The effects of human disturbance on vascular epiphyte in the Brazilian Atlantic Forest

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"What we have to practice today is solidarity,
one must not approach people to say
Here we come to give the charity of our
presence, to teach our science, to show you your
mistakes, your ignorance, your lack of basics.

We go with investigative zeal, and humble
spirit, to learn in great source of wisdom which is the
people."
Che Guevara

Declaration

The data collection and work presented in this thesis is all my own. Dr Cristina Banks-Leite did provide guidance throughout my thesis. Chapters are organized as papers, and I used “we” to recognize the role of my supervisor Dr Cristina. Data sources and software are referenced along the text. The support of different people is acknowledge as follows:

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Copyright Declaration

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Abstract

The high pressure that anthropogenic activities places on tropical forests are pushing species and communities to the brink of local, regional or global extinctions. However, the consequences of the loss of species and their ecosystem functions are not well known. My thesis addresses the causes and consequences of human disturbance on vascular epiphytes in the Brazilian Atlantic forest (BAF). I sampled understory and canopy, across a gradient of habitat loss, i.e. pastureland, human-modified forests (HMFs) and old-growth forest. I found that habitat loss has driven a net loss of 91% of species exclusive to old-growth, and 90% of individuals. I also found the edge effect to be a ubiquitous landscape process extending at least 500 m within forests habitats, leaving just 19.4% of the whole of the BAF suitable for forest-dependant epiphytes. However, whilst endemic species (habitat specialised species) are more prone to disappear as consequence of habitat loss, species with larger dispersal ranges and the ability to colonize different forest types flourish or endure the harsh conditions after disturbance. Consequently, HMFs have low functional richness and low functional redundancy, meaning low resilience, whereas old-growth forests exhibit high ecological resilience. Habitat transformation also leads to the loss of a large set of ecosystem functions related to pollination and water cycling across strata. Hence preserving large continuous forests are probably the only pragmatic conservation strategy for vascular epiphytes in highly human-modified landscapes. However, human-modified forests still provide limited ecosystem functions that may increase because of initiatives to improve habitat amount.

Table of content

List of figures

List of tables

1 General Introduction

The consistent pattern of the transformation of continuous old-growth forest to human-modified forests, pastureland, plantations and human infrastructures have impacted all attributes of biodiversity and the services they provide (Newbold *et al.*, 2015). Therefore, understanding the causes and consequences of forest transformation has become one of the main goals of linking ecology and social development.

The effects of habitat loss on community structure might comprise, but are not limited to, species loss, a decrease in abundance, shifts in community composition, and reduction of ecosystem function (Ewers & Didham, 2006; Didham, 2010; Ewers *et al.*, 2011). Old-growth forest remains the main repository of terrestrial biodiversity and ecosystem functions worldwide (Watson *et al.*, 2018; Gibson *et al.*, 2013), however, habitat loss has resulted in species, communities and populations having to find shelter in remnants of human-modified forests after disturbance. The value of these human-modified forests in terms of biodiversity conservation is under the spotlight as it is now the most representative landscape cover in the tropics.

The future of biodiversity, and the ecosystem functions provided by species, will likely depend heavily on the management of both old-growth and human-modified forests for conservation. Both forests play important roles in recruiting and preserving species pools and community dynamics (Einzmann & Zotz, 2016; Barlow *et al.*, 2007), and host significant species richness (e.g. Nöske et al., 2008; Werner & Gradstein, 2008; Flores-Palacios & Garcia-Franco, 2006; Köster, Friedrich, Nieder, & Barthlott, 2009).

My thesis provides empirical evidence of the value of both continuous old-growth forest and human-modified forests in protecting and maintaining species, populations, communities, and ecosystem functions.

1.1 Old-growth forests and human-modified forests

Old-growth forest represents the intact forests or mature forests (or in ecological climax) that are free of significant anthropogenic degradation (Watson *et al.*, 2018). Contrastingly, human-modified forests conceptually comprise second-growth forests, i.e. forests undergoing natural regeneration processes after complete clear-cut, and degraded, forests which are remnant of old-growth forests (Putz & Redford, 2010). Although old-growth and human-modified forests are structurally different, both play complementary roles in the conservation of biodiversity and ecosystem functions (Chazdon, 2014; Watson *et al.*, 2018).

In terms of global cover, the world's old-growth forests only account for 18-24% of total forest cover of the original cover (Intact Forest Landscape, Potapov et al., 2017; Human Footprint, Venter et al., 2016). Despite this reduced area, several studies have shown the importance of old-growth forests in maintaining local biota. For instance, old-growth forests accounts for 50% of native Singaporean biodiversity in just 0.25% of the total area of Singapore (Brook, Sodhl & Ng, 2003). Similarly, Barlow et al. (2007) found that 60% of the world's flora are restricted to old-growth forests. Old-growth forests are also highly important sinks for carbon sequestration; they contain 63% of the total aboveground carbon budget in the tropical Americas (Chazdon *et al.*, 2016).

In contrast, human-modified forests currently account for around 60% of global tropical forests cover (FAO 2010), and their area will continue to expand in the future through the conversion of primary forest (FAO 2015) and most importantly through the planned forest restoration of 300 million hectares worldwide (Bonn Challenge, 2011; Aichi target, 2011; New York Declaration on Forests, 2014). Despite the fact that human-disturbed forests do not show a comparable complexity to primary forests (Gibson *et al.*, 2013; Zotz, 2016), some researchers have found positive trends in forest restoration with recovery biodiversity and ecosystem functions. For instance, Barlow et al. (2007) showed that human-modified forests can retain up to 59% of old-growth species pool in the Amazon basin. Likewise, carbon sequestration is recovered over ~ 30 years in human-modified forest to approximately half of old-growth aboveground biomass (Gilroy *et al.*, 2014), and at the regional scale this forest type accounts for 25% of aboveground carbon sequestration in the tropical Americas (Chazdon *et al.*, 2016).

Despite their differences, old-growth and human-disturbed forests are exposed to the same threats to biodiversity, which includes changes of habitat area and connectivity and more importantly, edge effects (Watson *et al.*, 2018; Potapov *et al.*, 2017; Chazdon, 2014). As continuous old-growth forests are fragmented, there is an increasingly large area exposed to edge effects, with nearly 70% of the world's forests within 1 km of a forest edge (Haddad *et al.*, 2015a).

1.2 The ubiquitous impacts of edge effects

Wherever there is a creation of a forest fragment there is also creation of an edge and the edge surroundings will affect the dynamics and processes of the forest (Ries *et al.*, 2017). Edge effects are landscape processes that create abiotic changes to forest interiors (Ewers & Banks-Leite, 2013; Williams-Linera, Domínguez-Gastelú & García-Zurita, 1998), causing both positive and negative effects to the biotic component. Some species thrive by the opening of new edge habitats (Mascarúa López, Harper & Drapeau, 2006; Harper &

Macdonald, 2011), whereas others, such as the species dependent on forest interior conditions, may become locally extinct (Tabarelli, Peres & Melo, 2012).

The edge might be seen as a dynamic zone between “winners” and “losers” in disturbance. Recently, a worldwide study by Pfeifer et al. (2007) found that the abundance of 85% of vertebrate species were affected by forest edges, either positively (46%) or negatively (39%). The most consistent pattern however, is the resultant shift in community composition. In some cases, this leads to forest edge communities with little resemblance to communities in edge-free habitats (Ries *et al.*, 2017).

One of the most detrimental events occurring in the edge is the reduction in spatial diversity, i.e. the replacement of local biotas with alien species (McKinney & Lockwood, 1999). Local unique endemic species are replaced with already widespread species, negatively affecting phylogenetic diversity (Olden *et al.*, 2004), ecosystem functioning (Mitchell *et al.*, 2015), and potential repercussions for speciation (disscused in Olden et al., 2004). The effect of edges can also be translated into a reduction or shift in ecosystem functions provided by edge dwelling species. For instance, for productivity traits, functional diversity is lower on the edge, which reduces the potential of forests to store carbon (Razafindratsima *et al.*, 2018).

The influence of the edge can be partitioned into two components, the extent of the edge influence (the spatial scale), and the magnitude, i.e. the degree of the effect, (Chen, Franklin, & Spies, 1995; Harper et al., 2005). The higher the magnitude, the higher the edge effect and the lower the habitat quality. The larger the extent, the further the edge effect reaches into the forest and the lower the unaffected habitat amount. For instance, the extent of the edge effect is believed to reach up to 1km within forest habitat (Ewers & Didham, 2006), whereas the magnitude can affect negatively or positively local species richness (Harper *et al.*, 2005; Peyras *et al.*, 2013).

There are several difficulties in studying edge effects. The first is the idiosyncratic ecological response of species, as different species have more or less tolerance to the conditions in the edge. Secondly, the landscape components act synergistically. Forest habitats in human-modified landscapes are embedded in a matrix that modulates the resources or pressures to the focal habitat, the matrix domain (Driscoll *et al.*, 2013). Besides, there are additive effects associated to multiple edges of nearby fragments that can support other population via rescue events (Ries *et al.*, 2017). Thirdly, there is empirical difficulty in designing comprehensive studies to include the gradient habitat-no-habitat (such as matrix-edge-interior), and to provide abundance data, which provides species' preference of a particular habitat (Ries *et al.*, 2017).

In general, recent evidence on the impact on the biotic component of the forests suggests that edge effects are as important in driving biodiversity changes as habitat cover (Pfeifer *et al.*, 2017; Banks-Leite, Ewers & Metzger, 2010).

1.3 Habitat amount and core area

Human-modified forests, the matrix and edge effects all comprise a set of elements that constrain biodiversity and the expected habitat suitable for the maintenance or rescue of their ecosystem functions. Fahrig's (2013) habitat amount theory posits that species richness in a fragmented landscape is a product of the total sample area (e.g. plot, transect, quadrant), rather than a result of individual patch size and the fragment isolation in the landscape. This hypothesis deviates from MacArthur and Wilson (1967)'s "The island biogeography theory" to explain species richness on islands. MacArthur and Wilson (1967) predicted that smaller and more isolated islands have lower species richness than larger and less isolated ones.

The rationale behind Fahrig's hypothesis is that forest patches are not entirely embedded into a hostile matrix, as opposite to MacArthur and Wilson' (1967) "island biogeography theory". As such, plants and animals disperse across landscapes and the matrix imposes and modulates biotic and abiotic conditions that impact forest fragments. Hence, habitat amount predicts that species richness, in standardized sample sites, should increase with the total amount of the surrounded habitat which is the same as the target habitat, at a specific spatial scale. Therefore, the effects of habitat fragment size and isolation will be negligible on species richness in the sample sites, as long as the surrounding habitat amount is constant.

Species richness may also be affected by the amount of suitable core habitat that is available within a forest fragment. Laurance and Yensen's (1991) core area is a widely predictive spatially implicit model that estimates the habitat that remains unaffected by edge influence. The model has three components: total fragment area, total perimeter length, and a biological measure of the extent of edge effects on a particular group. This model has been adopted by ecologist and practitioners to model the effects of edge effects, reserve design, and management and restoration strategies (Laurance, 1991; Laurance and Yensen, 1991).

These complementary hypotheses bring together the possibility to estimate the suitable habitat for populations, species and communities dwelling in fragmented landscapes, by accounting for the effects of the edge influence and the amount of fragmented habitat in the landscape. Recently Lefebvre (2016) proposed and later demonstrated together with Pfeifer et al (2017) the use of a spatially explicit model to assess habitat fragmentation and its impact on species abundance. I used this approach here and provide my view of this approach in the general discussion.

1.4 Functional diversity

Trait-based ecology, i.e. the study of different levels of organization based on traits, has provided a mechanistic framework for the understanding of changes in assemblages to explain disturbance patterns in both natural and human-modified environments (Díaz *et al.*, 2016; Garnier, Navas & Grigulis, 2016). The success lies mainly in the predictable response of functional traits to different stressors and the potential to link of species responses to ecological processes (Villéger *et al.*, 2010; Funk *et al.*, 2016).

Organisms display a range of traits that may influence their ability to persist in and colonize altered habitats, i.e. response traits (Cornelissen *et al.*, 2003), and to impact their ecosystem processes, i.e. effect traits (Garnier, Navas & Grigulis, 2016). Response traits are characteristics that can therefore be used to help understand the mechanisms behind species sensitivity to habitat disturbance. For instance, low dispersal ability, drought-intolerance, low offspring production, habitat specialism, short lifespans, or short height, are all response traits that may promote a species vulnerability to extinction (Löbel & Rydin, 2009; Götzenberger *et al.*, 2012). On the other hand, effect traits are those which directly influence an ecosystem property, e.g. nutrient cycling, or trophic transfer (Diaz and Cabido, 2001). For instance, plant nectar production is a trait related to plant reproduction, but can influence ecosystem functions via food webs (Gotsch, Nadkarni & Amici, 2016). However, delimiting boundaries between a response and an effect trait is not a straight forward process because they usually overlap, particularly in the case of resource use. For instance, thick leaves provide a protective defence against herbivores (response), are a resistance trait to environmental stress (response), and are linked to nutrient cycling (effect).

Trait-based ecology studies rely on functional metrics as quantitative tools to understand trait diversity and the potential ecological functions in the community. Here we use functional structure for consistency with empirical and theoretical literature in community-level assembly processes and assembly rules (Mouchet *et al.*, 2010; Karadimou *et al.*, 2016; Garnier, Navas & Grigulis, 2016). Functional structure describes the distribution of traits by either the mean value or the variability in trait-space in a community (e.g. functional richness, divergence). The multivariate integrated association between species, traits and environmental conditions have been studied with RLQ and fourth-corner methods and these approaches have shown to be effective at disentangling patterns in functional trait space (Garnier, Navas & Grigulis, 2016).

1.5 Vascular epiphytes as a model group

Vascular epiphytes, plants that rely on a host for support (Schimper, 1903), are one the most species-rich groups in tropical forests, making up to 50% of all vascular flora at the local scale (Zotz & Bader, 2009). Following Zotz (2013a), I use the term vascular epiphytes to refer to epiphytes and hemiepiphytes of vascular plants. Epiphytes are physiologically different to their terrestrial counterpart. For instance, important biotic interactions in terrestrial plants, such as competition, pathogen attacks or herbivory, play minor roles on epiphyte plants (Zotz, 2016; G Zotz and Hietz 2001). However, the dependence upon a suitable host can also work as abiotic filtering (Ruiz-Cordova, Toledo-Hernández & Flores-Palacios, 2014; Woods, Cardelús & DeWalt, 2015; Einzmann *et al.*, 2014; Sáyago *et al.*, 2013).

Vascular epiphytes traits, such as absence of protective seed tissue (leading to limited seed banks formation; Benzing, 1990), high dispersal limitation of shade-dependent species, and higher mortality rate than tropical trees (Zuleta *et al.*, 2016), might create a bottleneck in epiphytes assemblages in human-modified landscapes. These characteristics make vascular epiphytes a unique model group to test the magnitude of human-induced disturbance in tropical forests. Likewise, the study of epiphytes will help to improve our understanding of the effects of habitat loss and fragmentation across the understory and canopy strata.

Vascular epiphytes play an important role in the functional stability of ecosystems via the regulation of forest hydrology (Pypker, Unsworth & Bond, 2006), the production of biomass (Hofstede,1993), nutrient fluxes (Clark, Nadkarni & Gholz, 2005), and facilitating animal life (Richardson, Rogers & Richardson, 2000). Experimental studies have shown they have a positive presence correlation with birds (Cruz-Angón & Greenberg, 2005), invertebrates (Cruz-Angón, Baena & Greenberg, 2009; Fernandez Barrancos, Reid & Aronson, 2017), and herpetofauna (McCracken & Forstner, 2014).

1.6 Disturbance on epiphytes: Winners and losers in habitat disturbance

Human disturbance has been shown to drive the reduction of epiphyte richness and abundance when comparing old-growth and human-modified forests (e.g. Kromer & Gradstein 2003; KÖster et al. 2009; Larrea & Werner 2010; Julia et al. 2016). This is likely because early stages of forest succession have fewer available resources and provide less suitable habitat than mature forests for the establishment of many epiphyte species. This also supports the pattern of slow recovery after disturbance found in ombrophilus forests (Cascante-Marin et al. 2008, 2009), especially for bromeliads and orchids, the most species-rich groups in epiphytes, that require 10–20 years to reach maturity (Schmidt & Zotz, 2002).

Nonetheless, this detrimental pattern that habitat loss exerts on species richness has similarly shown contradictory patterns in other studies (Hernández-Pérez & Solano, 2014; Kessler Michael., 2002). This trend is probably since numerous epiphyte species may benefit from the opening of new habitats so called “winners in disturbance”. For instance, whilst some bromeliads are restricted to particular shaded places in the forest and therefore high sensitive to drought-conditions in open areas (Martinelli *et al.*, 2008; Benzing, 2000), other species of the same family have high tolerance to drought and can colonize and disperse across fragmented landscapes (Marques *et al.*, 2014; Benzing, 2000; Einzmann & Zotz, 2017).

After experimental removal, drought-tolerant species arrive first, then local expansion occurs with no saturation of the host (Einzmann & Zotz, 2017), and assemblages slowly move towards more shade-preferred species as the tree becomes older and more complex aligning with Darwin's "island geological theory" and "species accumulation models" (Taylor & Burns, 2015; Woods, 2017). This dynamic of winners and losers in disturbance has shown that species have a set of strategies to cope with harsh environmental conditions. In case of drought, some species have developed eco-physiological traits to resist drought, i.e. drought-tolerance, whereas others avoid the loss of water via drought-avoidance traits (Males & Griffiths, 2017).

The species that are lost in disturbed habitats are generally those that dwell in wetter and shady portions of the forest or the tree and need more constantly humid microclimates (Cornelissen & Steege, 1989; Bianchi *et al.*, 2014; Wolf, 2005). In fact, drought and high exposure to solar radiation cause seed mortality and affects the survival of juvenile stages more so than for adults (Schmidt & Zotz, 2002; Zotz & Hietz, 2001; Hietz-Seifert, Hietz & Guevara, 1996; Benzing, 1990, 2000). For example, Zotz (2005) found the highest mortality (30-51%) in the early stages of the bromeliad *Vriesea sanguinolenta*. However, seedlings of other species of bromeliads can endure and germinate under experimental conditions of ca 30% C (Müller, Albach & Zotz, 2018).

Dispersal limitation also drives epiphyte community structure, because colonization of many species occurs within a close range from the mother, e.g. 30 m (Cascante-Marin et al. 2008, 2009), and individuals are genetically closely to those within 5 m distance (Trapnell, Hamrick & Nason, 2004). On the other hand, long-distance dispersal events also occur and at a rate sufficient to maintain local populations and connect the metacommunity in open areas, e.g. the atmospheric bromeliads in pastureland and matrix (Einzmann & Zotz, 2017; Einzmann, Zotz & Mi, 2017)

1.7 Functional strategies to cope with disturbance

Empirical studies on vascular epiphytes have explained disturbance tolerance at the local scale by linking a set of trait strategies to human forest transformation. A set of strategies seen in bromeliads and ferns make them the dominant groups of vascular epiphyte communities after habitat loss (Poltz & Zotz, 2011; Jian *et al.*, 2013; Mondragon & Calvo-Irabien, 2006). These traits, designed to cope with drought, include the photosynthetic pathway CAM (Rodrigues *et al.*, 2013; Benzing, 1990; Einzmann *et al.*, 2014), thick leaves, and the lack of water storage tissues (Benzing, 2000; John & Hasenstein, 2017; Rodrigues *et al.*, 2013).

Specifically, among the drought-avoidance and tolerance traits in atmospheric bromeliads there are low specific leaf area (SLA), high degree of succulence, thick leaves, and low epidermal water loss rate (EWL). Ferns however, invest less energy into their leaves (i.e., high SLA, low LDMC, low degree of succulence) and have a high EWL rate (Petter *et al.*, 2016; Woods, 2013). Experimental studies have found that dispersed seedlings, with no protective tissue, have higher mortality levels than seed protected species (Mondragon et al. 2015). These studies provide a baseline in our understanding of the response mechanisms behind local structures, especially in old-growth continuous forests, but the landscape scale is still vastly unexplored, especially in human-modified forests.

The causes and consequence of habitat loss and fragmentation are highly complex and need to be addressed from multiple angles, this is because an ecosystems stability and functions rely on the interconnection across taxa or functional entities. This is especially critical in the face of current anthropogenic pressures, which alter patterns of species composition within communities and the ecosystem functions they provide.

1.8 Thesis overview

My thesis presents original research and uses novel methods to determine the effect of anthropogenic disturbance and which drivers predict epiphytic plant community along a gradient of habitat loss. My study also provides a baseline to understand the reassembly of communities after human disturbance and estimates the capacity of human-modified forests to retain ecosystem functions provided by vascular epiphytes. Data chapters are arranged as manuscripts that are in preparation for submission. Therefore, there will be some repetition in the methods and bibliography sections. Literature cited throughout is provided at the end of the document.

Chapter 2 aimed to quantify the patterns of local and landscape determinants of habitat loss and fragmentation on epiphytes communities in the Brazilian Atlantic Forest (BAF). I accounted for the effects of the landscape, tree structure, elevation and rainfall on the diversity of epiphytes at canopy stratum. I here show one of the most dramatic effects of habitat loss and disturbance ever reported. These results suggest that the current population of seedlings and juveniles is unlikely to provide enough individuals for upcoming generations, due to the low population size in the patterns of ontogeny stages (vs old-growth forests). Additionally, I suggest reasons as to why epiphytes might be the most threatened group by habitat loss, which raises questions about the value of human-modified forest to preserve all components of biodiversity.

In Chapter 3, I quantified the extent and magnitude of edge effects on epiphyte communities in the BAF. I assessed the responses at the species and community level, as well as at the canopy and understory forest strata independently, which allowed me to decompose edge effects along the vertical as well as the horizontal gradient. I extended the predictions of edge influence across the whole BAF. This research questions the actual suitable habitat amount in the BAF to buffer anthropogenic forest disturbance.

In chapter 4, I explain and predict community and species trait patterns of vascular epiphytes in a highly human-modified landscape using life-history traits. This is the first study using life-history traits (response vs effect) to explain patterns in a vertical (among strata) and horizontal (matrix-edge-interior-control forests) gradient in a human-modified landscape. I also discuss the distribution patterns of response and effects traits and the functional structures of epiphytes communities along the horizontal and vertical gradient.

The final chapter of this thesis integrates the conclusions from each of my chapters to synthesize my findings. I also discuss the contributions that my doctoral research has made to the study of biodiversity change and habitat loss and identify future research directions.

Chapter 2.

The value of human-modified forests for the conservation of epiphyte communities

2 The value of human-modified forests for the conservation of epiphyte communities

2.1 Abstract

Human-modified forests – HMFs – now cover more area worldwide than primary forests, meaning it is increasingly important to understand their value in protecting global diversity. HMFs have been shown to preserve terrestrial plants, mammal, birds and invertebrates organism. However, their role in protecting vascular epiphytes remains unclear, because most epiphytes require large and old tree with humid and shaded conditions, features which are usually modified after disturbance. In this study, we assessed how adult and early ontogeny individuals of canopy epiphyte communities are affected by habitat loss and fragmentation. Our results show a net loss in HMFs of 91% of species exclusive to control forests, and 90% of individuals. Increasing forest cover within HMF did not increase species richness and abundance, but affected changes in community composition. Expectedly, the abundance of juveniles and seedlings was higher than of adults in control forests, however this pattern was shifted in HMFs, and we found no juveniles or seedlings in pastures. We here show one of the most dramatic effects of habitat loss and disturbance on any community, and our results also suggest that current bank of seedling and juveniles is unlikely to provide enough individuals for upcoming generations, due to the high mortality in early ontogeny stages. The future populations and communities of vascular epiphytes in HMF may be facing local or even regional extinction, hence efforts towards preserving large continuous pristine forests seems to be the only viable conservation option for vascular epiphytes.

2.2 Introduction

As the protection of large expenses of pristine forest becomes even more difficult, many now argue that the future of biodiversity will likely depend on the availability and appropriate management of human-modified forests – HMFs (Banks-Leite *et al.*, 2014; Wright & Muller-Landau, 2006). These arguments are supported by evidence from well-studied taxa, such as vertebrates and trees, which consistently show some level of resilience to habitat modification (Banks-Leite *et al.*, 2014; Gibson *et al.*, 2013; Mascarenhas & Mariano-neto, 2014). For instance, after habitat disturbance there is a change of functional groups in birds but there is not loss of functions (De Coster, Banks-Leite & Metzger, 2015). Epiphytes, however, are likely more sensitive than vertebrates and trees because their structural dependence on large trees, long generation cycles, dispersal limitation and sensitivity to microhabitat quality and availability (Petter *et al.*, 2016; Zotz, 2016). Currently, the responses of epiphytes to habitat disturbance at landscape scale are poorly known, and given the importance of these species to ecosystem functioning (see Zotz, 2016), it is imperative that the value of human-modified forests to protect and maintain this speciose community is fully understood.

HMF often comprise a suite of different types of forests: second-growth forests, forests undergoing natural regeneration processes after complete clear-cut, and degraded forests as remnant of old-growth forests (Putz & Redford, 2010). Under this conceptual umbrella, HMF already comprise the majority of the world's forests, and their prevalence is only likely to increase given on-going deforestation and reforestation (Chazdon, 2014). HMF play an important role in recruiting and preserving species pools and community dynamics (Einzmann & Zotz, 2016; Barlow *et al.*, 2007), despite the lower diversity and complexity than primary continuous forests (Gibson *et al.*, 2013; Zotz, 2016). HMFs might host similar number of species to control forests (Köster *et al.*, 2013, 2009; Nöske *et al.*, 2008; Larrea &

Werner, 2010; Flores-Palacios & García-Franco, 2008), and display some habitat structural characteristics similar to those of old-growth stands (Zanini *et al.*, 2014). For these reasons, it has been even suggested that HMF may buffer species from future extinction (Wright & Muller-Landau, 2006).

HMFs have been shown to preserve certain tropical forest species of trees, shrubs, birds and mammals (Chazdon, 2014; Farah *et al.*, 2017). HMFs, however, very rarely occur in large continuous areas, and thus are subjected to the same influence habitat fragmentation poses on continuous forests. Larger patch size, for instance, has been shown to influence colonization and succession in woody plant species (Yao *et al.*, 1999). Low forest cover in the landscape, on the other hand, has been found to drive losses in phylogenetic and functional diversity (Goncalves Rigueira, Bernardo-da-Rocha & Mariano-neto, 2013), whereas high connectivity improves the recruitment and rescuing of populations of disturbed forests from more preserved forests (Farah *et al.*, 2017; Young, Boyle & Brown, 1996; Brown & Kodric-Brown, 2016).

While the effects of fragmentation on terrestrial plant communities have been intensively studied (Haddad *et al.*, 2015b; Newbold *et al.*, 2015; Collins *et al.*, 2017; Brooks *et al.*, 2002), not much is known about vascular epiphytes at landscape scale, and there are reasons to believe that these species are more vulnerable than their hosts (Zotz, 2013). For instance, vascular epiphytes traits such as absence of protective seed tissue (leading to limited seed banks formation; Benzing, 1990), high dispersal limitation of shade-dependent species, and higher mortality rate than of tropical trees (Zuleta *et al.*, 2016) might create a bottleneck in epiphytes assemblages in human-modified landscapes. Furthermore, epiphytes propagules are affected by the host straits such as branch architecture, bark peelings, bark texture, and phenology that influence establishment and survival (Ruiz-Cordova, Toledo-Hernández & Flores-Palacios, 2014; Woods, Cardelús & DeWalt, 2015). Interestingly, however, important biotic interactions in terrestrial plants, such as competition, pathogen attacks or herbivory, play minor roles on epiphyte plants (Zotz, 2016; G Zotz and Hietz 2001).

Previous examinations of the relative importance of HMF upon epiphyte communities have been limited to small landscape scales, focused mainly on species richness and abundance (but see Einzmann, Döcke, and Zotz 2016; Gerhard Zotz 2016; Köster et al. 2009; Poltz and Zotz 2011; Taylor and Burns 2015). Most studies, to our knowledge, have not assessed how early ontogeny stages will respond to different habitat structure and landscapes conditions. In general, juvenile stages experience higher mortality than adults, hence, it is expected that early ontogeny stages may be more abundant in a population than adults (Mondragón *et al.*, 2015).

Our research explores how canopy epiphyte communities respond to habitat loss and fragmentation in the highly endangered Atlantic Forest. In particular, we assessed the extent to which epiphyte diversity, community composition and ontogeny stages in HMFs diverge from communities in the continuous forests. We also explore the effects of the landscape structure, habitat and macroclimatic characteristics in shaping patterns of species diversity and composition.

2.3 Material and methods

2.3.1 Study Area

The study area is located in the Brazilian Atlantic forest in Sao Paulo state, within the municipalities of Taubate, Sao Luiz do Paraitinga and Lagoinha (**Figure 2-1**). The study area has 28% forest cover in various successional stages, with an average fragment size of 15 ha across the landscape, and the matrix is dominated by pastureland and tree plantations. The altitude ranges from 860 m up to 1,470 m. The predominant types of soil are Latosol, and

Cambisol (RADAMBRASIL, 1983). The vegetation is predominantly characterized by Montane Ombrophilous Dense Forest (Veloso, Rangel-filho & Alves-Lima, 1991).

2.3.2 Sampled sites and environmental variables

Sites surveyed were part of the "Biodiversity and Ecosystem Functioning in Degraded and Recovering Amazonian and Atlantic Forests" (ECOFOR) research project funded by NERC (Grant Number NE/H016228/). Fieldwork was conducted from May 2015 to August 2016 in three habitat types: i) three open matrix sites dominated by species of Poaceae with sparse trees, hereafter "control pasture"; ii) three sites in an old-growth continuous forest in the Santa Virginia Nucleus of Serra do Mar State Park, hereafter "control forest"; and iii) twelve discrete fragments surrounded by pastures with isolated trees, hereafter "habitat fragments".

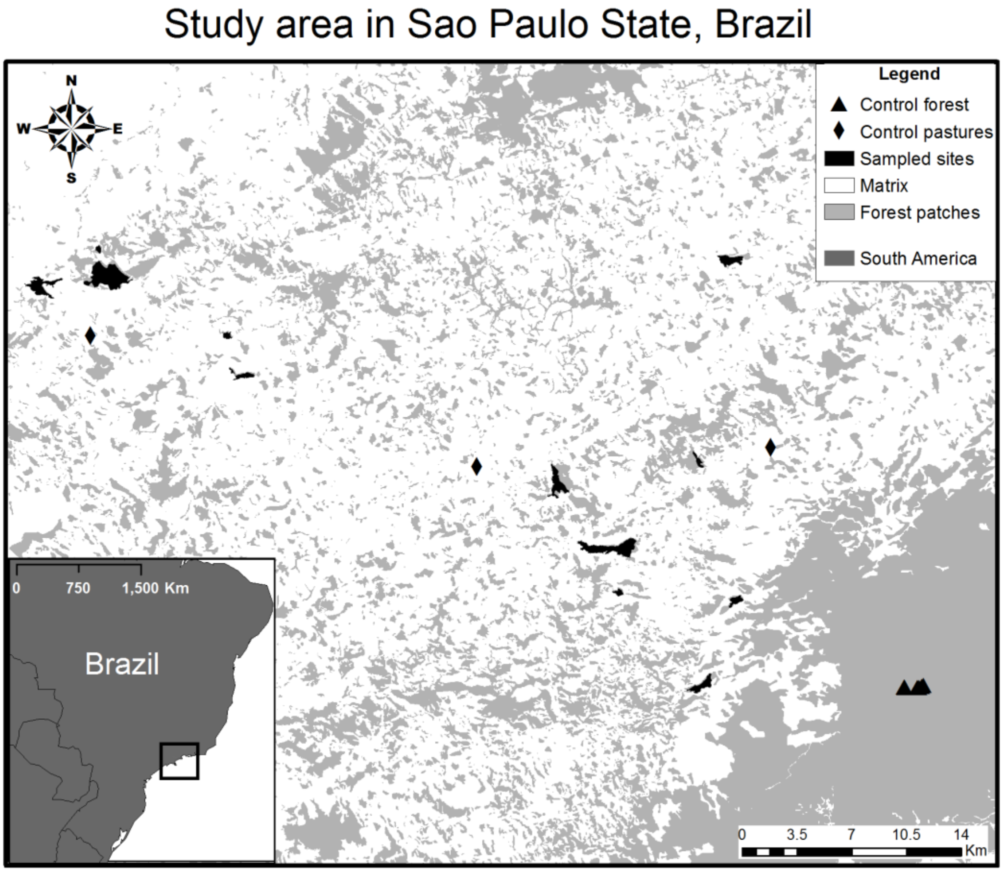
We combined maps provided by "Instituto florestal" (Instituto Florestal do Estado de São Paulo, 2012) and "SOS Mata Atlantica" (INPE, 2014), and from these maps we calculated patch size, connectivity, and forest cover for each site. Patch size and percentage of forest cover were calculated in ArcGIS 10.2 (ESRI Inc, 2014). Forest cover was extracted from radii of 500 m, 1000 m, 1500 m, 2000 m and 3000 m from the centroid of the studied plots (hereafter, FC.500, FC.1000, FC.1500 m, FC.2000, and FC.3000 m). Connectivity was estimated using the proximity index proposed by Whitcomb, et al. (1981) within 800m and 1500m radii in FRAGSTATS 4.2 (McGarigal, Cushman & Ene, 2012).

We obtained data from the "Departamento de Águas e Energia Elétrica" (http://www.hidrologia.daee.sp.gov.br) on the mean monthly rainfall from the past 15 years for seven stations located in the study area. The mean multiannual rainfall for each site was interpolated using the Spline interpolation method in ArcGis 10.2. Elevation was measured directly in the field using the Garmin device GPSMAP 62s.

Measures of habitat structure were represented by diameter at breast height (DBH in cm), tree height (m), and tree density (trees per plot) recorded from trees with DBH ≥10 cm.

2.3.3 Epiphyte sampling

Epiphytes were sampled in the canopy, which is defined as the section of the tree higher than 2 m from the ground until the outer branches. At each site we sampled five trees located in a rectangular plot (tree criteria's selection in Supplementary material 1). In the control forest, three 20 x 200 m plots were set-up. In habitat fragments and control pasture, the individual plot size was 10 x 250 m. The design comprised 18 sites (control pasture = 3, fragments = 12, and control reserve = 3) with five trees per site (n=90 trees). Plots in the fragments were *ca*. 100 m away from the edge (aiming to avoid edge effect), while in control pastures, plots were placed roughly 600 m (SD: 105.5 m) away from the nearest forest patch. Each tree was sampled using single rope technique, complemented with modified mountaineering and free climbing technique. Branches were reached manually up to 5 m from the main trunk, whilst outer branches were inspected by binoculars, and surveyed using a pole when possible. Data from individual trees were combined to conduct all analyses at the plot scale, because not all sampled trees supported epiphytes.



Source: SOS Mata Atlantica and
Instituto Florestal do Estado do Sao Paulo

Figure 2-1. Location of the study area. Forest cover (gray polygons) and matrix (in white) are delimited according to “Instituto florestal” and “SOS Mata Atlantica”. Three forest types were sampled; Control pastures (black triangle); Forest fragments (black polygon), and control forest (black rhombus).

The number of species and individuals were recorded from each tree. Following Sanford (1968) we defined an individual as a set of singular stems spatially separated from another set of stems of the same species. Individuals recorded were classified into three ontogeny stages, seedlings, juveniles and adults according to our expertise and literature from local floras. Seedlings were recognized as generally small-sized individuals, with radicle (embryonic root), hypocotyl (embryonic shoot), and cotyledons. Juveniles were considered as individuals with differentiated tissues like stem and or pseudobulbs, a developed root system, with an absence of floral structures and few individual plants per stand. Adult plants were identified as all individuals with evidence of developed floral structure, large ramets, many plants per stand and prominent root systems. Differentiation between ontogeny stages is difficult in the field and we recognised that potential errors might have occurred. However, we aimed to reduce systematic errors by validating our field observations with footage taken in the field (over 3000 photos and 6 hours of video). All dubious individuals were discarded. Species determination was conducted following specialized literature and consultancy of experts. Nomenclatural standardisation was based on "The Plant List" database names (The Plant List, 2010).

2.3.4 Statistical analysis

Total number of species, total abundance per plot and community composition were used as response variables. Abundance and species richness were log-transformed (log10 + 1) to improve normality. We measured community composition by using a Principal Coordinates Analysis (PCoA) based on Sørensen dissimilarity index calculated on a presence/absence matrix. We tested PCoA axis 1-3. canonical correspondence analysis -CCA was also tested, but due to high values (VIF> 35.91 before model selection; VIF= 18.20 after model selection; table S1) we did not use the outcome. Furthermore, CA and CCA are recommended when species display unimodal relationships with environmental gradients (ter Braak, 1985), which is revealed by a peak of abundance or presence when the optimal conditions are met. However, studies in human-modified landscapes have shown thresholds patterns or non-linear relationships with environmental variables at community level (e.g. Mascarenhas & Mariano-neto, 2014; Banks-Leite *et al.*, 2014; Martensen *et al.*, 2012).

We conducted a one-way analysis of variance ANOVA to compare species richness, total abundance, and community composition with habitat type (control pasture, fragments and control forest), followed by a *post hoc* Tukey test. Similarly, an ANOVA model was fitted for tree structure, where averaged tree height (m), averaged DBH (cm), and density (number of trees per plot) were used as response variables versus habitat type. We used Mantel tests to assess the spatial correlation of the community composition between habitats.

To determine which factors influence epiphyte species richness and abundance, we fitted independent linear models with Gaussian distribution family, with one response variable and one explanatory variable at a time. In all models we used averaged tree height per plot as an offset term to account for the effect of tree size in our diversity metrics (Flores-Palacios & García-Franco, 2001). The models included three set of predictors: 1) landscapes, represented by forest cover (relative), proximity index (log10), fragment area (ha); 2) forest structure, from DBH (averaged basal area in meters per plot as a proxy variable for crown area; O'Brien et al. 1995), and tree density (number of trees per plot); and 3) environment, from rainfall (multiannual average), and elevation (m.a.s.l.). Due to the high correlation of predictors within sets (Kendall's test, supplementary material), we aimed to select only one predictor per set. The best predictors were selected based upon adjusted R-squared, visual inspection of diagnostic plots and Akaike's criterion (AIC). Additionally we tested for additive and interaction effects between our set of predictors. However, due to high levels of collinearity (VIF < 10, Burnham & Anderson, 2002), interactions are not shown.

Due to the non-linear trend observed in the PCoA scores of community dissimilarity, we used independent generalized additive models (GAMs), to determine whether our set of predictors do influence community composition. We fitted our models with the maximum likelihood method "ML" and the tensor product smooth *te* on our set of predictors, and the smoothing *k* -term was iteratively tested to get the most parsimonious model. GAM models were compared with explained deviance (dev), estimate degrees of freedom (edf), and ANOVA (F-test) to determine the importance of terms for explaining composition dissimilarity.

To assess the influence of habitat types on ontogeny stages, we performed a nested ANOVA model using the total individuals per ontogeny stage (adult, juvenile and seedlings) as the response variable and habitat type as the explanatory variable. Additionally, we assessed the effect of our set of predictors on different ontogeny stages by fitting independent linear models, as explained before, to each ontogeny stage as the response variable (log10).

2.3.5 *Statistical analyses*

All analysis were conducted with R (R Core Team, 2017) with the packages "vegan" (version 2.2–1, Oksanen et al. 2015), "TaxonStand" (Cayuela *et al.*, 2012), "stargazer" (Hlavac, 2015), and "mgcv" (Wood, 2016).

2.3.6 *Ethic Statement*

Field work in habitat fragments was carried out on private properties with each landowner's permission. Sampling in the control forest was done under the permission COTEC: 260108 – 002.959/2016. We declare no conflict of interest.

2.4 Results

In total we surveyed 90 trees and recorded 173 epiphyte species, belonging to 19 families, including Orchidaceae (56 species) and Bromeliaceae (37 species) as the most common families. We were able to identify 79% of individuals at the species level and the remaining to morphospecies (36 morphospecies). The two most abundant species were *Octomeria gracilis* (579 individuals) and *Pleopeltis hirsutissima* (408 individuals). Tree height differed among habitats (F: 169.8, $p < 0.001$); trees in the control forest were on average the tallest (height = 18.6 m SD +/- 5m), followed by habitat fragments (height = 11.5m, SD +/- 6m) and control pastures (height =7.3m, SD +/- 2.2 m). Tree density and DBH did not differ between HMF and the control forest (F: 5.497, p: 0.341, df: 2; F:26.68, p:

0.379, df: 2, tree density and DBH respectively). Community composition across the fragmented landscape was not spatially auto-correlated (Mantel r: 0.3202, pr: 0.005)

The control forest had the highest richness and abundance among all habitats, with 6057 adult individuals from 155 species belonging to 19 families, followed by HMFs (566 ind/ 33 spp / 5 fam), and control pasture (54 ind/ 2 spp/1 fam). In terms of species richness (F-value: 153.7, $p < 0.001$) and total abundance (F-value: 28.35, $p < 0.001$), the control forest significantly differed from control pasture and HMFs. However, no difference was found between control pasture and HMFs (species richness, Tukey p-adjusted: 0.87; abundance Tukey p-adjusted: 0.99). Additive models showed forest cover as the only significant explanatory variable (table S3).

The first PCoA two axes were not significantly correlated to any environmental variable measured in our study, while PCoA axis three was significantly correlated to forest cover. For this reason, for now on we present the results for axis three only (see Ewers et al., 2017 for similar approach). Community composition significantly differed among habitats (F-value: 31.87 pr <0.001), following the pattern seen in species richness and total abundance. However, unlike species richness and total abundance, community dissimilarity revealed a difference between the control pasture and HMFs (F-value: 31.87 pr <0.001, df: 2; Figure 2-2; **Table 2**2).

The lack of change in species numbers and total abundance among control pasture and HMTFs might be because of the variability among HMTFs, values ranging between 0 and 12 for species richness, and 0 to 173 for total abundance, were three sites did not have a single species. Species identity did change between control pasture and HMTFs, where although we found that species such as *Tillandsia usneoides*, *T. polystachia*, *Polystachia estrellensis*, and *Serpocaulon catharinense* were capable to colonize both control pasture and HMTFs, other species such as *Zygopetalum maxillare*, *Anetium citrifolium*, *Begonia fulvosetulosa* were exclusive to the forest interior.

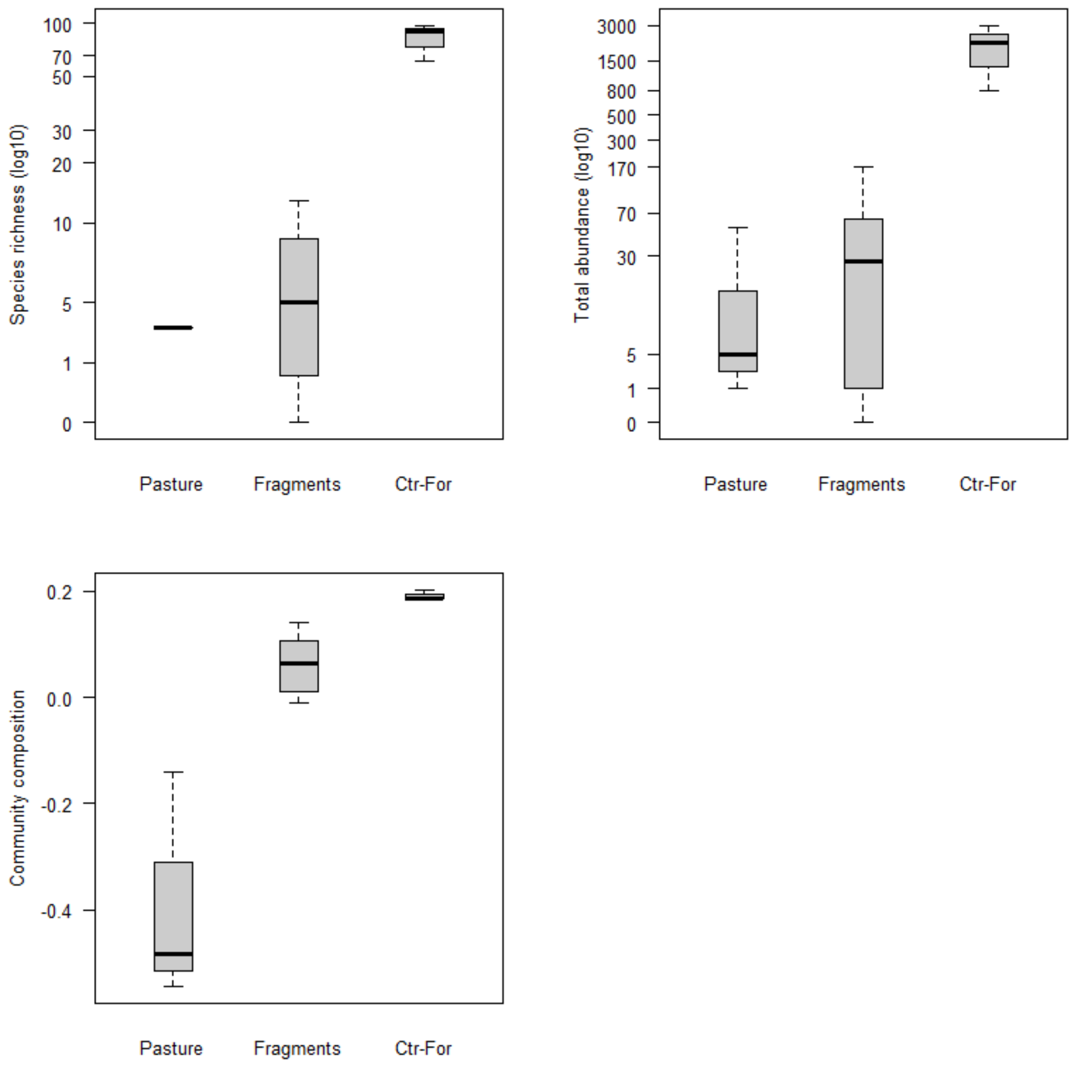


Figure 2-2 Habitat loss effect in (a) number of species, (b) total abundance of adult plants, and (c) community dissimilarity per plot. Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles.

Although species richness and total abundance increased as forest cover increased (FC.1000), this trend became negligible when the control forest was removed from the analysis (Richness t: 0.436, p: 0.6396; Abundance, t: 0.520, p: 0.6115; table S2). Community composition, on the other hand, was positively correlated with forest cover measured at 1000 m (k: 4, dev: 80.5%, edf: 2.543, pr < 0.001; Figure 2-3), and tree height (k: 4, dev: 83.3%, edf: 2.377, pr < 0.001; **Table S4**).

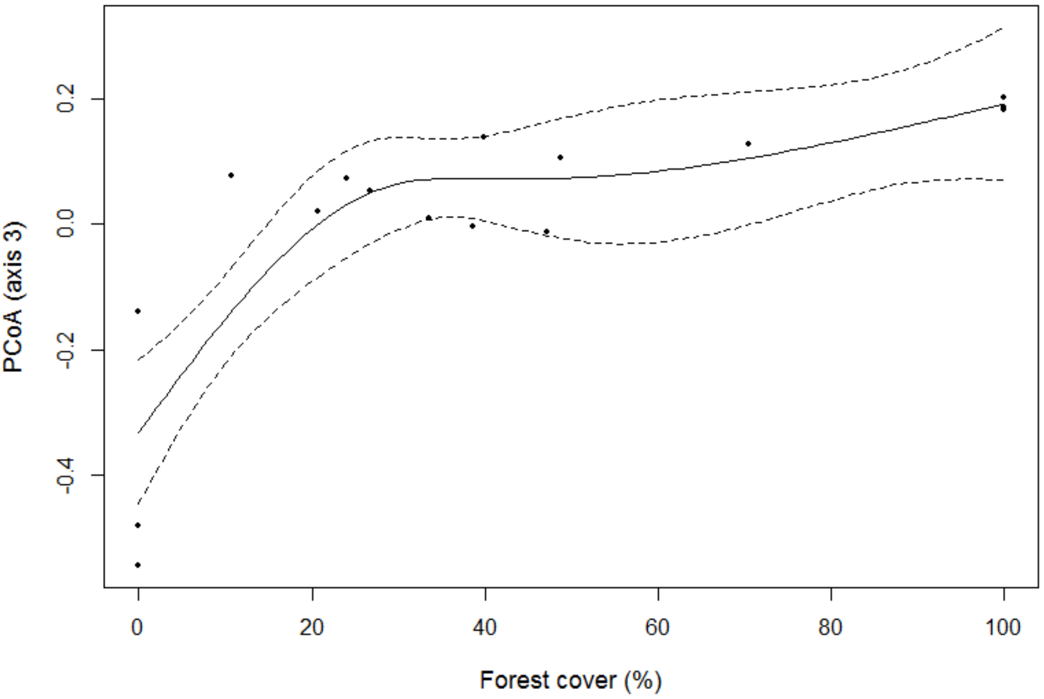


Figure 2-3. Community dissimilarity in vascular epiphytes along the percent of forest cover at 1000 m. Smoothed curves and 95% confidence intervals were obtained from general additive model (see methods).

The control forest had higher abundance of individuals in all ontogeny stages when compared to HMFs and control pastures (ANOVA; F-adults: 28.35; F-juveniles: 157.3; F-seedlings: 195.8; all p <0.001, n: 18, degrees of freedom: 17; Figure 2-4; S5). Seedlings and juveniles were two times more abundant than adults in the control forest (mean; adults: 2019, juveniles: 4439, seedlings: 4120), while in HMFs no significant differences were found among adults, juveniles and seedlings (mean; adults: 47, juveniles: 31, seedlings: 44). No juveniles or seedlings were found in control pastures. Juvenile and seedlings abundance were positively correlated with FC.1000 (t-value: 4.924, t-value: 0.055, p < 0.001, juveniles and seedlings respectively), and tree height (t-value: 5.024, t-value: -3.62, p < 0.001, juveniles and seedlings respectively), but this pattern became negligible when the control forest was removed from the analysis **Table 2**, p < 0.09).

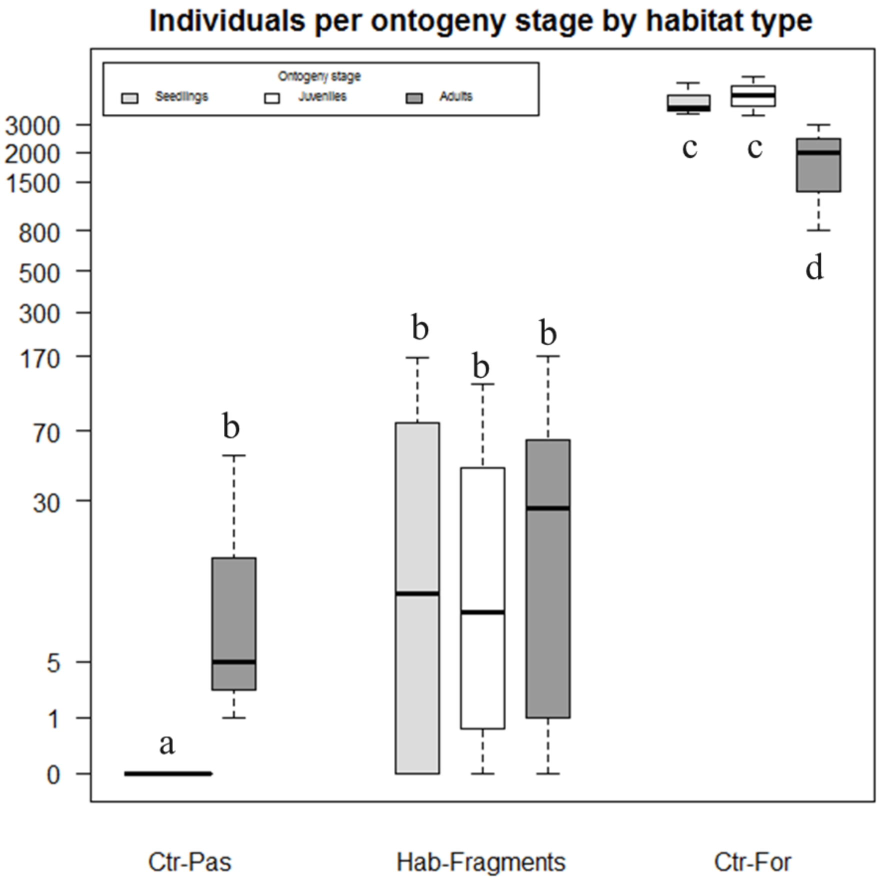


Figure 2-4. Ontogeny stages per habitat type of seedlings (light grey), juveniles (white), and adults (dark grey). Boxes show the median, 25th and 75th percentiles, error-bars show 10th and 90th percentiles. Letters showed the significant difference among stages and habitat types (Tukey HDS, table S4).

2.5 Discussion

Our results show that old growth forests provide a unique habitat for epiphytes that simply cannot be replaced by any other habitat, including large connected patches in human modified forests. The epiphyte community lost 81% of species, 91% of adult individuals, and suffered a drastic shift in species composition from old-growth to HMF. Low numbers of juvenile individuals to be recruited in HMFs is only going to exacerbate these differences in future. These dramatic impacts of habitat disturbance on forest species reinforce the idea that pristine or old-growth forests have unparalleled role in sustaining biodiversity in the tropics (Gibson *et al.*, 2013).

We have likely found one of the most detrimental effects of habitat modification on species richness and total abundance ever recorded at the landscape scale. Several meta-analyses have shown the adverse impact of human modification of the landscape on different taxa, but never to this extent. Newbold et al. (2015) modelled globally a net loss of 76.5% in species richness and 39.5% total abundance under human pressures, whilst Haddad et al. (2015) found a decrease of 13-75% in species richness of terrestrial plants, arthropods and birds in fragmentation experiments at global scale. Barlow et al. (2007), on the other hand, found that just 25% of the species pool in HMFs was unique to the Amazon primary forests. Plus, the magnitude of species net loss is comparatively higher than in others epiphyte studies, at local scale (up to 70%; Nöske et al., 2008; Köster et al., 2009), and landscape scale (65%; Köster, Nieder & Barthlott, 2011). Our findings point out that this net loss can go beyond these figures in the Atlantic Forest of Brazil. We found for instance, that several groups were absent in HMFs; orchids with pseudobulbs (*Xylobium variegatum*, *Zygopetalum maxillare*, species that may demand long time to develop, Stern, 2014); Hymenophyllaceae species (highly humidity-dependent species; Morton, 2015); and bird-dispersed species (e.g. Araceae, Gesneriaceae; Sheldon & Nadkarni, 2013).

Contrary to the trend found in terrestrial plants, forest area, connectivity and forest cover did not exert a positive effect on species richness or abundance in vascular epiphytes. For instance, Mascarenhas & Mariano-neto (2014) and Rocha-Santos et al. (2017) found in the Atlantic forest that forest cover has a positive effect on tree richness and abundance either linearly or showing threshold at 30% forest cover. Similarly, our results differed from the few available studies elsewhere testing the effect of landscape properties on epiphytes. Reid et al. (2016) showed that trees embedded in high forest cover landscapes hosted a high number of vascular understory species in Costa Rica, and Pereira Alvarenga & Pôrto (2007) found a positive effect of area and connectivity in Amazonian non-vascular epiphytes species richness. Although speculative, this lack of positive relationship between the landscape and vascular epiphytes is probably due to long history of modification in the Atlantic Forest and the high impact of habitat loss. The Atlantic forest has being drastically altered over the last 500 years, only 11% of the original forest remains (Ribeiro *et al.*, 2009) and fragments are within 1000 m of a forest edge (Haddad *et al.*, 2015b). Consequently, disturbance leads to a simplification in microhabitats along the vertical axis and among tree crowns were host trees are young, slim and fast-growing (Acebey *et al.*, 2003). This disturbance might have impacted propagule availability (Cascante-Marn *et al.*, 2009), resource availability (Ruiz-Cordova, Toledo-Hernández & Flores-Palacios, 2014), and provision of forest microhabitats for attachment, germination and establishment (González del Pliego *et al.*, 2016).

In terms of community composition, our results show that communities of HMFs might converge to communities in the control forest above 30% forest cover. Nonetheless, the lack of gaining species with forest cover, forest area, and connectivity, the low number of shared species with the control forest (15 spp), and the abundance of species associated to disturbed areas, such as *Pleopletis hirssutisima*, *P. pleopeltifolia* (species that tolerate water loss of 97%; Müller, Starnecker, & Winkler, 1981), *Serpocaulon* spp. and the Tillandsoids group (drought-tolerant species; Zotz, 2016), might suggest those species are consequence of extinction debt (Halley *et al.*, 2016).

The high species and abundance net loss, the dominance of generalist species in forest interiors, and the change in the ontogeny stage pattern between HMFs and control forest, might position vascular epiphyte plants as the most threatened taxa so far studied. Although this has been previously suggested by Zotz (2016) and Leão et al. (2014), our results go further by exploring the consequences of habitat disturbance on ontogeny stages. The observed pattern of total absence of early ontogeny stages in pastures and low abundance of seedlings and juveniles in HMF (contrasting to the control forest) might indicate that despite the resilience of adult individuals, HMF cannot provide enough resources to sustain the early ontogeny stages needed to maintain communities in the long term. This can potentially create a bottleneck for these populations in the future (Halpern, Gaines & Warner, 2005), specially due to the high seedling mortality of not-drought tolerant species (Winkler, Hülber & Hietz, 2005; Mondragón *et al.*, 2015). After all, the presence of a species does not imply a viable population in the future, resembling Janzen's 'living deads' definition (Janzen, 2001).

Preserving the remnant continuous forest seems to be the only option at the moment to preserve regional species pool. Our findings suggest that epiphytes are undergoing extinctions at the local and regional level in HMFs of the Atlantic Forest. The local extinction of vascular epiphytes have a cascading effect on other functional groups such as birds (Cruz-Angón & Greenberg, 2005), invertebrates (Cruz-Angón, Baena & Greenberg, 2009), herpetofauna (McCracken & Forstner, 2014), and mammals, therefore we expect reductions in ecosystem functioning. Other functions are also reduced as consequence of local epiphytes extirpations, such as CO2 sequestration via biomass production, interception, storage and evapo-transpiration of atmospheric water, and reduction in light along a strata (Gotsch, Nadkarni & Amici, 2016; and Zotz, 2016).

2.6 Supplementary material

2.6.1 *Tree selection*

Trees for canopy sampling were selected based on six criteria; i) healthy trees, and from ground inspection, ant, termite, bee and wasp colonies free; ii) trees with more than 90 cm of diameter at breast height (DBH); iii) positioned in an area with >20% of inclination from the ground; iv) as epiphytes show little host-species specificity trees of different species are preferred within each plot; v) low percent of liana cover; and vi) separated by a minimum distance of 10 m.

Table S1. variance inflation factor for canonical correspondence analysis -CCA- on community composition. Highlighted in grey variables after model reduction.

Variable	**VIF**
Habitat type (HMTF)	486.442.171
Habitat type (Ctr-Pas)	260.296.566
fc.1000	2.752.318.830
area.ha	916.606.466
p8	197.544.699
h.tree	543.453.442
elevation	35.906.967
pre	102.632.921
Habitat type (HMTF)	18.197.736
Habitat type (Ctr-Pas)	4.969.714
fc.1000	21.703.850

Table 2. Results for independent linear regression models on the number of species and total abundance recorded at the three habitat types. Regression models significant at $p \leq 0.05$ are marked with a star next to the estimate parameter. Standard error of the estimate and constant are also included, and adjusted r2. Highlighted in grey the best predictor per set.

		Pasture- HMTF -Control			**Pasture- HMTF**		
	Predictors	**Slope**	**t-value**	**Adj. R2**	**Slope**	**t-value**	**Adj. R2**
Species richness (log10)	FC.500	0.016	2.502	0.442	-0.008	-0.860	0.66
	FC.1000	***0.020****	***3.000***	***0.556***	***-0.009***	***-0.690***	***0.66***
	FC.1500	0.023**	3.420	0.62	-0.12	-1.360	0.69
	FC.2000	0.023**	3.469	0.635	-0.156	-0.280	0.69
	FC.3000	0.024**	3.669	0.656	-0.15	-1.650	0.71
	Area	0.004**	3.010	0.595	-0.008	-1.120	0.72
	Proximity.800	0.339*	2.630	0.463	*NC*	*NC*	*NC*
	Proximity.1000	0.335*	2.570	0.456	*NC*	*NC*	*NC*
	Tree.area	-0.002	0.383	0.063	0.012	0.620	-0.07
	Tree.den	-0.001	-0.061	0.1	0.029	0.042	-0.08
	Tree.H	***0.111******	***2.806***	***0.515***	***-0.099***	***-1.320***	***0.67***
	Elevation	0.003	2.570	0.295	0.005	2.340	0.4
	Rain	0.009	0.980	0.318	-0.007	-1.060	0.69
Total abundance (log10)	FC.500	0.037*	2.502	0.391	0.00072	0.029	0.47
	FC.1000	***0.040*****	***3.005***	***0.466***	***0.001287***	***0.042***	***0.483***
	FC.1500	0.044*	3.424	0.525	-0.1516	-0.120	0.497
	FC.2000	0.045*	3.469	0.529	0.0188	0.593	0.49
	FC.3000	0.046*	3.669	0.553	0.02627	0.710	0.5
	Area	0.007*	3.007	0.455	-0.01	-0.670	0.52
	Proximity.800	0.743*	2.625	0.403	*NC*	*NC*	*NC*
	Proximity.1000	0.734*	2.567	0.394	*NC*	*NC*	*NC*
	Tree.area	0.003	0.383	0.02	0.021	0.600	-0.093
	Tree.den	-0.0002	-0.061	-0.014	0.04	0.033	-0.11
	Tree.H	***0.238****	***2.805***	***0.448***	***0.0002***	***0.001***	***0.48***
	Elevation	0.009	2.568	0.32	0.0115	2.920	0.38
	Rain	0.011	0.980	0.089	-0.02	-1.750	0.571

Continuation
table S1

		Pasture-HMTF-Control			Pasture- HMTF		
	Predictors	**Slope**	**t-value**	**Adj. R2**	**Slope**	**t-value**	**Adj. R2**
Juveniles (log10)	FC.500	0.059***	4.173	0.6	0.02	1.09	0.71
	FC.1000	***0.062****	***4.924***	***0.67***	***0.025***	***1.15***	***0.71***
	FC.1500	0.066***	5.805	0.736	0.038	1.54	0.73
	FC.2000	0.067***	5.937	0.743	0.041	1.47	0.73
	FC.3000	0.067***	6.196	0.758	0.047	1.57	0.73
	Area (ha)	0.012***	5.274	0.691	0.001	0.119	0.69
	Proximity 800 m	0.970***	3.047	0.448	*NC*	*NC*	*NC*
	Proximity 1500m	0.970***	3.033	0.446	*NC*	*NC*	*NC*
	Tree area	0.008	0.827	0.058	0.041	1.12	0.14
	Tree density	0.005	0.096	-0.024	0.05	0.037	0.091
	Tree height	***0.383****	***5.024***	***0.686***	***0.147***	***0.97***	***0.71***
	Elevation	0.005	1.309	0.097	0.013	3.02	0.46
	Precipitation	0.025	1.989	0.237	-0.02	-1.21	0.71
Seedlings (log10)	FC.500	0.053***	-2.025	0.471	0.007	0.337	0.61
	FC.1000	***0.055****	***-2.035***	***0.524***	***0.00001***	***0.003***	***0.61***
	FC.1500	0.060***	-2.313	0.589	0.011	0.31	0.62
	FC.2000	0.060***	-2.235	0.59	0.008	0.24	0.61
	FC.3000	0.062***	-2.311	0.624	0.017	0.46	0.61
	Area	0.011***	-1.679	0.622	0.0024	0.22	0.61
	Proximity 800 m	0.851**	-1.435	0.339	*NC*	*NC*	*NC*
	Proximity 1500m	0.853**	-1.448	0.339	*NC*	*NC*	*NC*
	Tree area	0.009	-0.438	0.068	0.042	1.68	0.14
	Tree density	0.001	0.272	-0.017	0.1	0.07	0.05
	Tree height	**0.379*** **	**-3.62**	**0.639**	**0.17**	**0.96**	**0.64**
	Elevation	0.004	-0.831	0.049	0.012	2.08	0.36
	Precipitation	0.025	-1.558	0.228	-0.01	-0.78	0.62

Table S3. Results for additive linear regression models on the number of species and total abundance recorded at the three habitat types. Regression models significant at $p \leq 0.05$ on 14 degrees of freedom. Estimates and adjusted r2 are also included. Highlighted in grey the best predictor.

		Pasture-HMTF-Control		
Response variable	**Predictors**	**Estimate**	**t-value**	**p-value**
Species richness (r2= 0.44)	***FC.1000***	***0.039***	***3.537***	***0.003***
	Tree area	-0.004	-0.96	0.353
	Precipitation	-0.004	-0.563	0.582
Total abundance (r2= 0.55)	***FC.1000***	***0.072***	***3.308***	***0.0052***
	Tree area	-0.006	-0.698	0.467
	Precipitation	-0.017	-1.151	0.269

Table S4. Results for independent generalised additive models on community dissimilarity. Analysis based on the principal coordinate analysis axis 3, and percent landscape, forest structure and environmental predictors. Regression models significant at $p \leq 0.05$ are marked with a star next to the estimate parameter. Standard error of the estimate and constant are also included, and adjusted r^2. Highlighted in grey the best predictor per set.

	Predictors	**edf**	**F-value**	**p-value**	**R2**	**deviance**
Community composition	FC.500	2.542675	18.42476	0.000035***	0.77	80.5
	FC.1000	*2.64549*	*13.19897*	0.000363***	*0.78*	*79.3*
	FC.1500	2.675	15.71	0.000126***	0.74	78.4
	FC.2000	2.721427	14.87386	0.000179***	0.72	77.6
	FC.3000	2.708048	13.11369	0.000404***	0.69	75.3
	Area (ha)	2.848068	8.043562	0.002305***	0.62	69
	Proximity 800 m	2.393078	14.74065	0.000191***	0.74	76
	Proximity 1500 m	2.393	14.85	0.00018***	0.72	76.2
	Tree area	2.472993	21.18726	0.00002***	0.79	82.3
	Tree density	2.81916	15.56703	0.000139***	0.74	78.6
	Tree height	*2.376505*	*23.9872*	0.00005***	*0.8*	*83.3*
	Elevation	1.966249	1.797982	0.202835	0.17	27.8
	Precipitation	1.353234	0.17063	0.710108	-0.02	6.9

Table S5. Statistical summary of the interaction of abundance, habitat type and ontogeny stage. Tukey multiple comparisons of means 95% family-wise confidence level

set 1			set 2		diff	lwr	upr	p-adj
Ctr-For	Adults	vs	Seedlings	Ctr-Pas	2.02E+03	1007.64	3030.36	1.9E-06
Ctr-For	Adults	vs	Juveniles	Ctr-Pas	2.02E+03	1007.64	3030.36	1.9E-06
Ctr-For	Adults	vs	Adults	Ctr-Pas	2.00E+03	989.6399	3012.36	2.3E-06
Ctr-For	Adults	vs	Seedlings	HMTF	1.98E+03	1175.783	2774.884	0
Ctr-For	Adults	vs	Juveniles	HMTF	1.99E+03	1188.533	2787.634	0
Ctr-For	Adults	vs	Adults	HMTF	1.97E+03	1172.283	2771.384	0
Ctr-For	Adults	vs	Seedlings	Ctr-For	-2.10E+03	-3113.03	-1090.31	8E-07
Ctr-For	Adults	vs	Juveniles	Ctr-For	-2.42E+03	-3431.36	-1408.64	0
Ctr-For	Juveniles	vs	Seedlings	Ctr-Pas	4.44E+03	3427.64	5450.36	0
Ctr-For	Juveniles	vs	Juveniles	Ctr-Pas	4.44E+03	3427.64	5450.36	0
Ctr-For	Juveniles	vs	Adults	Ctr-Pas	4.42E+03	3409.64	5432.36	0
Ctr-For	Juveniles	vs	Seedlings	HMTF	4.40E+03	3595.783	5194.884	0
Ctr-For	Juveniles	vs	Juveniles	HMTF	4.41E+03	3608.533	5207.634	0
Ctr-For	Juveniles	vs	Adults	HMTF	4.39E+03	3592.283	5191.384	0
Ctr-For	Juveniles	vs	Seedlings	Ctr-For	3.18E+02	-693.027	1329.694	0.981
Ctr-For	Seedlings	vs	Seedlings	Ctr-Pas	4.12E+03	3109.307	5132.027	0
Ctr-For	Seedlings	vs	Juveniles	Ctr-Pas	4.12E+03	3109.307	5132.027	0
Ctr-For	Seedlings	vs	Adults	Ctr-Pas	4.10E+03	3091.307	5114.027	0
Ctr-For	Seedlings	vs	Seedlings	HMTF	4.08E+03	3277.45	4876.55	0
Ctr-For	Seedlings	vs	Juveniles	HMTF	4.09E+03	3290.2	4889.3	0
Ctr-For	Seedlings	vs	Adults	HMTF	4.07E+03	3273.95	4873.05	0
Ctr-Pas	Adults	vs	Seedlings	Ctr-Pas	1.80E+01	-993.36	1029.36	1
Ctr-Pas	Adults	vs	Juveniles	Ctr-Pas	1.80E+01	-993.36	1029.36	1
Ctr-Pas	Juveniles	vs	Juveniles	Ctr-Pas	4.26E-13	-1011.36	1011.36	1
Fragments	Adults	vs	Seedlings	Ctr-Pas	4.72E+01	-752.384	846.717	1
Fragments	Adults	vs	Juveniles	Ctr-Pas	4.72E+01	-752.384	846.717	1
Fragments	Adults	vs	Adults	Ctr-Pas	2.92E+01	-770.384	828.717	1
Fragments	Adults	vs	Seedlings	HMTF	3.50E+00	-502.18	509.1801	1
Fragments	Adults	vs	Juveniles	HMTF	1.63E+01	-489.43	521.9301	1
Fragments	Juveniles	vs	Seedlings	Ctr-Pas	3.09E+01	-768.634	830.467	1
Fragments	Juveniles	vs	Juveniles	Ctr-Pas	3.09E+01	-768.634	830.467	1
Fragments	Juveniles	vs	Adults	Ctr-Pas	1.29E+01	-786.634	812.467	1
Fragments	Juveniles	vs	Seedlings	HMTF	-1.28E+01	-518.43	492.9301	1
Fragments	Seedlings	vs	Seedlings	Ctr-Pas	4.37E+01	-755.884	843.217	1
Fragments	Seedlings	vs	Juveniles	Ctr-Pas	4.37E+01	-755.884	843.217	1
Fragments	Seedlings	vs	Adults	Ctr-Pas	2.57E+01	-773.884	825.217	1

Chapter 3.

The influence of edge effects on vascular epiphytes communities

3 The influence of edge effects on vascular epiphytes communities

3.1 Abstract

Edge effects are ubiquitous landscape processes influencing more than 70% of forests worldwide. However, little is known about how they impact epiphytes, and whether edge effects differentially impact communities in the canopy and understory strata. We sampled vascular epiphytes in the canopy of 270 trees and on the trunks of 3,127 trees in the Brazilian Atlantic Forest, to quantify the magnitude and extent of edge effects. Our results show that although understory stratum has low species richness and abundance, the community experienced similar magnitude of edge effects than the canopy community. The extent of edge effects was found to be at least 500 m, which means that just 0.24% of the forest present in the fragmented landscape studied was not affected by edge effects. We then extrapolated our findings to the whole realm of the Brazilian Atlantic Forest, and found that just 19.4% not affected by edge effects (3.3 Mha) and can therefore be considered habitat for epiphytes. Furthermore, the resources provided by the current forest fragments and the landscape itself might be insufficient to support future abundances of forest-dependant species, hence preserving large continuous “intact” forests are probably the only pragmatic conservation strategy for vascular epiphytes in highly human-modified landscapes.

3.2 Introduction

The world's old-growth forests currently account only for 18-24% of total forest cover (Intact Forest Landscape, Potapov et al., 2017; Human Footprint, Venter et al., 2016). Across human-modified forests, habitat disturbance manifests itself through changes in habitat area, connectivity and importantly, edge effects (Haddad *et al.*, 2015a). Edge effects are a landscape process that create abiotic changes that deeply affect forest dynamics and may cause both positive and negative effects to the biotic component (Pfeifer *et al.*, 2017; Banks-Leite, Ewers & Metzger, 2010; Ries *et al.*, 2017; Ewers & Banks-Leite, 2013; Williams-Linera, Domínguez-Gastelú & García-Zurita, 1998). Edge effects are an ubiquitous consequence of fragmentation and causes dramatic effects on fauna and flora (Ewers & Didham, 2008; Pfeifer *et al.*, 2017; Benchimol & Peres, 2015). To fully understand impacts of anthropogenic habitat disturbance on biodiversity and ecosystem functions, it is crucial that the magnitude and extent of edge effects are quantified for a large range of taxa (Ewers & Didham, 2006).

The impacts of edge effects can be partitioned into two components – the extent of edge influence (e.g. how far does the influence reach) and the magnitude of edge influence (e.g. how different edge conditions are to interior habitats, Chen, Franklin, & Spies, 1995; Harper et al., 2005). The extent of the edge effect has been shown to reach up to 1 km into forest habitat (Ewers & Didham, 2006; Pfeifer *et al.*, 2017), which dramatically reduces the amount of habitat for forest-dependant species given that nearly 70% of the world's remaining forests are within 1 km of an edge (Haddad *et al.*, 2015a). A large magnitude of edge effects has been detected in mortality rates of trees (Laurance *et al.*, 1998), as well as species richness, abundance and community composition of several taxa (Harper *et al.*, 2005; Peyras *et al.*, 2013). One of the major consequences of large extent and magnitude of edge effects is biotic homogenization, which is the replacement of local biota with non-indigenous species, or the replacement of local unique endemic species by species with large geographic ranges (McKinney & Lockwood, 1999). Biotic homogenization has a profound effect on ecosystem functioning via the disruption of food-web structures (Olden *et al.*, 2004), reduction of functional richness (Tabarelli, Peres & Melo, 2012) or shifts in ecosystem functions (De Coster, Banks-Leite & Metzger, 2015).

Various approaches have been proposed to quantify these two components of edge effects (Harper & Macdonald, 2011; Ewers & Didham, 2008); however, none could be reliably used to quantify edge effects in habitat fragments, where the presence of multiple edges interact to increase both extent and magnitude (Ewers & Didham, 2006; Banks-Leite, Ewers & Metzger, 2010; Malcolm, 1994). Recently, Lefebvre et al. (2016) developed a novel approach to estimate the impact of edge effects on species abundance and map them across landscapes. This approach incorporates a spatially-explicit model to integrate the potential spill-over effects from different habitats, distance from nearby edges, and the treatment of habitat quality as a spatial continuum. This approach overcome the issues regarding the synergistic effects of landscape elements and allows for the identification of species-specific responses (Ries *et al.*, 2017).

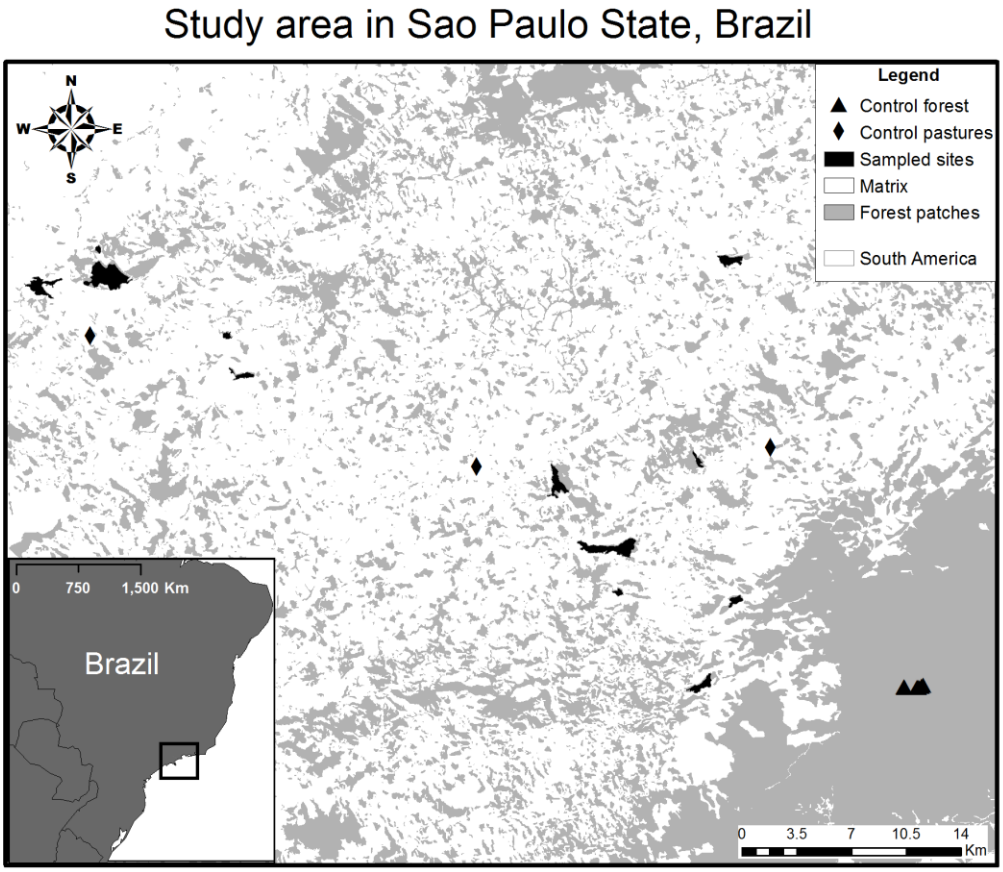
The reason why it is so advantageous to identify species-specific responses is that some species thrive in edge habitats (Mascarúa López, Harper & Drapeau, 2006; Harper & Macdonald, 2011), whereas others, such as the species-dependent on forest interior conditions, may become locally extinct (Tabarelli, Peres & Melo, 2012). Vascular epiphytes, i.e. plants that establish a commensal relationship with their host (Schimper, 1903), are no exception. Previous studies have shown increasing species richness at edges (Bernardi & Budke, 2010), whilst others revealed a reduction of species richness and abundance near edges (Bianchi *et al.*, 2014; Dias-Terceiro *et al.*, 2015; Parra-Sánchez, Armenteras & Retana, 2016). It is possible however that whether an epiphyte is positively or negatively affected is due where it is found along the forest's vertical axis - canopy and understory (Silva & Pôrto, 2013; Krömer, Kessler & Gradstein, 2007; Martínez-Meléndez, Pérez-Farrera & Flores-Palacios, 2008; Pos & Sleegers, 2010; Acebey *et al.*, 2003). Canopy communities may be less affected by edge effects than the understory because these species are more exposed to sunlight and wind, and experience longer periods of drought than their understory counterparts (Cervantes, Graham & Andrade, 2005; Didham & Ewers, 2014). The few available studies in edge effects comparing strata have found contradictory results (Normann, Tscharntke & Scherber, 2016; Stone, Catterall & Stork, 2018) (Vodka & Cizek, 2013). However, to our knowledge this has not yet been investigated in Neotropical systems.

Here we quantify the extent and magnitude of edge effects on understory and canopy epiphyte communities in the Brazilian Atlantic Forest (BAF). We specifically asked; what is the magnitude of edge effects on epiphytes, and does it differ between canopy and understory? And, what is the extent of edge effects and what its impact on the wider landscape? For the first question, our expectation is that understory species are more sensitive to edge effects than canopy species. Because the BAF is dominated by small fragments of human-modified forest of which ca. 80% are smaller than 50 ha and are highly isolated from nearby fragments (Ribeiro *et al.*, 2009; Haddad *et al.*, 2015a), we expect the extent of edge effects to be widespread and crossing the entire landscape.

3.3 Methods

3.3.1 Study area

The study area is located in the Brazilian Atlantic Forest (BAF), found within the municipalities of Taubaté, São Luiz do Paraitinga and Lagoinha, in the state of São Paulo (Figure 1). The study area has 28% forest cover in various successional stages, with an average fragment size of 15 ha, and a matrix dominated by pasturelands. The altitude ranges from 860 up to 1,470 m. The vegetation is predominantly characterized by Montane Ombrophilous Dense Forest species (Veloso, Rangel-filho & Alves-Lima, 1991). Studied sites were part of the “Biodiversity and Ecosystem Functioning in Degraded and Recovering Amazonian and Atlantic Forests” (ECOFOR) research project funded by NERC (Grant Number NE/H016228/). Fieldwork was conducted from May 2015 to July 2016 in two control habitats and the fragmented area (**Figure 3-1**).



Source: SOS Mata Atlantica and
Instituto Florestal do Estado do Sao Paulo

Figure 3-1. Map of the study area, showing the locations of fragments and sampling points. Study design Grey areas represent forest fragments, white the matrix, black the sampled forests, hexagons the control forests, and triangles the control matrix.

We designed our study to encompass the full range of habitats available in the landscape. Our sampling included six control sites; three of which were in open matrix sites dominated by species of Poaceae with sparse trees, hereafter "control pasture"; and the remaining three sites were located in an old-growth continuous forest in the Santa Virginia Nucleus of Serra do Mar State Park, hereafter "control forest". In the control pasture, plots were placed roughly 600 m (SD: 105.5 m) away from the nearest forest patch. We also sampled 12 fragments surrounded by pastures with isolated trees, and in each of these fragments, we sampled the interior, edge and adjacent matrix. Interior plots were surveyed at 100 m from the discrete border, and are hereafter referred to as "forest interior". Edge sites were defined at 30 m from the border line of the matrix, and are hereafter referred to as "forest edge", and isolated trees located at up to 100 m away from, and parallel to, the edge, are hereafter referred to as "matrix".

In the fragments' interior and edge plots and in the control pasture we sampled a plot of 10 x 250 m, subdivided into 25 subplots of 10 x 10 m. In the matrix, the sampled plots were placed parallel to the forest fragment preserving the same sample area of 2500 m^2 as the others. In the control forest, however, we surveyed a one-hectare plot (100 x 100 m) per site, with each plot subdivided into 10 subplots of 10 x 10 m each. This difference in protocol was due inconsistencies in ECOFOR's sampling design. In total we sampled 42 plots in 18 sites.

3.3.2 Epiphyte sampling

Epiphytes were sampled in the canopy and understory. The canopy was defined as the portion of the tree from the upper trunk, from the first bifurcation, to the outer branches, not taking mid trunk records. The canopy was sampled throughout Johansson's (1974) tree sections III to V, using single rope technique, complemented with modified mountaineering and free climbing technique. Branches were reached manually up to 5 m from the main trunk, whilst outer branches were inspected by binoculars, and surveyed using a pole when possible.

At each plot we sampled five trees (tree selection criteria in Supplementary material 1). In the fragmented area, the final design comprised 12 sites, with three plots (n=36) and five trees per plot (n=60), whereas the control forest had three sites with one plot per site (n=3), and five trees per plot (n=15).

In the understory, epiphytes up to 2 m high were recorded on trees with <10 cm diameter at breast height (DBH). In each plot, I surveyed ten subplots (10 x 10 m^2) as follows: five subplots where the tree for canopy sampling was surveyed, and an additional five subplots randomly selected within each plot (**Figure 3-2**). In the fragmented area, the final design comprised 12 sites, with three plots (n=36) and ten subplots per plot (n=360), whereas the control forest had three sites with one plot per site (n=3), and ten subplots per plot (n=30).

We recorded the number of species and individuals from each tree. Following Sanford (1968) we defined an individual as a set of singular stems spatially separated from another set of stems of the same species. All individuals in early ontogeny stages and morphospecies were excluded from analysis. Species determination was conducted following specialized literature and consultancy of experts. Nomenclatural standardisation was based on “The Plant List” database names (The Plant List, 2010).

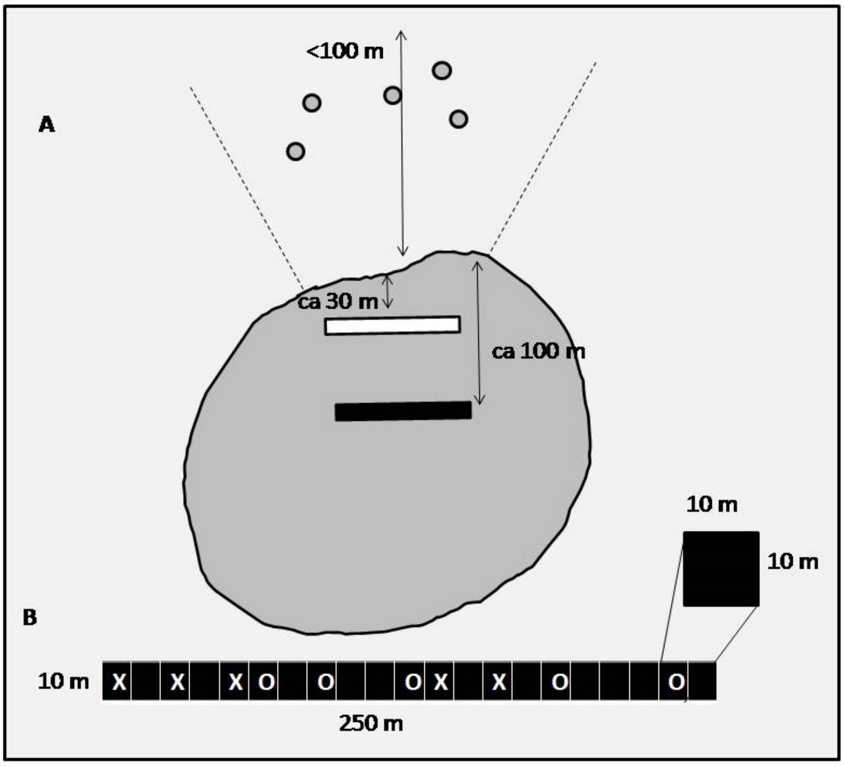


Figure 3-2. Sampling design for the human- modified forests. A) Black rectangle represents interior plot, white rectangle edge plot, arrows the distance from the edge fragment, and grey circles denote isolated trees in the matrix habitat. B) 10 x 250 plot, subdivided into 25 subplots of 10 x 10 m; letters represent an example of the sampling at the understory strata, -X- for canopy sampling and –O- for random sampling.

3.3.3 Response variables

Here we used only information about adult individuals (as they could be identified to species) to calculate species richness and total abundance. Community composition was analysed using species abundance matrix to calculate the Sørensen dissimilarity index from the median distance between each individual site per habitat and the control forest (hereafter community integrity). Community integrity was scaled up from 0-1, where larger numbers represent higher similarity to control forest.

3.3.4 Magnitude of edge effects

To analyse the magnitude, we fitted generalized linear mixed effect models. Observed values of species richness and abundance were modelled with a Poisson and negative binomial distribution respectively at plot scale. As fixed effects, we used three habitat types: forest interior, forest edge, and pasture without interaction term. As random effects, we had intercepts for the fragments to control for spatial dependency. Community integrity was fitted similarly with Gaussian distribution instead, and we test pairwise effects among plots using simultaneous linear hypothesis testing (function glht in R package multcomp; Hothorn, Bretz, & Westfall, 2008). We used likelihood ratio tests to determine parameter significance by comparing models with habitat type to a null model with no predictor. The proportion of variance explained by fixed effects was calculated as marginal R^2 (Nakagawa & Schielzeth, 2013). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity, normality, or spatial autocorrelation.

Additionally, we quantified the variation in species composition along the matrix-edge-interior gradient using non-parametric multivariate analysis of variance (PERMANOVA; Anderson, 2001), using 999 permutations of residuals with the method Bray-Curtis to account for the nested design of our study (plots within fragments).

3.3.5 Extent of edge effect

We mapped and quantified changes in the abundances of epiphyte species at the landscape-scale using the Lefebvre et al. (2016) approach, which allows us to characterize edge response and habitat preference per species based on their abundance. Here we briefly summarize the method, the full description can be found in Pfeifer et al. (2017) and at https://github.com/verol. This approach defines two spatially explicit metrics. The first is edge influence, which assesses the configuration of the landscapes and calculates local variations in percentage of tree cover within a 1-km radius. This metric ranges from 0 (in edge-free pixels) to 100 (pixels surrounded by a different habitat). The value of the edge influence represents a positive, negative, or no effect of edges, where forest habitats near the matrix have a negative value, matrix habitats near the forest a positive one, and values around zero corresponds to either "matrix core" or "forest core", respectively. In practice, edge influence characterises the extent of edge effects at both sides of the edge, and the sign determines the direction of the effect at the pixel level. The second metric is edge sensitivity of species, and this is a measure of preference for a certain habitat type. This metric ranges from 0.0 (no edge-sensitive species) to 1.0 (species exclusive to a particular habitat away from the edge), and the sign determines the direction of the preference (negative if the preference is to the matrix, positive if the preference is towards the forest, and zero towards either matrix core or forest core). Finally, species were categorised based on the most likely response to the edge of each species' abundance of the edge sensitivity of species via a naive Bayesian classifier included in BioFrag®. As follows, i) forest-core species will have a positive value of 1 or near to 1 (i.e. highest abundance in the forest interior); ii) forest-edge (i.e. highest abundance in forest edge); iii) matrix-core species had a value of minus 1 or near to -1 (i.e. highest abundance in matrix interior); and iv) matrix-edge (i.e. highest abundance in the matrix edge).

To assess edge influence and species sensitivity we used the species' abundance matrix and a matrix with the coordinates of our sampling sites. The land cover maps were based on Hansen et al. (2013) map, which defines tree cover as canopy closure for all vegetation taller than 5m, and each pixel has a value between 0 and 100%. We later complemented this map by combining maps provided by "Instituto florestal" (Instituto

Florestal do Estado de São Paulo, 2012), “SOS Mata Atlantica” (INPE, 2014) and MapBiomas (Biomap, 2018), to identify tree cover categories not identifiable from Hansen’s map, i.e. second-growth forests and degraded forests, and tree plantations. We also used a “mask” file that is a binary raster file to exclude urban areas.

We performed the modelling at five distances (250 m, 500 m, 750 m, 1000 m, and 2000 m), and selected the model with the highest rating based on the estimation of “how well the spatial distribution of the census points enables us to assess the species edge response” (Lefebvre, Pfeiffer M. & Ewers, 2016). We calculated the forest core area of the in ArcGIS software (ESRI, 2011) . We performed a one-way analysis of variance ANOVA between “edge Influence” scores and habitat type, followed by a *post hoc* Tukey test.

Finally, we extrapolated our edge influence predictions across the entire 143 million hectares covered by BAF. We used the combined map of “Instituto florestal” (Instituto Florestal do Estado de São Paulo, 2012), and “SOS Mata Atlantica” (INPE, 2014). We calculate the buffer area within forest fragments with discrete borders in ArcGis 10.1®.

3.3.6 Statistical analysis

Statistical analyses were conducted in R (R Core Team, 2017) with the packages “vegan” (version 2.2–1, Oksanen et al. 2015), “TaxonStand” (Cayuela *et al.*, 2012), “lme4” (Bates *et al.*, 2015), “MuMIn” (Barton, 2013), and “multcomp” (Hothorn, Bretz & Westfall, 2008). Extent was calculated with BioFrag (Lefebvre, Pfeiffer M. & Ewers, 2016),

3.3.7 Ethic statement

Fieldwork in the human-modified forests was carried out on private properties with each landowner’s permission. Sampling in the control forest was done under the permission COTEC: 260108 – 002.959/2016. We declare no conflict of interest.

3.4 Results

In total 270 trees in the canopy and 3,127 trees in the understory were surveyed. We found 14,489 individuals of epiphytes from 210 species, belonging to 18 families, including Orchidaceae (82 species) and Bromeliaceae (48 species) as the most common families. The most abundant species were *Pleopeltis hirsutissima* (1,375 individuals) and *Octomeria gracilis* (1,080 individuals).

The control forest hosted 167 species in total, 83% exclusive to this habitat type (154 spp), followed by forest interior with 55 spp in total and 18% exclusive (10 spp), forest edge with 33 spp and 15% exclusive (5 spp), and 18 spp in the matrix with just one spp exclusive to this habitat type. Seven species were found in all habitats i.e. *Aechmea vanhoutteana*, *Pleopeltis hirsutissima*, *Serpocaulon catharinae*, *S. latipes*, *Tillandsia gardneri*, and *T. geminiflora*. On the other hand, ten IUCN threaten species were exclusive of the reserve e.g. *Tillandsia polystachia*, *Rhipsalis crispata*, *Codonanthe carnosa*, *Nematanthus crassifolius*, *Cirrhaea loddigesii*, *Peperomia quadrifolia*, *P. subrubrispica* (Secretaria De Estado Do Meio Ambiente, Resolução Sma No 057, 2016).

3.4.1 *Magnitude in HTMF*

For the human-modified forests, we did not find significant differences between edge and interior at either canopy or understory species richness or abundance (Figure 3-3 and Table 3), despite the fact that we did not find a single individual in four of the edge sites in either strata. The only significant difference found was an increase in total abundance the canopy in the matrix (z= 3.7, $chi^2 = 4523$, p< 0.0001, marginal R^2= 55.1%; Figure 3-3).

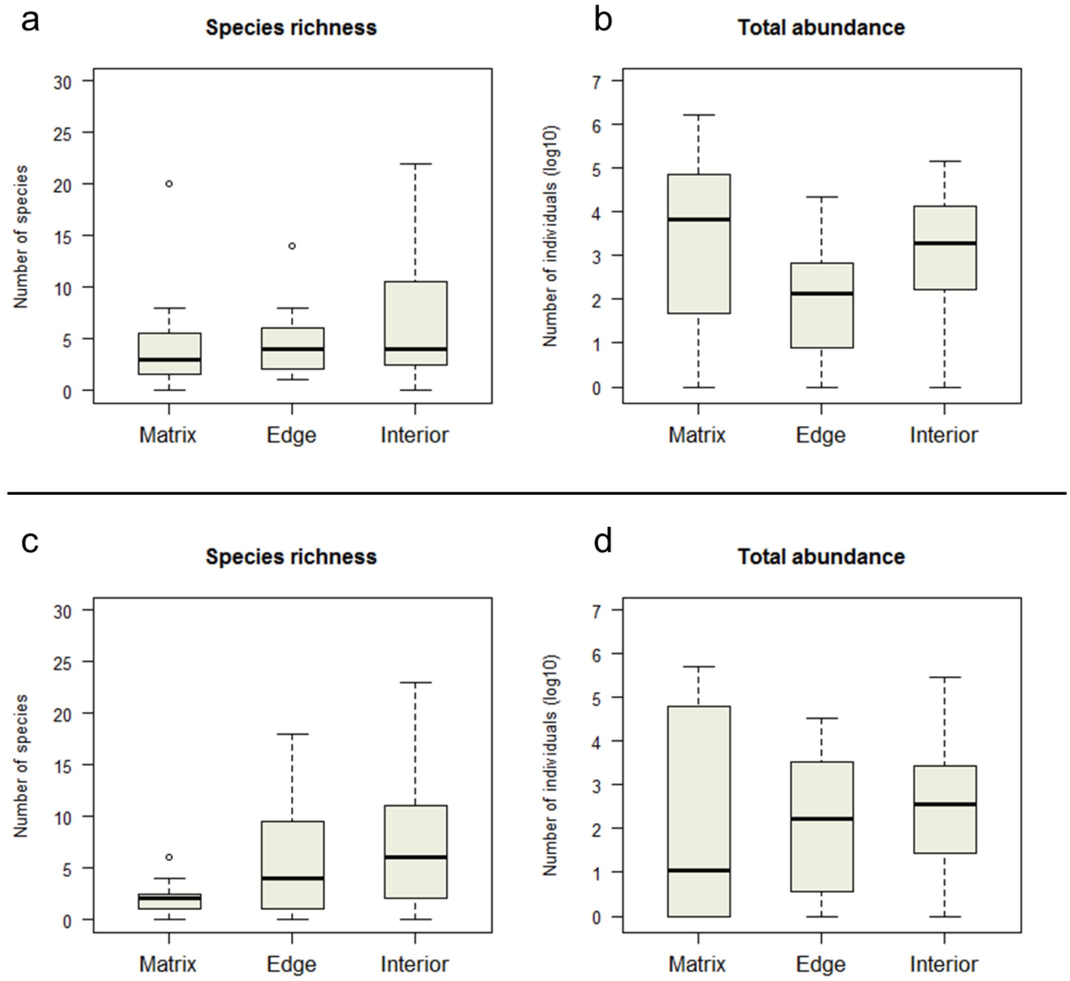


Figure 3-3. Species richness and total abundance of adult individuals along the canopy (A and B, respectively), and understory stratum (C and D, respectively) in HTMFs. Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles and points indicate the outliers. Ctr-Pas represents control pasture; Interior, forests interior; and Edge, is forest edge.

3.4.2 Community integrity

All habitats were significantly different from control forest communities (i.e. $p< 0.001$; Table 4 and Figure 3-74), showing that communities inhabiting the fragmented landscape have a poor resemblance to the communities in the control forest. Community integrity was consistently higher in forest interiors, then followed by edges, the matrix and controls pastures (note we did not find understory species in control pasture; Figure 3-74 and Table 4). All pairwise comparisons both at canopy and understory were not significantly different (Table 4, $p > 0.05$), showing that community composition does not change along the gradient.

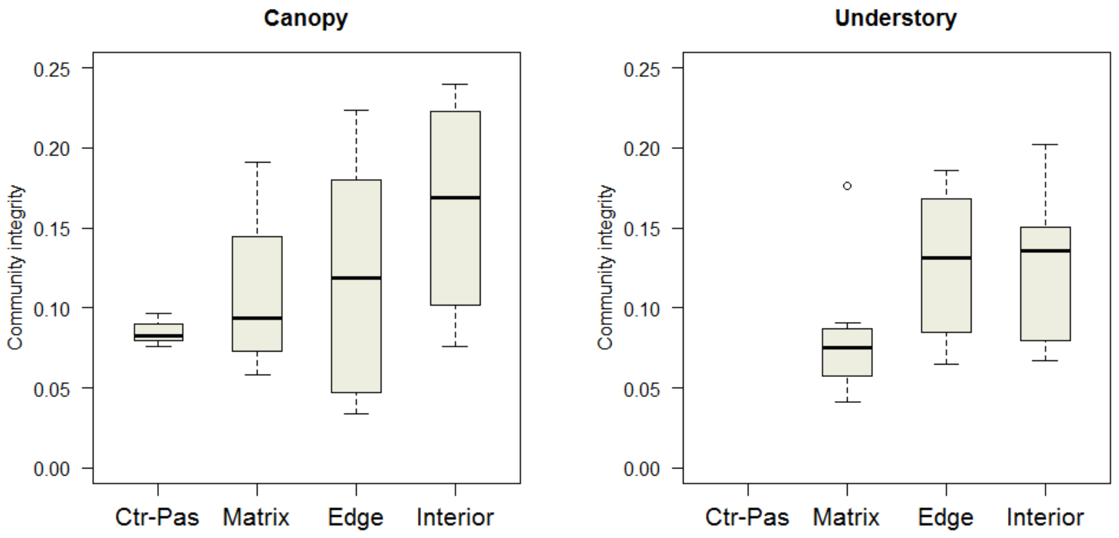


Figure 3-4. Community integrity in the canopy and understory strata. Control forest is taken as the comparison habitat type as community dissimilarity integrity with values is 1. Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles and points indicate the outliers. Ctr-Pas represents control pasture; Interior, forests interior; and Edge, is forest edge.

3.4.3 Extent of edge effect

We estimated that the edge extent reaches up to at least 500m (rating: 0.97; **Figure 3-5**) using BioFrag®. We found that the area unaffected by the edge is *ca.* 18,100 ha (6.96%), corresponding to 17,370 ha in the control forest (6.2% of the total landscape), and just 725 ha in the fragmented area (0.74% of the total landscape).

The edge influence (*EI,* Figure 3-5), the first metric assessing the configuration of the landscape and values ranges between 0 (in edge-free pixels) to 100 (pixels surrounded by a different habitat), shows that the control forest was practically unaffected by the edge influence (*EI* value: 1.4, SD +/- 0.02). We found a positive edge influence in the forest matrix and control pasture plots (matrix *EI value*: 26.9 SD +/- 6.3; ctr-pas *EI value*: 20.8 +/- 6.2). Forest edge and forest interior plots were negatively affected by the edge (mean, edge *EI value*: -21.9 SD +/- 9.3; interior *EI value*: -37.7 SD +/- 5.2).

The second metric, edge sensitivity, allowed us to categorised species based on their preference to a habitat. Species that rely on forest interior conditions so called “forest core species” were the most representative group in the canopy (83%, 149 spp), followed by forest edge (11 spp), and matrix edge species (3 spp). In contrast, the understory stratum was dominated by forest-edge species (50%, 36 spp), with 32% (25 spp) of its species considered forest core and 12.7% of its species (9 spp) considered matrix edge species. Matrix core species were restricted to the canopy with just one species.

Currently the Brazilian Atlantic Forest has only 17.5 Mha of forest (roughly 12% of its original extent of 143 Mha; Table 5), as remnants and regrowth. If we consider an edge extent of 500 m across the entire realm, then just 19.4% of this vegetated area can be considered core area (3.3 Mha). Nonetheless, much of this core area is found within large protected areas. If we consider just the fragments (c.a. 265.000), only 1.7% (4,586 fragments) of the entire realm have core area, and just 0.3 % of the fragments have core area < 150 ha (806 patches; **Figure 3-6**).

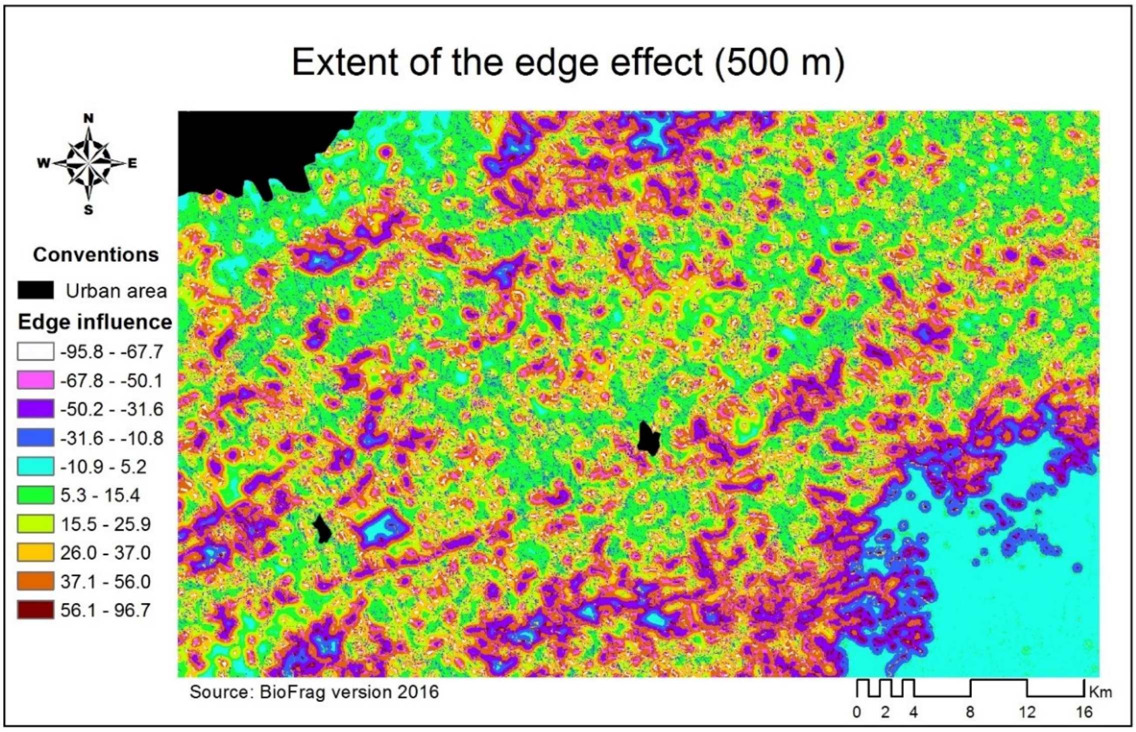
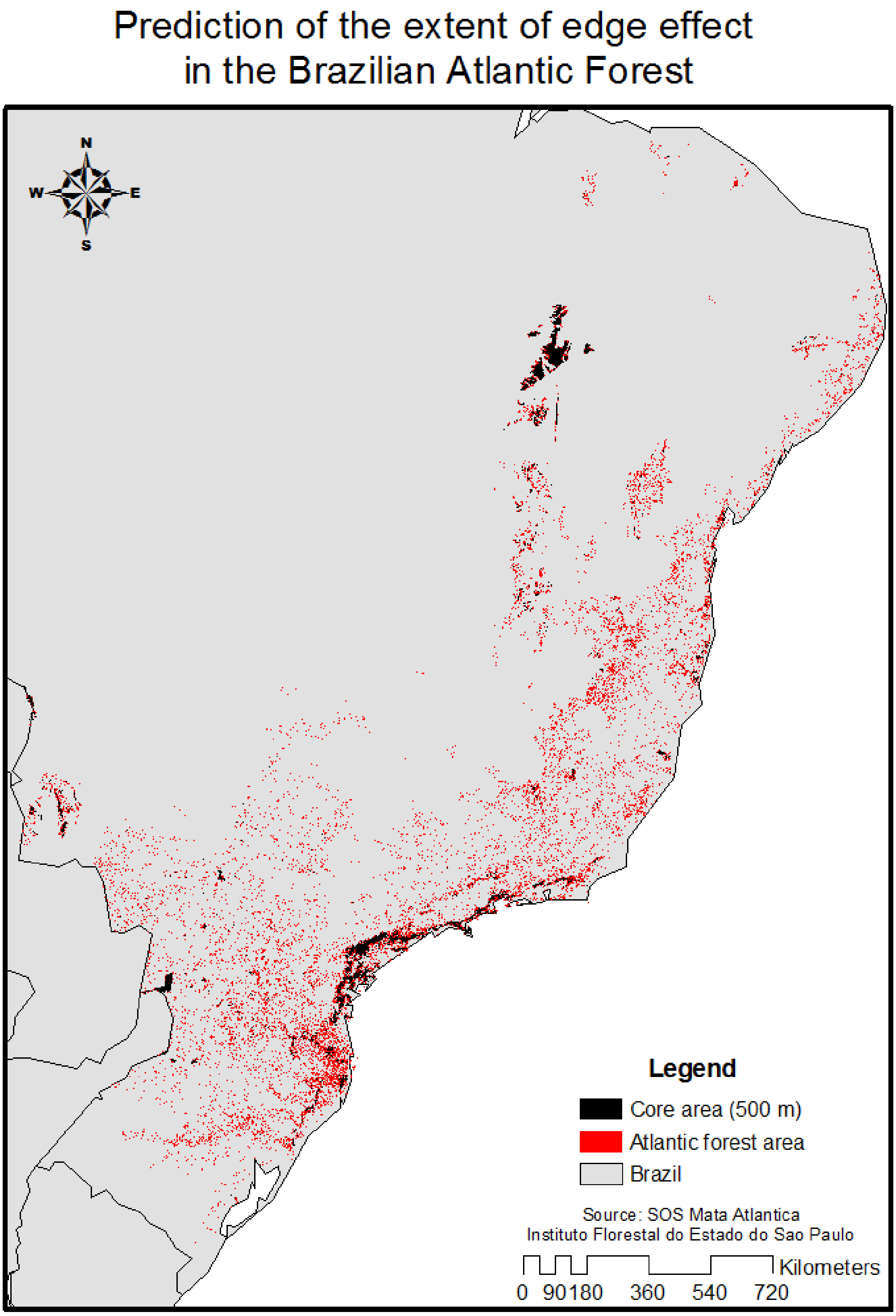


Figure 3-5. Map of the extent of the edge influence at 500 m. Depicting urban areas (black polygons), in colour the gradient of edge influence across the landscape, intensity according to convention. Depicting areas with low edge influence (-10.8 to 15.4), areas with negative edge influence (-10.9 to -95.8), and areas with positive edge influence (15.4 to 96.7).



Prediction of the extent of edge effect in the Brazilian Atlantic Forest

Source: SOS Mata Atlantica
Instituto Florestal do Estado do Sao Paulo

Figure 3-6. Prediction of the resultant core area (in black) of forest fragments 500 m away from the edge in the Brazilian Atlantic Forest (in red); Brazil land mask in grey.

3.5 Discussion

Our results provide evidence that: (i) the magnitude of the edge effects is similar in the canopy and understory, and that edge effects extend far into forest interiors (<500 m). This means that just 0.24% of the fragmented landscapes in our study area is not affected by edge effects and that the Brazilian Atlantic Forest has only 3.3Mha of habitat not affected by edges. Our results suggest that the future of vascular epiphytes in the BAF depends entirely on the protection of large areas of forest.

Although we found that community integrity, species richness and total abundance remained unaffected by edge effect across the "forest edge"-"forest interior" gradient. These results add support to the increasing evidence that edge effects might go up to 1 km into forests, because the process of species loss occurs alongside invasions from the matrix (Ewers & Didham, 2008; Pfeifer *et al.*, 2017). For instance, our results show a dramatic loss of species from control forests to fragmented landscapes, with 83% of species being restricted to control forests, specially of 10 species of conservation concern (VU and EX; Table 6). But we also found that six species of understory epiphytes were able to occur from the matrix to the interior, representing the colonization potential of non-native species into local communities. These species represent 50% of the total species pool of the matrix, 28% of the edge, and 17% of the interior, indicating a non-random species turnover, from forest-preferred to disturbed-tolerant species.

Using the approach developed by Lefbreve, we were able to estimate that the extent of edge influence can go at least 500 m inside the forests, which is beyond what our study design would allow (100 m). These results show how useful this model is for predicting edge effects in fragmented landscapes, as it allows researchers to better understanding the synergies in edge effects when multiple edges are in close contact. It is important to mention however that although we estimated a 500 m extent of edge influence, we cannot exclude the possibility that the effect of edges may extends further within the human-modified forests. The high degree of fragmentation in our landscape might have hampered the modelling process to explore further into the forest fragments. Nonetheless, our results also show that vascular epiphytes are more sensitive than the majority of vertebrates which are influenced by edge effects up to 200-400 m (Pfeifer *et al.*, 2017). These same authors found that 31% of the species were "forest core", while we found that 83% of the species were exclusive to control forest.

The future of epiphytes in the Brazilian Atlantic Forest is however quite uncertain. We estimated that only 19.4% of the current forest (3.3 Mha) provides habitat for the majority of epiphytes, and very few fragments have large core areas (0.3%, 806 forest fragments with >150 ha). The extent of effects of edges leave vascular epiphytes with a much-reduced amount of 'effective' habitat area in the landscape (Pfeifer *et al.*, 2017; Ries *et al.*, 2017; Didham & Ewers, 2012). Furthermore, intrinsic biological constraints of epiphytes species, such as very low seed survival (Mondragón, Valverde & Hernández-Apolinar, 2015), pronounced slow growth rate (Zotz, 2016), general higher mortality rate than of tropical trees (Zuleta *et al.*, 2016), and the absence of seed banks for later re-colonization (Zotz, 2016), reduce the likelihood of long term survival of forest-dependant epiphyte species. Therefore, the resources provided by the current forest fragments and the landscape itself might be insufficient to support future abundances of forest core species. This might imply that forest-core species are currently facing local extinction events in forest fragments, or they might already be undergoing a relaxation time as a product of habitat loss outside the control forest (Halley *et al.*, 2016)

Our study offers a novel view of the effects of human-modified forests to sustain biodiversity when edge effect is quantified across the vertical and horizontal gradient in a human-modified landscape. The conservation value of disturbed and second-growth forests has been acknowledged to maintain trees (Chazdon, 2014), birds, mammals, amphibians (Banks-Leite *et al.*, 2014), and invertebrates (Putz *et al.*, 2008), as well as in ecosystem functions provision (Chazdon, 2014). However, for epiphytes this might not be entirely true in highly modified landscapes. The general decline in abundance of forest core epiphytes species, the invasion of matrix species, together with the well documented slow recovery time after human disturbance of epiphytes communities (Woods & Dewalt, 2013; Martin, Newton & Bullock, 2013), make epiphytes one of the most sensitive groups to habitat loss studied so far. This dramatic impact of the edge effect on epiphyte species and communities might translate into a low provision of ecological functions of these human-modified forests. Epiphytes benefits several functional groups, such as birds (Cruz-Angón & Greenberg, 2005), invertebrates (Cruz-Angón, Baena & Greenberg, 2009), and herpetofauna (McCracken & Forstner, 2014), and many species decline after experimental removal of epiphytes. Other functions might also be reduced after extirpation of vascular epiphytes, such as carbon sequestration via biomass production, water regulation, and modulation in light intensity along the vertical gradient (rewied in Gotsch, Nadkarni & Amici, 2016; and Zotz, 2016).

Ideally, restoration strategies to maintain vascular epiphytes should be directed towards combining setting-aside areas to increase habitat amount at the landscape scale (Banks-Leite et al. 2014) with planned enlarging core area actions, via reducing the area-perimeter ratio and/or expanding the narrowest sections of large fragments and proposed the system. The amount of core habitat in a fragment provides a more ecological impact on communities than total area does (Didham & Ewers, 2012; Ewers & Didham, 2007). Nonetheless, core area favourable for epiphytes is a scarce asset in the BAF. Our prediction across the whole realm showed that the ca 20% of the fragments with core area this is less than 1 ha, which then raises an additional question of how much core area is enough (Fahrig, 2013). Furthermore, there is no guarantee that epiphytes would respond positively by solely increasing habitat amount without improving habitat quality, because of the low number of early ontogeny stages currently present in the landscape (chapter 1). For these reasons, protecting large continuous old-growth forests seems to be the only pragmatic strategy viable to maintain vascular epiphytes in highly human-modified landscapes by now.

3.6 Supplementary material

Table 3. Summary of linear mixed models of the magnitude of edge effect on epiphytes.

Mixed models			Estimate	Std. Error	z-value	Pr(<|z|)	Marginal R^2	Chi-sqr	p-value
Canopy	Species richness	**Intercept**	1.295	0.339	3.82	0.00013	0.11	159.1	0.0001
		edge	0.161	0.434	0.37	0.71054			
		matrix	0.753	0.424	1.78	0.07580			
	Total abundance	**Intercept**	3.217	0.404	7.97	0.00000	0.55	4523	0.0001
		edge	-1.004	0.578	-1.74	0.08215			
		matrix	2.107	0.569	3.70	0.00022			
Understory	Species richness	**Intercept**	1.534	0.393	3.91	0.00009	0.08	52.1	0.00001
		edge	-0.004	0.455	-0.01	0.99200			
		matrix	-0.129	0.526	-0.25	0.80700			
	Total abundance	**Intercept**	1.946	0.529	3.68	0.00001	0.31	2531	0.00001
		edge	0.200	0.747	0.27	0.79122			
		matrix	0.726	0.747	0.97	0.33820			

Table 4. Community integrity pairwise comparison at the canopy and understory. Independent linear mixed models fitted with “multcomp”.

	Pairwise comparison		Estimate	Std. Error	z- value	Pr(<|t|)
Canopy	Ctr-For	Interior	*-0.97192*	*0.013892*	*-69.963*	*<0.001*
	Ctr-For	Edge	*-0.99507*	*0.014069*	*-70.728*	*<0.001*
	Ctr-For	Matrix	*-0.96758*	*0.013892*	*-69.65*	*<0.001*
	Ctr-For	Ctr-Pas	*-0.98074*	*0.017231*	*-56.917*	*<0.001*
	Interior	Edge	-0.02315	0.009696	-2.387	0.113
	Interior	Matrix	0.00434	0.009438	0.46	0.9903
	Interior	Ctr-Pas	-0.00881	0.013892	-0.634	0.9681
	Edge	Matrix	0.027486	0.009696	2.835	0.418
	Edge	Ctr-Pas	0.014334	0.014069	1.019	0.8408
	Matrix	Ctr-Pas	-0.01315	0.013892	-0.947	0.8736
Understory	Ctr-For	Interior	*-0.55314*	*0.006928*	*-79.845*	*<0.001*
	Ctr-For	Edge	*-0.56243*	*0.007201*	*-78.108*	*<0.001*
	Ctr-For	Matrix	*-0.56297*	*0.007201*	*-78.183*	*<0.001*
	Interior	Edge	-0.00929	0.004932	-1.883	0.23
	Interior	Matrix	-0.00983	0.004934	-1.992	0.186
	Edge	Matrix	-0.00054	0.005309	-0.102	1

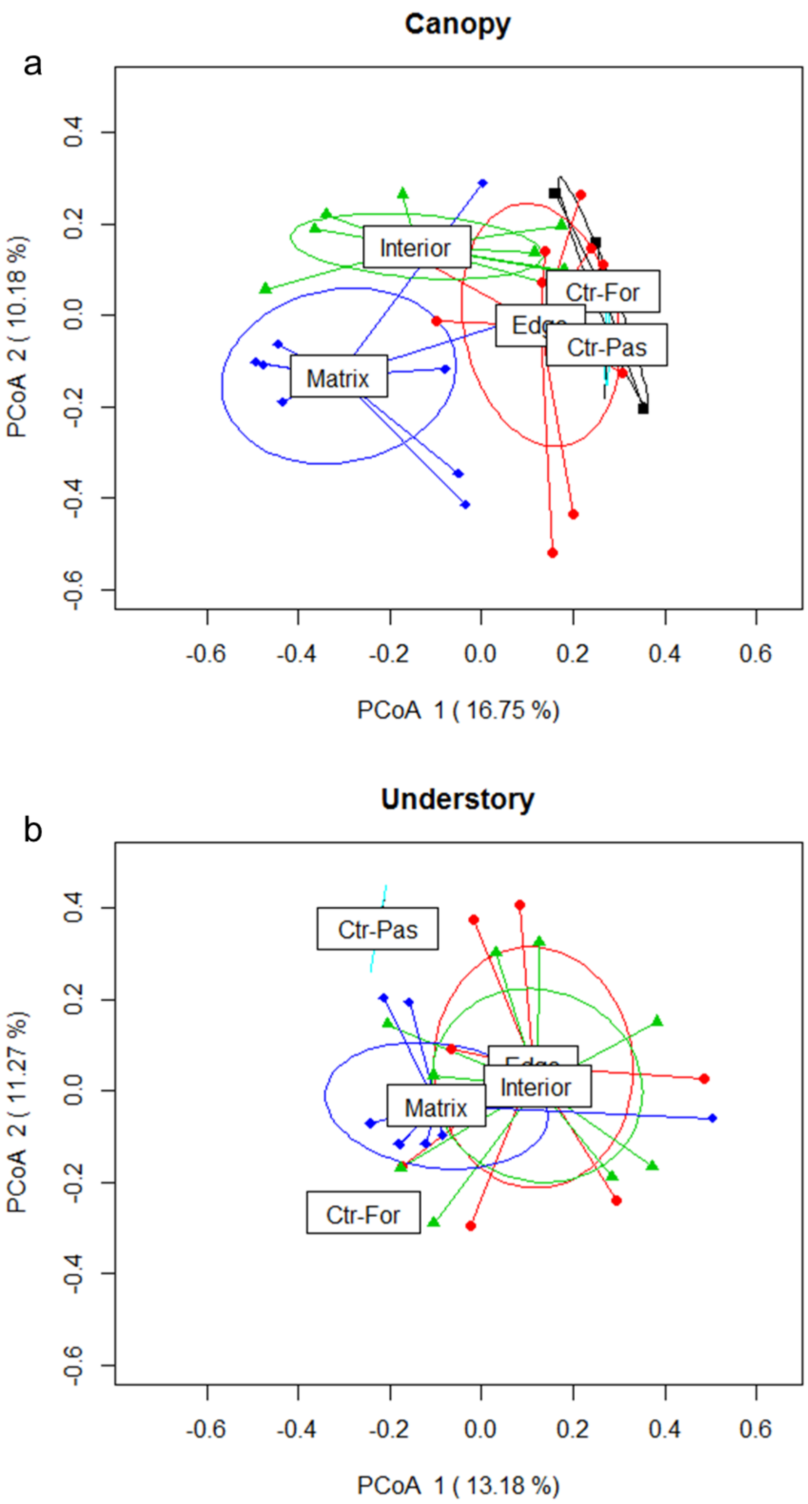


Figure 3-7. Community composition across the gradient of habitat loss. Across strata, canopy (a) and understory strata (b). Ctr-Pas: control pasture (cyan); Ctr-For: control (black); Interior: forest interior (green); Edge: forest edge (red). Dissimilarity based on Sorensen distance with abundance data.

Table 5. Summary of the predictions based on core area at 500 m away from the edge.

Range (ha)	Mean area	Total area	SD	Number of fragments	Presence in BAF %
>150	3957.49	3189737.2	20724.34	806	0.304
(50-150]	87.74	57295.3	28.38	653	0.246
(1 – 50]	0.58	673.1	0.58	1153	0.435
>1	0.29	252	0.28	868	0.328

Table 6. Threaten species in the study area. Source: Secretaria De Estado Do Meio Ambiente, Resolução Sma No 057, 2016. Categories following IUCN parameters. VU= vulnerable; CR; critical; EX: presumed extinct in the wild.

Species name	UICN status	Family
Tillandsia polystachia	VU	Bromeliaceae
Rhipsalis crispata	VU	Cactaceae
Codonanthe carnosa	VU	Gesneriaceae
Nematanthus crassifolius	VU	Gesneriaceae
Cirrhaea loddigesii	CR	Orchidaceae
Cirrhaea longiracemosa	VU	Orchidaceae
Grandiphyllum divaricatum	VU	Orchidaceae
Octomeria geraensis	EX	Orchidaceae
Peperomia quadrifolia	EX	Peperomiaceae
Peperomia subrubrispica	EX	Peperomiaceae

Chapter 4.

The stratification of ecosystem functions and functional resilience in human-modified forests

4 The stratification of ecosystem functions and functional resilience in human-modified forests

4.1 Abstract

Human-driven environmental changes in the habitat trigger positive and negative effects on species and communities. However, the mechanisms that underlie species responses to habitat disturbance and the potential to destabilize ecosystem functioning are still poorly understood. We used a set of life-history traits (response and effect traits) epiphytic plants sampled in the canopy and understory strata in the Brazilian Atlantic Forest (BAF) to assess the causes and consequences of habitat disturbance. The functional structure of old-growth forests, i.e. high functional richness and redundancy, indicates high ecological resilience, whereas the matrix-edge-interior gradient is comprised by low functional richness and low functional redundancy, meaning low resilience. We found that endemic species (habitat specialised species) are more prone to disappear as consequence of habitat loss, than species with larger dispersal range and ability to colonize different forest types. Habitat transformation also leads to the loss of a large set of functions related to pollination and water cycling across strata. Our results indicates that continuous old-growth forest is the only habitat that can maintain the full potential of ecosystem functions delivered by vascular epiphytes. Although limited, human-modified forests still provide ecosystem functions that can positively be influenced by landscape management actions such as increasing habitat amount.

4.2 Introduction

Human-induced disturbances are driving a sixth mass extinction (Barnosky *et al.*, 2011), however not all species are negatively affected. Although it is widely known that any taxa species may respond in a variety of ways to habitat changes, there is little understanding as to what mechanisms underlie species responses to habitat disturbance. Species extinction can also destabilize ecosystem functioning through the loss of functions these species perform and through changes in interactions with other species (Díaz & Cabido, 2001). Functional traits provide a useful approach for elucidating both the causes and consequences of species extinction in human-modified landscapes.

Functional traits encompass both (i) aspects of organisms that influence their ecology and performance in different habitats (i.e. response traits, McGill et al., 2006), and (ii) aspects related to the functions species perform in the ecosystem (i.e. effect traits; Garnier, Navas & Grigulis, 2016). Response traits comprise all characteristics that may be underlying a species response to habitat change, and can therefore be used to help understand the mechanisms behind species sensitivity. Species responses to abiotic stress may lead to changes in species abundances that might ultimately lead to local extinction (Suding, Goldberg & Hartman, 2004). For instance, low dispersal ability, absence of seed protection, drought-intolerance, are all traits that may promote species vulnerability to extinction in plants (McKinney & Lockwood, 1999; Sodhi *et al.*, 2008; Sodhi, Brook & Bradshaw, 2009). On the other hand, effect traits are those which directly influence an ecosystem property, e.g. nutrient cycling, trophic transfer (Díaz & Cabido, 2001). For instance, plant height and leaf phenology are traits related to plant transpiration and growth and these traits influence hydrological regulation of the ecosystem (references therein Díaz *et al.*, 2013).

Several metrics have been developed to capture different aspects of functional trait variation across sites. Measures of functional structure (Garnier et al, 2016) for instance, summarise variation in functional traits across species to provide a community-level estimate of functions provided. Functional structure, i.e. the community's trait distribution, encompasses functional richness or the volume of functional space occupied by the community, and functional divergence as the variability in trait abundance within a community (Mouchet *et al.*, 2010; Karadimou *et al.*, 2016; Garnier, Navas & Grigulis, 2016). These estimates may help unveil how species loss and community turnover affects the environment(Karadimou *et al.*, 2016; Flynn *et al.*, 2009).

Vascular epiphytes, plants that rely on a host for support (Schimper, 1903), are structurally different from their terrestrial counterparts, and intrinsic morphological traits might make epiphytes highly sensitive to disturbance in human-modified landscapes. For instance, most seeds lack a protective seed tissue (leading to limited seed bank formation; Benzing, 1990), shade-dependent species have high dispersal limitation (Victoriano-Romero *et al.*, 2017), adult mortality rate is higher compared to tropical trees (Zuleta *et al.*, 2016), and the dependence of seed establishment and colonization upon a suitable host requires trait matching between hosts and epiphytes (Einzmann et al. 2014; Sáyago et al. 2013; Ruiz-Cordova, Toledo-Hernández & Flores-Palacios, 2014; Woods, Cardelús & DeWalt, 2015). However, epiphytes also have a set of trait strategies to allow species to endure or even flourish in disturbed habitats. For instance, dominant traits in disturbed-tolerant assemblages are photosynthetic CAM pathway (Rodrigues *et al.*, 2013; Benzing, 1990; Einzmann *et al.*, 2014), presence of thick leaves (Woods, 2013), and large geographical range (Einzmann, Zotz & Mi, 2017).

The few available studies on trait-based ecology of vascular epiphytes have used response traits to explain trait matching between host and epiphyte (Köster, Nieder & Barthlott, 2011; Ruiz-Cordova, Toledo-Hernández & Flores-Palacios, 2014; Callaway *et al.*, 2002), and convergence of drought-avoidance strategies to tolerate extreme water limitation within host crowns in old-growth forests (Petter *et al.*, 2016; Woods, 2013). Experimental studies, on the other hand, have found that seeds with no protective tissue, have higher mortality levels than seed-protected species (Mondragon & Calvo-Irabien, 2006). These studies provide a baseline in our understanding of the species responses to local stressors, but it is still unclear to what leads this vastly speciose group to respond to habitat changes and the consequences after disturbance.

Vascular epiphytes play important roles in basic ecosystem functions such as pollination, hydrological regulation and carbon sequestration (Gotsch, Nadkarni & Amici, 2016). Several epiphytes provide reward for pollinators such as beetles, flies, bees, bats and hummingbirds (Gotsch, Nadkarni & Amici, 2016; and Zotz, 2016). For instance, a population of *Rhipsalis neves-armondii* provides resource for 14 species of insects, while an assemblage of bromeliads has found to provide nectar reward to 10 species of hummingbirds in Brazil (Martins & Freitas, 2018; Piacentini & Varassin, 2007). Epiphytes also impact ecosystem hydrological regulation via fog and rainfall interception, e.g. interception of up to 3 mm of precipitation, and water retention, e.g. up to 400% of individual dry weight, which is later release to the system (Hölscher *et al.*, 2004). Likewise, epiphyte biomass production adds to the carbon sequestration forests budget, e.g biomass production between 472-5339 kg ha-1 in primary forests in Brazil (Socher, Roderjan & Galvão, 2008; Petean, 2009). However, these functions are highly sensitive to human-disturbance. For instance, experimental removal of vascular epiphytes have been linked to a reduction of birds (Cruz-Angón & Greenberg, 2005), and invertebrates (Cruz-Angón, Baena & Greenberg, 2009), which may have cascading effects along food webs. Likewise, Kohler et al. (2007) reported dramatic biomass reductions when transforming an old-growth forest to a disturbed forests (from 2615 to 84 kg ha−1 after 30-years of restoration, respectively). This biomass reduction will impact the potential for carbon sequestration and hydrological regulation of human-modified forests.

However, we still do not know the magnitude and the loss or gain of functions of vascular epiphytes in human-disturbed habitats.

Our study aimed to quantify the effects of habitat disturbance in the functional structure of vascular epiphytes in a highly human-modified landscape using life-history traits. This is the first study using life-history traits (response and effect traits), to explain patterns in a vertical (canopy and understory), and habitat loss gradient (pasture-matrix-edge-interior-control forest) in a human-modified landscape. We specifically asked:

1. Which traits render species sensitive to habitat changes? It is expected that atmospheric bromeliads, with no storage water strategy and leaves with short-trichomes, will be dominant in disturbed habitats (Benzing, 2000; Zotz, 2016). In contrast, endemic species with unprotected seed-tissue are expected to prevail in the control forest.
2. What are the roles of the landscape and forest structure in shaping functional structure? We hypothesized that habitat disturbance will negatively impact functional richness, and there will be a significant loss or shift in ecosystem functions in the human-modified forests, because vascular epiphytes are in general highly sensitive to habitat loss (chapter 2 and 3).

Finally, because we carried out our analysis across strata, we in general expect that functional structure of epiphytes in the canopy stratum will be less affected by habitat loss because canopy assemblages are richer and have a better chance to disperse than understory species (Quaresma & Jardim, 2014; Arevalo & Betancur, 2006). Our empirical study on functional traits provides a baseline to understand the assembly of communities after human disturbance.

4.3 Methods

4.3.1 *Study area*

The study area comprises a landscapes of human-modified forests in different successional stages in the Brazilian Atlantic forest. Sites were located within the municipalities of Taubaté, São Luiz do Paraitinga and Lagoinha in the São Paulo state, with altitude ranging from 860 to 1,470 m (**Figure 4-1**). Site selection was done by the "Biodiversity and Ecosystem Functioning in Degraded and Recovering Amazonian and Atlantic Forests" (ECOFOR) research project funded by NERC (Grant Number NE/H016228/). The predominant vegetation in the region is Montane Ombrophilous Dense Forest (Veloso, Rangel-filho & Alves-Lima, 1991). The landscape has 28% forest cover including the reserve, and the matrix consists of pastureland and various small-sized (average 15 ha) forest fragments. Fieldwork was conducted between May 2015 and July 2016.

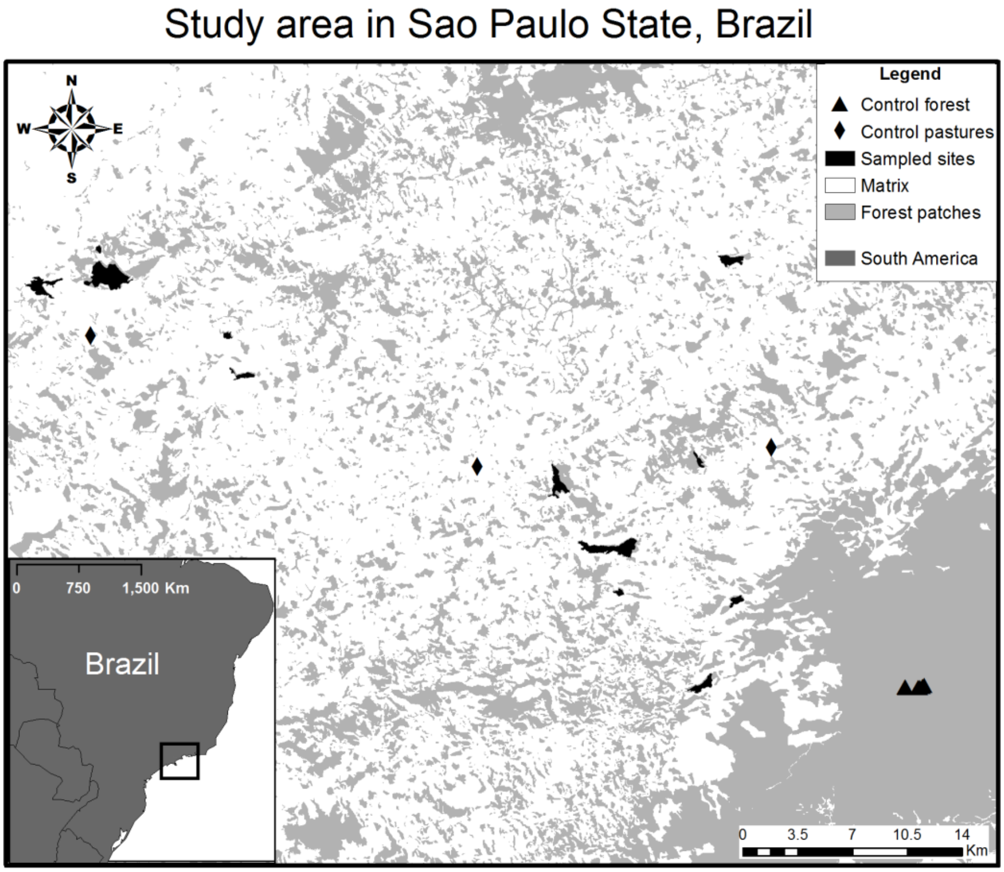
4.3.2 *Study design*

We sampled epiphytes across a wide range of habitats, including protected forest, fragments and open matrix. We defined two control sites: (1) three open matrix sites dominated by species of Poaceae with sparse trees, hereafter "control pasture", and (2) three sites in an old-growth continuous forest in the Santa Virginia Nucleus of Serra do Mar State Park, hereafter "control forest". In control pasture, sampled plots were located *ca* 600 m (SD: 105.5 m) away from the nearest forest edge. In the fragmented area, we selected twelve discrete forest fragments with hard edges, surrounded by pastures with isolated trees, and we sampled: (1) isolated trees located at up to 100 m away from and parallel to the edge, hereafter "matrix", (2) an edge plot which was defined at 30 m from the hard edge of the forest, hereafter "forest edge", and (3) an interior plot which was surveyed at 100 m from the discrete border, hereafter "forest interior" (**Figure 4-2**). In the fragmented area and control pasture all plots were 10 x 250 m, subdivided into 25 subplots of 10 x 10 m. In the matrix, plots had irregular shapes but preserved the same area of 2500 m^2 as the others plots. In the control forest, the plots were 100 x 100 m (Joly *et al.*, 2012) and were divided into ten subplots of 10 x 10 m each, plots were located *ca* 600 m (SD: 105.8 m) away from each other.

4.3.3 Epiphyte sampling

Epiphytes were sampled in the canopy and understory. The canopy, defined here as the section of the tree at the Johansson's (1974) zone 3, until the outer branches. We omitted the transitional tree segment between understory and canopy, known as section 2 (Johansson, 1974). Canopy was sampled using single rope technique, complemented with modified mountaineering and free climbing techniques. Branches were reached manually up to 5 m from the main trunk, whilst outer branches were inspected using binoculars, and surveyed using a pole when possible. At each plot, we sampled five trees (tree selection criteria in Supplementary material 1). In the understory, epiphytes at up to 2 m high were recorded on trees with <10 cm diameter at breast height (DBH). In each plot, ten subplots (10 x 10 m^2) were surveyed as follows; five subplots where the tree for canopy sampling was surveyed, and an additional five subplots randomly selected within each plot (**Figure 4-2**).

All dubious individuals were discarded. Species determination was conducted following specialized literature and consultancy of experts. Nomenclatural standardisation was based on "The Plant List, 2017" database names.



Source: SOS Mata Atlantica and
Instituto Florestal do Estado do Sao Paulo

Figure 4-1. Map of the study area, showing the locations of fragments and sampling points. Grey areas represent forest fragments, white the matrix, black the sampled forests, hexagons the control forests, and triangles the control matrix.

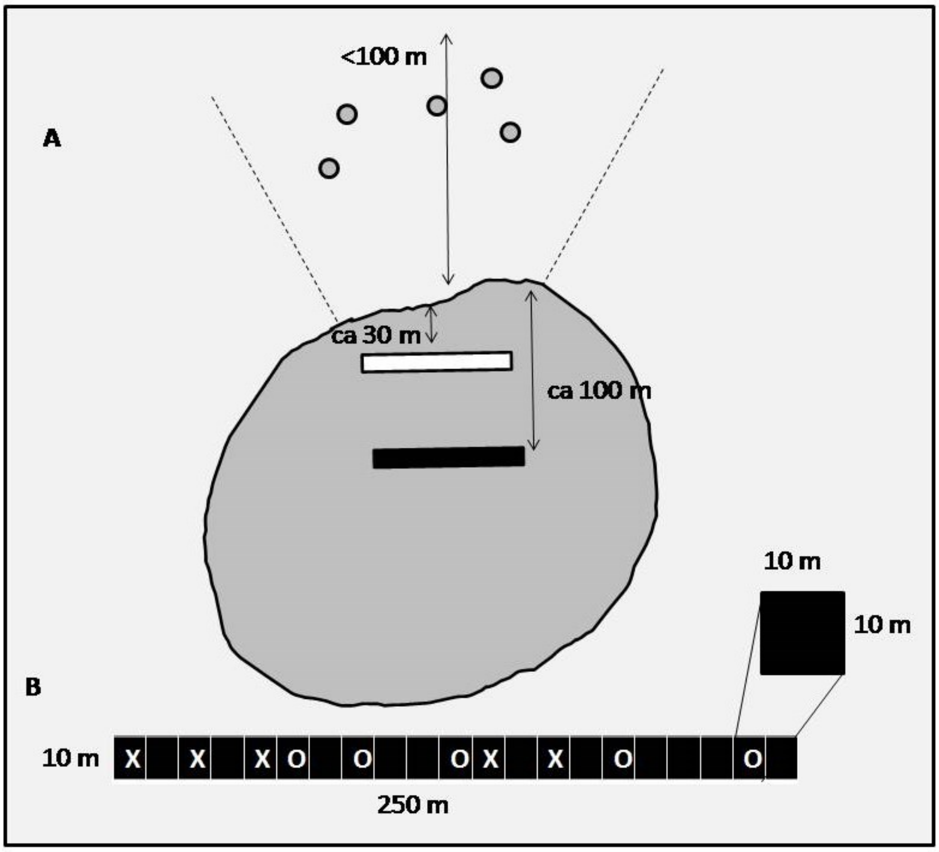


Figure 4-2. Sampling design. A) Black rectangle represents interior plot, white rectangle edge plot, arrows the distance from the edge fragment, and grey circles denote isolated trees for the matrix habitat. B) 10 x 250 plot, subdivided into 25 subplots of 10 x 10 m; letters represent an example of the sampling at the understory strata, X for canopy sampling and O for random sampling.

4.3.4 Life-history Traits

We studied the interspecific and community aspects of trait-based ecology. We collated information of a total of 200 epiphyte species (Supplementary material

Table 7 and page 174). Effects traits were selected based on their potential impact on ecosystem functioning such as rewards for pollinators, water regulation, i.e. water storage tissue (Gotsch, Nadkarni & Amici, 2016; Zotz, 2016). Response traits comprised a wide variety of dispersal features (dispersal syndrome, dispersal vector), adaptation to colonize adjacent niches (phyto-geographic domains, vegetation type, substrates exploited, and seed protection), strategies to capture atmospheric water (leaf ornamentation), and spatial distribution (geographic distribution, and endemism). See supplementary Information for further details and Supplementary Dataset for data availability (appendix 1). We used coarse categorical traits, as the detail level of ecological information is highly heterogeneous inter and intra specific in vascular epiphytes (Petter *et al.*, 2016; Woods, 2013). Information about functional traits was collated from different taxonomical treatments, flora datasets, and local floras, and by consulting experts (Goncalves-Salimena *et al.*, 2013; Borba *et al.*, 2002; Buzatto *et al.*, 2012; Newman, Manning & Anderson, 2014; Flora do Brasil, 2018). In total, we analysed 210 species with 100% of the selected traits information collated.

4.3.5 Environmental predictors

We used two sets of environmental predictors. The first set of predictors was the landscape metrics, in which we calculated patch size and forest cover for each site from the combined maps provided by "Instituto florestal" (Instituto Florestal do Estado de São Paulo, 2012) and "SOS Mata Atlântica" (INPE, 2014). Patch size and percentage of forest cover were calculated in ArcGIS 10.2 (ESRI Inc, 2014). Forest cover was extracted from radii of 500 m, 1000 m, 1500 m, 2000 m and 3000 m from the centre of the studied plots (hereafter, FC.500, FC.1000, FC.1500 m, FC.2000, and FC.3000 m). The second predictor was forest structure based on canopy openness and tree size. Canopy openness was assessed on each plot using fish-eye photography (16mm focal length) and analysed in GapLightAnalyzer® (Frazer, Canham & Lertzman, 1999). Tree size was measured with diameter at breast height (1.30 m above ground) recorded from trees with DBH ≥10 cm, as a proxy variable for crown area (O'Brien et al. 1995).

4.4 Data analysis

We performed two sets of analyses according to the trait type. For response traits, we used the RLQ and fourth-corner methods to analyse associations between species, traits and environmental predictors (Dray *et al.*, 2014). For effect traits, we tested the correlation of the environmental variables as predictors of functional structure, and the magnitude of functional loss or gains in functional guilds along the gradient.

4.4.1 Trait–environment-species relationships

We combined the RLQ and fourth-corner methods following Dray *et al.* (2014) protocol. The fourth-corner method has the advantage of statistically testing the significance of bivariate trait-environment relationships, whereas the RLQ analysis provides a summary of associations in the multivariate space. As discussed above we collated environmental variables (R), species traits (Q), and a species-by-site matrix with abundances (L). We first performed the RLQ analysis and tested our linkages based on the total inertia with the null hypothesis of no relationship of R and L (model 2), and no relationship between L and Q (model 4). Next, we performed the fourth-corner method to assess the significant associations of the RLQ space. We tested links between RLQ axes and traits (type test = "Q.axes"), and environmental variables (type test= "R.axes") using the false discovery rate to adjust p-values (significance level α = 0.05). All permutation tests were carried out at 4 999 iterations (Dray *et al.*, 2014).

4.4.2 Functional structure

We used effect traits to calculate two functional structure metrics, functional richness and Rao's quadratic entropy (hereafter Fric and RaoQ). Fric represents the diversity of traits within a community (Mouchet *et al.*, 2010). RaoQ is an abundance-weighted metric of divergence in trait-space (Mouchet *et al.*, 2010), which assumes that the traits of dominant species have stronger effects in the ecosystem (Grime, 1998). RaoQ has been used as a proxy of functional redundancy because it indicates a pattern of niche differentiation among species (Karadimou *et al.*, 2016), low RaoQ will indicate less divergent traits in the community and therefore a degree of redundancy. Functional metrics were calculated using Gower's dissimilarity matrix because it allows for both quantitative and qualitative traits.

The amount of niche space filled for the character would be expressed as a proportion of it:

$$Fric = \frac{SF_{ci}}{R_c}$$

Where FR_{ci}= the functional richness of functional character c in community i, SF_{ci} = the niche space filled by the species within the community, R_c= the absolute range of the character.

$$RaoQ = d_{ij} = \sum_{k=1}^{n} \sum_{l=1}^{n} w_{kl}(X_{ik} - X_{jk}) * (X_{il} - X_{jl})$$

“Where d_{ij} is the difference between the i-th and j-th species (d_{ij}= d_{ji} and d_{ii}= 0), n = the number of traits considered, X_{ik} = value of trait k in species i, and w_{kl}= elements of inverse of variance-covariance matrix of traits” (Botta-Dukat, 2005).

To test how functional richness and Rao’s quadratic entropy measures were affected by habitat changes, we fitted linear mixed effect models reflecting the nested structure of our data (plots within fragments). As fixed effects we used, landscape predictors: represented by forest cover (%), and forest fragment area in ha (log10); and forest structure predictors: DBH (averaged per plot) and canopy openness (% per plot). We tested the different radii of forest cover to find the most relevant spatial scale influencing epiphytes. Due to the high correlation of predictors within sets (Spearman’ correlation rank test **Table 8**), we aimed to select only one predictor per set. All models were fitted with a Gaussian error distribution at plot scale. We used likelihood ratio tests to determine parameter significance by comparing models independently to a null model with no predictor. The proportion of variance explained by fixed effects was calculated as pseudo R^2 (Nakagawa & Schielzeth, 2013). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity, normality, or spatial autocorrelation.

Additionally, we grouped species by functional guilds and analysed the impact of habitat type on the abundance of each functional guild to better understand which functions are lost across the gradient. We used generalized linear mixed model with penalized quasi-likelihood estimation (glmmPQL), to account for data over-dispersion using Poisson error distribution. We fitted total abundance per trait as our response variable, and habitat type as fixed term, and forest fragment as random effect. We tested whether terms in our models were significant using Wald $\chi 2$-tests (Hauck & Donner, 1977).

4.4.3 Statistical analysis

Statistical analyses were conducted in R (R Core Team, 2017) with the packages “vegan” (version 2.2–1,Dixon, 2003), “lme4” (Bates *et al.*, 2015), “FD” (Laliberté, Legendre & Bill Shipley, 2015), “MASS” (Venables & Ripley, 2002), and “multcomp” (Hothorn, Bretz & Westfall, 2008).

4.5 Results

In total, we found 200 species and 12,351 individuals from 18 families, including Orchidaceae (82 species) and Bromeliaceae (48 species) as the most speciose families, from a sampling of 270 canopy trees, and 3127 trees in the understory. Canopy had more species (179 vs 71 species) and held more individuals than the understory (10525 vs 1826 adult individuals).

4.5.1 Drivers of species sensitivity

We found significant signal of trait–environment-species relationships in the canopy, but we found no significant relationship in the understory. In the canopy, we found that the relationship between traits and environmental variables can be summarized by the first RLQ axis (88.7% of the cross-covariance between traits and environment). The global significance of the traits-environment relationships showed that environment did influence the distribution of species with fixed traits ("Model 2", $p < 0.001$), and that traits influenced the composition of species assemblages ("Model 4", $p < 0.0007$).

The positive values of the first RLQ axis show the association between endemism (r= 0.37, p-adj= 0.0064) with percentage of forest cover (1000m, r= 4.2048, p-adj= 0.0008), precipitation (r= 3.965, p-adj= 0.0008), and tree DBH (r= 3.719, p-adj= 0.0015). Those environmental descriptors were all higher in the control forest. We found several threatened endemic taxa of conservation concern in this forest, such as *Cirrhaea loddigesii* (CR), *Tillandsia polystachia* (VU), and *Wittrockia gigantea* (VU; IUCN 2000).

The negative values of the RLQ axis revealed the association of geographic distribution (r= -2.856, p-adj= 0.0049) and phyto-geographic domains (r= -3.021, p-adj= 0.0049) with distance to the control forest (r= -0.585, p-adj= 0.0008). The core species groups were the *Tillandsia* congeners group, ferns such as *Pleopeltis* group, and other *Polypodiace* species. These species are described as resistant to drought in the literature and have a large geographic range (Zotz, 2016; Benzing, 1990, 2000; Flora Flora do Brasil, 2018).

In the understory, although we found that the environmental predictors influenced the distribution of species with fixed traits ("Model 2", $p < 0.001$), these traits did not influence the composition of species assemblages ("Model 4", $p = 0.1824$). Therefore, no significant association in the RLQ space could be made, despite the high representation of the variance in the first two RLQ, 80.8%, and 11.4%, for axis 1 and 2, respectively.

4.5.2 Consequences for ecosystem functioning

Habitat type was the most important driver of functional structure of effect traits across strata (R2 marginal, **Table 9**). Canopy functional richness was significantly higher in the control forest than in the forest interior (t= -3.8, p<0.01), forest edge (t= -5.596, p< 0.01), matrix (t= -5.363, p< 0.01), and control pasture (t= -3.585, p< 0.01; figure 4.A). Although forest interior had higher functional richness, based on the estimates, none of the pairwise comparison were significant (**Table 9**). Functional richness in the understory stratum was not significantly influenced by any predictor (**Table 9**). In contrast, RaoQ was higher in the control forest, in both the canopy and understory strata, than: forest interior (canopy, t=-2.36, p= 0.03; understory, t= -1.93, p= 0.05), forest edge (canopy, t= -3.88, p< 0.01; understory, t= -3.08, p< 0.01), matrix (canopy, t= -3.31, p< 0.01; understory, t= -3.59, p< 0.01), and control pasture (canopy, t= -3.79, p< 0.01; Figure 4-3).

Forest cover at 500m was the second most important predictor. We found a positive correlation between forest cover with both functional richness (canopy, t= -3.79, p< 0.01) and RaoQ (canopy, t= 2.22, p= 0.04; understory, t= 3.176, p= 0.05). Lastly, fragment area was positively correlated with canopy functional richness (t= 4.85, p< 0.01). Forest structure did not correlate with either functional metrics or strata (**Table 9**).

For functional guilds, control forest holds all reward types and water strategies and these were significantly higher than in the fragmented area across strata (p< 0.05; Figure 4-4 and Figure 4-5; Table 10). We found that pollinator reward is more sensitive than water storage traits to habitat loss. Four reward strategies, i.e. oil, food, perfume and pollen, representing 17% in the understory (458 individuals), and 19% in the canopy (1715 individuals) of pollinator reward types in the control forest, are lost in the fragmented area (0 individuals; Figure 4-4 and Figure 4-5).

We also found a large shift in water storage strategies from water accumulated in the leaves, which represents 25% in understory and 43% in the canopy of the whole control forest water storage source, to "no-water storage" as the dominant strategy across strata in the disturbed forests (Table 11; Figure 4-5). Additionally, nectar reward, rhizome and tank traits are prevalent along the gradient across strata (with the exception of tank in the control pasture; Table 10; Figure 4-4).

In the canopy, nectar provision was the largest strategy, followed by none, all the other functions are lost in the fragmented area (**Table 11**). Forest interior has significantly more functions and individuals per strategy than forest edge, matrix and control pasture ($p< 0.01$; **Table 11**). For water cycling, rhizome is the most important strategy followed by none and tank (Table 5). Forest interior hold significantly higher abundance of rhizome, steam+leaves, and leaves than matrix-edge and control pasture ($p< 0.01$; **Table 11**). No-water storage tissue was significantly higher in the matrix and control pasture than in forest edge or interior ($p<0.01$).

In the understory, nectar reward and water storage types were not significantly affected by the gradient ($p> 0.05$; Figure 4-4, Figure 4-5). In contrast, the matrix is the most hostile habitat for leaves, stem and leaves+stem strategies, with no individuals present in this habitat type, whereas for rhizome and tank abundance was lower than forest interior (z-value= -3.122, p= 0.011; and z-value =-2.627, p= 0.044, rhizome and tank respectively; Table 10 and Figure 4-5).

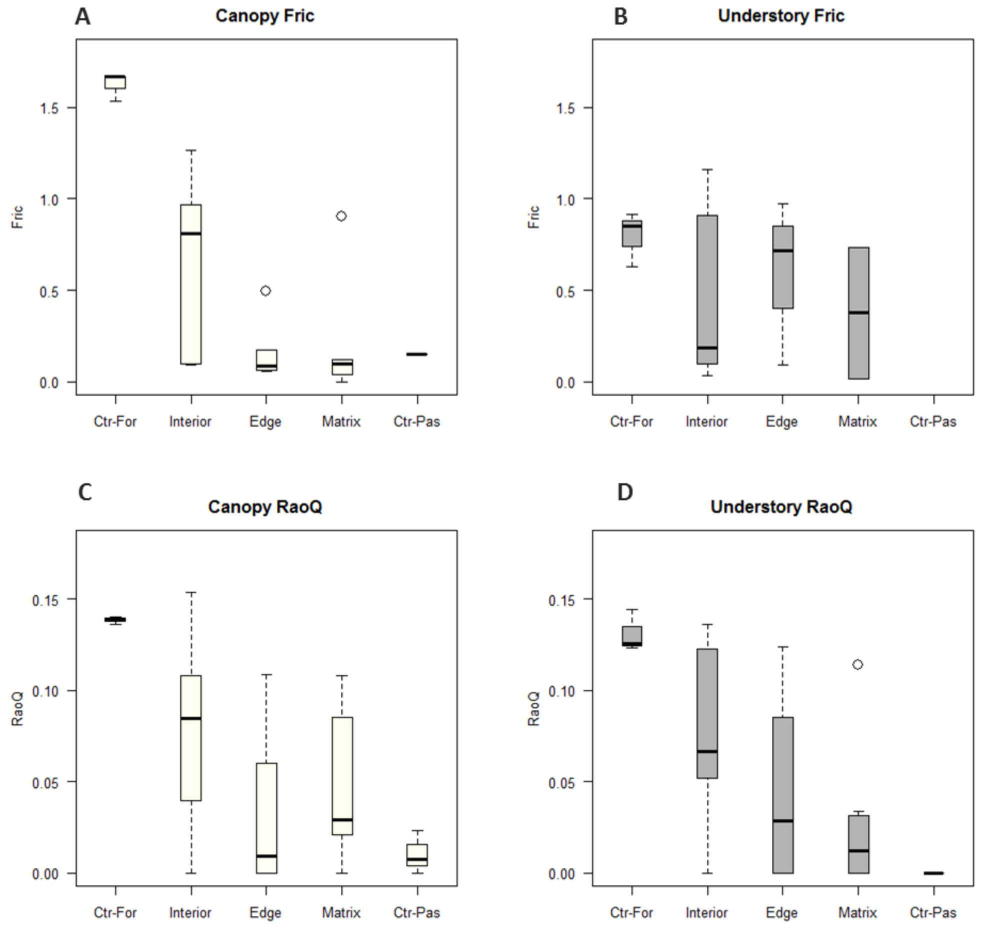


Figure 4-3. Functional richness and RaoQ along the canopy (A and B, respectively), and understory stratum (C and D, respectively). Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles and points indicate the outliers. Ctr-Pas represents control pasture; Ctr-For, control forest.

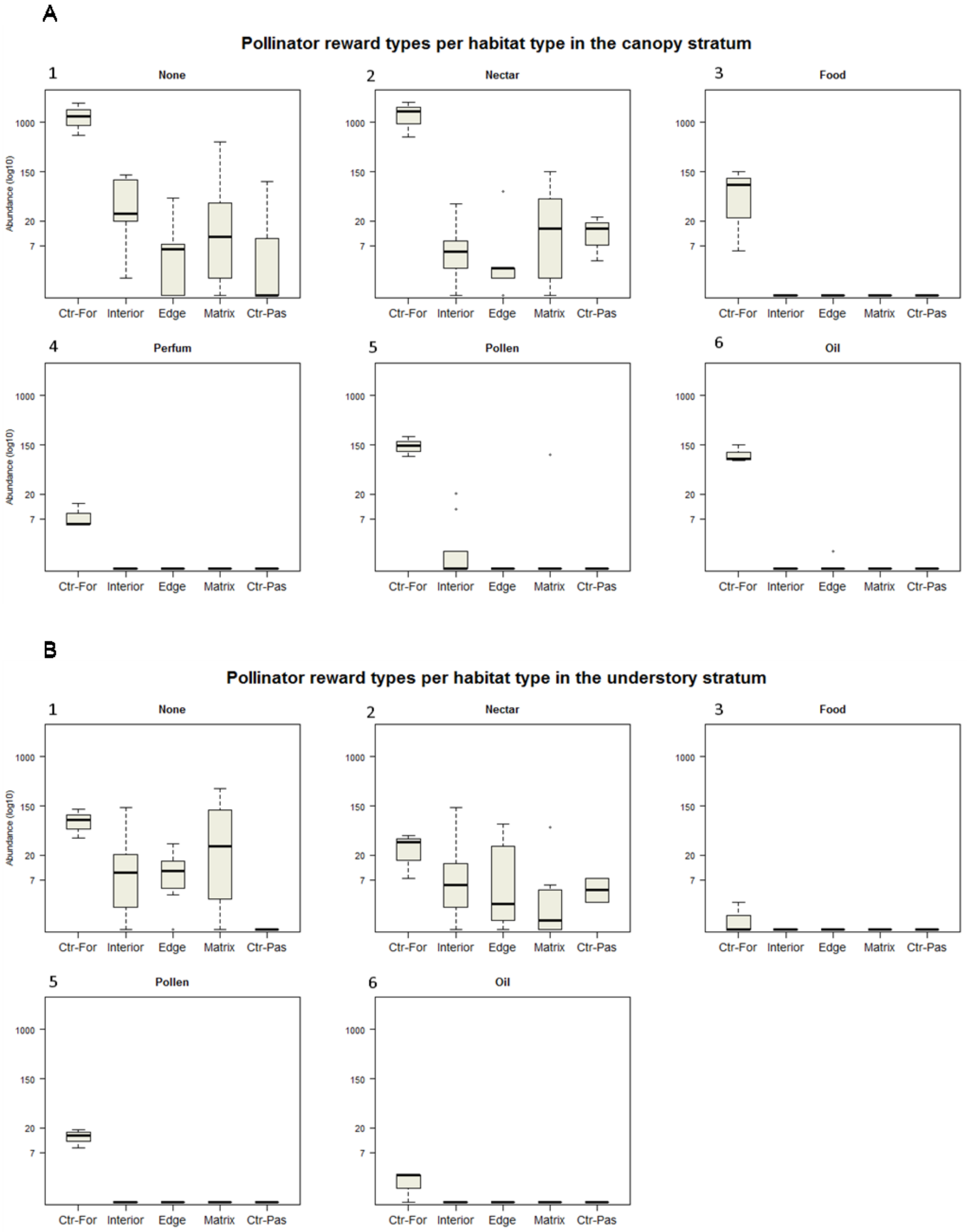


Figure 4-4. Total abundance of functional effect traits along the canopy (pane A), and understory stratum (pane B). Each pane comprises of: (1) for no reward, (2) nectar reward, (3) food, (4) perfume (absent in the understory), (5) pollen, (6) Oil. Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles and points indicate the outliers. Ctr-Pas= control pasture; Ctr-For= control forest.

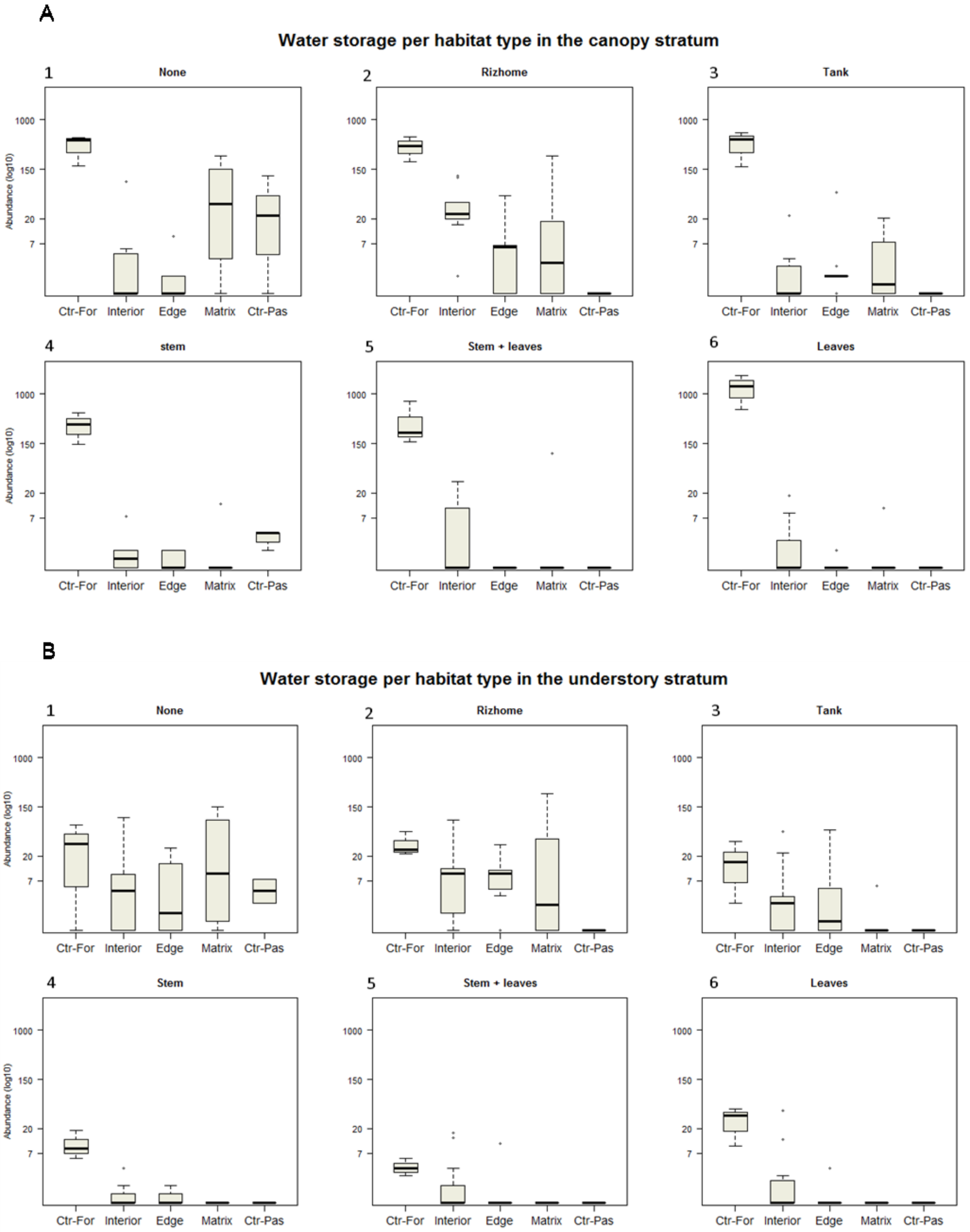


Figure 4-5. Total abundance the water storage effect traits along the canopy (pane A), and understory stratum (pane B). Each pane comprises of: (1) no tissue, (2) rhizome, (3) tank, (4) stem, (5) Stem+leaves, and (6) leaves. Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles and points indicate the outliers. Ctr-Pas= control pasture; Ctr-For= control forest.

4.6 Discussion

Our results showed a consistent negative effect of human disturbance across strata on the functional diversity of epiphytes. The old-growth continuous (control) forest plays an important role in hosting large number of highly diverse ecosystem functions delivered by vascular epiphytes that disappeared in human-modified forests. In contrast, traits related to dispersal and specialism seem to shape the distribution of traits along the gradient, with pastureland and matrix becoming increasingly dominated by fewer functional groups typical of generalist species.

The gradient of habitat types from continuous old-growth forest to pastureland, was found to be the major force shaping functional structure across strata. Old-growth continuous forest hosts the largest functional richness and functional redundancy (high RaoQ), which leads to high levels ecological resilience to local extinctions such as the intrinsic high mortality rate in epiphytes (Zuleta *et al.*, 2016). Hence, in the case that some species disappear, other species occupy a similar functional space, this resilience may maintain key functions and processes in the face of stresses or pressures, either by resisting or adapting to change. In contrast, in the fragmented landscape we found low ecological resilience, and most importantly that the disappearance of species would represent a reduction in ecological functions (Díaz & Cabido, 2001).

In the canopy, our results show that old-growth forest provide habitat for endemics which are dependent on large tree sizes, high forest cover and high precipitation (RLQ+fourth-corner), predictors which have been long documented to positively affect species richness and diversity of epiphytes (Krömer & Gradstein, 2003; Rodrigues & Neto, 2015; Zotz & Bader, 2009). Large trees have high microhabitat heterogeneity that leads to niche-partitioning, (Wagner, Bogusch & Zotz, 2013; Einzmann *et al.*, 2014). Likewise, high precipitation is highly associated with epiphytes because atmospheric water is the main way of water intake (Zotz & Hietz, 2001). Altogether, the conditions present in old-growth forests buffer the vulnerability of endemic epiphytes to extinction by promoting a variety of microhabitats.

In disturbed habitats, functionally similar species (low RaoQ), with a high dispersal range and high colonization capacity are dominant in the pastures and open areas (RLQ+fourth-corner). In open habitats, congeners of atmospheric bromeliads, such as *T. usneoides* and *T. flexuosa***,** are frequently reported to establish local populations (Einzmann, Zotz & Mi, 2017; Poltz & Zotz, 2011). The success of atmospheric bromeliads, i.e. bromeliads of reduced size, presence of non-functional roots, absorptive leaves and capacity to form massive populations, have been associated to high dispersal range, and drought tolerant traits, such as low leaf surface area, stomata protection by large trichomes (leptote trichomes), and high leaf succulence (Males & Griffiths, 2017).

No association between response traits and species composition was detected in the understory (model 4, RLQ+fourth-corner). This means that the species' abundances are structured along environmental gradients, i.e. the positions of species individuals on the gradient are not random (as seen in chapter three), but not due to differences in traits, because there is no link between species position on the gradients and their traits, or traits fail to capture differences in species niche positions. Notably, the understory has naturally lower microhabitat complexity than tree crowns which leads to patterns of fewer individuals (Benzing, 1990). This might be enhanced by the extent of edge effect that shifts temperature and humidity that would impact shifts shade-preferred towards drought-tolerant species after disturbance (Poltz & Zotz, 2011; Einzmann, Zotz & Mi, 2017; Ewers & Banks-Leite, 2013).

We found a large set of effect traits in old-growth forest disappearing in the human-modified landscape in both strata, showing that some functions are more vulnerable to habitat loss and fragmentation loss than others. Specifically, we report the disappearance of food, oils, and perfume pollinator rewards, and water storage strategies (leaves and stem in some species, and just leaves in others). The loss of pollinator rewards (by type or abundance) might have repercussions along food webs and pollination networks.

Likewise, diversity and abundance of wild bees have been found to decline as distance to natural habitat increase or after land use changes (Ricketts, 2004). Euglossinae bees are an example of this mutualistic relationship with endemic epiphytic orchids as the primary resource of fragrance, i.e. bee males collect oil and fragrance for mating purposes (Williams & Whitten, 1983). In the event of habitat disturbance, highly sensitive species, such as orchids (Sodhi *et al.*, 2008; Kindlmann, Meléndez-Ackerman & Tremblay, 2014), will disappear first and alongside a variety of pollinator rewards (such as food, oils, and perfume). In BAF, after habitat disturbance the Euglossinae composition also shifts, and specialist have been seen to reduce population and dispersal range, whilst more resilient species increase, e.g. *Euglossa carolina* and *Eulaema nigrita* represent 50% and 25% of local populations in HMFs (Ramalho, Gaglianone & Oliveira, 2009; Aguiar & Gaglianone, 2012; Ferronato *et al.*, 2017). Therefore, the extirpation of either, plant or pollinator, can disrupt the composition and the efficiency of pollinator's communities and networks, which would led to species extinctions and reduction of the resilience of the system (Bond, 1994; Wolowski, Ashman & Freitas, 2014).

Hydrological regulation is also affected by the loss and reduction of water storage traits, as we found the predominance of no-water storage strategy in disturbed habitats. This would impact local loss hydrological regulation, because lower plant size and no water storage tissues will reduce atmospheric water interception in the canopy and will impact evaporation from the foliage (interception loss) and the slow-redistribution to the ground (Stanton *et al.*, 2014; Van Stan & Pypker, 2015).

In contrast, a certain set of functions consistently appeared along the gradient and strata. We found that effect traits of nectar provision (pollinator reward) and tank water storage, are distributed across all the habitat gradient, albeit in much lower magnitude than in old-growth forest at habitat type scale. For instance, nectar reward is a rich resource produced constantly by bromeliads to attract hummingbirds and bats in disturbed and non-disturbed forests (Benzing, 2000; Piacentini & Varassin, 2007). Likewise, experimental studies have shown that tank species buffer canopy microclimate by increasing relative humidity (average 1.7%) and reducing temperatures by 0.5-2 ºC (Fernandez Barrancos, Reid & Aronson, 2017), and they provide 23 times more shelter for anurans, aquatic species and macro-invertebrates than branches with no tank bromeliads (Rangel *et al.*, 2017; Fernandez Barrancos, Reid & Aronson, 2017). The maintenance of these functions provides extra services in HTMFs. However, the low abundance of individuals, and the shift in population patterns (chapter 1), might suggest that the resilience of this forest type is low, and it might not be able to buffer population losses in the future.

Forest cover (500 m) positively influenced the number and the diversity of functions performed in the community. Therefore, increasing forest cover might promote more niches to become available due to improving habitat amount in the landscape (Fahrig, 2013). Our results differ from other studies which found that forest cover drives changes in ecosystem functions without affecting functional richness (De Coster, Banks-Leite & Metzger, 2015). These authors found that the decline of specialised species (i.e. those with particular combinations of traits) is compensated by newly occurring species that might be redundant with those already present. However, for vascular epiphytes in this highly modified landscape, the loss of forest cover significantly impacts functional richness and reduces functional diversity, which leads to reduced ecosystem function and lower resilient to disturbance. This is probably the result of the dramatic loss of species richness (90% species net lost) and abundance (91% individuals net lost), the significant shifts in community composition and ontogeny stages (chapter 2), and the high degree of edge influence in this landscape (chapter 3).

4.7 Conclusion

To sum up, the transformation of the landscape exerts a strong impact on a particular set of response traits, and reduces the potential of vascular epiphytes to provide ecosystem functions. This scenario is worrying because human-modified forest has become the most widespread type of forest worldwide (60%), and is expected to increase, either by the transformation of continuous landscapes, or by the recovery of abandoned areas (Hansen *et al.*, 2013). Certain conservation actions may positively influence the number and diversity of functions provided by vascular epiphytes in human-modified forests. Banks-Leite et al (2014) proposed an interesting initiative of maintaining or restoring at least 30% of forest cover in the BAF through set-aside programs. This initiative aims to preserve habitat amount at local landscape, which would have a cascading effect on non-exploited patches (Padmawathe, Qureshi & Rawat, 2004), allowing the persistence of large trees within forests (Wolf, 2005), and increase forest core area (as proposed in chapter 3), which may benefit the functional structure in epiphytes. However, in the meantime, continuous old-growth forest is the only habitat that can maintain the full potential of ecosystem functions delivered by vascular epiphytes.

4.8 Supplementary material

Table 7. Life-history functional traits of vascular epiphytes.

Effect traits

Associated function	**Trait**	**Variable type**	**Descriptor**
Pollination	Reward	Categorical	Absence
			Nectar
			Pollen/pseudopollen
			Essential oil
			Food resource
			Perfume
Local hydrological cycle	Water storage tissue	Categorical	None
			Rhizome
			Leaves
			Stem (pseudobulbs)
			Tank
			Combinate (stem+leaves; roots+leaves)

RESPONSE

Associated response	**Trait**	**Variable type**	**Descriptor**
Dispersal	Dispersal syndrome	Categorical	Wind
			Animal
			Wind/animal
	Seed protection tissue	Categorical	None
			Capsule
			Fruit
Adaptation	Inflorescence size	Continuous	Max length when adult (cm)
	Substrate	Categorical	Epiphytic
			Rupiculous
			Epiphytic/rupiculous
			Epiphytic/terrestrial
			Epiphyte / rupiculous / terrestrial

	Leaf size	Continuous	Max lenght when adult (cm)
	Leaf ornamentation	Categorical	Glabrous scales Trichomes (minute) Trichomes (organules)

Associated response	Trait	Variable type	Descriptor
Spatial distribution	Geographic distribution	Numeric	Number of states with confirmed location
	Phytogeographic domains	Categorical	1= Atlantic Forest 2= Cerrado 3= Caatinga 4=Amazon 5=Pampas
	Vegetation type	Categorical	0 = floresta ombrofila mista 1 = else where
	Endemic	Binary	0=non-endemic 1=endemic
Phylogenetic relationship	Taxonomical clade	Categorical nominal	Monocotyledons Eudicotyledons Pteridophyte

Table 8. Pairwise correlation of environmental variables used in RLQ-fourth corner method.

Pairwise comparison		Spearman correlation
d.tree	t.area.av	-33.94
d.tree	pre	-30.45
d.tree	co	-28.02
d.tree	area.ha	-8.18
d.tree	fc.3000	-6.60
d.tree	fc.2000	-5.45
d.tree	fc.1000	-1.97
d.tree	fc.500	11.34
d.tree	h	14.32
d.tree	pap.to	74.19
d.tree	pap.av	68.85
pap.av	co	-57.97
pap.av	pre	-29.57
pap.av	fc.500	31.48
pap.av	fc.1000	15.38
pap.av	fc.2000	8.63
pap.av	fc.3000	8.86
pap.av	h	32.47
pap.av	pap.to	76.80
pap.av	t.area.av	-1.38
pap.av	area.ha	-92.16
t.area.av	area.ha	41.03
t.area.av	fc.500	35.99
t.area.av	fc.1000	34.49
t.area.av	fc.2000	28.24
t.area.av	fc.3000	25.28
t.area.av	pre	46.30
t.area.av	co	9.13
t.area.av	h	57.12
h	area.ha	23.51
h	fc.500	32.77
h	fc.1000	31.05
h	fc.2000	24.44
h	fc.3000	22.01
h	pre	13.06
h	co	-7.45

Pairwise comparison		Spearman correlation
fc.1000	area.ha	80.35
fc.1000	fc.500	92.58
fc.2000	fc.500	82.05
fc.2000	area.ha	89.21
fc.2000	fc.1000	94.33
fc.3000	fc.500	74.63
fc.3000	fc.1000	87.28
fc.3000	area.ha	90.68
fc.3000	fc.2000	97.51
fc.500	area.ha	68.93
x.pesm	fc.3000	-64.32
x.pesm	fc.2000	-51.11
x.pesm	area.ha	-47.32
x.pesm	fc.1000	-32.83
x.pesm	pap.av	-25.87
x.pesm	pap.to	-25.49
x.pesm	fc.500	-24.12
x.pesm	d.tree	-20.13
x.pesm	d.tree.1	-20.13
x.pesm	h	-5.21
x.pesm	pre	33.48
x.pesm	co	13.22
x.pesm	t.area.av	51.99
co	fc.500	-48.74
co	fc.1000	-36.75
co	fc.2000	-31.34
co	fc.3000	-29.80
co	area.ha	-17.10
co	pre	-8.26
pre	fc.3000	37.53
pre	fc.2000	47.75
pre	fc.500	49.20
pre	fc.1000	53.60
pre	area.ha	58.24

Table 9. Summary of the linear mixed effect model for effect traits.

Canopy				Estimate	Std.	z	Pr(<|z|)
Fric	**C**	**-**	**I**	-0.95851	0.25225	-3.8	0.0014
	C	**-**	**E**	-1.45769	0.26051	-5.596	0.0010
	C	**-**	**M**	-1.39715	0.26051	-5.363	0.0010
	C	**-**	**P**	-1.4772	0.41199	-3.585	0.0028
	I	**-**	**E**	-0.49918	0.21303	-2.343	0.1242
	I	**-**	**M**	-0.43864	0.21399	-2.05	0.2311
	I	**-**	**P**	-0.51869	0.38536	-1.346	0.6501
	E	**-**	**M**	0.06054	0.2233	0.271	0.9987
	E	**-**	**P**	-0.01951	0.39081	-0.05	1.0000
	M	**-**	**P**	-0.08005	0.39081	-0.205	0.9996
RaoQ	**C**	**-**	**I**	-0.06414	0.02721	-2.357	0.1207
	C	**-**	**E**	-0.10561	0.02721	-3.881	0.0010
	C	**-**	**M**	-0.0913	0.02755	-3.313	0.0075
	C	**-**	**P**	-0.1281	0.03376	-3.794	0.0013
	I	**-**	**E**	-0.04147	0.01765	-2.349	0.1228
	I	**-**	**M**	-0.02715	0.01827	-1.486	0.5590
	I	**-**	**P**	-0.06396	0.02721	-2.35	0.1226
	E	**-**	**M**	0.01431	0.01827	0.783	0.9323
	E	**-**	**P**	-0.02249	0.02721	-0.826	0.9187
	M	**-**	**P**	-0.0368	0.02755	-1.336	0.6574

Understory				Estimate	Std.	z	Pr(<|z|)
Fric	**C**	**-**	**I**	-0.33263	0.28431	-1.17	0.636
	C	**-**	**E**	-0.28221	0.32118	-0.879	0.810
	C	**-**	**M**	-0.53883	0.37729	-1.428	0.471
	I	**-**	**E**	0.05042	0.22296	0.226	0.996
	I	**-**	**M**	-0.20619	0.29816	-0.692	0.897
	E	**-**	**M**	-0.25661	0.33151	-0.774	0.861
RaoQ	**C**	**-**	**I**	-0.05465	0.02838	-1.926	0.287
	C	**-**	**E**	-0.09068	0.02942	-3.082	0.016
	C	**-**	**M**	-0.10546	0.02941	-3.586	0.003
	I	**-**	**E**	-0.03603	0.01804	-1.997	0.252
	I	**-**	**M**	-0.05081	0.01825	-2.784	0.039
	I	**-**	**P**	-0.07629	0.0335	-2.278	0.141
	E	**-**	**M**	-0.01478	0.01959	-0.755	0.939

Table 10. Linear mixed effect model pairwise comparison between habitat types understory.

Understory				**Estimate**	**Std.**	**z**	**pr(<|z|)**
no reward	C	-	I	-1.584	0.7076	-2.239	0.1291
	C	-	E	-2.234	0.8407	-2.657	0.0446
	C	-	M	-0.03615	0.6646	-0.054	1
	I	-	E	-0.6496	0.6471	-1.004	0.8202
	I	-	M	1.548	0.422	3.669	0.0015
	E	-	M	2.198	0.623	3.528	0.0026
Nectar	C	-	I	-0.543	0.802	-0.677	0.9570
	C	-	E	-0.8322	0.8509	-0.978	0.8510
	C	-	M	-1.1552	0.9294	-1.243	0.7020
	I	-	E	-0.2892	0.5352	-0.54	0.9810
	I	-	M	-0.6122	0.6793	-0.901	0.8850
	E	-	M	-0.323	0.7296	-0.443	0.9910
No water	C	-	I	-0.543	0.802	-0.677	0.9570
	C	-	E	-0.8322	0.8509	-0.978	0.8510
	C	-	M	-1.1552	0.9294	-1.243	0.7020
	I	-	E	-0.2892	0.5352	-0.54	0.9810
	I	-	M	-0.6122	0.6793	-0.901	0.8850
	E	-	M	-0.323	0.7296	-0.443	0.9910
Rhizome	C	-	I	-1.274	0.8225	-1.549	0.4686
	C	-	E	-1.377	0.8979	-1.533	0.4791
	C	-	M	0.1416	0.7871	0.18	0.9997
	I	-	E	-0.1025	0.615	-0.167	0.9998
	I	-	M	1.416	0.4535	3.122	0.0109
	E	-	M	1.518	0.5983	2.538	0.0615
Stem	C	-	I	-4.055	1.027	-3.949	0.0004
	C	-	E	-4.747	1.056	-4.497	0.0001
	C	-	M	-30.94	79820	0	1
	I	-	E	-0.6923	0.3449	-2.007	0.1834
	I	-	*M*	*-26.88*	*79820*	*0*	*1*
	E	-	*M*	*-26.19*	*79820*	*0*	*1*
Stem + leaves	C	-	I	-0.4597	0.8938	-0.514	0.9800
	C	-	E	-1.494	1.001	-1.492	0.4820
	C	-	*M*	*-28.68*	*287700*	*0*	*1*
	I	-	E	-1.034	0.5964	-1.734	0.3300
	I	-	*M*	*-28.22*	*287700*	*0*	*1*
	E	-	*M*	*-27.19*	*287700*	*0*	*1*
Tank	C	-	I	-1.472	1.046	-1.407	0.5467
	C	-	E	-1.59	1.059	-1.501	0.4824
	C	-	M	-3.895	1.354	-2.876	0.0213
	I	-	E	-0.1184	0.3236	-0.366	0.9945

Understory				**Estimate**	**Std.**	**z**	**Pr(<|z|)**
Leaves	C	-	I	-2.713	1.034	-2.623	0.0426
	C	-	E	-5.6	1.308	-4.279	0.0001
	C	-	*M*	*-30.59*	*220000*	*0*	*1*
	I	-	E	-2.887	0.8373	-3.448	0.0030
	I	-	*M*	*-27.88*	*220000*	*0*	*1*
	E	-	*M*	*-24.99*	*220000*	*0*	*1*

Table 11. Summary of the linear mixed effect model pairwise comparison between habitat types.

Canopy				**Estimate**	**Std.**	**z**	**Pr(<|z|)**
No reward	C	-	I	-3.4359	0.5437	-6.319	0.0001
	C	-	E	-4.9877	0.9573	-5.21	0.0001
	C	-	M	-2.8819	0.4925	-5.852	0.0001
	C	-	P	-3.7102	0.9488	-3.911	0.0001
	I	-	E	-1.5517	0.9486	-1.636	0.449
	I	-	M	0.554	0.4671	1.186	0.741
	I	-	P	-0.2742	0.9699	-0.283	0.998
	E	-	M	2.1058	0.9226	2.282	0.136
	E	-	P	1.2775	1.2496	1.022	0.832
	M	-	P	-0.8282	0.9422	-0.879	0.896
Nectar	C	-	I	-5.0079	0.6538	-7.66	0.0001
	C	-	E	-5.2992	0.7009	-7.56	0.0001
	C	-	M	-3.7787	0.4785	-7.897	0.0001
	C	-	P	-4.6479	0.9434	-4.927	0.0001
	I	-	E	-0.2913	0.7865	-0.37	0.996
	I	-	M	1.2292	0.5999	2.049	0.228
	I	-	P	0.36	1.0395	0.346	0.997
	E	-	M	1.5205	0.6476	2.348	0.121
	E	-	P	0.6513	1.0698	0.609	0.972
	M	-	P	-0.8692	0.9392	-0.925	0.879
Oil	C	-	I	-26.1889	610.41	-0.043	1
	C	-	E	-4.774	301.40	-15.838	1
	C	-	M	-26.3001	644.92	-0.041	1
	C	-	P	-34.8955	30029.53	-0.001	1
	I	-	E	21.415	610.41	0.035	1
	I	-	M	-0.1111	887.99	0	1
	I	-	P	-8.7066	30035.74	0	1
	E	-	M	-21.5261	644.92	-0.033	1
	E	-	P	-30.1215	30029.53	-0.001	1
	M	-	P	-8.5954	30036.46	0	1
None water	C	-	I	-3.6881	0.743	-4.964	0.0001
	C	-	E	-5.8305	2.005	-2.908	0.0242
	C	-	M	-1.6711	0.421	-3.97	0.0001
	C	-	P	-2.1614	0.697	-3.1	0.0132
	I	-	E	-2.1424	2.083	-1.028	0.8197
	I	-	M	2.017	0.705	2.861	0.0278
	I	-	P	1.5267	0.916	1.667	0.4135
	E	-	M	4.1594	1.992	2.088	0.1952

Canopy				Estimate	Std.	z	Pr(<|z|)
Rizhome	C	-	I	-2.27E+00	0.4674	-4.859	0.0001
	C	-	E	-3.78E+00	0.8885	-4.252	0.0001
	C	-	M	-2.28E+00	0.4697	-4.863	0.0001
	C	-	P	-3.02E+01	526600	0	1
	I	-	E	-1.51E+00	0.9466	-1.592	0.4362
	I	-	M	-1.30E-02	0.5721	-0.023	1
	I	-	P	-2.80E+01	526600	0	1
	E	-	M	1.49E+00	0.9477	1.576	0.4463
	E	-	P	-2.65E+01	526600	0	1
	M	-	P	-2.80E+01	526600	0	1
Stem	C	-	I	-5.394	1.1035	-4.888	0.0001
	C	-	E	-7.1486	1.1699	-6.111	0.0001
	C	-	M	-8.1592	1.248	-6.538	0.0001
	C	-	P	-4.9041	1.3802	-3.553	0.0029
	I	-	E	-1.7547	0.4771	-3.678	0.0019
	I	-	M	-2.7653	0.7121	-3.884	0.0010
	I	-	P	0.4898	1.1465	0.427	0.9921
	E	-	M	-1.0106	0.8134	-1.242	0.7033
	E	-	P	2.2445	1.2105	1.854	0.3164
	M	-	P	3.2551	1.2861	2.531	0.0743
Stem + leaves	C	-	I	-6.02E+00	1.297	-4.643	0.0001
	C	-	E	-2.91E+01	11370	-0.003	1
	C	-	M	-5.40E+00	1.293	-4.176	0.0001
	C	-	P	-3.10E+01	159500	0	1
	I	-	E	-2.31E+01	11370	-0.002	1
	I	-	M	6.23E-01	0.2469	2.521	0.0492
	I	-	P	-2.50E+01	159500	0	1
	E	-	M	2.37E+01	11370	0.002	1
	E	-	P	-1.96E+00	159900	0	1
Tank	C	-	I	-6.12	0.8591	-7.123	0.001
	C	-	E	-5.2529	0.8414	-6.243	0.001
	C	-	M	-5.7986	0.8491	-6.829	0.001
	C	-	P	-30.2273	82571.75	0	1
	I	-	E	0.8671	0.283	3.064	0.012
	I	-	M	0.3213	0.3094	1.039	0.793
	I	-	P	-24.1073	82571.75	0	1
	E	-	M	-0.5458	0.2545	-2.145	0.1508
	E	-	P	-24.9745	82571.75	0	1
	M	-	P	-24.4287	82571.75	0	1

Canopy				**Estimate**	**Std.**	**z**	**Pr(<|z|)**
Leaves	C	-	I	-7.2564	0.9467	-7.665	0.001
	C	-	E	-10.5639	1.4218	-7.43	0.001
	C	-	M	-8.2991	0.9824	-8.448	0.001
	C	-	P	-31.4431	71697.33	0	1
	I	-	E	-3.3075	1.1013	-3.003	0.0144
	I	-	M	-1.0426	0.4007	-2.602	0.0481
	I	-	P	-24.1867	71697.33	0	1
	E	-	M	2.2648	1.1352	1.995	0.207
	E	-	P	-20.8792	71697.33	0	1
	M	-	P	-23.144	71697.33	0	1

Chapter 5.

General discussion

5 General discussion

In this thesis, I investigated how human-modification of the landscape in the Brazilian Atlantic Forest (BAF) impacts biodiversity and functional patterns. Specifically, the thesis has provided substantiated empirical evidence of the effects of anthropogenic induced disturbance on vascular epiphyte assemblages. Firstly, I assessed the differences in epiphyte diversity, community composition and ontogeny stages in the canopy stratum between continuous and human-modified forests (HMF). Secondly, I quantified and predicted the area most favourable for forest epiphyte species' abundances by looking at the magnitude and extent of edge effects. Finally, I used life-history traits to understand epiphyte species sensitivity to habitat loss and the potential consequences for ecosystem functioning. I have integrated novel and classic methods to unravel the different facets of habitat loss and fragmentation across the vertical as well the horizontal gradient of the forest.

The overall goal of this thesis was to provide quantitative evidence of the role of human-induced environmental changes on canopy plants. Here I will summarise the main findings of the chapters with respect to these three questions, explain how they fit in with the current state of scientific theory, and discuss the avenues of research they opened up.

5.1 The debate of old-growth forest vs human-modified forest

There is an increasing scientific, political and social interest in reforestation and recuperation of human-modified forests. From the scientific side, a plethora of approaches have been proposed for succession, restoration and landscape management, with the aim of supporting conservation decisions (Chazdon, 2014). From the political side, several worldwide initiatives have been agreed to restore forests and landscapes.

Throughout my thesis, I showed one of the most pervasive effects of habitat loss in many components of biodiversity in human-modified landscapes. Hence, my thesis supports the idea that old-growth continuous forest is without doubt the best, and probably the only shelter for many vascular epiphytes dwelling in such a highly fragmented landscape. Thus, showing evidence of the unparalleled role of old-growth forest in sustaining biodiversity in the tropics (Gibson *et al.*, 2013).

In contrast, human-modified forests present a totally uncertain future for epiphytes. The low numbers of seedlings and juvenile individuals in the HMFs will only exacerbate these differences in future. Furthermore, intrinsic biological constraints of epiphytes species, such as a very low seed survival (Mondragón, Valverde & Hernández-Apolinar, 2015), a pronounced slow growth rate (Zotz, 2016), a general higher mortality rate than of tropical trees (Zuleta *et al.*, 2016), and the absence of seed banks for later re-colonization (Zotz, 2016), reduces the likelihood of long term survival of forest-dependant epiphyte species in HMFs. After all, the presence of a species does not imply a viable population in the future, resembling Janzen's 'living deads' definition (Janzen, 2001). Woods and Dewalt (2013) found a recovery of 74% species richness and 75% community similarity in vascular epiphytes after 115 years of disturbance. However, these authors did not address the fundamental issue that HMFs are embedded (or not) in a fragmented landscape. This would imply that HMFs in low fragmented landscapes, such as the one found in Woods and Dewalt

(2013), is likely to be more prone to rescue events or mass effects than highly modified landscapes, like my study area, due to the habitat amount in the landscape (Fahrig, 2003, 2013). Therefore, the potential pervasive effects of lower structural connectivity would enhance the detrimental effect of habitat loss in epiphytes communities (Fahrig, 2003).

However, HMFs still harbour important ecosystem functions (chapter 4), especially in the canopy, that can potentially be managed to promote and enhance the offer of functional groups in the ecosystem. Changes alongside to forest restoration programs integrating trees and epiphytes might favour restoration as a whole. I argued that in the light of current political willingness in prioritization of conservation resources for management of HMFs, these activities should be addressed to preserve habitat amount and core area. Actions such as the conservation of non-exploited patches especially nearby protected areas (Padmawathe, Qureshi & Rawat, 2004), allowing the persistence of large trees within forests (Wolf, 2005), and increase forest core area (as proposed in chapter 3). Such actions align with Banks-Leite et al (2014) proposal of maintaining or restoring at least 30% of forest cover in the BAF through set-aside programs.

Although there is no guarantee that these actions would have a real impact on ecosystem functions provided by epiphytes, there are some complementary activities that can be carried out to increase the chances of success on epiphytes communities (discuss in Implication for forest conservation and management).

5.2 The core-area in the landscape as the suitable habitat amount for epiphytes

In chapter 3, my results strongly suggest that due to edge effects, the habitat “suitable” for epiphytes is much smaller than the current size of the forests in the landscape and BAF. I estimated that only 19.4% of the current forest in BAF have core areas (500 m inside the forests), and that 85% of the total species pool require forest core conditions. Hence, small forest fragments with the whole fragment less than 500 m away from sharp discrete edges might be unsuitable for epiphytes as they would be so heavily influenced by forest edge effects. These small "core-area" forest fragments may support some species, but will most likely have fewer abundances of species that demand forest core conditions, or may act as stepping stones (Pfeifer *et al.*, 2017; Ries *et al.*, 2017; Didham & Ewers, 2012).

In chapter 2 and 4, I found that forest cover (at 500 and 1000 m radius) was an important predictor for community composition and functional structure. On the other side, the patch size or proximity (as a measure for landscape connectivity) between the equal-sized sample sites used here did not influence epiphyte communities. These findings suggest that the suitable habitat for epiphytes is the combination of habitat amount and core area. Core area represents a free zone of edge-influence. Laurence and Yensen (1991) and later Didham and Ewers (2012), along with other empirical studies (Banks-Leite, Ewers & Metzger, 2010), showed that edge effects constrained the habitat for species and communities. Likewise, my results align with the habitat amount hypothesis (Fahrig, 2013). Fahrig posits that species richness in the landscape is a product of the sample area, rather than a result of patch size and the patch isolation effect.

The quantification of the habitat amount and the estimation of the core area free of edge influence would likely favour epiphytes and therefore might serve as better predictors of species abundance and community composition than each of them on their own. Lefebvre's (2016) approach accounts for the proximity and the effects of the surroundings as a continuum of the additive effects of multiple edges. These features and the ability to provide an estimation of the edge sensitive per species makes this spatially explicit model as one of the best to represent edge effects. However, it uses a fixed radius of 1 km of the local landscape. This fixed local landscape might constraint some taxonomical groups that are more or less sensitive to this radius. I found 500 m and 1000 m to be relevant for epiphytes, which in turn might be sufficient to do not present (dramatic) errors in the estimations, albeit a cross-validation should be carried to rule out completely this potential error (

Figure 5-1).

If possible edge effects and habitat amount should be quantified to calculate the suitable habitat for epiphytes communities, otherwise Lefebvre's (2016) approach offers a good alternative account for edge influence. The adequate quantification of the magnitude and extent of edge effects are one of the main goals to achieve in conservation management because it comprises a powerful force reducing the habitat suitable for species. For conservation purposes, it is important to find out where edge effects occur and where they do not occur, and so protected areas or large areas with core area are invaluable for the conservation of these species.

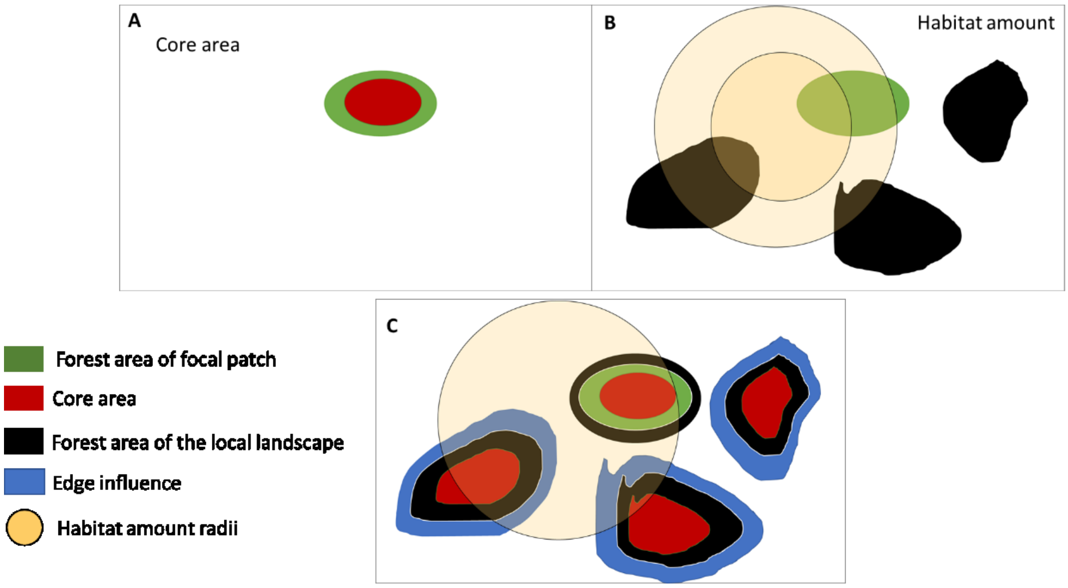


Figure 5-1. Schematic representation of the "core area", "habitat amount" and “edge influence” approaches. A) Core area based on Laurence and Yensen (1991), a spatially implicit model that does not account for the surroundings. B) Habitat amount based on Fahrig (2013), a spatial explicit approach that account for the habitat cover within a certain radius, so called “local landscape”. C) edge influence across the landscape as Lefebvre et al (2016) proposal. Representing, area of the focal habitat (green); core area after accounting for edge influence (red); forest fragments in the local landscape (black); edge influence (blue), and radius of the calculation of habitat amount (cream circle).

5.3 The causes and consequences of anthropogenic disturbance of habitats on vascular epiphytes

Species and community changes can destabilise ecosystem functioning through the loss of the functions these species perform and through changes in interactions with other species (Díaz & Cabido, 2001). Here I summarise the causes, vulnerabilities and consequences that anthropogenic disturbance exerts on epiphyte communities (**Figure 5-2**).

5.3.1 The causes

Habitat loss and fragmentation are the main forces that are driving changes in species worldwide (Fahrig, 2003; Barnosky *et al.*, 2011). After fragmentation fragmented forests are created and their boundaries are influenced by the surroundings. In chapter 2, I found lower species richness and abundance, and a shift in ontogeny patterns in HMFs compared to old-growth forests. In chapter 4, I also found a detrimental pattern in the functional structure of communities and guilds in HMFs. These results might suggest that species loss and functional structure are strongly linked. In agricultural landscapes, plant species richness and functional richness are more tightly linked together than both richness in mobile organisms, hence the loss of plant species would have direct effects on the number of ecosystem functions they perform more than would happen in animals (Flynn *et al.*, 2009). I found a positive relationship between species richness and functional richness (appendix Figure 11-3).

Forest cover and edge effects are also important drivers affecting the abundance of forest-core preferring species (chapter 3, and discussion 5.2). There is a widely consensus that forest edges affect communities in different levels and their response would be modulated by the way species interact with their contrasting habitat (Ries *et al.*, 2017; Haddad *et al.*, 2015a). In my study, edge effects reduce the habitat suitable for epiphytes and their effect is likely to be ubiquitous across BAF. In chapter 4, although not directly tested, there was a pattern of the reduction of more scarce strategies towards the edge and matrix. Functional diversity was also lower on forest edges for productivity traits, reducing the potential of forests to store carbon (Razafindratsima *et al.*, 2018).

5.3.2 Vulnerabilities of epiphyte species

Certain life-history, morphological, and physiological traits make some species more susceptible than others to disappearance after disturbance (Sodhi, Brook & Bradshaw, 2009).

For instance, large-sized, specialised species, with narrow distributions, and poor use of the matrix seem to be the response traits with high sensitivity to fragmentation and habitat loss (Henle *et al.*, 2004). My findings align with this general pattern; highly specialised species with short dispersal ranges, i.e. endemic epiphytes, are more prone to local extinction after disturbance (chapter 2 and 3). For instance, Brook et al. (2003) and Dodson and Gentry (1991) have both reported local extinction of endemic epiphyte orchids. Old-growth forest harbours this highly sensitive diversity. In my study I also found eight species of conservation concern and two species considered extinct in the wild in the Sao Paulo state (MAdESP, 2016). In contrast, traits associated with high dispersal ranges and high adaptability to colonize different forest types (as discussed in Chapter 4), provide other species with the ability to remain in the disturbance gradient (Males & Griffiths, 2017).

5.3.3 Consequences of the loss of species and ecosystem functions

The extinction of certain species has been shown to lead to biotic homogenization and cause cascading effects on ecological processes (Sodhi, 2008; Díaz *et al.*, 2013). I found a large disappearance of functional guilds which provide valuable resources for insects and herpetofauna, and hydrological cycling functions (Chapter 4). The functional redundancy hypothesis (or functional insurance, Naeem 1988) posits that resilient systems would be able to afford losses of certain groups because there would be another group with the same function that could replace them in their role. This resilience therefore counterbalances the effect of species extinctions. In chapter 4, I found that continuous old-growth forest hosts the largest functional richness and functional redundancy in the study area, which results in high ecological resilience to local extinctions that may aid these communities in coping with the potential losses of species or populations in the future. In contrast, the fragmented landscape has low ecological resilience, and most importantly, there were some functions that disappeared which might have impacts on ecological processes.

The consequence of preserving ecosystem functions by these epiphytes might have real economic impact. For instance, the addition of the canopy biomass could represent an increase of 2% in the carbon storage budget of an ecosystem (Gómez González *et al.*, 2017), which, although small, would represent an increment in REDD carbon credits for farmers and governments. However, more research is needed into how to best measure the ecosystem functions provided by epiphytes and the consequences of their loss.

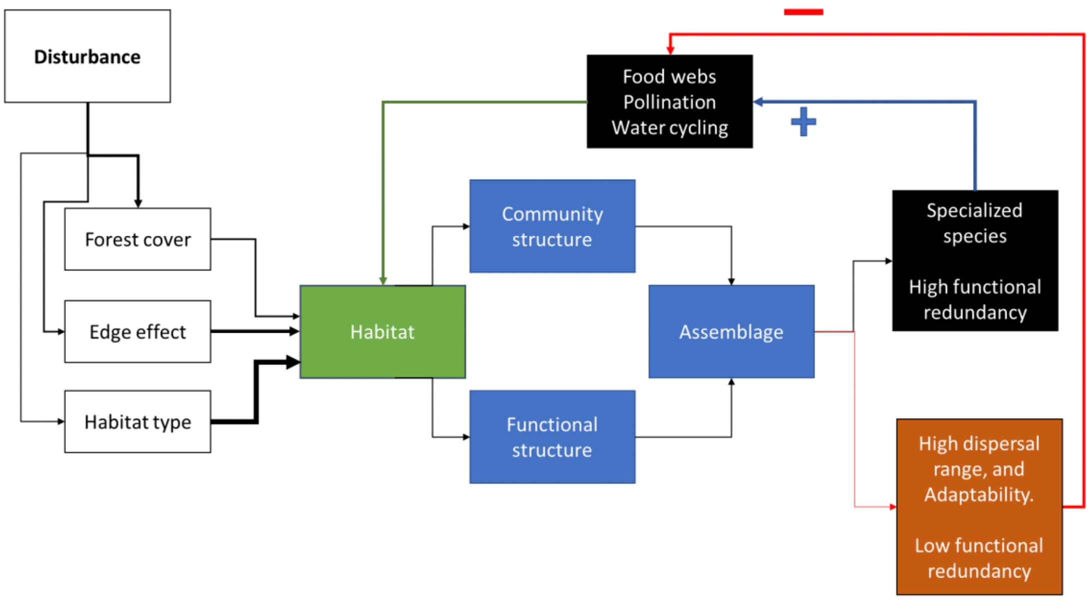


Figure 5-2. Schematic representation of the causes, vulnerabilities and consequences of human disturbance on vascular epiphytes communities. From left to right. Anthropogenic disturbance occur in the form of changes in forest cover and habitat type, and edge effects and exert pressure on habitats (the strength of line indicates the importance of the driver). These pressures are then act on community structure, i.e. species richness, abundance, community composition, and ontogeny, and the functional structure of the habitat, i.e. functional richness, divergence and functional guilds (blue boxes). The changes in the structure of communities and functions will then shape the community assemblage of either forest fragments or old-growth forests. These assemblages will be composed of species vulnerable to disturbance that will negatively impact the offer of ecosystem functions (red line low ecosystem resilience), or species with specialised functions that positively impact the ecosystem functions (blue line positive). Finally, these ecosystem functions feedback into the habitat which can either buffer or not buffer the impact of disturbance.

5.4 No time for global warming

A plethora of scientific evidence have shown that climate changes impose new requirements for many species to shift their ranges in order to remain within environmentally tolerable areas (Travis, 2003). Climate change models differ for the Atlantic forest although rising global temperature (RCP2.6 scenario: 0.4-1.6 ºC, and RCP8.5 scenario: 1.4-2.6 ºC) and increasing of precipitation are expected (IPCC, 2014). Recent models of climate change

(RCP2.6; RCP8.5) and ecological niche models in the Atlantic forest have suggested reduction of beta diversity and biotic homogenization by expansion of current species distributional limits rather than spatial turnover (Zwiener *et al.*, 2018)

Climate changes will impact epiphytes in many ways. First, Zotz and Bader (2009) found that the most important threat of climate change to vascular epiphytes is through changes in the altitude of cloud formation and altered precipitation patterns and fog. Atmospheric water is the main water source for many epiphytes. Therefore, alterations in hydrological patterns will have a dramatic effect on the distribution and abundance patterns of epiphytes. Second, the highly fragmented landscape enhance the pressure from the matrix to the forest interiors (Driscoll *et al.*, 2013). The type of matrix (pastureland or plantation) will modify edge effects and alien invasive species' susceptibility of the forests. For instance, in canopies a rise in liana densities as a result of edge effects is linked to driving changes in tree mortality and tree composition (Dislich & Mantovani, 2016; Schnitzer & Bongers, 2011). Third, abiotic changes might cause shifts in the life-cycle or body size of pollinators, which may lead to asynchrony in the pollinator-flowering relationship (Rafferty & Ives, 2011; Damon & Hernández-Ramírez, 2012).

The increasing temperature and reduced precipitation scenario provides an opportunity for pastureland, matrix, and forest edge-preferred species, such as atmospheric bromeliads, to become prevalent due to a set of physiological mechanisms to tolerate or avoid drought conditions (Males & Griffiths, 2017). These species can endure high temperature shifts between 3-4°C, plus their seed germination can endure temperatures of around 35°C (Müller, Albach & Zotz, 2018). Other strategies to cope with drought conditions have been reported in orchids widely spread in open habitats. For instance Zhang et al. (2016) found that *Coelogyne corymbosa* performes drought avoidance by enhancing water uptake and storage, and by reducing water losses, while co-occurring orchid *Pleione albiflora* employs a drought escape strategy, i.e. individuals complete their life cycle and remain dormant until more favoured conditions appear, by fixing carbon during growing season and minimizing transpiration by leaving a dormant pseudobulb. Furthermore, these species have an reproduction strategies such as the constant provision of rewards for long distance and wide spread pollinators, which will assist long distance pollination and ensure of pollination (Benzing, 2000)

However, some species might be stuck in an “ecological trap”, so these sessile species can be seen as remnants of past conditions, with current the habitat too hostile to harbour offspring, as Janzen’s “living dead” (Janzen, 2001). The species could also be maladapted to high temperature that experimentally have been shown to cause high leaf mortality, and low leaf longevity and production, as well as drastic mortality in the germination of shaded-preferred species such as some orchids and peperomias (Nadkarni & Solano, 2002; Winkler, Hülber & Hietz, 2005; John & Hasenstein, 2017). Hence, the current population of a species is potentially too small to ensure viable population sizes in the future.

Also, many epiphytes, such as orchids (Nunes *et al.*, 2017), have a specialized pollination system, so the disruption of the pollinator-flowering relationship would likely lead to reduction of population size (Mondragón, Valverde & Hernández-Apolinar, 2015). Consequently, detrimental cascading effect on species and ecosystem functions.

The pattern of “winners” and “losers” in the habitat loss and fragmentation is expected to be similar under rising temperature scenarios. Nonetheless, while these changes are expected in the near future for many other species, for epiphytes in the studied landscape, and probably to other similar highly fragmented landscape, it might be too late to wait for those disruptions, because these assemblages might have already paid (extinction debt), and due to the low population size will continue to pay (relaxation time), the price of human disturbance of the habitat.

5.5 Prediction of future of epiphytes communities in these fragmented landscapes

I demonstrated that the anthropogenic transformation of the landscape leads to reduction in population sizes, a shift in species composition and consequently to the loss of functional diversity and richness. Although my thesis did not directly assess extinction debt or relaxation time, it seems clear that these vascular epiphytes are undergoing an extinction process due to the low habitat amount at the landscape scale. Also, my findings identified community composition and the distribution of different ontogeny stages as strong indicators of habitat loss.

The future will be quite dramatic for vascular epiphytes. Species that do not tolerate disturbance will likely disappear in the fragmented area, primarily due to reduced population sizes. However, minimal loss in functional diversity is expected because most of the functions (e.g. nectar reward and tank water storage) are traits reported in wide spread species with a long-distance range and a high ability to colonise different type of forests. Therefore, these communities have probably surpassed the tolerance threshold and the remaining functional pool (along with the species with these traits) is the one that will either endure or thrive under harsh environmental conditions in highly fragmented landscapes.

6 Implication for forest conservation and management

My results support the notion that old-growth forests (or “intact forest” or “primary forest”) support an exceptional amount of diversity and ecosystem functions that are almost lost in fragmented landscapes. In addition, services associated to old-growth forests include water provision, indigenous and rural culture heritage, and direct and indirect impacts on human health (Watson *et al.*, 2018). Therefore, I join the voice of many researchers who argue that maintaining and improving the landscape and habitat quality of this forest type is imperative to safeguard ecosystem functions and biodiversity (Watson *et al.*, 2018; Gibson *et al.*, 2013).

On the other hand, recent initiatives which plan forest restoration of 300 million hectares worldwide make the improvement of human-disturbed forests the current conservation action (Bonn Challenge, 2011; Aichi target, 2011; New York Declaration on Forests, 2014). Although my results in the fragmented area showed highly disrupted patterns of biodiversity, it stills harbours opportunities to retain certain ecosystem functions. Restoration strategies to maintain vascular epiphytes should be directed towards combining setting-aside areas, to increase habitat amount at the landscape scale (Banks-Leite et al. 2014), with planned of enlarging core area actions, via reducing the area-perimeter ratio and/or expanding the narrowest sections of large fragments. The amount of core habitat in a fragment has a higher ecological impact on communities than the total area does (Didham & Ewers, 2012; Ewers & Didham, 2007). This initiative may preserve non-exploited patches (Padmawathe, Qureshi & Rawat, 2004), allowing the persistence of large trees within forests (Wolf, 2005), and increasing forest core area, which may benefit the functional structure in epiphytes.

Lastly, although speculative, a more active and extensive intervention strategy could be carried out to enrich habitat quality to rescue this group. For instance, focal initiatives, such as transplanting individuals from the richest forests, and ex-situ propagation programs might also be established to recover epiphyte communities. Indeed, Duarte (2013) found high adaptability of epiphyte individuals transplanted amongst different forest types. This measure is relatively inexpensive and has minimal impact on source populations if fallen plants are used (Fernandez Barrancos, Reid & Aronson, 2017; Reid *et al.*, 2016). Micro-propagation has also been successfully used to increase the population size of orchids, bromeliads and aroids, in a shorter time and with a lower mortality rate than under natural conditions (Zotz, 2016; Salazar Mercado and Cancino 2012). Unless some serious actions are taken, there is no future for many epiphyte species and populations in human-modified landscapes like the one studied here.

7 Methodological caveats

I here refer to the limitations of my research and methods that might have influenced my results. As such I will discuss three main caveats. 1) The control for the sampling design; 2) the use of a spatially explicit model to estimate the extent of edge effects (chapter 3), and 3) the use of life-history traits (chapter 4).

The sampling design was carried out by the Brazilian team of the Biodiversity and Ecosystem Functioning in Degraded and Recovering Amazonian and Atlantic Forests" (ECOFOR) research project. Therefore, the design was not explicitly made for epiphytes. Several methods have been proposed to assess vascular epiphytes (Zotz & Bader, 2011; Gradstein *et al.*, 2003; Wolf, Gradstein & Nadkarni, 2009; Flores-Palacios & García-Franco, 2001; Mendieta-Leiva & Zotz, 2015). To reduce potential bias associated to the experimental design, I ran two pilot activities before starting fieldwork. First, I randomly sampled 8 trees along two plots (edge and interior) in the fragmented forests to estimate the sampling effort. I found that due to the low species richness in the area two to three canopies would be enough for species richness (data not shown). However, because my study comprised canopies in the control forest and the richness was expected to be higher I decided to account five trees per plot bearing the recommendations of Zotz and Bader (2011) to sample the largest trees in the control forest

In chapter 3, we use few distance classes (matrix, edge, and interior) to capture edge effects, which was not enough to account for the whole magnitude (Ries *et al.*, 2017), and the assumption of equal habitat suitability across the landscape of the BioFrag® model (Pfeifer *et al.*, 2017). However, the direction in the community integrity pattern and the lower species richness and total abundance within the fragmented landscape (vs old-growth forest), demonstrating the pervasive edge effects (Haddad *et al.*, 2015a). Furthermore, the combination of a small core area in the landscape (629 ha), a large number of small patches (96% of total patches <100 ha), and a long history of fragmentation (Ribeiro *et al.*, 2009), means that the conditions favour only a few widely spread species, such as atmospheric Tillandsoids (Lôbo *et al.*, 2011; Tabarelli, Peres & Melo, 2012).

In chapter3, I used Biofrag® that assumes that all fragments are suitable for epiphytes and that they can host a representative number of species. Studies in epiphyte ecology have given contrasting patterns in their response to habitat disturbance (reviewed in Zotz, 2016). Werner et al. (2011) suggested that natural drier climate will host fewer epiphytes due to the low water availability and therefore the lower sampled richness could be an effect of natural drought conditions rather than disturbance. To rule out this caveat, I set-up one pilot plot within four of the forest fragments of the experimental design, with the same dimensions (10 x 250 m) and sampled trees in the same fashion. I found high levels of richness (observed richness) and the pilot plots were found to have similar forest structure as the sampled plots.

In chapter 4, the use of categorical traits, low statistical explanatory power and null model testing, may have influenced the power in unravelling the patterns of functional traits. Three main issues have been pointed out against the use of categorical groups in trait-based ecology studies. Firstly, coarse categories may mask variability and underestimate the important role that functional diversity plays in maintaining key ecosystem functions (Wright et al., 2006). Secondly, similar functional groups have been shown to respond differently to environmental variation (Funk, 2008; Firn et al., 2010, 2012; Han et al., 2012). Thirdly, the use of categorical groups may reduce the functional variability and therefore statistical power to reject a false null hypothesis (type II error). Despite these potential issues, the metrics and models used here were sufficient to reveal the pattern of habitat loss in the canopy. Furthermore, the identification of traits associated with dispersal and specialism align with findings from empirical studies based on physiological and morphological traits (Rodrigues et al., 2013; Poltz & Zotz, 2011; Stuntz & Gerhard Zotz, 2001; Cascante-Marín et al., 2006). In this regard, the lack of detectable patterns in response traits in the understory might be a result of traits that could not represent the variance in the gradient, hence it would be recommended to assess other traits related to dispersal and adaptation. Another potential caveat is the low explanatory power of functional structure metrics that might hamper our understanding of the patterns (below to 50%; e.g. Gagic et al. 2015; Jonason et al. 2017). However, the explained variation of our models oscillated between 19-68%, which reveals a rather conservative but consistent performance of our models. Despite of these caveats, the strong pattern in our study across metrics in functional structure implies that our method was appropriate to detect the dominant patterns along the gradient. Nonetheless, caution must be taken about the magnitude of the effect.

8 Future directions

8.1 Assembly rules

What can we infer about the ecological processes that drive community assembly? My study gives insights into the use of life-history functional traits to unravel the processes and mechanisms of community assembly of epiphytes in human-modified landscapes. I think that a step forward would be to refine the set of traits and functions at a global or regional scale to test whether there are deterministic or stochastic processes in operation. For instance, we could test the components of assembly or disassembly under different land-uses or degrees of modification of the landscape.

As stated before, epiphytes and terrestrial plants are inherently different. Biotic, neutral, and abiotic filters have been shown to influence assemblage and act simultaneously in terrestrial plants (Garnier, Navas & Grigulis, 2016). However, biotic filtering has shown no effect in shaping epiphytes communities due to several reasons: Intraspecific competition and facilitation are in general not important in shaping epiphytes communities due to low densities within and among host trees. We found low species densities per tree (0.08-0.78 species per tree, data not shown) which leads to a lower chance of intraspecific interaction (Mondragón, Valverde & Hernández-Apolinar, 2015). Pathogen attacks or herbivory are also unimportant for shaping assemblages, although few cases of floral structures herbivory attack have been seen in bromeliads and orchid (Zotz, 2016). Host specificity has been shown to be negligible in the majority of cases, where common epiphyte species interact with common hosts (Laube & Zotz, 2006; Wagner, Mendieta-Leiva & Zotz, 2015). Finally, high population dynamics in natural or disturbed habitats lead to unsaturated patterns within hosts (Einzmann & Zotz, 2017; Flores-Palacios & Garcia-Franco, 2006). Density-dependency has also been argued to be unimportant in shaping populations (Mondragón, Valverde & Hernández-Apolinar, 2015).

Vascular epiphytes are a great model group to study the rules governing community assembly by potentially reducing it to two mechanisms, stochasticity and abiotic ecological filtering. However, this remains untested either experimentally or empirically in the functional dimension of vascular epiphytes.

8.2 Phylogenetic signal

The dataset of functional traits compiled here might serve as the baseline for studies integrating functional traits, phylogeny, and ecosystem resilience. Functional traits are expected to be evolutionarily closely related among congener's species, because they tend to be ecologically similar and respond similarly to selection. Epiphytism is a life-growth form that comprises over 27,614 species represented in 913 genera in 73 families (Zotz, 2013b), where all species share the same constraint of the initial availability of a host tree.

Studying the combination of functional traits and phylogenetic signal, i.e. tendency to be more similar in closely related species than in distant relatives, will help to unravel patterns in the response of ecosystems and ecological processes to habitat loss (Harvey and Pagel 1991; Freckleton et al. 2002; Ackerly 2009). It is noteworthy that closely related species do not necessary show functional equivalence. For instance, orchids and bromeliads have evolved from adaptive radiation events that have resulted in a diverse number of species that colonise the canopy, understory, aquatic and rocky systems (Benzing, 2000; Jost, 2004; Givnish *et al.*, 2007).

It would be reasonable to test the extent of evolutionary diversification on the generation of trait diversification, which in turn may result in greater niche complementarity, and might have a role in ecosystem resilience to human disturbance.

9 Outreach activities

As a scientist one of my main responsibilities is to communicate my research and scientific findings to a wide variety of society. There is an increasing awareness of the need for more interaction between scientists and the general public (Devonshire & Hathway, 2014). However, the willingness of scientists to interact in person to the general public has been shown to be moderate (Rainie *et al.*, 2015). Here, I document two events organized by myself in the municipalities of Sao Luiz do Paraitinga and the National Park Serra do Mar, Sao Paulo Brazil.

The first activity was set-up in Sao Luiz do Paraitinga on 29th of July 2016. I set up three different stands to illustrate the life-cycle of epiphytes, the ecological interactions with other groups, and the uses of fruits and flowers by the rural communities. To this activity I invited the staff of the Serra do Mar Park, a musician to play the guitar and Ms Suzanna Martins a widely recognize Brazilian expert in bromeliads. The activity lasted 6 hours and we had around 200 students from the “Waldemar Rodrigues” primary and secondary school, ten communal leaders and around 50 more people from the general public. The second activity was carried out in the National Park with 25 staff, technicians, park guards and admin personal. This was a 4-hours workshop, two hours theory and two hours practice in the orchid nursery about orchid identification, conservation and ecosystem functions. These outreach activities were set up with the help of the local government of Sao Luiz do Paraitinga.

The scientific community and the public benefit from improving communication of basic scientific research in simple terms and to actively listen to the needs of society. I am very confident that having a science-literate or even sympathetic public has key implications for our society and for the perception that might come for public funding of research.

Figure 9-1 Outreach activities in Sao Luiz do Paraitinga. Feira ecologica "os tesouros escondidos do Vale do Paraiba". A) Escola municipal group 1 teachers and students. B) Students of secondary school testing GPS garmin device, laser, and canopy climbing gear. C) Students of primary school learning the difference between bromeliads. And D) school kids group 3 primary school in the demonstration of how epiphytes are pollinated. Photos from the author.

10 **Overall conclusion**

The transformation of the landscape by humans exerts negative impacts on all facets of the biodiversity of epiphytes, is a driving force in affecting a particular set of response traits and reduces the potential of vascular epiphytes to provide ecosystem functions. This scenario is worrying because human-modified forest has become the most widespread type of forest worldwide (60%), and is expected to increase, either by the transformation of continuous landscapes, or by the recovery of abandoned areas (Hansen *et al.*, 2013). However, in the meantime, continuous old-growth forest is the only habitat that can maintain the full potential of ecosystem functions delivered by vascular epiphytes.

The charismatic orchids, bromeliads and aroids are now scarce in a once picturesque landscape flourished with life and diversity. However, this colourful component of the flora can now only be seen in protected areas, where they bloom in harmony with bees, beetle, frogs and snakes that are usually supported by them. One last thing remaining in the HMTFs is the services that resilient epiphytes are still providing. This in turn, although I did not scientifically test of whether they will provide support for a future of populations, the remaining individuals give hope in case of improvements of habitat quality and active restoration actions.

11 Literature

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Appendix

Figure 11-1. Photos of the study area. Top pastureland, center HMFs, and bottom the canopy of old-growth forests.

Figure 11-2. Species found in the reserve. From top to bottom; *Zygopetallum maxillare*, *Tillandsia gardneri*, *Vriesea erythrodactylon*; and *Vriesea simplex*

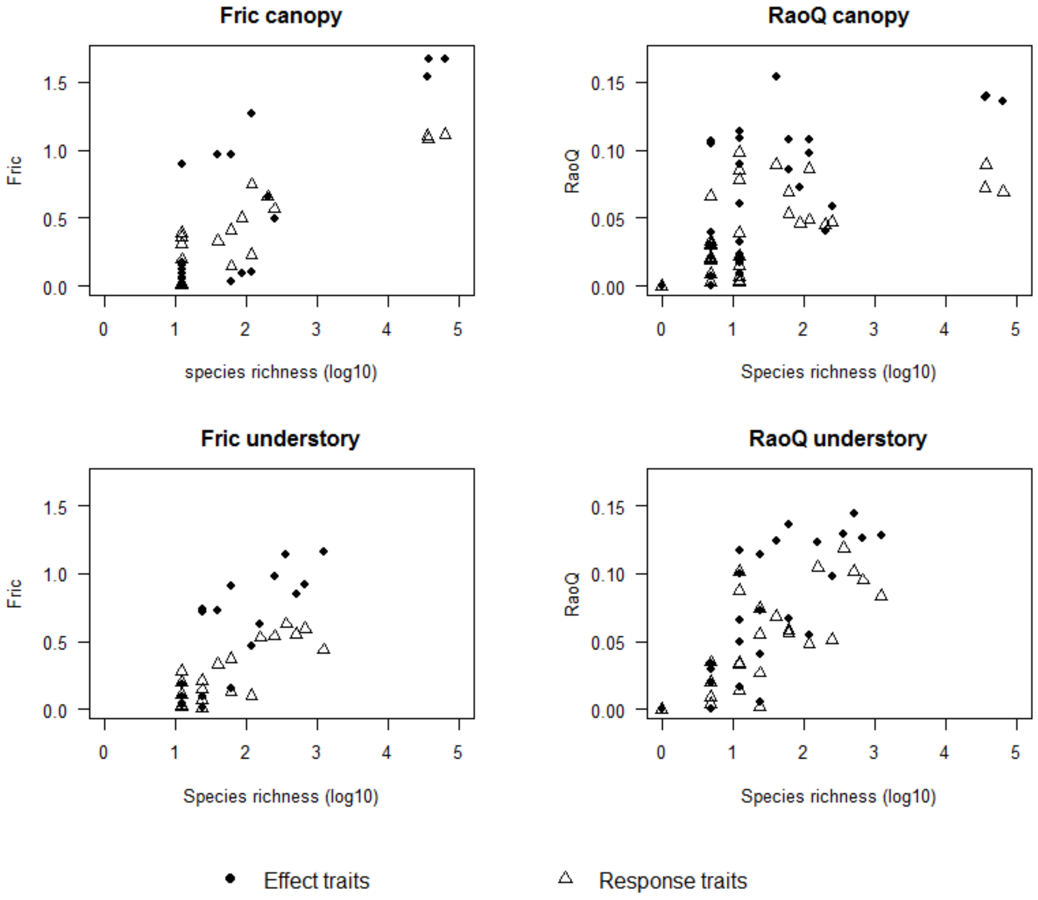

Figure 11-3. Functional richness and RaoQ relationship with species richness (log10)

11.1 Full dataset for life-history traits are available in:

https://www.dropbox.com/sh/1x6a28u198kpsed/AABeEnVNcJorSiwkgE-cVNB0a?dl=0