subtracted from the leaf area available for herbivory. Leaf damage measurements were taken from all plants including those already in-situ and transplanted plants.

4.3.4 Understory fauna

Every month, the leaves and stems of all plants within each plot were visually inspected for arthropods. Individuals were identified to order and their body length, from the most anterior part of the head to the tip of the abdomen, was estimated.

Formicidae were recorded as a separate group from other Hymenoptera. Lepidoptera were catalogued as adult or larval forms due to the significant impact the larvae have on herbivory rates. All recorded orders and functional categories are presented in Appendix A.

4.3.5 Data analysis

Analysis focused on the cumulative abundance of macro arthropod (body length ≥ 0.4 mm) groups, summed over the ten-month experimental period of repeated sampling. Formicidae were excluded from the analysis as they were too numerous to count accurately and their high abundance has potential to skew results. We analysed the response of two functional arthropod groups: predaceous and herbivorous; as well as total arthropod density and variation in the proportion of leaf damage. Firstly, data from control plots was analysed using generalised additive mixed model (GAMM) (Wood et al. 2017). Response variables were fitted against location, modelled as a two-level factor, and forest cover, modelled as continuous smooth functions. Forest cover was fitted using separate smooth terms for edge and interior locations and the significance of these smooth terms was recorded. Smooth terms were included to test for non-linear responses to forest cover, as detected by previous studies (Banks-Leite et al. 2014). Site was included as a random effect. Secondly, the difference between controls in paired edge and interior locations was calculated by subtracting edge from interior. Differences for each arthropod category and leaf damage were modelled separately against forest cover using GAMs. Finally, to test the effects of exclusion treatment we calculated the difference between control and exclusion for each interior and edge site for each of the response variables. This measure allowed us to better identify the impacts of distance to edge

and forest cover. The effect of forest cover at edge and interior sites on the response variables was modelled using GAMs, in the same manner as described above.

4.4 RESULTS

4.4.1 General trends in arthropod community

Over 11 paired sites and plots, a total of 1694 aboveground arthropods were sampled within the forest understory. Individuals were classified as one of 21 invertebrate taxa. Araneae were the most abundant taxon, comprising 30% of the arthropod community. Other frequently encountered groups were Hemiptera (26%), Coleoptera (11%), Lepidoptera larva (8%) and Orthoptera (6%). In combination, all other taxa amounted to 19% of the aboveground assemblage.

4.4.2 Effects of forest cover and distance to edge on arthropods

Total cumulative arthropod abundance was significantly greater at edge sites compared to interior ($t=3.72$, $p=0.00$, Fig. 4.2a). This effect was driven by increased densities of herbivorous arthropods at edges ($t=8.56$, $p=0.00$, Fig. 4.2a) but not by predaceous populations ($t=0.94$, $p=0.36$, Fig. 4.2a). The difference in herbivore density between edge and interior was positively correlated with forest cover ($F=16.98$, $p=0.00$, Fig 4.2b). This was due to a decrease in abundance within the interior as forest cover increased, whilst numbers at edge sites remained comparable in areas of high and low cover (Fig 4.2a). The difference in total arthropod abundance between edge and interior also increased with forest cover,

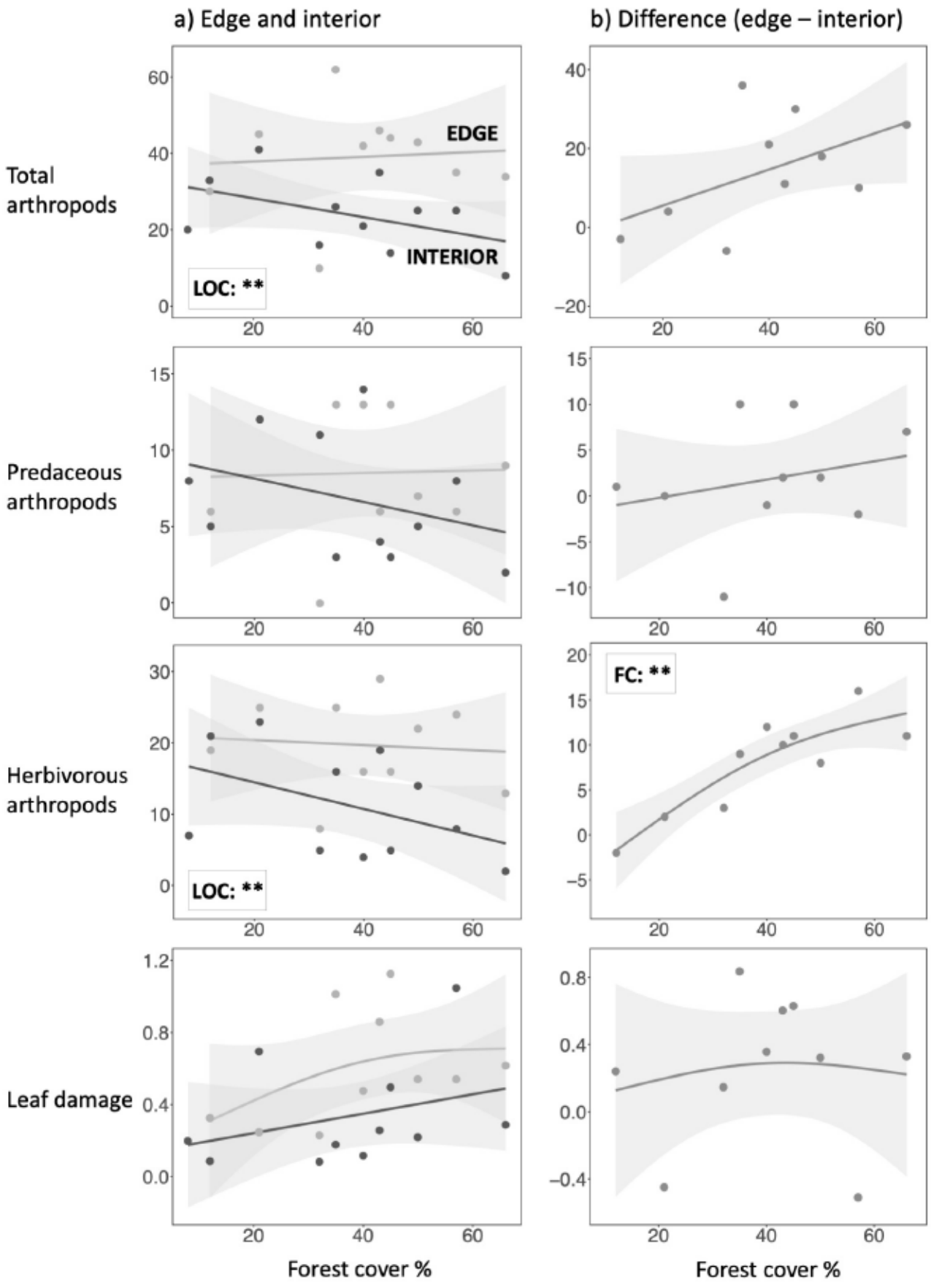

a) Edge and interior
b) Difference (edge – interior)
Total arthropods
Predaceous arthropods
Herbivorous arthropods
Leaf damage
EDGE
INTERIOR
LOC: **
FC: **
Forest cover %
Forest cover %

Figure 4.2a and b. The interacting effects of percentage forest cover and forest location on cumulative arthropod abundance (total, predaceous and herbivorous) and percentage leaf damage. Fig. 4.2a shows results of paired edge (light grey) and interior sites (dark grey) modelled with forest cover. Significant effects of location are reported on these plots. Fig. 4.2b shows the difference between paired sites along a gradient of forest cover, calculated for each site as edge minus interior. The significance of the smooth terms from generalised additive models are indicated here. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

although this effect was not significant (F=3.10, p=0.12, Fig 4.2b). Similarly, predaceous arthropods were not affected by forest cover (F=0.56, p=0.48, Fig 4.2b). Despite changes within the herbivore community, there was little corresponding variation in the proportion of leaf damage with location (t=1.85, p=0.08, Fig 4.2a) or with percentage forest cover (F=0.20, p=0.80, Fig 4.2b).

4.4.3 Trophic cascades along a gradient of forest cover

In all three invertebrate categories, the difference in observed abundance between exclosure and control plots was greater within the forest interior than forest edge (Fig. 4.3). Distance to edge had a significant impact on the mean difference in total arthropod abundance (t=7.19, p=0.00, Fig 4.3), predaceous (t=2.95, p=0.01, Fig. 4.3) and herbivorous groups (t=4.70, p=0.00, Fig. 4.3). There was a corresponding rise in the difference in percentage leaf damage between exclusion and control, which was also significantly greater at interior sites compared to edge (t=2.75, p=0.01, Fig 4.3.).

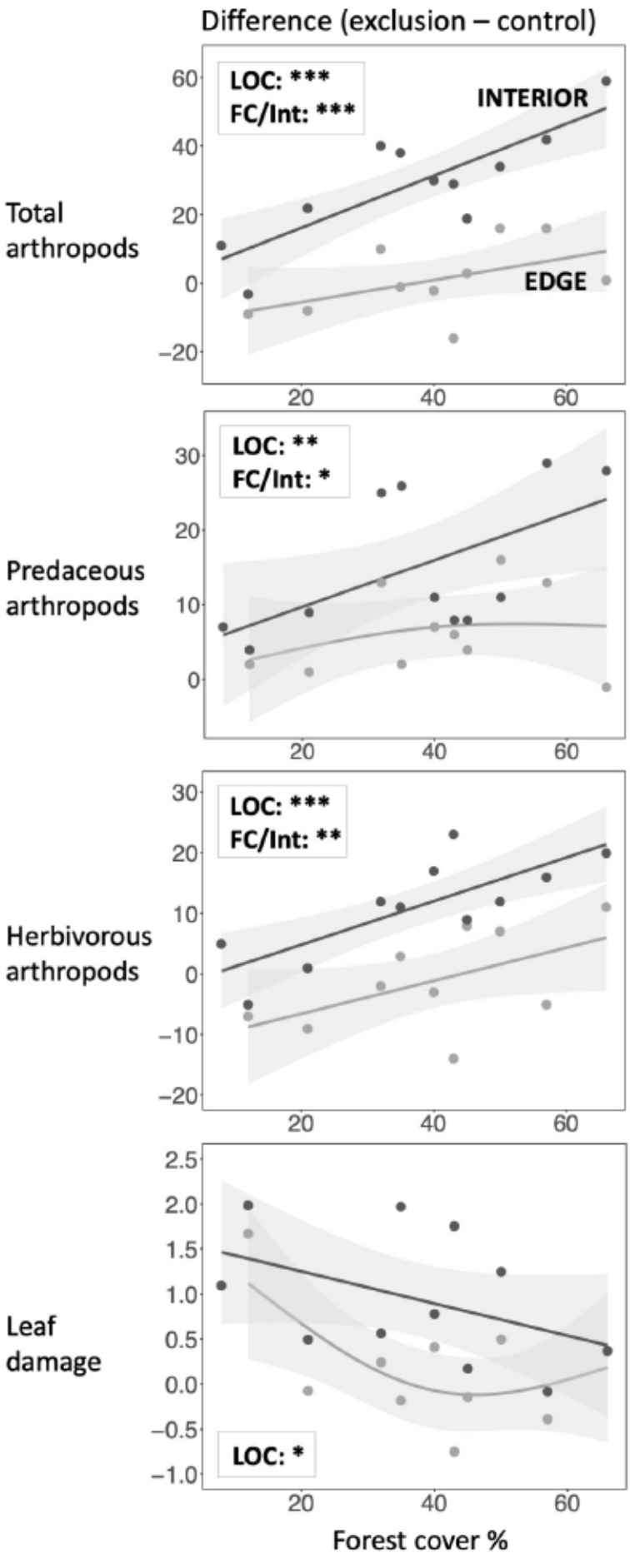

Difference (exclusion – control)
Total arthropods
LOC: ***
FC/Int: ***
INTERIOR
EDGE
Predaceous arthropods
LOC: **
FC/Int: *
Herbivorous arthropods
LOC: ***
FC/Int: **
Leaf damage
LOC: *
Forest cover %

Figure 4.3. The interacting effects of percentage forest cover and location on the difference in abundance of arthropods and percentage leaf damage. Difference was calculated for each site as exclusion minus control. Graphs show results for two functional arthropod guilds – predaceous and herbivorous – and all arthropods summed to give total abundance. Dark grey lines and points represent interior plots; light grey represents edge plots. Significant results of generalised additive models are reported on each graph. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Forest cover had a significant impact on the observed difference between exclusion and control plots, with difference in the abundance of both functional groups increasing as forest cover rises towards 70% (Predaceous: F=6.04, p=0.03; Herbivorous: F=10.58, p=0.00, Fig. 4.3). These trends were reflected in the patterns observed for total arthropod numbers, where differences in abundance were mediated by forest cover within the interior, but not at the edge (Interior: F=18.92, p=0.00; Edge: F=2.36, p=0.14, Fig 4.3). Despite the positive arthropod–forest cover relationship, there was no corresponding pattern with forest cover and difference in percentage leaf damage at either location (Interior: F=2.68, p=0.12; Edge: F=2.48, p=0.20, Fig. 4.3).

4.5 DISCUSSION

Our study shows that the top-down control of invertebrate populations by mammals and birds is mediated by habitat loss and fragmentation. Within forest interiors, the effect of vertebrate exclusion on both predaceous and herbivorous arthropods was greater at higher levels of forest cover. This positive correlation is likely due to shifts

in vertebrate functional guild composition, towards communities with a higher proportion of specialist insectivores in areas with more intact habitat. Despite these strong and significant patterns in herbivore density, there was no concurrent pattern in plant damage. The absence of such a relationship is not surprising given the highly inconsistent responses of herbivory to habitat loss (Magrach et al. 2014; Rossetti et al. 2017; Martinson & Fagan 2014; De Carvalho Guimarães et al. 2014). The generality of herbivore-plant interactions may confer them a degree of resilience to perturbation (Magrach et al. 2014). Equally the presence of omnivores in mid-trophic levels in degraded habitat may dampen trophic cascades (Pace et al. 1999). Edges remained impervious to the effects of exclusion, regardless of the scale of forest cover in surrounding habitat. The vertebrate communities found at the edges of habitat with differing levels of forest cover provide similar, low levels of top-down control on invertebrate populations.

Some tropical arthropod assemblages seem to be robust against the effects of habitat loss (Şekercioğlu et al. 2002), whilst others show significant shifts in abundance, richness and composition (Didham et al. 1998; Ricketts et al. 2001). In our study, only herbivorous arthropods exhibited any response to habitat loss, with the difference in abundance between forest locations correlating positively with forest cover (Fig. 4.2b). This trend was driven by a negative relationship between herbivore density and forest cover within the interior, whilst numbers at edge sites remained comparable along the gradient (Fig 4.2a). Changes in vertebrate functional guild composition are likely to be a contributing factor causing this trend. As specialist understory insectivores become more prevalent in areas of high forest cover (Banks-Leite et al. 2010), our results suggest top-down pressure on invertebrate populations

also increases. A similar trend, although non-significant, was observed for predaceous arthropods and the assemblage as a whole. This indicates that top-down control may be stronger for herbivorous groups – an idea which is at odds with previous findings that vertebrates prey indiscriminately, without preference for a particular arthropod guild (Mooney et al. 2010). There is some evidence to the contrary, which suggests that predation effects differ for invertebrate groups depending on local variation in surrounding vegetation density (Giffard et al. 2013). As plant communities do vary in small forest remnants compared to large (Benítez-Malvido & Martínez-Ramos 2003), so such structural heterogeneity between sites could explain the differential effects of insectivory on functional arthropod guilds.

Despite changes in herbivore density, rates of leaf damage within the interior were unaffected by habitat loss (Fig. 4.2a and b). The absence of a clear trend in herbivory reflects conflicting findings within the literature. Our results support the findings of two extensive meta-analyses where herbivory rates remained neutral to habitat modification, despite significant fluctuations herbivore numbers (Magrach et al. 2014; Rossetti et al. 2017). However, two other reviews provide evidence for significant and opposing trends in plant damage: diminished rates with fragmentation severity (Martinson & Fagan 2014) and higher herbivory with increased edge formation in fragments (De Carvalho Guimarães et al. 2014).

Vertebrate exclusion yielded significant results for all arthropod categories within forest interiors. The difference in total, predaceous and herbivorous densities between control and exclusion plots was significantly and positively correlated with percentage forest cover (Fig. 4.3). This lends further support to the idea that shifts in

vertebrate community composition with forest cover alter the strength of top-down control on the arthropod community. Vertebrate assemblages in larger fragments and continuous forest are known to be comprised of greater numbers of specialist insectivores than in smaller forest remnants (Bregman et al. 2014; Banks-Leite et al. 2010; Şekercioğlu et al. 2002; Banks-Leite et al. 2014). This functionally-important guild limits arthropod numbers and is thought to mitigate potential trophic cascades, which could give rise to increased plant damage. Mammal communities are also impoverished within small fragments and tend to be dominated by herbivores (Chiarello 1999).

Arthropods may be subject to different limiting factors in areas with low and high forest cover. The effect of exclusion on all arthropod categories increased consistently along the gradient of habitat loss, indicating that top-down predation pressure grew stronger in a similar way. In contrast, in control plots within the forest interior, the invertebrate assemblage as a whole did not appear to respond strongly to habitat loss, showing similar abundance in areas of low and high cover. Thus, in smaller fragments, where specialist vertebrate insectivores are scarce or entirely absent (Bregman et al. 2014; Banks-Leite et al. 2010; Şekercioğlu et al. 2002), other forces must be suppressing invertebrate populations. Small forest fragments tend to have more impoverished plant communities than larger patches and areas of continuous forest (Benítez-Malvido & Martínez-Ramos 2003). Therefore, at the lower end of the forest cover gradient, bottom-up forces such as plant quality and abundance could be controlling arthropod numbers. As forest cover reaches a threshold of 30%, the community integrity of vertebrate groups becomes closer to that of intact habitats (Banks-Leite et al. 2014). Thus, as forest cover rises and

resource availability becomes less of a constraint, the increasing number of vertebrate insectivores, and the top-down pressure they exert, may become the limiting factor for arthropod populations.

Interestingly, the positive correlation between forest cover and difference in herbivore density between control and exclusion did not translate into a corresponding pattern in leaf damage (Fig 4.3). Interspecific interactions, such as herbivory, are often classified as antagonistic and are thought to show a lower degree of specialisation than most mutualistic relationships (Poisot 2011). Although some plant-herbivore relationships are specific, many folivorous arthropods are generalists, consuming multiple plant species. It is the generality of these interactions that may increase their resilience to disturbances such as fragmentation and biodiversity loss (Magrach et al. 2014). Smaller forest remnants have a larger percentage of omnivorous arthropod species (Benitez-Malvido et al. 2016). These groups can switch feeding strategy depending on resource availability and may dampen the occurrence of trophic cascades (Pace et al. 1999). The increased density of mid-level omnivores and the generality of plant-herbivore interactions may account for absence of any relationship between trophic cascade strength and forest cover.

At forest edge sites, percentage of cover had little effect on measures of arthropod abundance or leaf damage (Figs. 4.2a and b). Similarly, exclusion caused no direct change in invertebrate communities and there was no evidence of a subsequent trophic cascade, regardless of increases in forest cover (Fig. 4.3). Even if surrounding habitat is comprised of forest with a high percentage cover, ecotone-

dwelling arthropods do not experience increased predation pressure. This corroborates previous results that insectivores that live within the forest interior actively avoid border areas (Banks-Leite et al. 2010; Pfeifer et al. 2017), despite the abundant prey available there (Didham et al. 1998). Ecotone zones along the gradient of forest cover may be similar in that the vertebrate community that exists there is not the limiting factor for arthropod populations.

Herbivorous arthropods, did benefit significantly by inhabiting forest edges compared to the interior sites (Fig 4.2a and b), corroborating findings from previous studies (Didham 1997; Wimp et al. 2011; De Carvalho Guimarães et al. 2014). A corresponding rise in the proportion of leaf damage also occurred at edge sites, which was also independent of forest cover. Although not significant, this rise suggests the increased abundance of arthropods does have a negative effect on plants in edge habitat. A combination of bottom-up and top-down factors is thought to drive the increased density of generalist herbivores in disturbed habitat (Wirth et al. 2008). Fast-growing, pioneer plants are more palatable for folivorous arthropods due to weaker defences and occur in greater quantities along forest borders (Coley & Barone 1996). Whilst a vertebrate community lacking a strong component of specialist insectivores is likely to exert less top-down control on invertebrate populations (Dale et al. 2007; Restrepo & Gomez 1998).

The impact of habitat loss, and associated changes in vertebrate diversity, on arthropod assemblages is clear. As habitat loss continues to accelerate (Hansen et al. 2013), it is likely that forested ecosystems will harbour increased invertebrate densities. The ability to predict how such shifts in faunal communities will affect

herbivory now, and in the future, continues to elude us. Further research is required to determine how both bottom-up and top-down mechanisms work in tandem to effect herbivory and how this varies along gradients of anthropogenic change. Effort should also be made to disentangle the confounding effects of edge and area on these processes (Ewers & Didham 2006; Banks-Leite et al. 2010).

CHAPTER 5

Discussion

As outlined in the first chapter, the positive biodiversity–ecosystem functioning (BEF) relationship is generally well received (Mace et al. 2012; Hooper et al. 2005). However, this idea has been built upon a body of work dominated by temperate studies, with only 13% occurring in the species-rich tropics (Clarke et al. 2017). The lack of tangible BEF examples from hyper-diverse biomes like the Atlantic Forest casts doubt on these widely-accepted notion. Species show varied responses to habitat modification and loss, but general trends in vertebrate diversity have emerged (Newbold et al. 2015; Banks-Leite et al. 2014; Pfeifer et al. 2017). Although less well-established, elevational patterns in bird and mammal communities, often show commonality (Rahbek 1995). With the positive BEF relationship in mind, it might be tempting to assume that ecosystem function varies in a corresponding manner to diversity along anthropogenic and elevational gradients. In this thesis, we aimed to test such assumptions by examining how trophic cascades on herbivory, caused by the exclusion of vertebrates, are mediated by habitat loss and environmental variation. Firstly, we aimed to establish how trophic cascades fluctuate along a naturally-occurring gradient of biodiversity, factoring out any anthropogenic influences. This was achieved by using the natural environmental and biotic variation that co-occurs with altitude and selecting sites within pristine tropical forests. Secondly, in areas of forest with high percentage cover, we assessed how distance to forest edge impacts the occurrence of trophic cascades. Finally, we determined how arthropod densities vary with vertebrate exclusion along a gradient of habitat loss and how this cascades to affect herbivory rates. In combination, these studies provide an overview of how environmental change and anthropogenic pressures can influence ecosystem dynamics and functioning.

5.1 How does biodiversity influence trophic cascades?

5.1.1 Occurrence of trophic cascades varies with gradient type

Collectively, our studies show that the mediation of trophic cascades on herbivory varies with gradient type. Most of the patterns presented here are caused by shifts in diversity and community composition with anthropogenic pressure and climatic change. Along elevational gradients in the Brazilian Atlantic Forest, we expect there to be varying diversity of vertebrates, invertebrates and plant, with fewer species at higher altitudes (Sanchez et al. 2013; Joly et al. 2012; Almeida-Neto et al. 2006; Eisenlohr et al. 2013; Lazzarotto & Lázzari 1998). As reported in chapter two, this naturally-occurring variation in species richness had implications for trophic cascade occurrence. Ecosystem dynamics remained resilient to vertebrate exclusion in the more diverse lowland forests, but not within the less rich highland habitat. At high elevations, the release of arthropods from top-down predation pressure elicited significant rises in numbers, which cascaded to affect herbivory rates. We suggest that the differential effects of exclusion may be due to increased diversity within mid- and producer levels of trophic tiers in lowland forests, which helps to buffer functions from perturbation in top trophic tiers.

The above findings raise the question: does the impoverished state of diversity in human-modified habitat make trophic cascades more likely if further disturbance occurs? Edges typically support a less diverse community of arthropods (Ewers & Didham 2006; Didham et al. 1998). So, given the findings of chapter two, it might be expected that low diversity within mid-trophic levels at would leave edge ecosystem vulnerable to further perturbation and trophic cascades would be common. However, we found the opposite trend. In chapter three, edges were unaffected by vertebrate

exclusion, whilst strong trophic cascades on plant damage occurred within forest interiors. It is worth noting at this point that the sites in chapters three and four were at altitudes above 1000 m asl and share characteristics with the high altitude sites in chapter two. Essentially, edge habitat supports only a depauperate vertebrate community, consisting of generalist, disturbance-adapted species (Banks-Leite et al. 2010; Dale et al. 2007). This impoverished community, with few specialist insectivores, exerts weak top-down control of arthropod populations (Kondoh 2003). Therefore exclusion, which simulates further vertebrate diversity loss, has no effect. Habitat loss and degradation has been found to cause the truncation of food webs, particularly the release of herbivorous guilds from predation pressure (Terborgh et al. 2016; Kondoh 2003; Kruess & Tscharntke 1994). In our study, food webs at edges are already simplified consisting of fewer trophic links than those within the interior.

5.1.2 Commonalities of vertebrate insectivory

Some trophic cascade theorists suggest that because vertebrate insectivores act as intra-guild predators, feeding on predaceous arthropods as well as herbivorous, they negate the impact of invertebrate predators on the community (Polis & Myers 1989; Polis & Holt 1992; Rosenheim et al. 1993). If this were the case, we would expect to see a buffering effect on trophic cascades, caused by the increased density of predatory arthropods (Ritchie & Johnson 2009). However, our results showed little evidence of trophic cascade mediation by predaceous arthropods. Rises occurred in arthropod density with exclusion, regardless of functional guild and usually elicited a corresponding increase in plant damage. This is in keeping with the outcomes of a recent meta-analysis, where vertebrate insectivores suppressed functional groups by a similar magnitude and caused subsequent decreases in herbivory rate (Mooney et

al. 2010). The exception to this occurred in the typically more diverse lowland forest, which experiences higher precipitation and temperatures. Exclusion in this forest caused an increase in aboveground predaceous invertebrates, but no concurrent rise in herbivore density. The rise in intermediate arthropod predators could mediate concurrent rises in folivorous invertebrate densities. This may be an example of how in more dynamic and diverse habitats, arthropods take on the functional roles of vertebrates and can buffer against perturbation (Halaj & Wise 2001; Schmitz et al. 2000).

Predation pressure exerted by the vertebrate community appears to be much stronger than that by insectivorous arthropods, despite the increased numbers of the latter with exclusion. The collective biomass of the insectivorous bird and mammal community would vastly outweigh that of arthropod predators. If all else were equal, as endotherms, vertebrates would still have much higher energy costs than ectothermic arthropods, necessitating much larger volumes of food (Nagy 1987). Higher biomass, greater metabolic demands and foraging over larger areas would increase the volume of prey consumed. Thus, it is to be expected that the predation pressure exerted by vertebrates is several orders of magnitude greater than that of the invertebrate community.

5.2 When is ecosystem function resilient to change?

Our research reveals which characteristics of ecosystems may prevent them from losing functionality in the wake of disturbance events. In chapter two, we found that the cascading effects of vertebrate exclusion were mediated by altitude. Lowland forests exhibited resilience to biodiversity loss, with only predaceous arthropods

responding to exclusion. In contrast, strong trophic cascades on herbivory were observed at high altitudes. We hypothesised that the difference in functioning between sites was caused by a declining pattern of biodiversity with altitude, corroborating previous findings (Strong 1992; Polis et al. 2000; Halaj & Wise 2001; Schmitz et al. 2000). In our study, the hotter, wetter lowland habitat is known to harbour higher levels of diversity and when this is concentrated in lower trophic levels, it may help to buffer ecosystem processes against perturbation. This is consistent with findings that the impact of herbivores is reduced in forests with more diverse producer assemblages (Jactel & Brockerhoff 2007). It may be that in diverse and dynamic ecosystems, functional roles can be fulfilled by multiple biotic groups. The results in lowland forests showed that in the absence of vertebrates, arthropods may take on the role of primary predator, limiting herbivore numbers and preventing trophic cascades.

In chapter two, we also see an example of how functional redundancy may buffer the belowground system from vertebrate biodiversity loss. We found that vertebrate exclusion did not trigger trophic cascades on decomposition or nutrient cycling at either high or low altitudes. Detritivorous species are numerous, but have very similar functional roles (Bradford 2002). Thus, unless the entire guild is negatively impacted, there will always be species to fulfil the decomposer role (Liiri et al. 2002). In logged forests, birds and small mammals fill functional roles left open by an impoverished arthropod community (Ewers et al. 2015).

Omnivores can feed at multiple trophic levels and are able to switch feeding strategy depending on resource availability. The presence of omnivores within communities

can dilute predation pressure and dampen trophic cascades (Polis et al. 2000; Polis & Myers 1989). They can act as a stabilising force for ecosystems in the aftermath of a disturbance event, shifting consumption to different trophic levels as relative abundances of resource species fluctuate (Fagan 1997). More recent, hypotheses however, suggest that omnivores can have stabilising and destabilising effects, depending on the dynamics of the ecosystem (Vandermeer 2006). Omnivorous arthropods survive well in degraded habitats (Benitez-Malvido et al. 2016) and could act as stabilisers in these impoverished environments. Thus, they may be a contributory factor for the neutral patterns of herbivory observed with forest cover in chapter four.

Within ecosystems, individual processes may be more or less robust to disturbance. Magrach (2014) distinguishes between mutualistic (e.g. seed dispersal) and antagonistic (e.g. herbivory) species interactions. The latter tend to be more generalised and this generality makes them less prone to disruption (Magrach et al. 2014). In chapters three and four cascades on herbivory occur with distance to edge but are not mediated by extent of forest cover. This suggests that the generality of the plant-herbivore relationships within the forest may be sufficient to buffer them from area effects, but not from stronger edge effects (Banks-Leite et al. 2010)

5.3 Caveats and limitations

As with the majority of field experiments, particularly those in dynamic natural systems, there are a number of limitations to our studies that warrant attention. These should be considered when interpreting the results presented in this thesis.

5.3.1 The validity of exclusion experiments

There are inherent issues with exclusion experiments. Some researchers argue that excluding the entire vertebrate community creates an unnatural scenario that does not represent real-world biodiversity loss. This is true in that extinction lags for sensitive species following disturbance would not be synchronous (Kuussaari et al. 2009) and the sudden extirpation of all vertebrates from an area of forest is highly unlikely. In the majority of cases, there would also be a subset of the excluded community that would persist within the degraded habitat and these species would have an impact on functioning. Thus, because of its all or nothing nature, exclusion cannot truly replicate how biodiversity loss would occur in real-world cases, nor how it would affect ecosystem functioning.

In excluding vertebrate predators, you invariably exclude vertebrate herbivores. This important group would ordinarily have a substantial impact on herbivory rate, with much greater consequences for plant mortality (Hulme 1994). As much of this thesis focussed solely on herbivorous activity of aboveground invertebrates, this may not be relevant. But for longer-term studies assessing how primary productivity is affected by vertebrate exclusion, this is of some importance. This problem may be more relevant for our belowground research. The increase in plant damage that would have occurred in the presence of vertebrate herbivores would have some influence on nutrient cycling (Metcalfe et al. 2014). Thus, any shifts in soil nutrient concentration that might occur with vertebrate exclusion (Dunham 2008), would have to take this into consideration.

The introduction of cages into dynamic tropical forest ecosystems will inevitably create microclimatic effects. In some cases, light intensity, temperature and wind speed are altered within exclosures (Luck et al. 1988). This has repercussions for plant communities in particular, but also affects herbivore activity and growth rate. The extent to which these microenvironments occur would depend on mesh size and type. In our study, the structure of the exclusion itself provided niches in which both predators and prey hid. Spiders were often observed making use of the corners to anchor webs. These favourable microhabitats may discourage arthropods from emigrating and behaving as they would have done under natural circumstances. Other issues include the fact that large arthropods, or those with wide wingspans, would also be excluded by the mesh. With a high biomass, these individuals would be likely to have a significant predatory or herbivorous impact inside the exclosure.

5.3.2 Experimental design and sampling

Across all of the experiments the number of sites came to 39 (three of which were destroyed). Each site was comprised of a control, procedural control and exclusion, giving a total of 117 plots to be sampled every month. We saw strong effects of the cumulative data in most cases, suggesting sample size was sufficient. For chapter four, an increased number of replicates along the gradient of forest cover, may have helped to elucidate trends in the highly variable rates of herbivory. Edge habitats are known to exhibit greater variability in biotic distribution and species interactions (Didham et al. 1998; Ewers & Didham 2006). In our studies, exclusion caused little response within this habitat type. Trends may have surfaced if a greater number of edges were sampled, including sites with different microclimatic and biotic characteristics.

We attempted to minimise the impacts of sampling on species and biotic interactions within experimental plots. To avoid disruption, arthropods were identified in situ, rather than being removed and identified in the laboratory. This precluded the ability of researchers to categorise individuals into morphospecies or to family level. Such information would have provided greater accuracy in determining functional roles of individuals, rather than the broad categorisation scheme used in our research. Soil sampling, by nature, is a destructive process. In taking cores, thin root networks would often be damaged and annelids were frequently bisected. This negative impact would have been ubiquitous across all plots, but it had potential adverse consequences for belowground dynamics and on nutrient cycling. We tried to minimise these deleterious effects by taking samples only once every three months.

Our exclusion experiment was conducted over a 10-month period. Responses of the aboveground ecosystem took only two or three months to manifest. Belowground systems, which are buffered against microclimatic effects (Ewers & Banks-Leite 2013), take longer to respond to biodiversity loss (Scherber et al. 2010). This brings into question whether our findings show the resilience of belowground dynamics or that changes simply did not occur within the experimental period. Exclusion over a longer timeframe would answer these queries.

5.3.3 Additional measures

Basic bird community information was gathered for the experimental sites, but the dataset was small, and few meaningful trends emerged. A more comprehensive

sampling of the vertebrate community, with trait-based data, would allow us truly to link variation in predator diversity with trophic cascades.

In a heterogenous and geologically complex environment like the Atlantic Forest, even sites in relative close proximity experience different microclimates (Carnaval & Moritz 2008). Given that climatic differences affect a wide array of biotic interactions, data specific to sites would have been useful. With this in mind, we did purchase dataloggers, which were to be installed at each of the 39 sites. However, during the import process into Brazil the dataloggers were withheld at customs.

5.4 Implications for conservation strategies

5.4.1 A focus on less biodiverse habitats

Typically, conservation strategies aim to conserve the greatest amount of biodiversity (Rands et al. 2010; Myers et al. 2000), focussing on designated 'hotspots'. Whilst there is merit in this approach, this may not, by default, preserve ecosystem function. Our results suggest that the avian and mammalian community that exists at 1,000 m asl has a strong component of specialist insectivores, which suppresses arthropod numbers and limits herbivory. The mitigation of trophic cascades on plant damage relies solely on this vertebrate community, with predaceous arthropods having little value for this control function. The occurrence of cascades with exclusion indicates that species richness at lower trophic levels may not be high enough to buffer against diversity loss within top tiers. Such reliance on specialist insectivores would make ecosystem functions vulnerable to the same pressures as the species providing the function. Conservation efforts may need to be

refocussed if their aim is to preserve ecosystem function as well as biodiversity. Alongside diversity inventories, the presence of specialist insectivores could be a good indicator with which to identify vulnerable habitat. Diversity measures would also need to be undertaken for assemblages that make up the lower trophic levels, to give an indication of function resilience.

The Atlantic Forest of Brazil is highly fragmented, with low connectivity between forest patches (Ribeiro et al. 2009). Clearance patterns of tropical forest for agriculture show that lowland flat areas are preferable to highland areas with steep terrain (Kinnaird et al. 2003). This means isolated forest remnants are often situated in inaccessible places of higher altitude. Given the findings of chapter two, their position at higher elevations may mean they harbour lower diversity and if disturbed, could be more prone to trophic cascades. To maintain viable specialist insectivore populations, and safeguard the functions they provide, efforts should be made to connect isolated patches. Indeed, even small fragments can maintain high levels of species diversity if they are connected to neighbouring areas of forest (Martensen et al. 2012).

5.4.2 Mitigation of edge effects

Our results in chapters three and four show that edge effects strongly influence the occurrence of trophic cascades on herbivory in tropical forests. Top-down predation pressure at edges is reduced because the specialist forest-dwelling insectivore community is absent from these degraded borders (Dale et al. 2007; Banks-Leite et al. 2010; Pfeifer et al. 2017). Conservation efforts, therefore, should focus on mitigating edge effects on the vertebrate community, so that a strong insectivore

contingent can be retained. How far edge effects penetrate into forest interiors can depend on several factors, including how open the understory structure is (Ewers & Banks-Leite 2013) and the surrounding matrix type (Prugh et al. 2008). Matrix habitats that share characteristics with the focal habitat are often less hostile for biotic assemblages than those that contrast highly (Prevedello & Vieira 2010). By interspersing natural forest patches with plantations, rather than pasture, edges may be softened (Hatfield 2018). Structural similarities between forest and plantations would weaken abiotic edge effects and decrease the distance they penetrate forest interiors. This would ensure a greater proportion forest remained habitable for sensitive species and could help to buffer against trophic cascades.

Although, trophic cascades on herbivory were not mediated by forest cover, a strong relationship did emerge between habitat loss and the effect of exclusion on invertebrates. However, further investigation is needed to determine the relative effects of area and edge on trophic cascades before basing conservation strategies on these findings.

5.4.2 Resilience of belowground systems

Our results show that aboveground systems in tropical forest are more sensitive to perturbation than those belowground. Both arthropod communities and ecosystem processes (decomposition and nutrient cycling) remained robust to changes in vertebrate diversity. As discussed, belowground biota and species interactions appear to be more resilient to disturbance than those aboveground (Scherber et al. 2010). However, there is evidence that the effects of biodiversity loss do trickle down to effect processes within the soil (Wardle et al. 2004; Dunham 2008). Thus, although conservation focus should be directed at maintaining a healthy

aboveground ecosystem, longer-term impacts on belowground systems should not be ignored.

5.5 Future directions

5.5.1 Edge, area and matrix effects

How biodiversity loss and associated ecosystem functioning vary in modified landscapes is dependent on multiple factors. In the landscape context, edge, area and matrix type can all have variable and interacting influences on biotic diversity and species interactions (Laurance et al. 2007). In chapter three, we found that edge effects were strong on trophic dynamics, with cascades on herbivory occurring only within forest interiors. In chapter four, however, we found that habitat loss mediated the responses of forest arthropods to vertebrate exclusion but did not affect herbivory in the same way. This indicates that edge and area effects may mediate tropic cascades to different extents and warrants further investigation. Indeed, in the degradation of tropical forests, edge effects can be as important as habitat area (Pfeifer et al. 2017). In some cases, area effects can all but disappear, after edge effects have been controlled for (Banks-Leite et al. 2010). Our experimental design incorporated fragments and continuous forests which were surrounded by only one type of matrix – pasture. The difference between forest and pastureland is stark, meaning edges can be abrupt and abiotic influences can permeate a substantial distance into forest interiors (Ewers & Banks-Leite 2013). Plantations share structural similarities with forests and these may help to mitigate edge effects on vertebrate communities (Hatfield 2018). Thus, we may see differential effects on trophic cascades, depending on the characteristics of adjacent matrix.

5.5.2 Relative impact of top-down and bottom-up effects

Our study focussed solely on the permeation of top-down effects through food chains. Most species interactions and patterns of diversity will be determined by a combination of top-down and bottom up-forces (Letourneau & Dyer 1998). Bottom-up processes originate from lower trophic levels and can limit herbivore density through food resource quality and availability (Hunter & Price 1992). Primary productivity and floristic diversity, composition and density all fluctuate along natural and anthropogenic gradients (Zhu et al. 2015; Tabarelli et al. 2008). Such variation will be likely to have cascading effects that flow up through the trophic chain to impact herbivory rates and arthropod densities. Indeed, in chapter four, we see how the relative importance of top-down and bottom-up processes in limiting arthropod numbers may vary along gradient of forest cover. Further research is needed to assess how ecosystem functioning is governed by these interacting processes. Predator exclusion experiments and plant manipulations could be performed in tandem to disentangle the relative strength of these processes.

5.6 Conclusions

Our work reveals how mechanisms that drive ecosystem function can vary along natural and anthropogenic gradients. Trophic cascades on herbivory were mediated by elevation and only occurred at high altitudes. We suggest that the level of biodiversity in natural habitats may be a key determinant of function resilience to perturbation. Edges strongly affect ecosystem functioning, whilst habitat loss affects arthropod communities but has a neutral effect on herbivory. This thesis reveals the properties of ecosystems which may confer resilience to disturbance and provides new insight into how conservation strategies should be redirected to focus on

ecosystem functioning, as well as biodiversity. We propose two new directions for future research which build on the findings here, including the contribution of bottom-up effects to ecosystem functioning. Further investigation is needed into how edge, area and matrix effects interact to influence trophic cascade strength. The latter question deserves urgent attention, given the accelerating rates of deforestation in the tropics (Hansen et al. 2013).

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APPENDIX A

Arthropod orders and categorisation into broad functional guilds

Table A.1. Aboveground functional arthropod groups

Macro-arthropods were categorised based on the dominant functional role of the order. The taxa reported here are arthropods of a body length greater than 0.3 cm and were sampled from leaves and stems of understory plants. To assess trophic cascade strength and interactions between functional groups, the following three categories were used: predaceous, herbivorous and omnivorous. Although these broad-scale classifications require generalisations for each order, it is sufficient for the purposes of this study. Some groups such as Lepidoptera, which have marked differences in diet between life stages were recorded as either adult or larva. In some cases, arthropods were identified only to class level e.g. Diplopoda. This occurred when further taxonomic expertise was required to identify to order level.

Arthropod taxon	Functional category
Araneae	Predaceous
Archaeognatha	Omnivorous
Blattaria	Omnivorous
Coleoptera	Omnivorous
Dermaptera	Omnivorous
Diptera	Omnivorous
Diplopoda	Omnivorous
Ephemeroptera	Omnivorous
(Formicidae)	(Excluded)
Hemiptera	Herbivorous
Hymenoptera	Omnivorous
Isopoda	Omnivorous
Lepidoptera	Herbivorous
Lepidoptera larva	Herbivorous
Mantodea	Predaceous
Neuroptera	Predaceous
Opiliones	Predaceous
Orthoptera	Herbivorous
Parasitiformes	Parasitic
Phasmatodea	Herbivorous
Plecoptera	Herbivorous
Trichoptera	Herbivorous

Table A.2. Belowground functional arthropod groups

Following the methods used for aboveground fauna, belowground macro-arthropods were defined as one of three functional groups: predaceous, detritivorous and omnivorous. The taxa reported here are arthropods of a body length greater than 0.3 cm and were sampled from leaf litter samples. Arthropod larvae were categorised as one broad group and some individuals were identified only to class level e.g.

Diplopoda. This occurred when further taxonomic expertise was required to identify to order level.

Arthropod taxon	Functional category
Amphipoda	Detritivorous
Araneae	Predaceous
Archaeognatha	Detritivorous
Arthropod larva	Predaceous
Blattaria	Detritivorous
Chilopoda	Predaceous
Coleoptera	Omnivorous
Collembola	Detritivorous
Dermaptera	Omnivorous
Diplopoda	Detritivorous
Diplura	Omnivorous
Diptera	Omnivorous
(Formicidae)	(Excluded)
Hemiptera	Detritivorous
Hymenoptera	Omnivorous
Isopoda	Detritivorous
Isoptera	Detritivorous
Lepidoptera larva	Detritivorous
Mantodea	Predaceous
Opiliones	Predaceous
Orthoptera	Omnivorous
Phasmatodea	Detritivorous
Symphyla	Detritivorous

APPENDIX B

Percentage forest cover of sites and GPS locations

Table B.1. Percentage forest cover and GPS locations of sites

Percentage forest cover was calculated at 800m radius from the patch centroid value. At each site there was a paired interior and edge set of plots, the interior being situated 100 m into the forest from the border with the surrounding matrix.

Site	Forest cover (%)	Easting	Northing
A	8	462410	7434231
B	12	452241	7440833
C	21	444448	7431675
D	32	455714	7439185
E	35	485620	7420193
F	40	485563	7420564
G	43	486404	7423808
H	45	483001	7421507
I	50	486711	7424155
J	57	474676	7428475
K	66	486989	7424365
L	71	472089	7432825

APPENDIX C

Variation in arthropod abundance between procedural and control plots

Table C.1. Variation in mean abundance of aboveground arthropods with altitude

The below table shows mean cumulative abundance of sites at low (below 100 m asl) and high (above 1000 m asl) altitude within the control (CO) and procedural controls (PC). The results of paired t-tests are also reported. Aboveground arthropods have been categorised as predaceous or herbivorous.

GROUP	LOW				HIGH			
	CO	PC	t	p	CO	PC	t	p
TOTAL	29.4	32.8	0.91	0.39	19.5	22.7	1.09	0.30
Predaceous	11.8	13.4	1.11	0.30	5.9	8.5	1.47	0.18
Herbivorous	13.9	14.6	0.21	0.84	8.6	8.9	0.15	0.88
Omnivorous	3.8	4.8	0.67	0.52	5.0	5.3	0.30	0.77

Figure C.1. Paired plots showing abundance of aboveground arthropods at sites of high and low altitude

Graphs show the cumulative abundance of the functional groups in all paired CO and PC plots in sites at varying altitude. Light grey points depict sites at high elevations and dark grey, low. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

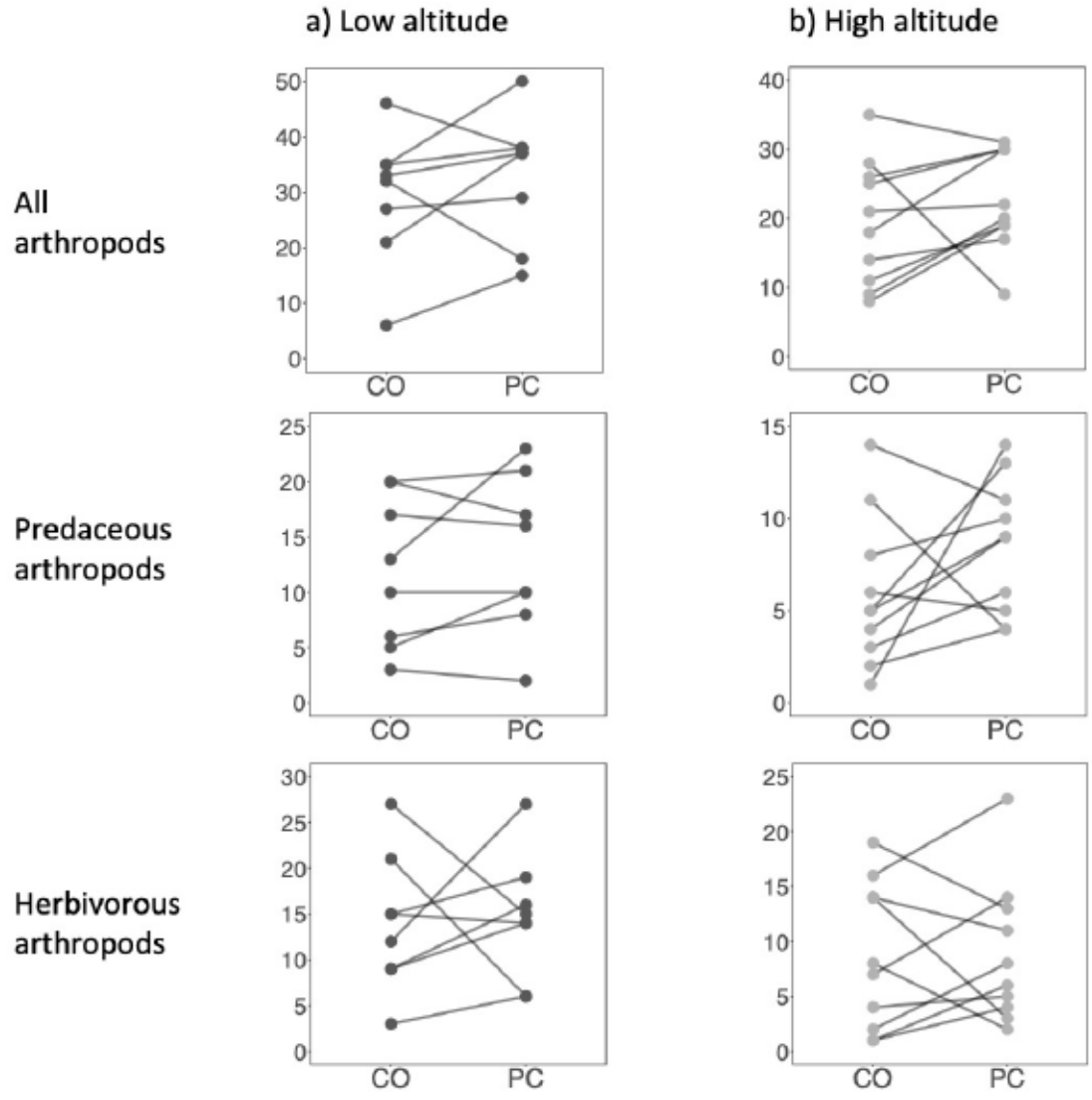


Table C.2. Variation in mean abundance of belowground arthropods with altitude

The below table shows mean cumulative abundance of sites at low and high altitude within the control (CO) and procedural controls (PC). Belowground arthropods have been categorised into the following functional groups: predaceous, detritivorous or omnivorous. Data have also been summed to give total arthropod abundance. The results of paired t-tests are shown.

GROUP	LOW				HIGH			
	CO	PC	t	p	CO	PC	t	p
TOTAL	27.5	27.5	0.00	1.00	26.1	31.4	1.49	0.17
Predaceous	4.5	6.1	1.26	0.25	7.5	8.9	1.18	0.27
Detritivorous	20.1	18.0	-0.48	0.64	13.0	16.4	1.25	0.24
Omnivorous	2.6	3.1	0.37	0.72	5.6	6.1	0.45	0.66

Figure C.2. Paired plots showing abundance of belowground arthropods at sites of high and low altitude

Graphs show the cumulative abundance of functional groups at all paired CO and PC plots at low and high elevations. Light grey points depict sites at high elevations and dark grey represents low altitude. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

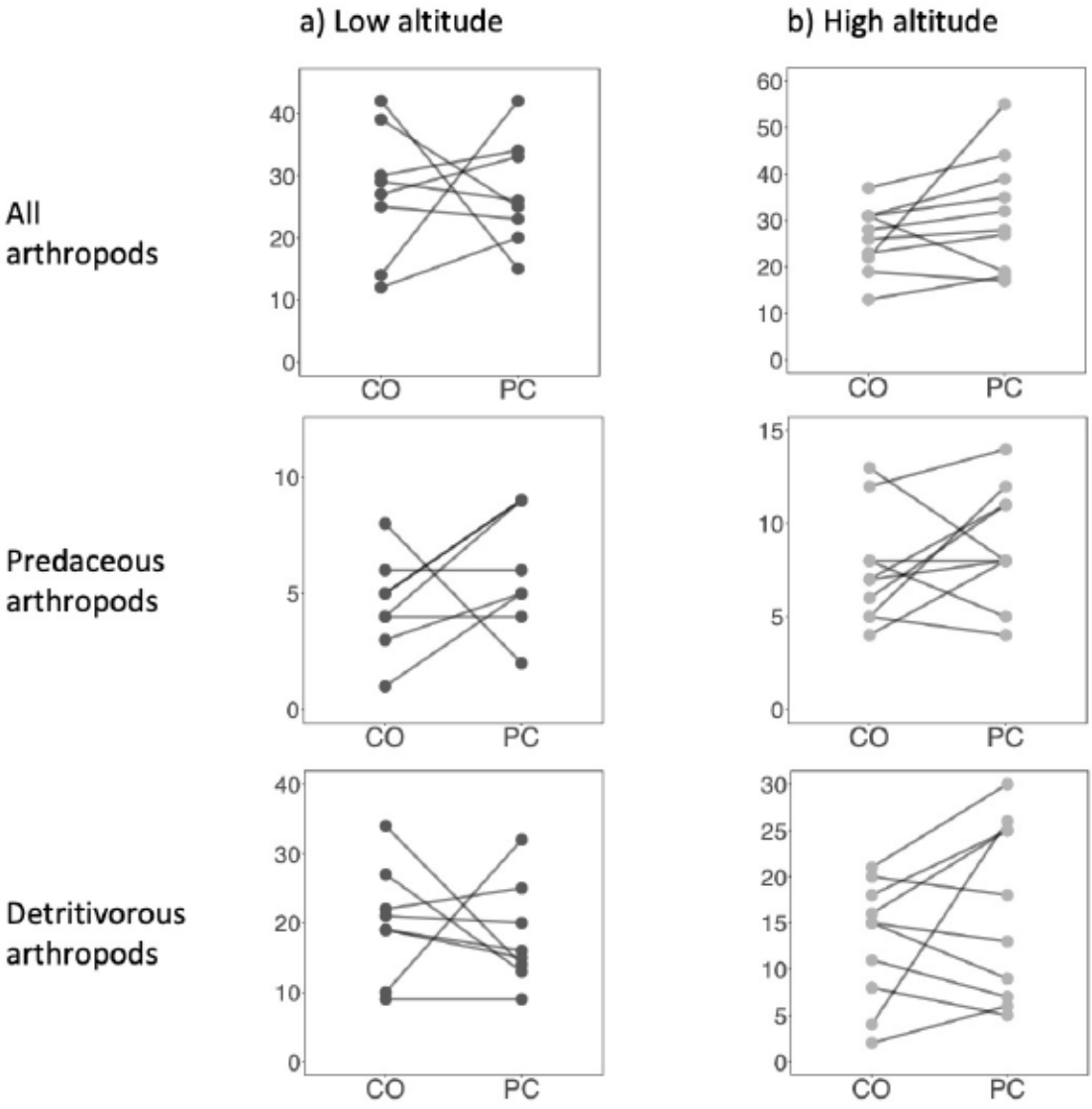

a) Low altitude
b) High altitude
All arthropods
Predaceous arthropods
Detritivorous arthropods
CO
PC

Table C.3. Variation in mean abundance of arthropods between edge and interior sites

The mean cumulative abundance of aboveground arthropod within control (CO) and procedural controls (PC) at interior and edge sites. The results of paired t-tests are also reported, and any significant results have been highlighted in bold font. Arthropods have been categorised as predaceous, herbivorous or omnivorous, and summed to give total arthropod abundance.

GROUP	INTERIOR				EDGE			
	CO	PC	t	p	CO	PC	t	p
TOTAL	11.9	13.1	0.50	0.65	25.3	27.4	1.05	0.33
Predaceous	3.3	4.4	1.18	0.28	**4.4**	**8.6**	**3.06**	**0.02**
Herbivorous	4.3	5.8	1.24	0.26	12.3	12.1	-0.05	0.96
Omnivorous	4.3	2.9	-0.89	0.41	8.6	6.7	-0.94	0.38

Figure C.3. Paired plots showing abundance of aboveground arthropods edge and interior sites

Graphs show the cumulative abundance of these groups in all paired CO and PC plots at edge and interior habitat. Light grey points depict edge sites and dark grey, interior. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

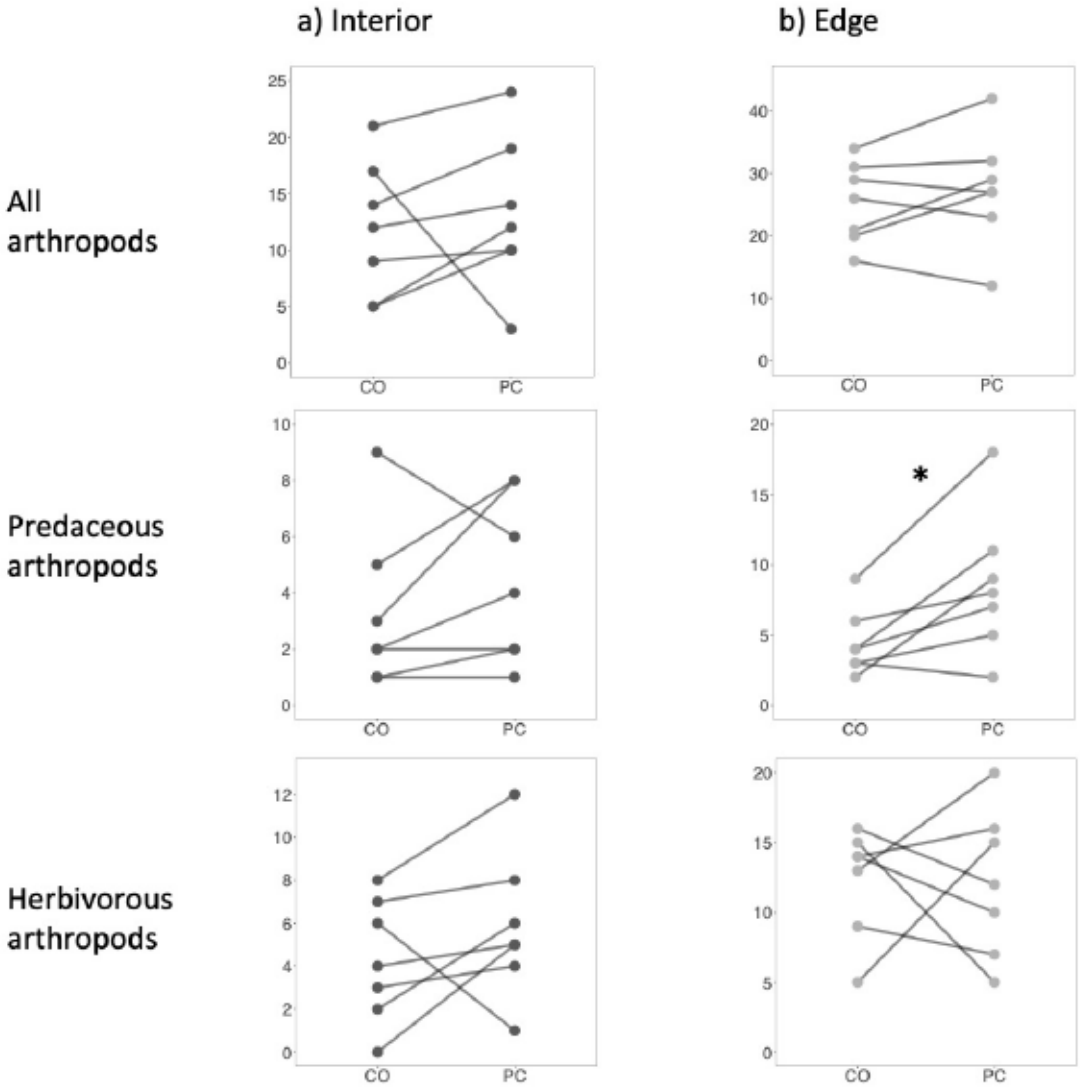

a) Interior
b) Edge
All arthropods
Predaceous arthropods
Herbivorous arthropods
CO
PC
*

Table C.4. Variation in the abundance of arthropod functional groups with forest cover at edge and interior sites

Table show the results of GAMMs, where cumulative arthropod abundance is modelled with treatment as a fixed effect and forest cover as separate smooth terms for control (CO) and procedural control (PC). Arthropods have been categorised as predaceous, herbivorous or omnivorous, and summed to give total arthropod abundance. Significant results are highlighted in bold font.

GROUP	INTERIOR					
	Treatment		s:CO		s:PC	
	t	p	F	p	F	p
TOTAL	0.99	0.34	3.05	0.10	1.63	0.22
Predaceous	1.59	0.13	0.70	0.41	1.95	0.25
Herbivorous	0.00	1.00	2.77	0.11	0.30	0.59
Omnivorous	-0.14	0.89	0.07	0.79	0.10	0.75

GROUP	EDGE					
	Treatment		s:CO		s:PC	
	t	p	F	p	F	p
TOTAL	0.65	0.52	0.03	0.85	0.58	0.46
Predaceous	**2.66**	**0.02**	0.00	0.95	2.31	0.15
Herbivorous	-0.25	0.80	0.12	0.73	0.16	0.70
Omnivorous	-1.00	0.33	1.60	0.35	0.20	0.66

Figure C.4. Plots showing the variation in arthropod abundance with forest cover at edge and interior sites

Graphs show cumulative abundance of aboveground arthropod along a gradient of percentage forest cover within CO and PC plots at interior and edge sites. Light grey points depict procedural control plots; dark grey represents controls. Asterisks represent p-values with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

