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ASSESSING THE EFFECTS OF LANDSCAPE STRUCTURE ON THE RELATIONSHIP BETWEEN SPECIES DIVERSITY AND FUNCTIONAL DIVERSITY

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Abstract

Promoting the conservation of multiple aspects of biodiversity in transformed landscapes is a fundamental challenge. Researchers have become increasingly interested in understanding not only how landscape structure affects the number of species that coexist in an area, but also the distribution of functional traits (i.e. functional diversity) that determine the relationship between species diversity and ecosystem functioning. As fragmented landscapes are becoming increasingly common, controlling landscape structure (i.e. both landscape configuration and composition) may help to promote the conservation of both taxonomic and functional diversity. Although we have a relatively good understanding of how landscape composition impact species richness over large spatial scales, less is known about how landscape configuration drives the relationship between species richness and functional diversity simultaneously. Furthermore, despite the conceptual support for trait-based frameworks, we still lack basic information on how different species traits explain species' responses and their potential to provide functions at different spatial scales. In this thesis, I addressed these issues to generate new insights around how landscape structure can be managed to potentially maximize the conservation of both taxonomic and functional diversity in human-dominated landscapes.

First, I conducted a systematic review on current approaches to evaluate how the influence of species traits on the relationship between environmental variables and ecological responses varies among scales (i.e. the scale-dependent role of traits; chapter 2). I show that there is a lack of studies comparing the effect of species traits on ecological responses at multiple scales. In addition, several ecological responses related to ecosystem functioning and species interactions such as seed dispersal, predation and multi-trophic networks have been widely overlooked. Importantly, the effects of landscape structure is also often ignored, and this makes it difficult to disentangle to what degree the responses of ecological systems across habitats, patches and landscapes are dependent on species traits. To address this gap, I then used data on bird ensembles collected in Brisbane (Australia) to test how landscape structure affects the distribution of species traits at different scales (chapter 3). I measured landscape composition and landscape configuration at two spatial resolutions: 100 m X 100 m and 1 km X 1 km. I found that depending on the scale of analysis, the strength of the association between species traits and landscape composition or configuration varies. At landscape scales, habitat configuration and the percentage of tree cover played a key role shaping the distribution of body sizes and dispersal capacities. Conversely, at local scales associations between the distribution of species traits and environmental variables were weak. Furthermore, the interaction between tree cover and fragmentation was important explaining trait distributions only at landscape scales. When tree cover was low at landscape scales, the presence of small-bodied species with low dispersal capacities depended mostly on having low levels of fragmentation. Although effects of fragmentation are stronger at landscape scales, habitat configuration is important determining trait distributions at local scales. Accounting for spatial scale can thus help to

find more general models of the effect of traits for predicting species responses to landscape change.

Then, I developed a spatially explicit meta-community model to quantify how the relationship between species diversity and functional diversity is driven by both habitat amount and fragmentation (chapter 4). I focus on the correlation between "response traits" (traits involved in species responses to environmental change) and "effect traits" (traits associated with species effects on ecosystem functioning). My model shows that the strength at which fragmentation modifies functional diversity in modified landscapes depends on the distribution of response traits and the correlation between response and effect traits. Finally, in chapter 5 I used my empirical data from Brisbane to disentangle the independent direct and indirect effects of landscape composition and configuration on bird functional diversity and species richness simultaneously. I evaluated the pathways through which landscape structure affects functional diversity in two main ways: 1) indirect effects through changes in species richness or 2) direct effects through redistribution in the abundances of particular traits. I show evidence that landscape structure acts differently on species richness compared to functional diversity. Landscape structure effects on species richness are consistent among different functional groups. However, patterns of functional diversity are more complex, vary among functional groups, and their dependence on the level of tree cover and fragmentation changes depending on the functional component evaluated. Importantly, although fragmentation does not always influence directly functional diversity, it can act indirectly through changes in species richness.

This thesis integrates different concepts of community and landscape ecology to understand how species richness and different components of functional diversity may respond to landscape structure. Crucially, the hypotheses presented here would simplify forecasting and understanding the mechanisms that drive functional diversity in different landscapes and represent an advance for generality in landscape ecology. In addition, it provides new evidence about the importance of evaluating species diversity–functional diversity relationships at different spatial scales. My study suggests that a focus on conserving species with particular traits at the local scale may be ineffective if attributes of landscape structure are ignored. In addition, the results presented in this thesis are key for understanding how urban growth might best be done to maximize the conservation of functional and taxonomic diversity.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Peer-reviewed papers:

- **Suárez-Castro A.F.,** Simmonds J., Mitchell M.G.E, Maron M. and Rhodes J.R. The Scale-Dependent Role of Biological traits in Landscape Ecology: A Review. Current Landscape Ecology Reports. 3(1), 12-22.

- Mitchell MGE, **Suarez Castro A.F.**, Martinez-Harms M, Maron M, McAlpine C.A, Gaston K.J, Johansen K, and Rhodes J.R. 2015. Landscape fragmentation and ecosystem services: a reply to Andrieu et al. Trends in Ecology & Evolution. doi:10.1016/j.tree.2015.09.002

- Mitchell MGE, **Suarez Castro A.F.**, Martinez-Harms M, Maron M, McAlpine C.A, Gaston K.J, Johansen K, and Rhodes J.R. 2015. Reframing landscape fragmentation's effects on ecosystem services. Trends in Ecology & Evolution 30:190-198

Conference abstracts:

- **Suárez-Castro A.F.**, Mitchell M.G.E, Maron M. and Rhodes J.R. Assesing the effects of landscape structure on the relationship between functional diversity and species diversity. Student Conference on Conservation Science, Brisbane, January 2015.
- **Suárez-Castro A.F.,** Mitchell M.G.E, Maron M. and Rhodes J.R Predicting the effects of landscape structure on bird functional diversity patterns: The importance of spatial configuration. Australasian Ornithological Conference, Adelaide, November 2015.
- **Suárez-Castro A.F.**, Mitchell M.G.E, Maron M. and Rhodes J.R. Predicting the effects of landscape structure on species diversity and functional diversity relationships. Society for Conservation Biology Oceania Conference, Brisbane, July 2016.
- **Suárez-Castro A.F.**, Mitchell M.G.E, Maron M. and Rhodes J.R. Predicting the effects of landscape fragmentation on the relationship between species richness and functional diversity. International Conference of Conservation Biology, Cartagena, Colombia. July 2017.

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Contributor	**Statement of contribution**
A.F. Suárez-Castro (Candidate)	Conceptualised paper (60 %) Performed literature review (80 %) Analysed data (100 %) Wrote the paper (100%) Edited paper (70 %)
J. Simmonds	Performed literature review (10 %) Conceptualised paper (5%) Wrote and edited paper (5 %)
M.G.E. Mitchell	Performed literature review (10 %) Conceptualised paper (5%) Edited paper (5 %)
M. Maron	Conceptualised paper (5 %) Edited paper (5 %)
J. R. Rhodes	Conceptualised paper (25 %) Edited paper (10%)

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Contributions by others to the thesis

The main outputs from this thesis are chapters 2 to 5 with myself as the lead author. Chapter 2 and Appendix B have been already published and chapters 3 to 5 are being prepared for submission in due course. The conceptualization of the research questions were produced in collaboration with my advisory team, Jonathan Rhodes, Martine Maron and Matthew G. E. Mitchell. I wrote the code for the model presented in Chapter 4, performed fieldwork to collect empirical data for chapters 3 and 5, did all data analysis and wrote the manuscripts and thesis for all the chapters.

Chapter 2 was written by myself and the contributions of the different authors are described in the preceding "Publications included in this thesis" section.

Chapter 3 will be submitted to the peer-reviewed journal *Landscape Ecology*. The conceptualization of the chapter was produced by myself, Jonathan Rhodes and Martine Maron. I conducted all the analysis and Jonathan Rhodes, Martine Maron and Matthew G. E. Mitchell provided feedback.

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Statement of parts of the thesis submitted to qualify for the award of another degree

None.

Research Involving Human or Animal Subjects

Animal ethics approval GPEM/047/15/ARCwas given for the period 17-Mar-2015 to 17-Mar-2018 by the University of Queensland Animal Ethics Committee (Appendix A).

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Australian birds, habitat loss, multiscale, functional redundancy, functional traits, landscape fragmentation, spatial scale, urban ecology

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FoR code: 0501, Ecological Applications, 70%

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Table of contents

List of figures

List of tables

Chapter 1
INTRODUCTION

1.1 Background to the problem

One of the most important questions in conservation science is how to predict the effects of environmental change on biological diversity that is relevant for ecosystem functioning (Díaz et al. 2013, Gross et al. 2017, Naeem and Wright 2003). For many years, it was assumed that maximizing the protection of taxonomic diversity was enough to achieve the conservation of other components of biodiversity (Myers et al. 2000). However, the range of functions provided by a community also depends on the diversity of functional trait states (i.e. functional diversity) (Díaz and Cabido 2001, Mayfield et al. 2010). Theoretical and empirical evidence is now showing that the relationship between species richness and functional diversity can take many shapes, from positive, to hump-shaped to non-significant (Laliberté et al. 2010, Mayfield et al. 2010, Safi et al. 2011). Thus, patterns of species richness, in some situations, tell us little about the ability of assemblages surviving in human-modified landscapes to provide ecosystem functions (de Bello et al. 2010, Mayfield et al. 2010, Petchey et al. 2007). Therefore, evaluating how different environmental factors influence species richness and functional diversity simultaneously is a research priority (Díaz et al. 2007, Mori et al. 2013).

One key environmental factor that affects functional diversity and species richness is landscape structure: the amount and spatial arrangement of different landscape elements (Dauber et al. 2003, Fahrig et al. 2011, Tscharntke et al. 2012). As highly fragmented landscapes are becoming more common with continuing anthropogenic habitat conversion (Haddad et al. 2015), understanding how landscape structure influences ecosystem functions in fragmented landscapes is of primary interest to maximize the outcomes of limited conservation resources. Empirical and theoretical evidence is showing that synergistic effects of habitat loss and fragmentation are fundamental for understanding ecosystem responses to environmental change (Bartlett et al. 2016, Didham et al. 2012, Ruffell et al. 2016). However, while previous work has demonstrated that the relationship between species richness and functional diversity can follows various trajectories in response to land-use change (Flynn et al. 2009, Luck et al. 2013, Newbold et al. 2013), less is known about how landscape configuration and landscape composition interact to affect functional diversity and its association with species richness.

During recent years, there has been important advances in using the concept of functional diversity as a basis for understanding the relationships among landscape change, species diversity and ecosystem functioning (Carmona et al. 2016, Mori et al. 2013, Petchey et al. 2007). Previous work has linked patterns in trait variation within and among species can allow for inferences about how landscape change affects species diversity (Suding et al. 2008, Mori et al. 2013, Palma et al. 2015), as well as the potential for different species to perform the same functional roles (Díaz et al. 2013, Laliberte et al. 2013). However, despite conceptual support for trait-based frameworks, we lack basic information about how traits' capacity to explain species responses to environmental change varies with the spatial scale of analysis. This information is critical for moving towards more general scale-dependent models of species and community distributions and dynamics. In this sense, scale-dependence and spatial configuration effects on species diversity-functional diversity relationships are emerging as important research topics in their own right over the next few years.

This introduction is divided into four sub-sections to describe the conceptual framework underlying this thesis. The first section, *"Functional diversity and its relationship with species diversity",* discusses current understanding of the relationship between species diversity and functional diversity in the context of landscape change. In addition, it defines the components of functional diversity and explains why functional traits matter for ecosystem functions. The second section "*The role of landscape structure*" discusses the importance of landscape structure in driving patterns of biodiversity and functional diversity. In the third section, "*Accounting for spatial scale*", I describe the importance of accounting for spatial scale for the relationship between species trait values and landscape structure. I then discuss the importance of applying these concepts in urban systems, by focusing on birds, the biological model I use in the empirical work of this thesis. Finally, I include a description of the thesis structure with a brief summary of each chapter. Key concepts used throughout this thesis are summarized in Table 1.1.

Table 1-1: Key definitions in the functional trait approach used in this thesis

Term	Definition	References
Assemblage	Phylogenetically related groups within a community that do not necessarily use the same resources.	(Fauth et al. 1996)
Community	A set of species occurring in the same place at the same time	(Fauth et al. 1996)
Ecosystem function	The changes in energy and matter over time and space occurring through biological activity, such as primary production, nutrient uptake, decomposition, and evapotranspiration.	Cardinale et al., 2007.
Ecosystem resilience	The capacity of a system to absorb disturbance so as to maintain the same controls on fundamental functions. Indicates how well a dynamic system continues functioning in times of environmental change. A high diversity of response traits in a community should, in theory, provide greater resilience.	(Sterk et al. 2013)

Ensemble	A phylogenetically bounded group of species that use a similar set of resources within a community.	(Fauth et al. 1996)
Fragmentation	The breaking apart of habitat, independent of habitat loss.	(Fahrig 2003)
Functional diversity	The variation of functional traits in an assemblage.	(Diaz and Cabido 2001, Laliberté and Legendre 2010)
Functional effect trait	A component of an organism’s phenotype that determines the organism’s effect on ecosystem functions.	(Luck et al. 2012, Suding et al. 2008)
Functional redundancy	The number of species contributing in a similar way to an ecosystem function. When multiple species have similar contributions to a focal function (that is, they have similar functional effect traits that are of interest), an ecosystem is better able to maintain key functionality while experiencing environmental change. Functional redundancy is an important characteristic of a community’s resilience to environmental change.	(Mayfield et al. 2010, Mori et al. 2013)
Functional response trait	A component of an organism’s phenotype that determines the organism’s response to environmental changes.	(Luck et al. 2012, Mori et al. 2013)
Functional traits	The phenotypic characteristics of an organism that affect its performance in providing functions and its fitness.	(McGill et al. 2006, Violle et al. 2007)
Landscape configuration	The spatial arrangement of landscape elements within a landscape	(Turner et al. 2001)
Landscape composition	The number of patch, land cover and habitat types represented on a landscape and their relative abundance	(Turner et al. 2001)
Landscape elements	All the quantifiable elements (e.g. Patches-Matrix-Corridors) that can be found in a specific landscape extent.	(Turner et al. 2001)
Landscape structure	The arrangement of landscape components, such as habitat patches or anthropogenic land-uses across a landscape. It includes landscape composition (how much of each land cover or land use that exists) and configuration (the spatial pattern of these land	(Mitchell et al. 2013, Tscharntke et al. 2012)

	cover or land use types).	
Response diversity	The diversity of species that can perform similar ecosystem functions but have different capacities to respond to disturbance, imparting greater resilience to the entire system.	(Mori et al. 2013)
Scale	Scale is composed of the spatial resolution (i.e. grain size) and spatial extent of analysis. Spatial resolution corresponds to the size at which ecological responses and/or environmental variables are measured, whereas spatial extent is the area defining the population or community under consideration.	(McGarigal et al. 2016)

1.2 Functional diversity and its relationship with species diversity

1.2.1 The need for functional traits approaches

A functional trait is a measurable property of an organism that affects that individual's capacity to thrive across an environmental gradient or to acquire and allocate energy and nutrients (McGill et al. 2006, Violle et al. 2007). For example, plant ecologists have used relatively easy traits to measure such as seed size, leaf longevity or wood density to link life history strategies with mean population growth rates (Adler et al. 2014). In addition, animal-based studies of functional diversity often consider behavioural characteristics (e.g. foraging behaviour) as traits (e.g. Luck et al. 2013). Traits can be classified depending on whether they explain how different individuals respond to disturbance (i.e. response traits) or how species contribute to ecosystem function (i.e. effect traits; Suding et al. 2008, Laughlin et al. 2014). For example, body size and nesting behaviour are response traits that affect species' tolerance to land use change (Belmaker et al. 2014, Brown and Graham 2015, Luck et al. 2012). In addition, effect traits such as tongue length and bill morphology in birds and insects influence pollination effectiveness and handling of fruit and seeds (Bartomeus et al. 2018, Luck et al. 2012, Pigot et al. 2016). Some traits can act as both response and effect traits. Dispersal capacity as an effect trait influences the movement of individuals in transformed landscapes and thus long distance seed dispersal. At the same time dispersal capacity can be a response trait, as species with limited dispersal capacity may suffer more from reduced landscape connectivity (Buchi et al. 2012, Luck et al. 2013).

Given limited budgets and the time needed to study the ecological aspects of all the species in a community, the possibility of inferring how environmental changes will influence ecosystem functioning by focusing on specific species traits seems a promising approach (Carmona et al. 2016, de Bello et al. 2010). Functional trait methods provide a more precise framework than functional group or guild approaches, because they characterise small functional differences between individuals and/or species that are ignored by functional groups (Carmona et al. 2016, Laliberté et al. 2010, Luck et al. 2012). In addition, the use of functional trait approaches allows for the quantification of the continuous variation in trait abundances across species (Messier et al. 2010, Spasojevic and Suding 2012, Violle et al. 2012). Based on this information, we can quantify how environmental change might affect the distribution of the abundance of traits related to ecosystem functioning across multiple scales (Mason et al. 2013, Villéger et al. 2008).This information can give more insight into community responses to disturbance than conventional species diversity metrics (Cadotte et al. 2011, Díaz et al. 2013).

The relationship between species richness and functional diversity in transformed landscapes depends on the distribution of response traits across species and the level of functional redundancy. Functional redundancy is the number of species that share similar effect traits and it implies that ecosystem functioning is largely unaffected if redundant species are removed, but decreases if the species lost have unique roles (Laliberté et al. 2010). By analysing functional redundancy patterns and the correlation between response and effect traits, it is possible to improve predictions about how biodiversity loss leads to loss in ecosystem function (Díaz et al. 2013, Suding et al. 2008). When effect traits correlated with response traits that provide low tolerance to landscape change, species more susceptible to landscape change may be more important providing specific functions. For example, large bees that are more susceptible to agricultural intensification can be more efficient in terms of pollination services (Suding et al. 2008). In this case, functional redundancy is low and functional diversity is expected to decline more rapidly than species richness with landscape change.

Despite the elegance of trait-base approaches, empirical evidence showing how functional traits drive species responses to landscape change that also considers landscape context and spatial scale is lacking (Bartomeus et al. 2018, Didham et al. 2016). Therefore, applying response-effect trait based approaches in spatially explicit ways constitutes an important research need. In addition, methods for functional trait approaches in fauna ecology substantially lag behind those in plant ecology (de Bello et al. 2010, Luck et al. 2012). Even though plants are excellent surrogates to measure some ecosystem functions (Díaz et al. 2007, Garnier et al. 2007, Laliberte et al. 2013), other functions such as pollination, pest control and seed dispersal are primarily produced by mobile faunal species that actively move between habitats and ecosystems (Cote et al. 2017, Kremen et al. 2007). As these species play essential roles translocating matter among and within patches, linking functional traits of these organisms to changes in landscape structure is a major research priority.

1.2.2 Functional diversity components

Here, I define the concept of functional diversity as the variation or dispersion of functional traits in an assemblage (Carmona et al. 2016, Villéger et al. 2008). Functional diversity is a multidimensional concept, and can be divided into functional richness, functional evenness and functional divergence (Figure 1.1). As such, it provides independent information on the distribution of species in functional trait space (Mouchet et al. 2010, Villéger et al. 2008). The components of functional diversity are defined as follows:

Functional richness: Represents the amount of functional space occupied by an assemblage. For a single-trait, the functional richness can be estimated as the difference between the maximum and minimum functional values present in the community (Mason et al. 2005). For multiple-trait studies, functional richness represents the volume filled in the trait dimensional space by the community of interest (Villeger et al. 2008). High functional richness indicates that the amount of functional volume occupied by a community is high and thus species interact with most of the resources potentially available to the community (Carmona et al. 2016).

Functional evenness: Functional evenness describes how regularly species abundances are distributed in functional space (Mouchet et al. 2010, Carmona et al. 2016). Functional evenness is higher when the distances between all nearest neighbour species pairs are identical and when all species have the same abundance. Conversely, functional evenness is low when some species are tightly packed along the functional trait range. Low functional evenness indicates that even when some species occupy all the functional trait space, some areas of the functional trait space are under-exploited.

Functional divergence: This component represents how far high species abundances are from the centre of the trait functional space (Carmona et al. 2016). Functional divergence is low when the most abundant species have functional traits that are close to the centre of the functional trait range. On the other hand, when the most abundant species have extreme functional trait values, divergence is high. High functional divergence indicates a high degree of niche differentiation, and thus low resource competition and increased ecosystem function as a result of more efficient resource use (Villéger et al. 2008, Carmona et al. 2016).

Another common index is functional dispersion which measures the distribution of species abundances within trait space, and it is closely related to Rao’s quadratic entropy (Laliberte and Legendre 2010). In this thesis, Rao’s Q has been used as an index of functional divergence in chapters 3 and 5, as it depends both on the range of functional space occupied by the community and on the similarity between species with the highest abundances (Mouchet et al. 2010). This index is strongly positively correlated with functional dispersion (Laliberte and Legendre 2010), given that both indices aim at estimating the dispersion of species in trait space, weighted by their relative abundances (Laliberte and Legendre 2010).

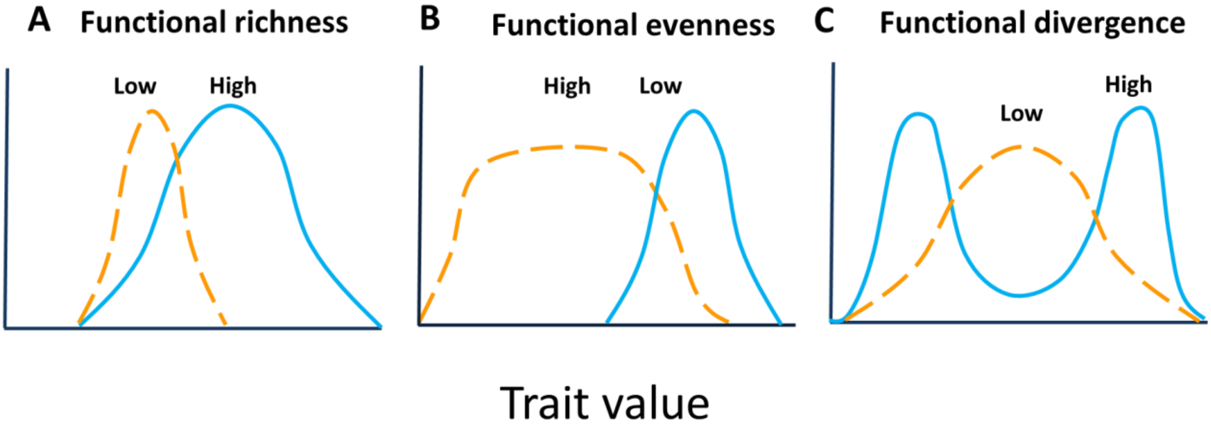

Figure 1-1: The components of functional diversity. See definitions in main text. Functional diversity components are complementary metrics of the distribution of functional trait values across the trait space. Even if functional richness (a) does not change, functional evenness (b) and functional divergence (c) may change depending on the distribution of abundances in the functional trait space. Adapted from Carmona et al. (2016).

As functional diversity components reflect complementary characteristics of the distribution of abundances and taxa in functional space, the values of functional richness, evenness and divergence can be different for the same assemblages occupying the same environmental gradient (Luck et al. 2013). For example, even though in some cases functional richness may not be affected by low amounts of habitat (e.g. Magnago et al. 2014), habitat loss and fragmentation can promote a redistribution of trait abundances across species by, for example, favouring individuals with high dispersal (Luck et al. 2013, Pakeman 2011, Sonnier et al. 2014a). In this case, functional evenness and functional divergence would change. This could reflect changes in community structure with important implications for ecosystem functioning (Laliberté and Legendre 2010, Laliberte et al. 2013). Particularly in areas where habitat amount is limited, the implications of changes in landscape structure on the relationship between functional diversity components and species richness are still mostly unknown.

1.2.3 The relationship between species richness and functional diversity

Previous work has shown that species richness and functional diversity follow different paths in response to landscape change (Flynn et al. 2009, Mayfield et al. 2010). Whereas for some groups functional diversity may show a linear increase with increasing species richness, other groups may show significant hump-shaped or even negative relationships. In some cases, even an increase in species richness can come at the expense of species with unique traits (Coetzee and Chown 2016, Mayfield et al. 2010). Landscape fragmentation can promote the dominance of species with traits associated with long-distance dispersal due to increased fragment isolation (Barbaro et al. 2014, Ding et al. 2013, Magnago et al. 2014). Furthermore, even though species richness may not be affected by fragmentation, habitat diversity can decrease in fragmented landscapes, which in turn favours generalist species with a more restricted set of functional traits (Munguia-Rosas et al. 2014).

There are multiple factors that may affect the effects of landscape structure on the relationship between species richness and functional diversity. These factors include the type of disturbance, the species pool size, as well as functional group identity (Flynn et al. 2009, Naeem and Wright 2003). A meta-analysis performed by Laliberte et al. (2010) in agricultural landscapes showed that declines in functional diversity of birds and mammals were steeper than predicted by species number. Conversely, these authors showed that changes in the functional diversity of plant assemblages were indistinguishable from changes in species richness. These results suggest that land-use intensification increases the vulnerability of functional effect groups independently of patterns of species richness. While much progress has been made in understanding the relationships among species richness and functional diversity in large-scale analyses that focus mostly on landscape composition (Flynn et al. 2009, Luck et al. 2013, Mayfield et al. 2010, Newbold et al. 2013, Palma et al. 2015), effects of landscape configuration have been widely overlooked. Most of the evidence showing that some ecosystem functions may be more susceptible than others to landscape configuration comes from analyses investigating species richness within functional groups. For example, frugivores and insectivores are highly susceptible to fragmentation when the amount of habitat is low (Bregman et al. 2014, Ikin et al. 2013). However, as I discussed above, analysis of the effects of fragmentation on functional groups ignores small functional differences between individuals and precludes predictive analyses using concepts like functional redundancy (McGill et al. 2006, Mayfield et al. 2010; Luck et al. 2012; Mori et al. 2013). Applying functional trait approaches in spatially explicit ways is a promising research area to understand how landscape structure affects ecosystem functioning in changing landscapes.

1.3 Bird functional diversity in urban systems

Understanding the impacts of urbanisation on biodiversity is currently a major priority in conservation biology (Alberti 2015, Devictor et al. 2007, Lin and Fuller 2013, Sushinsky et al. 2013). Cities are the places where most human population growth is happening, and by 2030 some estimates predict that urban land cover will increase by 1.2 million km^2 (Seto et al. 2012). Urban development primarily affects biodiversity through fragmentation and degradation of natural habitats. Although impacts vary with the frequency and intensity of environmental filters, including the loss and fragmentation of natural vegetation and increased disturbance from humans and exotic animals (Catterall et al. 2010, Litteral and Shochat 2017, Sol et al. 2014), a common outcome of urbanization is the simplification and homogenization of species composition (Devictor et al. 2007, Evans et al. 2011). This homogenization is predicted to result in a loss of the functioning and resilience of ecosystems (Ibarra and Martin 2015, Sonnier et al. 2014b). However, while the focus of previous research has been on the effects of urbanization on species composition and abundance, we know much less about the effects of urbanization on the relationship between species loss and ecosystem function.

Birds are an excellent group to link functional diversity patterns with urbanization effects on ecosystems because they respond rapidly to changes in landscape configuration and composition (Bregman et al. 2014, Catterall et al. 2010, Müller et al. 2013). In addition, they occupy a broad range of habitat types and ecological niches, and play an important role in linking patches at the landscape scale through processes such as seed dispersal, pest control and pollination (Heyman et al. 2017, Luck et al. 2013). In addition, they are easy to detect and observe and species are generally easy to identify in the field. Bird abundance and community composition in urban areas have been widely studied (Batáry et al. 2017, Litteral and Shochat 2017). There is empirical evidence from numerous regions showing that that bird community composition becomes increasingly impoverished with urban development, leading to the dominance of a few abundant species (Chamberlain et al. 2017, Devictor et al. 2007, Evans et al. 2009). In addition, species richness in urban areas is generally lower compared to the surrounding rural landscapes, although some studies have shown that areas with intermediate levels of urbanization may exhibit the highest richness (Batáry et al. 2017). Compared to the study of species richness, patterns of bird trait diversity across urbanization gradients are less well known.

There is growing evidence that bird species vary in their tolerance to urbanisation according to functional traits (Brown and Graham 2015, Croci et al. 2008, Evans et al. 2011). For example, species adapted to urban conditions tend to be omnivorous, medium-sized (40-100 g) species with high dispersal capacities (Croci et al. 2008, Evans et al. 2011, Sol et al. 2014). However, it is not clear how the relationship between the prevalence of these traits in urban environments and landscape structure changes depending on the spatial scale of analysis. Most studies have not asked direct questions about the effects of urban landscape structure on functional diversity and species diversity simultaneously. Furthermore, many studies often analyse a dichotomy between urban vs rural areas (Brown and Graham 2015, Evans et al. 2011, Sonnier et al. 2014b), but do not focus on differences across urban gradients of habitat loss and fragmentation.

There therefore remains a strong need to understand how patterns of urban development affect bird species diversity and functional diversity (Schütz and Schulze 2015). Urbanization can alter the potential of birds to promote restauration processes, control insect populations and even provide cultural services (Barber and Marquis 2011, Cox et al. 2018, Da Silveira et al. 2016). In this sense, besides affecting bird populations, changes in functional diversity could ultimately affect human health and well-being (Pollack et al. 2016). As landscape structure has been neglected in many studies that investigate the effects of land use change on functional diversity components, we lack understanding of the ecological trade-offs between species diversity and functional diversity associated with alternative urban growth patterns. In addition, separating the relative influence of landscape and local scale variables is fundamental for making spatially explicit decisions about urban biodiversity conservation (Batáry et al. 2017, Concepcion et al. 2015, Garden et al. 2010). The use of trait-based frameworks at multiple scales constitutes a novel approach to help decision makers to decide how to maximize the conservation of multiple aspects of biodiversity in urban areas.

1.4 The role of landscape structure and spatial scale

Landscape structure plays an important role in shaping species richness and the potential of communities to provide functions. Even though several authors have discussed the prevalence of the effects of habitat loss over those of habitat fragmentation (Fahrig 2003, Fahrig et al. 2011), empirical and theoretical evidence suggests that the effects of fragmentation on species diversity increase when there is little habitat in a landscape (Fahrig 2017, Hanski 2015, Rybicki and Hanski 2013, Tscharntke et al. 2012). Changes in configuration of landscape elements, patch size, edge effects and matrix type alter connectivity patterns (Fahrig et al. 2011, Mitchell et al. 2013), population persistence (Büchi and Vuilleumier 2014) and biotic interactions (Barbaro et al. 2014, Barnagaud et al. 2015, Villard and Metzger 2014). Furthermore, there is evidence that fragmentation can promote the occurrence of species with particular functional traits without substantially reducing species richness (Ding et al. 2013, Concepcion et al. 2015). Thus, although habitat loss has a bigger impact on biodiversity compared to the effects of fragmentation (Fahrig et al. 2011, Tscharntke et al. 2012), there is a need to investigate to what extent habitat configuration can mitigate the effects of habitat loss (Didham Raphael 2010, Didham et al. 2012, Villard and Metzger 2014).

Research on the effects of landscape configuration on functional diversity comes principally from studies that focus on the effects of patch size and isolation (de Frutos et al. 2015, Magnago et al. 2014, Ulrich et al. 2016). These studies have shown that fragmentation can affect functional diversity by modifying directly trait distributions and mediating the effects of habitat loss (Ibarra and Martin 2015, Magnago et al. 2014). For instance, fragmentation can promote traits associated with long-distance dispersal due to increased fragment isolation (Büchi and Vuilleumier 2012, 2014) These changes can be independent of the number of species if, for example, some species are replaced by stronger competitors with a new set of traits or if the abundance of species with less common traits increases (Coetzee and Chown 2016, Ding et al. 2013). In this sense, new research is needed to disentangle the ways in which configuration and composition variables contribute to functional diversity, either through changes in species richness or through independent changes in the distribution of functional traits.

Another important issue is accounting for the scale at which species traits best explain species responses to landscape structure (Jackson and Fahrig 2015, McGarigal et al. 2016, Miguet et al. 2016). How species traits affect ecological responses is likely to vary depending on the smallest unit of observation and the spatial extent over which observations are made. This is because biotic, abiotic and anthropogenic factors (and interactions among these) operating on species and communities at larger spatial scales can be quite distinct from those operating at smaller scales (de Bello et al. 2013a, Lavorel et al. 2013). For example, factors at regional and landscape scales such as the distribution of habitat types predominantly interact with species through traits like dispersal ability (Cadotte and Fukami 2005), while traits such as competitive ability and foraging behaviour may be more important in shaping species interactions at local scales (Ikin et al. 2014). In this sense, biological traits that determine the occurrence or abundance of species at the landscape scale may be less influential at the local or microhabitat scales. However, few studies have explored the relationship between landscape structure and species traits at different scales (Suárez-Castro et al. 2018), and most of them have focused on plant assemblages. As we are still unable to measure the net impact of landscape structure on functional diversity patterns across scales, we are limited in the extent to which we can apply trait-based frameworks to guide decision makers in changing landscapes.

1.5 Summary of the problem

In many cases, we are constrained by how much habitat we can conserve or how much urban or agricultural land is needed to protect multiple aspects of biodiversity (Ewers et al. 2010) (Fahrig et al. 2011). Thus, with increasingly fragmented landscapes, understanding how landscape structure influences ecosystem functions could help develop strategies that can maximize the outcomes of limited conservation resources (Mitchell et al. 2013). Knowledge of species traits could help to predict the effects of fragmentation on ecosystem function across species and regions (Ewers and Didham 2006, Kosydar et al. 2014, Kremen et al. 2007). However, despite conceptual support for trait-based frameworks, information about how different traits explain species responses at different spatial scales is scarce. As spatial patterns are scale dependent, there is a need to identify the local and landscape variables that best account for variation in trait diversity (de Bello et al. 2013a, Suárez-Castro et al. 2018). Furthermore, we still lack general hypotheses describing how changes to landscape structure drive the relationship between species richness and functional trait diversity. Much progress has been made in understanding how landscape composition impacts species richness and functional diversity over large spatial scales (Flynn et al. 2009, Mayfield et al. 2010), but less is known about the relative influence of landscape configuration on this process. This thesis will address these gaps using both theoretical and empirical approaches and evidence. The information provided by my thesis should help increase our ability to evaluate biodiversity–ecosystem function relationships at the spatial scales relevant to management, and establish guidelines to better prioritize biodiversity and ecosystem function-based conservation across landscapes (Luck et al. 2013, Mayfield et al. 2010).

1.6 Thesis aims and objectives

The overarching objective of this thesis is to contribute new evidence of how landscape structure affects species richness and functional diversity simultaneously. In chapter 2, I review current approaches used to evaluate how the influence of species traits on the relationship between environmental variables and ecological responses varies among scales (i.e. the scale-dependent role of traits). I then use bird ensemble data collected in Brisbane (Australia) to address one of the gaps identified in my review: increasing our ability to explain variation in trait values across local and landscape scales by including landscape structure variables (Chapter 3). In chapter 4, I develop a theoretical simulation model to quantify how the relationship between species richness and functional diversity is affected by both habitat amount and configuration. Finally, in Chapter 5, I use my empirical data from Brisbane to test some of the hypotheses that emerged from my theoretical model and evaluate the effects of landscape structure on both species richness and functional diversity for different functional groups.

My thesis addresses the following objectives:

1. Identify the main research gaps and opportunities around how the relationship between particular traits, environmental variables and ecological responses changes across scales.

2. Identify how spatial scale affects the relationship between landscape composition and configuration and bird trait distributions in urban environments.

3. Develop a spatially explicit analytical framework to quantify the effects of landscape structure on the relationship between species diversity and functional diversity.

4. Disentangle the ways in which landscape composition and configuration affect species richness and functional diversity for an urban bird assemblage.

1.7 Thesis outline

A brief overview of the six chapters is presented below, and depicted visually in Figure 1.2.

This thesis is structured as follows. First, in this chapter I have provided a critical summary of the key concepts and knowledge gaps relevant to the principal aim of my thesis. Next, there are four core chapters addressing each of the objectives mentioned in section 1.6. Finally, there is a conclusion chapter summarizing the main findings, conservation implications, and limitations of my thesis research, along with a description of the future research directions that have emerged.

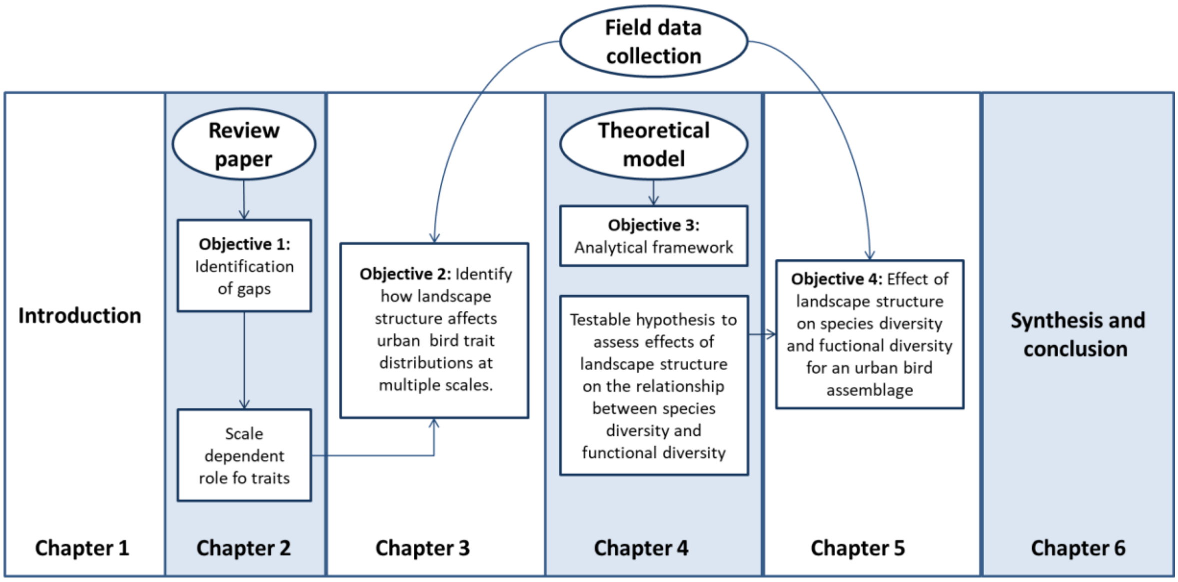

Figure 1-2: Conceptual diagram of flow of this thesis

CHAPTER 1: *Introduction.* This chapter provides an overview of the key topics explored in this thesis—the importance of functional trait diversity approaches, the role of landscape structure and spatial scale, bird trait diversity in urban environments—and outlines the overarching objective and specific questions addressed by this research.

CHAPTER 2: *The scale-dependent role of biological traits in landscape ecology: a review.* In this chapter, I describe current approaches used to evaluate how the influence of species traits on the relationship between environmental variables and ecological responses varies among scales (i.e. the scale-dependent role of traits). I quantify which traits and ecological responses have been assessed, and discuss the main challenges associated with quantifying the scale-dependent effect of traits and functional diversity metrics in real landscapes.

CHAPTER 3: *Associations between urban bird traits and environmental variables change across scales.* Here, I evaluate different landscape structure variables to explain variation in the trait values of an urban bird assemblage across local and landscape scales. I provide empirical evidence that the interaction between landscape configuration, landscape composition and spatial scale can explain contrasting patterns in the distribution of species traits that have been seen in previous studies. This will improve our understanding of how local and landscape elements affect the abundance and composition of bird ensembles in urban systems.

CHAPTER 4: *The effects of landscape structure on the relationship between species diversity and* *functional diversity.* In this chapter, I present a spatially explicit model to investigate how the relationship between species richness and functional diversity components is affected by landscape structure. This model links the concepts of functional redundancy, “response traits,” and “effect traits” to provide testable hypotheses about how fragmentation influences functional diversity at different levels of habitat amount. The hypotheses that emerge from this model provide an opportunity for testing across a broad range of real landscapes and communities in different regions.

CHAPTER 5: Effects of landscape structure on species richness and functional diversity in urban birds assemblages. Here, the hypotheses generated by the model in Chapter 4 are tested empirically using bird community data collected across the Local Government Area of Brisbane. I use a stratified random sampling approach at the landscape level to disentangle the independent direct and indirect effects of landscape composition and configuration on functional diversity and species richness simultaneously. This will help evaluate the mechanisms by which changes in landscape structure at landscape scales produce different responses in species diversity and functional diversity.

CHAPTER 6: *Synthesis and conclusion.* In this final chapter, I summarise the key findings of my research, with a major focus on how fragmentation modifies the relationship between functional diversity and species richness. I then outline the significant contribution that this research makes to the fields of landscape ecology and community ecology. Finally, I present recommendations relating to future research directions based on my key findings and the limitations of the project.

Chapter 2

THE SCALE-DEPENDENT ROLE OF BIOLOGICAL TRAITS IN LANDSCAPE ECOLOGY: A REVIEW

Accepted for publication in Current Landscape Ecology Reports

2.1 Abstract

To improve the application of trait-based approaches, we need to understand how the influence of species traits on the relationship between environmental variables and ecological responses varies among scales (i.e. the scale-dependent role of traits). In this chapter, I describe current approaches used to evaluate the scale-dependent role of traits. For this, I quantify which traits and ecological responses have been assessed, and discuss the main challenges associated with quantifying the scale-dependent effect of traits in real landscapes. Finally**,** I suggest ways forward for future research. I identify three main approaches used to evaluate the scale-dependent role of traits, based on whether: 1) traits are used as predictors or responses; 2) intraspecific variation of single traits is considered; or 3) trait diversity indices are used. This review shows that several ecological responses related to species interactions have been generally overlooked, and the interaction between species traits and landscape structure is not considered in many studies. The explicit inclusion of landscape structure effects in trait based approaches at multiple scales will benefit the integration between approaches from community ecology and landscape ecology. This is important if we want to describe the main mechanisms that operate simultaneously at multiple scales and predict the impact of landscape change on a broad range of ecological responses, including species diversity patterns and interspecific interactions.

2.2 Introduction

Conducting research across multiple spatial scales is important for evaluating community and species responses to landscape change (Levine 1992, Miguet et al. 2016). Species interact with the landscape at different scales, thus understanding how the influence of environmental variables on ecological responses changes across scales remains an important challenge (de Bello et al. 2013a, Jackson and Fahrig 2015, Miguet et al. 2016). Importantly, we can use species' traits to explain mechanistic links between environmental variables and ecological responses (Luck et al. 2012, McGill et al. 2006, Mori et al. 2013, Suding et al. 2008), as patterns in trait variation within and among species can allow for inferences about how spatial processes affect biodiversity across scales (De Bello et al. 2013b, Laughlin and Messier 2015, Messier et al. 2010, Moran et al. 2016). Currently, there is some understanding about how traits influence the scale at which species respond most strongly to particular environmental variables (i.e. the scale of effect approach) (Jackson and Fahrig 2015, Miguet et al. 2016). Yet, a different, but equally important perspective focuses on the need to understand how the effect of different traits varies with the scale at which environmental variables and/or species' responses are measured (i.e. the scale-dependent effect of traits).

The effect of traits on ecological responses depends on the spatial scales of measurement (Carmona et al. 2016, De Bello et al. 2013b, Levine 1992). This is because the way that biotic, abiotic and anthropogenic factors relate to species traits can be quite different when measured at continental, regional or landscape scales compared to small habitat patches or microhabitats (Chalmandrier et al. 2017, de Bello et al. 2012a). By identifying how the effects of traits vary with spatial scale, better predictions about how species may respond to specific environmental variables at particular scales should be possible. This information is critical for moving towards more general scale-dependent models of species and community distributions and dynamics.

I consider two components of scale (McGarigal et al. 2016): spatial resolution (i.e. grain size) and spatial extent (Figure 2.1). Spatial resolution corresponds to the plot size at which ecological responses, species traits and/or environmental variables are measured, whereas spatial extent is the area defining the population or community under consideration. Increasing the resolution helps to detect fine-scale associations between species traits and local environmental heterogeneity, as well as biotic interactions. For example, at fine resolutions, traits related to competitive ability and reproduction can shape interactions of species sharing similar resources (Chalmandrier et al. 2017, Gross et al. 2013). On the other hand, at coarse resolutions, the impacts of spatial patterns such as landscape fragmentation become more evident, and thus the importance of traits associated with dispersal capacity increases (Cote et al. 2017, Wilson and McTammany 2016). Large spatial extents tend to include a broad range of environmental conditions across gradients, and thus communities exhibit a wide range of trait values (Chalmandrier et al. 2017, Yang et al. 2014). In contrast, at small spatial extents, groups of species or individuals are defined by a more restricted number of suitable traits that represent adaptations to local conditions (de Bello et al. 2012b).

To understand the extent to which previous research has evaluated the scale-dependent effect of species traits, I undertook a systematic review of the literature from the past five years. I 1) identified the main approaches that have been used to describe the influence of traits on ecological responses to environmental changes at multiple scales; 2) identified which traits have been assessed for scale-dependent effects and 3) identified which major environmental variables and ecological responses have been measured and related to traits at the community and population levels. Based on my review, I point out that a more refined understanding of how traits drive species responses to environmental variables at different scales, will be of great benefit for understanding the ecological requirements (including optimal landscape structure) of species and ecological communities. I then identify future research challenges to address this. Detailed methods and references for the literature review are provided in Appendix B.

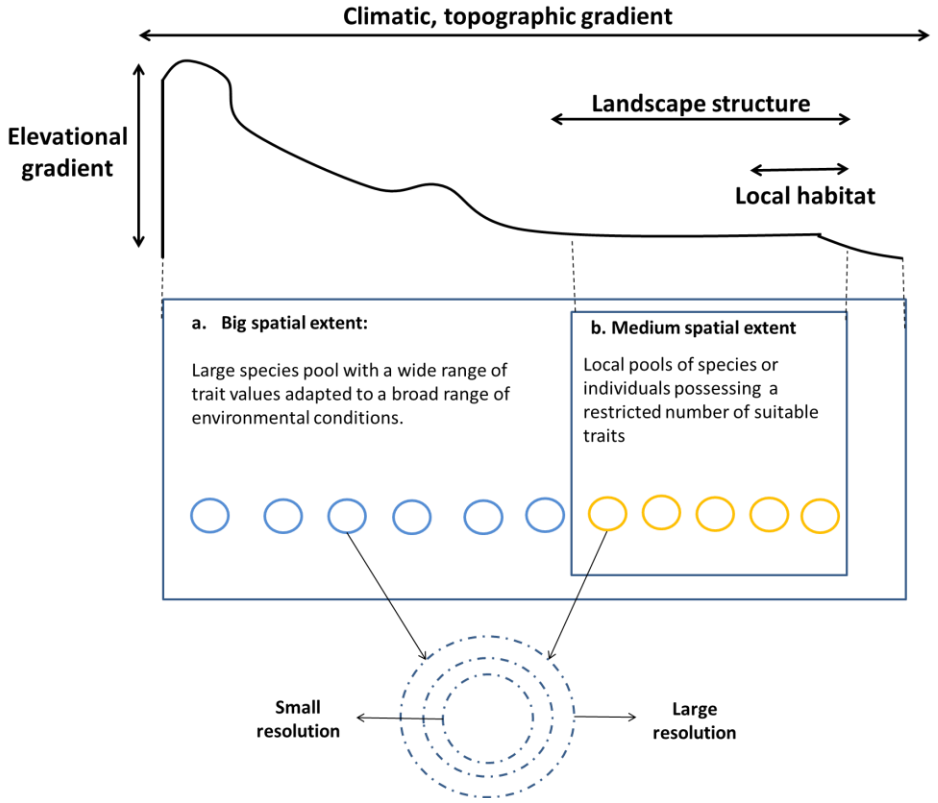

Figure 2.1: The components of spatial scale that affect trait-based inferences : 1) resolution (e.g. the plot area of the sampled community) and 2) extent, the total area that contains the population or assemblage under consideration. Broad spatial extents tend to include a broad range of environment variables (e.g. elevational and climatic gradients), whereas medium and small spatial extents reflect local habitat and landscape structure variables. Circles represent the plots used to measured ecological responses and/or environmental variables. All the plots (blue + yellow) could be analysed to discern the relationships between traits, environmental variables and ecological responses at large extents; while the yellow plots could be used to analyse these relationships at smaller extents. Individual plots can be of different size; the size of plot used in a specific study determines the spatial resolution of that study. Fine resolutions may be more appropriate to detect the influence of traits related to biotic interactions and local environmental heterogeneity, whereas at coarse resolutions ecological responses reflect the averaging effect of broad-scale environmental variables.

2.3 Methods

I was interested in and reviewed studies that: 1) measured explanatory environmental variables and/or ecological responses at more than one spatial scale (e.g. resolution, extent or both); 2) quantified species traits as predictors or response variables; and 3) evaluated how the relationships between particular set of traits, environmental variables and ecological responses change across scales. In this sense, this review does not focus on studies that only evaluate the scale at which environmental variables have their strongest effect on species with different traits (the scale of effect approach; Figure 2.2a) as this approach has received considerable attention and its importance has been discussed in recent reviews (Jackson and Fahrig 2015, Miguet et al. 2016).

I searched (March 27th 2017) for all papers published in the last five years, using the following search term sequence in Web of Science: TI (Title) = (scale or scale* or multi-scale or multi-scale or spatial) and TS (topic) = (trait or trait* or dispersal or size or size* or reproductive or foraging or behaviour) and TS = (scale or scale* or multi-scale or multi-scale*). To facilitate my search, I reviewed papers from 40 ecological journals most likely to publish papers on ecological responses to landscape change, and discarded all studies that did not include "scale" in the abstract. This produced a sample of 1540 papers (see Appendix B for details of search methodology). Most of the results were then eliminated based on the titles or the abstracts if they failed to meet one or more of the three criteria above. In cases where suitability could not be determined based on the abstract, an assessment was made after reading the methods and results sections. This process produced a set of 101 studies, which are listed in Table S2.

2.4 Approaches to evaluating the effect of traits in multi-scale studies

The approaches that I focus on in this review explicitly account for how the relationship between particular traits, environmental variables and ecological responses change across scales. This is important if we want to describe the key mechanisms that operate simultaneously at different scales and predict the impact of environmental variables on a broader range of ecological responses, including species diversity patterns and interspecific interactions (Table 2.1). I identified three different approaches: "species traits as predictors", "single trait expression across scales" and "trait diversity approaches". In the "species traits as predictors" approach (Figure 2.2b), different traits are used as predictors to identify how they moderate ecological responses to environmental change across scales. Here, the focus is in evaluating how interspecific variation in trait values affects ecological responses at different scales. For example, how the effect of dispersal capacity and competitive ability on species abundances differ among local, landscape and regional scales. In the "single trait expression across scales" and the "trait diversity" and approaches, traits are mainly used as response variables to identify how changes in intraspecific trait variation (Figure 2.2c) or trait diversity (Figure 2.2d), are related to particular environmental conditions at each spatial scale. In the approaches considered in this review, traits help to infer what set of environmental conditions have a stronger influence on species and communities at each scale.

Table 2-1: Main approaches used to evaluate the role of traits in multi-scale studies

Approach	Main research question	Examples of ecological responses of interest
Scale of effect	How do traits determine the scale at which environmental variables most strongly influence an ecological response?	Species presence and abundance patterns, physiological responses
Species traits as predictors	How does the effect of different traits vary with the scale of measurement of environmental variables and/or species' responses?	Species presence and abundance patterns, Biotic interactions (e.g. seed dispersal, pollination, parasitism), functional and species diversity patterns
Single trait variation across scales	How does the expression of a single trait for a particular species vary over different spatial scales and how do environmental variables moderate this variation? This includes studies that measure phenotypic plasticity or intraspecific variation.	Intraspecific trait variability (Variation in body size across scales, changes in home range and dispersal capacity related to changes in landscape structure at multiple scales)
Trait diversity	How do patterns of trait diversity (the variation or distribution of species traits in an assemblage) change across multiple scales?	Functional trait diversity, Species diversity patterns

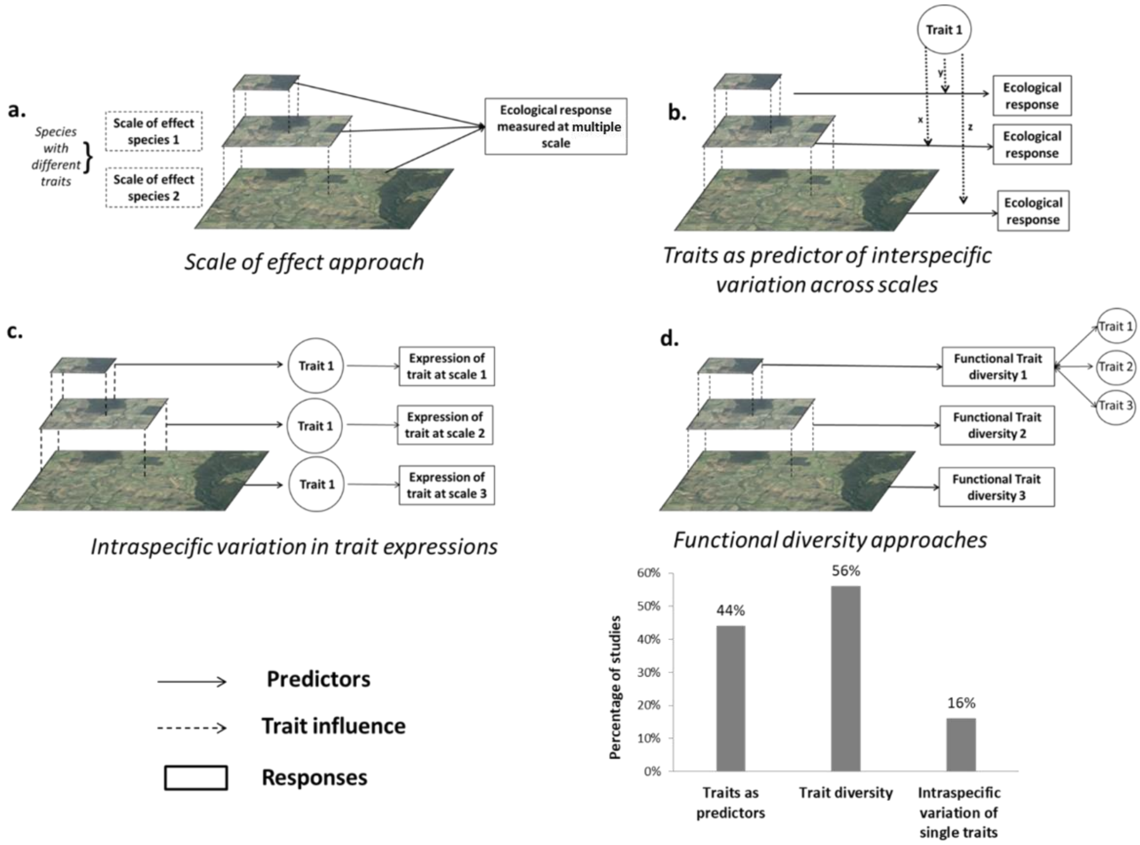

Figure 2-2: Approaches where traits are used to explain ecological responses at multiple scales (n = 101). Different landscape sizes show the different scales at which environmental variables are measured a) Scale of effect approach: studies aiming to identify which traits affect the scale at which environmental variables have their strongest effect; b) Traits as predictors: the effects of different traits on the relationship between environmental variables and ecological responses are measured at different scales; c) Studies that evaluate how the expression of single traits vary over different spatial scales and how environmental variables mediate such variation. d) The distribution of traits at particular scales is used to explain community assembly processes and to identify groups of species with similar traits that are affected in a similar fashion by biotic or abiotic conditions at different scales. In this case, researchers measure the abundance and frequency of trait values across species to infer how environmental variables shape community diversity patterns.

2.4.1 Species traits as predictors

I found 46 studies using the "species traits as predictors" approach. Studies of this type explicitly use traits as predictors to measure their moderating effect on the relationship between environmental variables and ecological responses at different spatial resolutions and/or extents (Figure 2.2b). It has been hypothesised that at broad spatial extents (e.g. landscape, region), environmental variables such as climate and topography influence species and communities based on sets of traits related to tolerance to disturbance, dispersal capacity and habitat specialization (Bourgeois et al. 2016, de Bello et al. 2013a, Mokany and Roxburgh 2010), while at smaller spatial extents, other traits, including diet and nesting behaviour operate through more localised environmental variables to influence species abundance (Ikin et al. 2014, Stirnemann et al. 2015). To test this, multivariate analyses may be used to measure how specific traits account for variation in ecological responses at each scale of interest (De Bello et al. 2013b, Gross et al. 2013). If variation in the effect of particular traits across scales is non-random, it can be hypothesized that this trait acts as a driving trait for a particular ecological response at some scales more than at other scales.

Studies that use this approach include those that identify species traits that explain variation in invasion area among species at different extents (e.g. Akasaka et al. 2012a, Barnagaud et al. 2015), as well as those that predict how species with different traits respond to land-use change or biotic conditions at different resolutions (e.g. Chalmandrier et al. 2017, Donadi et al. 2015, Mokany and Roxburgh 2010). For instance, Akasaka et al. (2012a) found that, irrespective of the resolution analysed, non-native species with clonality had significantly larger invasion areas than species without that attribute. Clonal reproduction enhanced competitive ability and establishment, promoting rapid expansion and maintenance within suitable habitats at fine and coarse resolutions. In contrast, traits related to species' colonization capacity, such as seed size, were only marginally related to invasion areas at coarser resolutions (i.e. 80 km^2 grid). This suggests that invasive plants are dispersal limited at large scales. In another example, Gilroy et al. (2015) showed that habitat specialization was a good predictor of bird species abundances in cloud forest zones in the Colombian Choco-Andes. However, this trait was strongly linked to amount of tree cover and the distance from forest only at within-farm spatial resolutions. Conversely, foraging plasticity was a strong predictor of species responses to distance from forest at coarser landscape resolutions, but not for responses to local habitat within each farm.

2.4.2 Single trait expression across scales

This approach includes studies that measure how the effect of environmental variables on the expression of a particular trait within species varies over different spatial scales (Fig 2.1c). At the population level, phenotypic plasticity can modify the expression of the same trait at different scales (Laughlin and Messier 2015, Messier et al. 2010, Violle et al. 2012). For example, there is evidence that the expression of morphological traits in response to variation in landscape structure may change at different spatial extents and resolutions (Cattarino et al. 2016, Miguet et al. 2016). Kaiser et al. (Kaiser et al. 2016) showed that, by altering temperature, urbanization affected butterfly size at fine resolutions (200 X 200 m), but these effects were not evident at broad resolutions (3 X 3 km). I found that 18 % of the reviewed studies analysed variation in trait expressions across different resolutions and/or extents. Most evidence on how environmental variables affect the expression of species traits and its effect on ecological responses comes from studies analysing trait variation across environmental gradients (e.g. levels of disturbance), rather than from analyses at multiple scales (Messier et al. 2010, Moran et al. 2016, Ryder et al. 2013). Some of these studies show that intraspecific variation in traits may lead to different ecological responses, such as changes in demographic attributes in terms of survival and reproduction (Cattarino et al. 2016, Kaiser et al. 2016). However, there is a lack of empirical evidence on this topic and more research effort is needed to address this gap.

2.4.3 Trait diversity

An approach that has become more popular in the last few years is to measure the frequency of trait values across species and relate this to community diversity patterns at different scales (54 studies, Figure 2.1d). The main objective of this approach is to identify groups of species with similar morphological, physiological or behavioural traits that are affected in a similar fashion by biotic or abiotic conditions at different scales (Aguiar et al. 2013, Carmona et al. 2012, Carmona et al. 2016, De Bello et al. 2013b). Recent multi-scale studies show how sets of environmental variables linked to fire regimes (Boiffin et al. 2015), grazing (Carmona et al. 2012) and urbanization gradients (Brice et al. 2016, Concepcion et al. 2015) explain variation in functional diversity indices at different scales. Variation in trait values across species reflect the spatial scale at which these environmental variables operate (De Bello et al. 2013b, Gross et al. 2013, Laliberte et al. 2013). For some assemblages, coexisting species tend to express more divergence in trait values at fine resolutions (10 × 10 cm subplots within larger plots), suggesting niche differentiation. Conversely, at broad resolutions and extents, environmental variables tend to filter species with similar traits and these patterns become more evident when disturbance increases (Chalmandrier et al. 2017, de Bello et al. 2013a). Thus, besides being important for analysing how landscape structure affects the distribution and abundance of individual species in habitat models, traits have become crucial to understanding how different sets of species maximize community-wide coexistence and hence measures of species diversity at different scales (Concostrina-Zubiri et al. 2014, Mayfield et al. 2010, Mori et al. 2013).

2.5 What traits have been used to understand the scale-dependent role of traits?

My review shows that traits related to size (e.g. body mass, plant height) and habitat specialization are most commonly used both at the species and the community level to explain the scale-dependent role of traits (Figure 2.3a). For animals, the most common trait was body size (n = 27) followed by habitat specialization (primary habitat and/or breadth of habitats used; n = 21), dispersal (n = 14), diet (n = 12) and various morphological traits (n = 11). How the effect of species competitive abilities on ecological responses change across scales is a topic that has received less attention, while traits associated with nesting and social behaviour have been investigated mostly in single-scale studies (Donner et al. 2013). Community level approaches are most common in plants, and generally evaluate easily measurable morphological traits such as height, seed mass and specific leaf area. These traits are used to describe reproductive abilities and tolerance to disturbance (e.g. Craven et al. 2016, Kazakou et al. 2014). Traits related to species interactions (e.g. morphological traits for pollination and reproduction, chemical defences for herbivory and social behaviour) are still mostly ignored in most multi-scale trait-based approaches. Although some studies included species or population attributes such as geographic range size, I did not take them into account in my analysis, since they are not a property of the organisms measured at the individual level (McGill et al. 2006) .

Of the studies that included multiple traits to calculate trait diversity indices, only 31% aimed to disentangle which particular set of traits were driving diversity patterns at each scale (Chalmandrier et al. 2017, Gross et al. 2013, Spasojevic et al. 2016b). Most community-level studies focused on evaluating how indices of functional diversity changed across spatial extents, without reporting the major combination of traits driving these differences. This information is fundamental to understand how species traits affect population responses and community dynamics at each scale (Bolnick et al. 2011, Laughlin and Messier 2015, Violle et al. 2012). For example, there is evidence that traits such as body size, dispersal capacity, trophic level and matrix tolerance increase or decrease a species' vulnerability to fragmentation and habitat loss (Bregman et al. 2014, Ewers and Didham 2006, Kosydar et al. 2014). However, multi-scale trait-based approaches still require information on how the interaction between these traits varies among microhabitats, patches and habitat types across landscapes. Using this information, it may be possible to explain, for example, whether edge sensitivity is primarily related to dispersal ability at the landscape scale (Ewers and Didham 2006), or if a much wider range of traits are influential in explaining this effect (Ries and Sisk 2010). More studies relating species traits and fragmentation patterns at multiple scales are needed to predict how changes to landscape structure affect biological communities.

2.6 What predictors have been measured to understand the scale-dependent role of traits?

Most studies I found focused on habitat or landscape composition variables, but less than 35% of the studies considered landscape structure predictors associated with both habitat amount and configuration. There are numerous examples of how changes in landscape structure variables can modify the effect of particular traits (Delattre et al. 2013, Moran et al. 2016). For example, matrix quality and fragmentation modify species mobility and fecundity through changes in mobility traits (Akasaka et al. 2012b, Delattre et al. 2013, Prokopenko et al. 2017, van Beest et al. 2011). The effect of dispersal capacity on community composition patterns may be higher in areas with complex topography, as there are more barriers for the movement of individuals. Conversely, flatter natural areas may increase connectivity, and thus the importance of dispersal capacity relative to landscape structure decreases. Thus, the spatial configuration of the landscape may have a greater effect on community composition than differences between dispersal capacities among species (Lauterbach et al. 2013, Moran-Ordonez et al. 2015). Ignoring the role of landscape structure may have consequences for the interpretation of how landscape change affects community dynamics and ecosystem functioning.

The importance of species traits for explaining ecological responses is highly dependent on environmental gradients that may affect the expression of traits (Albert et al. 2010, Garnier et al. 2007, Moreira et al. 2012). For example, differences in topography, disturbance level and elevation affect how traits such as plant height, nutrient concentration in leaves, and foraging behaviour influence population and community structure (Albert et al. 2010, Delattre et al. 2013, Garnier et al. 2007, Moreira et al. 2012, Spasojevic and Suding 2012). Most of the studies I reviewed measured environmental predictors at local habitat resolutions (Kazakou et al. 2014, Laliberte et al. 2013) and/or at broad extents (across continents, nations or regions) (Belmaker and Jetz 2013, Krasnov et al. 2015, Lauterbach et al. 2013). However, we lack trait-based studies combining both different resolutions and spatial extents that aim to detect the effect of environmental gradients on trait effects at local habitat resolutions (e.g. Boiffin et al. 2015, Concepcion et al. 2015, Kazakou et al. 2014, Perovic et al. 2015). In addition, in most of the studies (n = 72), trait measurements were averaged at the species level, ignoring how environmental variables may affect the expression of traits within species at different extents. Understanding how environmental predictors interact with scale to affect the influence of traits on ecological responses is a critical gap to be filled.

2.7 What ecological responses have been measured in multi-scale trait approaches?

I found that the main ecological responses that have been measured to understand species traits effects across scales include the analysis of multiple indices of diversity (e.g. beta diversity, functional and phylogenetic diversity; 48%) (Gilroy et al. 2015), taxonomic diversity (17% of studies), (Fig 2a) (Barnagaud et al. 2015, Chalmandrier et al. 2017), interspecific interactions (8%) such as parasitism (Barnagaud et al. 2015, Gunton and Poyry 2016) and predation (Green and Côté 2014), and patterns of single species occurrence and distribution (10%). Most work about community trait-based approaches come from studies on plant assemblages (38%) (Bourgeois et al. 2016, de Bello et al. 2013a) and to a lesser extent on invertebrates (23%) (Gothe et al. 2013, Wilson and McTammany 2016) and birds (14%) (Gilroy et al. 2015, Morante et al. 2016).

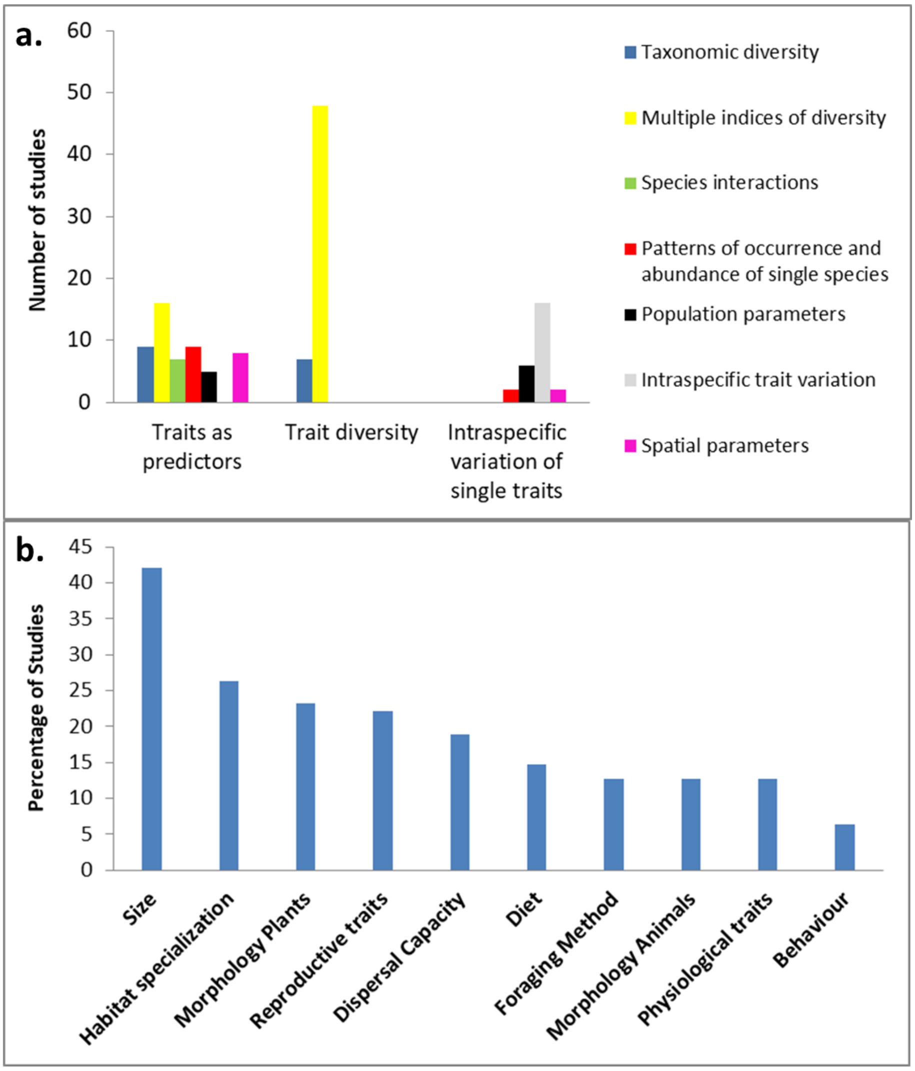

Figure 2-3: Ecological responses and traits analysed in multi-scale studies a) The main ecological responses and b) The main traits used in multi-scale studies for explaining the effects of traits on ecological responses at different scales. n = 101. An explanation of ecological responses and trait definitions is provided in Appendix B.

With respect to the “Single trait expression across scales” approach, I found that most studies did not evaluate how intraspecific trait variation could affect population responses such as reproduction success at multiple scales (Kaiser et al. 2016, Ryder et al. 2013). Changes in environmental conditions with increasing spatial extent can modify how a particular trait is expressed in a population, and this can affect population fitness and survival. However, since most studies describing species-environment relationships are still not adopting multi-scale frameworks (reviewed by McGarigal et al. 2016, Miguet et al. 2016), we have little understanding of how different environmental variables, including landscape structure, affect intraspecific variation of many traits across scales and its effect on ecological responses. This is despite the study of the impacts of landscape change on species traits, such as foraging behaviour and dispersal distance, being an active area of research (Carmona et al. 2016, Cote et al. 2017, Moran et al. 2016). Ignoring intraspecific trait variation at multiple scales may mask the effect of environmental variables on ecological responses, especially in landscape-scale studies that encompass strong environmental gradients and locally adapted populations (Spasojevic et al. 2016b).

Evaluation of the scale-dependent role of traits on species interactions such as predation, seed dispersal and pollination has been poorly addressed, and I found that only 8% of studies examined these processes (Figure 2.3b). Species interactions might be inferred from a small number of traits (Eklöf et al. 2013, Morales-Castilla et al.). However, more evidence is needed to infer whether the traits of interacting species groups are consistently related across spatial scales (Dehling et al. 2014). Some examples of advances in this area come from studies on host-parasite relationships. A meta-analysis by Gunton and Poyry (2016) tested the hypothesis that, within a landscape, the risk of an insect being attacked by a parasite is strongest at medium spatial resolutions, with respect to parasites' foraging range, whereas it is weak at fine resolutions. However, these authors also showed that there is a lack of evidence that this change in risk across scales depends on certain traits such as the level of specialization and whether the parasite is gregarious or not. In another example, (Barnagaud et al. 2015) found that the abundance patterns of the parasitic brown-headed cowbird (*Molothrus ater*) are influenced by specific hosts' ecological traits at fine resolutions within landscapes, rather than at coarse (regional or continental) spatial extents. These authors found that the effects of nest parasitism depend more on landscape structure and other environmental factors operating at landscape and patch scales than on specific associations with particular groups of species at larger scales. Therefore, evidence provided by these studies shows that the importance of species traits explaining species interactions is highly dependent on regional and landscape context.

2.8 Towards a better understanding of the scale-dependent effect of traits

Although traits can provide a mechanistic approach to evaluate the link between ecological responses and environmental variables, current understanding of the scale-dependent role of traits in shaping these relationships is still in its infancy. From my review, I identify three main gaps: 1) There is a lack of studies explicitly quantifying the relative effect of particular sets of traits on ecological responses across scales; 2) several ecological responses related to ecosystem functioning and species interactions such as seed dispersal, predation and multi-trophic networks have been widely overlooked, and 3) the effects of landscape structure are often ignored in many studies. While recognizing the challenges associated with evaluating the scale-dependent effect of traits in real landscapes, I discuss these gaps and provide some general recommendations for future progress.

Most community-level studies do not explicitly quantify the relative effect of single traits on ecological responses across spatial scales. Instead, studies measuring trait diversity tend to condense multiple traits in a single metric, and many of them do not test for how sensitive these metrics are to including different traits. Since species traits may represent different niche axes, aggregated information of functional metrics can overlook specific associations between environmental variables and community patterns at different scales (Butterfield and Suding 2013, Chalmandrier et al. 2017, Spasojevic et al. 2016b). Therefore, in order to explain the scale-dependent role of traits in heterogeneous landscapes, ecologists must 1) test for different sets of traits to represent the main variations in traits effects across scales (Laughlin and Messier 2015, Spasojevic and Suding 2012, Zhu et al. 2017) and 2) evaluate the congruence between trait diversity metrics and single-trait models.

Current research shows the importance of evaluating the congruence of functional diversity patterns with single-trait models. For example, Chalmandrier et al. (2017) classified traits as 'driving traits' if they had a significant pattern going in the same direction as the multi-trait functional diversity pattern and 'countering traits' if they showed a significant pattern going into the opposite direction. In this way, they showed how leaf dry matter content is more important for explaining the distribution of species at fine resolutions, whereas specific leaf area and height play a more important role structuring assemblages that respond in a similar way to environmental stressors at large extents (an entire landscape). More empirical evidence about how particular sets of traits drive trait diversity patterns across scales is needed, and the use of probability density function approaches to calculate functional diversity at multiple scales constitute a promising area of research (see Carmona et al. 2016) .

Understanding the scale-dependent role of traits requires the evaluation of how local ecological responses are context dependent across management practices or regions. Trait effects depend on multiple factors including the ecological response and the taxonomic group of interest, as well as inter-regional variation in landscape attributes such as matrix quality, road density or topography. For example, although it is assumed that dispersal traits may play an important role determining beta diversity when the spatial scale increases (De Bello et al. 2013b, Lauterbach et al. 2013), regional disturbances such as urbanization can moderate how strong the effect of dispersal capacity is at large spatial extents (Brice et al. 2016).. Further studies disentangling the effects of environmental variables, community composition, traits, and phylogeny are necessary to generalize findings of trait effects across regions. These studies may benefit from the current development of large databases (e.g. Kattge et al. 2011, Salguero-Gómez et al. 2015, Wilman et al. 2014) that allow the simultaneous extraction of trait values from a large number of species or populations, rather than on measurement of traits in the field (Kazakou et al. 2014).

My review found that research is scarce regarding the scale-dependent effect of species traits in processes such as competition, parasitism and trophic interactions. Some work has shown how fluxes of resources and individuals across different habitats influence each other's structure and dynamics (Kissling et al. 2012, Stouffer and Bascompte 2010, Wood et al. 2015). Other models have explicitly evaluated how traits of resistance to herbivory influence spatial patterns in plants (Anderson et al. 2015), and there is some empirical evidence showing that traits related to body size, body shape and behaviour help to predict predator-prey interactions across multiple extents, including individual prey foraging areas and entire landscapes (Green and Côté 2014). However, the study of the effects of traits on ecosystem processes such as food-web interactions is still very limited, and deriving generalities across scales is still a major challenge. In order to assess the impacts of human modification on ecosystem services, we need to understand how traits of interacting species groups and ecosystem functions are consistently related across spatial scales.

Although it is expected that the diversity of functional traits determines ecosystem functioning, we still lack information of how much trait diversity is needed to maintain multiple ecosystem functions within habitat types within landscapes, between landscapes and among regions (Nash et al. 2016, Spasojevic et al. 2016a). A key knowledge gap exists in our understanding of how species sharing similar functional traits respond to scale-specific disturbances. In addition, issues still remain in scaling up how local-scale diversity affects ecosystem processes at larger spatial scales (e.g. how functional diversity at the landscape scale influences the recovery of productivity after wildfires across landscapes (Spasojevic et al. 2016a) . To address this, tools used in large-scale studies of biodiversity (remote sensing and trait databases) can be combined with theoretical advances developed from small-scale experiments. This could help facilitate scaling up data on local trait variation to regional extents that are needed for understanding species interactions and ecosystem service management (Martinez et al. 2016, Spasojevic et al. 2016a).

Finally, studies tend to ignore how landscape structure and landscape context influence the scale-dependent role of traits; only a few empirical studies have addressed the impact of regional landscape context on local trait divergence in natural populations (Kaiser et al. 2016, Moran-Ordonez et al. 2015, Peringer et al. 2016). Generally, landscape ecologists focus on measuring landscape structure at varying spatial extents around sites/patches where the ecological response is measure, and then determine the scale at which species traits has the strongest effect on the ecological response (de Bello et al. 2013a, Jackson and Fahrig 2015, Miguet et al. 2016).. In contrast, multi-scale studies that focus on the scale-dependent role of traits generally use a hierarchical approach to compare ecological responses at local (plot scale) and regional scales that capture heterogeneity in conditions related with variables such as climate and topography. Studies that seek to link traits to ecological responses at the landscape scale must consider a hierarchical design where landscape structure is measured at multiple scales around plots distributed across an environmental gradient. This will allow for a more comprehensive understanding of how traits affect ecological responses in space, as well as guide management responses that explicitly account for trait effects across a wider range of spatial scales.

2.9 Conclusions

Over the past few decades, the dependence of ecological processes on drivers acting across a range of scales has been widely studied (Jackson and Fahrig 2015, Miguet et al. 2016, Mitchell et al. 2013). Theoretical and empirical evidence suggest that species responses to landscape change are determined partly by the spatial resolution and extent at which physical and biological attributes are measured and partly by the ecological traits of species (de Bello et al. 2012b, Ewers and Didham 2006, Flynn et al. 2009, Miguet et al. 2016). However, the study of the scale-dependent role of traits that drive ecological responses is still in its infancy. Furthermore, methodological developments in trait approaches for animal ecology substantially lag behind those currently used for plant ecology.

Without a proper quantification of variation in abiotic and biotic conditions at multiple scales in trait based approaches, it is still difficult to disentangle whether the responses of ecological systems are dependent on traits or on environmental variables acting across habitats, patches and landscapes. In addition, the effects of traits on ecological responses depend on the environmental context. Therefore, I advocate for the use of models that evaluate how variation in environmental conditions across regions and habitat types influence trait effects on ecological responses, as well as the measurement of landscape structure at a wider range of spatial extents and resolutions. The explicit inclusion of landscape structure effects in trait based approaches at multiple scales will benefit the integration between approaches from community ecology and landscape ecology. This is fundamental if we want to predict the impact of landscape change on a broad range of ecological responses, including species diversity patterns and interspecific interactions. This way, we could prevent missing essential information about the mechanisms that operate simultaneously at multiple scales to shape biological communities in changing landscapes.

Chapter 3

ASSOCIATIONS BETWEEN URBAN BIRD TRAITS AND ENVIRONMENTAL VARIABLES VARY ACROSS SCALES

To be submitted to Landscape Ecology

3.1 Abstract

The distribution of species traits along environmental gradients depends on the spatial scales of observation. Information about the relationship between species traits and landscape structure at fine scales is not necessarily helpful for predicting how these traits explain species responses at large scales. Thus, multi-scale approaches are necessary to understand the main factors that affect trait distributions across environmental gradients. I this chapter, I investigated the impacts of changes in landscape composition, landscape configuration (i.e. fragmentation) and their interaction on different bird species traits – namely body size, dispersal ability, clutch size and specialisation degree – across two spatial scales (1 hectare and 1km^2). At each scale, I examined if variation in the value of traits in urban bird communities is mostly due to landscape composition, landscape fragmentation, or both. Results of this analysis show that traits have different relationships with environmental variables depending on the scale of analysis. At landscape scales, landscape fragmentation and the percentage of tree cover played a key role shaping the distribution of body sizes and dispersal capacities. Conversely, at local scales associations between the distribution of species traits and environmental variables were weaker. Furthermore, the interaction between tree cover and fragmentation was important explaining trait distributions only at landscape scales. When tree cover was low at landscape scales, the presence of small-bodied species with low dispersal capacities depended mostly on having low levels of fragmentation. Although effects of fragmentation are stronger at landscape scales, habitat configuration is important determining trait distributions at local scales. I hypothesize that at local scales, fragmentation may increase heterogeneity and thus facilitates the presence of species with multiple traits for exploiting resources. However, when the percentage of tree cover is low (< 30 %) at local scales, fragmentation effects are negative and tend to homogenize the distribution of traits. This may reflect how increasing habitat heterogeneity facilitates the presence of species with multiple strategies for exploiting resources. Results of this study suggest that a focus on conserving species with particular traits at the local scale may be ineffective if attributes of landscape structure are ignored. Therefore, local actions aimed at increasing species richness that do not consider landscape structure effects may favour species that are already more adaptable to urban landscapes.

3.2 Introduction

Identifying the interaction between ecological community structure and the spatial scale of analysis is fundamental to understanding the effects of landscape structure on biodiversity more broadly (Jackson and Fahrig 2015, Miguet et al. 2016). Spatial processes and disturbance regimes vary across scales and so does the effect of environmental variables on species and communities. The effects of environmental variables depends on species traits, thus it is expected that the distribution of trait values in response to environmental variation will change depending on the scale of evaluation (de Bello et al. 2013a, Kazakou et al. 2014). Thus, information about the relationship between species traits and landscape structure at fine scales is not necessarily helpful for predicting how these traits respond at broader scales (Carmona et al. 2016, de Bello et al. 2013a). Multi-scale approaches are necessary to disentangle to what degree species' responses to environmental variables are dependent on traits (e.g. Boiffin et al. 2015, Kazakou et al. 2014).

In the review presented in chapter 2, I showed multiple examples of how the distribution of species traits along environmental gradients depends on the spatial scales of observation (Albert et al. 2010, Garnier et al. 2007, Moreira et al. 2012). For instance, at spatial resolutions of kilometres, an increase in landscape heterogeneity may favour species with high dispersal (Öckinger et al. 2010). In contrast, highly mobile species may not tolerate local conditions if they cannot find nesting sites and/or tolerate aggressive competitors (Ikin et al. 2014, Montague-Drake et al. 2011). Therefore, although the distribution of dispersal capacities may be a good indicator of effects of landscape change at coarse scales, at local scales, poor dispersers and mobile species may respond to landscape attributes in similar ways (Concepcion et al. 2015). However, most evidence on how landscape structure affects the distribution of species traits comes from studies across environmental gradients (e.g. levels of disturbance), rather than from analyses at multiple scales (Messier et al. 2010, Moran et al. 2016, Ryder et al. 2013).

Studying the impacts of urbanisation on biodiversity at multiple scales is a major priority in conservation biology (Alberti 2015, Evans et al. 2011, Lin and Fuller 2013). Cities are the epicenters of the net human population growth (Alberti 2015, Batáry et al. 2017), and separating the relative influence of landscape structure from patch and local scale variables is fundamental for making spatially explicit decisions about urban biodiversity conservation (Batáry et al. 2017, Concepcion et al. 2015, Garden et al. 2010). Urbanization can lead to biotic homogenisation through the replacement of non-urban specialist species with urban adapted species, which share traits necessary for exploiting the habitats that urban areas support (Croci et al. 2008, Evans et al. 2011, Müller et al. 2013, Sol et al. 2014). However, it is not clear how landscape structure influences the prevalence of different traits in urban environments across different spatial scales of analysis (Brown and Graham 2015, Evans et al. 2011, Sonnier et al. 2014b). Most studies often focused on coarse scale analyses such as evaluating the prevalence of particular traits in urban vs rural areas (Brown and Graham 2015, Evans et al. 2011, Sonnier et al. 2014b), which limits the potential of finding differences across gradients of habitat loss and fragmentation.

Here, I examine how accounting for spatial scale helps to explain the relationship between environmental change and the distribution of functional traits of an urban bird assemblage. In particular, I address the following question: which set of environmental variables explain variation of trait values across local (1 ha) and landscape (1 km) scales? I examine if variation in the value of traits in urban bird communities is mostly due to landscape composition, configuration, or both. I expect that traits will show different relationships with environmental variables depending on the scale of analysis. For example, the distribution of some traits such as dispersal capacity will be more affected by fragmentation and amount of vegetation at landscape scales, whereas other traits related to reproductive capacity (e.g. clutch size) will show stronger associations at local scales. This information will improve our understanding of how local and landscape elements affect the richness and functional composition of bird assemblages in urban systems.

3.3 Methods

3.3.1 Study area

I used empirical survey data to model the current distributions of bird species across the Brisbane Local Government Area (hereafter ‘Brisbane’) located on the eastern coast of Queensland, Australia (27°28′S, 153°07′E; Figure 3.1). This region has a mean altitude of 540 m (range: 300–940 m), mean minimum and maximum temperatures of 16·3 and 26·5 °C respectively and a mean annual precipitation of 1006 mm. During summer (December-March) average temperatures range from 21 - 29.8°C and the city has its highest average rainfall (426.6 mm). In winter (June – August), weather is generally dry and mild with mean temperatures between 11 - 21°C. Approximately half of the city (49 %) has tree canopy coverage (Jacobs 2014). Brisbane is also located in one of Australia’s most biodiverse regions, with more than 300 bird species recorded from 3100 km^2 within the greater Brisbane region, which includes urban and peri-urban habitats, as well as remnants of natural habitat. During recent decades, the city has experienced extensive land clearing and fragmentation as a consequence of rapid population growth (Brisbane City Council 2014), which in turn has promoted declines among woodland birds (Catterall et al. 2010).

3.3.2 Survey design

I selected sample units for bird surveys at two spatial scales: a landscape scale of (1 X 1 km) that encompasses gradients of different amounts of tree cover and fragmentation, and a local scale (1 ha: 100 X 100m) that encompasses gradients of the amount of vegetation at local scales. Although many bird species use areas larger than 1 km^2, most previous studies of effects of urbanization on bird diversity have commonly shown the scales at which predictor variables relate significantly to local bird assemblages are between 500 m^2 and 2000 m^2 (Litteral and Shochat 2017). In addition, the selection of this size allowed me to capture heterogeneity in landscape attributes while minimizing spatial mismatches between different sets of explanatory variables (Mitchell et al. 2016). Also, 1 km^2 tries to capture the size at which many local conservation planning actions are carried out, at about the size of a neighbourhood, within urban areas at the landscape scale. Tree cover was selected as the main vegetation variable to describe landscape structure since in the study area it is highly correlated to other metrics such as percentage of urbanization (Mitchell et al. 2016). In order to measure fragmentation, I used a "clumpiness" metric that measures spatial aggregation (McGarigal 2002). This metric is a reliable measurement for habitat fragmentation because it is relatively insensitive to variation in habitat extent (Wang et al. 2014).

Landscape units were selected by using stratified random sampling. First, I calculated tree cover for the entire Brisbane Local Government Area at the $1km^2$ resolution using ARCGIS 10.2.1 (Environmental Systems Research Institute). Each grid was classified according to each of the following tree cover categories: low (10-30%), medium (30-60%), and high (> 60 %). For each tree cover category (low, medium and high), I selected 16 landscape units stratified across different levels of fragmentation at the 1-km scale, ranging from low (clumpiness index > 0.8) to high (clumpiness index < 0.5) levels of fragmentation (Figure 3.1). All units were located below 100 m altitude to avoid biases related to changes in bird community structure associated with changes in elevation.

I then overlaid a 100 m x 100 m (1 ha) grid on the selected landscape units and performed a stratified random sampling based on the percentage of tree cover to select three sampling points within each landscape. These points corresponded to low (<30%), medium (30-60 %) and high (> 60 %) proportions of tree cover at the 1 ha scale In case a given level of tree cover at the plot scale was not available, a random point was chosen to keep the number of surveyed points equal across landscape units. This process resulted in the selection of 144 sampling points distributed across 48 landscape units. Although heterogeneity at local scales may be increase variability of environmental variables, the factorial design used in this analysis allows sampling local scale plots that represented three major vegetation conditions. In addition, the spatial replication of the same local conditions across landscapes helps to reduce variability across the analysed spatial extent.

3.3.3 Bird surveys

I used 5-minute point counts between dawn and 10 am to estimate bird density in each landscape unit. Each sampling point was sampled twice in each of two seasons: summer (January – March 2016) and winter (mid-May – August 2016) for a total of four repeat surveys. If a survey point was not accessible (e.g. could not be reasonably accessed on foot), I selected a new point in similar habitat identified on foot based on field conditions within the same 1ha grid cell. In order to avoid biases produced by local scale habitat variables on wetland birds (e.g. the presence of lakes), I excluded those species. I recorded distances of sightings using a range finder TruPulse 360B and each bird was recorded as seen, heard or flying over. Birds recorded as flying over were omitted in the statistical analyses to avoid biases in recording species at local scales. Each bird detection was assigned to one of five distance classes from the site (0–10 m, 10–20 m, 20-40 m, 40–50 m, and > 50 m).

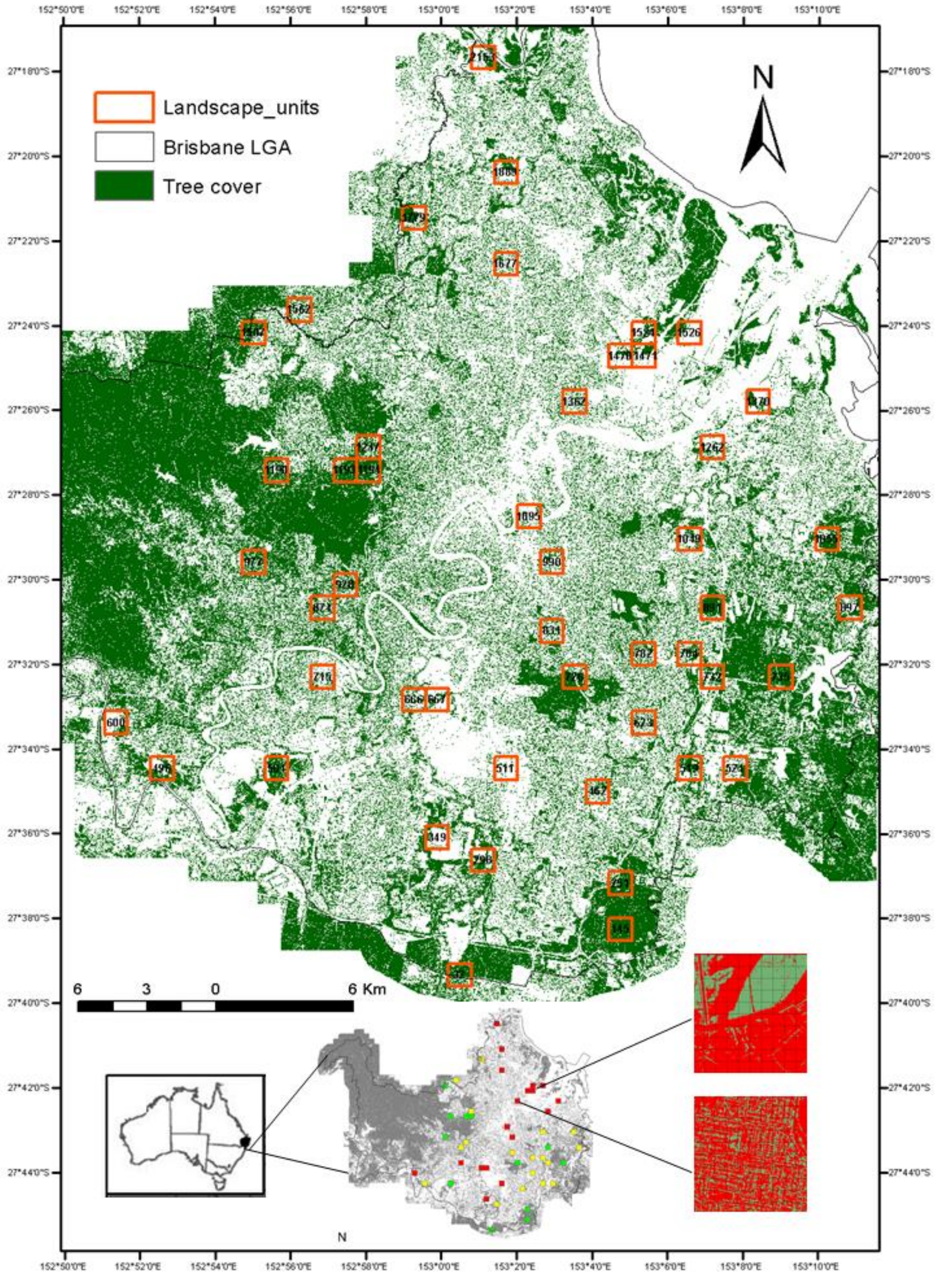

Figure 3-1: Brisbane Local Government Area showing the landscape units used in this study. Landscape units were first selected based on tree cover (red < 30 %, yellow 30-60%, green > 60 %). Each of these categories was stratified across different levels of fragmentation, ranging from low (clumpiness index > 0.8) to high (clumpiness index < 0.5) levels. Two units with similar levels of tree cover and different levels of landscape configuration are highlighted.

3.3.4 Species traits

I selected traits based on previous analyses that have explored their capacity to predict species responses to environmental degradation in urban environments (Croci et al. 2008, Evans et al. 2011, Sol et al. 2014). These traits included body size, habitat plasticity, dispersal capacity and clutch size. Trait values were sourced from an unpublished traits database derived from the Handbook of Australian, New Zealand and Antarctic Birds (Luck, unpublished data) and from Garnett et al. (2015). In addition, Fraser et al. (2017) provided the values for dispersal capacity based on calculations for each species following Garrard et al. (2012) model. This model predicts median dispersal distance based on data on wingspan and body mass collated from published studies world-wide, and predicts that birds with a higher wingspan to mass ratio will have longer median dispersal distances. Collinearity between the selected traits across sites was tested using Spearman's correlation test (Appendix C Table C1). Correlations (range 0.16 –0.36) were considered low, and therefore, all traits were retained for analysis.

Body size can be linked to many system properties (Fritschie and Olden 2016) and strongly relates to a range of other traits in birds, including metabolic rate, foraging behaviour and longevity. Habitat plasticity is an absolute measure that represents the level of habitat specialisation associated with a given species, and it has been used in previous work to explain responses of urban birds to fragmentation and urbanization (Keinath et al. 2017). A diversity of habitat use strategies should confer greater capacity to adapt to landscape change for a given bird community. Although habitat plasticity is a characteristic that may be associated with several traits (e.g. nesting behaviour, competitive ability), I included it to reflect how specialist species would typically perceive their habitat as more restricted than generalists (Öckinger et al. 2010). Values of habitat plasticity were taken from Luck's unpublished database. This metric is based on the frequency of occurrence of a species across thirteen different habitat types (Luck et al. 2013). Finally, mean clutch size was used because species with small clutch size tend to be less resilient to environmental change (Luck et al. 2012).

3.3.5 Environmental variables

Based on a review of the literature concerning bird and wildlife distributions in urban areas (e.g.Batáry et al. 2017, Catterall et al. 2010, Evans et al. 2011, Litteral and Shochat 2017), I chose variables that have been related to the impact of urban form and landscape structure conditions on urban bird diversity at both local and landscape scales. These were: the proportion of each cell that was impervious surface and build infrastructure, the proportion of each cell that was treed (% tree cover), the clumpiness, this is the level of aggregation of vegetation patches in each cell (as an inverse measure of fragmentation), and average vegetative vertical heterogeneity. These variables were calculated in each sampling unit at both local (1ha) and landscape scales (1k). High resolution LiDAR data from which I extracted these variables are available for Brisbane (Brisbane City Council, year 2009) and the collinearity among these variables is low (Appendix C, Table C2). In order to measure vegetative vertical heterogeneity, I used foliage height diversity (FHD) as a relative abundance measure that describes how evenly the vegetation is distributed across each of the vertical stratums (Caynes et al. 2016, Mitchell et al. 2016). To characterise vegetation vertical structure, I used a foliage projective cover layer produced by Caynes et al. (2016). Based on modified methods from Miura and Jones (2010),The LiDAR data was separated into five distinct vertical vegetation layers based on discrete height intervals, including very low (≥ 0.15 to <1 m), low (≥ 1 to <2 m), medium (≥ 2 to <5 m), high (≥ 5 to <10 m) and very high vegetation (≥ 10 m). Caynes et al. (2016) obtained a measure of relative vegetation density within each vertical layer by calculating the ratio between the number of LiDAR returns within each vertical layer to the total number of returns from that layer and below. To quantify total vegetation vertical complexity over discrete height intervals, foliage height diversity (FHD) was calculated for each raster cell. FHD is defined as:

$$FHD=-\sum^{R}_{i=1} p_i \ln p_i$$

where p_i is the proportion of total foliage from the *ith* vegetation layer and R_i denotes the final ratio value for each vertical layer. FHD values are high where vegetation is more evenly distributed across the vertical strata and low where vegetation is less evenly distributed. I calculated a mean FHD value for all areas with tree cover at the local and landscape scale. In order to measure fragmentation, I used a “clumpiness” metric that measures spatial aggregation (McGarigal 2002). This metric is a reliable measurement for habitat fragmentation because it is relatively insensitive to variation in habitat extent (Wang et al. 2014). Clumpiness values range from −1 when vegetation is maximally disaggregated to 1 when vegetation is maximally aggregated (McGarigal et al. 2002) with values above 0 representing more aggregated vegetation and values below 0 more disaggregated. In order to calculate clumpiness, I used the 2-m tree cover data layer for both the local and the landscape scales, defining patches as 4-neighbour contiguous cells of tree cover (e.g. Von Neumann neighbourhood).. Metrics of landscape structure were calculated using FRAGSTATS (v4.2.598) (McGarigal 2002).

3.3.6 Data analysis

3.3.6.1 Abundance estimates

Multiple-covariate distance sampling (Thomas et al. 2010) was used to fit detection functions to the observed data separately for each species and to test the importance of environmental and observer factors thought to influence detection probability. I fitted alternative models to the observed distribution of detections using half-normal or hazard key functions using season, detection type (i.e. if the bird was seen or only heard) and percentage of tree cover at the 1 ha resolution as potential covariates of detection probability of each species. For species recorded infrequently (< 30 records), a common detection function was generated by grouping infrequently recorded species with more common species expected to have similar detectability. (Alldredge et al. 2007). These groupings were based on similarities in diet (i.e. frugivorous, nectarivorous, insectivorous or omnivorous) and main foraging stratum (canopy, understory, ground; see Appendix C, Table C3). For each sampling site, I then calculated density estimates and analytical 95% confidence intervals for each species from the model that were best supported by the Akaike information criteria AIC. The abundance of each species at the 1km scale was estimated as the average of the abundances across the three sites surveyed in each landscape unit.

3.3.6.2 Model selection

For each spatial scale and each trait, I calculated the average trait value of a community, weighted by the relative abundance of the species (community weighted mean, hereafter CWM) using the CWM index of the FD package in R statistical environment (ver. 3.3.2; www.r-project.org). The CWM of traits has been extensively used to study the functional trait structure of communities and how this structure affects ecosystem functioning (Díaz et al. 2007). I log-transformed CWMs in order to approximate a normal distribution of the data and then standardized the CWMs (each trait separately) by subtracting the arithmetic mean and dividing by the standard deviation. At the 1km scale, CWM was calculated using all the species recorded within each landscape unit, whereas only the species recorded at each sampling point were used to calculate CWM at the local scale (1ha).

To identify if variation in trait community weighted means across the environmental gradient at each scale were mostly due to landscape composition (i.e. build infrastructure, tree cover, vegetative vertical heterogeneity), configuration (fragmentation level) or both, I used generalise additive models (hereafter GAMs). Following Wüest et al. (2017), I fitted GAMs for the community weight means as a function of the environmental predictors while accounting for between-trait correlation:

$\text{traitij} = \text{f(envi)} + \text{ukj} + \varepsilon\text{ij}$ Equation 3.1

Where $f(\text{env}_\text{i})$ is the smooth term of an environmental variable in site i, trait_{ij} is the community weight mean of a trait j in site i, u_{kj} represents a random effect that enables the model to fit specific smoothers for each trait j and each predictor k (see equation 3.1). Correlation between traits was accounted for by defining an unstructured correlation structure on u_{kj} with a different parameter for every possible pair of traits. Modelling traits jointly performs better compared to modelling each trait independently since it accounts for correlations between traits and yields less uncertainty in trait CWM predictions (Wüest et al. 2017). In addition, the use of GAMs avoids assumptions about the exact shape (e.g. linear, curvilinear, exponential) of ecological responses and local environmental gradients, which are unknown in many cases (Wüest et al. 2017). In order to minimize overfitting in GAM models, I allowed for a maximum of five degrees of freedom in the smoothers to avoid overly complex responses.

To test if variation in the value of traits in urban bird communities is due to variation in landscape composition, configuration, or both at each spatial scale, I created a full model with all environmental variables and their interactions as fixed terms. All terms were then dropped individually from this model and compared with chi-square likelihood ratio tests, and all terms whose removal did not result in a significant p-value ($\alpha = 0.05$) were considered as non-significant. The explanatory power of the best fitting model using root mean square error (RMSE) of predicted versus observed trait CWM-values. Models with the lowest RMSE have the best absolute fit. In addition, I calculated the marginal R^2, which represents the proportion of variance explained by the predictors. Trait-specific values were calculated for each of these indices. To assess the significance of smooth terms for each trait in the best model, I used approximate p-values of Wald tests implemented in the mgcv (Wood Simon 2010) and 'MuMIn' (Bartón 2014) packages in R. In this case, the null hypothesis is that the smooth term was zero.

3.4 Results

A total of 84 terrestrial bird species were observed during the survey period, none of which have been listed as nationally threatened (IUCN 2017). At the landscape scale, species richness in the highly urbanized areas (percentage of build infrastructure > 70 %) varied from 13 to 24 species, whereas in low urbanized areas (percentage of build infrastructure < 30 %) varied from 22 to 41 species.

The importance of environmental variables to explain trait community weight mean (CWM) changed depending on the spatial scale analysed. At landscape scales, the inclusion of vegetation vertical structure of the vegetation did not improve model performance explaining the distribution of traits across the city (likelihood ratio test $p = 0.22$). Conversely, removing this variable caused a decline in model fit at local scales ($p < 0.005$). Dropping fragmentation or tree cover reduced the performance of models at both scales ($p < 0.0001$). However, the interaction between these two variables was important in improving model fit only at landscape scales (Local scale model: $p = 0.99$, Landscape scale model: $p < 0.005$). The best models for each scale are presented in Table 3.1.

Table 3-1: Best GAMs models using environmental variables as predictors of community weight mean for four different bird traits at the landscape scale (1 km) and the local scale (1 ha). The root mean square error (RMSE) and the proportion of variance explained (R2) by the model for each trait are shown. Predictors: Build infrastructure (BI); Fragmentation (F); tree cover (T); vegetation height diversity (V). Significance levels: * $0.05 < p < 0.1$, ** $0.01 < p < 0.05$. *** NS: not significant.

Trait specific RMSE	Trait specific R^2

	Best model	**Body size**	**Clutch size**	**Dispersal**	**Habitat Plasticity**	**Body size**	**Clutch size**	**Dispersal**	**Habitat Plasticity**
Landscape scale (1 X 1 km)	CWM = T** + F*** + I^{*}*+ F:T***	0.15	0.19	0.13	0.11	0.44	0.09	0.43	0.1
Local scale (1 ha)	CWM = T^{NS} + F** + I^{NS} + V**	0.25	0.35	0.27	0.11	0.17	0.13	0.19	0.03

Models at the landscape scales had a better absolute fit and a higher deviance explained compared to local scale models (Table 3.1). Differences in trait-specific RMSE and R^2 indicate that, at landscape scales, body size (RMSE = 0.15; $R^2 = 0.45$) and dispersal (RMSE = 0.13; $R^2 = 0.43$) were more strongly driven by the selected environmental variables than clutch size (RMSE = 0.35; $R^2 = 0.13$) or habitat plasticity (RMSE = 0.11; $R^2 = 0.10$). At landscape scales (1 km^2), smooth terms of the interaction between dispersal and body size with tree cover ($p < 0.005$ and fragmentation ($p =0.005$) were highly significative. Species in areas with low tree cover and high fragmentation had high dispersal capacity and medium to large body sizes (Figure 3.2a-b). However, when fragmentation was low, assemblages in areas with low levels of tree cover (around 25 %) supported a higher proportion of species with low dispersal capacities (small dispersal community weight mean; Fig 3.2b). The interaction between dispersal and body size with fragmentation was also significant at local scales ($p <0.0005$), and more-fragmented areas with medium amounts of tree cover were associated with lower mean body size (Fig 3.2 d).

3.5 Discussion

The effect of urbanisation on bird species traits is greater at landscape scales and weaker at local scales. At landscape scales, habitat configuration and the percentage of tree cover plays a key role shaping the distribution of body sizes and dispersal capacities. When tree cover was low at landscape scales, the presence of small-bodied species with low dispersal capacities depended mostly on having low levels of fragmentation. In addition, the influence of landscape configuration determining trait distributions at both scales may reflect how increasing habitat heterogeneity facilitates the presence of species with multiple strategies for exploiting resources (Evans et al. 2011, Marzluff 2005). In contrast, tree cover and built infrastructure were poor predictors of trait distributions at local scales. Although the maintenance of small patches at local scales can help to preserve taxonomic diversity (Sekercioglu and Sodhi 2007) , results of this study suggest that this may not be the best alternative to reduce homogenization of bird assemblages, since trait diversity in urban areas is mainly driven by landscape rather than local scale variables.

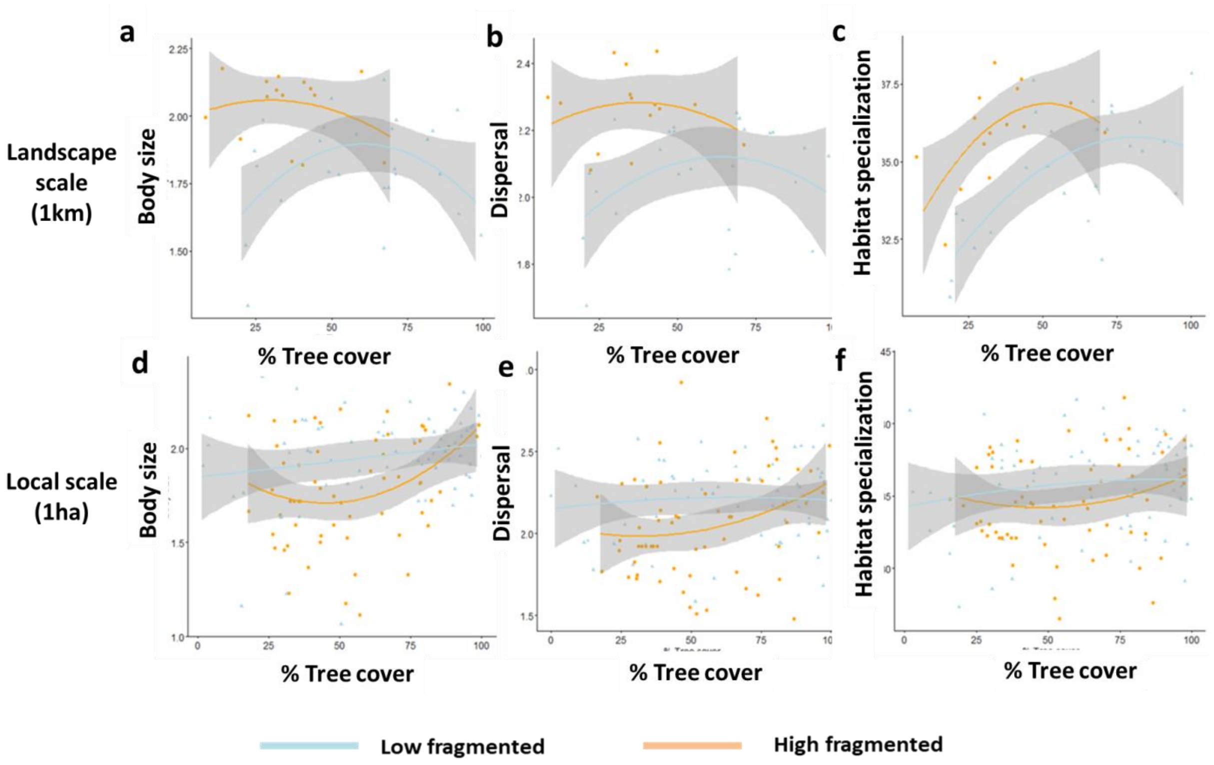

Figure 3-2: Relationship between traits community weighted mean and percentage of tree cover across an urbanization gradient at the landscape (1km) (a-c) and the local scale (1ha) (d-f). The two lines represent different levels of fragmentation. Orange: high fragmentation (clumpiness < 0.5); blue: low fragmentation (clumpiness > 0.5). Effects of tree cover on the distribution of trait values were only significant at landscape scales, whereas effects of fragmentation were significant at both local and landscape scales.

None of the distributions of the traits evaluated were affected in a similar way by environmental variables at both scales. At landscape scales, small species with low dispersal capacities were negatively affected by loss of tree cover, particularly in more-fragmented areas. Previous studies have reported fragmentation and percentage of built infrastructure reducing reproductive capacity of smaller-bodied species and increasing survival of larger-bodied species (Brown and Graham 2015, Evans et al. 2011). At local scales, however, the relationship between species traits and compositional variables (tree cover and build infrastructure) was weak. This might be because of the matrix surrounding remnant habitat patches with similar levels of fragmentation and habitat amount can be quite diverse in urban areas (Garden et al. 2010, Ikin et al. 2013, Litteral and Shochat 2017). Heterogeneity at local scales may facilitate the presence of aggressive species (Shochat et al. 2010) and the availability of finding suitable nesting sites (Marzluff et al. 2007). The influence of these factors on species occurrence may not be mediated by species' size or dispersal capacities, but for behavioural traits that were not take into account in this analysis.

Results of this study show that fragmentation plays an important role driving the distribution of traits at both scales. At the landscape scale, the negative effects of habitat loss and fragmentation are more evident in species with low mobility and low habitat plasticity that are more likely to rely on heterogeneous habitat patches with moderate to low edge effects. On the other hand, highly mobile species, which are able to move among distant habitat fragments, are expected to be less sensitive to landscape configuration (Öckinger et al. 2010, Schleicher et al. 2011). However, highly mobile species can also be negatively affected at local scales by fragmentation through its effect on nesting and reproduction (Ikin et al. 2014). In this case, fragmentation may increase the prevalence of adverse factors, such as nest predation, and facilitate the presence of aggressive species (Montague-Drake et al. 2011). Fragmentation also decreases the proportion of habitat specialists at landscape scales, particularly at medium (< 50 %) and low (< 25 %) amounts of tree cover. This may explain adverse effects on species with high dispersal capacities but with low habitat plasticity. The interaction between fragmentation and spatial scale could explain mixed results from previous studies, ranging from positive effects of dispersal on species occurrence at the landscape level (Devictor et al. 2008) to non- significant effects of urbanization on both highly and poorly mobile birds (Concepcion et al. 2015). These results emphasise the need for multi-scale approaches to properly quantify the importance of species traits and landscape structure shaping urban assemblages.

A focus on conserving species with particular traits at the local scale may be ineffective if attributes of landscape structure are ignored. Local actions such as garden planting (Catterall 2004, French et al. 2005) could be ineffective if the objective is to implement conservation initiatives that target species less tolerant to landscape change (e.g. small-bodied species with low dispersal capacities). Previous work has shown that revegetating urban spaces may increase species richness, but this favours species that are already more adaptable to urban landscapes (Archibald Carla et al. 2017). If landscape structure is inappropriate, enhancing revegetation at local scales may not attain the desired conservation outcomes for species more sensitive to urbanization. Therefore, variation in habitat quality at landscape scales may be more relevant in explaining species distributions in urban landscapes (Donnelly and Marzluff 2006, Melles 2003, Sandström et al. 2006). The results presented here agree with those of previous studies showing that in Brisbane, conservation of bird assemblages in remnants depends mostly on the interaction between patch remnant size and connectivity (Catterall et al. 2010) (Shanahan et al. 2011). Although big generalist species with high dispersal capacities tend to dominate in urban bird assemblages (Devictor et al. 2007, Sol et al. 2014) , heterogeneity caused by landscape change can promote communities with a higher diversity of traits in urban areas(Litteral and Shochat 2017).

There are a few key areas for future research that will help explain the mechanisms of spatial structuring in urban bird assemblages at multiple scales. To improve the reach of these results, linking this information with regional patterns is still needed. The results presented in this study must be compared with analyses of how landscape structure affects trait distributions in surrounding non-urban areas

(Evans et al. 2011). For example, by evaluating the distribution of reproductive and dispersal traits across multiple extents, it might be possible to test how dispersal processes over large distances interact with matrix types to maintain local-scale functional diversity (Benchimol and Peres 2015, Delattre et al. 2013). This will allow for a more comprehensive understanding of how trait values distributions could be extrapolated in space, and could guide management responses that explicitly account for trait effects at a wider range of spatial scales. More research is also needed in understanding trade-offs between multiple sets of traits, including how bird dispersal patterns are associated with other traits such as competitive ability and how this drives community responses to landscape change. In addition, including other metrics of trait distribution may help to understand the main findings of this study. Here, weighted mean trait values were used, but ignoring intraspecific variation may mask the effect of environmental variables on ecological responses, especially in landscape-scale studies that encompass strong environmental gradients and locally adapted populations (Spasojevic et al. 2016b).Finally, accounting for local disturbances associated with habitat fragmentation, such as noise levels and presence of competitive aggressive species may provide additional insights into why species with specific traits may decline. Based on this information, we can develop the most efficient strategies to manage urban species at landscape and local scales.

Chapter 4

EFFECTS OF FRAGMENTATION ON FUNCTIONAL DIVERSITY AND ITS ASSOCIATION WITH SPECIES RICHNESS

To be submitted to Ecography

4.1Abstract

Promoting the conservation of multiple aspects of biodiversity in transformed landscapes is a fundamental challenge. We need to understand not only how landscape structure affects species diversity, but also the distribution of functional traits (i.e. functional diversity) that determine the relationship between species diversity and different ecosystem processes. However, we still lack information about how landscape structure drives the relationship between species richness and functional diversity simultaneously. Here, I use a spatially explicit model to generate hypotheses about how changes to landscape structure drive the relationship between species and different components of functional diversity across human-dominated landscapes. I focus on the correlation between "response traits" (traits involved in species responses to environmental change) and "effect traits" (traits associated with species effects on ecosystem functioning).The strength at which fragmentation modifies functional diversity in modified landscapes depends on the distribution of response traits and the correlation between response and effect traits. I show that: 1) when present, the effect of fragmentation on functional diversity tends to be negative and becomes evident when the correlation between response and effect traits increases; 2) indirect effects of fragmentation through changes in species richness are strong in communities with a low divergence in response traits and 3) direct effects of fragmentation are evident in communities with a high divergence in the distribution of response traits and a high correlation between response and effect traits. The generation of the hypotheses presented in this Chapter provides a good opportunity to test them across a broad range of real landscapes and communities in different regions.

4.2 Introduction

Predicting how landscape change affects the relationship between species diversity and ecosystem functioning is a central question in conservation biology (Mayfield et al. 2010). For many years, it was assumed that maximizing the protection of taxonomic diversity was enough to achieve the conservation of other components of biodiversity (Myers et al. 2000). However, the range of functions provided by a community is thought to largely depend on the diversity of functional trait states across species (i.e. functional diversity; Díaz and Cabido 2001, McGill et al. 2006). Since functional diversity is not necessarily associated to species richness (Laliberté et al. 2010, Mayfield et al. 2010), taxonomic diversity, in some situations, tells us little about the ability of assemblages to provide ecosystem functions. As such, conservationists and ecologists have called for a more comprehensive view of biodiversity that does not only focus on maximizing species richness, but also functional diversity that might affect the potential of an assemblage to maintain ecosystem functions (Cadotte et al. 2011, Cernansky 2017).

A key environmental factor that determines species richness and functional diversity is landscape fragmentation; the breaking apart of habitat, independent of changes in habitat amount (Fahrig 2003). Empirical and theoretical evidence suggests that landscape fragmentation plays an important role in shaping biodiversity, especially when there is little habitat in a landscape (Hanski 2015, Rybicki and Hanski 2013). Fragmentation can alter functional diversity directly by, for example, promoting the occurrence of medium-sized species with high dispersal capacities. In this case, changes in patterns of trait abundances (e.g. an increase in the proportion of high dispersers) within a community may occur even if species richness remains constant (Sonnier et al. 2014a). In addition, fragmentation can act indirectly on functional diversity by affecting species richness (Rybicki and Hansky 2013). This occurs when species richness and functional diversity are correlated and thus factors that affect species richness indirectly affect functional diversity (de Bello et al. 2010, Mouchet et al. 2010, Petchey and Gaston 2006). For example, if functional diversity is positively correlated with species richness, it is expected that less-fragmented landscapes, which may have higher species richness (Rybicki and Hanski 2013), would have high functional diversity as well. By simultaneously affecting species richness and functional diversity, fragmentation may change the strength of the association between these components, as it has been shown with changes in landscape composition (Laliberté et al. 2010, Flynn et al. 2009). As fragmented landscapes become increasingly common (Haddad et al. 2015, Mitchell et al. 2013, Villard and Metzger 2014), disentangling effects of landscape fragmentation relative to the effects of habitat loss is of particular interest to maintain functional diversity.

The response-effect-trait framework can help to identify which traits drive species responses to fragmentation and their effect on ecosystem functioning (Luck et al. 2012, McGill et al. 2006, Mori et al. 2013, Suding et al. 2008). Species responses to landscape change are thought to be directed by their "response traits" (Mori et al. 2013). Those species with response traits that allow persistence in fragmented landscapes are most likely to persist compared to those without compatible response traits (Mori et al. 2013, Suding et al. 2008). For example, species with traits that enhance reproductive capacity favour colonization of small patches of habitat (Belmaker and Jetz 2013, Henle et al. 2004). In addition, habitat specialists tend to be less common across landscapes, and thus more likely to be absent from small isolated remnant patches (Keinath et al. 2017). The species that persist contribute to ecosystem functioning and these functions are reflected in the distribution of "effect traits" (de Bello et al. 2010, Díaz et al. 2004, Suding et al. 2008). Examples of effect traits include tongue length that influence pollination effectiveness and bill morphology that influence the handling of fruits and seeds in different animal groups (Galetti 2013, Garibaldi Lucas et al. 2015, Luck et al. 2012).

By evaluating the correlation between response and effect traits, we may predict the main paths by which fragmentation affects functional diversity. When response traits values that make species susceptible to fragmentation are not correlated with effect traits, the loss of species does not necessarily translates to losses of specific effect functional traits from the community. In this case, fragmentation effects on functional diversity will be less associated to changes in species richness (Carmona et al. 2012, Laliberté et al. 2010, Luck et al. 2013). On the other hand, when response and effect traits are highly correlated, there is a high chance that species responding in a similar way to fragmentation also provide functions that are not provided by other species (Suding et al. 2008). In this case, the association between species richness and functional diversity will be strong, as the loss of those species sharing similar response traits can alter significantly patterns of functional diversity (Mori et al. 2013). However, the rate at which species are lost will depend on how many of them share similar response traits (Mori et al. 2013, Batáry et al. 2017). In this sense, we also need to account for patterns of distribution of response traits across species to infer potential effects of fragmentation on functional diversity.

Currently, we lack spatially-explicit understanding that can provide general hypotheses of how changes to fragmentation drive functional diversity and its association with species richness as habitat is lost. Previous spatially explicit metacommunity models have evaluated the factors that drive coexistence of species with different dispersal and reproductive traits (Buchi et al. 2012, 2014), or that drive species-area relationships (e.g. Rybicky and Hanski 2013). Other studies (Suding et al. 2008, Mori et al. 2013) have presented trait-based response–effect frameworks that differentiate the community response to environmental change (predicted by response traits) and the effect of that change on ecosystem processes (predicted by effect traits). In this chapter, I present a spatially explicit model that integrates these concepts to evaluate how fragmentation affects the association between species richness and different components of functional diversity. These components are the number of different trait values present in a community (i.e. functional richness), the distribution of the abundance of those values (i.e. functional evenness), and the degree to which the abundance of a community is distributed toward the extremities of the occupied trait space (i.e. functional divergence) (Carmona et al. 2016, Villéger et al. 2008). Based on the results of this model, I derive a series of testable hypotheses about the trajectories of change we would expect for species and functional diversity as habitat amount and fragmentation change.

4.3Methods

4.3.1 Model description

I used a modified version of a spatially explicit metacommunity simulation model that integrates elements of the models described by Büchi and Vuilleumier (2014), Jackson and Fahrig (2012), and (Rybicki and Hanski 2013) (R code provided in Appendix D). My model considers multi-species communities that are characterized by their response trait values, and where these are either highly or

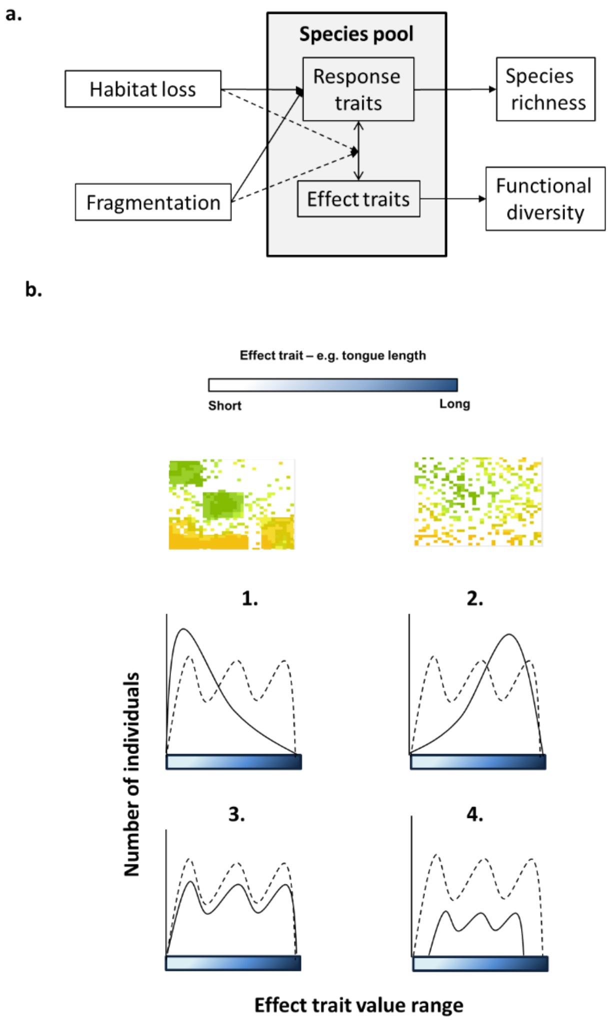

Figure 4-1: Potential paths by which fragmentation and habitat loss can influence functional diversity.a) Fragmentation can affect functional diversity directly by changing the abundance patterns of effect traits. The level at which fragmentation affects directly functional effect diversity will depend on the correlation between response and effect traits. Fragmentation can also affect indirectly functional diversity by altering patterns of species richness. In addition, fragmentation can moderate the association between species richness and functional diversity by changing the correlation between response and effect traits. One-headed arrows represent causal pathways between variables. Dashed arrows represent moderating effects b) Examples of direct and indirect effects of fragmentation on functional diversity for a community with high correlation between response (e.g. dispersal) and effect (e.g. tongue length) traits. 1 and 2 represent direct effects whereas 3 and 4 represent cases of indirect effects. 1., fragmentation pattern benefits low dispersers and thus species with short tongues without changing species richness; 2. Fragmentation pattern benefits high dispersers and thus species with longue tongues without altering species richness: 3. Fragmentation pattern maintain high levels of species richness. In this case, the chance of maintaining high levels of functional diversity will depend on the correlation between response and effect traits. 4. Fragmentation pattern affects negatively species richness and filter both high and low dispersers.

slightly correlated with effect traits. The species reproduce, disperse, survive and compete for space in landscapes with different levels of habitat amount and different patterns of habitat fragmentation (Figure 4.2).

Landscapes are represented as grids where cell values represent a continuous measure of habitat type so that cells with similar values correspond to similar habitat types. The edge of the grid-based landscape was modelled as a torus, with the bottom row adjoining the top row and the right-most column adjoining the left-most column. Each cell had a fixed carrying capacity that can support a maximum number of individuals, which is constant across all cells in the landscape. Dispersing organisms could not settle if a grid cell reached carrying capacity, and thus carrying capacity was used as a proxy for competition of different individuals for space. Performance of a species in a particular grid cell was determined by the distance between the habitat type value of each cell the optimum habitat type values based on the response trait values of that species. The interaction between community dynamics and the spatial distribution of habitat type values determines outcomes in terms of patterns of species diversity and functional diversity.

4.3.2 Landscape generation

I created fractal landscapes of 1089 (33 x 33) cells using the midpoint displacement algorithm (Saupe 1988). I assumed that habitat types were spatially autocorrelated, thus grid cells with similar values tended to be close to each other (fractal dimension D = 2, to generate all landscapes). To ensure that there was an even representation of habitat values across the landscape and avoid bias towards particular habitat types, I transformed the normally-distributed raw values generated by the midpoint displacement algorithm to a uniform distribution, U (0,1). To do this, I used the following transformation:

$$z = \frac{1}{2} Erfc\left(\frac{-y}{\sqrt{2}}\right) \qquad \text{Equation 4.1}$$

Where z is a uniform distributed value, y is a Gaussian distributed value, and *Erfc* is the complementary error function (Weisstein 2006).

I simulated the removal of habitat in each landscape, by creating a second fractal landscape that served as a “habitat loss grid”. Values of grid cells in the “habitat loss grid” were distributed uniformly based on equation 4.1, and corresponded to the relative probability of the cell being removed from the original fractal landscape. Based on these probabilities, I removed a set number of cells that I assumed become unsuitable for reproduction and settlement by any species. To simulate fragmentation, I manipulated the distribution of cells within the “habitat loss” grid to simulate maximal (fractal dimension D = 3) to low (fractal dimension D = 2) levels of fragmentation (Figure 4.2a).

4.3.3 Species response traits

Species differed based on three response traits: niche optimum (μ_s), niche breadth (σ_s) and dispersal ability (ϕ_s). I chose niche optimum and niche breadth since they affect habitat suitability and specialisation of species by influencing their reproductive capacity in different habitats, whereas dispersal ability plays a fundamental role in determining the impacts of habitat fragmentation on species diversity (Büchi and Vuilleumier 2014, Cattarino et al. 2016). In real communities, niche optimum and breadth corresponds to an expression of multiple traits including diet, morphology and foraging strategies(Laughlin and Messier 2015). However, for simplicity, I assumed that one trait is the main determinant of each of niche optimum and breadth, but this model could be extended to include multiple traits if needed.

I assume that niche optimum and niche breadth control the number of offspring each species can produce in different habitats. The niche optimum constitutes the habitat value where each species has the greatest reproductive capacity, while niche breadth corresponds to the range of habitat values where the species can reproduce. For each cell, individuals reproduce based on their reproductive rates $R_s(H_i)$ such that:

$$R_s(H_i) = \frac{1}{\sigma_s\sqrt{2\pi}} exp\left[-\frac{1}{2}\left(\frac{H_i-\mu_s}{\sigma_s}\right)^2\right]. \qquad \text{Equation 4.2}$$

where $R_s(H_i)$ depends on the deviation from the individual niche optimum μ_s in the habitat (H_i) value for the cell i that the individual is located in, as well as the niche breadth (σ_s). Values of $R_s(H_i)$ were rounded to the nearest integer to produce a discrete numeric value of offspring in each simulation step. Species with large niche breadths tend to be able to reproduce in a wider range of suitable habitats and thus are more generalist than species with the smaller niche breadths. However, their reproductive rate in their optimum habitat is lower compared to specialists (Büchi and Vuilleumier 2014).

I specified dispersal ability as a trait that affects the probability that individuals disperse a distance d between cells. This probability is described by a negative exponential distribution:

$$D_s(d) = \frac{1}{\phi_s}\exp\left(\frac{-d}{\phi_s}\right) \qquad \text{Equation 4.3}$$

where $D_s(d)$ is the dispersal kernel of species s, and ϕ_s is the mean dispersal ability for the species (Büchi and Vuilleumier 2014).

4.3.4 Distribution of response traits

Following Kraft et al. (2007) and Mouchet et al. (2010), I simulated sets of 150 species to generate communities with different distributions of response traits (Figure 4.2b). For simplicity, I controlled the distribution of one response trait: niche breadth. I used this trait since the distribution of specialist (narrow niche breadth) versus generalist species (broad niche breadth) is a major determinant of communities' tolerance to landscape change (Büchi and Vuilleumier 2014). Communities could have a high representation of specialist species that are more dependent to one particular habitat type. In contrast, communities could have a high proportion of generalist species that are able to reproduce in a wide range of habitat types. In each simulation I started with a uniform distribution of dispersal abilities in each community and allowed fragmentation and habitat loss to filter for specific dispersal strategies after community dynamics. For each community, niche optimum also followed a uniform distribution across species, taking values between 0 and 1 (Table 4.1).

To simulate different distributions of niche breadths, I used a beta distribution with different mean and variance parameters (equation 4.4; Table 4.1):

$$Var(y_i) = \frac{m_i(1 - m_i)}{(1 + p_i)} \qquad \text{Equation 4.4}$$

where $Var(y_i)$ is the variance of niche breadth (y_i) across individuals in a community i, m_i is the mean niche breadth value for the community i and p_i is a precision parameter that controls the variance of y_i across the entire community.

4.3.5Correlation between response and effect traits

To test how landscape structure might affect each community's capacity to provide functions, I used a continuous theoretical effect trait "ET1" that follows a uniform distribution between 0 and 1. This distribution ensures that different values of the effect trait are equally represented in each community. In order to achieve different levels of redundancy, I controlled the correlation coefficient between response and effect traits using a bivariate beta distribution based on the method described by (Dias et al. 2008). A low correlation coefficient implies a high chance of having effect trait values spread randomly across different response trait values, whereas a high correlation implies a high chance of particular effects trait values being associated with particular response trait values.

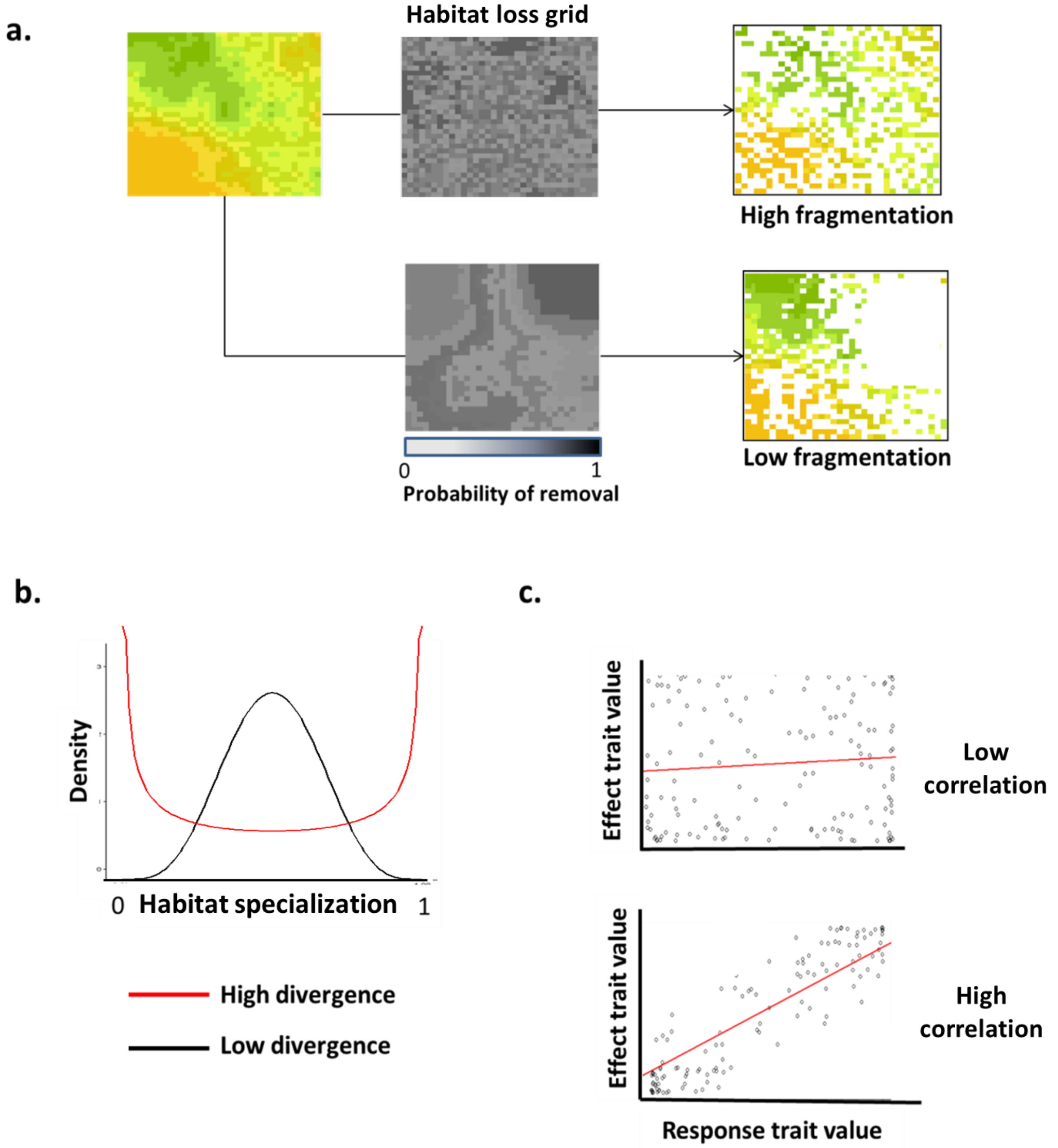

Figure 4-2: Main components of the model used to infer the effects of fragmentation on the relationship between species richness and functional diversity a) Fractal landscapes represent landscapes with different amounts of habitat and the configuration of habitat patches. Cells with similar colours represent similar habitat types. High fractal dimension represent situations where habitat is removed with high levels of fragmentation. b) Communities with different distributions of response traits are achieved by sampling different distributions of niche breadths. c) Communities with different levels of correlation between effect and response traits.

Table 4-1 List of parameters used to generate the species pools and the fragmentation patterns

	Parameter	Phase	Values
Functional Traits	Niche optimum (μ_s)	Reproduction	U(0,1)
	Niche breadth (σ_s)	Reproduction	Beta(m, p_i) m = (0.5), p_i = (5,50)
	Dispersal ability (ϕ_s)	Dispersal	U(0,1)
	Effect trait (ET)	Functional effect diversity	U(0,1)
Landscapes	Fractal algorithm (D)	Spatial structure of the habitat	2
	Fractal algorithm (D)	Fragmentation pattern	2,3

4.3.6 Community dynamics

I used a demographic model to simulate the dynamics of each community in each landscape. Demographic processes were simulated in the following sequence: (1) reproduction, (2) mortality, and (3) dispersal. After reproduction, individuals survive based on a probability of 0.5 for each species. In this way, I did not assume a specific survival strategy for each species and kept mortality as a fixed factor in my analysis. All juveniles disperse a random distance (d) during each time step, drawn from the dispersal kernel that depended on their dispersal ability ϕ_s (Equation 4.3). The initial direction of the movement was chosen by drawing a uniform random number between 0 and 2π. Then, individuals adopted a movement behaviour where the directions of successive movement steps were correlated (Van Dyck and Baguette 2005). For this, I used a wrapped Cauchy distribution with a mean direction equal to the previous direction (Fletcher Jr 2006). If individuals did not find a suitable cell because it had reached its carrying capacity (K = 10) or if it was not suitable for reproduction ($R_s(H_i)$ was less than 1) or settlement the individual moved again and looked for a different cell. Individuals could not move more than five times in one time step and died if they could not find a suitable cell. For simplicity, I did not explicitly model mortality during movement. Once all the individuals dispersed and settled they became adults, reproduced and a new time step started.

4.3.7 Experimental design

Simulations were conducted using a factorial experimental design, in which the total amount of habitat, the fragmentation pattern, the distribution of response traits, and the correlation between response and effect traits in the community were varied. I considered two different levels of fragmentation for the habitat removal process: low (*D*=2) and high (*D*=3). For each fragmentation level, habitat was removed at four levels: 60%, 70%, 80% and 90% habitat loss. I focused on medium and low levels of habitat amount, as this is the range where previous studies have found the largest effects of fragmentation on communities and species (Hanski 2015, Rybicki and Hanski 2013). In addition, I controlled for the distribution of abundances of niche breadths within the trait value range for each community (Hereafter "divergence" Carmona et al. 2016). For this, I used equation 4.4. If divergence is low, few species are distributed in the extremes of the trait value range, and thus it is expected that most species will respond similarly to landscape change. In contrast, if divergence is high, many species are distributed in the extremes of the trait value range, and thus many species will respond differently to landscape change. I tested the effects of fragmentation patterns on four types of communities with different distributions of niche breadths and different levels of correlation between effect and response traits (Table 4.1, Figure 4.2b-c): 1) Low divergence in the response trait, high correlation; 2) High divergence in the response trait, low correlation; 3) Low divergence in the response trait, low correlation and 4) High divergence in the response trait, high correlation.

The simulations were initialised by randomly allocating individuals to habitat cells in each landscape until each cell reached carrying capacity (K = 10 individuals). Then community dynamics were simulated in each fragmented landscape until species richness varied by less than 10 % from time step to time step for at least 100 time steps, or until the community went extinct. For each of the 32 unique combinations of factors (four types of communities, by four levels of habitat amount, by two types of fragmentation patterns), I replicated community dynamics 50 times, resulting in a total of 1600 simulation runs. A new landscape and a new community were simulated in each run.

4.3.8 Statistical analysis

I characterized species richness and the distribution of the effect trait in each community at the end of each simulation using the TPD package in R version 3.1.3 (Carmona et al. 2016). This package calculates functional diversity using trait probability density functions that represent the distribution of probabilities of observing each possible trait value in a given ecological unit. For each simulation, I calculated functional divergence, functional evenness, and functional richness (Mason and De Bello 2013).

I used structural equation modelling (SEM; Grace 2006) to examine the pathways through which habitat loss and fragmentation affect each component of functional effect diversity (i.e. functional evenness, functional divergence or functional richness). I created a different model for each functional diversity component establishing a causal path between species richness and functional diversity to account for indirect effects of habitat amount and fragmentation. I also included a moderator term for habitat loss and fragmentation to detect their influence on the association between functional diversity components and species richness (moderated mediation *sensu* Preacher et al. (2007). To evaluate if the patterns of response trait divergence influenced effects of habitat loss and fragmentation, I created a model including all the community types. In addition, I created models for each community type to evaluate the paths by which fragmentation effects changed depending on the level of correlation between response and effect traits. The Tucker – Lewis index (TLI) was used to check how overall model fit improved relative to compared with an expected "true" model that best explains the response variable based on the presented set of predictors. A value of 0.95 or larger indicates good model fit (Weston and Gore 2006). I also used the root mean square error of approximation (RMSEA) to measure absolute model fit, where values < 0.06 indicate good fit (Weston and Gore 2006). Models with high RMSEA and low TLI were rejected and some relationships were removed until I found a well-fitting and ecologically meaningful model (Shipley 2000). Direct and indirect effects of each environmental predictor on functional diversity were analysed by calculating standardized path coefficients of the final selected model (Grace 2006). All SEMs were created using the R package *lavaan* (Rosseel 2012) in R version 3.1.3 (R Core Team, 2015)

4.4 Results

The full model (TLI = 0.995 and RMSE = 0.04) including all the community types show that both habitat loss (p < 0.001) and fragmentation (p < 0.005) have a negative effect on all the components of functional diversity. In addition, the correlation between response and effect traits was key determining the relative importance of direct and indirect effects of landscape fragmentation on functional diversity. Effects of habitat loss were more constant than effects of fragmentation, and for the same amount of habitat loss, communities with a high correlation of response and effect traits tended to be more negatively affected compared to communities with low correlations (Figure 4.3, Table 4.2). This pattern was maintained for all the components of functional diversity independently of the distribution of response traits (Figure 4.3, Table 4.2).

Effects of fragmentation on functional diversity depended on three main factors: the correlation between response and effect traits, the distribution of response traits and the functional component evaluated. Models for communities with high effect- response trait correlations included significant direct fragmentation effects (p < 0.05, Table 4.2) and had a good fit (TLI = 0.95 and RMSE = 0.03). In these communities, components of functional diversity tended to be lowest in fragmented landscapes compared to non-fragmented landscapes (Figure 4.3). However, depending on the distribution of response traits, the prevalence of direct effects or effects mediated by changes in species richness was different. When the divergence in the distribution of response traits was low, indirect effects on all the components of functional diversity were always significant ($p < 0.01$, Table 4.2). In contrast, when the divergence in response traits increased, direct effects were prevalent (Table 4.2). For communities with a low correlation between effect and response traits, negative effects of fragmentation were only significant for functional richness ($p < 0.01$), particularly when the divergence in the distribution of response traits increased (Table 4.2). I did not find significant effects of fragmentation on either functional evenness or functional divergence of communities with low correlations of response and effect traits (Table 4.2).

Moderating effects of fragmentation on the association between species richness and functional diversity were only evident for functional richness in communities with a high divergence in the distribution of response traits (TLI = 0.985 and RMSE = 0.05). In this case, functional richness decreased faster than species richness in fragmented landscapes, particularly when species richness was low (Figure 4.4). For all the community types analysed, I did not find any evidence that the association between species richness and functional evenness or functional divergence was affected by fragmentation (Table 4.2).

4.5 Discussion

4.5.1Effects of fragmentation on functional diversity and its association with species richness

The results of this model provide new evidence that landscape configuration is important driving patterns of species richness and functional diversity. My results agree with previous work showing that habitat amount tends to filter species more strongly than fragmentation (Fahrig and Triantis 2013). However, my model shows that a redistribution of trait abundances as a result of changes in habitat configuration is expected depending particular factors (Sonnier et al. 2014a). Based on the results presented here, general patterns of fragmentation effects on functional diversity and its association with species richness can be found: 1) the effect of fragmentation on functional diversity tends to be negative and becomes evident when the correlation between response and effect traits increases; 2) indirect effects of fragmentation through changes in species richness are strong in communities with a low divergence in response traits and 3) direct effects of fragmentation are evident in communities with a high divergence in the distribution of response traits and a high correlation between response and effect traits. Testing these patterns across different regions and landscape contexts will help to understand the mechanistic pathways through which fragmentation influence functional diversity and species richness.

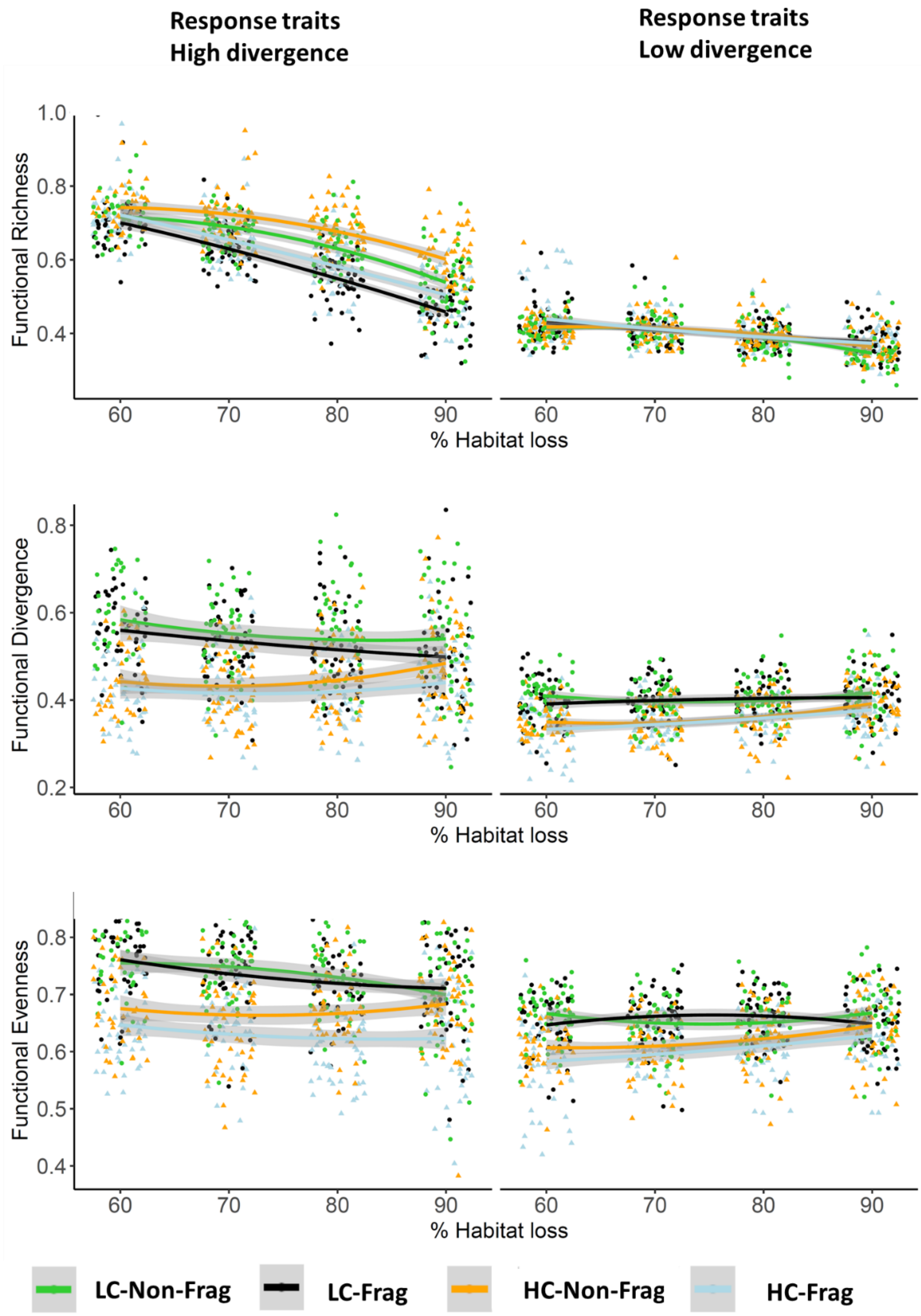

Figure 4-3: Relationship between functional diversity components and habitat amount showing the trends for two fragmentation types. Panels on the left correspond to a community with high divergence in the distribution of niche breadth values, whereas panels on the right correspond to communities with low divergence in the distribution of niche breadths. Shaded areas represent the 95 % confidence interval. LC : Low correlation between response and effect traits; HC: High correlation between response and effect traits; Frag: High fragmented landscape; Non-Frag: Low fragmented landscape.

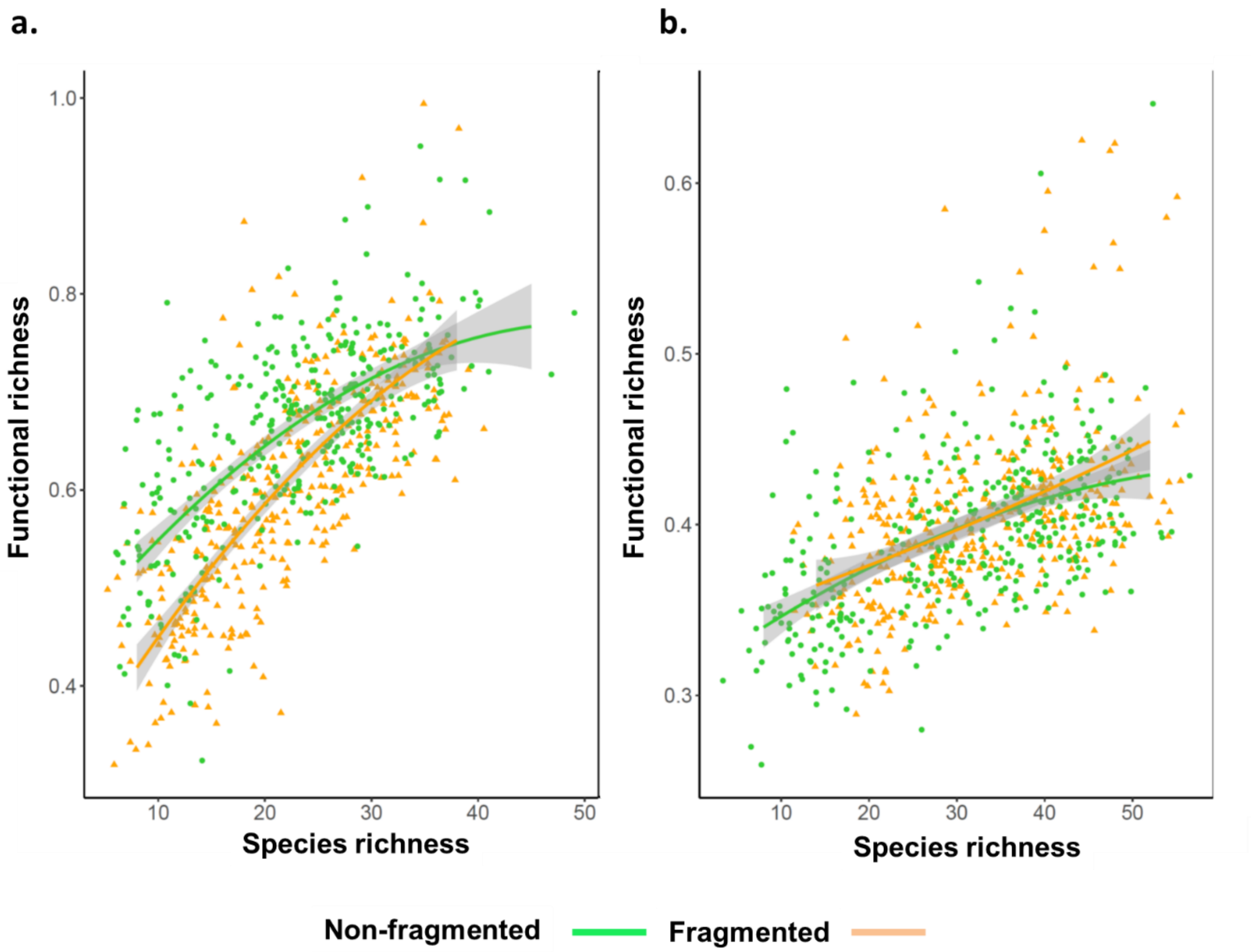

Figure 4-4: Association between species richness and functional richness for different types of communities with a) high divergence and b) low divergence in the distribution of response traits. The lines represent two levels of fragmentation. In communities with high divergence in the distribution of response traits, fragmentation increases the rate of decline in functional richness for a given number of species. Shaded areas represent confidence intervals.

Table 4-2: Direct, indirect (mediated by changes in species richness) and moderating effects of fragmentation and habitat loss on different components of functional diversity for communities with different distributions of response traits and different levels of correlation between response and effect traits. FRic = Functional richness; FDiv = Functional divergence; FEve = Functional evenness. Significant effects are bolded.

				Low correlation				High correlation			
	Distribution of response traits			Estimate	Std.Err	z-value	P(>|z|)	Estimate	Std.Err	z-value	P(>|z|)
Fric	High divergence	Direct effects	Habitat loss	**0.00**	**0.00**	**-2.89**	**0.00**	**0.00**	**0.00**	**-3.04**	**0.00**
			Fragmentation	**-0.06**	**0.01**	**-8.75**	**0.00**	**-0.06**	**0.01**	**-9.93**	**0.00**
		Correlation	Species richness	**0.01**	**0.00**	**3.12**	**0.00**	**0.01**	**0.00**	**3.24**	**0.00**
		Indirect effects	Fragmentation	**-0.01**	**0.01**	**-1.90**	**0.06**	**-0.01**	**0.00**	**-3.08**	**0.00**
			Habitat loss	**0.00**	**0.00**	**-2.98**	**0.00**	**0.00**	**0.00**	**-3.05**	**0.00**
		Moderating effects	Fragmentation	**0.003**	**0.001**	**6.503**	**0.00**	**0.00**	**0.04**	**2.94**	**0.00**
	Low divergence	Direct effects	Habitat loss	0.00	0.00	0.66	0.51	0.00	0.00	0.04	0.97
			Fragmentation	0.01	0.01	1.27	0.21	0.00	0.00	0.62	0.53
		Correlation	Species richness	**0.00**	**0.00**	**3.34**	**0.00**	**0.00**	**0.00**	**3.55**	**0.00**
		Indirect effects	Fragmentation	**0.00**	**3.00**	**0.00**	**0.01**	**0.00**	**0.00**	**2.69**	**0.01**
			Habitat loss	**0.00**	**0.00**	**-3.22**	**0.00**	**0.00**	**0.00**	**-3.41**	**0.00**
FDiv	High divergence	Direct effects	Habitat loss	0.00	0.00	-0.24	0.81	**0.00**	**0.00**	**1.75**	**0.08**
			Fragmentation	-0.02	0.01	-1.88	0.06	**-0.02**	**0.01**	**-1.94**	**0.05**
		Correlation	Species richness	0.00	0.00	1.36	0.17	0.00	0.00	1.09	0.28
		Indirect effects	Fragmentation	0.00	0.00	-1.47	0.14	0.00	0.01	-0.88	0.38
			Habitat loss	0.00	0.00	-1.30	0.20	0.00	0.00	-1.02	0.31

	Low divergence	Direct effects	Habitat loss	0.00	0.00	-0.15	0.88	0.00	0.00	-0.60	0.55
			Fragmentation	-0.01	0.01	-0.75	0.45	-0.01	0.01	-0.96	0.34
		Correlation	Species richness	0.00	0.00	-0.98	0.33	**0.00**	**0.00**	**-2.94**	**0.00**
		Indirect effects	Fragmentation	0.00	0.00	-0.76	0.45	**0.00**	**0.00**	**-2.17**	**0.03**
			Habitat loss	0.00	0.00	0.91	0.36	**0.00**	**0.00**	**2.82**	**0.01**
Feve	High divergence	Direct effects	Habitat loss	0.00	0.00	-1.36	0.18	0.00	0.00	1.05	0.29
			Fragmentation	0.00	0.01	0.10	0.92	**-0.04**	**0.01**	**-3.86**	**0.00**
		Correlation	Species richness	0.00	0.00	1.20	0.23	0.00	0.00	1.57	0.12
		Indirect effects	Fragmentation	0.00	0.00	-1.27	0.21	0.00	0.00	-1.44	0.15
			Habitat loss	0.00	0.00	-1.21	0.23	0.00	0.00	-1.55	0.12
	Low divergence	Direct effects	Habitat loss	0.00	0.00	-1.37	0.17	**0.00**	**-0.45**	**0.65**	**0.00**
			Fragmentation	0.00	0.01	-0.40	0.69	**-0.01**	**0.01**	**-2.26**	**0.02**
		Correlation	Species richness	0.00	0.00	-1.39	0.17	**0.00**	**0.00**	**-2.31**	**0.02**
		Indirect effects	Fragmentation	0.00	0.00	-1.53	0.13	**0.00**	**0.00**	**-2.10**	**0.04**
			Habitat loss	0.00	0.00	1.37	0.17	**0.00**	**0.00**	**2.33**	**0.02**

Direct fragmentation effects on functional diversity that are independent of changes of species richness are common in communities with a high divergence in the distribution of response traits. Previous work shows that landscape change can promote changes in the distribution of functional traits without substantially reducing species richness (Concepcion et al. 2015, Ding et al. 2013). This could happen, for example, if some species are replaced by stronger competitors with a new set of traits (i.e. changes in functional richness), if the abundance of species with less common traits increases (i.e. changes in functional evenness) or if the centroid of the mean trait distribution is changed (changes in functional divergence). These changes will have an impact on functional diversity while species richness remains constant (Sonnier et al. 2014a). Since fragmentation tends to filter species that share similar traits (Carneiro et al. 2016), the diversity of functional traits may decrease abruptly in fragmented landscapes for a given number of species. This could be particularly evident when groups of species that share similar response traits that make them more susceptible to fragmentation. Although the main effects of fragmentation on functional evenness and functional divergence were negative, fragmented landscapes can lead to an increase in these components at low levels of species richness (Figure 4.3, Table 4.2). These can reflect that only the most adapted species that maximize the use of resources in high fragmented areas will persist (Ding et al., 2013, Ibarra and Martin 2015). These results may explain the homogenization in the distribution of functional traits that has been found across multiple human dominated landscapes (Devictor et al. 2007, Ibarra and Martin 2015, Sonnier et al. 2014b).

Indirect effects of fragmentation through changes in species richness are preponderant when the divergence in response traits is low. In this case, my model reflects cases where species richness and functional diversity are correlated and thus factors that decrease species richness are expected to indirectly decrease functional diversity (de Bello et al. 2010, Mouchet et al. 2010, Petchey and Gaston 2006). When the divergence in the distribution of response traits decreases, there is a high chance that multiple species respond in a similar way to landscape change. For example, fragmentation has a strong negative effect on large bodied species (Bartlett et al. 2016, Bregman et al. 2014) or high trophic groups (Bartlett et al. 2016). If these species share similar effect traits, fragmentation will have an important role hindering particular functions such as seed dispersal for large-fruited trees (Bovo et al. 2018). In addition, if the correlation between response and effect traits is high, losing one particular species can affect significantly functional diversity, as fewer species contribute in a similar way to any given ecosystem function (Mori et al. 2013). In this case, patterns of functional diversity will mostly depend on species richness.

Results of this study suggest that we should avoid fragmentation to maintain high levels of functional diversity at the landscape scale. Although fragmentation can increase heterogeneity in habitats and have some positive effects on species richness and species abundance (Fahrig 2017), my model shows that increasing fragmentation reduces functional diversity for a given amount of habitat. In addition, I show evidence that functional richness can decrease more abruptly in fragmented landscapes when there is a high divergence in the distribution of response traits. As shown in previous studies, functional richness is more correlated to species richness and generally decreases as habitat is lost (Flynn et al. 2009, Mayfield et al. 2010). This is supported by empirical evidence (Ding et al. 2013, Magnago et al. 2014) showing that fragmentation selects against species with extreme trait values and so trait values tend to converge (Barbaro et al. 2014). In contrast, large habitat patches allow the persistence of more specialist species (Rybicki and Hanski 2013). Thus, less-fragmented landscapes that have not reached low amounts (< 30 %) of remnant vegetation tend to promote the persistence of species with extreme trait values (Carmona et al. 2016, Mason and De Bello 2013). Results of this study also suggest that functional evenness increases when fragmentation is low. Therefore, independently of the number of species and the amount of habitat available, large or interconnected habitat patches will not only promote a higher functional richness (Bovo et al. 2018), but also a higher chance that species with extreme and less common traits use available resources more efficiently at the landscape level (Magnago et al. 2014).

4.5.2Limitations and future research

As with all models, I made a series of assumptions that may limit the generality of these findings. First, I used a single trait to describe both the distribution of response traits and effect trait diversity. Second, my model assumes that there is a strong relationship between species traits and local environmental conditions, even though the effects of traits might depend on regional context that is ignored in this study. Finally, I ignore the frequency of disturbances that can alter relationships between species richness and functional traits. Here, I describe potential avenues of research that can provide more insights in these topics.

A crucial avenue of research involves identifying which set of traits have the largest influence on species' responses to fragmentation. Values of functional diversity metrics depend on which traits and how many traits are included (Mouchet et al. 2010, Zhu et al. 2017). In my model, I used niche breadth to represent a combination of traits that favoured reproduction in particular habitats. However, multiple traits such as body size, trophic level and matrix tolerance increase or decrease a species' vulnerability to fragmentation and habitat loss, and therefore define niche breadth (Ewers and Didham 2006) (Laughlin and Messier 2015). In addition, survival and competitive traits act with spatial heterogeneity to promote the coexistence of distinct dispersal strategies (Cattarino et al. 2016) (Büchi and Vuilleumier 2014, 2016) . Therefore, a selection process evaluating correlations between traits in real landscapes is needed before testing effects of habitat configuration on functional diversity.

Previous research shows that factors related to regional context (e.g. regional disturbance) can modify the effects of species traits on ecological functions. Unfortunately, there is a lack of empirical tests that evaluate how fragmentation drives functional diversity across different disturbance frequencies.

Empirical evidence comes mostly from analyses that focus on landscape composition (e.g.Flynn et al. 2009, Luck et al. 2013) or from tests comparing functional group diversity across patches of different size in the same landscape (e.g. Benchimol and Peres 2015, Bregman et al. 2014). Future research should focus on discerning how factors such as matrix type and composition, the scale of analysis, species interactions and spatial autocorrelation of habitat types affect the hypotheses provided by my model (Biswas et al. 2016). For example, by evaluating the distribution of reproductive and dispersal traits across landscapes with different matrix type and levels of spatial autocorrelation of habitat types, it might be possible to test how dispersal processes are affected to maintain local-scale functional diversity.

Finally, competitive and mutualistic interactions among species with similar ecological traits have an important role in shaping community structure in heterogeneous landscapes (Barbaro et al. 2014, Bregman Tom et al. 2015). In my model, carrying capacity was used as a proxy for competition of different individuals for space. However, further work need to quantify how spatial context moderates the role of species interactions in driving trait distributions. For instance, the spatial autocorrelation of habitat types may affect movement behaviour, as well as the probability of species interacting (Barbaro et al. 2014, Biswas et al. 2016). This opens an opportunity to analyse how landscape configuration drives functional diversity by altering the frequency at which species interact. In addition, accounting for disproportionate effects of key species that may drive community structure is needed. For example, an increase of a single native species affected by anthropogenic habitat alteration can introduce substantial ecological dysfunction (Maron et al. 2013). Such information would complement inferences about how environmental filtering processes lead to patterns of trait diversity across systems with different spatial contexts.

4.5.3 Conservation and management implications

Highly fragmented landscapes are becoming ever more common with continuing anthropogenic habitat conversion (Haddad et al. 2015). Thus, understanding how landscape configuration influences ecosystem functions in fragmented landscapes will help maximize the ability of limited conservation resources to achieve landscapes that provide multiple functions. If for example, there is low correlation between response and effect traits in a group of frugivorous species, my results suggest that focusing resources on protecting patches that maximize taxonomic diversity may be enough to ensure high levels of seed dispersal. However, when the correlation between effect and response traits increases (e.g. pollinator ensembles where different species are associated with different crops), the potential to manage landscape configuration to protect both species richness and functional diversity becomes more restricted. In this case, planning at the landscape scale requires a deeper understanding of the trade-offs and synergies between the conservation of taxonomic diversity and functional diversity with limited resources.

My results support the idea that habitat fragments should be protected in clusters rather than as randomly scattered fragments (Rybicki and Hanski 2013), since when fragmentation has an effect on diversity, it is always negative. There is empirical evidence that functional diversity increases with patch size (Benchimol and Peres 2015, Bregman Tom et al. 2015) and this may explain the positive effects of maintaining spatial aggregations of habitat as habitat is lost across a landscape. However, preserving large habitat patches is not always possible, and there are many examples where managing the spatial configuration of remnant habitat is necessary. For example, although urban environments tend to have negative impacts on biodiversity, ecological impacts of urbanization might be mitigated by managing the composition and spatial pattern of the remaining habitat (Lin and Fuller 2013, Villard and Metzger 2014). Collecting empirical evidence of functional diversity along the gradient of large patches to networks of small patches will help develop strategies to manage the growth of urban and agricultural landscapes and conserve both species and functional diversity.

Chapter 5

EFFECTS OF LANDSCAPE STRUCTURE ON SPECIES RICHNESS AND FUNCTIONAL DIVERSITY IN URBAN BIRDS ENSEMBLES

To be submitted to Journal of Applied Ecology

5.1 Abstract

Analysing the simultaneous effects of landscape structure on species richness and functional diversity is necessary to propose strategies that maximize the conservation of both. Here, I use structural equation modelling to show how landscape composition (the percentage of tree cover and built infrastructure), landscape configuration (fragmentation level) and vegetation structure interact to drive functional diversity and species richness of urban bird ensembles in Brisbane, Australia. My approach allows disentangling the pathways through which landscape structure (i.e. landscape composition and configuration) affect functional diversity in two main ways: 1) indirect effects through changes in species richness or 2) direct effects through redistribution in the abundances of particular traits. Effects of landscape structure on species richness are consistent among different ensembles: fragmented landscapes in areas with high percentage of built infrastructure have low levels of species richness. However, patterns of functional diversity are more complex. Direct effects of landscape composition on functional diversity were more common in frugivorous/nectarivorous, whereas direct effects of fragmentation were more evident in insectivorous ensembles. In addition, effects of landscape composition mediated by changes in species richness were more common than indirect effects of fragmentation These results are key for understanding how urban growth might best be done to maximize the conservation of functional and taxonomic diversity.

5.2 Introduction

Evaluating the relationship between species richness and functional diversity is necessary if we want to maximize the conservation of both in changing landscapes. If species richness and functional diversity are strongly related, similar conservation strategies could achieve both. However, previous work (including the model presented in chapter 4) has demonstrated that the relationship between species richness and functional diversity can vary from positive to negative or non-significant (Flynn et al. 2009, Laliberté et al. 2010, Mayfield et al. 2010). In particular, fragmentation can affect this relationship by modifying trait distributions and mediating the effects of habitat amount on both species and traits (Ibarra and Martin 2015, Magnago et al. 2014). However, most progress in this area comes from large-scale analyses that focus on landscape composition (Flynn et al. 2009, Luck et al. 2013), and the broader effects of landscape structure on this relationship have been widely overlooked.

Effects of landscape structure on functional diversity can be both direct and indirect (Sonnier et al. 2014a). Fragmentation and habitat loss can act directly on functional diversity by filtering species with certain traits that make them more tolerant to landscape change (Barbaro et al. 2014, Ding et al. 2013, Magnago et al. 2014). For instance, fragmentation can promote traits associated with long-distance dispersal due to increased fragment isolation (Büchi and Vuilleumier 2012). These changes can be independent of the number of species surviving in a community (Büchi and Vuilleumier 2014, Magnago et al. 2014). In addition, landscape structure can act indirectly on functional diversity by affecting species richness. This occurs when species richness and functional diversity are correlated and thus factors that decrease species richness are expected to indirectly decrease functional diversity (de Bello et al. 2010, Mouchet et al. 2010, Petchey and Gaston 2006). For example, if functional diversity is positively correlated with species richness, it is expected that less-fragmented landscapes, which may have higher species richness (Rybicki and Hanski 2013), would have high functional diversity as well. Analysing direct and indirect effects of landscape structure on functional diversity can help unpack the drivers that differentially affect species richness and functional diversity.

In the previous chapter, I showed that fragmentation effects on functional diversity depend on the distribution of response traits across species and its correlation with effect traits. These two factors will affect the community functional redundancy, this is, the number of species contributing in a similar way to a particular ecosystem function. Functional redundancy may affect the prevalence of direct and indirect effects of landscape structure on functional diversity. If functional redundancy is low, then functional diversity would decrease rapidly as species with less common traits are lost (Laliberté et al. 2010). This is an example of indirect effects of landscape structure on functional diversity through declines of species richness (Mayfield et al. 2010). Since habitat amount tends to filter species more strongly than fragmentation (Fahrig et al. 2011), a redistribution of trait abundances as a result of changes in habitat amount rather than on habitat configuration is expected. Conversely, when functional redundancy is high, changes in functional diversity will be less mediated by changes in species richness (Carmona et al. 2012, Laliberté et al. 2010, Luck et al. 2013), and thus direct effects of landscape structure will become common. In this case, certain types of habitat configuration can alter patterns of trait abundances in a community (e.g. favour large species) without any conspicuous changes in species richness.

Understanding direct and indirect drivers of how landscape structure alters functional diversity is important is important in urban environments. Cities constitute important locations of landscape transformation and are on of the fastest-growing land-use type globally (Seto et al. 2012). Although urban environments tend to have negative impacts on biodiversity, the ecological impacts of urbanization might be mitigated by managing the spatial pattern of the remaining habitat (Villard and Metzger 2014). For example, a compact, high-density growth form may reduce local extinctions and improve species' distributions when relatively large patches with good habitat quality are preserved (Hanski 2015). On the other hand, sprawling growth may have adverse effects on native species richness, but may help to maintain friendlier wildlife matrices that enhance connectivity and potential ecological functions at larger scales (Fahrig 2017, Soga et al. 2014). Land sharing and land sparing constitute two extremes that are not necessarily exclusive, and evaluating what happens along the gradient of possibilities is fundamental to propose strategies to manage the spatial arrangement of landscape elements (Fischer et al. 2014, Lin and Fuller 2013). However, analyses in urban areas have mostly focused on the effects of tree cover on species richness (Batáry et al. 2017), and there is a lack of studies about the simultaneous effects of landscape structure on both species richness and functional diversity.

In this chapter, I test how the amount of tree cover, vertical vegetation structure and landscape fragmentation simultaneously influence species diversity and functional diversity of urban bird assemblages using Brisbane as a case study. I evaluate this for different functional groups and provide evidence showing how fragmentation modifies the impacts of habitat loss on different functional indices. Specifically, I ask: 1) how does landscape structure affect both species richness and functional diversity components of an urban bird assemblage? And 2) How do different attributes of landscape structure affect directly and indirectly through changes in species richness functional diversity for different ensembles? I focus in two groups, frugivorous/nectarivorous and insectivorous birds, since they are associated with different functions and have different levels of functional redundancy in Brisbane. In addition, previous work has shown that, in urban areas, insectivorous birds tend to be more affected by fragmentation than frugivorous birds (Evans et al. 2011, Sol et al. 2014)}. Based on the results of my theoretical model (chapter 4), I expect that direct effects of fragmentation on the functional diversity will mostly depend on the level of functional redundancy. In addition, I expect that landscape composition will have a bigger influence than landscape configuration on functional diversity of frugivorous species (a group with low functional redundancy in the study area) than on insectivorous species (which has high functional redundancy). Based on these results, I discuss how urban growth could be managed to potentially maximize the conservation of both taxonomic and functional diversity.

5.3 Methods

The analyses presented here are based in the data collected in the Brisbane Local Government Area as explained in sections 3.2.1 and 3.2.2. In this chapter, however, I focus only on measuring associations at the 1 km^2 resolution.

5.3.1 Data analysis

5.3.1.1 Functional trait diversity indices and species richness calculation

In chapter 3, I explored which traits best explained bird species responses to habitat loss and fragmentation across Brisbane (i.e., response traits). In this chapter, I focus on effect traits – the traits that relate to the performance of functions - to infer how landscape structure affects the capacity of bird ensembles to contribute to specific ecosystem functions. For this, I selected four effect traits: dispersal capacity and body size, foraging plasticity and diet. Body size can be linked to many system properties (White et al. 2007) and may represent a universal trait to predict the effects of landscape structure on ecosystem functioning (Séguin et al. 2014). Dispersal capacity and foraging behaviour are important traits in the dynamics of pollination, seed dispersal, and pest control (Lundberg and Moberg 2003). Luck et al. (2013) provided values of foraging plasticity based on the frequency with which a particular species has been recorded using different foraging behaviours in different Australian regions.

Trait values of each effect trait were sourced from an unpublished traits database derived from the Handbook of Australian, New Zealand and Antarctic Birds (Luck, unpublished data). In addition, Fraser et al. (2017) provided values of dispersal capacity for each species using a model presented by Garrard et al. (2012). This model predicts median dispersal distance based on data on wingspan and body mass collated from published studies world-wide, and predicts that birds with a higher wingspan to mass ratio will have longer median dispersal distances.

I also classified bird species into different functional groups based on diet: frugivorous, nectarivorous and insectivorous following Wilman et al. (2014). These authors translated verbal descriptions of bird diets from multiple sources into standardized, semi-quantitative information about the relative importance of different food categories. I defined insectivores as those whose diet is more than 60% arthropods. These species are more likely associated with pest control. Nectarivorous and frugivorous birds were those that include more than 60% of their diet on fruits and nectar, and they most likely contribute to pollination and seed dispersal (see Appendix C Table C3 for a complete list of species recorded in this study and their trait values). Frugivorous and nectarivorous birds were grouped into a single group since most species (e.g. rainbow lorikeet *Trichoglossus chlorolepidotus*, brown honeyeater *Lichmera indistincta*) that use plant resources include nectar and fruits in their diet. In order to test the hypothesis that the effects of fragmentation are more evident in groups of species with high functional redundancy, I calculated functional redundancy for each of the insectivorous and frugivorous groups taking into account all the species I recorded during my surveys. For this, I used the function “redundancy” of the package TPD (Carmona et al. 2016) in R.3.3. Functional redundancy of insectivorous birds was higher (15.8) than frugivorous/nectarivorous birds (10.6). In addition, the number of insectivorous species recorded is higher (41) than the number of frugivorous/nectarivorous (25) and thus insectivorous species are expected to have higher redundancy.

For each of these functional groups, I quantified species richness, functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) at a 1 km^2 resolution using the total number of individuals recorded in each landscape unit (see section 3.3. for data collection methodology). As explained in previous chapters, functional richness corresponds to the range of trait values in a given area and reflects how much functional space is occupied by a community. Functional evenness quantifies if the functional trait space is evenly occupied by the community (Villéger et al. 2008).

Functional evenness values will be lower when some parts of the functional space are empty while others are densely populated (Mouchet et al. 2010). Functional divergence measures to what extent dominant species diverge in their trait values using trait dissimilarity weighted by species abundance (Mason et al. 2005). All diversity calculations were performed with the dbFD function implemented in the FD package in R (R Development Core Team, (Laliberté and Legendre 2010)).

5.3.1.2 Data analysis

I used structural equation modelling (SEM; Grace 2006) to examine the pathways through which habitat loss and fragmentation affect each functional diversity component. I created a different model for each functional diversity component establishing a causal path between species richness and functional diversity to account for indirect effects of landscape structure. Environmental variables were the percentage of built infrastructure (impervious surface + buildings), percentage of tree cover, vertical vegetation structure complexity, fragmentation measured as the level of aggregation of patches. The hypothetical model for the causal relationships among these factors is given in Figure 5.1.

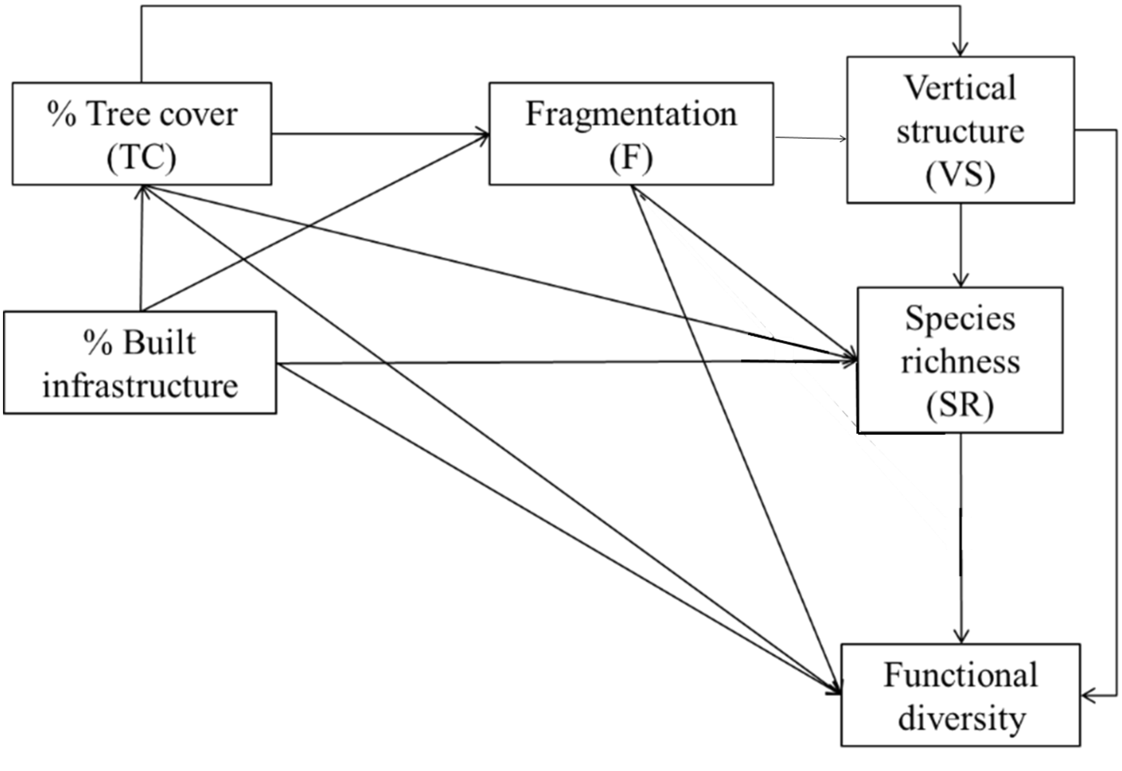

Figure 5-1: Theoretical model showing the main relationships between landscape structure and species richness and functional diversity. Built infrastructure affects both the amount and the spatial aggregation of tree cover. In addition, tree cover and fragmentation affect vertical structure across Brisbane (Mitchell et al. 2016). All the components of landscape structure affect directly patterns of species richness, and this may drive changes in functional diversity (indirect effects). In addition, landscape structure can affect directly functional diversity without necessarily changing species richness by

promoting the abundance of species with particular traits (direct effects). One-headed arrows represent causal pathways between variables.

For each functional component (i.e. functional evenness, functional divergence or functional richness), I constructed the model presented in figure 5.1. I then tested the fit of this model using a maximum likelihood method, based on a Chi squared distribution to check how overall model fit improved relative to an expected model that best explains the response variable based on the presented set of predictors. If $p \geq 0.05$, I considered that the two models were not statistically different from each other. If $p < 0.05$, the model was rejected and I started adding quadratic terms and removing some relationships until I found a well-fitting and ecologically meaningful model (Shipley 2000). In addition, I used the Tucker – Lewis index (TLI) to check how overall model fit improved relative to the alternative models. A value of 0.95 or larger indicates good model fit(Weston and Gore 2006). I also used the root mean square error of approximation (RMSEA) to measure absolute model fit, where values < 0.06 indicate good fit (Weston and Gore 2006). The model with the lower RMSEA and the highest TLI was considered as the best.

I analysed the direct and indirect effects of each environmental predictor on functional diversity by calculating standardized path coefficients of the best fitting model (Grace 2006). The significance of the individual paths coefficients was analysed and *p* values lower than 0.05 were denoted as significant. If both direct and indirect effects were significant, I found evidence that landscape structure acted on functional diversity both by modifying species richness and by redistributing trait abundances across species. All SEMs were created using the R package *lavaan* (Rosseel 2012), and all continuous variables were log-transformed prior to analyses.

5.4 Results

5.4.1 Effects of landscape structure on species richness and functional diversity for the urban bird assemblage

For all the functional diversity components and the functional groups, the SEMs including tree cover, percentage of built infrastructure and fragmentation had the best overall fit (x^2= 1.243, p = 0.27, TLI= 1, RMSEA = 0.048, df = 10). Adding the relationship between vegetation structure and functional diversity did not improve overall model fit (x^2= 9.3, p = 0.01, TLI= 1, RMSEA = 0.435, df = 14). Therefore, SEM results show that at the 1 km^2 resolution, the vertical structure of the vegetation does not help to explain the effects of landscape structure on either species richness or the functional components evaluated.

Landscape composition and configuration affect species richness and functional diversity differently.

At the assemblage level, both fragmentation (standardize path coefficient = -0.30) and the percentage of built infrastructure (standardized path coefficient = -0.75) negatively affect species richness. This relationship was different when functional diversity components were evaluated. In this case, both functional richness (Figure 5.2a) and functional evenness were unaffected directly by fragmentation, tree cover or built infrastructure. The only component that was directly affected by landscape structure was functional divergence that decreased significantly when both fragmentation ($p < 0.05$; standardized path coefficient of – 0.43) and built infrastructure increased ($p < 0.05$; standardized path coefficient of – 0.37) (Figure 5.2b).

5.4.2 Effects of landscape structure on species richness and functional diversity for the urban bird ensembles

Drivers of species richness among insectivorous and frugivorous/nectarivorous species were similar, but direct effects on functional components were more variable (Table 5.1). Increasing fragmentation reduced functional richness and functional divergence in the insectivorous ensemble, whereas it did not have a clear effect on the nectarivorous/frugivorous ensemble (Figure 5.3 a-d). For frugivorous/insectivorous birds, functional diversity is mostly driven by landscape composition rather than on fragmentation (Table 5.1). For example, tree cover had a significant positive effect on functional richness of this ensemble, whereas built infrastructure played an important role decreasing functional evenness (Figure 5.3f). In contrast, models did not show direct effects of tree cover and built infrastructure on functional evenness or functional richness of insectivorous species (Figure 5.3 e-f).

The level of functional redundancy was not an indicator of the prevalence of indirect effects of landscape structure on functional diversity. Independently of the ensemble evaluated, species richness mediated the effects of built infrastructure on all the components of functional diversity (Table 5.1). In addition, indirect effects of fragmentation had a negative influence on functional evenness of frugivorous/nectarivorous, but no effects were detected for functional evenness of insectivorous (Figure 5.3, Table 5.1). In contrast, fragmentation had an indirect negative impact on functional divergence of insectivorous, whereas functional divergence of frugivorous/nectarivorous increased with species richness independently of the fragmentation level (Figure 5.3, Table 5.1).

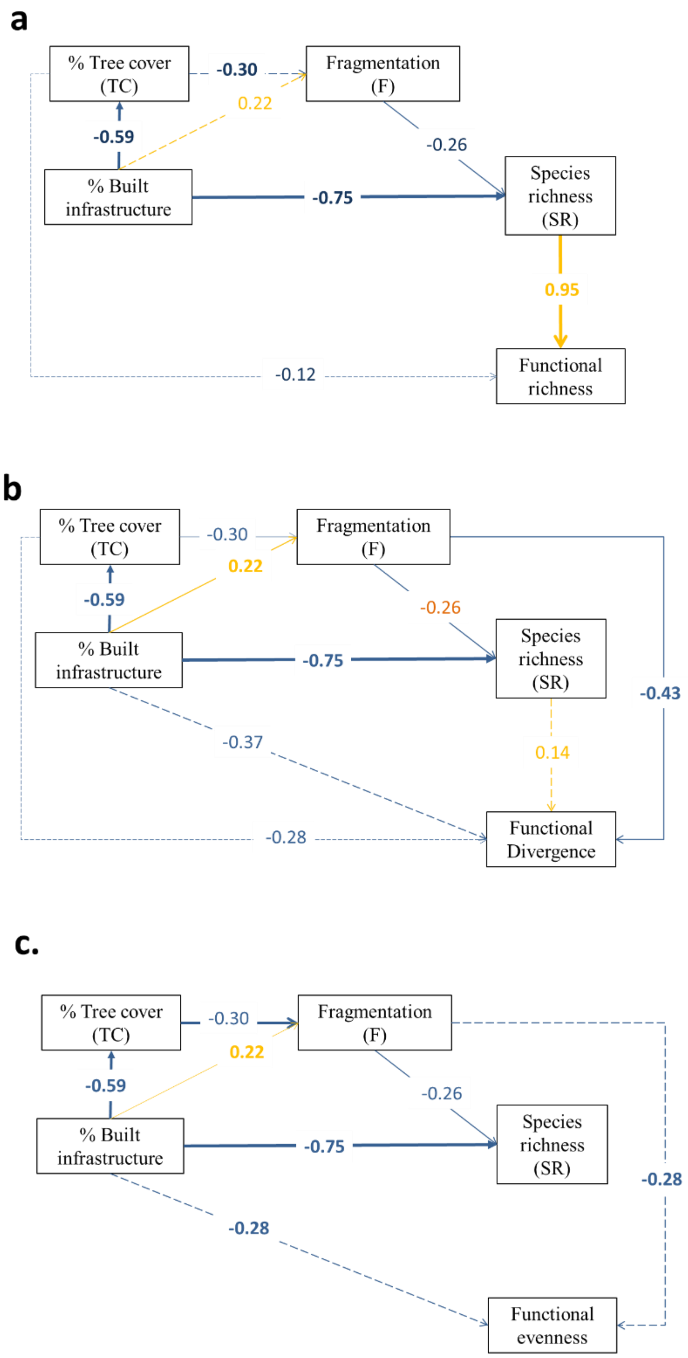

Figure 5-2: Structural equation models showing the effects of landscape structure on different functional components for the urban bird assemblage. Numbers between arrows indicate standardized path coefficients, which allow for comparing relationship strengths within a model; a) Functional richness, b) Functional divergence and c) Functional evenness. One-headed arrows represent causal pathways. Yellow arrows: Positive effects, Green arrows: Negative effects. The intensity of the colour represents the strength of the relationship. Solid lines denote significant effects whereas dashed lines denote non-significant effects

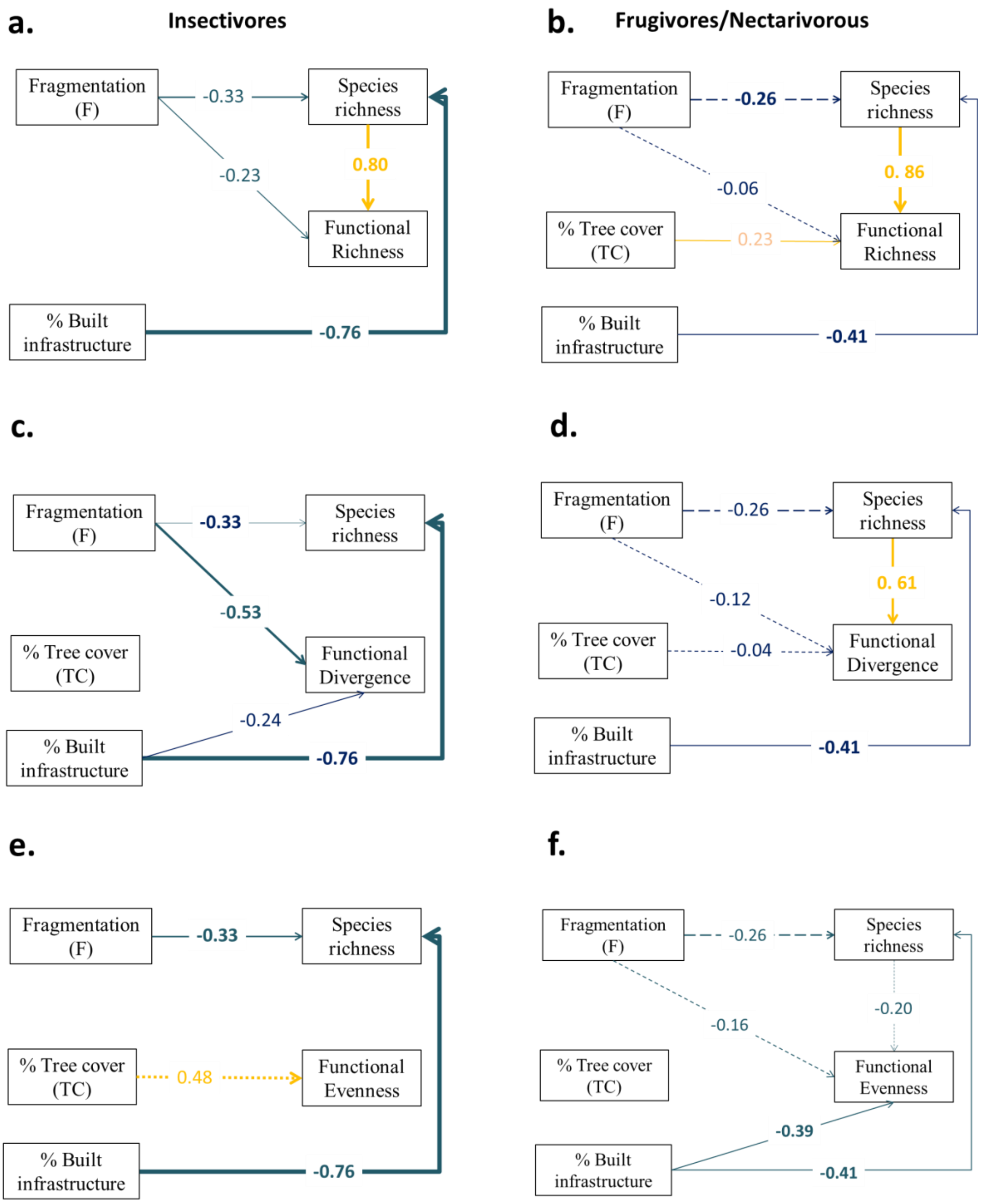

Figure 5-3: Structural equation models showing the direct effects of landscape structure on different functional components for the insectivorous and the frugivorous ensembles. Numbers between arrows indicate standardized path coefficients, which allow for comparing relationship strengths within a model; a, b) Functional richness; c, d) Functional divergence; and e, f) Functional evenness. Orange arrows: Positive effects, Blue arrows: Negative effects. The intensity of the colour represents the strength of the relationship. Dashed lines represent non-significant relationships.

Table 5-1: Direct and indirect effects of different attributes of landscape structure on different components of functional diversity for the two ensembles evaluated. FRic = Functional richness; FDiv = Functional divergence; FEve = Functional evenness. Significant effects are bolded.

			Frugivorous/Nectarivorous				**Insectivorous**			
			Estimate	**Std. Err**	**z-value**	**P(>|z|)**	**Estimate**	**Std. Err**	**z-value**	**P(>|z|)**
Fric	Direct effects	Built infrastructure	-0.32	0.18	2.37	0.00	-0.51	0.41	-1.24	0.22
		Tree cover	2.31	1.22	1.9	0.04	1.14	0.82	1.40	0.16
		Fragmentation	-2.38	2.04	1.17	0.24	**-7.59**	**2.35**	**3.22**	**0.00**
		Species richness	**0.40**	**0.03**	**13.24**	**0.00**	**0.30**	**0.08**	**4.01**	**0.00**
	Indirect effects	Tree cover	-0.19	0.13	-1.47	0.14	-0.30	0.22	-1.42	0.16
		Fragmentation	-4.97	3.04	1.64	0.10	**-7.77**	**3.10**	**2.50**	**0.01**
		Built infrastructure	**-0.87**	**0.26**	**-3.33**	**0.00**	**-1.94**	**0.47**	**-4.11**	**0.00**
FDiv	Direct effects	Built infrastructure	-0.03	0.23	-0.12	0.91	0.48	0.25	1.95	0.45
		Tree cover	-0.11	0.27	-0.42	0.68	**-0.31**	**0.9**	**0.1**	**0.00**
		Fragmentation	-1.51	1.99	-0.76	0.45	-9.5	2.01	4.7	0.47
		Species richness	**0.16**	**0.03**	**6.18**	**0.00**	0.03	0.04	0.68	0.49
	Indirect effects	Tree cover	0.03	0.07	0.45	0.66	**-0.21**	**0.06**	**-3.66**	**0.00**
		Fragmentation	-1.97	1.21	1.64	0.10	**-2.34**	**1.36**	**1.73**	**0.08**
		Built infrastructure	**-0.34**	**0.12**	**-2.81**	**0.01**	**-0.59**	**0.15**	**-3.96**	**0.00**
Feve	Direct effects	Built infrastructure	**-0.03**	**0.01**	**-2.86**	**0.00**	0.02	0.01	1.73	0.09
		Tree cover	0.00	0.02	0.18	0.86	-0.02	0.02	-1.42	0.16
		Fragmentation	-0.07	0.06	1.14	0.26	-0.12	0.07	1.76	0.08
		Species richness	**-0.01**	**0.00**	**-3.43**	**0.00**	0.00	0.00	-1.05	0.29
	Indirect effects	Tree cover	0.00	0.01	-0.17	0.86	0.01	0.01	1.31	0.19
		Fragmentation	**0.08**	**0.03**	**-2.40**	**0.02**	0.03	0.03	-1.14	0.26
		Built infrastructure	**0.01**	**0.01**	**2.58**	**0.01**	0.01	0.01	1.13	0.26

5.5 Discussion

My approach allowed me to disentangle the independent direct and indirect effects of landscape composition and configuration on bird functional diversity and species richness. Although direct effects of landscape structure on species richness are consistent among bird ensembles, within-group functional diversity responded differently depending on the ensemble considered. In addition, I provide evidence that landscape composition and configuration affect species richness and functional diversity differently. My results suggest that in ensembles with low redundancy, changes in functional diversity are mostly driven by landscape composition, whereas the relative effects of landscape configuration increase in ensembles with high redundancy. These results highlight the importance of accounting for the independent effects of different aspects of landscape structure to explain changes in functional diversity in human-dominated landscapes (Laliberte et al. 2013, Luck et al. 2013, Mayfield et al. 2010).

Landscape composition drives functional diversity both directly by filtering species with particular traits and indirectly by altering patterns of species richness. Since species richness and functional richness tend to be correlated (Mouchet et al. 2010), the highly negative effects of built infrastructure on species richness can lead to declines in functional richness. In addition, negative direct effects of built infrastructure on functional richness likely reflect a homogenization in the distribution of a reduced number of common traits (Batáry et al. 2017, Coetzee and Chown 2016). My results suggest that even if tree cover does not affect directly species richness of frugivorous/nectarivorous, managing urban tree cover can promote high levels of functional richness. This may be achieved by preserving a good diversity of planted trees in urban areas that facilitate the presence of species with multiple requirements (Catterall 2004, Sewell and Catterall 1998). Although landscape composition does not have a clear effect on functional richness of insectivorous, negative effects of built infrastructure on functional divergence suggest that there is a reduction in abundance for species with extreme trait values. In this case, managing tree cover to preserve high functional richness does not necessarily enhance functional diversity in highly urbanized areas, since built infrastructure tend to homogenize the distribution of certain traits (Croci et al. 2008).

The level of functional redundancy is an indicator of the prevalence of direct effects of fragmentation on both functional richness and functional divergence. In frugivorous/nectarivorous, there is a high variation in dispersal and body size traits and thus in responses to habitat configuration across species (Coetzee and Chown 2016, de Frutos et al. 2015, Magnago et al. 2014). In this sense, the effects of landscape configuration on frugivorous become less evident. For insectivorous, there is a high redundancy for traits such as dispersal and body size and these traits predict how species may rely on heterogeneous habitat patches with moderate to low edge effects (Catterall et al. 2010, Shanahan et al. 2011). Therefore, a reduction in functional divergence is associated with a decrease in the abundance of small sized species with low dispersal capacities in fragmented landscapes (Brown and Graham 2015, Evans et al. 2011). My results show that reductions in functional divergence of insectivorous can be expected even if species richness is not altered. These results concur with several studies of both simulated communities (Mouchet et al. 2010, Villéger et al. 2008) and real avian assemblages (Ding et al. 2013, Ibarra and Martin 2015) showing that changes in functional diversity may appear independent of changes in species richness.

Despite the contrasting responses between different functional components and ensembles, it may be possible to establish some guidelines to promote the conservation of functional diversity in urban areas. Since responses of the components of functional diversity to landscape structure are mixed (Schütz and

Schulze 2015), it is clear that maintaining the capacity of bird ensembles to provide multiple functions is more challenging than protecting species richness. However, at least for some groups, we could benefit from understanding how landscape structure promotes positive relationships found between species richness and functional richness/divergence. Previous work in the study region has found that bird assemblages in remnant forest patches varied little with patch size above 10–20 ha, but below this threshold, they became increasingly dominated by large-bodied species (Catterall et al. 2010). Additional work in the area has shown that landscape connectivity has a greater influence on bird species richness than patch area (Litteral and Shochat 2017, Shanahan et al. 2011). Thus, preserving connected, medium-sized patches might be the best option to preserve both functional diversity and species richness in Brisbane. For this approach to be successful, the negative impacts of fragmentation should be reduced by promoting the conservation of landscape elements that attenuate the effects of the landscape matrix on both the area-sensitivity and/or dispersal behaviour of bird species.

This study is a first step to understand the effects of landscape structure on functional diversity, but more analysis are needed to link this findings to effects on ecosystem functioning. For example, several studies indicate that birds, besides reducing herbivorous insect populations, may also increase plants productivity and biomass (Barber and Marquis 2011, Mäntylä et al., 2011). In cities, this could have important implications for the conservation of green spaces that provide habitat for other species as well as cultural services. However, it is unknown at what extent the diversity of dispersal and body size traits influence increases in plant biomass, or if this is mostly driven by the presence of specific trait values within the community. It is important to note that, although results of this study describe changes in functional diversity at the landscape level, effects of fragmentation are scale dependent, and opposite forces operate simultaneously to shape species assemblages at the fragment scale. For example, previous work has found that bird insectivory increases at edges and in small forest fragments (Barbaro et al. 2014, González-Gómez et al. 2006), and this increase may be explained by a greater regularity of trait abundance distributions in edge than in interior bird assemblages (Barbaro et al. 2014). Testing this hypothesis requires information at the patch scale that I did not include in my analyses here. In addition, my study focused on understanding how landscape structure affects general patterns of community structure, but I did not identify individual species within ensembles that can have disproportionate effects on ecosystem functions, and this remains an important issue.

5.6 Conclusions

Results from this study show that it is possible to disentangle the pathways through which fragmentation and landscape composition affect functional diversity of groups with different levels of functional redundancy. This has important implications for understanding how landscape change (e.g. urban growth) might best be done to maximize the conservation of functional and taxonomic diversity.

Avoiding fragmentation would help to maintain high levels of functional diversity for insectivorous ensembles with high redundancy of traits associated with vulnerable responses to landscape change. In contrast, the weak direct effects of fragmentation on functional diversity of frugivorous species suggest that landscape composition (i.e. percentage of built infrastructure and native vegetation) is the main driving force of functional diversity in this group, whereas fragmentation acts mostly indirectly through effects on species richness. Instead of promoting certain habitat configurations, actions such as street tree plantings that help avoid species richness loss ought also to maintain high functional diversity for that group (Catterall et al. 2010, Lim and Sodhi 2004, Sewell and Catterall 1998). For these actions to be successful, accounting for the relative effects of landscape attributes on functional diversity is crucial if we want to propose management strategies for multiple groups of species in transformed landscapes.

Chapter 6
SYNTHESIS

Conserving multiple aspects of biodiversity in transformed landscapes is a fundamental challenge (Laliberté et al. 2010, Luck et al. 2013). As fragmented landscapes become increasingly common, controlling the spatial arrangement of landscape elements may help to promote the conservation of both taxonomic and functional diversity. In this context, the use of species' traits to predict how species richness and functional diversity may follow independent paths after landscape change is a potentially powerful approach (Díaz et al. 2013, Mori et al. 2013). However, despite the conceptual support for trait-based frameworks, we still lack basic information on how different traits explain species responses at different spatial scales (Chapter 2). Furthermore, to date there have been few attempts to provide general hypotheses of how changes to landscape structure drive the relationship between species richness and functional trait diversity. Much progress has been made in understanding how landscape composition impact functional diversity over large spatial scales (Flynn et al. 2009, Mayfield et al. 2010). However, less is known about how the landscape configuration and landscape composition interact to affect the relationship between species diversity and functional diversity.

To address these gaps, the overarching objective of this thesis was to provide novel evidence of how landscape structure drives species richness and functional diversity simultaneously. For this, I divided my analyses into four main chapters. In Chapter 2, I reviewed current approaches used to evaluate how the influence of species traits on the relationship between environmental variables and ecological responses varies among scales (i.e. the scale-dependent role of traits). I then used bird assemblage data collected in Brisbane (Australia) to address one of the gaps identified in my review: including landscape structure variables to explain variation of trait values across local and landscape scales (Chapter 3). In Chapter 4, I developed a theoretical simulation model to quantify how the relationship between species richness and functional diversity is driven by both habitat amount and configuration. Finally, I used my empirical data to test some of the hypothesis of my theoretical model and evaluated the effects of landscape structure on both species richness and functional diversity components for different functional groups (Chapter 5).

In this concluding chapter, I summarise the main findings from each Chapter of this thesis, and discuss their implications for the management of landscape structure in transformed landscapes. I then synthesise the major contributions, discuss challenges and limitations, and recommend future research directions.

6.1 Main findings

6.1.1 The scale-dependent role of biological traits in landscape ecology: a review

In Chapter 2, I completed the first quantitative synthesis of the main approaches used to evaluate how patterns in trait variation within and among species are related to environmental variables across scales (De Bello et al. 2013b, Laughlin and Messier 2015, Messier et al. 2010, Moran et al. 2016). I identified which ecological responses have been measured and related to traits at the community and population levels in multi-scale studies. Based on my review, I identified three main gaps: 1) there is a lack of studies explicitly quantifying the relative effect of particular sets of traits on ecological responses across scales; 2) several ecological responses related to ecosystem functioning and species interactions such as seed dispersal, predation and multi-trophic networks have been widely overlooked, and 3) the effects of landscape structure are often ignored.

This chapter constitutes a step towards better integration of landscape ecology and community ecology to improve inferences about the relationship between species traits and multiple ecological responses. I emphasized that without a proper quantification of spatial scale effects in trait-based approaches, it is difficult to disentangle to what degree the responses of ecological systems across habitats, patches and landscapes are dependent on species traits. I advocated for the use of models that evaluate how variation in landscape structure across regions and habitat types at coarse scales interacts with local variables to determine the effects of traits on ecological responses. In this way, we can ensure that we capture the essential mechanisms that operate simultaneously at multiple scales to shape biological communities in changing landscapes.

6.1.2 Associations between urban bird traits and environmental variables change across scales

One of the main gaps I identified in Chapter 2 was the need to disentangle how landscape structure acts on trait distributions at multiple spatial scales. This is necessary if we want to understand how species sharing similar traits may be more or less tolerant to landscape change at a range of scales relevant to management (Concepcion et al. 2015, de Bello et al. 2013a). In this chapter, I provided empirical evidence that the interaction between landscape configuration, landscape composition and spatial scale can explain contrasting patterns about variations in the distribution of species traits at different scales. At landscape scales, fragmentation (landscape configuration) and percentage of tree cover (landscape composition) played a key role shaping the distribution of body sizes and dispersal capacities. At local scales, however, the relationship between landscape composition and species traits was weak. Furthermore, I showed that fragmentation plays an important role driving the distribution of traits at both scales. In particular, increasing fragmentation at landscape scales negatively affected small species with low dispersal capacities in areas of low tree cover. Conversely, fragmentation at local scales increased spatial heterogeneity that allowed for the persistence of species with a diverse set of traits (e.g. both high and low dispersers). Thus, although dispersal can explain biotic homogenization at the landscape scale as a consequence of the dominance of highly mobile species (Devictor et al. 2008) at local scales birds with different dispersal capacities are affected by similar factors, including competition for nesting sites and the presence of aggressive species (Concepcion et al. 2015). Accounting for differences in trait distributions across multiple scales spatial scale can thus help to find more general models of the effect of traits for predicting species responses to landscape change.

6.1.3 Effects of fragmentation on the relationship between species richness and functional diversity

In Chapter 4, I presented a theoretical model aimed to generate hypotheses about how fragmentation drives the relationship between species richness and multiple components of functional diversity, while controlling for habitat amount. This is the first model that shows how the correlation between response and effect traits and the distribution of response traits can be used to predict fragmentation effects on species richness and functional diversity for multiple communities. Results of my model showed that: 1) when present, the effect of fragmentation on functional diversity tends to be negative and becomes evident when the correlation between response and effect traits increases; 2) indirect effects of fragmentation through changes in species richness are strong in communities with a low divergence in response traits and 3) direct effects of fragmentation are evident in communities with a high divergence in the distribution of response traits and a high correlation between response and effect traits. The generation of the hypotheses presented in this chapter provides a good opportunity to test them across a broad range of real landscapes and communities in different regions.

6.1.4 Effects of landscape structure on species richness and functional diversity in urban bird assemblages

In Chapter 5, I tested some of the hypotheses generated by the theoretical model developed in Chapter 4. Here, I disentangled how landscape structure drives the functional diversity directly or indirectly by changes in species richness. I did this for different components of functional diversity and functional groups with different levels of functional redundancy. Previous research evaluating the effects of landscape configuration on functional diversity has mostly focused on comparing patches with different size or isolation levels (Ibarra and Martin 2015, Magnago et al. 2014). My study goes further and focuses on multiple landscapes with different levels of habitat amount and fragmentation. By using a stratified random sampling approach at the landscape level, I could disentangle the independent direct and indirect effects of landscape composition and configuration on functional diversity and species richness simultaneously. I provided evidence that landscape structure acts differently on species richness and functional diversity. Further, the effects of landscape structure on species richness were consistent among different functional groups. However, patterns of functional diversity varied among groups and were less dependent upon tree cover and fragmentation. I showed that although fragmentation sometimes does not act directly on functional diversity, it can affect it indirectly, through changes in species richness.

6.2 Major contributions

My thesis advances our knowledge of the effects of landscape structure on multiple components of biodiversity, and in particular functional trait diversity. I draw from the fields of landscape ecology, functional ecology, community ecology, and environmental management. My findings are relevant to ecologists and practitioners/managers with an interest in preserving biodiversity in human-modified landscapes. I did a systematic review and generated theoretical and empirical evidence. By doing this, I was able to identify the main knowledge gaps, simulate different scenarios to provide specific hypotheses and test them in real landscapes. This approach allowed me to generate new insights around how landscape change can be managed to potentially maximize the conservation of both taxonomic and functional diversity. The overarching contributions of my project are detailed below.

I provided new evidence that not only landscape composition but also landscape configuration is important in driving patterns of species richness and functional diversity. Most previous studies have focused on analysing effects of fragmentation on species richness and functional diversity independently (Magnago et al. 2014, Perovic et al. 2015), but my study goes further by analysing how fragmentation drives the relationship between these components (Chapter 4-5). In addition, previous work has drawn different conclusions about the relative importance of the mechanisms underlying fragmentation effects across differing taxa, and some studies even argue about the utility of the 'habitat fragmentation' concept in general (Fahrig and Triantis 2013). Usually, fragmentation effects are best tested with studies on individual species rather than on communities, as the latter typically consist of species with dissimilar habitat requirements (Hanski 2015). I showed that trait based approaches are useful for seeking more general patterns of fragmentation effects on multiple components of biodiversity at the community level. This was achieved by comparing communities and functional groups with dissimilar distribution of trait values. I show that it may be possible to explain multi-species responses to fragmentation based on species traits.

i. The theoretical model I developed brings together different concepts from functional ecology within a landscape ecology framework. Previous spatially explicit metacommunity models have evaluated the factors that drive coexistence of species with different dispersal and reproductive traits (Buchi et al. 2012, 2014), or that drive species-area relationships (e.g. Rybicky and Hanski 2013). Other studies (Suding et al. 2008, Mori et al. 2013) have presented trait-based response–effect frameworks that differentiate the community response to environmental change (predicted by response traits) and the effect of that change on ecosystem processes (predicted by effect traits). The model presented in my thesis is the first to integrate these concepts to predict how species richness and different components of functional diversity may respond to fragmentation. Furthermore, I then explicitly tested these hypotheses with empirical data and provided evidence that different components of landscape structure may influence the relationship between species richness and functional diversity in real landscapes. Empirical evidence that the mechanisms that led to these hypotheses operate in many ecosystems would simplify biodiversity forecasting and represent an advance for generality in community and landscape ecology.

ii. An important challenge for empirical studies is to account for the correlation between the total amount of habitat and the degree of fragmentation. Effective research on the impacts of habitat loss versus fragmentation requires tools that can empirically test whether environmental variables are causally related, and if so, account for the indirect effects that these causal relationships imply (Ruffell et al. 2016). The study design used in this thesis allowed me to infer the independent and joint effects of different compositional and configurational variables on functional diversity. In addition, both my theoretical model and the structural equation models I used to analyse my empirical data helped me to unpack the drivers of functional diversity and species richness in my study area. Based on these analyses, I show that the relative effects of habitat loss and fragmentation on functional diversity can be inferred by analysing functional redundancy patterns.

iii. Studies in urban areas have shown that the ability of traits to explain species responses to urbanization varies among regions (Brown and Graham 2015, Croci et al. 2008, Evans et al. 2011). However, it is not clear how much of this variation is due to differences in the spatial scale at which landscape structure influences the distribution of traits (Chapter 2). Thus, the underlying mechanisms that account for patterns of bird trait diversity after urban land use change remain unclear. I presented new evidence of how the interaction between landscape structure and spatial scale drives the distribution of urban bird functional traits. I showed that urbanisation affects bird species traits at landscape scales more strongly than at local scales. Thus, trait-based inferences about species responses to landscape change could be improved by addressing the scale issue. This information could help to reconcile previous contrasting results about the importance of species traits explaining species responses to landscape change across different regions.

6.3 Conservation implications

Landscape ecologists tend to focus on how attributes of the surrounding landscape affect the site scale responses of species with different biological traits. Management prescriptions guided by this knowledge will influence species or assemblages at sites, but not necessarily result in the intended biodiversity outcome beyond this scale. My study suggests that a focus on conserving species with particular traits at the local scale may be ineffective if attributes of landscape structure are ignored. In urban systems, for example, local actions such as planting native gardens (Catterall et al. 2010, French et al. 2005)have been proposed to promote species diversity peaks in areas with moderate levels of urbanization . This is because the heterogeneity produced by intermediate levels of urbanization can promote the coexistence of species using different resources (Batáry et al. 2017). However, this might be ineffective if the objective is to implement conservation initiatives that target species less tolerant to landscape change, such as small-bodied species with low dispersal capacities (Brown and Graham 2015). Local actions aimed at increasing species richness that do not consider landscape structure effects may favour species that are already more adaptable to urban landscapes (Archibald Carla et al. 2017).

Highly fragmented landscapes are becoming ever more common due to anthropogenic habitat conversion (Haddad et al. 2015). In this context, understanding how landscape structure influences the relationship between species richness and functional diversity will help maximize limited conservation resources. If, for example, there is high redundancy in an assemblage of frugivorous species, my results suggest that focusing resources on protecting well-connected, medium-sized patches may be enough to ensure high levels of seed dispersal. However, the potential to manage landscape configuration to protect both species richness and functional diversity becomes more restricted when there is low functional redundancy. In this case, a limited number of key species providing one specific function may be highly susceptible to habitat loss. Even if landscape configuration is managed to maximize species richness (Jackson and Fahrig 2015, Rybicki and Hanski 2013), rapid declines in functional diversity are expected if unique species are lost (Coetzee and Chown 2016, Laliberte et al. 2013). In this case, managing landscape structure for particular targets (e.g. species with key effect traits) may be more realistic than trying to maximize multiple aspects of biodiversity.

When habitat configuration matters, my results support the idea that habitat fragments should be protected in clusters rather than as randomly scattered fragments (Rybicki and Hanski 2013), as when fragmentation has an effect on functional diversity, it tends to be negative. Although fragmentation can increase heterogeneity in habitats and have some positive effects on species richness and species abundance (Fahrig 2017), evidence suggest that this is at expense of species with unique traits (Coetzee and Chown 2016). In addition, there is empirical evidence that functional diversity increases with patch size (Benchimol et al. 2015, Bregman et al. 2015) and this may explain the positive effects of avoiding fragmentation when habitat is lost. However, preserving or restoring large patches is not always possible, and there are multiple examples where managing the spatial configuration of remnant habitat is necessary to protect biodiversity (Haddad et al. 2015, Villard and Metzger 2014). Although urban environments tend to have negative impacts on biodiversity, ecological impacts of urbanization might be mitigated by managing the composition and spatial pattern of the remaining habitat (Lin and Fuller 2013, Sushinsky et al. 2013). When habitat amount is limited. When habitat amount is limited, my results show that fragmentation must be avoided at landscape scales to maximize functional diversity

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6.4 Limitations and future research

In this section, I discuss the primary limitations of the contributions of my thesis, and suggest future research directions to advance this work.

6.4.1 The different components of scale

In Chapter 3, I addressed how landscape structure explains variation of trait values across local (1 ha) and landscape (1 km^2) scales. To improve the reach of these results, linking this information with regional patterns is still needed. The results presented in this thesis must be compared with analyses of how landscape structure affects trait distributions in surrounding non-urban areas (Evans et al. 2011). For example, by evaluating the distribution of reproductive and dispersal traits across multiple extents, it might be possible to test how dispersal processes over large distances interact with matrix types to maintain local-scale functional diversity (Benchimol and Peres 2015, Delattre et al. 2013). This will allow for a more comprehensive understanding of how trait values distributions could be extrapolated in space, and could guide management responses that explicitly account for trait effects at a wider range of spatial scales.

In Chapter 5, I was interested in understanding how landscape attributes affected simultaneously functional diversity and species richness at a single scale. The next step will be to evaluate how variables at local and coarser scales operate simultaneously to shape species assemblages at the fragment and the regional scale. Patch level analyses can show how heterogeneity produced by fragmentation may increase functional diversity at local scales, even if it decreases at landscape scales. For example, previous work has found that bird insectivory increases at edges and in small forest fragments (González-Gómez et al. 2006), and this increase may be explained by higher levels of functional evenness and functional divergence in edge compared to interior bird assemblages. Comparing patterns of functional diversity between the edge and the patch interior will help to detect edge effects that can increase heterogeneity in trait distributions at local scales. Also, accounting for spatial autocorrelation of the functional diversity components at more than one scale can help to disentangle the effects of large-scale and local scale filters shaping community structure (Biswas et al. 2015). Positive spatial autocorrelation means the functional diversity values of nearby locations are more similar than distant ones, and therefore there is a higher influence of large scale environmental filters. Conversely, negative spatial autocorrelation means functional diversity is more dissimilar in nearby locations, and therefore local scale processes such as competition are expected to occur (Fortin and Dale 2005). It is thus necessary to identify the spatial signature of multiple ecological processes that are potentially acting at different spatial scales by contrasting positive and negative components of spatial autocorrelation for different components of functional trait diversity.

6.4.2 Synergistic effects of fragmentation and multiple environmental variables

Recent advances in our understanding of the ecological effects of habitat fragmentation show the strong context dependence of ecosystem responses, including time lags in population decline, and synergistic interactions between habitat fragmentation and other factors such as frequency of disturbances, topography and climate (Didham et al. 2012, Ewers and Didham 2006, Tscharntke et al. 2012). I only evaluated a subset of environmental variables, but future research should focus on discerning how factors such as matrix type, patch characteristics (e.g shape and edge contrast) affect the results provided by my work (Biswas et al. 2015, Carmona et al. 2016). For example, hostile landscape matrixes may act in synergy with habitat configuration to increase the proportion of species with high dispersal abilities (Buchi et al. 2012). Furthermore, the frequency of disturbances can increase the role of one trait over others (e.g. reproductive capacity becomes more important than dispersal) (Büchi and Vuilleumier 2014, 2016) and thus a further step will consist in running my model again changing the frequency of habitat removal.

In addition, including information about factors such as soil types and topography, which affect non-random patterns of land clearing, should be considered in future analyses. Since the loss and retention of native vegetation is rarely random among landscapes, the amount of remaining native vegetation may not necessarily reflect a good measure of habitat quality (Simmonds et al. 2017). For example, different areas with high amounts of tree cover are on sandy soils that do not provide a good habitat for several species (Watson 2011), which can impact the range of trait values that can be found. This might explain why I did not find clear effects of tree cover on functional richness for the functional groups analysed. Accounting for these effects in future analyses is needed to better understand the relative effects of habitat amount and fragmentation.

6.4.3 Accounting for species interactions

One of the main gaps I identified during my dissertation is the need to quantify how spatial context moderates the role of species interactions in driving trait distributions. Recent evidence is suggesting that competition and mutualism can drive effects of environmental change on trait diversity (Adler et al. 2013, Barbaro et al. 2014; Bregman et al. 2015). For example, although it is supposed that competitive interactions should generate trait dispersion patterns due to limiting similarity process (Gallien 2017, Maynard et al. 2017), competition can also lead to patterns of trait clustering when it acts synergistically with landscape change(Gallien et al. 2017). However, empirical tests of synergistic effects of species interactions and disturbance on functional diversity are lacking. In addition, the spatial autocorrelation of habitat types may modify the probability of species interacting (Biswas et al. 2015; Barbaro et al. 2015). This opens an opportunity to analyse how landscape configuration drives functional diversity by altering the frequency at which species interact. In addition, accounting for disproportionate effects of key species that may drive community structure is needed. For example, an increase of a single native species affected by anthropogenic habitat alteration can introduce substantial ecological dysfunction (Maron et al. 2013). Such information would complement inferences about how environmental filtering processes lead to patterns of trait diversity across systems with different spatial contexts.

6.4.4 Improving trait-based frameworks

The ability to effectively use a trait framework is becoming controversial because most studies have not clearly related specific traits to specific threats or functions (Bartomeus et al. 2018, Didham et al. 2016). Despite some generalities that emerge across taxa associated with large species, specialists, and higher trophic levels being in general more sensitive to fragmentation (Ewers and Didham 2006)(Bartlett et al. 2016), there is substantial variation in the response of the species with those traits to landscape change. I have discussed that this must be due in part to how spatial scale affects the relationship between species traits and environmental variables. However, comparisons of how single traits explain species responses across regions are needed. Ecological studies that collect rigorous empirical evidence about how traits influence species responses and their potential to provide functions is a major research priority (Didham et al. 2016). In addition, there is a need to quantify the functional effects of trait variation on clear measurements of performance, rather than just assuming invariant species-level trait correlates of ecosystem functions (McGill 2015, Didham et al. 2016).

By using continuous trait variations in my simulated model, I avoided issues related to ignoring intraspecific variation in trait-based approaches (Messier et al. 2010). However, trait values for my empirical analyses were sourced from the literature rather than being measured directly in the field, which was out of the scope of this project. Thus, the analyses presented in chapters 3 and 5 are based on mean trait values of species. In addition, the predictions of my theoretical model are largely based on whether response and effect traits are in general positively, negatively, or uncorrelated (e.g. large bodied species have a high pollination efficiency). However, the evaluation of how traits are correlated across different taxa is an important question that has not yet been answered. Besides collecting primary information in the field, analysis of trait variation using values reported in multiple trait databases may help to solve these issues.

6.5 Concluding remarks

Trait based analyses constitute a powerful approach to understanding and predicting the effects of landscape structure on functional diversity and species diversity. However, as stated by several authors, we are still far to ensure we are adequately equipped to make conservation decisions based on trait theory across different landscapes (Bartomeus et al. 2018, Didham et al. 2016). Experimental tests are needed to understand which traits are important for explaining ecological responses in different contexts. Furthermore, we need to evaluate how many traits are appropriate to study effects of environmental change on ecological responses at different scales of observation (Suárez-Castro et al. 2018). This thesis constitutes an advance in trying to find general patterns about the effects of landscape structure on functional diversity. However, testing the hypotheses presented here requires accounting for context dependence of ecosystem responses, as well as the synergistic interactions between habitat fragmentation, species interactions and other components of global environmental change (Didham et al. 2012, Ruffell et al. 2016). A better integration and communication between the fields of landscape and community ecology is needed if we want to advance in this area.

REFERENCES

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. and Franco, M. (2014) Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences 111(2), 740-745.

Aguiar, F.C., Cerdeira, J.O., Martins, M.J. and Ferreira, M.T. (2013) Riparian forests of S outhwest E urope: are functional trait and species composition assemblages constrained by environment? Journal of Vegetation Science 24(4), 628-638.

Akasaka, M., Takada, M., Kitagawa, R. and Igarashi, H. (2012a) Invasive non-native species attributes and invasion extent: examining the importance of grain size. Journal of Vegetation Science 23(1), 33-40.

Akasaka, T., Akasaka, M. and Nakamura, F. (2012b) Scale-independent significance of river and riparian zones on three sympatric Myotis species in an agricultural landscape. Biological Conservation 145(1), 15-23.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. and Lavorel, S. (2010) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Functional Ecology 24(6), 1192.

Alberti, M. (2015) Eco-evolutionary dynamics in an urbanizing planet. Trends in Ecology & Evolution 30(2), 114-126.

Alldredge, M.W., Simons, T.R. and Pollock, K.H. (2007) A Field Evaluation of Distance Measurement Error in Auditory Avian Point Count Surveys. The Journal of Wildlife Management 71(8), 2759-2766.

Anderson, K.E., Inouye, B.D. and Underwood, N. (2015) Can inducible resistance in plants cause herbivore aggregations? Spatial patterns in an inducible plant/herbivore model. Ecology 96(10), 2758-2770.

Archibald, C., McKinney, M., Mustin, K., Shanahan Danielle, F. and Possingham Hugh, P. (2017) Assessing the impact of revegetation and weed control on urban sensitive bird species. Ecology and Evolution 7(12), 4200-4208.

Barber, N.A. and Marquis, R.J. (2011) Light environment and the impacts of foliage quality on herbivorous insect attack and bird predation Oecologia 166: 401.

Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I. and Brockerhoff, E.G. (2014) Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. Diversity and Distributions 20(2), 149-159.

Barnagaud, J.Y., Papaix, J., Gimenez, O. and Svenning, J.C. (2015) Dynamic spatial interactions between the native invader Brown-headed Cowbird and its hosts. Diversity and Distributions 21(5), 511-522.

Bartlett, L.J., Newbold, T., Purves, D.W., Tittensor, D.P. and Harfoot, M.B.J. (2016) Synergistic impacts of habitat loss and fragmentation on model ecosystems. Proceedings of the Royal Society B: Biological Sciences 283(1839).

Bartomeus, I., Cariveau, D.P., Harrison, T. and Winfree, R. (2018) On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. Oikos 127(2), 306-315.

Bartón, K. (2014) "MuMIn: multi-model inference. R package version 1.10. 0.".

Batáry, P., Kurucz, K., Suarez-Rubio, M. and Chamberlain, D.E. (2017) Non-linearities in bird responses across urbanization gradients: A meta-analysis. Global Change Biology, 24(3):1046-1054.

Belmaker, J. and Jetz, W. (2013) Spatial Scaling of Functional Structure in Bird and Mammal Assemblages. American Naturalist 181(4), 464-478.

Belmaker, J., Parravicini, V. and Kulbicki, M. (2014) Ecological traits and environmental affinity explain Red Sea fish introduction into the Mediterranean. Global Change Biology 20(2), 680-680.

Benchimol, M. and Peres, C.A. (2015) Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. Journal of Ecology 103(2), 408-420.

Biswas, S.R., Mallik, A.U., Braithwaite, N.T. and Wagner, H.H. (2016) A conceptual framework for the spatial analysis of functional trait diversity. Oikos 125(2), 192-200.

Boiffin, J., Aubin, I. and Munson, A.D. (2015) Ecological controls on post-fire vegetation assembly at multiple spatial scales in eastern North American boreal forests. Journal of Vegetation Science 26(2), 360-372.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. and Vasseur, D.A. (2011) Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26(4), 183-192.

Bourgeois, B., Gonzalez, E., Vanasse, A., Aubin, I. and Poulin, M. (2016) Spatial processes structuring riparian plant communities in agroecosystems: implications for restoration. Ecological Applications 26(7), 2103-2115.

Bovo, A.A.A., Ferraz, K.M.P.M.B., Magioli, M., Alexandrino, E.R., Hasui, É., Ribeiro, M.C. and Tobias, J.A. (2018) Habitat fragmentation narrows the distribution of avian functional traits associated with seed dispersal in tropical forest. Perspectives in Ecology and Conservation 16(2) 90-96.

Bregman Tom, P., Lees Alexander, C., Seddon, N., MacGregor Hannah, E.A., Darski, B., Aleixo, A., Bonsall Michael, B. and Tobias Joseph, A. (2015) Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. Ecology 96(10), 2692-2704.

Bregman, T.P., Sekercioglu, C.H. and Tobias, J.A. (2014) Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biological Conservation 169, 372-383.

Brice, M.H., Pellerin, S. and Poulin, M. (2016) Environmental filtering and spatial processes in urban riparian forests. Journal of Vegetation Science 27(5), 1023-1035.

Brown, L.M. and Graham, C.H. (2015) Demography, traits and vulnerability to urbanization: can we make generalizations? Journal of Applied Ecology 52(6), 1455-1464.

Büchi, L. and Vuilleumier, S. (2012) Dispersal Strategies, Few Dominating or Many Coexisting: The Effect of Environmental Spatial Structure and Multiple Sources of Mortality (Dispersal Strategies in a Metacommunity). PLoS ONE 7(4), e34733.

Büchi, L. and Vuilleumier, S. (2014) Coexistence of Specialist and Generalist Species Is Shaped by Dispersal and Environmental Factors. The American Naturalist 183(5), 612-624.

Büchi, L. and Vuilleumier, S. (2016) Ecological strategies in stable and disturbed environments depend on species specialisation. Oikos 125(10), 1408-1420.

Butterfield, B.J. and Suding, K.N. (2013) Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. Journal of Ecology 101(1), 9-17.

Cadotte, M.W., Carscadden, K. and Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48(5), 1079-1087.

Cadotte, M.W. and Fukami, T. (2005) Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. Ecology Letters 8(5), 548-557.

Carmona, C.P., Azcárate, F.M., Bello, F., Ollero, H.S., Lepš, J. and Peco, B. (2012) Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. Journal of Applied Ecology 49(5), 1084-1093.

Carmona, C.P., Francesco de, B., Norman, W.H.M. and Jan, L. (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. Traits Without Borders: Integrating Functional Diversity Across Scales Trends in Ecology & Evolution 31, 382-394.

Carneiro, M.S., Campos, C.C.F., Beijo, L.A. and Ramos, F.N. (2016) Anthropogenic Matrices Favor Homogenization of Tree Reproductive Functions in a Highly Fragmented Landscape. PLoS ONE 11(10), e0164814.

Cattarino, L., McAlpine, C.A. and Rhodes, J.R. (2016) Spatial scale and movement behaviour traits control the impacts of habitat fragmentation on individual fitness. Journal of Animal Ecology 85(1), 168-177.

Catterall, C. (2004) Birds, garden plants and suburban bushlots: where good intentions meet unexpected outcomes. Pp 21 - 31 in Urban Wildlife: more than meets the eye, edited by Daniel Lunney and Shelley Burgin 2004. Royal Zoological Society of New South Wales, Mosman, NSW

Catterall, C.P., Cousin, J.A., Piper, S. and Johnson, G. (2010) Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? Diversity and Distributions 16(4), 559-570.

Caynes, R.J.C., Mitchell, M.G.E., Wu, D.S., Johansen, K. and Rhodes, J.R. (2016) Using high-resolution LiDAR data to quantify the three-dimensional structure of vegetation in urban green space. Urban Ecosystems 19(4), 1749-1765.

Cernansky, R. (2017) Biodiversity moves beyond counting species. Nature 546, , 22–24

Chalmandrier, L., Münkemüller, T., Colace, M.P., Renaud, J., Aubert, S., Carlson, B.Z., Clément, J.C., Legay, N., Pellet, G., Saillard, A., Lavergne, S. and Thuiller, W. (2017) Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. Journal of Ecology 105(1), 277-287.

Chamberlain, D., Kibuule, M., Skeen, R. and Pomeroy, D. (2017) Trends in bird species richness, abundance and biomass along a tropical urbanization gradient. Urban Ecosystems 20(3), 629-638.

Coetzee, B.W.T. and Chown, S.L. (2016) Land-use change promotes avian diversity at the expense of species with unique traits. Ecology and Evolution 6(21), 7610-7622.

Concepcion, E.D., Moretti, M., Altermatt, F., Nobis, M.P. and Obrist, M.K. (2015) Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos 124(12), 1571-1582.

Concostrina-Zubiri, L., Pescador, D.S., Martinez, I. and Escudero, A. (2014) Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. Biodiversity and Conservation 23(7), 1757-1770.

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D. and Baguette, M. (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. Ecography 40(1), 56-73.

Cox, D.T.C., Hudson, H.L., Plummer, K.E., Siriwardena, G.M., Anderson, K., Hancock, S., Devine-Wright, P. and Gaston, K.J. (2018) Covariation in urban birds providing cultural services or disservices and people. Journal of Applied Ecology 55(5), 2308-2319.

Craven, D., Filotas, E., Angers, V.A. and Messier, C. (2016) Evaluating resilience of tree communities in fragmented landscapes: linking functional response diversity with landscape connectivity. Diversity and Distributions 22(5), 505-518.

Croci, S., Butet, A. and Clergeau, P. (2008) Does Urbanization Filter Birds on the Basis of Their Biological Traits. The Condor 110(2), 223-240.

Da Silveira NS, Niebuhr BBS, Muylaert RdL, Ribeiro MC, Pizo MA (2016) Effects of Land Cover on the Movement of Frugivorous Birds in a Heterogeneous Landscape. PLoS ONE 11(6): e0156688

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A. and Wolters, V. (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture, Ecosystems and Environment 98(1), 321-329.

de Bello, F., Janecek, S., Leps, J., Dolezal, J., Mackova, J., Lanta, V. and Klimesova, J. (2012a) Different plant trait scaling in dry versus wet Central European meadows. Journal of Vegetation Science 23(4), 709-720.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A. and Sveriges, l. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation 19(10), 2873-2893.

de Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F. and Thuiller, W. (2013a) Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography 36(3), 393-402.

de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, K., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger, L., Lavergne, S., Lepš, J. and Pärtel, M. (2012b) Functional species pool framework to test for biotic effects on community assembly. Ecology 93(10), 2263-2273.

de Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H.C., Lavorel, S. and Sykes, M.T. (2013b) Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. Journal of Ecology 101(5), 1237-1244.

de Frutos, A., Navarro, T., Pueyo, Y. and Alados, C.L. (2015) Inferring Resilience to Fragmentation-Induced Changes in Plant Communities in a Semi-Arid Mediterranean Ecosystem. PLoS ONE 10(3): e0118837.

Dehling, D.M., Topfer, T., Schaefer, H.M., Jordano, P., Bohning-Gaese, K. and Schleuning, M. (2014) Functional relationships beyond species richness patterns: trait matching in plant-bird mutualisms across scales. Global Ecology and Biogeography 23(10), 1085-1093.

Delattre, T., Baguette, M., Burel, F., Stevens, V.M., Quénol, H. and Vernon, P. (2013) Interactive effects of landscape and weather on dispersal. Oikos 122(11), 1576-1585.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. and Couvet, D. (2008) Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography 17(2), 252-261.

Devictor, V., Julliard, R., Couvet, D., Lee, A. and Jiguet, F. (2007) Functional Homogenization Effect of Urbanization on Bird Communities. Conservation Biology 21(3), 741-751.

Dias, C.T.D.S., Samaranayaka, A. and Manly, B. (2008) On the use of correlated beta random variables with animal population modelling. Ecological Modelling 215(4), 293-300.

Díaz, S. and Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16(11) 646-655

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., Torres-Espuny, L.d., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. and Zak, M.R. (2004) The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15(3), 295-304.

Díaz, S., Lavorel, S., Bello, F.d., Quétier, F., Grigulis, K. and Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences 104(52), 20684-20689.

Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P. and Pearse, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecology and Evolution 3(9), 2958-2975.

Didham RK. 2010. Ecological consequences of habitat fragmentation. In: Encyclopedia of life sciences. Chichester: John Wiley & Sons Ltd

Didham, R.K., Kapos, V. and Ewers, R.M. (2012) Rethinking the conceptual foundations of habitat fragmentation research. Oikos 121(2), 161-170.

Didham, R.K., Leather, S.R., Basset, Y. and Stewart, A. (2016) Circle the bandwagons – challenges mount against the theoretical foundations of applied functional trait and ecosystem service research. Insect Conservation and Diversity 9(1), 1-3.

Ding, Z., Feeley, K.J., Wang, Y., Pakeman, R.J. and Ding, P. (2013) Patterns of bird functional diversity on land-bridge island fragments. Journal of Animal Ecology 82(4), 781-790.

Donadi, S., van Der Heide, T., Piersma, T., van Der Zee, E.M., Weerman, E.J., van de Koppel, J., Olff, H., Devine, C., Hernawan, U.E., Boers, M., Planthof, L. and Klemens Eriksson, B. (2015) Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. Oikos 124(11), 1502-1510.

Donnelly, R. and Marzluff, J.M. (2006) Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. Urban Ecosystems 9(2), 99-117.

Donner, D.M., Anderson, D., Eklund, D. and St. Pierre, M. (2013) Large-scale forest composition influences northern goshawk nesting in Wisconsin. Journal of Wildlife Management 77(3), 495-504.

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de Sassi, C., Galetti, M., Guimarães, P.R., Lomáscolo, S.B., Martín González, A.M., Pizo, M.A., Rader, R., Rodrigo, A., Tylianakis, J.M., Vázquez, D.P. and Allesina, S. (2013) The dimensionality of ecological networks. Ecology Letters 16(5), 577-583.

Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D. and Gaston, K.J. (2011) What makes an urban bird? Global Change Biology 17(1), 32-44.

Evans, K.L., Newson, S.E. and Gaston, K.J. (2009) Habitat influences on urban avian assemblages. Ibis 151(1), 19-39.

Ewers, R.M. and Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81(1), 117-142.

Ewers, R.M., Marsh, C.J. and Wearn, O.R. (2010) Making statistics biologically relevant in fragmented landscapes. Trends in Ecology & Evolution 25(12), 699-704.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34(1), 487-515.

Fahrig, L. (2017) Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics 48(1), 1-23.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. and Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14(2), 101-112.

Fahrig, L. and Triantis, K. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40(9), 1649-1663.

Fauth, J.E., Bernardo, J., Camara, M., W. J. Resetarits, J., Buskirk, J.V. and McCollum, S.A. (1996) Simplifying the Jargon of Community Ecology: A Conceptual Approach. The American Naturalist 147(2), 282-286.

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G. and von Wehrden, H. (2014) Land Sparing Versus Land Sharing: Moving Forward. Conservation Letters 7(3), 149-157.

Fischer, J. and Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16(3), 265-280.

Fletcher Jr, Robert J. (2006) Emergent Properties of Conspecific Attraction in Fragmented Landscapes. The American Naturalist 168(2), 207-219.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. and DeClerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12(1), 22-33.

Fraser, H., Hauser, C.E., Rumpff, L., Garrard, G.E. and McCarthy, M.A. (2017) Classifying animals into ecologically meaningful groups: A case study on woodland birds. Biological Conservation 214, 184-194.

French, K., Major, R. and Hely, K. (2005) Use of native and exotic garden plants by suburban nectarivorous birds. Biological Conservation 121(4), 545-559.

Fritschie, K.J. and Olden, J.D. (2016) Disentangling the influences of mean body size and size structure on ecosystem functioning: an example of nutrient recycling by a non-native crayfish. Ecology and Evolution 6(1), 159-169.

Galetti, M.G., R., Côrtes, M.; Fadini, R.; Von Matter, S.; Leite, A.; Labecca, F.; Ribeiro, T.; Carvalho, C.; Collevatt, R.; Pires, M.; Guimarães, P. Jr.; Brancalion, P.; Ribeiro, M.; Jordano, P. (2013) Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. Science 340, 6.

Gallien, L. (2017) Intransitive competition and its effects on community functional diversity. Oikos 126(5), 615-623.

Gallien, L., Zimmermann, N.E., Levine, J.M., Adler, P.B. and Wootton, T. (2017) The effects of intransitive competition on coexistence. Ecology Letters 20(7), 791-800.

Garden, J.G., McAlpine, C.A. and Possingham, H.P. (2010) Multi-scaled habitat considerations for conserving urban biodiversity: native reptiles and small mammals in Brisbane, Australia. Landscape Ecology 25(7), 1013-1028.

Garibaldi Lucas, A., Bartomeus, I., Bommarco, R., Klein Alexandra, M., Cunningham Saul, A., Aizen Marcelo, A., Boreux, V., Garratt Michael, P.D., Carvalheiro Luísa, G., Kremen, C., Morales Carolina, L., Schüepp, C., Chacoff Natacha, P., Freitas Breno, M., Gagic, V., Holzschuh, A., Klatt Björn, K., Krewenka Kristin, M., Krishnan, S., Mayfield Margaret, M., Motzke, I., Otieno, M., Petersen, J., Potts Simon, G., Ricketts Taylor, H., Rundlöf, M., Sciligo, A., Sinu Palatty, A., Steffan-Dewenter, I., Taki, H., Tscharntke, T., Vergara Carlos, H., Viana Blandina, F., Woyciechowski, M. and Devictor, V. (2015) EDITOR'S CHOICE: REVIEW: Trait matching of flower visitors and crops predicts fruit set better than trait diversity. Journal of Applied Ecology 52(6), 1436-1444.

Garnett, S.T., Duursma, D.E., Ehmke, G., Guay, P.-J., Stewart, A., Szabo, J.K., Weston, M.A., Bennett, S., Crowley, G.M., Drynan, D., Dutson, G., Fitzherbert, K. and Franklin, D.C. (2015) Biological, ecological, conservation and legal information for all species and subspecies of Australian bird. Scientific Data 2, 150061.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J., Thébault, A., Vile, D. and Zarovali, M.P. (2007) Assessing the Effects of Land-use Change on Plant Traits, Communities and Ecosystem Functioning in Grasslands: A Standardized Methodology and Lessons from an Application to 11 European Sites. Annals of Botany 99(5), 967-985.

Garrard, G.E., McCarthy, M.A., Vesk, P.A., Radford, J.Q. and Bennett, A.F. (2012) A predictive model of avian natal dispersal distance provides prior information for investigating response to landscape change. Journal of Animal Ecology 81(1), 14-23.

Gilroy, J.J., Medina Uribe, C.A., Haugaasen, T. and Edwards, D.P. (2015) Effect of scale on trait predictors of species responses to agriculture. Conservation Biology 29(2), 463-472.

González-Gómez, P.L., Estades, C.F. and Simonetti, J.A. (2006) Strengthened insectivory in a temperate fragmented forest. Oecologia 148(1), 137-143.

Gothe, E., Angeler, D.G. and Sandin, L. (2013) Metacommunity structure in a small boreal stream network. Journal of Animal Ecology 82(2), 449-458.

Grace, J.B. (2006) Structural equation modeling and natural systems / James B. Grace, Cambridge, UK ; New York : Cambridge University Press, Cambridge, UK ; New York.

Green, S.J. and Côté, I.M. (2014) Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. Journal of Animal Ecology 83(6), 1451-1460.

Gross, N., Bagousse-Pinguet, Y.L., Liancourt, P., Berdugo, M., Gotelli, N.J. and Maestre, F.T. (2017) Functional trait diversity maximizes ecosystem multifunctionality. Nature Ecology & Evolution 1, 0132.

Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.L., García-Gómez, M., Valencia-Gómez, E. and Maestre, F.T. (2013) Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. Journal of Ecology 101(3), 637-649.

Gunton, R.M. and Poyry, J. (2016) Scale-specific spatial density dependence in parasitoids: a multi-factor meta-analysis. Functional Ecology 30(9), 1501-1510.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X. and Townshend, J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1(2).

Hanski, I. (2015) Habitat fragmentation and species richness. Journal of Biogeography 42(5), 989-993.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. and Settele, J. (2004) Predictors of Species Sensitivity to Fragmentation. Biodiversity & Conservation 13(1), 207-251.

Heyman, E., Gunnarsson, B. and Dovydavicius, L. (2017) Ecology and Conservation of Birds in Urban Environments. Murgui, E. and Hedblom, M. (eds), pp. 465-488, Springer International Publishing, Cham.

Ibarra, J.T. and Martin, K. (2015) Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. Biological Conservation 192, 418-427.

Ikin, K., Barton, P.S., Stirnemann, I.A., Stein, J.R., Michael, D., Crane, M., Okada, S. and Lindenmayer, D.B. (2014) Multi-Scale Associations between Vegetation Cover and Woodland Bird Communities across a Large Agricultural Region. PLoS ONE 9(5).

Ikin, K., Beaty, R.M., Lindenmayer, D.B., Knight, E., Fischer, J. and Manning, A.D. (2013) Pocket parks in a compact city: how do birds respond to increasing residential density? Landscape Ecology 28(1), 45-56.

Jackson, H.B. and Fahrig, L. (2012) What size is a biologically relevant landscape? Landscape Ecology 27(7), 929-941.

Jackson, H.B. and Fahrig, L. (2015) Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24(1), 52-63.

Jacobs, B.M., N.; Delaney, C. (2014) Benchmarking Australia's Urban Tree Canopy: An I-Tree Assessment, Final Report, University of Technology Sydney, Sydney (Australia).

Kaiser, A., Merckx, T. and Van Dyck, H. (2016) The Urban Heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. Ecology and Evolution 6(12), 4129-4140.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin Iii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G. and Ozinga, W.A. (2011) TRY – a global database of plant traits. Global Change Biology 17(9), 2905-2935.

Kazakou, E., Violle, C., Roumet, C., Navas, M.L., Vile, D., Kattge, J. and Garnier, E. (2014) Are trait-based species rankings consistent across data sets and spatial scales? Journal of Vegetation Science 25(1), 235-247.

Keinath, D.A., Doak, D.F., Hodges, K.E., Prugh, L.R., Fagan, W., Sekercioglu, C.H., Buchart, S.H.M. and Kauffman, M. (2017) A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26(1), 115-127.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J., Montoya, J.M., Römermann, C., Schiffers, K., Schurr, F.M., Singer, A., Svenning, J.C., Zimmermann, N.E. and O'hara, R.B. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography 39(12), 2163-2178.

Kosydar, A.J., Conquest, L.L. and Tewksbury, J.J. (2014) Can life histories predict the effects of habitat fragmentation? a meta-analysis with terrestrial mammals. Applied Ecology and Environmental Research 12(2), 505-521.

Kraft, Nathan J.B., Cornwell, William K., Webb, Campbell O. and Ackerly, David D. (2007) Trait Evolution, Community Assembly, and the Phylogenetic Structure of Ecological Communities. The American Naturalist 170(2), 271-283.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Stanko, M., Morand, S. and Mouillot, D. (2015) Assembly rules of ectoparasite communities across scales: combining patterns of abiotic factors, host composition, geographic space, phylogeny and traits. Ecography 38(2), 184-197.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T.a., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J. and Ricketts, T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters 10(4), 299-314.

Laliberté, E. and Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91(1), 299-305.

Laliberte, E., Norton, D.A. and Scott, D. (2013) Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. Journal of Vegetation Science 24(5), 834-834.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A. and Mayfield, M.M. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13(1), 76-86.

Laughlin, D.C. and Messier, J. (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends in Ecology and Evolution 30(8), 487-496.

Lauterbach, D., Romermann, C., Jeltsch, F. and Ristow, M. (2013) Factors driving plant rarity in dry grasslands on different spatial scales: a functional trait approach. Biodiversity and Conservation 22(10), 2337-2352.

Lavorel, S., Storkey, J., Bardgett, R.D., Bello, F., Berg, M.P., Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S. and Harrington, R. (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. Journal of Vegetation Science 24(5), 942-948.

Levine, J.M. (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology 73(6), 1943-1967.

Lim, H.C. and Sodhi, N.S. (2004) Responses of avian guilds to urbanisation in a tropical city. Landscape and Urban Planning 66(4), 199-215.

Lin, B.B. and Fuller, R.A. (2013) FORUM: Sharing or sparing? How should we grow the world's cities? Journal of Applied Ecology 50(5), 1161-1168.

Litteral, J. and Shochat, E. (2017) Ecology and Conservation of Birds in Urban Environments. Murgui, E. and Hedblom, M. (eds), pp. 135-159, Springer International Publishing, Cham.

Luck, G.W., Carter, A. and Smallbone, L. (2013) Changes in Bird Functional Diversity across Multiple Land Uses: Interpretations of Functional Redundancy Depend on Functional Group Identity. PLoS ONE 8(5), e63671.

Luck, G.W., Lavorel, S., McIntyre, S. and Lumb, K. (2012) Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. Journal of Animal Ecology 81(5), 1065-1076.

Lundberg, J. and Moberg, F. (2003) Mobile Link Organisms and Ecosystem Functioning: Implications for Ecosystem Resilience and Management. Ecosystems 6(1), 0087-0098.

Mäntylä, E., Klemola, T. and Laaksonen, T. (2011). Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators Oecologia 165(1), 143:151

Magnago, L.F.S., Edwards, D.P., Edwards, F.A., Magrach, A., Martins, S.V. and Laurance, W.F. (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. Journal of Ecology 102(2), 475-485.

Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., Clarke, M.F., Loyn, R.H., Mac Nally, R., Davidson, I. and Thomson, J.R. (2013) Avifaunal disarray due to a single despotic species, Diversity and Distributions 19(12) 1468-1479.

Martinez, O.J.A., Fremier, A.K., Gunter, S., Bendana, Z.R., Vierling, L., Galbraith, S.M., Bosque-Perez, N.A. and Ordonez, J.C. (2016) Scaling up functional traits for ecosystem services with remote sensing: concepts and methods. Ecology and Evolution 6(13), 4359-4371.

Marzluff, J.M. (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems 8(2), 157-177.

Marzluff, J.M., Withey, J.C., Whittaker, K.A., David Oleyar, M., Unfried, T.M., Rullman, S. and Delap, J. (2007) Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. The Condor 109(3), 516-534.

Mason, N.W.H., Bello, F.d. and Wilson, B. (2013) Functional diversity: a tool for answering challenging ecological questions. Journal of Vegetation Science 24(5), 777-780.

Mason, N.W.H. and De Bello, F. (2013) Functional diversity: a tool for answering challenging ecological questions. Journal of Vegetation Science 24(5), 777-780.

Mason, N.W.H., Mouillot, D., Lee, W.G. and Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111(1), 112-118.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. and Vesk, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Global Ecology and Biogeography 19(4), 423-431.

Maynard, D.S., Crowther, T.W. and Bradford, M.A. (2017) Competitive network determines the direction of the diversity–function relationship. Proceedings of the National Academy of Sciences 114(43), 11464-11469.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: Spatial Pattern Analysis

Program for Categorical Maps. . Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html.

McGarigal, K., Wan, H., Zeller, K., Timm, B. and Cushman, S. (2016) Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31(6), 1161-1175.

McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21(4), 178-185.

Melles, S.G., S.; Martin, K. (2003) Urban Bird Diversity and Landscape Complexity: Species–environment Associations Along a Multiscale Habitat Gradient. Ecology and the Society 7(1), 22.

Messier, J., McGill, B.J. and Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters 13(7), 838- 848.

Miguet, P., Jackson, H., Jackson, N., Martin, A. and Fahrig, L. (2016) What determines the spatial extent of landscape effects on species? Landscape Ecology 31(6), 1177-1194.

Mitchell, M.G.E., Bennett, E.M. and Gonzalez, A. (2013) Linking Landscape Connectivity and Ecosystem Service Provision: Current Knowledge and Research Gaps. Ecosystems 16(5), 894-908.

Mitchell, M.G.E., Wu, D., Johansen, K., Maron, M., McAlpine, C. and Rhodes, J.R. (2016) Landscape structure influences urban vegetation vertical structure. Journal of Applied Ecology 53(5), 1477-1488.

Mokany, K. and Roxburgh, S.H. (2010) The importance of spatial scale for trait-abundance relations. Oikos 119(9), 1504-1514.

Montague-Drake, R.M., Lindenmayer, D.B., Cunningham, R.B. and Stein, J.A. (2011) A reverse keystone species affects the landscape distribution of woodland avifauna: a case study using the Noisy Miner (Manorina melanocephala) and other Australian birds. Landscape Ecology 26(10), 1383-1394.

Morales-Castilla, I., Matias, M.G., Gravel, D. and Araújo, M.B. (2015) Inferring biotic interactions from proxies. Trends in Ecology & Evolution 30(6), 347-356.

Moran-Ordonez, A., Pavlova, A., Pinder, A.M., Sim, L., Sunnucks, P., Thompson, R.M. and Davis, J. (2015) Aquatic communities in arid landscapes: local conditions, dispersal traits and landscape configuration determine local biodiversity. Diversity and Distributions 21(10), 1230-1241.

Moran, E.V., Hartig, F. and Bell, D.M. (2016) Intraspecific trait variation across scales: implications for understanding global change responses Global Change Biology 22(1) 137-150.

Morante, J.C., Arroyo-Rodriguez, V. and Faria, D. (2016) Patterns and predictors of beta-diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. Journal of Animal Ecology 85(1), 240-250.

Moreira, B., Tavsanoglu, Ç. and Pausas, J. (2012) Local versus regional intraspecific variability in regeneration traits. Oecologia 168(3), 671-677.

Mori, A.S., Furukawa, T. and Sasaki, T. (2013) Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews 88(2), 349-364.

Mouchet, M.A., Villéger, S., Mason, N.W.H. and Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24(4), 867-876.

Müller, N., Ignatieva, M., Nilon, C.H., Werner, P. and Zipperer, W.C. (2013) Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment. Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P.J., McDonald, R.I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K.C. and Wilkinson, C. (eds), pp. 123-174, Springer Netherlands, Dordrecht.

Munguia-Rosas, M.A., Jurado-Dzib, S.G., Mezeta-Cob, C.R., Montiel, S., Rojas, A. and Pech-Canche, J.M. (2014) Continuous forest has greater taxonomic, functional and phylogenetic plant diversity than an adjacent naturally fragmented forest. Journal of Tropical Ecology 30, 323-333.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. Nature 403, 853.

Naeem, S. and Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology Letters 6(6), 567-579.

Nash, K.L., Graham, N.A.J., Jennings, S., Wilson, S.K. and Bellwood, D.R. (2016) Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. Journal of Applied Ecology 53(3), 646-655.

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioğlu, Ç.H., Alkemade, R., Booth, H. and Purves, D.W. (2013) Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B: Biological Sciences 280(1750).

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. and Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13(8), 969-979.

Pakeman, R.J. (2011) Multivariate identification of plant functional response and effect traits in an agricultural landscape. Ecology 92(6), 1353-1365.

Palma, A.D., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Börger, L., Hudson, L.N., Lysenko, I., Newbold, T., Purvis, A. and Kaplan, I. (2015) Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. Journal of Applied Ecology 52(6), 1567-1577.

Peringer, A., Schulze, K.A., Stupariu, I., Stupariu, M.S., Rosenthal, G., Buttler, A. and Gillet, F. (2016) Multi-scale feedbacks between tree regeneration traits and herbivore behavior explain the structure of pasture-woodland mosaics. Landscape Ecology 31(4), 913-927.

Perovic, D., Gamez-Virues, S., Borschig, C., Klein, A.M., Krauss, J., Steckel, J., Rothenwohrer, C., Erasmi, S., Tscharntke, T. and Westphal, C. (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. Journal of Applied Ecology 52(2), 505-513.

Petchey, O.L., Evans, K.L., Fishburn, I.S. and Gaston, K.J. (2007) Low functional diversity and no redundancy in British avian assemblages. Journal of Animal Ecology 76(5), 977-985.

Petchey, O.L. and Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. Ecology Letters 9(6), 741-758.

Preacher, K.J., Rucker, D.D. and Hayes, A.F. (2007) Addressing Moderated Mediation Hypotheses: Theory, Methods, and Prescriptions. Multivariate Behavioral Research 42(1), 185-227.

Pigot, A.L., Bregman, T., Sheard, C., Daly, B., Etienne, R.S. and Tobias, J.A. (2016) Quantifying species contributions to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. Proceedings of the Royal Society B: Biological Sciences 283(1844), 1-7

Pollack, L., Ondrasek, N.R. and Calisi, R. (2017) Urban health and ecology: the promise of an avian biomonitoring tool. Current Zoology 63(2), 205-212.

Prokopenko, C.M., Boyce, M.S. and Avgar, T. (2017) Extent-dependent habitat selection in a migratory large herbivore: road avoidance across scales. Landscape Ecology 32(2), 313-325.

Ries, L. and Sisk, T.D. (2010) What is an edge species? The implications of sensitivity to habitat edges. Oikos 119(10), 1636-1642.

Rosseel, Y. (2012) lavaan: An R Package for Structural Equation Modeling. Journal of Statistical Software; Vol 1, Issue 2 (2012).

Ruffell, J., Banks-Leite, C. and Didham, R.K. (2016) Accounting for the causal basis of collinearity when measuring the effects of habitat loss versus habitat fragmentation. Oikos 125(1), 117-125.

Rybicki, J. and Hanski, I. (2013) Species–area relationships and extinctions caused by habitat loss and fragmentation. Ecology Letters 16, 27-38.

Ryder, J.J., Pastok, D., Hoare, M.J., Bottery, M.J., Boots, M., Knell, R.K., Atkinson, D. and Hurst, G.D.D. (2013) Spatial variation in food supply, mating behavior, and sexually transmitted disease epidemics. Behavioral Ecology 24(3), 723-729.

Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K. and Diniz-Filho, J.A.F. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. Philosophical Transactions of the Royal Society B: Biological Sciences 366(1577), 2536.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D.A., Brinks, E., Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., Wille, J., Zeh, S., Davison, R., Vieregg, D., Baudisch, A., Altwegg, R., Colchero, F., Dong, M., Kroon, H., Lebreton, J.D., Metcalf, C.J.E., Neel, M.M., Parker, I.M., Takada, T., Valverde, T., Vélez-Espino, L.A., Wardle, G.M., Franco, M. and Vaupel, J.W. (2015) The compadre Plant Matrix Database: an open online repository for plant demography. Journal of Ecology 103(1), 202-218.

Sandström, U.G., Angelstam, P. and Mikusiński, G. (2006) Ecological diversity of birds in relation to the structure of urban green space. Landscape and Urban Planning 77(1), 39-53.

Saupe, D. (1988) The Science of Fractal Images, pp. 71-113, Springer-Verlag New York, Inc.

Schleicher, A., Biedermann, R. and Kleyer, M. (2011) Dispersal traits determine plant response to habitat connectivity in an urban landscape. Landscape Ecology 26(4), 529-540.

Schütz, C. and Schulze, C.H. (2015) Functional diversity of urban bird communities: effects of landscape composition, green space area and vegetation cover. Ecology and Evolution 5(22), 5230-5239.

Séguin, A., Harvey, É., Archambault, P., Nozais, C. and Gravel, D. (2014) Body size as a predictor of species loss effect on ecosystem functioning. Scientific Reports 4, 4616.

Sekercioglu, C.H. and Sodhi, Navjot S. (2007) Conservation Biology: Predicting Birds' Responses to Forest Fragmentation. Current Biology 17(19), R838-R840.

Seto, K.C., Güneralp, B. and Hutyra, L.R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences 109(40), 16083-16088.

Sewell, S.R. and Catterall, C.P. (1998) Bushland modification and styles of urban development: their effects on birds in south-east Queensland. Wildlife Research 25(1), 41-63.

Shanahan, D.F., Miller, C., Possingham, H.P. and Fuller, R.A. (2011) The influence of patch area and connectivity on avian communities in urban revegetation. Biological Conservation 144(2), 722-729.

Shipley, B. (2000) A New Inferential Test for Path Models Based on Directed Acyclic Graphs. Structural Equation Modeling: A Multidisciplinary Journal 7(2), 206-218.

Shochat, E., Lerman, S.B., Anderies, J.M., Warren, P.S., Faeth, S.H. and Nilon, C.H. (2010) Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. BioScience 60(3), 199-208.

Soga, M., Yamaura, Y., Koike, S. and Gaston, K.J. (2014) Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? Journal of Applied Ecology 51(5), 1378-1386.

Sol, D., González-Lagos, C., Moreira, D., Maspons, J. and Lapiedra, O. (2014) Urbanisation tolerance and the loss of avian diversity. Ecology Letters 17(8), 942-950.

Sonnier, G., Jamoneau, A. and Decocq, G. (2014a) Evidence for a direct negative effect of habitat fragmentation on forest herb functional diversity. Landscape Ecology 29(5), 857-866.

Sonnier, G., Johnson, S.E., Amatangelo, K.L., Rogers, D.A. and Waller, D.M. (2014b) Is taxonomic homogenization linked to functional homogenization in temperate forests? Global Ecology and

Biogeography 23(8), 894-902.

Spasojevic, M.J., Bahlai, C.A., Bradley, B.A., Butterfield, B.J., Tuanmu, M.N., Sistla, S., Wiederholt, R. and Suding, K.N. (2016a) Scaling up the diversity-resilience relationship with traitdatabases and remote sensing data: the recovery ofproductivity after wildfire. Global Change Biology 22(4), 1421-1432.

Spasojevic, M.J. and Suding, K.N. (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. Journal of Ecology 100(3), 652-661.

Spasojevic, M.J., Turner, B.L. and Myers, J.A. (2016b) When does intraspecific trait variation contribute to functional beta-diversity? Journal of Ecology 104(2), 487-496.

Sterk, M., Gort, G., Klimkowska, A., van Ruijven, J., van Teeffelen, A.J.A. and Wamelink, G.W.W. (2013) Assess ecosystem resilience: Linking response and effect traits to environmental variability. Ecological Indicators 30, 21-27.

Stirnemann, I., Ikin, K., Gibbons, P., Blanchard, W. and Lindenmayer, D. (2015) Measuring habitat heterogeneity reveals new insights into bird community composition. Oecologia 177(3), 733-746.

Stouffer, D.B. and Bascompte, J. (2010) Understanding food-web persistence from local to global scales. Ecology Letters 13(2), 154.

Suárez-Castro, A.F., Simmonds, J.S., Mitchell, M.G.E., Maron, M. and Rhodes, J.R. (2018) The Scale-Dependent Role of Biological Traits in Landscape Ecology: A Review. Current Landscape Ecology Reports 3(1), 12-22.

Suding, K.N., Lavorel, S., Chapin Iii, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. and Navas, M.L. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14(5), 1125-1140.

Sushinsky, J.R., Rhodes, J.R., Possingham, H.P., Gill, T.K. and Fuller, R.A. (2013) How should we grow cities to minimize their biodiversity impacts? Global Change Biology 19(2), 401-410.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. and Burnham, K.P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of Applied Ecology 47(1), 5-14.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., Van der Putten, W.H. and Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Review 87(3), 661-685.

Turner, M G., Gardner, R.H., O'Neill, R. (2001). Landscape Ecology in Theory and Practice. Pattern and Processes. XIV, 406 Springer-Verlag New York

Ulrich, W., Lens, L., Tobias, J.A. and Habel, J.C. (2016) Contrasting Patterns of Species Richness and Functional Diversity in Bird Communities of East African Cloud Forest Fragments. PLoS ONE 11(11) e0163338.

van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M. and Mysterud, A. (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? The Journal of animal ecology 80(4), 771.

Van Dyck, H. and Baguette, M. (2005) Dispersal behaviour in fragmented landscapes: Routine or special movements? Basic and Applied Ecology 6(6), 535-545.

Villard, M.A. and Metzger, J.P. (2014) Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51(2), 309-318.

Villéger, S., Mason, N.W.H. and Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89(8), 2290-2301.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. and Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution 27(4), 244-252.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. (2007) Let the concept of trait be functional! Oikos 116(5), 882-892.

Wang, X., Blanchet, F.G., Koper, N. and Tatem, A. (2014) Measuring habitat fragmentation: An evaluation of landscape pattern metrics. Methods in Ecology and Evolution 5(7), 634-646.

Watson, D.M. (2011) A productivity-based explanation for woodland bird declines: poorer soils yield less food. Emu - Austral Ornithology 111(1), 10-18.

Weisstein, W.E. (2006) Distribution Function, From MathWorld--A Wolfram Web Resource, From MathWorld--A Wolfram Web Resource.

Weston, R. and Gore, P.A. (2006) A Brief Guide to Structural Equation Modeling. The Counseling Psychologist 34(5), 719-751.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J. and Enquist, B.J. (2007) Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22(6), 323-330.

Wilman, H., Belmaker, J., Simpson, J., De La Rosa, C., Rivadeneira, M.M. and Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95(7), 2027-2027.

Wilson, M.J. and McTammany, M.E. (2016) Spatial scale and dispersal influence metacommunity dynamics of benthic invertebrates in a large river. Freshwater Science 35(2), 738-747.

Wood, S.A., Russell, R., Hanson, D., Williams, R.J. and Dunne, J.A. (2015) Effects of spatial scale of sampling on food web structure. Ecology and Evolution 5(17), 3769-3782.

Wood Simon, N. (2010) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B

(Statistical Methodology) 73(1), 3-36.

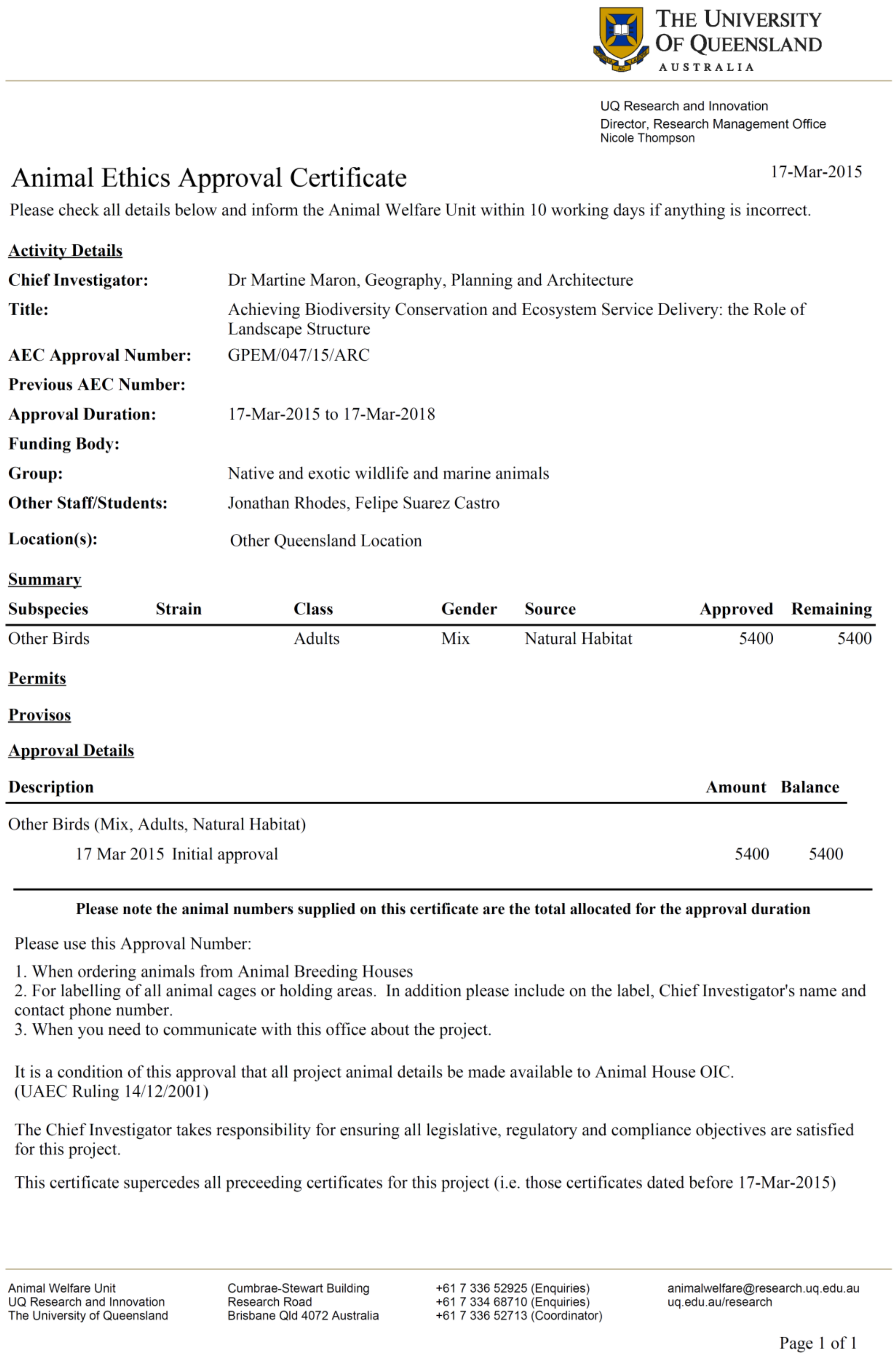
Wüest, R.O., Münkemüller, T., Lavergne, S., Pollock, L.J. and Thuiller, W. (2017) Integrating correlation between traits improves spatial predictions of plant functional composition. Oikos 127(3), 472-481.

Yang, J., Zhang, G.C., Ci, X.Q., Swenson, N.G., Cao, M., Sha, L.Q., Li, J., Baskin, C.C., Slik, J.W.F. and Lin, L.X. (2014) Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. Functional Ecology 28(2), 520-529.

Zhu, L., Fu, B., Zhu, H., Wang, C., Jiao, L. and Zhou, J. (2017) Trait choice profoundly affected the ecological conclusions drawn from functional diversity measures. Scientific Reports 7(1), 3643.

Zuur, A.F., Ieno, E.N. and Smith, G.M. (2007) Analysing Ecological Data by Alain F. Zuur, Elena N. Ieno, Graham M. Smith, New York, NY : Springer New York, New York, NY.

APPENDIX A



THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

Animal Ethics Approval Certificate

17-Mar-2015

Please check all details below and inform the Animal Welfare Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Dr Martine Maron, Geography, Planning and Architecture
Title:	Achieving Biodiversity Conservation and Ecosystem Service Delivery: the Role of Landscape Structure
AEC Approval Number:	GPEM/047/15/ARC
Previous AEC Number:	
Approval Duration:	17-Mar-2015 to 17-Mar-2018
Funding Body:	
Group:	Native and exotic wildlife and marine animals
Other Staff/Students:	Jonathan Rhodes, Felipe Suarez Castro
Location(s):	Other Queensland Location

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Other Birds		Adults	Mix	Natural Habitat	5400	5400

Permits

Provisos

Approval Details

Description	Amount	Balance
Other Birds (Mix, Adults, Natural Habitat)		
17 Mar 2015 Initial approval	5400	5400

Please note the animal numbers supplied on this certificate are the total allocated for the approval duration

Please use this Approval Number:

1. When ordering animals from Animal Breeding Houses
2. For labelling of all animal cages or holding areas. In addition please include on the label, Chief Investigator's name and contact phone number.
3. When you need to communicate with this office about the project.

It is a condition of this approval that all project animal details be made available to Animal House OIC. (UAEC Ruling 14/12/2001)

The Chief Investigator takes responsibility for ensuring all legislative, regulatory and compliance objectives are satisfied for this project.

This certificate supercedes all preceeding certificates for this project (i.e. those certificates dated before 17-Mar-2015)

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Page 1 of 1

APPENDIX B

A review of the literature on the scale-dependent role of traits from 2012 to March 2017

Search criteria:

I searched (March 27th 2017) for all papers published in the last five years, using the following search term sequence in Web of Science: TI (title) = (Scale Or Scale* Or Multiscale Or Multi-Scale Or Spatial) And TS (topic) = (Trait Or Trait* Or Dispersal Or Size Or Size* Or Reproductive Or Foraging Or Behaviour). This procedure resulted in over 30,000 results. All studies that did not include "scale" in the abstract were discarded. I then filtered these results by selecting 40 ecological journals most likely to publish papers on ecological responses to landscape change, resulting in a total of 1540 records (Table S1). For my analysis, we selected studies based on the following criteria:

1) Environmental predictors and ecological responses were measured at multiple spatial scales. I defined spatial scale as the smallest/shortest unit of observation (i.e. grain) and the spatial extent or duration over which observations are made (i.e. extent).
2) The ecological response variable was directly measured, not inferred e.g. from a model.
3) Species traits were explicitly included as predictors or response variables for explaining the relative influence of environmental factors on ecological responses at each measured scale. I use the term trait in its broader sense and included morphological, physiological features related to species survival and reproduction, as well as traits related to species-specific habitat preferences (i.e. habitat specialization).
4) Measured trait effects or responses were explicitly reported from tables or graphs and based on quantitative analyses. Thus, I did not take into account papers that discussed potential links between traits, environmental variables and ecological responses from the text portions of the papers.

Most of the results were then eliminated based on the titles or the abstracts, because they failed to meet one or more of the criteria above. In cases where suitability could not be determined based on the abstract, I eliminated additional papers after reading the methods and results sections. This process produced a set of 101 studies, which are listed in table S2.

I placed each of these studies according to the three approaches analysed in my review: "Species traits as predictors", "Single trait expression across scales" and "Trait diversity approaches". For this, I answered each of the following questions:

- *Does the study quantify trait effects at multiple spatial scales?* The study quantifies how the effect of different traits on the response variables varies with the spatial scale of measurement.

- *Does it quantify trait distributions at multiple spatial scales?* The study quantifies how trait diversity patterns (The variation or dispersion of functional traits in an assemblage) change with scale.
- *Does it quantify effects of scale on traits?* The study evaluates how the expression of a single trait for a particular species varies over different spatial scales and how environmental variables moderate this variation.

The proportion of papers categorized into each approach is shown in Fig. 1. Next, I determined the type of traits and ecological responses measured in each study (results in Fig. 1b). I used the following categories:

Species traits

- *Size:* Length, height or body mass. I excluded traits such as seed size from this category as they were used for explaining the relative dispersal or reproductive abilities of the species.
- *Habitat specialization:* Principal habitat requirements and capacity to use various habitats.
- *Morphology Plants/animals:* Any structural or morphological trait except body mass/length or plant size. For plants morphological traits included specific leaf area, growth form and stem width and thickness, whereas for animals traits included body shape, wing size and shape, beak width, tail length, and tarsus length
- *Reproductive traits:* Offspring size, clonality, seed production, number of broods per year, number of eggs per clutch, mating behaviour.
- *Dispersal Capacity:* Any trait related to the area or distance over which a species moves across the landscape (e.g. home range size, dispersal strategy, dispersal vector)
- *Diet:* Main type of food items consumed.
- *Foraging Method:* Food procurement methods and main foraging locations. Studies about habitat selection are not included.
- *Physiological traits:* Leaf dry matter content, leaf nitrogen concentration, leaf carbon concentration.
- *Behaviour:* Traits related to nesting or social behaviour

Ecological responses

- *Interspecific interactions:* Studies evaluated the relationships between different species that affected survival, reproduction and/or growth rates for at least one species involved in the interaction. Interactions may include parasitism, competition, predation, pollination or herbivory.

- *Multiple indices of diversity:* The study reported quantitative measures that reflect how many different types of species and functional traits can be found in a particular assemblage across scales. Trait diversity could be measured with different indices, including functional richness, functional evenness, functional divergence, community weighted means or any multivariate analyses aimed at determining the optimal trait combination for a given environment.
- *Spatial parameters:* The studies characterized spatial relationships between biotic and abiotic variables at multiple scales. Measurements included the spatial aggregation of species among an environmental gradient, functional connectivity patterns or metacommunity analyses.
- *Patterns of species abundances:* The study reported the abundance of each species independently at each scale of observation.
- *Taxonomic diversity:* Studies that only focused on calculating indices of taxonomic diversity (e.g. taxonomic alpha, beta or gamma diversity) for biological assemblages at multiple scales.

Table B1 List of journals searched for papers on species traits explaining ecological responses to landscape change at multiple scales between 2012 and March 2017. In parenthesis, the number of studies

Journal	Number of papers
Agriculture Ecosystems & Environment	1
American Naturalist	2
Behavioral Ecology	3
Biodiversity and Conservation	2
Biogeosciences	1
Biological Conservation	1
Biotropica	1
Conservation Biology	1
Diversity and Distributions	5
Ecography	5
Ecological Applications	1
Ecological Indicators	2
Ecology	6
Ecology and Evolution	3
Ecology Letters	1
Ecosphere	1
Evolutionary Ecology	1
Evolutionary Ecology Research	1
Freshwater Science	1
Functional Ecology	3
functonal ecology	1
Global Change Biology	1
Global Ecology and Biogeography	3

Insect Conservation and Diversity	2
Journal of animal ecology	1
Journal of Animal Ecology	3
Journal of Applied Ecology	3
Journal of Ecology	8
Journal of Evolutionary Biology	1
Journal of Plant Ecology	1
Journal of Vegetation Science	9
Journal of Wildlife Management	1
Landscape Ecology	3
Marine ecology progress series	3
Molecular Ecology	1
Oecologia	3
Oikos	5
Plant Ecology	2
Plos One	4
Science of The Total Environment	1
Urban Ecosystems	1

Table B2. Articles used in the 2012-2017 review of the empirical literature on the scale-dependent role of traits, numbered alphabetically.

1. Aguiar FC, Cerdeira JO, Martins MJ, Ferreira MT. Riparian forests of Southwest Europe: are functional trait and species composition assemblages constrained by environment? Journal of Vegetation Science. 2013;24(4):628-38. doi:10.1111/jvs.12009.
2. Akasaka M, Takada M, Kitagawa R, Igarashi H. Invasive non-native species attributes and invasion extent: examining the importance of grain size. Journal of Vegetation Science. 2012;23(1):33-40. doi:10.1111/j.1654-1103.2011.01332.x.
3. Akasaka T, Akasaka M, Nakamura F. Scale-independent significance of river and riparian zones on three sympatric Myotis species in an agricultural landscape. Biological Conservation. 2012;145(1):15-23. doi:10.1016/j.biocon.2011.08.017.
4. Albouy C, Leprieur F, Le Loc'h F, Mouquet N, Meynard CN, Douzery EJP et al. Projected impacts of climate warming on the functional and phylogenetic components of coastal Mediterranean fish biodiversity. Ecography. 2015;38(7):681-9. doi:10.1111/ecog.01254.
5. Allen AM, Mansson J, Sand H, Malmsten J, Ericsson G, Singh NJ. Scaling up movements: from individual space use to population patterns. Ecosphere. 2016;7(10). doi:10.1002/ecs2.1524.
6. Auffret AG, Aggemyr E, Plue J, Cousins SAO. Spatial scale and specialization affect how biogeography and functional traits predict long-term patterns of community turnover. Functional Ecology. 2017;31(2):436-43. doi:10.1111/1365-2435.12716.
7. Barnagaud JY, Papaix J, Gimenez O, Svenning JC. Dynamic spatial interactions between the native

invader Brown-headed Cowbird and its hosts. Diversity and Distributions. 2015;21(5):511-22. doi:10.1111/ddi.12275.

8. Bartlett MK, Zhang Y, Yang J, Kreidler N, Sun SW, Lin L et al. Drought tolerance as a driver of tropical forest assembly: resolving spatial signatures for multiple processes. Ecology. 2016;97(2):503-14. doi:10.1890/15-0468.1.

9. Bastos R, D'Amen M, Vicente J, Santos M, Yu HR, Eitelberg D et al. A multi-scale looping approach to predict spatially dynamic patterns of functional species richness in changing landscapes. Ecological Indicators. 2016;64:92-104. doi:10.1016/j.ecolind.2015.12.025.

10. Bauder JM, Castellano C, Jensen JB, Stevenson DJ, Jenkins CL. Comparison of Movements, Body Weight, and Habitat Selection Between Translocated and Resident Gopher Tortoises. Journal of Wildlife Management. 2014;78(8):1444-55. doi:10.1002/jwmg.790.

11. Bell DM, Bradford JB, Lauenroth WK. Scale dependence of disease impacts on quaking aspen (Populus tremuloides) mortality in the southwestern United States. Ecology. 2015;96(7):1835-45. doi:10.1890/14-1184.1.

12. Belmaker J, Jetz W. Spatial Scaling of Functional Structure in Bird and Mammal Assemblages. American Naturalist. 2013;181(4):464-78. doi:10.1086/669906.

13. Bino G, Ramp D, Kingsford RT. Niche evolution in Australian terrestrial mammals? Clarifying scale-dependencies in phylogenetic and functional drivers of co-occurrence. Evolutionary Ecology. 2013;27(6):1159-73. doi:10.1007/s10682-013-9631-5.

14. Boiffin J, Aubin I, Munson AD. Ecological controls on post-fire vegetation assembly at multiple spatial scales in eastern North American boreal forests. Journal of Vegetation Science. 2015;26(2):360-72. doi:10.1111/jvs.12245.

15. Bourgeois B, Gonzalez E, Vanasse A, Aubin I, Poulin M. Spatial processes structuring riparian plant communities in agroecosystems: implications for restoration. Ecological Applications. 2016;26(7):2103-15. doi:10.1890/15-1368.1.

16. Brice MH, Pellerin S, Poulin M. Environmental filtering and spatial processes in urban riparian forests. Journal of Vegetation Science. 2016;27(5):1023-35. doi:10.1111/jvs.12425.

17. Brun P, Payne MR, Kiorboe T. Trait biogeography of marine copepods - an analysis across scales. Ecology Letters. 2016;19(12):1403-13. doi:10.1111/ele.12688.

18. Burbrink FT, Myers EA. Body size distributions at community, regional or taxonomic scales do not predict the direction of trait-driven diversification in snakes in the United States. Global Ecology and Biogeography. 2014;23(4):490-503. doi:10.1111/geb.12139.

19. Campbell DR, Bischoff M, Lord JM, Robertson AW. Where have all the blue flowers gone: pollinator responses and selection on flower colour in New Zealand Wahlenbergia albomarginata. Journal of Evolutionary Biology. 2012;25(2):352-64. doi:10.1111/j.1420-9101.2011.02430.x.

20. Carmona CP, Azcarate FM, de Bello F, Ollero HS, Leps J, Peco B. Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall.

Journal of Applied Ecology. 2012;49(5):1084-93. doi:10.1111/j.1365-2664.2012.02193.x.

21. Chalmandrier L, Münkemüller T, Colace MP, Renaud J, Aubert S, Carlson BZ et al. Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. Journal of Ecology. 2017;105(1):277-87. doi:10.1111/1365-2745.12658.

22. Chalmandrier L, Munkemuller T, Gallien L, de Bello F, Mazel F, Lavergne S et al. A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns. Journal of Vegetation Science. 2013;24(5):853-64. doi:10.1111/jvs.12031.

23. Coetzee BWT, le Roux PC, Chown SL. Scale effects on the body size frequency distributions of African birds: patterns and potential mechanisms. Global Ecology and Biogeography. 2013;22(4):380-90. doi:10.1111/j.1466-8238.2012.00793.x.

24. Cohen M, Bilodeau C, Alexandre F, Godron M, Andrieu J, Gresillon E et al. What is the plant biodiversity in a cultural landscape? A comparative, multi-scale and interdisciplinary study in olive groves and vineyards (Mediterranean France). Agriculture Ecosystems & Environment. 2015;212:175-86. doi:10.1016/j.agee.2015.06.023.

25. Colzani E, Siqueira T, Suriano MT, Roque FO. Responses of Aquatic Insect Functional Diversity to Landscape Changes in Atlantic Forest. Biotropica. 2013;45(3):343-50. doi:10.1111/btp.12022.

26. Concepcion ED, Moretti M, Altermatt F, Nobis MP, Obrist MK. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos. 2015;124(12):1571-82. doi:10.1111/oik.02166.

27. Concostrina-Zubiri L, Pescador DS, Martinez I, Escudero A. Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. Biodiversity and Conservation. 2014;23(7):1757-70. doi:10.1007/s10531-014-0683-9.

28. Craven D, Filotas E, Angers VA, Messier C. Evaluating resilience of tree communities in fragmented landscapes: linking functional response diversity with landscape connectivity. Diversity and Distributions. 2016;22(5):505-18. doi:10.1111/ddi.12423.

29. da Silva PM, Berg MP, Serrano ARM, Dubs F, Sousa JP. Environmental factors at different spatial scales governing soil fauna community patterns in fragmented forests. Landscape Ecology. 2012;27(9):1337-49. doi:10.1007/s10980-012-9788-2.

30. Dahirel M, Seguret A, Ansart A, Madec L. Dispersal-related traits of the snail Cornu aspersum along an urbanisation gradient: maintenance of mobility across life stages despite high costs. Urban Ecosystems. 2016;19(4):1847-59. doi:10.1007/s11252-016-0564-y.

31. de Bello F, Lavorel S, Lavergne S, Albert CH, Boulangeat I, Mazel F et al. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography. 2013;36(3):393-402. doi:10.1111/j.1600-0587.2012.07438.x.

32. De Bello F, Vandewalle M, Reitalu T, Lepš J, Prentice HC, Lavorel S et al. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. Journal of Ecology. 2013;101(5):1237-44. doi:10.1111/1365-2745.12139.

33. Dehling DM, Topfer T, Schaefer HM, Jordano P, Bohning-Gaese K, Schleuning M. Functional relationships beyond species richness patterns: trait matching in plant-bird mutualisms across scales. Global Ecology and Biogeography. 2014;23(10):1085-93. doi:10.1111/geb.12193.

34. Donadi S, van Der Heide T, Piersma T, van Der Zee EM, Weerman EJ, van de Koppel J et al. Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. Oikos. 2015;124(11):1502-10. doi:10.1111/oik.02100.

35. Dunck B, Algarte VM, Cianciaruso MV, Rodrigues L. Functional diversity and trait-environment relationships of periphytic algae in subtropical floodplain lakes. Ecological Indicators. 2016;67:257-66. doi:10.1016/j.ecolind.2016.02.060.

36. Emerson SE, Brown JS, Whelan CJ, Schmidt KA. Scale-dependent neighborhood effects: shared doom and associational refuge. Oecologia. 2012;168(3):659-70. doi:10.1007/s00442-011-2144-4.

37. Fiser Z, Altermatt F, Zaksek V, Knapic T, Fiser C. Morphologically Cryptic Amphipod Species Are "Ecological Clones" at Regional but Not at Local Scale: A Case Study of Four Niphargus Species. Plos One. 2015;10(7). doi:10.1371/journal.pone.0134384.

38. Frye GG, Connelly JW, Musil DD, Forbey JS. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology. 2013;94(2):308-14.

39. Fu H, Yuan GX, Zhong JY, Cao T, Ni LY, Xie P. Environmental and Ontogenetic Effects on Intraspecific Trait Variation of a Macrophyte Species across Five Ecological Scales. Plos One. 2013;8(4). doi:10.1371/journal.pone.0062794.

40. Geheber AD, Geheber PK. The effect of spatial scale on relative influences of assembly processes in temperate stream fish assemblages. Ecology. 2016;97(10):2691-704. doi:10.1002/ecy.1503.

41. Gilroy JJ, Uribe CAM, Haugaasen T, Edwards DP. Effect of scale on trait predictors of species responses to agriculture. Conservation Biology. 2015;29(2):463-72. doi:10.1111/cobi.12422.

42. Gothe E, Angeler DG, Sandin L. Metacommunity structure in a small boreal stream network. Journal of Animal Ecology. 2013;82(2):449-58. doi:10.1111/1365-2656.12004.

43. Green SJ, Côté IM. Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. Journal of Animal Ecology. 2014;83(6):1451-60. doi:10.1111/1365-2656.12250.

44. Gross N, Börger L, Soriano-Morales SI, Le Bagousse-Pinguet Y, Quero JL, García-Gómez M et al. Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. Journal of Ecology. 2013;101(3):637-49. doi:10.1111/1365-2745.12063.

45. Gunton RM, Poyry J. Scale-specific spatial density dependence in parasitoids: a multi-factor meta-analysis. Functional Ecology. 2016;30(9):1501-10. doi:10.1111/1365-2435.12627.

46. Hamann E, Kesselring H, Armbruster GFJ, Scheepens JF, Stocklin J. Evidence of local adaptation to fine- and coarse-grained environmental variability in Poa alpina in the Swiss Alps. Journal of Ecology. 2016;104(6):1627-37. doi:10.1111/1365-2745.12628.

47. Harmon-Threatt AN, Ackerly DD. Filtering across Spatial Scales: Phylogeny, Biogeography and

Community Structure in Bumble Bees. Plos One. 2013;8(3). doi:10.1371/journal.pone.0060446.

48. Heap SM, Stuart-Fox D, Byrne PG. Reduction in site fidelity with smaller spatial scale may suggest scale-dependent information use. Behavioral Ecology. 2015;26(2):543-9. doi:10.1093/beheco/aru230.

49. Henry LA, Navas JM, Roberts JM. Multi-scale interactions between local hydrography, seabed topography, and community assembly on cold-water coral reefs. Biogeosciences. 2013;10(4):2737-46. doi:10.5194/bg-10-2737-2013.

50. Hitt NP, Roberts JH. Hierarchical spatial structure of stream fish colonization and extinction. Oikos. 2012;121(1):127-37. doi:10.1111/j.1600-0706.2011.19482.x.

51. Hough-Snee N, Laub BG, Merritt DM, Long AL, Nackley LL, Roper BB et al. Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds. Ecosphere. 2015;6(10). doi:10.1890/es15-00064.1.

52. Izen R, Stuart YE, Jiang YX, Bolnick DI. Coarse- and fine-grained phenotypic divergence among threespine stickleback from alternating lake and stream habitats. Evolutionary Ecology Research. 2016;17(3):437-57.

53. Kaiser A, Merckx T, Van Dyck H. The Urban Heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. Ecology and Evolution. 2016;6(12):4129-40. doi:10.1002/ece3.2166.

54. Kang M, Chang SX, Yan ER, Wang XH. Trait variability differs between leaf and wood tissues across ecological scales in subtropical forests. Journal of Vegetation Science. 2014;25(3):703-14. doi:10.1111/jvs.12118.

55. Kazakou E, Violle C, Roumet C, Navas ML, Vile D, Kattge J et al. Are trait-based species rankings consistent across data sets and spatial scales? Journal of Vegetation Science. 2014;25(1):235-47. doi:10.1111/jvs.12066.

56. Khimoun A, Eraud C, Ollivier A, Arnoux E, Rocheteau V, Bely M et al. Habitat specialization predicts genetic response to fragmentation in tropical birds. Molecular Ecology. 2016;25(16):3831-44. doi:10.1111/mec.13733.

57. Korallo-Vinarskaya NP, Vinarski MV, Khokhlova IS, Krasnov BR. Body size and coexistence in gamasid mites parasitic on small mammals: null model analyses at three hierarchical scales. Ecography. 2013;36(4):508-17. doi:10.1111/j.1600-0587.2012.07779.x.

58. Koyanagi T, Kusumoto Y, Yamamoto S, Okubo S, Iwasaki N, Takeuchi K. Grassland plant functional groups exhibit distinct time-lags in response to historical landscape change. Plant Ecology. 2012;213(2):327-38. doi:10.1007/s11258-011-9979-y.

59. Krasnov BR, Shenbrot GI, Khokhlova IS, Stanko M, Morand S, Mouillot D. Assembly rules of ectoparasite communities across scales: combining patterns of abiotic factors, host composition, geographic space, phylogeny and traits. Ecography. 2015;38(2):184-97. doi:10.1111/ecog.00915.

60. Laliberte E, Norton DA, Scott D. Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. Journal of Vegetation Science. 2013;24(5):834-

. doi:10.1111/jvs.12044.

61. Larsen S, Ormerod SJ. Anthropogenic modification disrupts species co-occurrence in stream invertebrates. Global Change Biology. 2014;20(1):51-60. doi:10.1111/gcb.12355.

62. Lauterbach D, Romermann C, Jeltsch F, Ristow M. Factors driving plant rarity in dry grasslands on different spatial scales: a functional trait approach. Biodiversity and Conservation. 2013;22(10):2337-52. doi:10.1007/s10531-013-0455-y.

63. Liu JJ, Wu DY, Peng XY, Zhou SR, Bradshaw CJA. Exogenous and endogenous determinants of spatial aggregation patterns in Tibetan Plateau meadow vegetation. Journal of Plant Ecology. 2013;6(4):277-85. doi:10.1093/jpe/rts041.

64. Luza AL, Goncalves GL, Hartz SM. Phylogenetic and morphological relationships between nonvolant small mammals reveal assembly processes at different spatial scales. Ecology and Evolution. 2015;5(4):889-902. doi:10.1002/ece3.1407.

65. Maciejewski K, Cumming GS. Multi-scale network analysis shows scale-dependency of significance of individual protected areas for connectivity. Landscape Ecology. 2016;31(4):761-74. doi:10.1007/s10980-015-0285-2.

66. Marini L, Ockinger E, Battisti A, Bommarco R. High mobility reduces beta-diversity among orthopteran communities - implications for conservation. Insect Conservation and Diversity. 2012;5(1):37-45. doi:10.1111/j.1752-4598.2011.00152.x.

67. Marsh DM, Cosentino BJ, Jones KS, Apodaca JJ, Beard KH, Bell JM et al. Effects of roads and land use on frog distributions across spatial scales and regions in the Eastern and Central United States. Diversity and Distributions. 2017;23(2):158-70. doi:10.1111/ddi.12516.

68. Martin AR, Rapidel B, Roupsard O, Van den Meersche K, Virginio ED, Barrios M et al. Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. Functional Ecology. 2017;31(3):604-12. doi:10.1111/1365-2435.12790.

69. Moran-Ordonez A, Pavlova A, Pinder AM, Sim L, Sunnucks P, Thompson RM et al. Aquatic communities in arid landscapes: local conditions, dispersal traits and landscape configuration determine local biodiversity. Diversity and Distributions. 2015;21(10):1230-41. doi:10.1111/ddi.12342.

70. Morante JC, Arroyo-Rodriguez V, Faria D. Patterns and predictors of beta-diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. Journal of Animal Ecology. 2016;85(1):240-50. doi:10.1111/1365-2656.12448.

71. Mouchet MA, Burns MDM, Garcia AM, Vieira JP, Mouillot D. Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): environmental filtering consistently overshadows competitive exclusion. Oikos. 2013;122(2):247-57. doi:10.1111/j.1600-0706.2012.20411.x.

72. Nash KL, Graham NAJ, Jennings S, Wilson SK, Bellwood DR. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. Journal of Applied Ecology. 2016;53(3):646-55. doi:10.1111/1365-2664.12430.

73. Nichols E, Uriarte M, Bunker DE, Favila ME, Slade EM, Vulinec K et al. Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. Ecology. 2013;94(1):180-9.

74. Pardo I, Roquet C, Lavergne S, Olesen JM, Gomez D, Garcia MB. Spatial congruence between taxonomic, phylogenetic and functional hotspots: true pattern or methodological artefact? Diversity and Distributions. 2017;23(2):209-20. doi:10.1111/ddi.12511.

75. Pavoine S, Vela E, Gachet S, de Belair G, Bonsall MB. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. Journal of Ecology. 2011;99(1):165-75. doi:10.1111/j.1365-2745.2010.01743.x.

76. Penone C, Kerbiriou C, Julien JF, Julliard R, Machon N, Le Viol I. Urbanisation effect on Orthoptera: which scale matters? Insect Conservation and Diversity. 2013;6(3):319-27. doi:10.1111/j.1752-4598.2012.00217.x.

77. Peringer A, Schulze KA, Stupariu I, Stupariu MS, Rosenthal G, Buttler A et al. Multi-scale feedbacks between tree regeneration traits and herbivore behavior explain the structure of pasture-woodland mosaics. Landscape Ecology. 2016;31(4):913-27. doi:10.1007/s10980-015-0308-z.

78. Perovic D, Gamez-Virues S, Borschig C, Klein AM, Krauss J, Steckel J et al. Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. Journal of Applied Ecology. 2015;52(2):505-13. doi:10.1111/1365-2664.12394.

79. Petit S, Fried G. Patterns of weed co-occurrence at the field and landscape level. Journal of Vegetation Science. 2012;23(6):1137-47. doi:10.1111/j.1654-1103.2012.01421.x.

80. Rejou-Mechain M, Flores O, Bourland N, Doucet JL, Feteke RF, Pasquier A et al. Spatial aggregation of tropical trees at multiple spatial scales. Journal of Ecology. 2011;99(6):1373-81. doi:10.1111/j.1365-2745.2011.01873.x.

81. Ryder JJ, Pastok D, Hoare MJ, Bottery MJ, Boots M, Knell RK et al. Spatial variation in food supply, mating behavior, and sexually transmitted disease epidemics. Behavioral Ecology. 2013;24(3):723-9. doi:10.1093/beheco/ars209.

82. Saito VS, Cianciaruso MV, Siqueira T, Fonseca-Gessner AA, Pavoine S. Phylogenies and traits provide distinct insights about the historical and contemporary assembly of aquatic insect communities. Ecology and Evolution. 2016;6(9):2925-37. doi:10.1002/ece3.2081.

83. Siefert A. Spatial patterns of functional divergence in old-field plant communities. Oikos. 2012;121(6):907-14. doi:10.1111/j.1600-0706.2011.19706.x.

84. Smith AB, Sandel B, Kraft NJB, Carey S. Characterizing scale-dependent community assembly using the functional-diversity-area relationship. Ecology. 2013;94(11):2392-402. doi:10.1890/12-2109.1.

85. Sobral FL, Cianciaruso MV. Functional and phylogenetic structure of forest and savanna bird assemblages across spatial scales. Ecography. 2016;39(6):533-41. doi:10.1111/ecog.00903.

86. Spasojevic MJ, Turner BL, Myers JA. When does intraspecific trait variation contribute to

functional beta-diversity? Journal of Ecology. 2016;104(2):487-96. doi:10.1111/1365-2745.12518.

87. Sutherland C, Elston DA, Lambin X. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology. 2012;93(11):2465-73.

88. Tan CH, Pratchett MS, Bay LK, Graham EM, Baird AH. Spatial and temporal variation in fecundity among populations of Acropora millepora on the Great Barrier Reef. Marine Ecology Progress Series. 2016;561:147-53. doi:10.3354/meps11936.

89. Tilley A, Lopez-Angarita J, Turner JR. Effects of scale and habitat distribution on the movement of the southern stingray Dasyatis americana on a Caribbean atoll. Marine Ecology Progress Series. 2013;482:169-79. doi:10.3354/meps10285.

90. Trisos CH, Petchey OL, Tobias JA. Unraveling the Interplay of Community Assembly Processes Acting on Multiple Niche Axes across Spatial Scales. American Naturalist. 2014;184(5):593-608. doi:10.1086/678233.

91. Troia MJ, Gido KB. Functional strategies drive community assembly of stream fishes along environmental gradients and across spatial scales. Oecologia. 2015;177(2):545-59. doi:10.1007/s00442-014-3178-1.

92. Van Looy K, Piffady J, Floury M. At what scale and extent environmental gradients and climatic changes influence stream invertebrate communities? Science of the Total Environment. 2017;580:34-42. doi:10.1016/j.scitotenv.2016.12.009.

93. van Moorter B, Bunnefeld N, Panzacchi M, Rolandsen CM, Solberg EJ, Saether BE. Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology. 2013;82(4):770-80. doi:10.1111/1365-2656.12045.

94. Vergara PM, Saura S, Perez-Hernandez CG, Soto GE. Hierarchical spatial decisions in fragmented landscapes: Modeling the foraging movements of woodpeckers. Ecological Modelling. 2015;300:114-22. doi:10.1016/j.ecolmodel.2015.01.006.

95. Vergara PM, Soto GE, Moreira-Arce D, Rodewald AD, Meneses LO, Perez-Hernandez CG. Foraging Behaviour in Magellanic Woodpeckers Is Consistent with a Multi-Scale Assessment of Tree Quality. Plos One. 2016;11(7). doi:10.1371/journal.pone.0159096.

96. Villalobos F, Arita HT. Morphological diversity at different spatial scales in a Neotropical bat assemblage. Oecologia. 2014;176(2):557-68. doi:10.1007/s00442-014-3039-y.

97. Wilson JB, Stubbs WJ. Evidence for assembly rules: limiting similarity within a saltmarsh. Journal of Ecology. 2012;100(1):210-21. doi:10.1111/j.1365-2745.2011.01891.x.

98. Wilson MJ, McTammany ME. Spatial scale and dispersal influence metacommunity dynamics of benthic invertebrates in a large river. Freshwater Science. 2016;35(2):738-47. doi:10.1086/685732.

99. Yang J, Zhang GC, Ci XQ, Swenson NG, Cao M, Sha LQ et al. Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. Functional Ecology. 2014;28(2):520-9.

100. Yuan ZQ, Gazol A, Lin F, Wang XG, Ye J, Suo YY et al. Scale-dependent effect of biotic

interactions and environmental conditions in community assembly: insight from a large temperate forest plot. Plant Ecology. 2016;217(8):1003-14. doi:10.1007/s11258-016-0626-5.

101. Zimmermann B, Nelson L, Wabakken P, Sand H, Liberg O. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behavioral Ecology. 2014;25(6):1353-64. doi:10.1093/beheco/aru134.

APPENDIX C

Table C1: Values of the Spearman correlation test for the traits selected in this study

	Body mass (g)	**Clutch size**	**Habitat specialization**	**Dispersal**
Body.mass	1	0.21	-0.12	0.31
Clutch.size.y	0.21	1	-0.1	-0.24
Habitat_Plasticity	-0.12	-0.1	1	0.56
dispersal	0.31	-0.24	0.56	1

Table C2: Values of the Spearman correlation test environmental variables used as predictors in this study

	% Tree cover	**Built infrastructure**	**Clumpiness**	**Vertical structure**
% Tree cover	1	-0.6	-0.42	0.71
Built infrastructure	-0.6	1	0.34	0.6
Clumpiness	-0.42	0.34	1	0.39
Vertical structure	0.71	0.6	0.39	1

Table C3: Trait values for bird species recorded in Brisbane during 2016 that were taken into account in the statistical analysis of this thesis

Species	Common name	Diet	Foraging strata	Body mass (g)	Clutch size	Habitat plasticity	Diet Plasticity	Foraging behaviour plasticity
Acanthiza nana	Yellow thornbill	Invertebrate	Tree/shrub	6.19	3.1	39	8	11
Acanthiza pusilla	Brown thronbill	Invertebrate	Tree/shrub	7.62	2.9	42	14	13
Acanthorhynchus tenuirostris	Eastern spinbell	Omnivore	Tree/shrub	16.00	2.2	42	8	9
Acridotheres tristis	Common myna	Omnivore	Ground	116.43	4	17	27	16
Acrocephalus australis	Australian Reed-Warbler	Invertebrate	Ground	24.80	3.1	31	8	15
Alectura lathami	Australian Brush turkey	Plant/Seed	Ground	2333.06	22	14	23	5
Alisterus scapularis	Australian King Parrot	Plant/Seed	Tree/shrub	232.26	4.5	29	20	15
Anthochaera chrysoptera	Little wattlebird	Fruits/Nectar	Tree/shrub	67.80	1.7	37	15	14
Cacatua galerita	Sulphur crested cockatoo	Plant/Seed	Ground	720.43	2.5	47	17	13
Cacatua sanguinea	Little corella	Plant/Seed	Ground	523.69	2.6	27	13	9
Cacomantis flabelliformis	Fan tailed cuckoo	Invertebrate	Ground	49.80	1.1	38	5	12
Chrysococcyx basalis	Horsfield's Bronze-Cuckoo	Invertebrate	Tree/shrub	23.12	1	45	11	5
Cisticola exilis	Golden headed cisticola	Invertebrate	Tree/shrub	7.80	3.6	43	8	5
Climacteris picumnus	Brown treecreper	Invertebrate	Tree/shrub	28.94	2.7	36	10	14
Colluricincla harmonica	Grey shrike thrush	Invertebrate	Tree/shrub	65.80	2.9	45	18	15
Colluricincla megarhyncha	Little shrike thrush	Invertebrate	Tree/shrub	32.34	2.4	17	12	9
Columba livia	Rock dove	Plant/Seed	Ground	354.20	1.8	20	12	10
Coracina novaehollandiae	Black faced cuckoshrike	Omnivore	Tree/shrub	118.00	2.5	45	14	18
Cormobates leucophaea	White throated treecreper	Invertebrate	Tree/shrub	22.00	2.5	28	10	13
Corvus orru	Torresian crow	Omnivore	Ground	507.96	4.6	22	25	8
Cracticus nigrogularis	Pied butcherbird	Omnivore	Ground	128.00	2.8	42	26	11
Cracticus tibicen	Australian Magpie	Invertebrate	Ground	284.87	3.3	50	26	20
Cracticus torquatus	Grey butcherbird	Omnivore	Tree/shrub	82.88	3.2	46	18	10
Dacelo novaeguinae	Laughing kookaburra	Invertebrate	Ground	333.80	3	34	10	14
Dicaeum hirundinaceum	Mistletoebird	Fruits/Nectar	Tree/shrub	12.00	2.7	31	13	9
Dicrurus bracteatus	Spangled drongo	Invertebrate	Tree/shrub	85.53	3.4	19	17	9

Elanus axillaris	Black shouldered kite	VertFishScav	Tree/shrub	270.10	3.4	43	9	24
Entomyzon cyanotis	Blue faced honeyeater	Invertebrate	Tree/shrub	105.26	2.6	33	13	16
Eolophus roseicapilla	Galah	Plant/Seed	Ground	325.33	4.5	35	17	11
Eopsaltria australis	Eastern yellow robin	Invertebrate	Tree/shrub	20.15	2.3	34	11	13
Eurystomus orientalis	Dollarbird	Invertebrate	Tree/shrub	143.02	3.5	26	5	10
Geopelia humeralis	Bar shouldered dove	Plant/Seed	Ground	128.42	2	15	8	5
Gerygone levigaster	Mangrove gerygone	Invertebrate	Tree/shrub	6.20	2.8	13	5	9
Gerygone olivacea	White throated gerygone	Invertebrate	Tree/shrub	6.72	2.8	37	5	10
Glossopsitta pusilla	Little lorikeet	Fruits/Nectar	Tree/shrub	39.40	4	31	10	8
Grallina cyanoleuca	Magpie-lark	Invertebrate	Ground	82.57	3.8	50	11	14
Hirundo neoxena	Welcome swallow	Invertebrate	Tree/shrub	14.70	3.8	55	5	16
Lichenostomus chrysops	Yellow faced honeyeater	Fruits/Nectar	Tree/shrub	17.30	2.4	36	20	10
Lichmera indistincta	Brown honeyeater	Fruits/Nectar	Tree/shrub	11.18	1.9	19	10	10
Lonchura castaneothorax	Chesnut breasted manikin	Plant/Seed	Ground	11.00	5	14	8	10
Malurus cyaneus	Superb fairy wren	Invertebrate	Ground	10.00	7.3	44	17	16
Malurus lamberti	Variegated fairy wren	Invertebrate	Tree/shrub	8.04	2.9	31	8	10
Malurus melanocephalus	Red backed fairy wren	Invertebrate	Tree/shrub	7.90	2.4	18	5	11
Manorina melanocephala	Noisy miner	Omnivore	Tree/shrub	60.22	2.8	34	18	14
Megalurus timoriensis	Tawny grassbird	Invertebrate	Ground	37.50	3.2	17	7	5
Meliphaga lewinii	Lewins honeyeater	Fruits/Nectar	Tree/shrub	33.58	2.2	31	16	15
Melithreptus albogularis	White throated honeyeater	Invertebrate	Tree/shrub	14.01	2	14	10	12
Merops ornatus	Rainbow bee eater	Invertebrate	Tree/shrub	29.50	4.7	42	5	13
Monarcha melanopsis	Black faced monarch	Invertebrate	Tree/shrub	22.70	2.3	22	5	9
Myiagra inquieta	Restless flycatcher	Invertebrate	Tree/shrub	20.90	3.3	26	5	15
Myiagra rubecula	Leaden flycatcher	Invertebrate	Tree/shrub	12.05	1.9	29	7	13
Myzomela sanguinolenta	Scarlet honeyeater	Fruits/Nectar	Tree/shrub	8.34	2	15	9	11
Neochmia temporalis	Red browed finch	Omnivore	Tree/shrub	11.00	5.2	48	13	12
Ocyphaps lophotes	Crested pigeon	Plant/Seed	Ground	204.00	2	32	13	5
Oriolus sagittatus	Olive backed oriole	Fruits/Nectar	Tree/shrub	95.20	2.2	30	20	13
Pachycephala pectoralis	Golden whistler	Invertebrate	Tree/shrub	30.36	2.2	43	10	19

Pachycephala rufiventris	Rufous whistler	Invertebrate	Tree/shrub	22.48	2.6	42	14	15
Pardalotus punctuatus	Spotted pardalote	Invertebrate	Tree/shrub	8.70	3.1	45	9	13
Pardalotus striatus	Striated pardalote	Invertebrate	Tree/shrub	11.44	3.8	41	13	13
Petrochelidon ariel	Fairy martin	Invertebrate	Tree/shrub	10.84	3.5	39	5	10
Petroica rosea	Rose robin	Invertebrate	Tree/shrub	8.20	3	22	5	16
Philemon citreogularis	Little friabird	Omnivore	Tree/shrub	60.56	2.4	26	16	12
Philemon corniculatus	Noisy friabird	Omnivore	Tree/shrub	100.71	3	35	22	10
Platycercus adscitus	Pale headed rosella	Plant/Seed	Tree/shrub	111.00	6	18	18	5
Platycercus elegans	Crimson rosella	Plant/Seed	Tree/shrub	123.86	4.4	35	21	7
Plectorhyncha lanceolata	Stripped honeyeater	Fruits/Nectar	Tree/shrub	40.56	3	33	17	13
Psophodes olivaceus	Eastern whipbird	Invertebrate	Tree/shrub	62.36	2	32	11	10
Rhipidura albiscapa	Grey fantail	Invertebrate	Tree/shrub	7.80	1.9	45	13	15
Rhipidura leucophrys	Willie wagtail	Invertebrate	Tree/shrub	20.70	3	47	8	23
Rhipidura rufifrons	Rufous fantail	Invertebrate	Tree/shrub	NA	1.9	34	5	19
Scythrops novaehollandiae	Channel billed cuckoo	Fruits/Nectar	Tree/shrub	683.99	3	13	11	8
Sericornis frontalis	White browed scrub wren	Invertebrate	Ground	13.23	2.1	44	13	11
Sphecotheres vieilloti	Australasian figbird	Fruits/Nectar	Tree/shrub	108.00	2.7	24	17	10
Strepera graculina	Pied currawong	Omnivore	Tree/shrub	298.86	3.1	31	24	22
Streptopelia chinensis	Spotted dove	Plant/Seed	Ground	159.00	1.9	15	9	5
Taeniopygia bichenovii	Double-barred Finch	Invertebrate	Ground	10.00	4.3	21	9	5
Threskiornis molucca	Australian ibis	Omnivore	Tree/shrub	1794.89	3	29	14	10
Todiramphus sanctus	Sacred kingfisher	Invertebrate	Ground	52.96	4.3	28	9	21
Trichoglossus chlorolepidotus	Scaly breasted lorikeet	Fruits/Nectar	Tree/shrub	87.10	2.9	14	16	5
Trichoglossus haematodus	Rainbow lorikeet	Fruits/Nectar	Tree/shrub	113.25	2	44	19	9
Vanellus miles	Masked lapwing	Invertebrate	Ground	387.00	3.5	42	14	20
Zosterops lateralis	Silvereye	Omnivore	Tree/shrub	11.00	2.6	49	24	20

Table C4: Groups used to calculate average density estimates in Brisbane for birds recorded in this project during 2016. The model with the lowest AIC and the coefficient of variation (CV) is shown. Potential covariates were season (s) and percentage of tree cover (t); hn = half detection function. The model with the lowest AIC shows the variable (in brackets) that accounted for variation in detection probability.

			Number of counts					
Group characteristics	**Species**	**Common name**	**Summer**	**Winter**	**Total**	**Models with lowest AIC**	**Density (ha)**	**CV**
Invertebrates; Tree/Shrub < 10 g	*Acanthiza nana*	Yellow thornbill	0	3	3	hn (s)	0.03	1.97
	Gerygone levigaster	Mangrove gerygone	6	8	14	hn (s)	0.14	1.97
	Gerygone olivacea	White throated gerygone	1	6	7	hn (s)	0.07	1.97
	Acanthiza pusilla	Brown thronbill	4	8	12	hn (s)	0.12	1.97
	Rhipidura albiscapa	Grey fantail	5	38	43	hn (s)	0.43	1.97
	Petroica rosea	Rose robin	0	4	4	hn (s)	0.04	1.97
	Pardalotus punctuatus	Spotted pardalote	0	11	11	hn (s)	0.11	1.97
	Zosterops lateralis	Silvereye	6	16	22	hn (s)	0.22	1.97
	Eopsaltria australis	Eastern yellow robin	18	17	35	hn (s)	0.35	1.97
	Rhipidura rufifrons	Rufous fantail	4	7	11	hn (s)	0.11	1.97
Fruit/Nectar; Tree/Shrub; 12-18 g	*Dicaeum hirundinaceum*	Mistletoebird	4	18	22	hn (s)	0.22	2.94
	Melithreptus albogularis	White throated honeyeater	22	18	40	hn (s)	0.4	2.94
	Acanthorhynchus tenuirostris	Eastern spinbell	3	8	11	hn (s)	0.11	2.94
	Lichenostomus chrysops	Yellow faced honeyeater	7	52	59	hn (s)	0.59	2.94
Omnivore; Tree/Shrub/80 - 120 g	*Entomyzon cyanotis*	Blue faced honeyeater	16	9	25	hn (t+s)	0.25	0.03
	Manorina melanocephala	Noisy miner	311	199	510	hn (t+s)	5.1	0.03
	Acridotheres tristis	Common myna	17	6	23	hn (t+s)	0.23	0.03
Invertebrates; Ground; <10 g	*Cisticola exilis*	Golden headed cisticola	2	7	9	hn (t)	0.09	0.17
	Malurus melanocephalus	Red backed fairy wren	20	14	34	hn (t)	0.34	0.17

	Malurus lamberti	Variegated fairy wren	12	7	19	hn (t)	0.19	0.17
	Malurus cyaneus	Superb fairy wren	29	28	57	hn (t)	0.57	0.17
	Sericornis frontalis	White browed scrub wren	8	12	20	hn (t)	0.2	0.17
Plant/Seed; Tree/Shrub; > 120 g	*Platycercus adscitus*	Pale headed rosella	12	8	20	hn (s)	0.2	1.64
	Platycercus elegans	Crimson rosella	0	3	3	hn (s)	0.03	1.64
	Alisterus scapularis	Australian King Parrot	11	4	15	hn (s)	0.15	1.64
	Eolophus roseicapilla	Galah	8	3	11	hn (s)	0.11	1.64
	Cacatua sanguinea	Little corella	8	6	14	hn (s)	0.14	1.64
Plant/Seed; Ground; > 120 g	*Geopelia humeralis*	Bar shouldered dove	13	10	23	hn (t+s)	0.23	1.43
	Streptopelia chinensis	Spotted dove	34	8	42	hn (s)	0.42	1.43
	Columba livia	Rock dove	6	0	6	hn (s)	0.06	1.43
	Ocyphaps lophotes	Crested pigeon	29	38	67	hn (s)	0.67	1.43
Finches; Ground; <10 g	*Taeniopygia bichenovii*	Double-barred Finch	4	2	6	hn (t)	0.06	4.20
	Neochmia temporalis	Red browed finch	8	6	14	hn (t)	0.14	4.20
	Lonchura castaneothorax	Chesnut breasted manikin	0	3	3	hn (t)	0.03	4.20
Invertebrate; Tree/Shrub;10-20g	*Petrochelidon ariel*	Fairy martin	3	2	5	hn (t+s)	0.05	0.13
	Pardalotus striatus	Striated pardalote	48	58	106	hn (t+s)	1.06	0.13
	Myiagra rubecula	Leaden flycatcher	6	2	8	hn (t+s)	0.08	0.13
	Hirundo neoxena	Welcome swallow	15	10	25	hn (t+s)	0.25	0.13
	Myiagra inquieta	Restless flycatcher	0	2	2	hn (t+s)	0.02	0.13
Invertebrate; Ground/Shrub; >25 g	*Acrocephalus australis*	Australian Reed-Warbler	3	3	6	hn (t+s)	0.06	3.40
	Megalurus timoriensis	Tawny grassbird	4	8	12	hn (t+s)	0.12	3.40
Lorikeets	*Glossopsitta pusilla*	Little lorikeet	0	5	5	hn (t+s)	0.05	0.06
	Trichoglossus chlorolepidotus	scaly breasted lorikeet	25	26	51	hn (t+s)	0.51	0.06
	Trichoglossus haematodus	Rainbow lorikeet	221	134	355	hn (t+s)	3.55	0.06
Invertebrate;Tree/Shrub; > 24g	*Pachycephala rufiventris*	Rufous whistler	9	24	33	hn (t+s)	0.33	1.52
	Chrysococcyx basalis	Horsfield's Bronze-Cuckoo	0	2	2	hn (t+s)	0.02	1.52
	Climacteris picumnus	Brown treecreper	1	1	2	hn (t+s)	0.02	1.52

	Merops ornatus	Rainbow bee eater	11	7	18	hn (t+s)	0.18	1.52
	Pachycephala pectoralis	Golden whistler	0	15	15	hn (t+s)	0.15	1.52
	Colluricincla megarhyncha	Little shrike thrush	1	3	4	hn (t+s)	0.04	1.52
	Cormobates leucophaea	White throated treecreper	12	14	26	hn (t+s)	0.26	1.52
Fruit/Nectar; Tree/Shrub; >40 g < 100 g	*Plectorhyncha lanceolata*	Stripped honeyeater	5	1	6	hn (t+s)	0.06	0.11
	Cacomantis flabelliformis	Fan tailed cuckoo	3	7	10	hn (t+s)	0.1	0.11
	Oriolus sagittatus	Olive backed oriole	5	4	9	hn (t+s)	0.09	0.11
	Sphecotheres vieilloti	australasian figbird	33	11	44	hn (t+s)	0.44	0.11
Invertebrate; Tree/Shrub;60-90g	*Colluricincla harmonica*	Grey shrike thrush	8	9	17	hn (t)	0.17	1.98
	Dicrurus bracteatus	Spangled drongo	8	4	12	hn (t)	0.12	1.98
Single	*Myzomela sanguinolenta*	Scarlet honeyeater	0	64	64	hn (s)	0.64	0.06
	Lichmera indistincta	Brown honeyeater	49	83	132	hn (t+s)	1.32	0.09
	Rhipidura leucophrys	Willie wagtail	24	22	46	hn (t+s)	0.46	0.06
	Meliphaga lewinii	Lewins honeyeater	39	28	67	hn (t+s)	0.67	0.07
	Psophodes olivaceus	Eastern whipbird	18	10	28	hn (s)	0.28	0.05
	Grallina cyanoleuca	Magpie-lark	56	42	98	hn (s)	0.98	0.08
	Cracticus torquatus	Grey butcherbird	130	64	194	hn (t+s)	1.94	0.06
	Philemon corniculatus	Noisy friabird	14	25	39	hn (t+s)	0.39	0.05
	Coracina novaehollandiae	Black faced cuckoshrike	35	6	41	hn (s)	0.41	0.14
	Cracticus nigrogularis	Pied butcherbird	120	98	218	hn (s)	2.18	0.07
	Cracticus tibicen	Australian Magpie	104	69	173	hn (s)	1.73	0.08
	Dacelo novaeguinae	Laughing kookaburra	26	12	38	hn (s)	0.38	0.08
	Corvus orru	Torresian crow	185	140	325	hn (s)	3.25	0.04
	Cacatua galerita	Sulphur crested cockatoo	36	29	65	hn (s)	0.65	0.06
	Alectura lathami	Australian Brush turkey	15	24	39	hn (s)	0.39	0.19
	Strepera graculina	Pied currawong	28	19	47	hn (s)	0.47	0.07
	Vanellus miles	Masked lapwing	19	21	40	hn (t+s)	0.4	0.23
	Threskiornis molucca	Australian ibis	21	17	38	hn (s)	0.38	0.18

APPENDIX D

Script of the model used in chapter 4 to test the effects of fragmentation on functional diversity and species richness.

```
######Community model, effects of fragmentation on species richness and functional diversity####
##############################Andrés Felipe Suárez Castro#############################

scPATH="m:/Users/uqasuare/Desktop/CODE_FSC/CODE_COMMUNITIES_2017Aug.R"

source(scPATH)

library(plyr)
library(vegan)
library(FD)
library(BBmisc)
library(pracma)
library(gridExtra)
library(ggplot2)
library(snowfall)
library(CircStats)

#----------------------------------------------------------------------------------------#
#  CREATE COMMUNITIES BASED ON BETA DISTRIBUTIONS   #
#----------------------------------------------------------------------------------------#

####This is the list of parameters to create the communities###

#rep.cap = runif(0.1,0.9,0.5) #reproductive capacities. Three means of a beta distribution: 0.1 (low =high survival),0.5(medium = medium survival),0.8(high = low survival)
#Nicheopt = runif(0.1,0.9,0.5)     #Niche breadth. Two means of a beta distribution: 0.1 (specialists),0.5(generalists)
mean.op = c(0.5,0.5,0.5,0.5) # different mean values for niche optimum. These values will represent the mean for different communities
prec = c(2,2,2,2) # precision parameter to calculate the variance of the beta distribution, for fixed ?, the larger the value of the parameter, the smaller the variance of y.
Disp.cap = c(0.5, 0.5,0.5,0.5) #Dispersal capacity means. Mean of a beta distribution that will represent the rates of decay for a negative exponential distribution: 0.1 (HIGH dispersal capacity),0.5(MEDIUM dc), 0.8 (LOW dispersal capacity)
Dispcap.prec=c(5,5,5,5) #precision parameter for the beta distribution of dispersal capacity

####This is the list of parameters to create the landscapes###
```

```
p = c(1)          #amount of habitat for fractal landscapes
H.val = c(0.1,0.5,1)    #degrees of habitat clustering for habitat types. 1 = high spatial autocorrelation
of habitats.

####Combine the `parameters to generate the experimental design###

landscap.par<-expand.grid(H.val,p) #landscape parameters
exp.design <- data.frame(mean.op, prec,Disp.cap,Dispcap.prec)

#parallel setup to run multiple communities simultaneously
sfInit(parallel=TRUE,cpus=24)

#export data, functions and libraries to workers
sfExportAll()
sfClusterEval(library(plyr))
sfClusterEval(library(vegan))
sfClusterEval(library(FD))
sfClusterEval(library(BBmisc))
sfClusterEval(library(pracma))
sfClusterEval(library(snowfall))
sfClusterEval(library(CircStats))

#---------------------------------------------------------------------------------------#
#LOW FRAGMENTATION, HIGH DIVERGENCE IN RESPONSE TRAITS
#-------------------------------------------------------------------------------------##

allland<-generate.lands(landscap.par)

system.time(community_1<-generate.comms(exp.design,0.1,0.7,1000,150,10,allland[[2]],10,0.5,0.5))

#60% habitat lost
landscape<-generate.lands(landscap.par)
landscape_60_clustered<-habloss_biased(landscape[[2]],landscape[[3]],60)
community_1b_2Sep<-sfLapply(community_1,remove_cells,landscape_60_clustered)
system.time(sim_clustfrag_HD60_2Sep<-
sfLapply(community_1b_2Sep,comm.dynamics,600,landscape_60_clustered,10,60,0.5,0.5))
save(sim_clustfrag_HD60_2Sep,file="sim_clustfrag_HD60_2Sep.RData")
communityb_HD<-sim_clustfrag_HD60_2Sep[[1]][[1]]
rm(sim_clustfrag_HD60_2Sep)

#70% habitat lost
landscape<-generate.lands(landscap.par)
landscape_70_clustered<-habloss_biased(landscape[[2]],landscape[[3]],70)
community_1c_2Sep<-sfLapply(community_1,remove_cells,landscape_70_clustered)
system.time(sim_clustfrag_HD70_2Sep<-
sfLapply(community_1c_2Sep,comm.dynamics,600,landscape_70_clustered,10,70,0.5,0.5))
save(sim_clustfrag_HD70_2Sep,file="sim_clustfrag_HD70_2Sep.RData")
```

```
communityc_HD<-sim_clustfrag_HD70_2Sep[[1]][[1]]
rm(sim_clustfrag_HD70_2Sep)

#80% habitat lost
landscape<-generate.lands(landscap.par)
landscape_80_clustered<-habloss_biased(landscape[[2]],landscape[[3]],80)
community_1d_2Sep<-sfLapply(community_1,remove_cells,landscape_80_clustered)
system.time(sim_clustfrag_HD80_2Sep<-
sfLapply(community_1d_2Sep,comm.dynamics,600,landscape_80_clustered,10,80,0.5,0.5))
save(sim_clustfrag_HD80_2Sep,file="sim_clustfrag_HD80_2Sep.RData")
communityd_HD<-sim_clustfrag_HD80_2Sep[[1]][[1]]
rm(sim_clustfrag_HD80_2Sep)

#90% habitat lost
landscape<-generate.lands(landscap.par)
landscape_90_clustered<-habloss_biased(landscape[[2]],landscape[[3]],90)
community_1d_2Sep<-sfLapply(community_1,remove_cells,landscape_90_clustered)
system.time(sim_clustfrag_HD90_2Sep<-
sfLapply(community_1d_2Sep,comm.dynamics,600,landscape_90_clustered,10,90,0.5,0.5))
save(sim_clustfrag_HD90_2Sep,file="sim_clustfrag_HD90_2Sep.RData")
communitye_HD<-sim_clustfrag_HD90_2Sep[[1]][[1]]
rm(sim_clustfrag_HD90_2Sep)

simulation_HDCLUST_2Sep<-
rbind(communityb_HD,communityc_HD,communityd_HD,communitye_HD)

#------------------------------------------------------------#
# HIGH FRAGMENTATION, HIGH DIVERGENCE IN RESPONSE TRAITS
#------------------------------------------------------------##

system.time(community_1<-generate.comms(exp.design,0.1,0.7,1000,150,10,allland[[2]],10,0.5,0.5))

#60% habitat lost
landscape<-generate.lands(landscap.par)
landscape_60_unclustered<-habloss_random(landscape[[2]],60)
community_1b_2Sep<-sfLapply(community_1,remove_cells,landscape_60_unclustered)
system.time(sim_rand_HD60_2Sep<-
sfLapply(community_1b_2Sep,comm.dynamics,600,landscape_60_unclustered,10,60,0.5,0.5))
save(sim_rand_HD60_2Sep,file="sim_rand_HD60_2Sep.RData")
communityb_UHD<-sim_rand_HD60_2Sep[[1]][[1]]
rm(sim_rand_HD60_2Sep)

sfStop()
```

#Functions used in the code to generate the landscapes and simulate community dynamics

```
#-----------------------------------------------------------------------------#
#  CREATE COMMUNITIES BASED ON BETA DISTRIBUTIONS   #
#----------------------------------------------------------------------------#

#The following functions calculate all the parameters for the beta distribution
#calculate the trait value distribution for each community based on the mean of trait values
#Formula from #r is the Target (Spearman) correlation #n is the number of samples

beta_correlated <- function(exp.design, r1, r2, n){
 rho1 <- 2 * sin(r1 * pi/6)    # Pearson correlation
 rho2 <- 2 * sin(r2 * pi/6)    # Pearson correlation
 P <- toeplitz(c(1,rho1,rho2))# Correlation matrix
 d <- nrow(P)          # Dimension
 ## Generate sample
 U <- pnorm(matrix(rnorm(n*d), ncol = d) %*% chol(P))
 #niche_breadths
 alpha <- 1
 beta <- 1
 rep.cap<-c(1)

 x1_beta <- qbeta(U[,1], alpha, beta)
 x2_beta <- qbeta(U[,2], alpha, beta)
 x3_beta <- qbeta(U[,3], alpha, beta)

 Nbre<-expand.grid(x1_beta,rep.cap)
 Nbre_05<-expand.grid(x2_beta,rep.cap) # low correlation with effect traits
 Nbre_01<-expand.grid(x3_beta,rep.cap) # high correlation with effect traits

 #disp_capacity
 alpha_disp <- exp.design[[3]]
 beta_disp <- exp.design[[4]]

 x1_beta_disp <- qbeta(U[,1], alpha_disp, beta_disp)
 x2_beta_disp <- qbeta(U[,2], alpha_disp, beta_disp)
 x3_beta_disp <- qbeta(U[,3], alpha_disp, beta_disp)

 Disp_cap<-expand.grid(x1_beta_disp,rep.cap)
 Disp_cap_05<-expand.grid(x2_beta_disp,rep.cap)
 Disp_cap_01<-expand.grid(x3_beta_disp,rep.cap)

 Nicheopt<-runif(n)
 Surv<-0.5
 df<-
data.frame(Nicheopt,Nbre[,2],Nbre[,1],Disp_cap[,1],Surv,Nbre_01[,1],Nbre_05[,1],Disp_cap_01[,1],
Disp_cap_05[,1])
return(df)
}
```

```
#### Based on the community mean the following functions calculate all the parameters for the beta distribution for individuals###

betafi <- function(community,Nind) #Nind is the number of individuals to generate. x is a dataframe that includes a column with the trait value mean for a specific community
{
 comms1<-list()
 for (i in 1:nrow(community))
 {
  var<-((1-community[i,1])*community[i,1])/(1+100)
  alpha <- ((1 - community[i,1]) / var - 1 / community[i,1]) * community[i,1] ^ 2
  beta <- alpha * (1 / community[i,1] - 1)
  Nicheoptimum <- rbeta (Nind, alpha, beta)
  comms1[[i]]<-data.frame(Nicheoptimum,community[i,])
  comms1[[i]]<-comms1[[i]][,c(1,3:15)]
 }
 return(do.call(rbind,comms1))
}

#generate number of individuals by species
ComSpecies <- function(ComMatrix,Nsp)
{
 NumCom <- length(ComMatrix) / Nsp
 Output <- matrix(NA,nrow=Nsp,ncol=NumCom)
 for (i in 1:NumCom)
 {
  Output[,i] <- ComMatrix[(((i - 1) * Nsp) + 1):(i * Nsp)]
 }
 return(Output)
}

#--------------------------------------------------------------------------#
# FRACTAL ALGORITHM TO GENERATE LANDSCAPES        #
#--------------------------------------------------------------------------#

MidPointFM2D_NS <- function (x, maxlevel=5, sigma=1, H=x, addition=1, SD=1) # generate a matrix of values based on midpoint displacement method
{
 f3 <- function(delta, x0, x1, x2)
 {
  (x0+x1+x2)/3 + delta * rnorm(1,mean=0,sd=SD) # average 3 points and displacement
 }
 f4 <- function (delta, x0, x1, x2, x3)
 {
  (x0+x1+x2+x3)/4 + delta * rnorm(1,mean=0,sd=SD) # average 4 points and displacement
 }
 N <- 2^maxlevel # dimension of matrix
```

```
 X <-matrix ( , N+1, N+1) # empty matrix
 delta <- sigma
 # set intial 4 random corners of the matrix
 X [1,1] <- delta*rnorm(1,mean=0,sd=SD)
 X [1,N+1] <- delta*rnorm(1,mean=0,sd=SD)
 X [N+1,1] <- delta*rnorm(1,mean=0,sd=SD)
 X [N+1,N+1] <- delta*rnorm(1,mean=0,sd=SD)
 D <- N # set step/limit
 d <- N/2 # set step/limit
 for (stage in 1:maxlevel)
 {
  delta <- delta*0.5^(0.5*H)
  # start moving on a 2D matrix with i=x and j=y
  for (i in seq(d+1, N-d+1, by=D))
  {
   for (j in seq(d+1, N-d+1, by=D))
   {
    X[i,j] <- f4 (delta, X[i+d, j+d], X[i+d, j-d], X[i-d, j+d], X[i-d, j-d]) # find the point where diagonals cross eachother
   }
  }
  # diplacement of external points (optional)
  if (addition == 1)
  {
   for (i in seq(1, N+1, by=D))
   {
    for (j in seq(1, N+1, by=D))
    {
     X[i,j] <- X[i,j] + delta*rnorm(1,mean=0,sd=SD)
    }
   }
  }
  delta <- delta*0.5^(0.5*H) # reduce the displacement
  # find boundary grid points(they have only 3 surrounding points each)
  for (i in seq(d+1, N-d+1, by=D))
  {
   X[i,1] <- f3 (delta, X[i+d, 1], X[i-d, 1], X[i, d+1])
   X[i,N+1] <- f3 (delta, X[i+d, N+1], X[i-d, N+1], X[i, N-d+1])
   X[1,i] <- f3 (delta, X[1, i+d], X[1, i-d], X[d+1, i])
   X[N+1,i] <- f3 (delta, X[N+1, i+d], X[N+1, i-d], X[N-d+1, i])
  }
  # find interior grid points (first iteration would be negative step and it is also not needed for grid purposes, therefore conditional)
  if (D<N)
  {
   for (i in seq(d+1, N-d+1, by=D))
   {
    for (j in seq(D+1, N-D+1, by=D))
```

```
    {
     X[i,j] <- f4 (delta, X[i, j+d], X[i, j-d], X[i+d, j], X[i-d, j])
    }
   }
   for (i in seq(D+1, N-D+1, by=D))
   {
    for (j in seq(d+1, N-d+1, by=D))
    {
     X[i,j] <- f4 (delta, X[i, j+d], X[i, j-d], X[i+d, j], X[i-d, j])
    }
   }
  }
  # displacement of corner and middle points (optional)
  if (addition == 1)
  {
   for (i in seq(1, N+1, by=D))
   {
    for (j in seq(1, N+1, by=D))
    {
     X[i,j] <- X[i,j] + delta*rnorm(1,mean=0,sd=SD)
    }
   }
   for (i in seq(d+1, N-d+1, by=D))
   {
    for (j in seq(d+1, N-d+1, by=D))
    {
     X[i,j] <- X[i,j] + delta*rnorm(1,mean=0,sd=SD)
    }
   }
  }
  D <- D/2
  d <- d/2
 }
 return(X)
}

#######transform the raw values to a uniform distribution######


transform.uniform<- function(landscape)

{
 landscap<-as.vector(landscape)
 Y <- (landscape - mean(landscape))/sd(landscape)
 Z <- 0.5 *erfc(-Y / sqrt(2))
 transform.landscape<- matrix(Z, nrow=dim(landscape)[1],ncol=dim(landscape)[1])
 return(transform.landscape)
}
```

```
#--------------------------------------------------------------------------------#
#  APPLY FRACTAL ALGORITHM TO GENERATE LANDSCAPES    #
#---------------------------------------------------------------------------------#

generate.lands<-function(exp.design)
{
 landscap.par<-exp.design[1,"H.val"]
 allland<-transform.uniform(MidPointFM2D_NS(exp.design[1,"H.val"]))
 allland<-apply(landscap.par,1,MidPointFM2D_NS)
 landscap<-list()
 for (i in 1:ncol(allland))
 {
  landscap[[i]]<- matrix(allland[,i], nrow=sqrt(nrow(allland)),ncol=sqrt(nrow(allland)))
 }
 allland<-lapply(landscap, transform.uniform)
 return(allland)
}


######Functions of habitat loss###############


# Remove habitat randomly to generate high fragmentation
habloss_random<-function(landscape,hab.loss) # hab.loss is the % of cells to replace with non-suitable
habitat

{
 cell.loss<-round((length(landscape)*hab.loss)/100)
 suitcells<-which(landscape!=-1)
 cells.rep <- sample(suitcells, cell.loss,replace=FALSE)  # draw random values from [1, length(vec)]
 landscape[cells.rep] <- -1
 return(landscape)

}

# Remove habitat in clusters. Low fragmentation
habloss_biased<- function(landscape, frag_layer,hab.loss)
{
 data<-data.frame(c(frag_layer))
 data$cell<-1:1089
 data$celllandscape<-c(landscape)
 cell.loss<-round((length(landscape)*hab.loss)/100)
 for (i in 1:nrow(data))
              {
          if(data[i,"celllandscape"]==-1){
          data[i,1]<-0
       }
```

```
    }
  #data<-subset(data,celllandscape!=-1)
  cells.rep <-sample(seq_len(nrow(data)), cell.loss, prob=data[,1])
  landscape[cells.rep] <- -1
  return(landscape)
}

#Count the number of individuals in each cell of the landscape

count.inds <- function(comm.position)
{
 #Initiatlize a 33x33 matrix with 0
 spp.counts<-matrix(nrow=33,ncol=33, rep(0, 33*33))
 for(i in 1:nrow(comm.position))
 {
  # fill the location
  spp.counts[comm.position[i,"X1"],  comm.position[i,"X2"]  ]  <-  spp.counts[comm.position[i,"X1"],
comm.position[i,"X2"] ] +1
 }
 return(spp.counts)
}

assign.position <- function(community,landscape,K)
{
 positions<-data.frame(which(landscape[,]>-2,arr.ind=TRUE),position=1:length(landscape),inds=0)
 for (i in 1:nrow(positions))positions[i,"cell.value"]<-landscape[positions[i,"row"],positions[i,"col"]]
 positions<-positions[rep(seq_len(nrow(positions)), each=K),]
 positions<-positions[sample(nrow(positions),nrow(positions),replace = FALSE),]
 community<-community[sample(nrow(community),K*(dim(landscape)[1]^2),replace = TRUE),]
 community$X1<-positions$row
 community$X2<-positions$col
 community$cell.value<-positions$cell.value
 community$count<-0
 return(community)
}
#-----------------------------------------------------------------------------#
#    CALCULATE REPRODUCTION, DISPERSAL, MORTALITY
#----------------------------------------------------------------------------#

# Survival function
surviv<-function(test.com)
            {
                        for (i in 1:nrow(test.com))
            {
                        test.com[i,"Survi"]<-0.5
            test.com[i,"survival"]<-rbinom(1,1,(test.com[i,"Survi"]))
         }
   survivors<-subset(test.com, test.com$survival!=0)
```

```
   return(survivors)
}

#Reproduction function

reproduction<-function(adults)
{
 for (i in 1:nrow(adults))
 {
  adults[i,16]<-dnorm(adults[i,"cell.value"],adults[i,"Nicheoptimum"],adults[i,"Nbre"])
  if(round(adults[i,16]>1))adults[i,16]<-1
 }
 new.ind <- adults[rep(row.names(adults), round(adults[,16])), 1:15]
 return(new.ind)
}

#Function survival reproduction

surv.rep<-function(test.com,landscape,K)
{
 juveniles<-reproduction(test.com)
 juveniles$count<-0
 survivors<-surviv(test.com)
 new.test.com <-survivors[1:15]
 if (nrow(juveniles)>0)
 {
  new.generation<-disper_fun(juveniles,landscape,new.test.com,K)
 }else
 {
  survivors<-survivors[1:15]
  survivors$count<-survivors$count+1
  new.generation<-survivors
 }

 return(new.generation)#add a matrix with the number of individuals

}
#------------------------------------------------------#
#              DISPERSAL FUNCTIONS     #
#------------------------------------------------------#

#Simulate individual movement:

disp.juv<- function(juveniles,landscape,ind_positions, K)
 {
  posavailable<-sum(ind_positions$indsavailable)

  lattice_size<-dim(landscape)
```

```
  posx<-juveniles[[12]]
  posy<-juveniles[[13]]
  #calculate distance of dispersal based on dispersal capacity
  dist<-rexp(1, juveniles[[4]])
  if(dist>30)dist<-30
  if(dist==0)dist<-1
  theta<-runif(1,0,2*pi)
  x<-cos(theta)*dist
  y<-sin(theta)*dist
  if (round(x+posx)!=33)
  {
   newposx<-round(x+posx) %% lattice_size[1]#new x position
  }else{
   newposx<-33
  }
  if (round(y+posy)!=33)
  {
   newposy<-round(y+posy) %% lattice_size[2]#new x position
  }else{
   newposy<-33
  }
  juveniles[[12]]<-newposx
  if (juveniles[[12]]==0)juveniles[[12]]<- 1
  juveniles[[13]]<-newposy
  if (juveniles[[13]]==0)juveniles[[13]]<- 1
  juveniles[[16]]<-(nrow(landscape)-(nrow(landscape)-
juveniles[[12]]))+(nrow(landscape)*(juveniles[[13]]-1))
  juveniles[[17]]<-landscape[juveniles[[12]],juveniles[[13]]]
  steps<-0
  while(steps<5 & dnorm(juveniles[[17]],juveniles[[1]],juveniles[[3]])<0.5){
   steps<-steps+1
   dist<-rexp(1, juveniles[[4]])
   if(dist==0)dist<-1
   if(dist>30)dist<-30
   theta<-rwrpcauchy(1, theta, rho=exp(-1))
   x<-cos(theta)*dist
   y<-sin(theta)*dist
   if (round(x+posx)!=33)
   {
    newposx<-round(x+posx) %% lattice_size[1]#new x position
   }else{
    newposx<-33
   }
   if (round(y+posy)!=33)
   {
    newposy<-round(y+posy) %% lattice_size[2]#new x position
   }else{
    newposy<-33
```

```
    }
    juveniles[[12]]<-newposx
    if (juveniles[[12]]==0)juveniles[[12]]<- 1
    juveniles[[13]]<-newposy
    if (juveniles[[13]]==0)juveniles[[13]]<- 1
    juveniles[[16]]<-(nrow(landscape)-(nrow(landscape)-
juveniles[[12]]))+(nrow(landscape)*(juveniles[[13]]-1))
    juveniles[[17]]<-landscape[juveniles[[12]],juveniles[[13]]]
   }
  return (juveniles)
}

disper_fun<-function(juveniles,landscape,current.community,K)
 {
  #calculate current numbers of individuals in each cell
  position.land<-count.inds(current.community)
  #calculate number of available positions in each cell
  indsavailable <- c(K-position.land)
  ind_positions<-data.frame(position=1:length(landscape),indsavailable=indsavailable)
  #subset available cells in the landscape
  ind_positions<-subset(ind_positions,!ind_positions$position %in% which(landscape[,]==-1))
  #count the number of available cells
  posavailable<-sum(ind_positions$indsavailable)
  current.community$count<-current.community$count+1
  count_steps<-0
  while(posavailable>0 & nrow(juveniles)>0 & count_steps<10){
   juveniles$ID<-paste("Juv", 1:nrow(juveniles), sep = "")
   if(nrow(juveniles)>posavailable)
   {
    juvtodisp<-(juveniles[sample(nrow(juveniles),posavailable),])
   }else{
    juvtodisp<-juveniles
   }
   count_steps<-count_steps+1
   juveniles<-juveniles[!(juveniles$ID %in% juvtodisp$ID),]
   #apply dispersal function
   juvdispersed<-apply(juvtodisp[1:15],1,disp.juv,landscape,ind_positions,K)
   juvdispersed<-as.data.frame(t(juvdispersed))
   juvdispersed<-juvdispersed[c(1:13,17,15)]
   names(juvdispersed)<-names(current.community[1:15])
   juvdispersed$position<-(nrow(landscape)-(nrow(landscape)-
juvdispersed$X1))+(nrow(landscape)*(juvdispersed$X2-1))
   juvdispersed$ID<-paste("Juv", 1:nrow(juvdispersed), sep = "")
   juvnotdispersed<-juvdispersed[!(juvdispersed$position %in% ind_positions$position),]
   juvdispersed<-juvdispersed[!(juvdispersed$ID %in% juvnotdispersed$ID),]
   freq<-count(juvdispersed,"position")
   ind_positions2<-ind_positions[!(ind_positions$position %in% freq$position),]
   ind_positions<-ind_positions[ind_positions$position %in% freq$position,]
```

```
   for (i in freq[,"position"])
   {
    ind_positions[which(ind_positions$position == i),"indsavailable"]<-ind_positions[which(ind_positions$position == i),"indsavailable"]-freq[which(ind_positions$position == i),2]
   }
   overloadpos<-subset(ind_positions,ind_positions$indsavailable<0)
   if (nrow(overloadpos)>0)
   {
    juvdispersed$ID<-paste("Juv", 1:nrow(juvdispersed), sep = "")
    juvtodisp<-juvdispersed[juvdispersed$position %in% overloadpos$position,]
    for (i in overloadpos[,"position"])
    {
     juvtodisp[which(juvtodisp$position == i),"remove"]<-overloadpos[which(overloadpos$position == i),][[2]]*-1
    }
    juvtodisp <- split(juvtodisp, juvtodisp[16], drop=TRUE)
    juveniles_disp<-list()
    for (i in 1:length(juvtodisp))
    {
     if (nrow(juvtodisp[[i]])>juvtodisp[[i]][1,"remove"])
     {
      juveniles_disp[[i]]<-juvtodisp[[i]][sample(nrow(juvtodisp[[i]]), juvtodisp[[i]][1,"remove"]), ]
     }else{
      juveniles_disp[[i]]<-juvtodisp[[i]]
     }
    }
    juveniles_disp<- do.call(rbind, juveniles_disp)
    juvdispersed<-juvdispersed[!(juvdispersed$ID %in% juveniles_disp$ID),]
    juvtodisp<-juveniles_disp
    names(juvtodisp)<-names(current.community)
    juveniles<-rbind(juvtodisp[1:15],juveniles[1:15])
   }
   juveniles<-rbind(juveniles[1:15],juvnotdispersed[1:15])
   current.community<-rbind(juvdispersed[1:15],current.community)
   position.land<-count.inds(current.community)
   indsavailable <- c(K-position.land)
   ind_positions<-data.frame(position=1:length(landscape),indsavailable=indsavailable)
   ind_positions<-subset(ind_positions,!ind_positions$position %in% which(landscape[,]==-1))
   posavailable<-sum(indsavailable)
  }
 new.generation <- current.community
 return(new.generation)
}
```

```
#------------------------------------COMMUNITY DYNAMICS--------------------------------------------------
```

```
comm.dynamics <-function(community,generations,H.val,p,
            K,habloss,shapebeta1,shapebeta2,clustered=NULL)
{

 initial_diversity<-fundiv_total(community, community[,c("Species", "Nbre","Nbre_05")])
 landscap.par<-expand.grid(H.val,p)
 allland<-generate.lands(landscap.par)
 if(missing(clustered)) {
  landscape<-habloss_random(allland[[1]],habloss)
 }else {
  landscape<-habloss_biased(allland[[1]],allland[[2]],habloss)
 }
 test.com<-remove_cells(community,landscape)
 diver<-list()
 community_matrix<-list()
 for (i in 1:generations)
 {
  test.com<-surv.rep(test.com, landscape,K)
  #diver[[i]]<-list(speciesdiv(test.com),fundiv(test.com),count(test.com, "Species"))
  if (nrow(count(test.com, "Species"))<1)
  {
   break
  }
  if (i %in% c(1,generations/2,generations))
  {
   fun.div_05<-fundiv_total(test.com, test.com[,c("Species", "Nbre","Nbre_05")])
   fun.div_01<-fundiv_total(test.com, test.com[,c("Species","Nbre","Nbre_05","Disp.cap")])
   #fun.div_Nbre<-fundiv_total(community, community[,c("Species","Nbre")])
   fun.div_01$Nbre<-fun.div_01$CWM[,1]
   fun.div_01$Nbre_2<-fun.div_01$CWM[,2]
   fun.div_01$Disp.cap<-fun.div_01$CWM[,3]
   fun.div_05$Nbre<-fun.div_05$CWM[,1]
   fun.div_05$Nbre_2<-fun.div_05$CWM[,2]
   fun.div_05$Disp.cap<-fun.div_01$CWM[,3]#I put the same value of div_05 here
   fun.div_01<-do.call(cbind,fun.div_01)
   colnames(fun.div_01)[which(names(fun.div_01) == "CWM.Nbre_01")] <- "CWM.Nbre_05"
   fun.div_05<-do.call(cbind,fun.div_05)
   community_matrix[[i]]<-test.com
   diver[[i]]<-rbind.fill(fun.div_01,fun.div_05)
   diver[[i]]$generation<-i
```

```
  }
 }
 diver<-do.call(rbind.fill,diver)
 diver$shapebeta1<-shapebeta1
 diver$shapebeta2<-shapebeta2
 diver$hab<-habloss
 if(missing(clustered)) {
  diver$frag<-"FRAGMENTED"
 }else {
  diver$frag<-"NON-FRAGMENTED"
 }
 diver$Hlands1<-H.val[[1]]
 diver$Hlands2<-H.val[[2]]
 return(list(diver, community_matrix,initial_diversity))
}

###########################################################
#Calculate FD using trait probability distributions (Carmona et al. 2016)
###########################################################

fundiv_total <- function(test.com,traits)
{

 TPDs_d1 <- TPDs(species = test.com$Species, traits)
 test.com<-test.com[order(test.com$Species),]
 abundance<-(count(test.com,"Species"))
 abundance2<-as.data.frame(t(abundance[,2]))
 colnames(abundance2)<-abundance$Species
 rownames(abundance2)<-"1"
 TPDc_d1 <- TPDc(TPDs = TPDs_d1, sampUnit = abundance2)
 RED_comm_d1 <- as.data.frame(REND(TPDc = TPDc_d1))
 FRED<-as.data.frame(redundancy(TPDc_d1))
 colnames(RED_comm_d1)<-c("FRic","FEve","FDiv")
 colnames(FRED)<-c("Fred","nbsp")
 return(cbind(RED_comm_d1,FRED))
```