Tests of community assembly across spatial scales in Neotropical birds

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Abstract

Species diversity varies dramatically across the surface of the Earth. A key step in the accumulation of species diversity is the ability of species to coexist in biological communities. Thus, identifying the mechanisms underlying community assembly is a major challenge for ecologists seeking to explain patterns in species diversity and composition. Recently some consensus has been reached on the set of processes that influence community assembly: speciation, demographic stochasticity, niche-based fitness trade-offs among species and dispersal. However, it is unclear how the importance of a particular process changes with spatial scale, which interactions exist among processes at large spatial scales and the extent to which niche-based resource partitioning among species explains differences in diversity among communities. Neotropical birds offer an ideal opportunity to address these uncertainties because of their high diversity and the existence of detailed information on their evolutionary history and ecology. In this thesis, I first use trait and phylogenetic metrics of community structure to show that both habitat filtering and interspecific competition shape community composition at the scale of individual bird territories (~1–2 ha). Second, I use simulations of community assembly to show that trait-based metrics of community structure outperform phylogenetic metrics for detecting niche-based community assembly, and that both sets of metrics often have low power when multiple processes influence community composition. Third, taking a trait-based, species-level approach, I show that both habitat filtering and interspecific competition influence species occurrence at regional scales (~75000 km^2), and interact with dispersal ability so that their effect on species occurrence is increased for species with greater dispersal ability. Finally, using a combination of trait- and isotope-based methods to quantify resource partitioning, I show that species' niche widths do not change and niche overlap is reduced at high compared to low species richness. Taken together, these results suggest that both habitat filtering and interspecific competition (i.e. niche-based processes) influence community assembly from local to regional scales. However, at least at regional scales, the degree to which these processes are important for determining the occurrence of any given species depends on that species's dispersal ability. They also suggest, based on niche-based interspecific competition influencing community composition, that differences in species richness among communities are in part explained by differences among sites in the breadth of available niche space, not by increased ecological specialisation or niche overlap.

Ithaka

As you set out for Ithaka
hope the voyage is a long one,
full of adventure, full of discovery.
Laistrygonians and Cyclops,
angry Poseidon – don't be afraid of them:
you'll never find things like that on your way
as long as you keep your thoughts raised high,
as long as a rare excitement
stirs your spirit and your body.
Laistrygonians and Cyclops,
wild Poseidon – you won't encounter them
unless you bring them along inside your soul,
unless your soul sets them up in front of you.

Hope the voyage is a long one.
May there be many a summer morning when,
with what pleasure, what joy,
you come into harbors seen for the first time;
may you stop at Phoenician trading stations
to buy fine things,
mother of pearl and coral, amber and ebony,
sensual perfume of every kind –
as many sensual perfumes as you can;
and may you visit many Egyptian cities
to gather stores of knowledge from their scholars.

Keep Ithaka always in your mind.
Arriving there is what you are destined for.
But do not hurry the journey at all.
Better if it lasts for years,
so you are old by the time you reach the island,
wealthy with all you have gained on the way,
not expecting Ithaka to make you rich.

Ithaka gave you the marvelous journey.
Without her you would not have set out.
She has nothing left to give you now.

And if you find her poor, Ithaka won't have fooled you.
Wise as you will have become, so full of experience,
you will have understood by then what these Ithakas mean.

(C.P. Cavafy, *Collected Poems*. Translated by Edmund Keeley and Phillip Sherrard)

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Despite my own interest in natural history, I was not a fan of biology as a high school student and spent a lot of time being told I had not coloured in the Golgi apparatus correctly. Evolution was only introduced into the South African school syllabus in 2008! When told that my undergraduate major in geography and economics would include a first year biology course, I was not too excited. However, the excellent lectures and field courses given by George Branch, Jeremy Midgley, Tony Verboom and William Bond at the University of Cape Town were awesome, and I switched majors immediately. I am forever grateful to them for this. At Oxford, I have been fortunate to have Nathalie Seddon and Joe Tobias as my supervisors. They have given me a lot of freedom to pursue my own ideas, but were always available to meet to discuss my research. Away from Oxford, both Owen Petchey and Bob Ricklefs hosted me on lab visits and were instrumental in conceptualising many of the analyses in this thesis.

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CHAPTER 1

General Introduction

Species diversity varies dramatically across the surface of the Earth. For example, a single 110 x 110 km quadrat in the Peruvian Andes may contain as many as 900 bird species (Hawkins et al. 2003), while the same size area at higher latitudes may support only 40 species (Orme et al. 2005). Likewise, species composition changes, often considerably, between assemblages at both local and regional scales, even when the accompanying change in species diversity is low. For example, adjacent forest plots in Amazonia may share only 55% of their tropical tree species (Condit et al. 2002). At larger spatial scales, to the extent that changes in species composition among assemblages reflect changes in the overlapping of species ranges, these changes in composition result from the substantial variance among species in their geographic ranges. Range size varies by more than 12 orders of magnitude among species as a whole, and by several orders of magnitude even within families (Brown et al. 1996; Sexton et al. 2009). Although many of these patterns have been recognised since natural historians began cataloguing diversity across the globe in the 18th century, and are increasingly well documented (e.g. Hillebrand 2004), identifying the mechanisms underlying them remains a major challenge for community ecology and evolutionary biogeography (Darwin 1859; Wallace 1869; Gaston 2000).

There are perhaps two main reasons that ecologists have had difficulty in identifying general pattern–process relationships for species diversity and composition. First, the results of manipulative experiments seldom scale up to explain phenomena over larger areas (Lawton 1999; Ricklefs 2006). Second, in larger scale observational studies, many patterns in the diversity, abundance and distribution of species may have multiple, often non-mutually exclusive, explanations. For example, species relative abundance distributions may be equally well explained by models from neutral theory that assume demographic equivalence among species and by those from niche theory based on deterministic fitness differences among species (Volkov et al 2003; Rosindell et al. 2012). In addition, there is the seemingly ubiquitous role of historical contingency on community structure (Ricklefs 1987; Cornell and Lawton 1992). Combined, these factors have led to the proliferation of hypotheses to explain species diversity maintenance and differences in species composition (Palmer (1994) identified 120 different hypotheses) that make any synthesis difficult, and have led some to conclude that the search for generality in community ecology is "unworkable" (Lawton 1999).

However, recently some broad consensus has begun to emerge regarding the processes that may influence species composition and diversity. This developing consensus has followed largely from two key debates at the centre of contemporary community ecology. First, since Hubbell's (2001) formulation of neutral theory there has been intense debate over whether community assembly is better explained by either deterministic niche-based or stochastic neutral models of species co-occurrence, especially for plant communities (Hubbell 2001; Ricklefs and Renner 2012). Second, on-going argument over the appropriate spatial scale at which to consider community assembly (e.g. Ricklefs 2008; Brooker et al. 2009) has led to the realization that neither local nor regional approaches can in isolation show the importance of different community assembly mechanisms. Thus, a more integrated view of community assembly is now focussed on the full set of processes that may influence species composition and diversity for a given system: selection (i.e. deterministic niche dynamics), ecological drift (i.e.

stochastic neutral dynamics), dispersal and speciation (Vellend 2010). As a result, attention is now focussed on developing a more integrated analytical approach to understanding the dynamics of communities, incorporating factors such as species evolutionary history, competition and dispersal ability estimates (Webb et al. 2002; Pavoine and Bonsall 2011; Weiher et al. 2011). This conceptual synthesis coupled with ever increasing data on species traits, evolutionary histories and geographic distributions, suggests that hope remains for generality over contingency in community ecology (Vellend 2010; Rosindell et al. 2012).

Community ecology: A brief history

Vellend (2010) defined selection in community ecology as the existence of "deterministic fitness differences between individuals of different species". Selection defined this way is essentially synonymous with the concept of species niches that dominated thinking in community ecology for much of the last century. In the first half of the 20th century, population models (Lotka 1923; Volterra 1926) and microcosm experiments led Gause (1934) to state emphatically that "complete competitors cannot coexist". Thus, species coexistence requires trade-offs in the relative competitive ability (i.e. resource-use efficiency) of species under different environmental conditions and species densities, resulting in negative density-dependent selection on species populations (Chesson 2000). In the field, Grinnell (1917) was the first to articulate the niche concept when describing the distribution of a bird species, the California thrasher, with respect to climate and habitat. Elton (1927; 1946) adopted a different perspective on species niches, focussing on local assemblages within a single habitat and describing food webs and community membership in the context of the competitive exclusion of ecologically similar species.

These two perspectives can be described, respectively, as the population and individual components of the niche (Holt 2009; Ricklefs 2010), where the individual component is defined by the role a species plays in a local assemblage, particularly as a consumer of resources. Hutchinson (1957) formalised these two basic concepts of niche theory as the species' niche, encompassing the set of conditions (abiotic and biotic) under which births exceeded deaths for a given species. This inclusion of biotic and abiotic factors distinguished between the fundamental and realised niche. Following from this, MacArthur and Levins (1967) suggested that the ecological similarity of competing species limited community membership and that a combination of resource diversity and ecological specialisation set a limit to species richness (Hutchinson 1959; MacArthur 1972). The concept of niche partitioning was applied similarly at both the local assemblage (MacArthur 1958) and population scale (Whittaker 1967). The result was a model, described as 'local determinism' (Ricklefs 2004), in which local-scale species interactions determined the membership of saturated communities, for which there was a strong correlation between diversity and the physical environment (MacArthur 1972; Diamond 1975; Cornell 2012).

In contrast to the niche-based perspective, regional-scale explanations based on the age and environmental stability of a region, which had originally lead thinking on gradients in species richness (e.g. Wallace 1869) were initially dismissed in the development of community ecology. However, the species diversity and composition of a community depends fundamentally on that of the regional species pool (Ricklefs 1987; Ricklefs and Schluter 1993; Ricklefs 2004). The importance of regional effects is illustrated by the existence of a positive correlation between local and regional diversity (Ricklefs 1987; Cornell and Lawton 1992) and of "diversity anomalies", where the diversity of an equally sized area with similar habitat qualities varies greatly between regions (Latham and Ricklefs 1993). These observations led to the consideration of speciation as a key process in explaining patterns in community ecology. For example, communities within a geographically more complex region may have increased diversity due to geographic complexity promoting allopatric speciation, as has been suggested for plants in Asia versus North America (Qian and Ricklefs 2000) and birds in Amazonia (Naka et al. 2012). Yet although historical contingencies play an important role in a model that incorporates regional effects on diversity (Cornell and Lawton 1992; Ricklefs 2004), within this framework species diversity and composition are still viewed largely as the outcome of deterministic processes (Ricklefs 2012).

The absence of obvious niche partitioning among tropical forest tree species as well as the unpredictability with respect to species identity of the replacement of individuals led Hubbell (2001) and others (e.g. Bell 2000; Bell 2001) to question the importance of deterministic niche-based processes, and put forward a neutral theory of biodiversity. Hubbell's model lacks any niche structure; instead, individuals of different species are demographically equal—intraspecific competition equals interspecific competition—and species diversity and composition are determined by the stochastic outcome of random births, deaths and speciation. This stochastic component in community dynamics due to random birth-death processes is known as ecological drift. The assumption of demographic equivalence has generated fierce criticism criticised by many ecologists, based both on natural history observations of trait differences among species (Purves and Turnbull 2010) and studies demonstrating either negative density-dependence in population dynamics (Comita et al. 2010; Johnson et al. 2012) or a seeming absence of ecological drift (Ricklefs and Renner 2012). However, there is some experimental support for demographic equivalence in insect communities (Park 1948; Siepielski et al. 2010). Moreover, a distinction often missed in debate over the fit of purely neutral models is that demographic equivalence is not required for ecological drift to influence community assembly. For example, when the number of individuals in a community decreases or niche-based processes are relatively weaker, or both, the presence of niche-based processes merely makes certain community outcomes more likely, but does not guarantee any particular outcome (Nowak 2006; Vellend 2010).

Finally, dispersal is important for community assembly, but its importance was also relatively neglected in the early development of community ecology. To be sure, dispersal is included as a key process in both the regional perspective put forward by Ricklefs (1987; 2004) and neutral theory (Hubbell 2001; Rosindell et al. 2012). However, the metacommunity concept that explicitly addresses linkages between different spatial scales in community ecology has placed the most emphasis on the influence of dispersal on species composition (Leibold et al. 2004; Holyoak et al. 2005). The dispersal of individuals integrates the effect of local community dynamics, such as species interactions within a larger region (Shmida and Wilson 1985; Leibold et al 2004). Indeed, Ricklefs (2004; 2008) has argued that because local species abundances reflect ecological interactions integrated across regional scales, ecological communities make sense only as regional entities and local communities exist only as point estimates of overlapping regional species distributions. In contrast, metacommunity ecology recognises ecological interactions at local scales, while stressing the importance of dispersal in mediating the role of drift and selection through mass effects and source-sink dynamics in structuring communities across spatial scales (Holyoak et al. 2005).

Unresolved questions

Within this more inclusive framework, a very general theory of community ecology can be articulated in which speciation and dispersal add species to communities, while selection (i.e. niche-based processes) and ecological drift and dispersal shape species relative abundances (Vellend 2010). However, there is intense debate as to how the relative importance of these processes for patterns of species richness and composition changes across both taxonomic groups and spatial scales (McGill 2010; Weiher et al. 2011; Chave 2013). Here I outline three research areas in which our understanding is still particularly limited.

First, this expanded conceptual framework is rarely specific with regard to the spatial scales at which different processes, such as niche-based selection and dispersal limitation, have greatest influence (Levin 1992; Swenson et al. 2006; McGill 2010; Chase and Myers 2011). For example, the influence of interspecific competition on species composition is expected to be strongest at the scale of direct interactions among individuals, such as the canopy size of trees, and to become progressively weaker as spatial scale increases (Weiher and Keddy 1995; Vamosi et al. 2009). Conversely, habitat filtering is expected to be weak at small spatial scales, but dominant at larger scales encompassing increased environmental variation among communities (Harper 1977; Weiher and Keddy 1995). However, the generality of this shift is poorly understood because: (1) previous studies of species composition have focussed largely on only a few taxonomic groups, especially plants, and have produced mixed results (Vamosi et al. 2009; McGill 2010); and (2) when multiple processes influence community assembly and vary in their relative importance, the power of metrics of community structure to detect the influence of a particular niche-based process is unclear (Kraft et al. 2007; Aiba et al. 2013). A bias towards systems such as plant communities, where the spatial scale of interactions between individuals is likely to be highly circumscribed, may underestimate the signature of competition at larger scales. For example, recent studies suggesting that interspecific competition is a key factor in limiting species geographic distributions in birds (Pigot and Tobias 2012; Laube et al. 2013) propose that competition is an important influence on community composition at regional scales.

Second, the dispersal of individuals across space integrates community dynamics within a larger region so that species occurrence within a given community reflects in part the integration of ecological processes across larger spatial scales (Leibold et al. 2004; Urban et al. 2008). Based upon this, metacommunity theory predicts that dispersal and environmental filtering as well as dispersal and interspecific competition should interact to influence species occurrence (Leibold et al. 2004; Holyoak et al. 2005; Urban et al. 2008). For example, environmental filtering and interspecific competition may be less important predictors of species occurrence for more dispersive species because high dispersal ability distributes individuals into habitats regardless of their ecological suitability (Holyoak et al. 2005). However, because most studies consider only the main and not the interaction effects of the environment, interspecific competition and dispersal ability on species occurrence, they inevitably yield an incomplete picture of the influence of these processes (Vellend 2010; Laube et al. 2013). Therefore, to better understand the mechanisms underlying species composition patterns, it is essential to consider how dispersal interacts with environmental filtering and interspecific competition to influence species occurrence. In addition, the few studies that have considered these interactions have tended to do so only at small spatial scales (Cadotte 2006), with the result that the degree to which these interaction effects are scale dependent remains unclear.

Third, if niche-based interspecific competition is important in shaping community composition, how resource partitioning among species constrains species richness needs clarification (Hutchinson 1959; Belmaker et al. 2011; Ricklefs 2012). Positive correlations between species richness and net primary productivity at regional–global scales support the hypothesis that resource availability or the breadth of available niche space limits species richness (Currie 1991; Hurlbert and Jetz 2010). Alternatively, for a given availability of niche space, species richness may increase as species are more tightly packed into niche space, either due to increased ecological specialisation (i.e. narrower niches) (MacArthur 1972; Belmaker et al. 2011) or increased niche overlap (Klopfer and MacArthur 1961; Le Bagousse-Pinguet et al. 2013), thus decoupling species richness from available niche space. Despite these contrasting predictions, the extent to which greater resource space or niche packing contribute to species richness gradients is poorly resolved due in large part to the difficulty of quantifying resource availability and its partitioning among species (e.g. Pianka 1975).

Study system

Neotropical birds provide an ideal system within which to explore the mechanisms underlying patterns in species diversity and composition. Neotropical bird species richness varies enormously both latitudinally and along elevation gradients (Orme et al. 2005), encompassing a gradient in climate and vegetation comparable to that found from the equator to the poles. In the tropical Andes, there is as much as a fivefold increase in bird species richness as one descends from high elevation grassland and cloudforest communities to lowland tropical forest in Amazonia (Terborgh 1977; Walker et al.

2006). Compared to temperate regions, Neotropical bird communities also offer larger sample sizes of year-round resident species that are likely to compete over space and resources. Birds also play key ecological roles as seed dispersers, pollinators and predators (e.g. Galetti et al. 2013), and their exclusion from a system can have negative impacts upon human welfare. For example, the exclusion of insectivorous birds from coffee plantations has been shown to significantly reduce crop yields (Maas et al. 2013; Karp and Daily 2013). Thus given the prospect of rapid global environmental change, understanding what shapes species occurrence and community composition is also a major concern for conservation and management (Walther et al. 2002; Parmesan 2006).

Birds make good subjects for community-level research because they are relatively easy to identify, survey and catch. Furthermore, morphological measures, such as beak and tarsus length, provide well-supported indices of both diet and microhabitat resource use (Miles and Ricklefs 1984; Miles et al. 1987; Grant and Grant 2006). Dietary resource partitioning among bird species can also be quantified using stable isotope analysis of blood (Inger and Bearhop 2008). However, although stable isotope analysis offers a potentially powerful tool for assessing niche partitioning in species rich avian communities, its efficacy in this regard has not been tested. In addition, morphological measures can also be used to quantify dispersal ability. For instance, Kipp's distance—the distance between the longest primary and the first secondary feather—has been shown to predict both natal dispersal distances (Dawideit et al. 2009) and flight performance (Claramunt et al. 2011). Finally, extensive background information exists on both species geographical distributions (Orme et al. 2005) and their phylogenetic relationships (Jetz et al. 2012). In the neotropics in particular, there is an especially well-sampled phylogeny for the ovenbirds, one of the major South American bird radiations (Derryberry et al.

2011). Neotropical bird communities thus offer the potential for extensive analyses of how the importance of particular community assembly processes changes at different spatial scales, of how assembly processes interact to influence species composition and of how resource partitioning might constrain species richness.

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CHAPTER 2

Unravelling the complex interplay of community assembly processes acting on multiple niche axes across spatial scales

ABSTRACT

The importance of spatial scale in ecology is the focus of intensive debate, with many studies concluding that biodiversity is structured by species interactions at small scales, and habitat filtering at larger scales. However, delimiting scales at which niche-based processes act is difficult because many approaches potentially integrate separate community assembly patterns across multiple niche axes, and may therefore struggle to identify overlapping processes. Here, I use simulations to evaluate the power of phylogenetic and trait-based metrics to detect competition and habitat filtering under multiple assembly scenarios. I then test for both processes at a range of spatial scales in a Neotropical bird assemblage, using functional traits to derive niche axes. Simulations revealed that multi-niche-axis metrics—including phylogenetic structure and functional diversity—have low power to detect competition and habitat filtering when a mix of processes acts across niche axes, whereas single-niche-axis metrics were better able to deal with this complexity. Applying these more focused metrics to observed communities revealed that competition and habitat filtering act together at local scales. I results challenge the view that competition and habitat filtering are partitioned across scales, and suggest that many standard phylogenetic and trait methods may produce misleading evidence of such partitioning by merging the signals of multiple processes. Taken together, these findings highlight the importance of single-niche-axis approaches for testing community assembly models.

INTRODUCTION

The study of differences in species resource-use strategies and their importance for understanding species coexistence has dominated ecology throughout much of the last century, with evidence for ecological niche partitioning discovered in communities as diverse as yeast cell cultures, plants and birds (Gause 1934; Stubbs and Wilson 2004; Lovette and Hochachka 2006). Over the last decade, most attention has focused on clarifying the importance of niche-based processes in structuring communities relative to purely neutral models (Hubbell 2001; Chase and Myers 2011). This debate has led to a more balanced consensus on the total set of processes that can be involved in community assembly, including niche-based habitat filtering and interspecific competition, as well as dispersal and demographic stochasticity (Vellend 2010; Weiher et al. 2011). However, this expanded conceptual framework is rarely specific with regard to the spatial scales at which different processes have greatest influence, and the potential interaction of these processes across scales remains unclear (Levin 1992; Swenson et al. 2006; McGill 2010; Chase and Myers 2011).

It is generally assumed that interspecific competition is strongest at the scale of direct interactions, such as the canopy size of trees, and becomes progressively weaker as spatial scale increases (Weiher and Keddy 1995; Vamosi et al. 2009). Conversely, habitat filtering is expected to be weak at small spatial scales, but dominant at larger scales encompassing increased environmental variation among communities (Harper 1977; Weiher and Keddy 1995). The classic signature of this variation is a niche differentiated pattern of regular spacing or overdispersion in the trait values of co-occurring species at small scales (MacArthur and Levins 1967; Ricklefs and Travis 1980), shifting to the opposite pattern of clustering of species' trait values within communities at larger scales

(Weiher and Keddy 1995; Cavender-Bares et al. 2009). Yet, the generality of this shift is poorly understood because previous studies have focused on only a few taxonomic groups and produced mixed results (Vamosi et al. 2009; McGill 2010).

One source of uncertainty relates to analytical techniques. Most recent studies of community assembly across scales apply phylogenetic or trait-based metrics that are sensitive to both overdispersion and clustering (e.g. Cavender-Bares et al. 2006). In addition, many of these metrics either combine multiple traits into a single analysis (e.g. FD; Petchey and Gaston 2002), or do so indirectly in the case of phylogenetic methods. These metrics have been used to detect non-random patterns across multiple niche axes, and have the advantage that they may provide an integrated overview of community structure. However, when different niche-based assembly processes act on separate niche axes independently, or else exert combined effects on the same niche axis, a potential drawback is that 'multi-niche-axis' metrics may combine the signals of contrasting assembly processes (Swenson and Enquist 2009). These approaches may therefore obscure the niche-based assembly processes involved at a given scale if one process masks another, or multiple processes erase each other's signal by generating seemingly random patterns associated with neutral dynamics (Kraft et al. 2007; Weiher et al. 2011). This may help to explain the high proportion (82%) of results failing to reject random assembly in previous studies of plant communities (Götzenberger et al. 2012). The use of metrics testing assembly processes on single niche axes may increase rates of detection and reveal different patterns across spatial scales, but this possibility remains to be tested.

A related issue is that most analyses exploring community assembly processes across scales have focused either on plants or microbes (e.g. Cadotte 2006; Swenson and Enquist 2009; Kraft and Ackerly 2010), as these are highly amenable to observational and experimental tests comparing across spatial scales. In contrast, it is relatively difficult to define communities and delimit sampling scales in mobile animal species, particularly vertebrates (Vamosi et al. 2009). Because of this longstanding research bias, our knowledge of the ecological and evolutionary patterns describing communities is primarily based on systems (plants, microbes) where the spatial scale of interactions between individuals is likely to be highly circumscribed, perhaps underestimating the signature of competition at larger scales. In addition, most previous studies in animals have focused either across many habitats at large scales or within single habitat types at small scales (Vamosi et al. 2009), a factor that may bias analyses and potentially explains the perceived shift from habitat filtering to competitive interactions as spatial scale decreases.

I addressed these issues by using a multi-scale sampling design to assess patterns in the structure of Neotropical bird communities across multiple habitats at local spatial scales (0.8–6.4 ha). As a first step, I used principal components analysis to derive independent trait axes linked to candidate niche axes. I then used community assembly simulations on this dataset to evaluate the power of both broad (i.e. 'multi-niche-axis') and focused (i.e. 'single-niche-axis') metrics to detect assembly processes under various scenarios. These simulations provide an important framework for I study as it is largely unknown how most metrics of community phylogenetic or trait structure vary in their sensitivity to a given niche-based assembly process when multiple processes operate on the same and on different niche-axes, particularly when different processes vary in their relative strength (Aiba et al. 2013). Finally, I tested for assembly processes in the observed bird communities across spatial scales using an array of phylogenetic and functional trait metrics.

Tropical insectivorous birds provide an excellent system for this approach. First, they are relatively easily encountered in low-stature montane habitats, and can be efficiently surveyed to generate 'point communities'—i.e. assemblages of species with high likelihood of interaction because their home ranges overlap at a single point. Second, many species hold territories year-round and defend them against heterospecifics (Robinson and Terborgh 1995), suggesting that competitive exclusion may extend considerably further than the size of individual organisms, and potentially over local (Jankowski et al. 2010) and even regional scales (Pigot and Tobias 2013). Finally, the link between morphological traits and ecology is relatively well established in birds, as the avian beak is a classic index of trophic niche (Hutchinson 1959; Schoener 1965; Grant and Grant 2006), and other biometric measurements such as tarsus and wing length can be related to foraging manoeuvre, microhabitat and substrate use (Miles and Ricklefs 1984), helping us to identify candidate sets of traits that represent key niche axes potentially important in community assembly (see Appendix S1).

My simulations and analyses are designed to clarify processes at small spatial scales, where the drivers of vertebrate community structure are still unclear, and yet where many of the most interesting dynamics of community assembly related to species interactions and habitat selection are likely to take place (Vamosi et al. 2009). This uncertainty constrains our understanding of how niche-based processes govern patterns of species richness and turnover. For example, range boundaries are proposed to be limited in birds by both habitat filtering (Pigot et al. 2010) and competition (Terborgh and Weske 1975; Jankowski et al. 2010), but the spatial dynamics of these processes remain contentious (Gotelli et al. 2010). Moreover, understanding how these factors interact across local scales has important implications for ecological forecasting techniques, including the modeling of species distribution and abundance under environmental change (McGill et al. 2006; Gotelli et al. 2010).

METHODS

Study site and survey methods

I conducted surveys during July–November 2010 in the Kosnipata Valley at Wayqecha Biological Research Station, Peru (13°10'35"S 71°35'20"W). I used a Garmin GPS 60CSX device to establish a plot of 72 survey points at regular intervals of 120 m on a grid layout (Fig. 1). The grid covered an elevation range of 2570–3050 m and contained two major habitat types—montane cloud forests and high elevation 'puna' grassland—in roughly equal proportion (Fig. 1; Fig. S1). A third shrub habitat type was present in areas where the ecotone between the cloud forest and grassland was wider. The shrub habitat type typically had vegetation lower than 4m and an understory dominated by grasses. These habitat types differ markedly in the foraging substrates and vegetation structures available to insectivorous birds, providing the opportunity for habitat filtering within the study grid. For a full description of vegetation types and topography across the site, see Gibbon et al. (2010).

An advantage of focusing on cloud forest and adjacent grassland habitats is that birds are relatively easy to survey because of lower diversity and greater visibility, in comparison with other tropical habitats such as lowland rainforests. They are nonetheless more diverse than temperate habitats, and in particular offer larger sample sizes of year-round resident species that are likely to compete over space and resources. I conducted standardized audial and visual bird surveys at all 72 points. Surveys focused on circular areas with 50 m radius centred on each point, ensuring that neighbouring communities were non-overlapping. Communities therefore consisted of birds occurring in an area of approximately 0.8 ha, with the study grid designed so that neighbouring survey points could be clustered to produce larger communities (1.6, 3.2 and 6.4 ha; Fig. 1). See Appendix S1 for a full description of survey methods.

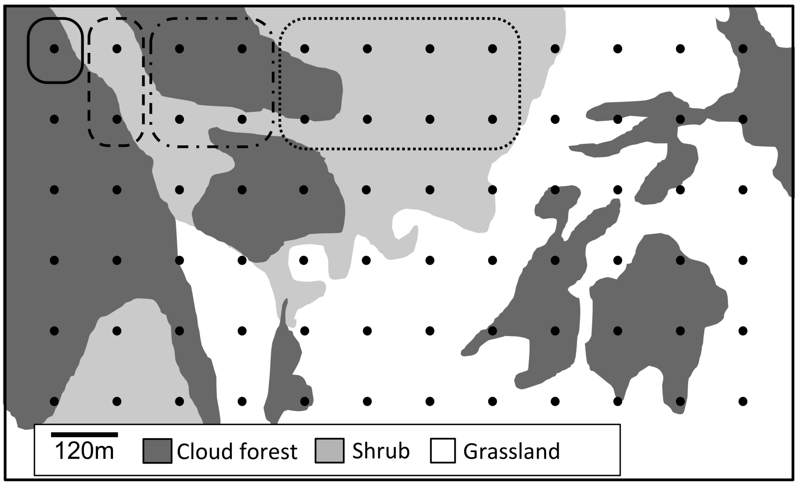

Figure 1. Diagram of the study grid. Rectangles (viewed from top left) indicate how the 72 survey points were grouped to create communities at four different scales: 0.8 ha (solid line), 1.6 ha (dashed line), 3.2 ha (dash-dot line), 6.4 ha (dotted line). Sample size was 72 communities for the smallest spatial scale, 12 communities for the largest. The relationship between points and habitats is shown in gray-scale; see Fig. S1 for a satellite image.

The total area of the study site is small enough (~80 ha) that most study species are able to disperse across the site within minutes, and even the most non-dispersive species (e.g. *Scytalopus*) are potentially able to do so within a single generation. This is important as null models of community assembly assume that dispersal among communities is not limited, whereas many empirical studies may violate this assumption (Cavender-Bares et al. 2009), particularly those focusing at larger scales (e.g. Graham et al. 2009).

Functional traits and associated niche axes

As most community assembly models apply to interactions within trophic levels (Hubbell 2001; Cavender-Bares et al. 2009), I restricted my analyses to bird species with primarily insectivorous diets. In addition, for bird communities: (1) it is expected that interspecific competition will be strongest among species within trophic guilds (Cody 1974), (2) using a single trophic guild ensures that trait-based tests for the effect of competition on community structure can use a set of functional traits that more accurately capture differences in foraging ecology among species, and (3) the relationship between morphology and foraging ecology is relatively well known for insectivorous species (Miles et al. 1986). I measured six functional traits (beak length, beak width, beak depth, wing length, tail length and tarsus length) from 1–70 (mean ± SE = 11.54 ± 2.43) individuals. Data for most species were sampled from individuals captured by mist-netting at the study site, with missing trait values for seven species measured on museum specimens from localities as close as possible to the study site. Measurements of live birds and museum specimens were taken using standard procedures described in Appendix S1.

Intraspecific variation in functional traits may reduce the power to detect non-random patterns in the spacing of trait values within communities. In my dataset, the proportion of variance in trait values explained by species (84.5–94.7%) was far greater than that explained by intraspecific differences (5.3–15.5%) for 20 well-sampled species ($n > 5$ individuals; Table S2). I therefore used mean trait values normalized with log transformations for all analyses, following previous trait-based studies (Stubbs and Wilson 2004; Kraft et al. 2008).

Focusing tests for a given niche-based assembly process on appropriate functional traits raises the challenge of identifying and delimiting relevant niche axes. For example, if foraging differences are accentuated among coexisting species to reduce interspecific competition, it seems sensible to focus tests for the signature of competitive exclusion (i.e. overdispersion) on key trophic traits such as beak shape (Hutchinson 1959; Schoener 1965). However, the link between traits and niche axes is not always clear, and sets of traits often provide information about the same or overlapping niche axes. In my dataset, functional traits were strongly positively correlated (r = 0.28–0.84), largely through their association with overall body size. Therefore, to prevent these trait correlations biasing trait-based analyses towards detecting only those processes acting on niche axes associated with body size, I used ordination techniques to derive independent trait axes.

I explored two methods of reducing trait correlations using PCA. First, following previous studies (e.g. Ingram and Shurin 2009; Swenson and Enquist 2009), I obtained niche axes by entering all traits into a single PCA. Second, I used a novel two-step PCA process to ensure that functional trait axes were not only independent, but mapped onto interpretable niche axes (Fig. S2). Specifically, following Miles et al. (1987), I classified (1) beak dimensions as trophic traits related to prey item selection, and (2) wing, tail and tarsus lengths as locomotory traits related to foraging substrate and manoeuvre. I performed PCAs on trophic and locomotory traits separately, and then performed a further PCA using the first components from both the trophic and locomotory PCAs to derive an index of body size (Fig. S2). This two-step approach was designed to generate three largely independent indices—trophic traits, locomotory traits, and overall body size—all related to different aspects of the foraging niche (see Appendix S1). When I compared both PCA approaches, I found that the two-step process outperformed the one-step process in separating candidate niche axes (see ‘Functional traits’ in Results and

Table S3 and S4). Thus, outputs from the two-step process were included in all further analyses.

Multi-niche-axis metrics

I used two standard metrics—functional diversity (FD; Petchey and Gaston 2002) and convex hull volume (CHV; Cornwell et al. 2006)—both of which test concurrently for habitat filtering and niche differentiation. FD is a measure of how dispersed a set of species is in trait space (Petchey and Gaston 2002), while CHV is the smallest convex set in trait space enclosing all of the species trait values within a community, and is analogous to a multivariate measure of the range of community trait values (Cornwell et al. 2006). FD and CHV are generally applied to sets of multiple functional traits and, because they also test for two patterns concurrently, can be classified as 'multi-pattern, multi-niche-axis' metrics. I calculated FD and CHV using all three trait axes derived from the two-step trait PCA (Fig. S2). Because I did not know a priori the relative importance of these three functional trait axes for community assembly, I standardized the axes to have a mean of zero and unit variance so that each axis would have equal weight in the calculation of FD and CHV (Villéger et al. 2008). FD measures for each survey point were standardized by the FD of the total species pool so that variation in FD ranged from 0 to 1. For both FD and CHV, results using unstandardized axes were very similar to those reported here (Table S7).

Another source of 'multi-pattern, multi-niche-axis' metrics that are now widespread in community ecology are phylogenetic analyses (Cavender-Bares et al. 2009). A standard assumption of community phylogenetic models is that multiple niches are phylogenetically conserved, and thus that co-occurring species should be more related than expected by chance under habitat filtering but less related than expected by chance under competitive exclusion (Kraft et al. 2007; but see Mayfield and Levine 2010). To test this, I constructed a molecular phylogeny for all species in the study community (Fig. 2; see Appendix S1 for all information on genetic extraction, sequencing and tree building methodology). I assessed the phylogenetic signal in functional traits using Blomberg's K statistic (Blomberg et al. 2003), and in habitat type using D (Fritz and Purvis 2012), both with 1000 permutations. I selected the metrics Mean Phylogenetic Distance (MPD) and Mean Nearest Taxon Distance (MNTD) because they are used widely and have been the subject of previous power analyses (Kraft et al. 2007). MPD is the mean of the pairwise phylogenetic distances between co-occurring species and is most sensitive to tree-wide patterns of phylogenetic clustering and evenness. MNTD is the mean of the phylogenetic distances separating each species from its closest co-occurring relative and is most sensitive to patterns of phylogenetic clustering or evenness at the tips of the phylogeny (Webb et al. 2002; Kraft et al. 2007).

Single-niche-axis metrics

I assessed community structure on each of the three trait axes separately using metrics I classified as either 'multi-pattern, single-niche-axis', because they test for both major assembly patterns (clustering and overdispersion), or as 'single-pattern, single-niche-axis', because they are used to test for only one assembly pattern. I focused on three 'multi-pattern, single-niche-axis' metrics: (1) FD applied to a single trait axis, (2) Variance (the variance in species values within a community along a single trait axis), and (3) Range (the range in species trait values within a community, i.e. the single-niche-axis equivalent of CHV). Both Variance and Range have previously been used predominantly as a measure of trait clustering (e.g. Stubbs and Wilson 2004; Kraft and Ackerly 2010). I also focused on one ‘single-pattern, single-niche-axis’ metric, SDNDr, the standard deviation of the distances between neighbouring species along a single trait axis, divided by the trait range of the community. SDNDr is used to detect only the regular spacing in species trait values predicted by competitive exclusion (Kraft and Ackerly 2010).

Power analyses of phylogenetic and trait metrics

To evaluate the statistical performance of both multi-niche-axis and single-niche-axis metrics I conducted a series of simulations. These were designed to assess the power of the metrics to detect two separate processes—habitat filtering and competitive exclusion based on limiting similarity—operating over multiple niche axes, and across a range in the relative importance of each process. I assembled 1000 communities of nine species (the median species richness in my dataset) for each of five scenarios in the relative importance of habitat filtering to competitive exclusion, varying from the sole action of one process to a 50:50 mix in the importance of both processes. I assembled communities using three uncorrelated trait axes to generate realistic scenarios for the combined action of habitat filtering and competitive exclusion on the same niche axis and, simultaneously, of each process on separate niche axes during the assembly of a community. The body size trait axis from the two-step PCA was subjected to habitat filtering and limiting similarity, the locomotory axis to habitat filtering only, and the trophic trait (beak shape) axis to limiting similarity only. I also performed simulations where the axes were switched so that the locomotory trait axis was subjected to habitat filtering and limiting similarity and the body size axis to habitat filtering only. This was done to investigate whether the distribution of a trait's values in the species pool had an effect on the power of the metrics.

Each community simulation started with all 41 species recorded at the study site and species were removed using the algorithms of Kraft et al. (2007). First, the habitat-filtering algorithm selected an optimal body size and locomotory trait value at random from within the observed range for these traits and species furthest from this optimum—by Euclidean distance—were eliminated. Second, the limiting-similarity algorithm detected the pair of species with the smallest Euclidean distance between them and eliminated one of the pair at random, repeating this process until the desired local community species richness was reached. Species pair distances were calculated within either the body size by beak shape trait space, or the locomotory trait by beak shape trait space, depending on the simulation. To vary the relative importance of habitat filtering and competitive exclusion, the number of species eliminated due to either process was adjusted, with the 50:50 assembly scenario resulting in an equal number (16) being eliminated by each process.

The observed value, as well as the null model mean and standard deviation from 999 null communities, were calculated for each multi- and single-niche-axis metric for each simulated community. To enable calculation of the phylogenetic metrics, I constructed a community phylogeny for each simulated community by selecting, from the phylogeny for all species at the study site, the nine species in each simulated community. For all metrics, I used a null model that drew species at random from the species pool while maintaining the species richness for each community. It was not necessary to use a null model that maintained species occurrence frequency because there was no species occurrence frequency structure in the dataset independent of that generated by the assembly algorithms I applied. To test the power of the metrics to reject a false null hypothesis of random assembly, I drew sets of 20 communities, sampling at random without replacement, from the set of 1000 communities simulated for a given scenario of habitat filtering to competitive exclusion. This procedure yielded 50 sets of local communities for each of the five assembly scenarios. Wilcoxon signed-ranks tests were then performed on each of these 50 sets of 20 local communities allowing the proportion of tests rejecting the null model for a given scenario to be recorded. The Wilcoxon signed-ranks test assessed whether the distribution of the differences between the observed, simulated local community values and their respective null model means was shifted away from zero. For all 'multi-pattern' metrics, a two-tailed test was used with a shift in observed values below zero indicative of clustering and a shift above zero of overdispersion (Kraft et al. 2008; Kraft and Ackerly 2010). However, following previous studies (e.g. Kraft et al. 2008; Kraft and Ackerly 2010), a one-tailed test for a shift below zero was used for SDNDr because this 'single-pattern' metric is designed to test only for the reduced standard deviation in neighbour distances (regular spacing). I note that the method of using Wilcoxon signed-ranks tests to evaluate the power of the metrics at the aggregate level of multiple individual communities is likely to yield higher estimates of power than that obtained when testing individually for the deviation of single communities from the null model (Kraft and Ackerly 2010). All simulations and metric analysis was performed in R (R Core Team 2013). See Appendix S1 for further details of analytical techniques and R code.

Tests of bird community assembly across scales

To determine if phylogenetic and trait patterns in the observed communities deviated from those expected by chance, I used the independent swap algorithm (Gotelli and

Graves 1996) on the total species by community matrix to generate a null distribution of 999 random communities for each observed community, at each spatial scale (0.8–6.4 ha; Fig. 1). The independent swap null model was used to provide a more conservative test of assembly processes by maintaining observed species occurrence frequencies in the null model communities to control for affects on species occurrence in the observed data unrelated to habitat filtering and competitive exclusion. Following the protocol for the power analyses, I used Wilcoxon signed-ranks tests to assess significant deviation from the null model. Because the signal of niche-based processes might be masked from MPD and MNTD analyses owing to their assessment of pattern across the whole phylogeny, I also tested if individual clades were filtering into specific habitat types. To achieve this, I grouped taxa by their primary habitat type (forest or non-forest; see Appendix S1) and used the nodesig analysis in Phylocom (Webb et al. 2008) to test whether taxa descended from each node were over- or under-represented in a habitat type.

Further tests of habitat filtering

An absence of trait clustering in communities at larger spatial scales could result from an increase in habitat heterogeneity encompassed within communities, as this could lead to a more dispersed functional trait set within communities. To assess the role of this relationship, I used a correlogram and mantel tests to quantify the degree of habitat (vegetation structure) heterogeneity across scales. To quantify vegetation structure, a single observer estimated the percentage cover of tree, shrub and grass by eye within a 20m x 20m square centred on each survey point. Trees were classed as non-grass vegetation higher than 4m. The tree canopy was defined as the upper surface of tree foliage covering an area of at least 5m by 5m. Maximum canopy height was estimated visually, to the nearest metre, by placing a pole of set length (2m) against the base of the tallest vegetation and standing a set distance (10m) from the base of the vegetation. These habitat variables were selected because they were relatively easy to survey in steep terrain and capture the variation in foraging substrates available to insectivorous birds. I arcsin transformed the percentage cover estimates and performed a PCA on all vegetation data, retaining the first component as a measure of vegetation structure. I then used least squares regression to test whether there was a relationship between habitat and the rank of mean trait values for each community at the smallest spatial scale. See Appendix S1 for full details of spatial autocorrelation analysis.

RESULTS

Community data

The total species pool across all 72 points comprised 41 species (Table S8). To assess whether the observed species richness was a reasonably accurate indication of community composition, I estimated species richness for the study site with a Chao II incidence-based estimator (Chao 1987) implemented in *EstimateS* version 8.2.0 (http://viceroy.eeb.uconn.edu/estimates/). Observed species richness was 91% of estimated species richness for the study site. In addition, at the scale of individual survey points, the mean proportion of new species detected at a survey point levelled off at <0.05 species per visit after five visits (Fig. S3). Thus, my surveys captured a high proportion of bird diversity across the study site.

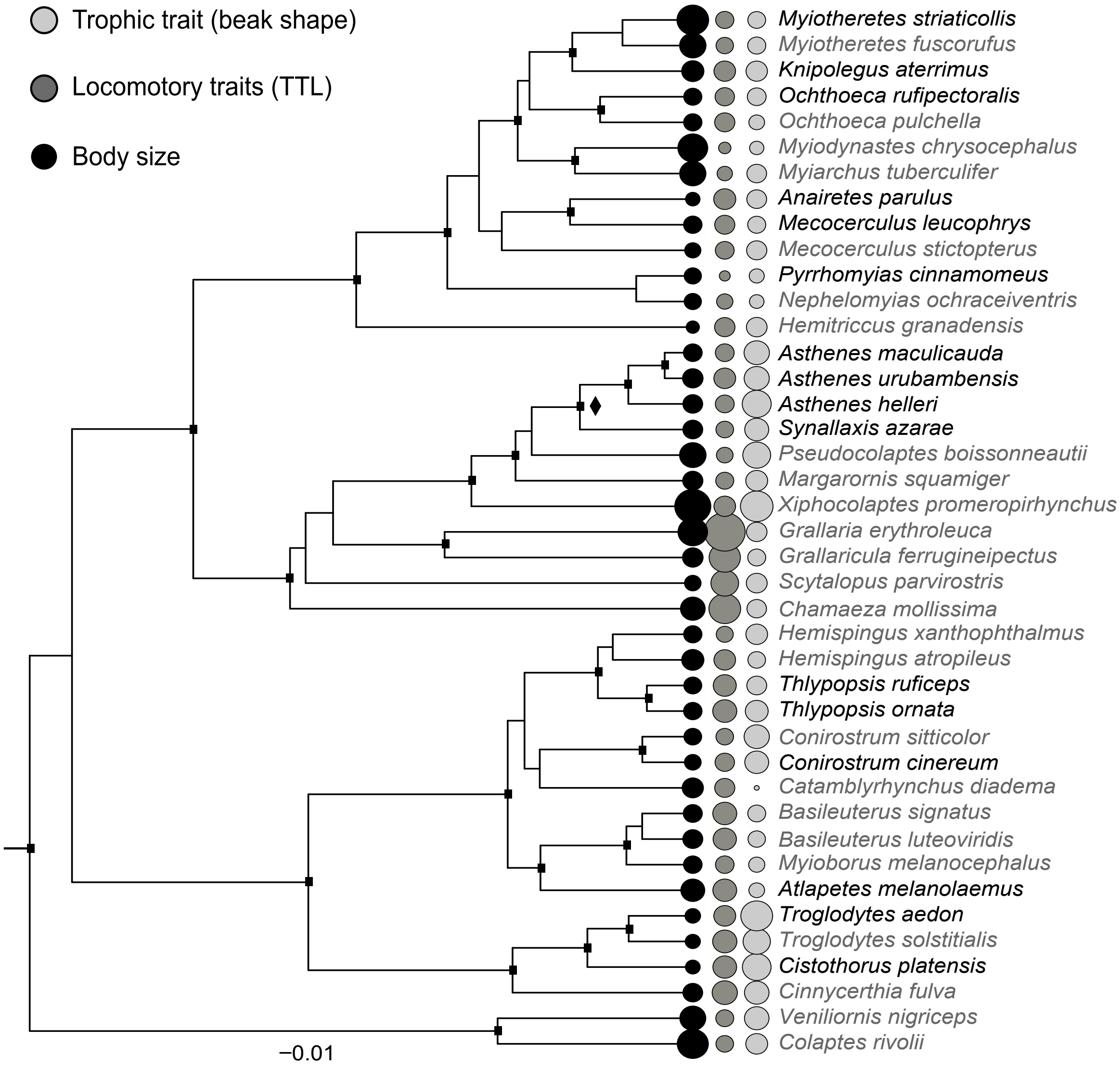

Figure 2. Maximum clade credibility tree inferred from analysis of mitochondrial DNA regions for all study species, labeled as occurring primarily in forest (gray names) or grassland and shrubby vegetation (black names). Diamond (♦) indicates the only node significantly over-represented by a particular habitat (non-forest). Nodes with squares indicate posterior probability support >95%; other node values are given in Figure S4; scale bar indicates sequence divergence. The size of data circles represents the value of scaled traits: trophic traits (PC2; beak shape), locomotory traits (PC2; tarsus to tail length ratio) and body size (PC1).

Functional traits

The first principal component (PC) of a standard PCA including all six functional traits explained 70% of the variation in the traits, and represented an index of body size (Table S3). The second PC explained 15% of variation, and was an index of tarsus to tail length ratio. The third PC explained 7% of the variation and represented a tail length to beak width ratio. In contrast to the first two axes, this axis is less easily interpreted as an ecological niche axis because it potentially provides information on a mix of prey item selection and foraging location (see Appendix S1). PC axes four to six also represented indices combining both foraging and locomotory traits (Table S3). Because the standard PCA produced ambiguous niche axes, I compare the results against a two-step PCA in which the first step is focused on describing candidate niche axes (separating trophic and locomotory traits) (Fig. S2).

Using this two-step process, the first PC for locomotory traits (tail, wing and tarsus length) explained 62% of the variation in these traits and represented locomotory trait size, with increasing values associated with a longer tarsus, wing and tail (Fig. S2; Table S4). The second PC explained 28% of the variation and represented the tarsus to tail length ratio, with increasing values associated with a longer tarsus and shorter tail. It was highly correlated (r = 0.97) with the equivalent output (second PC) from the standard PCA. The first PC for trophic traits (beak length, width and depth) explained 85% of the variation in these traits, and was an index of beak size with increasing values associated with longer, wider and deeper beaks (Fig. S2; Table S4). The second PC for trophic traits explained 10% of the variance and was an index of beak shape with increasing values associated with longer and narrower beaks. The first PC of the body size PCA, on the locomotory trait and beak size axes, explained 94% of the variation (Fig. S2;

Table S4), and was an index of overall body size with increasing values associated with an increase in all trophic and locomotory traits. It was very highly correlated ($r = 0.99$) with the first PC of the standard PCA.

In all further analyses of community structure I used the body size, tarsus to tail length, and beak shape axes from the two-step PCA because they are realistic—as shown by the correlation with two axes from the standard PCA approach—and because they also provide an index of beak shape as an additional, more interpretable axis of the foraging niche.

Power analyses

Simulations revealed that, when the only active process during community assembly was either habitat filtering or competitive exclusion, standard trait-based 'multi-pattern, multi-niche-axis' metrics—FD and CHV—had high power to detect the correct assembly process (Fig. 3 and Fig. S6). However, of particular importance to delimiting the scale at which processes operate, when habitat filtering and competition were both active in community assembly at a ratio of 75:25, or 50:50, FD and CHV had low or very low power to detect the dominant process or either process, and detected competition over habitat filtering in the 50:50 scenario. Although when the ratio of habitat filtering to competition was 25:75 they had relatively high power to detect competition as the dominant process. The 'multi-pattern, multi-niche-axis' phylogenetic metrics—MPD and MNTD—generally had even lower power to detect habitat filtering and competition than the trait-based metrics (Fig. 3 and Fig. S6).

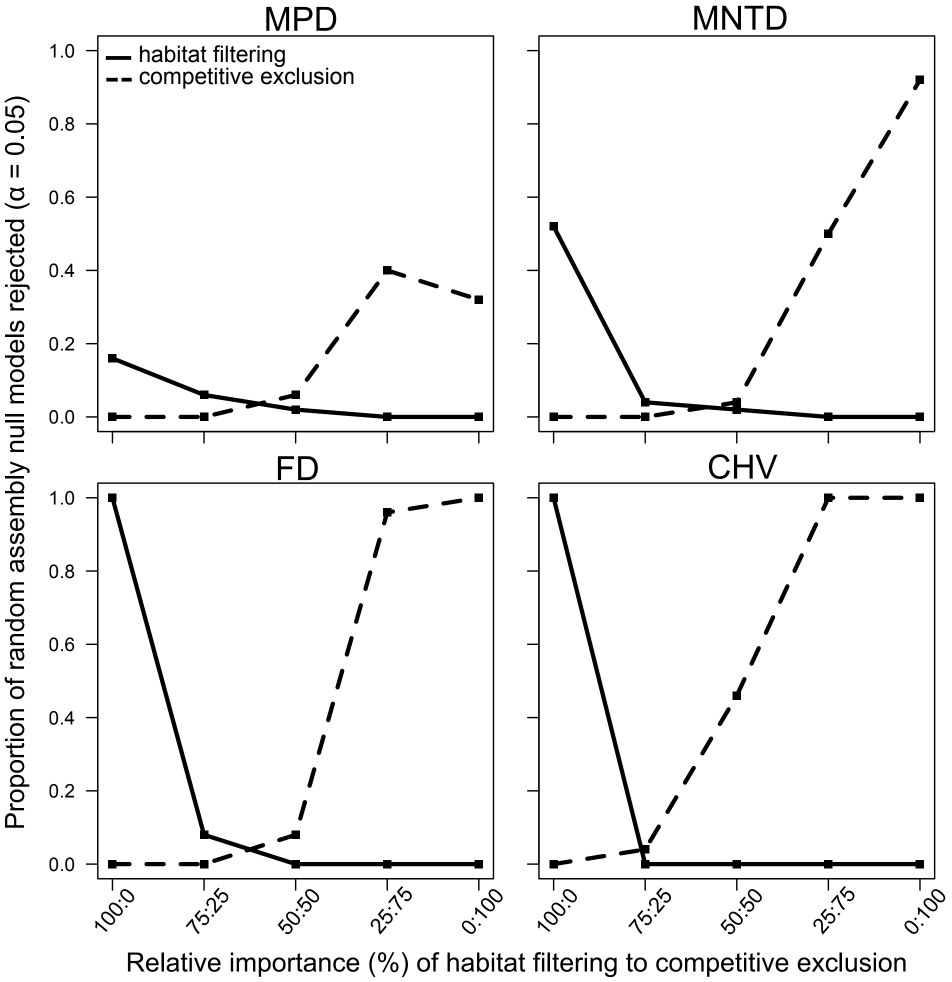

Figure 3. The power of multi-pattern, phylogenetic and functional trait metrics—mean phylogenetic distance [MPD]; mean nearest taxon distance [MNTD]; Functional diversity [FD]; Convex hull volume [CHV]—to reject correctly the random community assembly null model in favor of either habitat filtering or competitive exclusion. Assembly models were tested under five scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. Each metric was calculated using multiple niche axes, and each species is a composite of three traits: body size, locomotory traits and beak traits. During community assembly simulations, body size was subjected directly to habitat filtering and competitive exclusion, locomotory traits to habitat filtering only, and beak shape to competitive exclusion only. See methods for further details of trait and community simulations, null models, and statistical tests.

In contrast, the trait-based ‘multi-pattern, single-niche-axis’ metrics—FD, Variance, and Range—had high power to detect the signature of competition at all levels of its relative importance when used on a trait axis (beak shape) on which only competition was acting directly (Fig. 4 and Fig. S7). Variance and Range also had high power to detect habitat filtering at all levels of its relative importance when it was the only process acting directly on body size (Fig. 4), but these metrics were not as successful in detecting the signature of habitat filtering when it was the only process acting directly on locomotory trait structure (Fig. S7). ‘Multi-pattern, single-niche-axis’ metrics also improved on ‘multi-pattern, multi-niche-axis’ metrics by more often detecting the dominant niche-based process when multiple processes were active on a single niche axis (body size; Fig. S6 and Fig. S7). However, the main difficulty for ‘multi-pattern, single-niche-axis’ metrics arose when there was the combination of habitat filtering and competition acting directly on the same niche axis, as under these scenarios FD, Variance, and Range were also often unable to reject the random assembly null model (Fig. 4 and Fig. S7). In addition, FD and Variance (for body size; Fig. 4), and Variance and Range (for locomotory traits; Fig. S7) detected regular spacing when competitive exclusion had not acted directly on the axis being tested, but was the sole process active in community assembly (i.e. acting on other trait axes).

The ‘single-pattern, single-niche-axis’ metric, SDNDr, had low power to detect competition on beak shape, the axis on which only competition was acting directly, but had higher power to detect competition on the body size axis (Fig. 4 and Fig. S7). However, SDNDr was also sensitive to habitat filtering on all three trait axes.

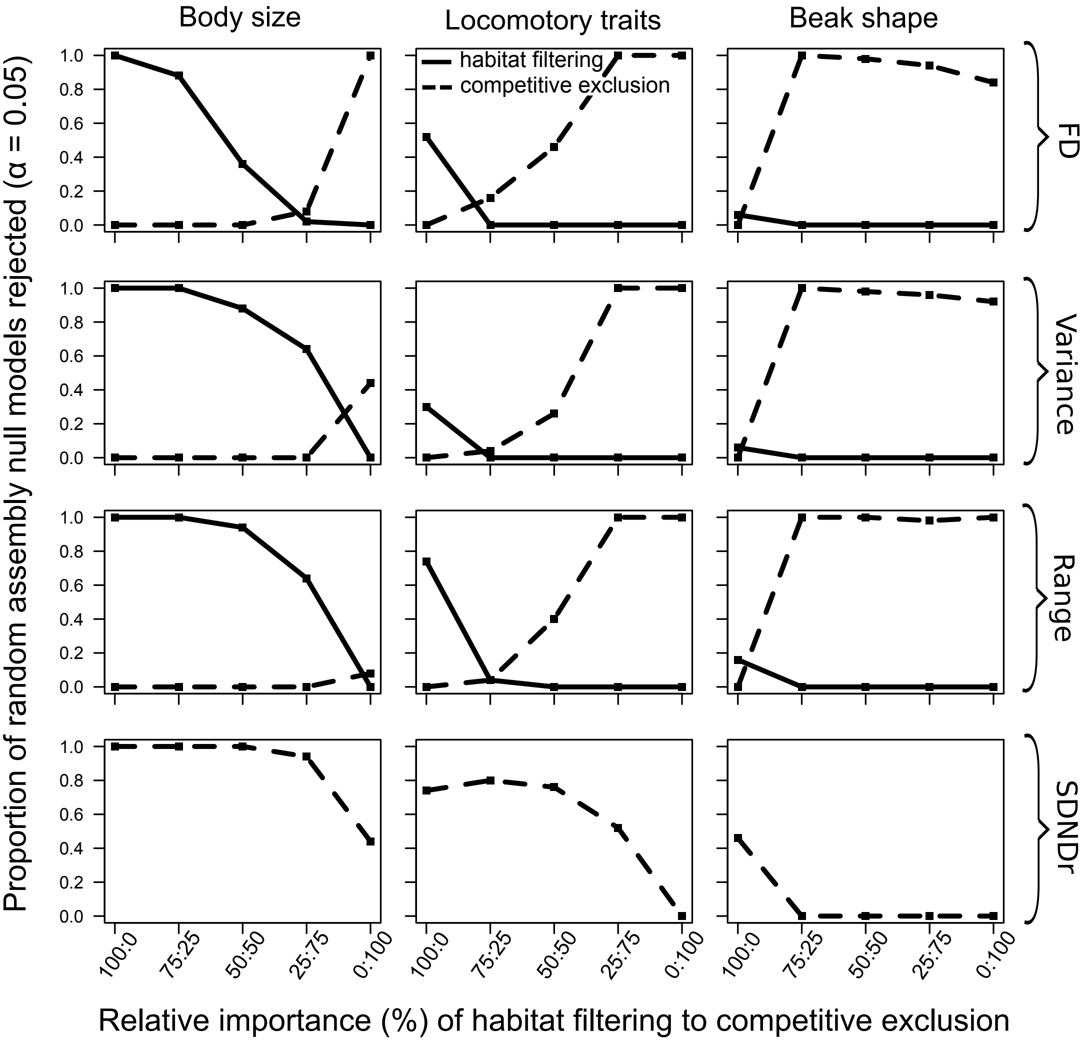

Figure 4. The power of multi-pattern and single-pattern trait metrics, calculated using only a single niche axis, to reject the random assembly null model in favor of either habitat filtering or competitive exclusion. Assembly models were tested under five scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. Functional Diversity [FD] and Standard deviation in neighbour distances divided by range [SDNDr]. Each species is a composite of three traits: body size, locomotory traits and beak traits. During community assembly the locomotory trait axis was subjected directly to habitat filtering and competitive exclusion, body size to habitat filtering only, and beak shape to competitive exclusion only. SDNDr is a single-pattern metric focused only on the detection of competitive exclusion and so a one-tailed test was used. See methods for further details of trait and community simulations, null models, and statistical tests.

Multi-niche-axis tests of bird community assembly

For trait-based metrics, I found no significant deviation from the random assembly null model expectation for bird community structure at any spatial scale for either FD or CHV (Table 1; Fig. 5). Thus, according to these metrics community structure appeared to be purely stochastic. The only pattern that approached significance was of reduced volume (i.e. trait clustering) in observed CHV values at the 0.8 ha scale (Table 1).

When I tested the assumption of phylogenetic signal in traits I found that species body size, beak shape (trophic trait) and tarsus to tail length ratio (locomotory trait) showed significantly more phylogenetic signal than expected if the distribution of trait values were random with respect to phylogeny, but were less conserved than expected from a Brownian motion model of trait evolution (Table S5). Phylogenetic signal in primary habitat type was not significantly different from that expected under either a random, non-phylogenetic model (estimated $D = 0.65$, $P = 0.1$) or a Brownian motion model (estimated $D = 0.65$, $P = 0.09$). When I focused on community phylogenetic structure I found that observed structure was not significantly different from the null model at any spatial scale for either MNTD or MPD (Table 1). Some habitat filtering was evident, at least at the study site scale, as the node at the base of the *Synallaxis* and *Asthenes* clade was significantly over-represented in non-forest habitat (Fig. 2). However, this was the only node significantly over- or under-represented in any habitat type.

Table 1. Results of 'multi-pattern, multi-niche-axis', trait and phylogenetic tests for habitat filtering and interspecific competition using functional diversity (FD), convex hull volume (CHV), mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD).

	Trait-based metric				Phylogeny-based metric			
Spatial scale (ha)	FD	*P*	CHV	*P*	MPD	*P*	MNTD	*P*
0.8	0.125 ± 0.11	0.26	0.014 ± 0.11	0.06	0.130 ± 0.10	0.38	0.030 ±0.11	0.91
1.6	0.002 ± 0.15	0.88	–0.130 ± 0.13	0.16	0.000 ± 0.15	0.80	–0.140 ± 0.17	0.38
3.2	0.010 ± 0.22	0.96	–0.175 ± 0.20	0.26	0.050 ± 0.20	0.52	0.050 ± 0.42	0.73
6.4	0.006 ± 0.43	1.00	0.088 ± 0.40	0.36	0.140 ± 0.24	0.43	0.050 ± 0.42	0.91

Note: Values are Mean SES ± SE (SES = standard effect sizes, calculated as observed value – null model mean, divided by sd of the null model distribution, averaged across all observed communities at each spatial scale). Positive SES indicates even spacing; negative SES indicates clustering (relative to the expected null model trait spacing or relatedness of the community.

Table 2. Results of ‘multi-pattern, single-niche-axis’ and ‘single-pattern, single-niche-axis’ trait metric tests for habitat filtering and interspecific competition across spatial scales.

	FD		Variance		Range		SDNDr	
Trait and Spatial scale (ha)	SES ± SE	*P*	SES ± SE	*P*	SES ± SE	*P*	SES ± SE	*P*
Body size (PC1):								
0.8	0.050 ± 0.10	0.11	0.032 ± 0.13	0.28	0.042 ± 0.12	0.70	–0.012 ± 0.13	**<0.05**
1.6	–0.111 ± 0.20	0.77	–0.013 ± 0.18	0.96	–0.024 ± 0.17	0.87	–0.033 ± 0.17	0.48
3.2	0.196 ± 0.18	0.10	–0.011 ± 0.24	0.83	0.114 ± 0.23	0.42	0.124 ± 0.21	0.86
6.4	–0.127 ± 0.31	1.00	-0.039 ± 0.44	0.82	–0.147 ± 0.44	0.82	–0.157 ± 0.33	0.46
Trophic traits (PC2)†:								
0.8	–0.142 ± 0.15	0.82	–0.115 ± 0.14	0.78	–0.166 ± 0.14	0.76	–0.235 ± 0.13	**<0.05**
1.6	–0.077 ± 0.22	0.65	–0.114 ± 0.18	0.88	–0.079 ± 0.19	0.58	–0.069 ± 0.20	0.15
3.2	–0.126 ± 0.30	0.47	–0.059 ± 0.30	0.93	–0.067 ± 0.29	0.93	–0.120 ± 0.25	0.25
6.4	–0.094 ± 0.28	0.16	–0.069 ± 0.40	0.65	–0.087 ± 0.29	0.25	0.004 ± 0.31	0.33
Locomotory traits (PC2)‡:								
0.8	–0.138 ± 0.11	0.28	–0.085 ± 0.10	**<0.01**	–0.123 ± 0.10	**<0.05**	–0.191 ± 0.08	**<0.01**
1.6	–0.159 ± 0.16	0.17	–0.065 ± 0.15	0.30	–0.098 ± 0.14	0.46	–0.144 ± 0.13	**<0.05**
3.2	–0.169 ± 0.27	0.58	–0.034 ± 0.23	0.67	–0.093 ± 0.23	0.67	–0.196 ± 0.17	0.11
6.4	–0.034 ± 0.41	0.73	0.043 ± 0.33	0.65	–0.030 ± 0.32	0.65	–0.171 ± 0.25	0.25

Note: values are Mean SES ± SE (SES = standard effect sizes, calculated as observed value – null model mean, divided by SD of the null model distribution, averaged across all observed communities at each spatial scale).

P-values are for Wilcoxon signed-ranks tests.

†Beak shape.

‡Tarsus to tail length ratio.

Single-niche-axis tests of bird community assembly

In contrast to multi-niche-axis metrics, single-niche-axis approaches revealed complex non-random patterns of trait values within communities at smaller spatial scales (Table 2; Fig. 5). Specifically, I detected the signal of both clustering and regular spacing in locomotory traits at small spatial scales (0.8–1.6 ha), and the signal of regular spacing in body size and trophic traits (beak shape) at the smallest spatial scale (0.8 ha). The 'multi-pattern, single-niche-axis' metrics—Variance and Range—detected clustering in species trait values for tarsus to tail length ratio, with significantly reduced values for tarsus to tail length ratio in observed communities at the 0.8 ha scale. Beak shape and body size showed no significant reduction in Variance or Range at any spatial scale. The 'single-pattern, single-niche-axis' metric, SDNDr, detected a pattern of regular spacing of species trait values for body size, tarsus to tail length ratio, and beak shape, as the observed community values for these traits were significantly shifted below the null model expectation within communities at the 0.8 ha scale. At the 1.6 ha scale only tarsus to tail length ratio showed significant regular spacing. No traits showed clustering or regular spacing at larger spatial scales.

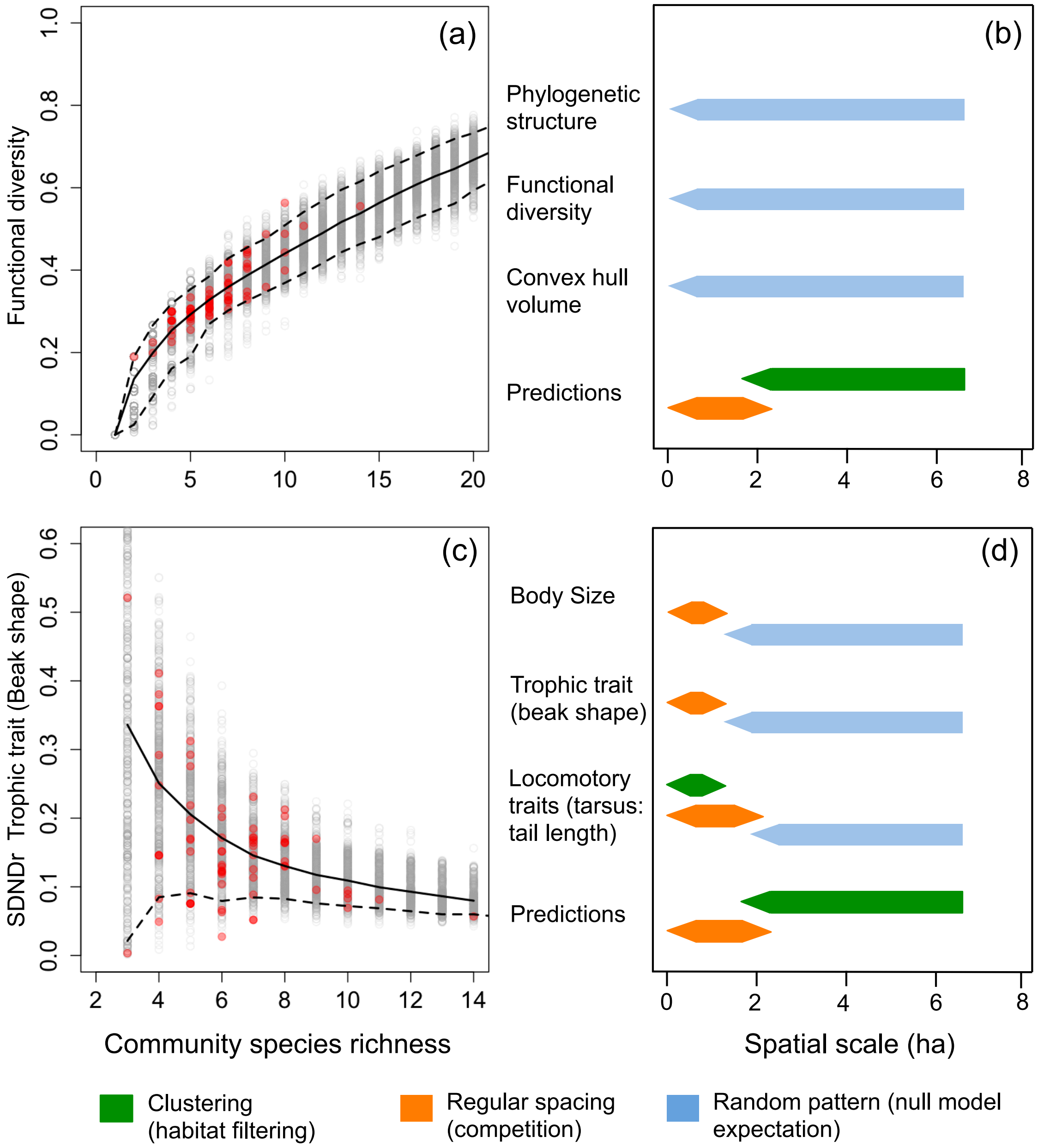

Figure 5. (a) Observed community functional diversity (FD) values (red) do not differ significantly from the distribution of null community values (gray) at the 0.8 ha scale; mean (solid line) and 95% confidence interval (dashed lines). (b) No 'multi-pattern, multi-niche-axis' phylogenetic or trait-based test rejects the null model at any spatial scale. (c) The distribution of a 'single-pattern, single-niche-axis' metric (SDNDr) is significantly shifted below the null expectation mean, suggesting that beak shapes are more regularly spaced than expected under random assembly at the 0.8 ha scale. Only one interval is indicated because the test is one-tailed. (d) Testing individual trait axes using single-niche-axis metrics yielded significant deviation from the null expectation, consistent with habitat filtering and competition structuring communities at smaller scales.

The role of habitat heterogeneity

The first PC (Habitat PC1) from the habitat PCA explained 71% of the variation in habitat data and was interpreted as an index of vegetation structure (Table S6); increasing values are associated with more forested habitat, including increased maximum canopy height and tree cover, and decreased grass and shrub cover. There was spatial autocorrelation in vegetation structure across 0.8 ha survey sites (Mantel test: $r = 0.23$, $P < 0.001$, $N = 72$, 10,000 permutations). However, this effect decayed to zero at distances greater than those separating neighbouring 0.8 ha survey points (Fig. S5), indicative of increased habitat heterogeneity for communities at larger spatial scales.

At the 0.8 ha scale, there was a positive relationship between vegetation structure (log Habitat PC1) and the rank in the null distribution of community mean tarsus to tail length ratios ($\beta = 1.94$, $r^2 = 0.25$, $P < 0.001$, $N = 72$). This shows that tarsus to tail length ratios were higher than expected by chance for species in forested sites, and lower for those in non-forest sites. These results imply that communities at larger spatial scales encompass forest and non-forest vegetation, and thus contain sets of species with both higher and lower than expected tarsus to tail length ratios, weakening the signal of habitat filtering (i.e. clustering in tarsus to tail length).

DISCUSSION

Disentangling multiple assembly processes

My simulation analyses show that multi-niche-axis phylogenetic and trait-based metrics have low power to detect competition and habitat filtering when these processes act simultaneously on community assembly. This confirms previous suggestions that such metrics—because they measure the net effect of different assembly processes—may be ineffective at differentiating niche-based processes from neutral dynamics because multiple niche-based processes can cancel each other out (Kraft et al. 2007; Swenson and Enquist 2009; Weiher et al. 2011). Similarly, I show that these methods can oversimplify assembly dynamics by detecting a single niche-based process when multiple processes co-occur. This problem can arise either when subordinate processes are overlooked, or when multiple processes are equally influential, in both cases exaggerating the impression that assembly processes occur in isolation rather than in combination.

These findings cast doubt on numerous trait-based analyses using multi-niche-axis metrics to detect processes acting simultaneously. This approach is often supported with reference to previous simulation studies, several of which have shown FD and CHV to be powerful metrics for detecting niche-based processes. However, these studies either did not evaluate trait metrics under conditions when both habitat filtering and interspecific competition act simultaneously (e.g. Mouchet et al. 2010), focused community assembly on single trait axes (Mason et al. 2013), or applied assembly processes equally across all trait axes (e.g. Aiba et al. 2013; Mason et al. 2013). Therefore, previous studies do not address many of the cases in community assembly where multiple processes differ in their relative importance across multiple niche axes (Chesson 2000), as seems likely when testing for assembly processes across spatial scales.

When I applied multi-niche-axis trait (FD and CHV) and phylogenetic (MPD and MNTD) metrics to the observed study communities, none of them detected significant deviations from the random assembly null model expectations (Table 1 and Fig. 5). Although the absence of any phylogenetic or trait clustering may be relatively uninformative, as the influence of habitat filtering is often assumed to be weak at these scales (0.8–6.4 ha), the lack of evidence for overdispersion of functional traits or phylogenetic relationships is perhaps more surprising, as these are signals of species interaction that are expected to strengthen as spatial scale decreases (Swenson et al. 2007; Cavender-Bares et al. 2009). Nonetheless, an absence of both clustering and overdispersion in traits and phylogenies has been reported fairly widely in plants and animals at local scales, and is typically interpreted as evidence for a neutral model of community assembly (e.g. Gómez et al. 2010; Thompson et al. 2010).

A strongly contrasting set of patterns was detected when I applied single-niche-axis metrics (FD, Variance, Range, and SDNDr) to simulated and observed community data. Simulations revealed that these metrics are able to detect the action of both competition and habitat filtering across a wide range in the relative importance of either process (Fig. 4). In conjunction, empirical tests showed that both assembly processes act together to structure tropical bird assemblages (Table 2 and Fig. 5). These non-random patterns reject neutral assembly models, and suggest instead that habitat filtering and interspecific competition act simultaneously on locomotory traits, while interspecific competition acts on body size and beak shape, at the 0.8–1.6-ha scale. Much previous work has debated the scales at which habitat filtering and interspecific competition are influential in community assembly, with broad agreement that habitat filtering is most important at larger scales and niche differentiation at smaller scales (Weiher and Keddy 1995; Swenson et al. 2006; Weiher et al. 2011). However, my results contradict this view by suggesting that both habitat filtering and interspecific competition structure bird communities at small spatial scales by acting simultaneously on the same and independently on separate niche axes.

Differences in the results of multi- and single-niche-axis approaches to the observed community datasets agree with contrasts in the expected power of these alternative approaches obtained from my simulation study. I have shown that, when multiple processes act together, multi-niche-axis metrics either fail to detect any assembly process, or else detect a single process when two are operating in conjunction, even if both are equally prevalent. I thus infer that random patterns in trait and phylogenetic structure detected by multi-niche-axis metrics may simply be an emergent property of the simultaneous action of contrasting niche-based processes, even when one process is dominant. Here, it is important to differentiate between detecting the presence of an assembly process and its relative importance. Metrics focussed on single axes may be less likely to combine the signal of multiple processes and thus more likely to detect the full set of processes present in community assembly at a given scale. In contrast, multi-axis metrics may provide an integrated assessment of community assembly, but can often have low power to detect even dominant processes over random assembly and will generally only detect a single process. The key point is that such multi-niche-axis metrics may therefore generate misleading evidence of either neutrality or the partitioning of assembly processes across scales.

Implications for bird community assembly

The regular spacing detected in functional traits associated with locomotion and foraging is consistent with interspecific competition at the 0.8–1.6 ha scale, and implies that bird communities are structured by competitive exclusion through direct interspecific territory defence or indirect competition for resources. Although the evidence I present aligns closely with longstanding ideas about the importance of beak differences (Hutchinson 1959; Schoener 1965) and foraging microhabitat divergence (MacArthur 1958; MacArthur and Levins 1967) in promoting co-occurrence, it suggests that the spatial scale of these interactions can be highly localized. One possible reason is that the size of individual territories for many study species is likely to be only 1–2 ha (Kikuchi 2009), meaning that competing species can potentially co-occur in larger communities without coming into direct contact, thus weakening the signal of competitive exclusion. The reduced likelihood of direct competition at larger plot sizes may also explain why Gómez et al. (2010) found no evidence of competition structuring Neotropical antbird communities in plots of 100 ha, as the mean territory size of their study species is only ~5 ha (Terborgh et al. 1990). Also, by focusing within a single family, as opposed to all insectivorous bird species in a community, Gómez et al. (2010) may have excluded important interspecific competitive interactions.

Single-niche-axis metrics revealed not only regular spacing, but also clustering in functional traits, suggesting habitat filtering at small spatial scales (0.8–1.6 ha). The positive relationship I detected between vegetation structure and the mean locomotory trait (tarsus to tail length ratio) value of a community at the 0.8 ha scale suggests that habitat filtering is related to traits associated with foraging manoeuvre and substrate use, and specifically the consistent differences between traits in forest versus non-forest sites. This relationship between habitat type and community mean tarsus to tail length ratio also suggests that trait clustering is likely not due to a competitive hierarchy in these locomotory traits (Mayfield & Levine 2010; HilleRisLambers et al. 2012). I found no evidence of habitat filtering above a scale of 1.6 ha, probably because larger scale communities (3.2–6.4 ha) contained higher habitat heterogeneity, and thus aggregated small-scale communities with both higher and lower trait values. Community ecology studies generally predict an increasing importance of habitat filtering at larger spatial scales (Weiher and Keddy 1995; McGill 2010), and the fact that the relationship between habitat filtering and spatial scale is reversed in my study emphasizes that it is not spatial scale per se, but rather the degree of habitat heterogeneity that drives habitat filtering (Willis et al. 2010). This is a critical point suggesting that more attention should be focused on measuring environmental variables relevant to communities, and testing their effects on habitat-related niche axes, particularly at finer scales.

I have interpreted the regular spacing of functional traits as evidence of competitive exclusion, and clustering as evidence of habitat filtering, following many previous studies. However, I acknowledge that other processes may contribute to these patterns. For example, it has been proposed that social information gathering could influence spacing between conspecifics and even heterospecifics, potentially shaping community structure (Seppänen et al. 2007). Although I cannot rule out the contribution of social interaction among species, this process seems unlikely to lead to pervasive overdispersion or even clustering in functional traits at the scales I detect, particularly as most of the study lineages hold year-round territories. In addition, intraspecific variation could affect community dynamics by altering species' niche widths (Bolnick et al. 2011). Although this may lead to changes in patterns of niche overlap, the overwhelming majority of trait variation was among species and not individuals (Table S2), and I suspect that intraspecific variation is unlikely to drive the patterns I have detected. Considering only insectivorous species and within this set only traits related to foraging manoeuvre and prey item selection, it is possible that niche axes along which interspecific competition occurs may have been excluded. For example, competition for nesting sites or selection to reduce nest density and thus nest predation through the avoidance of nesting near species with similar nest site preferences (Martin 1993) may influence local co-occurrence patterns in birds, and occur among species of different trophic levels. Indeed, if nest site competition is important and if nesting behaviour is phylogenetically conserved, a broader phylogenetic sampling of the community would be appropriate to test for overdispersion because while some of the clades within the community phylogeny are exclusively insectivorous (e.g. Furnariidae), others have more closely related non-insectivorous relatives present within the study site (e.g. Conirostrum). Finally, migratory behaviour is another trait not considered here that may allow for the mediation of competitive interactions among species at times of low resource availability and thus the co-occurrence of more similar species than expected by chance when resource availability is high. However, while migration may be an important trait governing co-occurrence for more temperate avian communities, the majority of the insectivorous species surveyed for this study are resident and hold territories year-round (Merkord 2010).

My results add to a growing body of work seeking to understand the role of deterministic and stochastic processes across scales (Levin 1992; Chase and Myers 2011). The finding that species interactions and habitat filtering have strongest influence at small scales, on the order of individual territory sizes, may help to explain why random processes appear to dominate in structuring biodiversity across regional scales (Ricklefs 2011). However, my results are also consistent with the idea that niche-based processes minimize spatial overlaps between species sharing similar ecologies, potentially driving broad-scale species distribution patterns, particularly in tropical systems where the ranges of ecological competitors often abut (Terborgh and Weske 1975; Jankowski et al. 2010; Pigot and Tobias 2013). Further research is needed to determine whether similar processes structure communities in temperate systems where species only hold territories during the breeding season, potentially altering the intensity and spatial scale of competition (Gotelli et al. 2010).

Implications for tests of community assembly

Although my findings highlight problems with current multi-niche-axis trait and phylogenetic analytical approaches, they do not imply that such approaches should be abandoned. On the contrary, as confirmed by my simulations, these multi-niche-axis methods can provide an important tool for detecting whether any particular niche-based assembly process is dominant (e.g. Petchey et al. 2007). Moreover, multi-niche-axis trait-based metrics may make fewer assumptions about which niche axes are relevant to community assembly and can provide links between community assembly and ecosystem function (Cadotte et al. 2009; Thompson et al. 2010), while the equivalent phylogenetic approaches allow for analyses to be conducted when potentially important traits are difficult to measure (Cavender-Bares et al. 2009). Given these advantages, an important target for future research is to investigate whether the sensitivity of such 'multi-pattern, multi-niche-axis' metrics can be increased, for example by systematically adjusting the weighting of a trait to test for its influence on the overall trait pattern.

Until such methods are developed, single-niche-axis metrics can provide a useful solution because—as my analyses demonstrate—they are better able to detect and tease apart the signals of multiple assembly processes, particularly when these processes act on separate niche axes. In addition, by focusing on single axes these metrics can make it much easier to interpret the action of niche-based processes on specific niche axes. An inherent challenge of single-niche-axis methods is to approximate niche axes from trait data, and I have shown that this is not always achievable using the classic approach of a multivariate PCA, as this may combine information from multiple niche axes on a single principal component axis. As an alternative, I introduce a novel technique of performing separate PCAs on groups of traits according to their acknowledged relevance to particular niche axes (Fig. S2). The main advantage of this approach is that specific tests of assembly processes can be focused exclusively on independent niche dimensions identified by *a priori* hypotheses. For example, species interactions can be tested on trophic traits separately from locomotory traits, as some of the latter are not expected to mediate interspecific competition, and indeed may blur the signal of competitive exclusion.

My results suggest that single-niche-axis metrics can struggle in two different scenarios. First, the power of multi-pattern metrics is reduced when multiple processes act on a single niche axis. Second, both multi-pattern and single-pattern metrics can sometimes wrongly detect the signal of a process when that process is absent on the trait axis being tested but of high relative importance on another axis, even when the axes are uncorrelated (Fig. 4). For example, my simulations show that SDNDr, a single-pattern metric for competition, is also sensitive to habitat filtering and so should be interpreted cautiously if other metrics detect clustering on the same axis. Similarly, the lower power of SDNDr to detect regular spacing in the trophic trait (beak shape) dataset suggests that some single-pattern metrics may have lower power for trait axes with lower variance, where perhaps assembly patterns are weaker than on axes with higher variance. Thus, I recommend against the use of multi-pattern metrics such as Variance and Range in single-pattern, one-tailed hypothesis tests, as has been advocated previously (e.g. Kraft and Ackerly 2010; Aiba et al. 2013). I also recommend the complementary use of both multi-pattern and single-pattern metrics focused on single niche-axes as this can enable detection of insensitivity or error in the metrics. Further research is required to develop metrics that are sensitive to only one of clustering or overdispersion, and that are also robust to differences in trait variance and to the action of assembly processes across multiple axes.

The simulation approach used in this study applied a habitat filter where a predefined number of species furthest away from the randomly selected trait value were removed from the species pool. Although this process might appear to select an optimum trait value it is actually a binary (i.e. in/out) filter on community membership. Evidence for strong binary filters on community does exist. For example, the ability to tolerate freezing temperatures acting as a binary habitat filter in high latitude plant communities (Woodward and Williams 1987). However, other habitat filters may instead act as optimality filters where species closer to a trait optimum have higher fitness while those further away are still able to survive and reproduce at the site. Species further away from the trait optimum may then be more susceptible to exclusion due to interspecific competition or other biotic interactions. In this study, some foraging substrates available in forest habitats (e.g. gleaning insects from twigs and leaves in the mid-story and canopy) are absent in the grassland and thus the habitat filter on community membership may be closer to a binary than an optimality filter for some forest species. In contrast, for other species such as terrestrial foraging insectivores foraging substrate features may act more as an optimality filter on community membership as particular foraging substrates are reduced but not absent in either grassland or forest. In addition, biotic interactions not considered here such as the influence of avian malaria pathogens on community membership may also act as optimality filters or even binary-like filters in extreme cases where mortality is close to 100% for some species, such as has occurred with the introduction of avian malaria to Hawaii (Atkinson et al. 1995). The effect of optimality filters on community composition is expected to be more evident in patterns of abundance than in species occurrence. This is because species further from the trait optimum for a given site have lower fitness at that site, resulting in lower abundance but not necessarily absence from the site. Thus, further work considering optimality filters should use models of community assembly and diversity metrics that incorporate abundance information.

The study of community assembly processes has advanced rapidly in recent decades, driven in part by the development of sophisticated analytical techniques (Cavender-Bares et al. 2009). In general, the tendency has been to develop methods for pooling together as much information as possible, with recent studies even advocating the combined analysis of multiple trait and phylogenetic axes (Cadotte et al. 2013). While such all-inclusive approaches have a number of advantages, my analyses indicate that they can obscure the nuances of community assembly over time and space. This finding supports a recent counter-trend in community ecology which proposes, not the integration of datasets, but their subdivision into niche axes before analysis (see Adler et al. 2013). I suggest that studies of community assembly need to consider both inclusive and more targeted approaches to tease apart the influence of multiple assembly processes on community structure.

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CHAPTER 3

Detecting the influence of niche-based processes on community assembly: an evaluation of functional and phylogenetic metrics

ABSTRACT

Functional trait and phylogenetic diversity measures have been widely used to distinguish between niche-based (e.g. competition and habitat filtering) and neutral models of community assembly. However, because these metrics often fail to detect non-random community structures, an improved understanding of their statistical performance under conditions closer to those in natural communities is required. Here, I use simulations to explore the power of single and multi-trait-axis metrics to detect clustering and overdispersion under four commonly expected scenarios: (1) multiple niche-based processes influence community assembly; (2) niche-based processes vary widely in their relative importance; (3) niche-based processes act on only partly overlapping sets of traits, and the number of traits sampled for metric calculation that have been exposed to a given process varies; (4) for the traits exposed to a given niche-based process, the signal of the process varies among the traits. Metrics often had low power to reject random assembly when multiple niche-based processes were important for community assembly. Trait metrics had greater power than phylogenetic metrics. Most trait metrics detected clustering better than overdispersion, and had lowest power when competition was dominant. Single-trait-axis metrics outperformed multi-trait-axis metrics when a combination of processes was active in community assembly, but only when applied to traits exposed to a single assembly process. The power of multi-trait-axis metrics to detect a particular process was increased both when the proportion of traits exposed to the process was increased among the sampled traits used to calculate the metric, and when one of these sampled traits was of greater relative importance for that process. Convex hull volume and the ratio of the minimum to the maximum branch length of the minimum spanning tree were the most robust multi-trait-axis metrics for detecting clustering and overdispersion, respectively. These results suggest that trait diversity measures should be preferred to phylogenetic metrics whenever possible. In addition, to increase multi-trait-axis metric power, rather than screening all traits, traits should be grouped by their hypothesized relevance for a specific niche-based process, and the appropriate set of metrics applied to test for non-random structure in each set.

INTRODUCTION

The structure of biological communities should reflect the ecological and evolutionary processes that determine their assembly (Elton 1946; MacArthur and Levins 1967; Webb et al. 2002). Many studies have therefore used metrics of community functional trait and phylogenetic structure to test for the influence of niche and neutral processes in community assembly (reviewed in Cavender-Bares et al. 2009; Vamosi et al. 2009; Pavoine and Bonsall 2011; Götzenberger et al. 2012). Empirical research has focussed on the detection of trait or phylogenetic clustering due to habitat filtering, and on overdispersion (evenness) due to negative biotic interactions, especially interspecific competition, with results suggesting that either one or both of these niche-based processes influences community assembly (Kraft et al. 2008; Ingram and Shurin 2009; Vamosi et al. 2009). In addition, several trait and phylogenetic metrics of community structure used in community ecology are also frequently used to test for relationships between biodiversity and ecosystem functioning (e.g. Cadotte et al. 2009; Mouillot et al. 2011). Thus, trait and phylogenetic diversity measures are central to much contemporary ecological research that seeks to identify the mechanisms underlying community assembly and ecosystem functioning, and to draw links between these (Pavoine and Bonsall 2011; Naeem et al. 2012).

However, we still lack an understanding of the ability of these metrics to detect individual niche-based community assembly processes when community assembly is more complex than the simple, deterministic action of a single niche-based process (Kraft and Ackerly 2010; Mouchet et al. 2010). Complex community assembly scenarios involving multiple processes are expected to be relatively common in nature (Vellend 2010), with empirical evidence for multiple niche-based assembly processes operating across multiple trait axes (Ingram and Shurin 2009; Spasojevic and Suding 2012; Kraft and Ackerly 2010). Research is thus shifting away from asking if an individual assembly process is valid to instead asking what set of processes is present and what is the relative importance of each assembly process. Uncertainty concerning the performance of trait and phylogenetic metrics when multiple processes influence community assembly therefore limits the interpretation of many existing empirical studies (Götzenberger et al. 2012; Aiba et al. 2013), complicating the selection of appropriate metrics for future research.

Recent simulation studies suggest that when multiple niche-based processes such as habitat filtering and competitive exclusion influence community assembly, both trait and phylogenetic metrics may decrease in their power to detect a given process (Kraft and Ackerly 2010; Aiba et al. 2013; Chapter 2 of this thesis). However, these studies considered only a limited set of scenarios, failing to address four key factors necessary for an improved understanding of metric performance under more complex community assembly scenarios. First, most existing metrics can be classified into two groups: those that measure trait patterns on single trait axes and those that measure patterns in multiple-trait-axis space. Due to the likelihood of phylogenetic signal in multiple species traits, phylogenetic metrics are generally interpreted as multi-trait-axis metrics. Previous studies assessing the performance of single-trait-axis metrics constructed artificial communities using only a single trait axis (Kraft and Ackerly 2010; Mason et al. 2012; but see Chapter 2 of this thesis). Thus the ability of single-trait-axis metrics to detect assembly processes under more realistic, multiple-trait-axis community assembly remains unclear. Second, many metrics may detect both clustering and overdispersion. Multi-trait-axis metrics of this type, by presumably integrating multiple axes of niche space, are thought to provide more inclusive assessments of community structure and thus identify the dominant niche-based process governing community assembly (Cornwell et al. 2006; Petchey et al. 2007). However, there is no reason to assume that multi-trait-axis metrics will necessarily detect the dominant niche-based process (e.g. Swenson and Enquist 2009). Indeed an influential simulation study by Kraft et al. (2007) on the power of community phylogenetic metrics suggested that these metrics would have reduced power to detect non-random structure when both habitat filtering and competition act during community assembly, but tested metric performance only for scenarios where a single assembly process was active. Therefore, for multi-trait-axis metrics we require a better understanding of how their power to detect niche-based processes changes across a wide range in the relative importance of each niche-based process, especially when multiple niche-based processes influence community assembly. Third, previous simulation studies that have considered multiple trait axes in community assembly applied niche-based assembly processes equally to all trait axes (Mouchet et al. 2010; Aiba et al. 2013). Yet, this is unlikely to be the prevailing case in nature where instead niche-based processes such as habitat filtering and competition may act on different, nested or only partly overlapping sets of traits (Spasojevic and Suding 2012; Ingram and Shurin 2009; Chapter 2 of this thesis). Moreover, in any empirical treatment there will likely be unequal sampling of the trait axes exposed to each process, especially when traits are not independent. Therefore, I need to know how robust multi-trait-axis metrics are to changes in the number of trait axes used in an analysis that have been exposed to one or more niche-based process. Finally, the signals of particular niche-based processes are likely to vary across different traits. For example, interspecific competition related to foraging location may be stronger than that for prey item selection in birds (MacArthur

1958). Thus, overdispersion may be more pronounced for traits related to foraging substrate and manoeuvre (e.g. tarsus length) than for those related to prey item selection (e.g. beak shape). However, this is rarely known a priori, and so most studies simply scale traits to have equal variance, and thus equal weight, in the calculation of multi-trait-axis metrics (Petchey and Gaston 2006; Cadotte et al. 2009; Villéger et al. 2008). The consequence of this re-scaling for the ability to detect niche-based assembly processes is unclear.

Here, to address these four uncertainties in metric performance, I evaluated the statistical power of phylogenetic, multi- and single-trait-axis metrics to detect clustering due to habitat filtering, and overdispersion due to limiting-similarity-based competition, under the following conditions: (1) community assembly involving multiple trait axes; (2) across a wide range in the relative importance of competition and habitat filtering for community assembly; (3) competition and habitat filtering acting on only partly overlapping sets of trait axes, and with variation in the number of traits exposed to either process used in metric calculations; and (4) when traits differed in the signal of either competition or habitat filtering, and were scaled before analyses. In addition, because variation in the proportion of species from the regional pool that are present in the local community is known to affect metric performance (Kraft et al. 2007; Aiba et al. 2013), I evaluated metric performance at three species richness levels. I discuss the robustness of the metrics under the different scenarios, and provide guidelines for the use of the metrics to test for the influence of niche-based processes on community structure and for estimating the relative importance of niche-based processes.

METHODS

Community assembly simulations

I generated 1000 regional communities, each consisting of 100 species. The phylogenetic relationships for each regional community were simulated under a constant-rate pure birth model. Each species had three trait values (traits X, Y and Z). Traits were continuous, and species trait values for each regional community were evolved under a constant-rate Brownian motion model. The variance under Brownian motion for each trait was set to one and the covariance among traits was set to zero (Fig. 1a). This resulted in the same order of magnitude for the variance for each trait. To test how an increase in the relative importance of a trait axis for either competition or habitat filtering affected metric power, two additional sets of 1000 regional communities with unequal trait variances were simulated. In one set, the variance of trait Y, and in the other set, the variance of trait Z was increased to 10, while the remaining trait variances were fixed at one (Fig. 1b). Thus, in total, there were three sets of 1000 regional communities.

This simulation approach generated regional pool phylogenies that were ultrametric, had a distribution of tree topological imbalances centred around zero (Colless Imbalance = 0.22 ± 0.02 [mean ± se]; Fig. S1 in Appendix S2), and phylogenetic signal in traits matching that expected under Brownian motion (median Blomberg's K = 0.92; Fig. S2 in Appendix S2). Thus the vast majority of the regional phylogenies lie within the parameter space in which community phylogenetic metrics are expected to have the greatest power to detect habitat filtering and limiting-similarity-based competition (Kraft et al. 2007; Vellend et al. 2011). The correlation among traits was low (Fig. S3 in Appendix S2), so there was no need for the use of ordination techniques to derive independent trait axes.

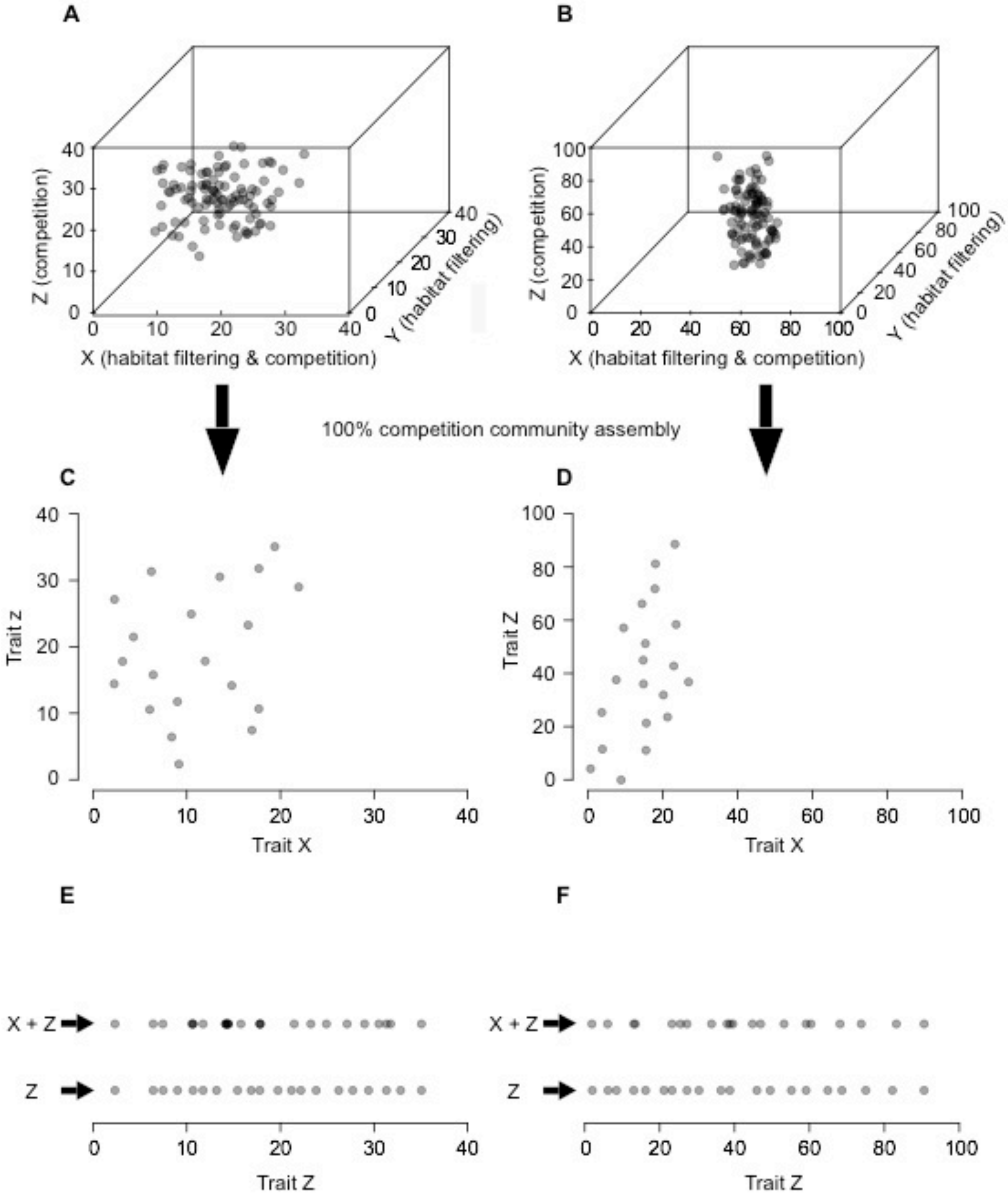

Figure 1. Trait values for the 100 species in the regional species pool for (A) the equal trait variance assembly model and (B) increased variance in trait Z. Species overlapping in trait space are shown as darker shading. Species trait values for the 20 species in the local community after community assembly under limiting-similarity-based competition showed more even spacing along both trait axes for the equal trait variance (C) than the unequal variance scenario (D). However, the spacing of species trait values along trait axis Z showed less even spacing in the unequal (F) vs the equal (E) variance scenario (labelled as X+Z in E and F). Overdispersion on trait Z was greater still when competition was focussed on only trait Z (labelled as Z in E and F).

Each local community simulation started with all 100 species in a regional pool, and species were removed until a given local species richness was reached (Fig. 1). Because variation in the proportion of species from the regional pool that are present in the local community is known to affect metric performance (Kraft et al. 2007; Kraft and Ackerly 2010), local richness values of 20, 50, and 80 were set for the equal trait variance scenario. So that multiple processes operated on only partly overlapping sets of traits, habitat filtering was applied to traits X and Y, and competition was applied to traits X and Z.

Local communities were assembled from regional communities in two steps. First, in the habitat-filtering algorithm a 'local optimum' value for trait X and Y was selected at random from within the range observed in the regional community. Species were then removed based on their Euclidean distance from this point in trait space. Second, the limiting-similarity algorithm detected the pair of species with the smallest Euclidean distance between them in X by Z trait space and removed one species in the pair at random, repeating this process until the target local species richness had been reached. The phylogeny for each simulated local community was generated by pruning the species absent from the local community. These habitat filtering and competition algorithms have been used in previous assessments of metric power and are designed to generate trait distributions that mimic those found under the most deterministic form of the two assembly processes (Kraft et al. 2007; Kraft and Ackerly 2010; Mouchet et al 2010). The elimination of species based on Euclidean distance gave traits with larger variance greater importance in determining species occurrence. This is because distances among species along the high variance trait axis will be, on average, greater than those along the axes with lower variance (Fig. 1c and d).

To generate local communities under varying relative strengths of habitat filtering and competition, I varied the percentage of species removed via each process. I explored scenarios ranging from all species being removed due to a single process (100:0) to an equal number of species being removed due to each process (50:50) (i.e. Habitat filtering and limiting similarity in percentages of 100:0, 80:20, 60:40, 50:50, 40:60, 20:80, 0:100 respectively). Therefore each regional species pool in a set of 1000 was used to generate seven local communities, so that for the equal trait variance scenario 7000 communities were generated for each of the three local species richness levels. A further 7000 communities were generated for each of the two unequal trait variance scenarios, yielding 35000 communities in total. The packages Geiger (Harmon et al. 2008), Picante (Kembel et al. 2010), and apTreeshape (Bortolussi et al. 2006) in R (R Core Team 2013) were used for simulating phylogenies and traits, and for calculating phylogenetic descriptive statistics. R code for performing the community simulations is available in the supplementary materials (Appendix S2).

Trait and phylogenetic metrics

On the basis that they have been used frequently in past studies of community assembly and ecosystem functioning (Pavoine and Bonsall 2011; Petchey and Gaston 2006; Cadotte et al. 2009), I selected the following metrics: two phylogenetic metrics, mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD); seven multi-trait-axis metrics: functional diversity (FD), convex hull volume (CHV), functional divergence (FDiv), functional dispersion (FDis), minimum nearest neighbour distance (minNND), mean nearest neighbour distance (MNND), and the ratio of the shortest to the longest distance in a minimum spanning tree connecting species in multidimensional trait space (min/maxMST); and three single-trait-axis metrics: Trait range, trait variance and the standard deviation of the distances between neighbouring species along a trait axis, divided by the trait range (SDNDr) (see Table 1). In addition, with the exception of CHV, all trait-based, multi-trait-axis metrics were also applied to individual trait axes as single-trait-axis metrics.

Table 1: Metrics used for measuring community functional trait or phylogenetic structure. I indicate (with crosses) whether each metric is used as a multi (M) or single (S) trait-axis metric, and whether the metric is used to detect overdispersion (O) or clustering (C).

Metric	Abbreviation	Description	M	S	O	C	Reference
Mean phylogenetic distance	MPD	Mean of the pairwise phylogenetic distances between co-occurring species.	X		X	X	Webb et al. (2002)
Mean nearest taxon distance	MNTD	Mean of the phylogenetic distances separating each species from its closest co-occurring relative.	X		X	X	Webb et al. 2002
Functional diversity	FD	Measure of how dispersed species are in trait space. The sum of the branch lengths that connect species in the local community on a dendrogram of all species in the regional community, constructed using hierarchical clustering of species traits.	X	X	X	X	Petchey and Gaston (2002)
Convex hull volume	CHV	Smallest convex set in trait space enclosing all of the species trait values within the community. Analogous to a multivariate measure of the range of community trait values.	X		X	X	Cornwell et al. (2006)
Functional dispersion	FDis	Mean distance of species trait values to the centroid of multidimensional trait space. Single-trait-axis version uses mean on a trait axis instead of centroid.	X	X	X	X	Laliberté and Legendre (2010)
Functional divergence	FDiv	The deviation of the distances between species trait values and the centroid of the trait space from the mean distance of all species to the centroid. Single-trait-axis version uses mean on a trait axis instead of	X	X	X	X	Villéger et al. (2008)

Table 1(*Cont.*)

Metric	Abbreviation	Description	M	S	O	C	Reference
Minimum nearest neighbour distance	minNND	The minimum distance between two species in trait space.	X	X	X	X	Weiher et al. 1998; Stubbs and Wilson (2004)
Mean nearest neighbour distance	MNND	Mean distance between nearest neighbour species in trait space	X	X	X	X	Ricklefs and Travis (1980); Stubbs and Wilson (2004)
	minmaxMST	The ratio of the shortest to the longest distance in a minimum spanning tree connecting species in trait space.	X	X	X	X	Stubbs and Wilson (2004)
Range	Range	Trait range in the community		X	X	X	
Variance	Variance	Trait variance in the community		X	X	X	
	SDNDr	The standard deviation of the distances between neighbouring species along a trait axis, divided by the trait range in the community.		X	X		Kraft and Ackerly (2010)

Calculating trait and phylogenetic metrics

Multi-trait axis metrics were calculated using all three trait axes for each local community, and also for all paired combinations of the three trait axes (XY, XZ and YZ). Single-trait-axis metrics were calculated on each of the three trait axes for each local community. To test the robustness of the metrics to the scaling of trait axes to have equal variance, all of the metric calculations were performed, both with and without scaling traits, for the unequal trait variance scenarios. R code for calculating metrics and applying a range of null models was modified from the R packages picante (Kembel et al. 2010) and FD (Laliberté and Shipley 2012) and is available in the supplementary materials (Appendix S2).

Power analyses

For each simulated local community, the observed value, as well as the mean and standard deviation from 999 null model communities, was calculated for each metric. I used a null model that drew species at random from the regional species pool while maintaining the species richness of each local community. It was not necessary to use a more constrained null model such as the independent swap because there was no structure to the species occurrence data independent of that generated by the community assembly algorithms.

The analysis of each metric's power to reject the random assembly null model was performed in two steps. First, 100 sets of 10 local communities were generated for each of the seven ratios of habitat filtering to competition within an assembly scenario. This was done by selecting communities at random, without replacement, from the 1000 communities for a given ratio of habitat filtering to competition. Second, a Wilcoxon signed-ranks test was performed on each set of local communities and the proportion of tests rejecting the null hypothesis, out of the 100 tests for a given ratio of habitat filtering to competition, was recorded. This provided an estimate of the power of each metric. The Wilcoxon signed-ranks test assessed whether the distribution of the differences between local community metric values and their respective null model means was shifted significantly away from zero. A shift in observed values below zero is indicative of clustering and a shift above zero is indicative of overdispersion. Two-tailed tests were used for all metrics able to detect both clustering and overdispersion (See Table 1). However, following previous studies, a one-tailed test for a shift below zero was used for SDNDr because this metric is designed to test only for the reduction in the standard deviation of neighbour distances predicted to result from limiting-similarity-based competition (Kraft and Ackerly 2010; Aiba et al. 2013). To evaluate how metric performance was affected by the relative importance of traits for habitat filtering and competition, scaling traits before metric calculation and local species richness, I plotted the difference in a metric's power to reject the null model between the assembly scenario with 50 species and equal trait variance, and each of the alternative trait variance and species richness scenarios.

RESULTS

Comparison of multi and single-trait-axis metrics when: (1) community assembly involves multiple traits, and (2) niche-based processes vary in their relative importance.

Phylogenetic metrics had low power to detect competition, and only MNTD had high power to detect habitat filtering when it was the sole process important in community assembly (Fig. 2; Fig. 5). In contrast, when all three traits were used in metric calculation, trait-based, multi-trait-axis metrics generally had high power to reject the random assembly null model when only one niche-based process was important for community assembly (Fig. 2; Fig. 5). Exceptions to this were FDiv and min/maxMST for habitat filtering and FDiv for competition. When both habitat filtering and competition were active in community assembly, the power of most multi-trait-axis metrics to reject random assembly was reduced (Fig. 2). For the phylogenetic metrics, power was lowest when habitat filtering and competition were of equal importance or when competition dominated. Again, the trait-based multi-trait-axis metrics had generally higher power than phylogenetic metrics, but did still have very low power to reject random assembly at some combination of habitat filtering and competition (Fig. 2). Two exceptions to this were minNND and min/maxMST that maintained high power to detect competition at all levels of the relative importance of this process (Fig. 2). For habitat filtering, CHV was the most powerful metric, having high power to detect this process until habitat filtering was responsible for only 20% of species absences.

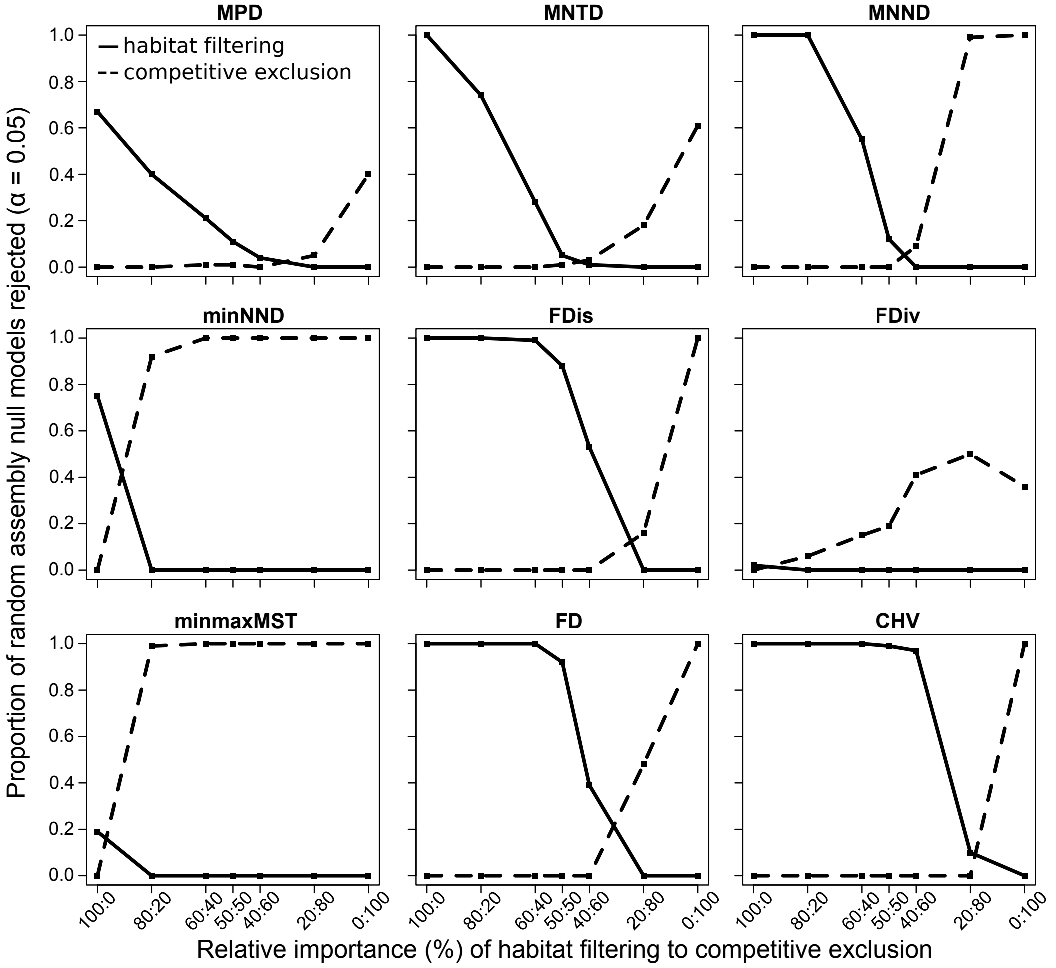

Figure 2. The power of phylogenetic and trait-based, multi-trait-axis metrics to reject the random assembly null model in favour of either habitat filtering or competitive exclusion when each metric was calculated using all three traits: trait X exposed to habitat filtering and competition, Y to habitat filtering, and Z to competition. See Table 1 for descriptions of each metric. The metrics were tested under seven community assembly scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. See methods for further details of trait and community simulations, null models, and statistical tests.

When trait metrics were applied to each trait axis individually, there was marked variance in metric performance both among metrics and across trait axes. Interestingly, and in strong contrast to their power as multi-trait-axis metrics, min/maxMST and minNND had very low power to reject the random assembly null model for any single trait axis, and at all combinations of habitat filtering and competition (Fig. 3; Fig. 5). Again, as in the multi-trait-axis case, FDiv had low power to detect either habitat filtering or competition. When applied to the trait that was directly exposed to both competition and habitat filtering, MNND, FDis, FD, range and variance had high power to detect habitat filtering when it was dominant, but low power to detect competition unless it was the sole process important for community assembly (Fig. 3; Fig. 5). Of these metrics, range was the most powerful for detecting habitat filtering on this axis, and had higher power to detect this process than CHV calculated using all three traits (Fig. 5). When applied to the trait that had been directly exposed only to habitat filtering, these same metrics had high power to detect habitat filtering at all levels of its relative importance (Fig. 3). For the trait axis that was directly exposed only to competition, FD, FDis and range, had greater power to detect competition than when these metrics were calculated using all three trait axes (Fig. 5). However, the power of these metrics to reject random assembly on this trait axis when competition was the less important process was still low (Fig. 3). In contrast, SDNDr had slightly higher power to detect competition when this process was relatively weak, but had only intermediate power when competition was dominant (Fig. 3). Furthermore, contrary to its use as a single-trait metric for overdispersion, SDNDr was sensitive to trait clustering on both traits exposed to habitat filtering (traits X and Y) (Fig. 3). Thus FD, FDis and variance were the most powerful single-trait-axis metrics for detecting competition (Fig. 5).

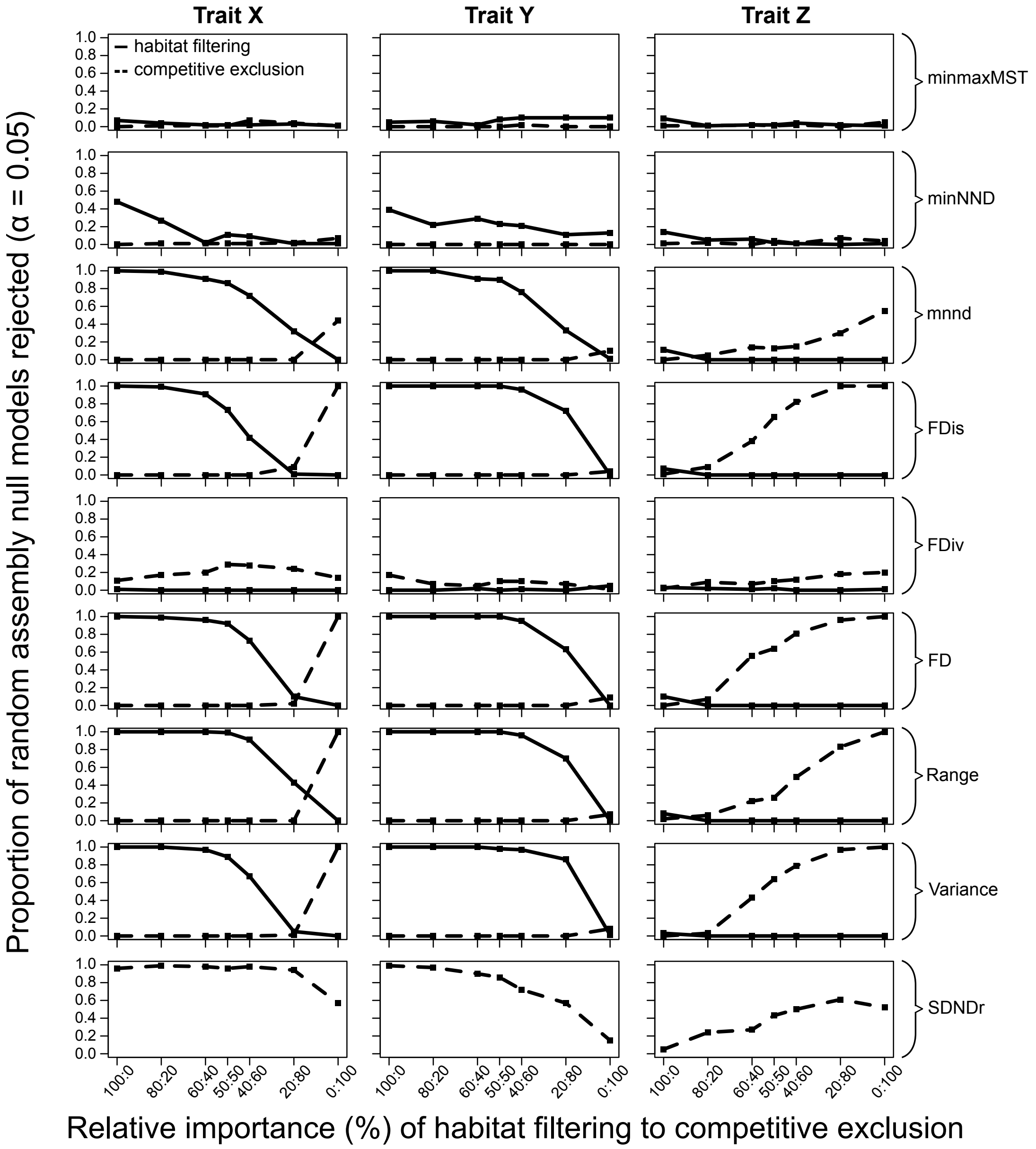

Figure 3. The power of trait-based, single-trait-axis metrics to reject the random assembly null model in favour of either habitat filtering or competitive exclusion. Trait X was directly exposed to habitat filtering and competition, trait Y to habitat filtering only and trait Z to competition only. See Table 1 for descriptions of each metric. The metrics were tested under seven community assembly scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. SDNDr is a single-pattern metric focused only on the detection of overdispersion associated with competitive exclusion and so a one-tailed test was used.

Changing the number of traits sampled that have been exposed to a given niche-based process.

The power of multi-trait-axis metrics to reject random assembly depended upon the number of trait axes used that had been exposed to a given niche-based process (Fig. 4; Fig. 5). MNND, FD, FDis and CHV all had greater power to detect a given niche-based process when the number of sampled traits that had been exposed to that process was increased. This effect was strongest for min/maxMST and minNND. These metrics had high power to detect competition at all levels of its relative importance, but only when competition had acted on both trait axes used in the analysis (Fig. 4; Fig. 5). When the number of sampled trait axes that had been exposed to competition and habitat filtering was equal, MNND, FD, FDis and CHV all had greater power to detect habitat filtering than competition, and lowest power when competition was dominant (Fig. 4). However, the propensity of these metrics to detect habitat filtering over competition was less for this scenario than when they were evaluated for the single trait axis on which both habitat filtering and competition had acted (Fig. 5). CHV maintained the highest power to detect habitat filtering across all of the two trait combinations (Fig. 4; Fig. 5).

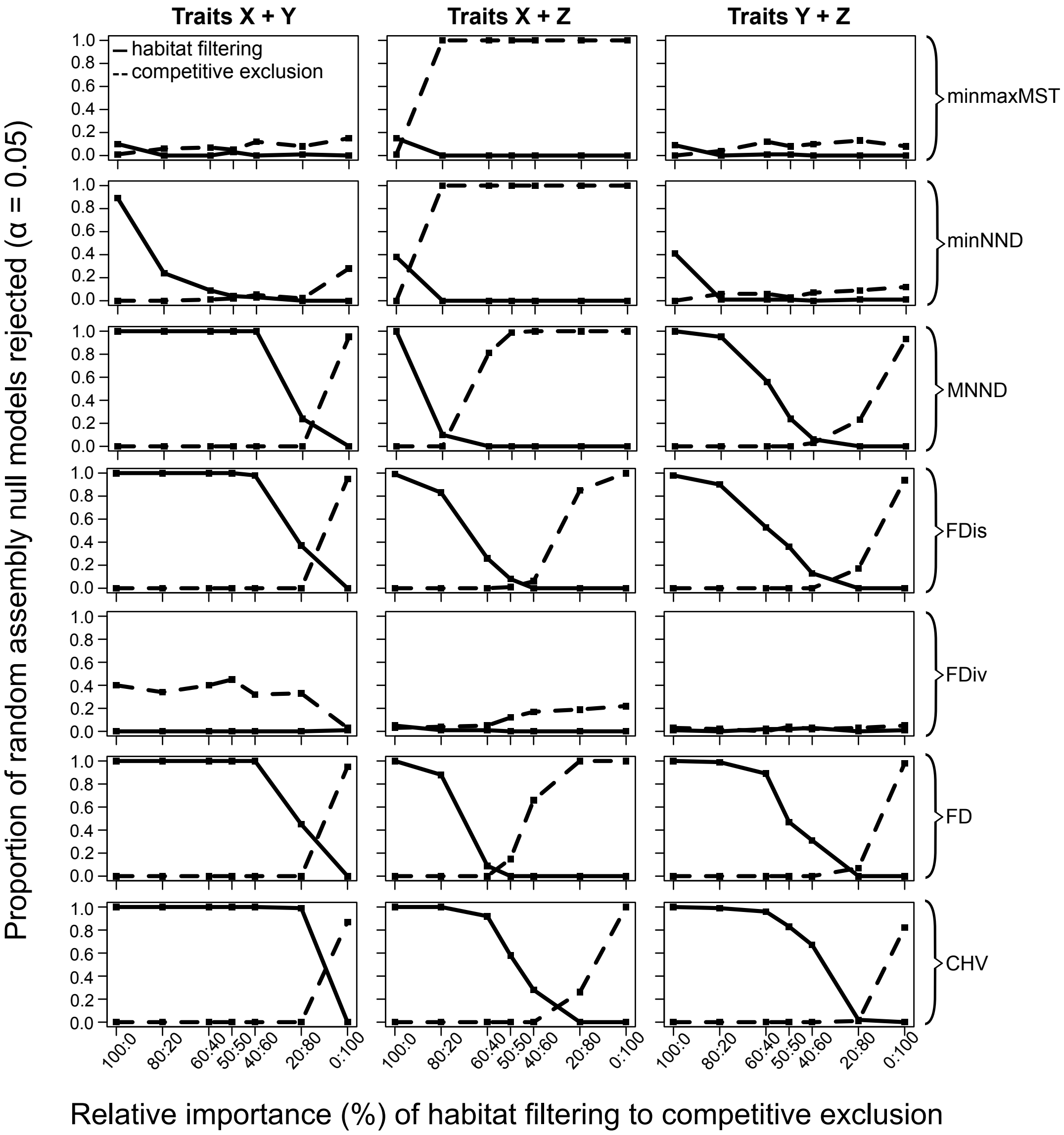

Figure 4. The power of trait-based, multi-trait-axis metrics to reject the random assembly null model in favour of either habitat filtering or competitive exclusion when multi-trait-axis metrics used combinations of two traits. Trait combinations differ in the proportion of the traits directly exposed to either habitat filtering or competition. Trait X was directly exposed to habitat filtering and competition, trait Y to habitat filtering only and trait Z to competition only. See Table 1 for descriptions of each metric. The metrics were tested under seven community assembly scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. See methods for further details of trait and community simulations, null models, and statistical tests.

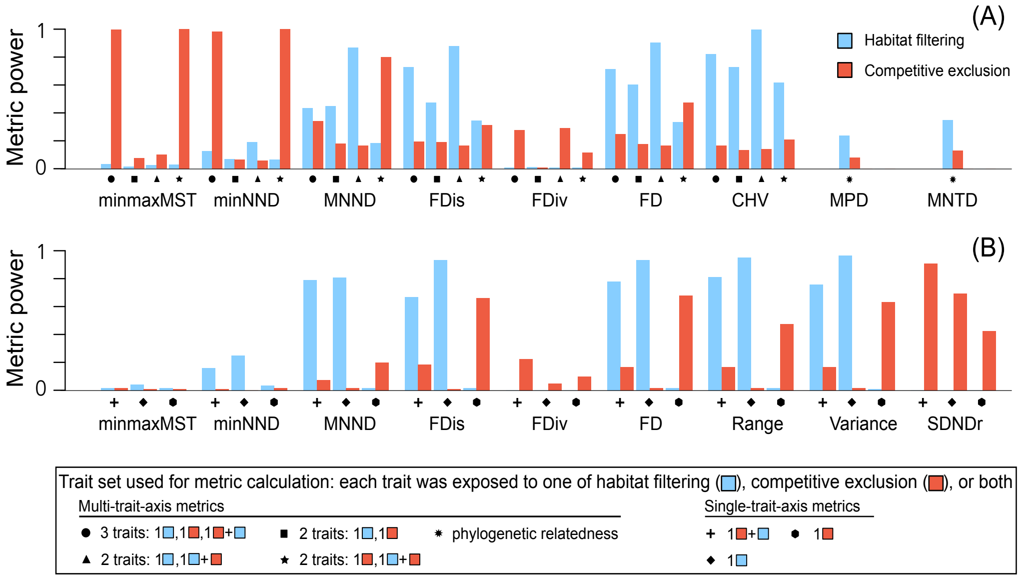

Figure 5. The power of (A) multi and (B) single-trait-axis metrics to detect clustering due to habitat filtering (blue) and overdispersion due to interspecfic competition (red) during community assembly. The symbol below each pair of bars denotes the set of traits used to calculate the metric. The height of each bar is the proportion of times, over the entire range in relative importance (20%–100%) of the respective process in community assembly, that the metric detected this process. The high power for SDNDr is misleading due to this metric responding to both habitat filtering and competition (see Discussion).

Scaling traits

There were marked differences among metrics in their response to a change in the signal of habitat filtering or competition on a trait axis. Increased variance of the trait directly exposed only to competition strengthened the pattern of overdispersion on this trait axis (Fig. 1e and d). However, this had little or no effect on the power of minNND, min/maxMST, CHV or single-trait-axis metrics to detect either competition or habitat filtering, regardless of the trait axes sampled or whether traits had been scaled before analysis (Fig. S4). In contrast, for MNND, FD and FDis, when traits remained unscaled, power to detect competition increased and to detect habitat filtering decreased when the trait directly exposed only to competition was used in metric calculation (Fig. 6; Fig. S4). Scaling of the traits to have equal variance before metric calculations adjusted the power of this set of metrics to be the same as when each trait had equal variance in community assembly (Fig. 6; Fig. S5).

Increased variance of the trait directly exposed only to habitat filtering (trait Y) increased the signal of clustering on this trait axis. Except for min/maxMST and minNND, when trait Y was used in metric calculation, the power of trait-based multi-trait-axis metrics to detect habitat filtering increased and to detect competition decreased (Fig. 6; Fig. S6). For trait combinations excluding trait Y the effect on metric power was the opposite (Fig. 6; Fig. S6). In addition, the power of single-trait-axis metrics to detect habitat filtering on trait Y increased. However, in contrast, for the trait exposed to both habitat filtering and competition, the power of single-trait-axis metrics to detect habitat filtering decreased and to detect competition increased (Fig. 6; Fig. S6). When traits were scaled, the power of multi-trait-axis metrics was adjusted toward that for the equal trait variance scenario, but only for trait combinations including trait Y and notable differences in metric power remained between the scaled and unscaled trait scenarios (Fig. 6; Fig. S7).

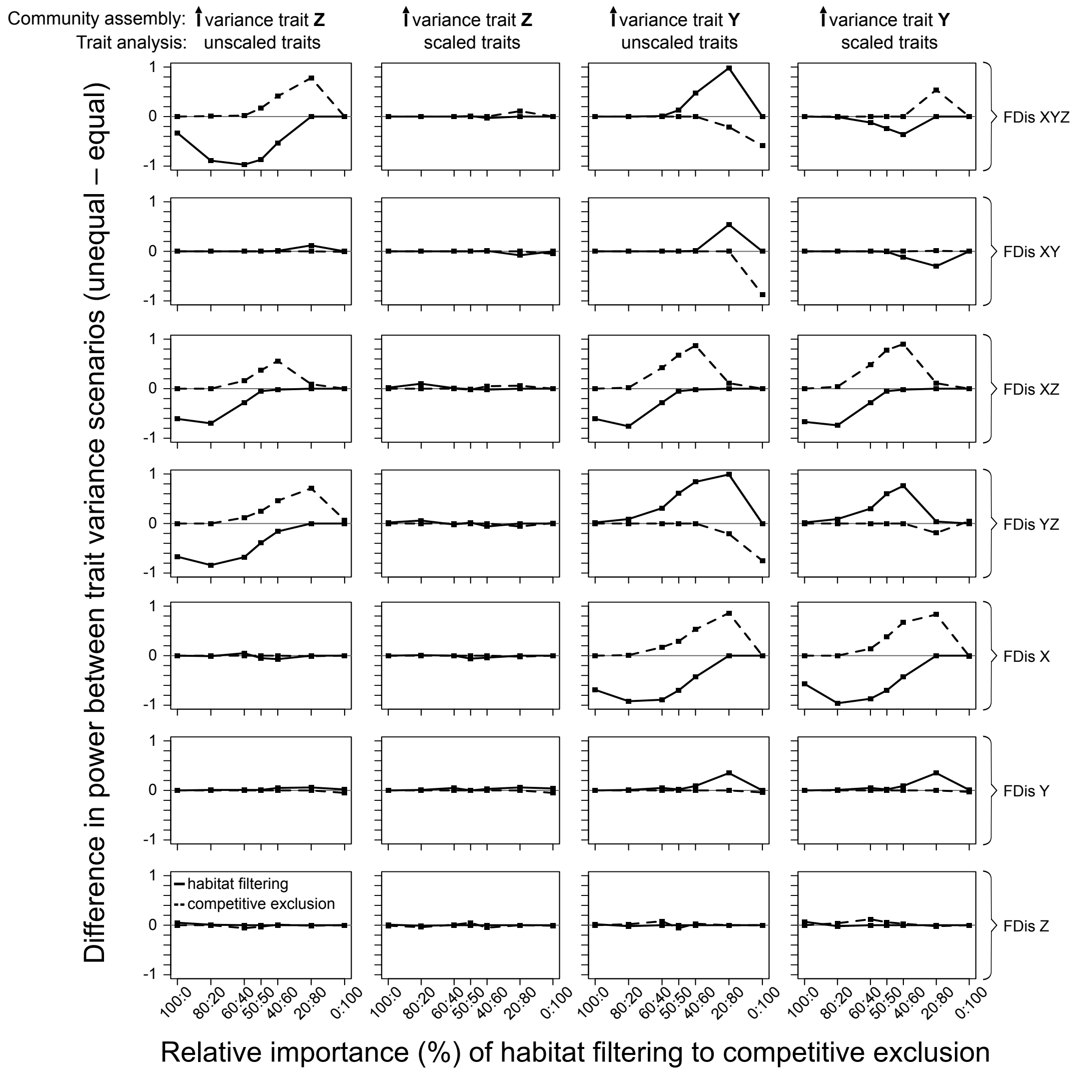

Figure 6. The difference in the power (proportion of random assembly null models rejected) of Functional dispersion [FDis] to detect habitat filtering and competition between the community assembly model in which a single trait had greater variance, and therefore importance, for either competition (trait Z) or habitat filtering (trait Y), and that in which each trait had equal variance. The metrics were tested under seven community assembly scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. Similar results were obtained for MNND, FD, CHV, variance and range, but differed for FDiv, minNND and min/maxMST (Figures S4-7). See methods for further details of trait and community simulations, null models, and statistical tests.

Local species richness

SDNDr, min/maxMST and minNND were not affected by a decrease in the number of species from the regional pool that were present in the local community (Fig. S8). However, for all other trait-based metrics, power to detect competition increased and to detect habitat filtering decreased in response to this change in species richness. In contrast, MPD, a phylogenetic metric, showed a slight increase in power to detect habitat filtering. When local species richness was increased, the most pronounced effect on trait-based multi-trait-axis metrics was when the metrics used all three trait axes. In this scenario, these multi-trait-axis metrics decreased in their power to detect competition and, except for min/maxMST and minNND, increased in their power to detect habitat filtering (Fig. S9). When using only combinations of two traits, the response of multi-trait-axis metrics was variable, most often with little change or a decrease in power to detect competition. The single-trait-axis metrics variance and range also showed little change in power, but did decrease in power to detect competition on trait Z. Both phylogenetic metrics decreased in power to detect habitat filtering.

DISCUSSION

Functional trait and phylogenetic diversity metrics failed in many instances to reject the random assembly null model. This was often the case when a combination of habitat filtering and competition was important for community assembly, and despite the fact that community assembly was based upon only purely deterministic, niche-based processes (Fig. 5). In addition, when the null model was rejected, many of the metrics detected the niche-based process that was of lower relative importance in community assembly, most often habitat filtering over competition (Figs 2, 3 and 4). The power of the metrics to detect non-random patterns in community structure was affected by the following: the relative importance of habitat filtering and competition in community assembly (Figs 2, 3 and 4); the number of trait axes sampled that had been exposed to a specific niche-based process (Figs 4 and 5); the importance of a trait axis for a niche-based process (Fig. 6); and local species richness. However, there were strong differences among metrics in their robustness to these factors, making possible the careful selection of metrics to mitigate these effects and thus improve the power of tests for the influence of niche-based processes on community assembly.

Multi- vs. single-trait-axis metric performance

Trait-based metrics generally had much greater power than phylogenetic metrics to detect non-random patterns in community structure (Fig. 2; Fig. 5). This is surprising given that relatively strong phylogenetic signal in species traits—Blomberg's K ≈1 for traits on regional phylogenies—is commonly expected to result in trait and phylogenetic metrics having similar power (Cavender-Bares et al. 2009). This was the case even when the ratio of local to regional richness was within the range for which these phylogenetic metrics have previously been shown to have high power (Kraft et al. 2007). However, Kraft et al. (2007) did not compare phylogenetic with trait metrics and did not consider the combined action of habitat filtering and competition on metric performance, where my results show that the power of phylogenetic metrics was lowest. Furthermore, while they did not evaluate widely used metrics, Mason and Pavoine (2013) showed that for a more complex model of niche-based assembly along a stress gradient, phylogenetic metrics had low power to detect trait-based assembly processes, even when trait conservatism was strong. Similarly, recent experimental studies have shown that phylogenetic diversity may be only weakly associated with competition-mediated species coexistence (Bennett et al. 2013; Best et al. 2013; but see Violle et al. 2011). The limited ability of phylogenetic diversity measures to detect niche-based processes may thus be relatively pervasive, even in comparatively simple assembly scenarios. This highlights the need to move beyond the use of phylogenetic diversity as a proxy for trait diversity. Although phylogenies remain useful for assessing the influence of evolutionary history on community dynamics (Swenson 2013), researchers should continue to increase the collection of relevant trait data for testing contemporary niche-based community assembly mechanisms.

Trait-based metrics had high power to detect habitat filtering and competition when only a single process was important for community assembly. In contrast, and in agreement with recent work by Aiba et al. (2013), many multi-trait-axis metrics had very low power to reject the random assembly null model when a combination of competition and habitat filtering was important for community assembly. Interestingly, I found that this region of low power does not necessarily correspond to the scenario in which habitat filtering and competition are of equal relative importance. Instead, because many commonly used multi-trait-axis metrics (MNND, FDis, FD and CHV) have greater power to detect trait clustering than overdispersion, the lowest power to reject random assembly in fact occurs when competition is of greater relative importance (Figs 2 and 4).

It has been suggested that single-trait-axis metrics are better able than multi-trait-axis metrics to detect the influence of multiple niche-based processes on community assembly (Spasojevic and Suding 2012; Chapter 2 of this thesis). However, I found that the ability to detect non-random assembly was generally even lower for single-trait-axis metrics when a combination of habitat filtering and competition was important for assembly. Although an exception to this was the high power of trait range for the detection of habitat filtering. Only when single-trait-metrics happen to be applied to a trait that is subject to a single assembly process is power increased compared to multi-trait approaches. This is especially the case given that SDNDr—the single-trait-axis metric designed to detect only overdispersion—often failed to differentiate between overdispersion and clustering. Thus, because multiple niche-based processes are likely important in community assembly (Vellend 2010), this generally lower metric power when multiple niche-based processes are active may explain in part why only 18% of trait-based tests for habitat filtering and limiting similarity in plant communities have rejected random assembly (Götzenberger et al. 2012).

However, a key finding is that when communities are assembled under both competition and habitat filtering, the power to detect a given process increased dramatically when the proportion of analysed traits exposed to that process in community assembly was increased. CHV had the highest power of all the metrics to detect clustering across all levels of habitat filtering's relative importance, when both traits sampled for analysis had been directly exposed to habitat filtering (Fig. 5). Likewise, minNND and min/maxMST had the highest power to detect overdispersion at all levels of competition's relative importance when two of the sampled traits had been directly exposed to competition. This effect on metric power has been overlooked previously because studies of trait-based metrics under multiple assembly processes applied niche-based processes equally to all trait axes (e.g. Aiba et al. 2013). Yet, empirical studies suggest that habitat filtering and competition likely act on only partly overlapping sets of trait axes (Spasojevic and Suding 2012; Chapter 2 of this thesis). Thus, rather than using all functional traits together, emphasis should be placed on grouping trait axes into sets, each hypothesized to be important for a given niche-based process, and then each tested separately using the appropriate multi-trait-axis metrics. Although this approach requires additional biological information, this information is often available (e.g. Wright et al. 2004 for plants); using it in this way provides for stronger tests for the presence of a process rather than more exploratory approaches that simply screen all functional traits for which data are available.

The reason min/maxMST and minNND had low power when used as single-trait-axis metrics is because both use minimum nearest neighbour distance. When limiting-similarity-based competition acts across ≥2 trait axes, species will be overdispersed within this multidimensional space, but will most likely still overlap in trait values when viewed along a single dimension, especially if traits are uncorrelated (Fig. 1c–f). Thus, if competition occurs across multiple traits, but is tested for using only one of these, the minimum nearest neighbour distance may be zero or close to zero and therefore not significantly above the null model expectation. Because SDNDr uses neighbour distances along only a single trait axis, the overdispersion of species in multiple dimensions also likely explains the low power of this metric to detect overdispersion, in contrast to previous tests based upon assembly simulations along individual trait axes (Kraft and Ackerly 2010; Aiba et al. 2013).

Scaling traits

When a trait axis sampled for a multi-trait-axis metric was of greater relative importance for a given niche-based process (i.e. had stronger signal from that process), the power of MNND, FD, FDis and FDiv to detect the process increased at the expense of their power to detect a process generating an opposing signal. This behaviour of the metrics is useful when the process of interest is that for which the sampled trait has greater importance, but is not so useful when it prevents the detection of processes generating opposing signals, even when these are dominant in community assembly. Scaling traits to have equal variance adjusted metric power to be the same as that for the equal trait variance scenario, but only for the scenario when the strength of the signal of overdispersion varied between traits directly exposed to competition. However, CHV, min/maxMST and minNND were robust to variation in the relative importance of traits for competition and habitat filtering and thus can be used without having to scale traits to have equal variance.

Species richness

When local species richness was raised to include a greater portion of the regional species pool, the power of trait-based metrics to detect habitat filtering increased and to detect overdispersion decreased. The opposite effects on metric power occurred when local species richness was decreased. For community assembly simulated on individual trait axes, Kraft and Ackerly (2010) found this same inverse relationship between local species richness as a proportion of the regional pool and the power of single-trait-axis metrics to detect overdispersion. However, Aiba et al. (2013) found the opposite pattern for single-trait-axis metrics across a wide range of assembly scenarios, suggesting that the relationship between metric power and species richness is more complex.

Estimating the relative importance of niche-based processes

When using trait-based and phylogenetic or multi-trait-axis metrics, the detection of significant clustering or overdispersion has been cited as evidence for the dominance of either habitat filtering or competition, respectively, in community assembly (e.g. Petchey et al. 2007). However, this study has demonstrated that multi-trait-axis metrics often fail to reject random assembly when a single niche-based process is very dominant in community assembly. Of even more concern for inferring the dominance of a process, I found that all multi-trait metrics often detect a subordinate over a dominant process in community assembly.

In contrast, recently developed alternative methods are able to identify whether niche-based or neutral processes are dominant in community assembly, but are not able to differentiate among niche-based processes (Shipley et al. 2012). Phylogenetic and trait-based mixed-modelling methods offer a possible solution by partitioning variation in species occurrence data among particular traits (e.g. Ives and Helmus 2011).

Simulation framework

Following Kraft et al. (2007) and Mouchet et al. (2010), the simulation framework used in this study applied habitat filtering and then limiting similarity sequentially to generate local communities from the species pool. Thinking of community assembly as a process whereby species pass through a sequence of filters, first abiotic and then biotic in order to occur in a given local community is intuitively appealing and has a long history in community ecology (Weiher and Keddy 1995; Vamosi 2010). This is because the abiotic conditions of a site must fall within the fundamental niche (physical tolerance limits) of a given species before that species is able to interact with other species that may occur within that site's local community. However, abiotic and biotic filtering processes may occur simultaneously in natural communities where a species's competitive ability is a function of the local habitat conditions (HilleRisLambers et al. 2012), or the sequence of filters might be reversed when interspecific competition at large spatial scales acts to remove species from the regional pool before microenvironmental heterogeneity acts as a habitat filter within the local community. In simulations of community assembly, Aiba et al (2013) removed species one at a time from a source pool to create a local community, and for each removal selected at random whether the species removed was due to habitat filtering or limiting similarity, approximating more the simultaneous action of the two filtering processes. Similar to the results of this study they found minNND and minmaxMST to be the best metrics for detecting limiting similarity, but that CHV had low power to detect habitat filtering likely due to the reduction in trait volume of the local community being less under their simulation approach than when habitat filtering acts first. The application first of a limiting similarity filter and then a habitat filter to the species pool may change the power of the metrics observed in this study, but this change is not expected to be large. Metrics such as CHV and range that assess the total volume of trait space occupied may have slightly decreased power to detect habitat filtering due to an increased chance that a species that is a relative outlier from the trait optimum occurs in the local community because species closer to the trait optimum have already been removed by competition. Likewise metrics such as minNND and minmaxMST that assess structure within the trait volume may have slightly lower power to detect competition because some of this limiting similarity structure should be removed when habitat filtering is applied second.

GUIDELINES: **Detecting trait clustering and overdispersion**

(1) Trait-based metrics should be preferred over phylogenetic metrics when testing for the influence of niche-based processes on community assembly. This is because they have greater power than phylogenetic metrics to detect clustering and overdispersion, especially when both limiting similarity and habitat filtering are important in assembly.

(2) Only include data on the functional traits thought to be relevant for the niche-based processes hypothesized to influence community assembly at the spatiotemporal scale of interest (Aiba et al. 2013; Götzenberger et al. 2012). This approach promotes the formation of more specific hypotheses before analysis, increasing metric power to reject random assembly when a higher proportion of traits have been exposed to niche-based processes (Aiba et al. 2013).

(3) Use ordination techniques to generate orthogonal trait axes more likely to represent distinct niche axes to increase the use of unique information about organism function in trait-based tests. Strong correlation among traits suggests that they are associated with a singular trade-off in function (Laughlin 2014). Because the metrics combine additively signals of assembly processes on separate traits, the use of multiple correlated traits will bias the metrics by upweighting the signal of any niche-based processes acting on the niche axis/axes with which the correlated traits are associated.

(4) Trait axes should be grouped based upon the niche-based processes for which they are hypothesized to be important, and the appropriate trait-based metrics applied to each set. A trait axis may belong to more than one set . Increasing the number of trait axes used in a metric's calculation that have been directly exposed to a given niche-based process increases the power of multi-trait-axis metrics to detect that process.

(5) CHV is recommended as the most powerful metric overall for detecting trait clustering, as it was relatively robust to trait scaling and changes in local species richness. Variance and range were

the most powerful single-trait-axis metrics for detecting trait clustering. For overdispersion, min/maxMST and minNND are recommended because they were the most powerful metrics, and were robust to trait scaling and changes in species richnesss. However, min/maxMST and minNND had low power to detect overdispersion when only a single sampled trait axis had been exposed to competition. Thus, one of FD, FDis, or variance should be used as complementary metrics.

(6) Null model selection should be tailored to the specifics of the study (e.g. spatial scale, habitats, assembly processes), as a good null model randomises only those structures in the data that are relevant to the process/es of interest (Gotelli and Graves 1996). A detailed statement should be included about the processes influencing assembly that are controlled for by the null model (Götzenberger et al. 2012).

(7) Although contrary to many simulation and empirical studies that have used one-tailed tests (e.g. Aiba et al. 2013; Kraft and Ackerly 2010), a two-tailed test should be used to test for deviations from random assembly whenever a metric has the ability to detect both clustering and overdispersion by deviating to opposite sides of the null model expectation.

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CHAPTER 4

Dispersal ability and ecological similarity interact to shape species occurrence in a diverse radiation of birds

ABSTRACT

The influence of environmental conditions on species occurrence is well accepted, but there is intense debate over the importance of dispersal and interspecific competition, especially at regional scales. Empirical treatments have typically focussed on the influence of only a single assembly process on species occurrence. However, this narrow focus yields an incomplete picture of the importance of these processes because dispersal integrates ecological conditions across the regional distribution of a species. Thus, to better understand regional diversity patterns, it is necessary to recognise how environmental filtering, interspecific competition, biogeographic history and dispersal interact to shape species occurrence. I used data on phylogenetic relatedness, functional traits and dispersal ability for a large continental bird radiation (ovenbirds) to model species occurrence probabilities at the regional scale, considering interactions among assembly processes. First, emphasizing the importance of including interactions, the influence of competition on species occurrence was only detected when interaction effects were considered. Second, the effects of environmental filtering and interspecific competition on species occurrence probability were greater for species with greater dispersal ability. These results show that interactions between both interspecific competition and dispersal ability and environmental filtering and dispersal ability influence regional-scale community composition in ovenbirds. They also suggest that more dispersive species are closer to equilibrium with the spatial ecological niche extent at regional scales.

INTRODUCTION

The geographic distribution of a species may be influenced by numerous factors, including environmental conditions, biogeographic history, species interactions and dispersal (Sexton et al. 2009). Furthermore, to the extent that community species composition reflects the overlapping of species' geographic distributions, it is also influenced by these same factors (Ricklefs 2004; Ricklefs 2008). Thus, a focus on the determinants of species distributions and regional-scale species occurrences may be more informative about the processes that drive species composition patterns than studies of co-occurrence in a given local community (Ricklefs 2008; Ricklefs 2011). The vast majority of empirical work on species range limits and regional-scale occurrence patterns has emphasized the importance of environmental filters in setting range boundaries (Sexton et al. 2009). In contrast, the extent to which species interactions limit regional-scale species occurrence remains controversial, especially with respect to interspecific competition (Sexton et al. 2009; Wiens 2011). Examples of ecological release on islands and elevational range expansion in the absence of ecologically similar species imply that competition is important in limiting species ranges (MacArthur 1972; Terborgh and Weske 1975). In addition, studies of community composition, trait and phylogenetic structure have focussed extensively on interspecific competition, providing some support for its role in limiting species co-occurrence, but almost exclusively at small spatial scales (e.g. Stubbs and Wilson 2004; Kraft and Ackerly 2010). However, that species distributions often appear largely individualistic at regional scales suggests that competition has little influence on species occurrence at large spatial scales (Davis and Shaw 2001; Ricklefs 2011). Similarly, there is mixed empirical support for differences in dispersal ability driving variation in range size and regional-scale occurrence among species (Lester et al. 2007; Sexton et al. 2009), despite the perceived importance of dispersal ability for range expansion (Gaston 2003)—e.g. in recolonizing formerly glaciated regions (Svenning and Skov 2007).

Most studies consider only individual effects of the environment, interspecific competition or dispersal ability on species occurrence (Vellend 2010). However, this approach inevitably yields an incomplete picture of the importance of these processes. This is because the dispersal of individuals across space links assemblage dynamics within a larger region so that the occurrence of a species within a given community reflects in part the integration of ecological processes across larger spatial scales (Leibold et al. 2004; Ricklefs 2008; Urban et al. 2008). Based upon this, metacommunity theory predicts that species dispersal will moderate the effect of both environmental filtering and interspecific competition on species occurrence (Leibold et al. 2004; Urban et al. 2008; Urban et al. 2013). Environmental filtering and interspecific competition are predicted to be less important in determining species occurrence for highly dispersive species because high dispersal distributes individuals of these species into habitats regardless of their ecological suitability, often termed mass effects (Fig. 1A and C) (Holyoak et al. 2005; Urban et al. 2008). Alternatively, species with poor dispersal ability may be less able to colonize the full spatial extent of ecologically suitable habitat available to them (Gaston 2003; Sexton et al. 2009). Thus, environmental filtering and interspecific competition may be more important predictors of species occurrence for more dispersive species because these species may be closer to equilibrium with the ecological limits to their spatial extent than less dispersive species (Fig. 1B and D) (Holyoak et al. 2005; Sexton et al. 2009). In addition, which one of these two forms the interaction effects between dispersal ability and environmental filtering and dispersal ability and interspecific competition take may be scale-dependent. At small spatial scales, where large geographic barriers to dispersal (e.g. rivers) are absent, high dispersal ability may lead to mass effects that reduce the importance of environmental filtering and competition for predicting species occurrence. In contrast, at large spatial scales, high dispersal ability may increase long distance dispersal events across biogeographic barriers (Burney and Brumfield 2009), allowing more dispersive species to colonize a larger proportion of ecologically suitable habitat and thus be closer to equilibrium with ecological limits. The few empirical studies to consider these interactions have focussed almost exclusively at small spatial scales (Cadotte 2006; Vellend 2010), thus potentially enhancing the view that competition is unimportant in shaping species composition. Finally, dispersal ability may interact with the evolutionary history of a species to influence species occurrence. For example, the importance of dispersal ability for determining regional-scale species occurrence may be greater for younger species because they have had less time available to disperse (Böhning-Gaese et al. 2006; Paul et al. 2009). Thus, to better understand the mechanisms shaping patterns of species composition, it is essential to consider how dispersal ability interacts with environmental filtering and interspecific competition, as well as with biogeographic history to influence regional-scale species occurrence.

Testing for the influence of interaction effects on species composition has in part been limited by the longstanding focus in community ecology on simple summary statistics of community composition, trait or phylogenetic structure (e.g. Elton 1946; Diamond 1975; Cardillo 2011). The use of these community-level metrics to identify interaction effects typically requires complicated null models and species pool delimitations, the results of which are often consistent with multiple alternative hypotheses, especially at the regional scale (Colwell and Winkler 1984; Cardillo 2011). For example, a 'checkerboard' pattern of closely related species occupying mutually exclusive regions is consistent with competitive exclusion, but allopatric speciation followed by insufficient time for dispersal back into sympatry may generate the same pattern (Mayr 1942; Barraclough and Vogler 2000).

In contrast, focussing on species-level occurrence patterns at regional scales may provide a more straightforward way to include the effect of multiple processes on species composition (e.g. Ricklefs 2011; Algar et al. 2013), and thus to test for the influence of interactions among them. For example, species-level analyses can more easily account for the time a species has had to disperse into a regional community and therefore better differentiate the influence of competitive exclusion from the history of allopatric speciation (Algar et al. 2013). However, a weakness of the species-level approach at regional scales has been the pseudoreplication and spatial autocorrelation inherent in assessing species occurrence using 100 km x 100 km grids because this scale is much smaller than the range of most species (Jetz and Fine 2012). One potential solution to this is the use of ecoregions as the scale at which to assess species occurrence, as has been done for community-level analyses (Gómez et al. 2010; Cardillo 2011). Being delimited by broad-scale patterns in vegetation composition and at large spatial scales (Olson et al. 2001), ecoregions are less prone to the problems of spatial autocorrelation inherent in species occurrence data generated using grid cells. Moreover, although area varies among ecoregions, in contrast to grid cells set at a similarly large spatial scale, ecoregions are delimited so that macroecological variables are similar within ecoregions but differ among them. Thus habitat filtering within ecoregions may be relatively limited increasing the potential for species interactions. Ecoregions are also large enough to capture effects of long-distance dispersal and biogeographic history (Gómez et al. 2010). Thus, ecoregions make sense as the unit of species occurrence with which to test for the interactive effects of dispersal, interspecific competition and environmental filtering at regional scales.

Still, two further major limitations of the species-level approach have been the difficulties of quantifying species dispersal ability and of identifying potential competitive interactions among species for inclusion in species distribution models (Araújo and Luoto 2007; Laube et al. 2013). For example, studies have typically quantified the degree of dispersal limitation among sites using dispersal cost estimates based on habitat suitability, thus making it difficult to separate the influence of environmental filtering from that of dispersal (e.g. Algar et al. 2013). However, because how species interact with the environment is a function of their phenotype, one potential solution to this limitation is to use a trait-based approach. For example, in birds, wing shape is a proxy for dispersal ability (Dawideit et al. 2009; Claramunt et al. 2011), and beak size and tarsus length are indicative of prey item selection and foraging substrate use (Miles et al. 1987; Grant and

Grant 2010). Therefore, increased similarity between two species in traits important for resource use can act as a proxy for an increased degree of interspecific competition between them (Schoener 1965; Ricklefs and Travis 1980; Algar et al. 2013). Likewise, increased dissimilarity of a focal species to the species resident within a region provides an estimate of the decreased environmental suitability of that region for the focal species (McGill et al. 2006; Belmaker and Jetz 2013). In addition, the use of a trait-based measure of dispersal ability should enable the effect of dispersal ability to be separated from that of environmental filtering, a common difficulty in empirical studies of species range limits (Urban et al. 2012; Algar et al. 2013). Thus, the interactions between dispersal and competition and dispersal and environmental filtering predicted to affect species occurrence can be translated into trait-based hypotheses at the regional scale (Fig. 1). Furthermore, these hypotheses are testable within a generalised linear mixed modelling framework: a methodological approach that recent simulation studies suggest has greater power to detect phylogenetic and trait-based influences on species occurrence patterns than methods that rely only on community-level metrics coupled with randomization tests (Ives and Helmus 2011; Jamil et al. 2013).

Here, I use a phylogenetic generalised linear mixed model (PGLMM) approach to test for the interactive effects of dispersal ability and mean trait similarity (environmental filtering), dispersal ability and nearest neighbour trait distance (interspecific competition), and dispersal ability and species age on species-level occurrence probabilities at the ecoregion scale in ovenbirds. Unlike community-level metrics of trait and phylogenetic diversity (see Chapters 2 and 3 of this thesis) the PGLMM approach has species as the unit of analysis, and models the occurrence dynamics of each species as opposed to comparing community-level patterns in traits or relatedness to null model based expectations. This species-level approach allows for the fitting of observed occurrence data to hypotheses about the underlying influences (e.g. interaction effects between dispersal and competition) on the distribution of species among communities that do not require the development of complicated null models, as is the case for community-level diversity metrics. In addition, a PGLMM approach can account for non-independence in the occurrence of each species due to phylogenetic relatedness as well as partition variance in species occurrences among traits and phylogeny, allowing for the development of predictive models of species co-occurrence not easily possible when using community-level metrics. (Ives and Helmus 2011; Jamil et al. 2013).

Ovenbirds are an ideal study system to test for interactive effects on regional-scale species occurrence for the following reasons: the clade represents a diverse continental radiation (293 species in South and Central America) with a highly resolved and well-sampled phylogeny (Derryberry et al. 2011); all ovenbird species are predominantly insectivorous, allowing differences in resource-use to be quantified using relatively simple ecomorphological traits (e.g. beak length and shape); and wing morphology can be used as a surrogate for dispersal ability in this group (Claramunt et al. 2011). Furthermore, previous studies on ovenbirds suggest: (1) that interspecific competition based on similarity in beak morphology limits range overlap among species (Pigot and Tobias 2012), and (2) that high dispersal ability based on wing morphology inhibits rates of speciation and thus by implication, species ranges (Claramunt et al. 2011). Therefore, a key next step is to integrate these processes with environmental filtering and biogeographic history to test for interaction effects on regional-scale species occurrence in this group.

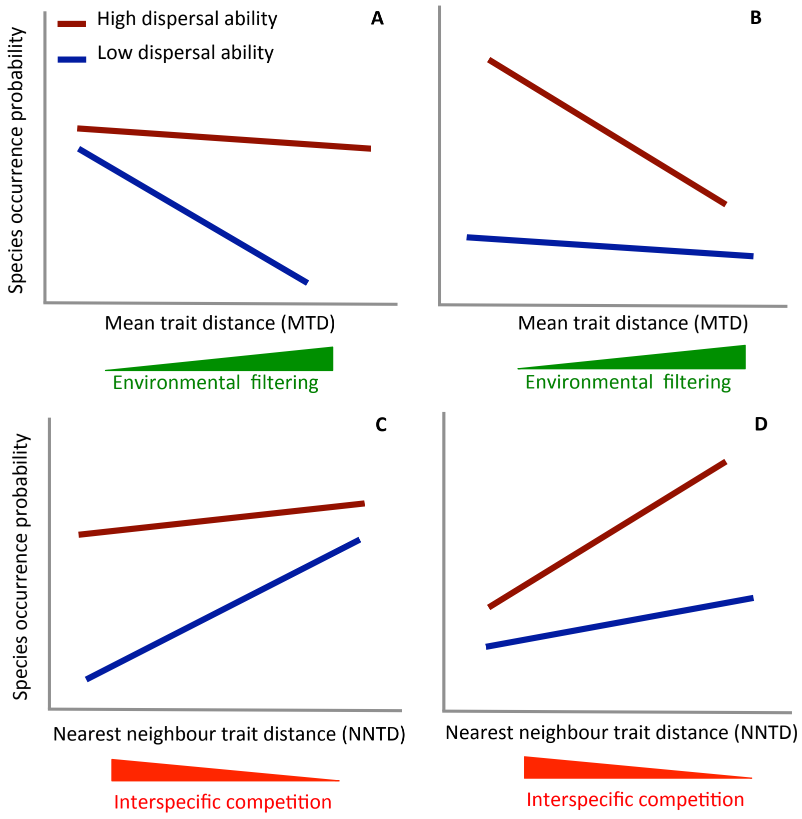

Figure 1. Potential interactions between dispersal ability, environmental filtering and interspecific competition. Species occurrence probability is predicted to decrease with an increase in the mean trait distance (MTD) of a species to the regional community, a proxy for environmental filtering, but the effect of MTD may either decrease (A) or increase (B) for species with greater dispersal ability. Species occurrence probability is predicted to increase with an increase in the nearest neighbour trait distance (NNTD) of a species to the regional community, a proxy for interspecific competition, but the effect of NNTD may either decrease (C) or increase (D) for species with greater dispersal ability.

METHODS

Species occurrence data

Species not present in the ovenbird phylogeny (Derryberry et al. 2011) and offshore island endemics were excluded from analysis, resulting in a sample of 284 out of 293 species. Species range polygons for the ovenbirds were obtained from Orme et al. (2005), and species ranges were updated to reflect recent taxonomic revisions consistent with the lineages in the ovenbird phylogeny (Derryberry et al. 2011). Regional-scale species occurrence data were generated in two stages by overlaying range polygons first on biome, and then ecoregion maps for South and Central America (Olson et al. 2001). Ecoregions are relatively large areas (range: 323–1987000 km^2, median: 74840 km^2 for South and Central America) containing distinct assemblages delimited based primarily upon vegetation composition, and they are nested within larger biomes (e.g. tropical moist broadleaf forest) (Olson et al. 2001). The lake, rock and ice, and mangrove biomes were not considered because these do not provide habitat used by ovenbirds. This resulted in 139 ecoregions among 10 biome types. Species were recorded as occurring within a biome if more than 5 percent of their range polygon area overlapped with the biome. Regional-scale occurrence for a species was recorded as presence or absence within ecoregions, but only for the ecoregions in the biomes in which the species occurred. This was done to account for environmental filtering among sets of ecoregions at the biome scale (e.g. temperate forest vs. desert biome) that might otherwise overwhelm any signal of regional-scale dispersal and interspecific competition, especially as species with highly diverged macrohabitat preferences are unlikely to interact. A species was recorded as present within an ecoregion if >10% of the ecoregion area was overlapped by the species range. Because some species have small ranges, species for which range overlap was less <10% of the ecoregion, but >10% of the species range were also recorded as present (this was a small number of cases). To account for uncertainty in range maps, I also recorded species occurrence with the threshold on biome overlap raised from 5 to 20%. When biome assignment was based on >5% of the focal species range overlapping the biome, 21% of species were restricted to a single biome and 87% of species ranges overlapped with 3 or fewer biomes.

Dispersal ability

I quantified dispersal ability using the hand-wing index following Claramunt et al. (2011). This index is standardized for wing length and is related to the aspect ratio of the wing. It is equivalent to that developed by Kipp (1958), except that the difference between the length of the closed wing and the distance from the carpal joint to the tip of the first secondary feather were used instead of direct measurements between feather tips (Claramunt et al. 2011). This index is a robust surrogate for flight and dispersal ability in birds, correlating with flight performance (Claramunt et al. 2011), natal dispersal distance (Dawideit et al. 2009) and migratory behaviour (Baldwin et al. 2010; Lockwood et al. 1998). This estimate of dispersal ability is also negatively related to the degree of genetic differentiation among populations of lowland Neotropical forest bird species across biogeographic barriers (Burney and Brumfield 2009) and the rate of speciation within ovenbirds, implying that more dispersive ovenbird species maintain larger ranges that are resilient to the range division and population isolation necessary for speciation. Thus, the hand-wing index provides a surrogate for dispersal ability that has relevance on both a contemporary ecological and an evolutionary scale.

Trait-based measures of ecological similarity

Ecological similarity was quantified based on five morphological trait measurements: beak length, beak depth, beak width, tarsus length and wing length. These traits are closely related to prey item selection and foraging substrate use in birds (Grant 1968; Miles and Ricklefs 1984; Miles et al. 1987), and thus may be subject to both competitive exclusion and environmental filtering

(Ricklefs and Travis 1980; Chapter 2 of this thesis). Trait measurements were taken by Derryberry et al. (2011), with both these data and additional measurements provided by S. Claramunt, yielding an average of 5.02 ± 0.21 [mean ± s.e.] specimens per species. Following log-transformation of individual trait values, the average trait values for each species were used in a phylogenetic principal component analysis (PCA) (Revell 2009). Phylogenetic PCA accounts for phylogenetic non-independence in trait data, assuming a Brownian motion model of trait evolution (Revell 2009), which has been shown to provide a better fit to these trait data than either a delta or OU model (Derryberry et al. 2011).

Using the distances among species in morphological space described by the five axes of the phylogenetic PCA (Table S1), I calculated two metrics of ecological similarity for each species and ecoregion combination. The mean trait distance (MTD) was calculated as the average of all the pairwise Euclidean distances in trait space from the focal species to the species resident within the ecoregion. Following Algar et al. (2013), the nearest neighbour trait distance (NNTD) was calculated as the inverse of the Euclidean distance between the focal species and the closest species in trait space within the ecoregion. To make model interpretation easier, I multiplied NNTD by negative one, and then added the minimum value to all observations so that trait dissimilarity increases as NNTD increases, analogous to MTD. Ecoregions for which the focal species was the only resident species were excluded from further analyses as it was not possible to estimate MTD and NNTD for these. Both of these metrics may capture the signal of environmental filtering and competitive exclusion. However, MTD should be better suited to detecting an effect of environmental filtering because it quantifies the distance a focal species is, on average, from the areas of occupied niche space within an ecoregion. In contrast, NNTD should better detect an effect of interspecific competition on species occurrence because it quantifies the ecological similarity of the focal species to its closest potential competitor for resources within the ecoregion.

Phylogenetic data and biogeographic history

I used the maximum clade credibility tree for the Furnariidae from Derryberry et al. (2011), generated based on multiple nuclear and mitochondrial genes with nodes dated using a relaxed clock Bayesian approach. When estimating divergence times, Derryberry et al. (2011) placed no restrictions on tree topology so that topological uncertainty was factored into divergence date estimates. The time that a focal species had been diverged from its closest relative within an ecoregion was included as a main effect in the trait-based analysis. Species divergence time from an ecoregion community is predicted to have a positive effect on species occurrence probability if species absences are explained by insufficient time for dispersal back into the ecoregion following allopatric speciation.

Statistical analyses

I implemented phylogenetic generalised linear mixed models (PGLMM) using a Bayesian Markov chain Monte Carlo estimation approach in the MCMCglmm package (Hadfield 2010) in R version 3.0.1 (R Core Team 2013). Species occurrence was fitted as a binary response variable (0 = absence, 1 = presence) using a binary distribution with a logit link. Flat non-informative priors with a uniform low degree of belief were set for all analyses. However, residual variance cannot be calculated for binary response variables and was therefore fixed to one (Hadfield 2010). Prior to analysis, explanatory variables were mean centred and standardised by dividing by two standard deviations. This was done to enable the easy interpretation of parameter estimates on both main and interaction effects as standardized effect sizes (Gelman 2008; Schielzeth 2010). I specified the following interactions: MTD by hand-wing index, NNTD by hand-wing index, NNTD by species age and species age by hand-wing index. All explanatory variables included in interaction effects were also included as main effects, and ecoregion area was included as an additional main effect. To assess the effect of excluding these interactions on the inference of the importance of each process for determining species occurrence, PGLMMs were also run with only main effects specified. The correlation among fixed effect explanatory variables was generally low (pearson's r: –0.23 to 0.30) and thus collinearity did not hinder model interpretation. In each PGLMM, biome, ecoregion and species identity were fitted as random effects, specifying the estimation of random intercepts to account for variation among biomes and ecoregions in mean occurrence probabilities, and to account for inter-specific variation due to the repeat sampling of species (Grueber et al. 2011; Hadfield 2010). Although ecoregion is nested within biome, specification of nested random effects is not required in MCMCglmm as the package fits two, cross-classified sets of random effects. Phylogenetic non-independence in occurrence probabilities among species was accounted for by specifying a phylogenetic covariance matrix as a random effect (Hadfield 2010; Hadfield and Nakagawa 2010). Finally, although the estimation of random slopes for random effects is desirable, this was not possible here due to resultant reductions in the ability to achieve model convergence.

All models were run for 110,000 iterations, sampling every 100 iterations after a burnin of 10,000 iterations, and used slice sampling to improve sampling efficiency. To check model convergence and ensure proper mixing, I visually inspected trace plots of the posterior parameter estimates and checked that autocorrelation between successive sampled iterations was less than 0.1 (Hadfield 2010). All runs converged rapidly and the effective sample size of parameter estimates was typically ~1000. Because minimum adequate models can inflate Type 1 error rates, I report the results of full models (Hadfield 2010) and assess significance using Bayesian credible intervals and P values. P values reported here are the number of iterations for which the parameter estimate had the opposite sign to that reported, divided by the total number of iterations, and multiplied by two. I do not use differences in DIC scores because this measure of model support is not appropriate for non-Gaussian hierarchical models (J. Hadfield pers. com.). However, Bayes Factors might be applied within the PGLMM approach used here to provide estimates of the importance of the model terms allowing a more nuanced interpretation of the relative contribution of each effect to species occurrence patterns.

Null model tests

Type 1 error rates for the observed model results were estimated based on sets of null species occurrences generated by randomly shuffling species ranges (i.e. occurrence data) among species across the tips of the phylogeny. This null model generated appropriate null expectations for the interaction terms in the observed model by randomizing the following associations: species dispersal ability with species occurrence; age with species occurrence; and species trait similarity and species co-occurrence. The null model maintained ecoregion species richness, the geographic location of ranges (although their species identity was shuffled) and the association between species traits and phylogenetic relatedness. The Bayesian PGLMM approach was computationally intensive. Generalized linear mixed models using maximum likelihood estimation, with ecoregion within biome as a nested random effect, and accounting for phylogenetic non-independence by specifying species within genus as a nested random effect, were faster and yielded qualitatively similar results for the observed model (Table S4 in Appendix 3). Thus each of the 100 sets of null occurrence data were analysed using the lme4 package in R (Bates 2005). The expected probability of an interaction in the observed model was estimated as the proportion of times the observed interaction (with the same signs on the main effects) was significant in the null occurrence data.

RESULTS

Ecoregion species richness ranged from 1 to 94, with the most species rich regions in the Andes and Amazonia (Fig. 2). In addition, for the species present in an ecoregion, species ranges overlapped, on average, more than half of the ecoregion area (proportion overlap: 0.58 ± 0.006 [mean ± s.e.]). Thus, the likelihood of species interactions occurring among the species present within an ecoregion is high.

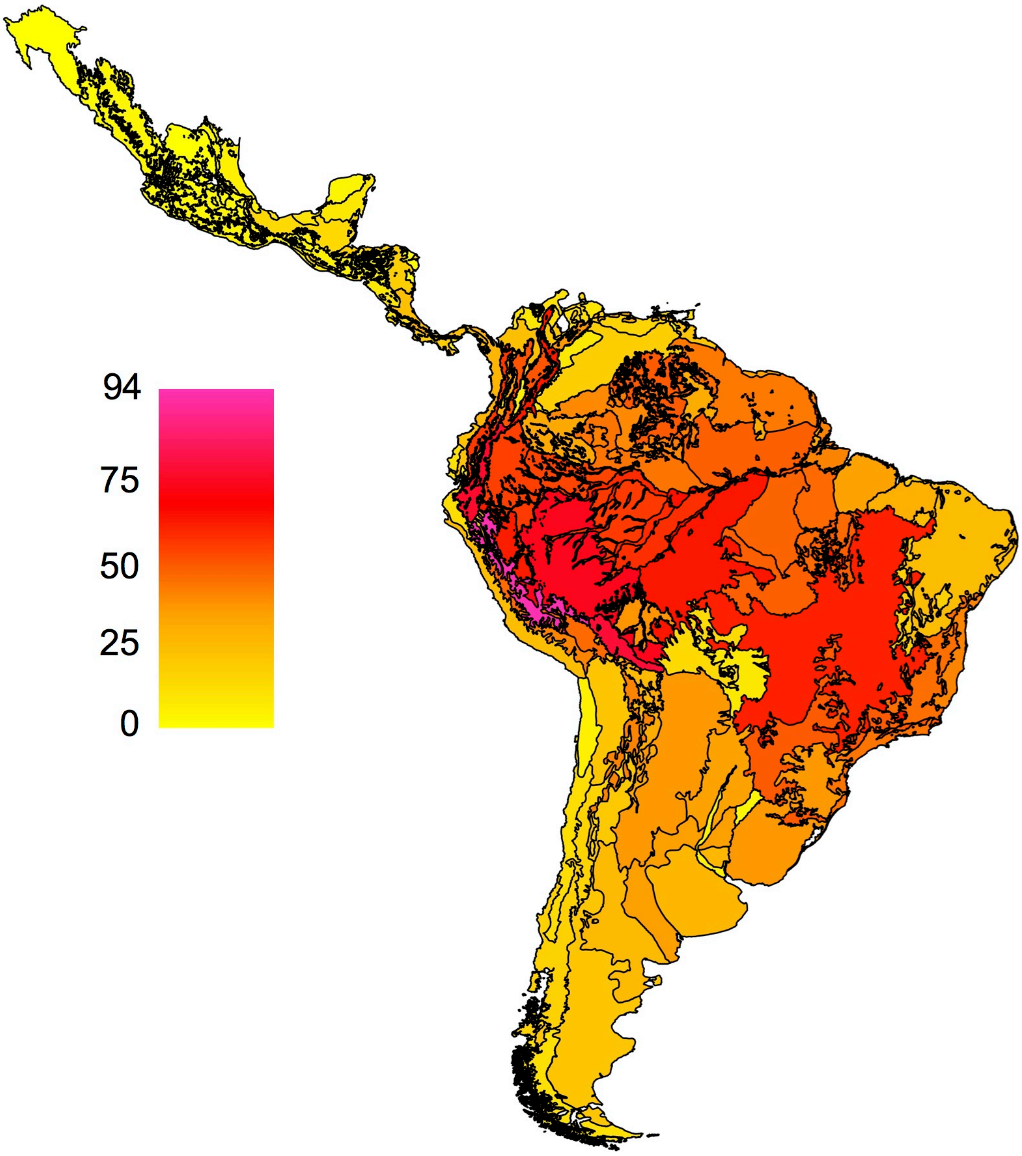

Figure 2. Furnariidae (ovenbirds and woodcreepers) species richness for each of 146 ecoregions. Seven ecoregions were excluded from the study (see methods).

When interaction effects among dispersal ability, mean trait distance (MTD), nearest neighbour trait distance (NNTD) and species age were not considered, the probability of a species occurring in an ecoregion increased with increased ecoregion area and with an increase in species hand-wing index (dispersal ability) (Table S2 in Appendix 3). In addition, consistent with an effect of environmental filtering, species occurrence probability decreased with an increase in the MTD of a species from the ecoregion community. However, there was no significant effect of NNTD, species age or the time a species had been diverged from its closest relative within the ecoregion on species occurrence probability.

When interaction effects were included, there was a significant interaction between MTD and dispersal ability. Species occurrence probability declined with increased MTD to the ecoregion community, and this decline was steeper for species with an increased hand-wing index (Fig. 3a). Thus, the trait similarity of a species to the ecoregion community was a more important predictor of species occurrence probability for species with greater dispersal ability. There was also a significant interaction between NNTD and dispersal ability (Table 1). Species occurrence probability increased with increased NNTD, consistent with an effect of interspecific competition, and this increase was greater for species with higher dispersal ability (Fig. 3b). Thus, the trait similarity of a species to the single species most similar to it in the ecoregion was a more important predictor of species occurrence probability for species with greater dispersal ability. While there was a significant positive effect of species age on species occurrence probability, there was no significant interaction between species age and dispersal ability (Table 1). There was also no significant effect of divergence time. However, there was a significant interaction between species age and NNTD, where the effect of NNTD on species occurrence probability decreased with increasing species age (Table 1; Fig. 3c). When the interaction model was run with the threshold in range overlap for biome assignment raised from 5 to 20%, the results were similar, but for a significant positive effect of divergence time and the absence of a significant interaction between

MTD and dispersal ability (Table S3 in Appendix 3). The expected probability of the interactions in the model being significant based on a null model where the associations between species traits, range size, and species co-occurrences were randomized was low (Table 2).

Table 1 Trait-based model of species-level occurrence probability at the ecoregion scale, considering interactions among dispersal ability, a species' trait-based similarity to the ecoregion and species age. Species assignment to biomes used the 5% percent range overlap threshold.

Parameter	Estimate	CI	ESS	P
(Intercept)	–0.473	(–2.142, 1.686)	712	
NNTD	0.100	(–0.052,0.230)	1000	0.174
MTD	–0.951	(–1.180, –0.733)	1000	<0.001
HWI	0.448	(–0.070, 0.908)	1000	0.074
Species age	0.469	(0.068, 0.910)	1000	0.036
Divergence time	–0.152	(–0.344, 0.033)	1000	0.096
Ecoregion Area	0.754	(0.373, 1.112)	1000	<0.001
NNTD x Species age	–1.152	(–1.439, –0.855)	1000	<0.001
NNTD x HWI	0.800	(0.475, 0.800)	904	<0.001
MTD x HWI	–0.663	(–1.106, –0.218)	1000	0.004
HWI x Species age	–0.335	(–0.827, 0.259)	1000	0.226

NNTD = trait distance to the nearest neighbour in ecoregion community; MTD = mean trait distance to ecoregion community; HWI = hand-wing-index, an estimate of dispersal ability. Parameter estimates are standardized effect sizes, standardized on 2 SD following Gelman (2008). Estimate = mean value from the posterior distribution for the parameter; CI = 95% credible interval; ESS = effective sample size in the posterior distribution; P = Bayesian p-value (see methods).

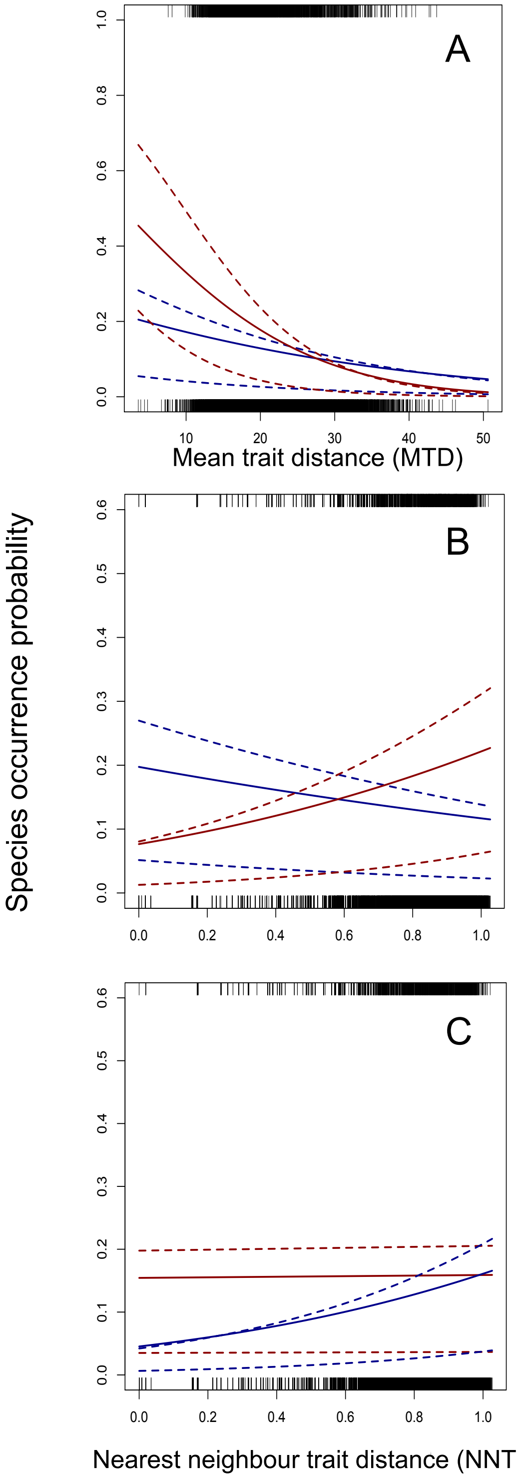

Figure 3. Interactions between: (a) MTD and dispersal ability; (b) NNTD and dispersal ability; and (c) NNTD and species age (Myr). The interactions (a and b) are plotted for dispersal ability at one standard deviation above the mean [red] and one standard deviation below the mean [blue] value for all 284 species, and for age (c) at 0.5 Myr [blue] and 5Myr [red]. Median species age was 3.45 Myr. All fixed effect variables not in the interaction were held at their mean value. Dashed lines are the lower 25% and upper 75% quartiles due to variation in probability of occurrence from the random effects.

Table 2 The expected probability of observing, as significant, the same interactions as were found with the observed data (see Table 1), based on a null model of species occurrence that shuffled species ranges at random among the tips of the phylogeny.

Interaction term	Expected probability*
Trait-based model	
NNTD x Species age	0.07
NNTD x HWI	0.04
MTD x HWI	0.04
HWI x Species age	0.01

* Proportion of times the observed interaction (with the same signs on the main effects) was significant out of 100 null model datasets.

DISCUSSION

I modelled ecoregion-scale occurrence probabilities for 284 ovenbird species, considering the potential for interactions between the following: dispersal ability and species age; dispersal ability and interspecific competition; and dispersal ability and environmental filtering. While there was no significant interaction between dispersal ability and species age, the effects of both mean trait distance (MTD)—a proxy for environmental filtering—and nearest neighbour trait distance (NNTD)—a proxy for interspecific competition—on species occurrence probability were greater for species with higher dispersal ability (Fig. 3). Moreover, it was only when interaction effects were included that the influence of NNTD on regional-scale species occurrence patterns was detected (Tables 1 and S2).

Dispersal ability and species age

Species age and hand-wing index (a proxy for dispersal ability) both had a positive effect on species occurrence probability, but there was no significant interaction between them. These results are thus consistent with the prediction that less dispersal limited species, both in terms of time for dispersal (species age) and dispersal ability, will be able to colonize more ecoregion assemblages within their ecological niche than more dispersal limited species (Gaston 2003;Paul et al. 2009). The hypothesis that dispersal ability limits regional-scale species occurrence more for younger species because they have had less time to disperse (Böhning-Gaese et al. 2006; Paul et al. 2009) is not supported. However, that dispersal ability had a positive effect on species occurrence may also reflect: (1) high dispersal maintaining populations in ecologically unsuitable regions through mass effects (Holyoak et al. 2005; Urban et al. 2008) and (2) that speciation rate declines with increased dispersal ability in ovenbirds (Claramunt et al. 2011), suggesting that more dispersive species have higher occurrence probabilities because they resist range division across the dispersal barriers separating many ecoregions (e.g. rivers in Amazonia). The consideration of interactions between dispersal ability and environmental filtering and dispersal ability and interspecific competition allowed for the separation of these potential influences of dispersal ability on species occurrence.

Interaction of dispersal ability and environmental filtering

The negative effect on the occurrence probability for a species of an increase in its mean trait distance (MTD) to the ecoregion community suggests an effect of environmental filtering on species occurrence among ecoregions. This is consistent with the finding that environmental filtering structures ecoregion-scale species composition in antbirds, another large neotropical bird radiation (Gómez et al. 2010). It is also perhaps expected given that ecoregion delimitation is based primarily upon differences in vegetation composition (Olson et al. 2001). Thus, ecoregions should describe relatively distinct habitats for ovenbirds, leaving a signature of species sorting among habitat types in morphological traits such as tarsus length that are related to foraging substrate and microhabitat use (Miles and Ricklefs 1984; Miles et al. 1987).

However, this interpretation is incomplete because species MTD interacted with dispersal ability such that the effect of MTD on occurrence probability was more negative for species with greater dispersal ability. Therefore, ovenbird ecoregion assemblages are most likely insufficiently connected by dispersal for mass effect dynamics among species populations in different ecoregions to influence regional-scale species occurrence. Instead, the observed interaction suggests that species occurrence for species with greater dispersal ability is more limited by the environmental suitability of an ecoregion than for less dispersive species. This is consistent with a model where more dispersive species are better able to colonize the spatial extent of environmentally suitable ecoregions, making species occurrence for these species relatively more dependent on environmental conditions. Although this study is possibly the first to show this result for vertebrates, there is some existing evidence for this relationship from plant ecology studies. The predictability of local-scale (~4m^2) plant species occurrence based on environmental conditions has been shown to increase with increased dispersal ability (Ozinga et al. 2005). Furthermore, when more dispersive grassland plant species were planted outside of their predicted local environmental niche (0.33 km^2 study area), they had lower fitness compared to less dispersive species (Moore and Elmendorf 2006).

The observed interaction between dispersal ability and environmental filtering fits with the expectation that dispersal may enhance the effect of environmental filtering at larger spatial scales. However, the spatial scale at which this observed interaction is detected should depend on a combination of dispersal barrier strength at a given scale and on species dispersal ability, such that species with greater dispersal ability show the observed interaction only at scales with stronger dispersal barriers. The majority of ovenbird species occupy niches associated with low dispersal (e.g. understory insectivores) (Salisbury et al. 2012). Thus, the range of dispersal abilities within ovenbirds may have resulted in the detection of only an effect of increased dispersal ability leading to increased importance of environmental filtering. In contrast, the opposite effect, where increased dispersal ability decreases the importance of environmental filtering, may be more apparent at the ecoregion scale for groups with higher dispersal ability. For example, many large frugivorous bird species may more easily cross the barriers (e.g. rivers) separating some ecoregions (Burney and Brumfield 2009). Indeed, metacommunity theory suggests that species sorting is most likely to produce a close match between species composition and the environment at intermediate levels of dispersal (Mouquet and Loreau 2002). Thus, considering the interaction of dispersal ability and environmental filtering across a wider range of species dispersal abilities may recover this unimodal relationship at the ecoregion scale.

Interaction between dispersal ability and interspecific competition

Species occurrence probability increased with increased NNTD (i.e. increased dissimilarity) of a species to the most similar resident species in the ecoregion. This is consistent with interspecific competition—also termed niche incumbency—limiting regional-scale species occurrence. It has been shown previously that the dynamics of range overlap between sister species in ovenbirds were consistent with a model in which interspecific competition limits species ranges (Pigot and Tobias 2012). My results broaden this finding to competition mediating regional-scale co-occurrence among ecologically similar species in this clade, irrespective of relatedness. In doing this they add to a small, but growing number of studies (e.g. Pigot and Tobias 2012; Algar et al. 2013; Laube et al. 2013) that suggest that factors other than environmental filtering shape regional-scale species occurrence patterns.

The effect of NNTD on occurrence probability was only detected when the interaction effect between NNTD and dispersal was included. Similar to MTD and environmental filtering, the effect of NNTD on species occurrence probability was greater (a more positive slope) for species with higher dispersal ability. This does not support a model where mass effects allow species with greater dispersal ability to occupy ecoregions where they might otherwise be competitively excluded. Instead, in line with the interpretation for MTD, this interaction is suggested to result from more dispersive species being better able to reach suitable sites without close competitors, thus making trait similarity to potential competitors a more important limit on occurrence for these species. When viewed from the perspective of dispersal, this interaction suggests that dispersal ability is a less important predictor of occurrence for species that have a more similar potential competitor in an ecoregion. This may be because in this case interspecific competition limits occurrence, despite the species ability to disperse into the region. This interpretation is consistent with previous work suggesting that species of *Sylvia* warbler with greater dispersal ability showed greater range filling only when the number of potential competitors near the species range margin was low (Laube et al. 2013). Again, as for MTD, the shape of this relationship may be unimodal, and vary with both species dispersal ability and spatial scale.

However, when species that are most closely related are also more similar in traits, an alternative explanation for the positive effect of NNTD on species occurrence is that insufficient time has passed since speciation for closely related, ecologically similar species to disperse back into sympatry (Mayr 1942; Barraclough and Vogler 2000). This explanation seems reasonable given the predominance of allopatric speciation in birds (Phillimore et al. 2008) and the association of increased speciation rates with low dispersal ability in ovenbirds (Claramunt et al. 2011). Indeed, the finding of a decreased importance for NNTD as a predictor of species occurrence for older species would seem to support this (Fig. 3c). However, there are two reasons to suggest that this is not the case. First, a species's divergence time from its closest relative in the ecoregion should capture the effect of time for dispersal back into sympatry more directly than an interaction between species age and NNTD. Instead, divergence time was either not significant, or when the threshold for biome overlap was raised to 20% and there was a positive effect of divergence time, the interaction between NNTD and age remained unchanged. Second, if dispersal limitation in the form of insufficient time for dispersal back into sympatry was the dominant explanation for the decreased importance of NNTD with increased species age, then it would be expected that increased dispersal ability would also decrease the importance of NNTD, but as already discussed I found the opposite relationship. Thus an alternative explanation for the decreased importance for NNTD as a predictor of species occurrence for older species is that older species have diverged more in traits related to reproductive isolation, where incomplete reproductive isolation limits co-occurrence of younger close relatives through costly interspecific sexual interactions (Hochkirch et al. 2007; Gröning and Hochkirch 2008). Analyses of the type presented here quantifying NNTD for traits such as plumage and song, related to aggressive interspecific interactions and reproductive isolation, may help to further clarify the relative roles of these processes.

Null models

The null model shuffled species ranges across the tips of the phylogeny. One consequence of this approach was the removal of any phylogenetic signal in the spatial location of species ranges. Under a more mechanistic, spatial model of allopatric speciation, if range dynamics are sufficiently slow, there should be phylogenetic signal in range locations, even when species range size and occurrence are independent of species traits. Thus, a spatially explicit null model may generate either higher or lower co-occurrence among ecologically similar species than that predicted by the null model used here if speciation occurs predominantly either across or within the ecoregions of a biome, respectively. In Amazonia, where many of the ecoregions in this study are located, ecoregion boundaries often correspond with river barriers that form geographic boundaries for many bird species (Naka et al. 2012; but see Gascon et al. 2000 for frogs and small mammals), such that allopatric speciation across ecoregions may be expected. Thus, a spatially explicit null model should predict lower co-occurrence of ecologically similar species than the null model used here, further supporting environmental filtering in the observed data. With respect to NNTD, this effect was partially accounted for by including divergence time as a covariate. Nevertheless, the use of more mechanistic null models that include the spatial dynamics of speciation should be considered for future studies of regional-scale species occurrence.

CONCLUSION

I found that dispersal ability, environmental filtering and interspecific competition influence species-level occurrence probabilities at the regional scale. Furthermore, the degree to which species were sorted among ecoregions, based on both environmental filtering and interspecific competition, increased with greater species dispersal ability. Thus, ecological limits to species occurrence are more important predictors of species occurrence for more dispersive species, suggesting that these species are closer to equilibrium with their spatial ecological niche at regional scales. These results also suggest that there is predictability in species-level occurrence patterns at the regional scale, and that the consideration of interactions between dispersal, environmental filtering, interspecific competition and biogeographic history is a key step in revealing the importance of each of these processes. Thus, my results make clear that the inclusion of interspecific variation in dispersal ability and of scale-dependency in the interactions between community assembly processes is a crucial next step for metacommunity theory. Moreoever, building upon recent simulation studies (Urban et al. 2012; Urban et al. 2013), they emphasize the need to consider these same factors when modelling the impacts of global environmental change on species distributions.

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CHAPTER 5

Niche space constrains species richness in Andean birds: insights from dietary niches and functional traits

ABSTRACT

A ubiquitous pattern for numerous taxa is for species richness to increase dramatically as one descends from high to mid–low elevations. Two potential mechanisms underlying this pattern are the tighter packing of species into available niche space due to increased ecological specialisation (i.e. narrower niches) or greater niche overlap, or both. However, due in part to the difficulty of quantifying resource partitioning among species, few studies have examined ecological specialisation and niche overlap across diversity gradients and thus, the importance of these mechanisms remains unclear. I tested these two hypotheses for forest insectivorous bird communities situated at opposite ends of an Andean elevation gradient, which shows a threefold increase in diversity. Niche width and overlap were quantified using isotopic analysis of species diet and variance in functional traits. Contrary to the ecological specialisation hypothesis, niche width (intraspecific trait variance) did not differ between high and low species richness. Furthermore, contrary to the niche overlap hypothesis, overlap in species dietary niches was lower at high species richness. Taken together, these results imply that bird species richness along the elevation gradient does not increase in response to tighter niche packing, but instead is constrained by the breadth of available niche space.

INTRODUCTION

Species richness varies dramatically across space in both the terrestrial and marine environment (Roy et al. 1998; Hillebrand 2004), often declining with increasing latitude (Hillebrand 2004) and altitude (Rahbek 1995). Longstanding ecological theory asserts that coexisting species must differ in their use of shared, limiting resources (Gause 1934; MacArthur and Levins 1967). However, the role of resource partitioning in explaining patterns of species richness remains unclear (Hutchinson 1959; Belmaker et al. 2011; Ricklefs 2012).

One prominent explanation for biodiversity gradients is that the species richness at a site is related to the variety or breadth of available resources (niche space) that can be partitioned among species to reduce interspecific competition and allow for coexistence (MacArthur 1965; Tilman 1982; Hurlbert and Jetz 2010). This explanation provides an equilibrial model of species richness, where gradients in diversity arise because the species richness at each site is close to a resource-determined species carrying capacity (Rabosky 2013; Cornell 2013). However, two alternative explanations exist that are also based on resource partitioning. First, increased ecological specialisation (narrower species' niches) is predicted to allow for increased species richness (Hutchinson 1959; MacArthur 1972). Specialisation enables greater species coexistence for a given level of resource diversity because it reduces interspecific competition through a finer partitioning of resources. Second, species in high diversity sites may tolerate overlapping resource use to a greater extent, exhibiting greater niche overlap than those in low diversity environments, thereby allowing more species to coexist (Klopfer and MacArthur 1961; May and MacArthur 1972). In both cases, species diversity increases as species are more tightly packed into available niche space, decoupling the relationship between species richness and ecological resource breadth (Pianka 1966; Jablonski et al. 2006; Rabosky 2009). However, species diversity in this model may still reach a steady state if interspecific competition limits diversification (Rabosky 2013). Despite these contrasting predictions, the extent to which greater resource space or niche packing contributes to species richness gradients is unresolved.

A key reason for this lack of consensus is the difficulty of quantifying resource availability and its partitioning among species (e.g. Pianka 1975). Thus, whilst positive correlations between species richness and net primary productivity at regional–global scales support resource availability limiting species richness (Currie 1991; Hurlbert and Jetz 2010), few studies have quantified the degree of ecological specialisation and niche overlap across either latitudinal or altitudinal gradients (Armbruster 2006; Schemske et al. 2009; Ghosh-Harihar and Price 2013).) In a meta-analysis, Vázquez and Stevens (2004) found little evidence for increased ecological specialisation at lower latitudes. However, more recent studies on ecological specialisation have yielded conflicting results, with evidence for both increased (Dyer et al. 2007) and unchanged (Novotny et al. 2006) ecological specialisation across latitudinal diversity gradients in herbivorous insects, and for both increased and decreased trait overlap across diversity gradients in plants (Hulshof et al. 2013; Le Bagousse-Pinguet et al. 2013). In birds, Belmaker et al. (2011) found that species had more specialised diets and habitat preferences in more species rich assemblages, and Marra and van Remsen (1997) found that species niche breadth was narrower and niche overlap less in foraging microhabitat use in a tropical compared to a temperate understory insectivorous bird community. Moreover, Salisbury et al. (2012) showed that ecological specialisations associated with reduced dispersal ability were more common in tropical avifaunas, suggesting a non-equilibrial model in which specialisation results in increased allopatric diversification, thus contributing to increased species richness. However, a detailed study of resource use in Old World warblers showed that, within species, populations were more specialised in species poor assemblages, suggesting an equilibrial model where reduced resource availability limits species richness (Ghosh-Harihar and Price 2013). Accordingly, given the limited empirical understanding of hypotheses of niche packing and species richness and the centrality of resource partitioning in theories of biodiversity, further comparison of specialisation and niche overlap across diversity gradients is clearly needed.

Here, I compare ecological specialisation and niche overlap between assemblages of forest-dwelling insectivorous birds at opposite ends of an Andean elevation gradient that has a threefold increase in bird species richness for this group. Important differences exist in how environmental factors such as seasonality, suggested to contribute to diversity gradients, co-vary with latitude but not elevation (Körner 2007). Despite these differences, similarities in diversity gradients across latitude and elevation occur, making the assessment of niche dynamics across elevation potentially useful in identifying mechanisms underlying diversity gradients more generally (Brown 2001; Hulshof et al. 2013).

I used two complementary approaches to quantify ecological specialization and niche overlap among species: (1) variance in species stable isotope signatures related to dietary resource use and (2) variance in species functional traits related to prey item selection, foraging substrate use and foraging movements. Stable isotope analysis overcomes many of the practical difficulties associated with more time-consuming and often more invasive approaches to assessing resource partitioning among species (e.g. stomach and faeces contents analysis; Rosenberg and Cooper 1990). Indeed, the analysis of $\partial^{13}C$ and $\partial^{15}N$ isotope ratios has been increasingly used as a way to quantify and partition species trophic niches (Bearhop et al. 2004, Newsome et al. 2007), especially in birds (e.g. Herrera et al. 2003; Young et al. 2010; Bodey et al. 2013). Thus, stable isotope analysis provides a potentially powerful tool for assessing niche dynamics across a larger number of species, improving on previous tests of the relationship of niche width and overlap to species richness. Trait-based approaches assume that trait variability within a population reflects variability in resource use (Roughgarden 1972; Violle et al. 2012), with some evidence that increased beak shape variation is related to increased dietary niche width in birds (Hsu et al. 2013). Recent insights from trait-based community ecology have provided a framework for the use of intra and inter-specific trait variation in testing niche-based hypotheses of community assembly

(Bolnick et al. 2011; de Bello et al. 2011; Violle et al. 2012). The ratio of intraspecific trait variation (niche width) to the trait variance of all individuals in the community (community niche width) has been shown to be a robust metric of trait overlap among species (Violle et al. 2012; de Bello et al. 2011; de Bello et al. 2013).

Therefore, if increased species richness at low elevation is associated with increased ecological specialisation (i.e. narrower niches) allowing tighter niche packing, intraspecific trait variation is predicted to be lower for species in the low elevation community. Alternatively, if increased species richness is associated with increased niche overlap driving niche packing, the ratios of intraspecific to total community trait variance and of intraspecific to total community isotopic variance are predicted to be higher in the low elevation community. Furthermore, the percentage of total community variance in isotope values explained by species identity is predicted to be lower.

METHODS

Study sites

This study was conducted in the Peruvian Andes at two sites separated in elevation by 2770 m. The Wayqecha Biological Research Station in the Kosnipata valley (13°10'35"S 71°35'20"W) covers an elevational range of 2600–3050 m asl and the Centro de Investigación y Conservación de Río Los Amigos (CICRA) in Madre de Dios (12°34′07″S, 70°05′57″W) covers a range of 280–300 m asl. Wayqecha contains a mix of montane cloudforest and high elevation grassland habitats, while vegetation at CICRA consists of a mix of Amazonian habitats, dominated by terra firme and flood plain forest.

Data collection

I restricted my sample to a single trophic level—insectivorous birds—to allow for a more interpretable comparison of fine-scale dietary and trait-based niche widths among species. Because a single prey type may have different isotopic signatures in different habitats, estimates of species dietary niche width from isotopic analysis may capture components of both the diversity in habitats used and prey items consumed by a species (Matthews and Mazumder 2004; Flaherty and Ben-David 2010; Cummings et al. 2012). Therefore, increased species generalization in habitat and dietary resource use may have opposing effects on niche width estimates that are difficult to separate without detailed additional data on species foraging behavior (Flaherty and Ben-David 2010). In order to control for these potentially confounding effects of species' generalisation in diet and habitat use on niche width, I sampled only species classified as forest habitat specialists. Habitat classification was based on habitat preference data in del Hoyo et al. (1992-2012), Parker et al. (1996) and Schulenberg et al. (2007). Based on species elevational ranges for this region (Walker et al. 2006) and on research station species records, the resident species pool for forest insectivores was estimated to be 59 species for Wayqecha and 197 for CICRA. In addition, isotopic analysis may incorrectly estimate a narrow niche (low variance) for a generalist species when, in contrast to individual specialisation, all individuals take the same broad range of prey items. However, blood isotope ratios used here reflect diet over relatively short time scales and thus are unlikely to underestimate niche width for populations of individual generalists as diet variability among individuals should still exist at short time scales (Bearhop et al. 2004).

Fieldwork was conducted at Wayqecha between July and September 2010, and at CICRA between August and September 2012. Mist-nets were set between ground level and 3 m in forested habitats, opened at first light and kept open until one hour before dark. They were checked every 20 minutes. For each captured individual, a small blood sample (0.1–0.2 ml) was collected by wing venipuncture of the brachial (ulnar) vein and stored in 1 ml of absolute ethanol at room temperature. In addition, measurements were taken for six morphological traits closely related to foraging substrate use, foraging movement and prey item selection in birds: beak width, beak depth, beak length, wing length, tail length and tarsus length (Schoener 1965; Miles and Ricklefs 1984; Miles et al. 1986). A total of 153 individuals from 19 species were sampled for both isotopes and trait measurements at Wayqecha, and 553 individuals from 88 species at CICRA. See Chapter 1 of this thesis for a detailed description of trait measurement protocols. To obtain a more complete sample of the trait diversity at each site, for those species in a site's resident species pool that were not sampled by mist-net capture, data on species trait means were obtained from museum specimen measurements (provided by C. Sheard and T. Bregman) made following the same measurement protocols.

Sample preparation and isotopic analysis

Approximately 0.7 mg of blood from each sample was dried in a drying oven at 50°C for 48 hours prior to being homogenized for analysis. C and N isotope ratios were measured by continuous-flow isotope ratio mass spectrometry, using a Costech ECS 4010 elemental analyser interfaced with either a Thermo Fisher Scientific Delta XP Plus or a Thermo Fisher Scientific Delta V Plus IRMS. Three internal laboratory standards were analysed for every 10 blood samples, and measurement precision of both $\partial^{13}C$ and $\partial^{15}N$ was estimated to be $\leq 0.2‰$. Because some samples were run on different mass spectrometers, all sample C and N values were normalized by subtracting the mean C and N value of the internal laboratory standard gel (a solution of 2 g Fluka gelatin [Sigma Aldrich] to 20 ml distilled water) for the run in which they were analysed. Internal laboratory standards are regularly calibrated against International Atomic Energy Agency and National Institute of Standards and Technology stable isotope reference materials.

Statistical analysis

Bayesian standard ellipses were used to estimate species dietary niche widths based on isotopic data using the *SIAR* package in R (Jackson et al. 2011), with niche width estimates taken as the median standard ellipse area from the posterior distribution. Bayesian standard ellipses are relatively unbiased and more robust with respect to small sample sizes than other available methods to estimate niche width, such as convex hull volume (Jackson et al. 2011). Following Jackson et al. (2011), I used the correction for small sample sizes and estimated niche width only for species with 10 or more sampled individuals. This sample size threshold resulted in similar sampling intensity for the two sites (14% of the species pool for Wayqecha and 11% for CICRA). When comparing species niche widths between sites, it is necessary to correct for potential differences in the baseline variation in prey $\partial^{13}C$ and $\partial^{15}N$ values (Syvaranta et al. 2013). Thus, I estimated the total community niche width as the standard ellipse area of all sampled individuals at a site—again representing a similar sampling intensity of species per site (32% of the species pool for Wayqecha and 44% for CICRA)—and then divided each species niche width by the niche width of its community. This accounted for baseline isotopic variation between sites by comparing variance in species dietary resource use as a proportion of the variance displayed by the community at a site, providing a measure of niche packing as a fraction of community niche space and a metric of niche overlap the same as that calculated using intraspecific and total trait variance ratios. To account for potential phylogenetic non-independence, I calculated phylogenetic signal in species dietary niche width using Pagel's lambda in the R package *caper* (Orme et al. 2011). Estimates of phylogenetic relationships across species were obtained from a recent time calibrated molecular phylogenetic tree (downloaded from www.birdtree.org) (Jetz et al. 2012). To account for phylogenetic uncertainty, I repeated my analysis across 500 trees drawn at random from the posterior distribution. Phylogenetic signal in niche width was zero across the distribution of phylogenies, so t-tests were used to compare species niche widths between sites. To further test for differences in niche overlap between high and low species richness sites, following Bodey et al. (2013), I used MANOVA to partition the total variance in $\partial^{13}C$ and $\partial^{15}N$ among species and residual variance for each site, using only species for which ≥ 5 individuals were sampled (20% of the species pool for both sites). I used Wilk's lambda (Λ) to assess significance and report partial eta squared (η^2) values as estimates of explained variance.

A two-step principle components analysis (PCA) was used to reduce redundancy in functional traits. First, traits were grouped according to their importance for prey item selection (beak traits) or foraging maneuver and substrate use (wing, tail and tarsus), and a separate PCA applied to each trait set after log-transformation of individual trait values. Species not sampled in the field were represented by mean trait values from museum specimens. Second, a further PCA was then performed using the first PCs (indices of trait size) from each of these separate analyses (see Chapter 1 for a detailed description of this method). This generated four trait axes: beak shape, tarsus length:tail length ratio, size, and beak size:body size ratio (see Table S1 in Appendix S4 for PCA summary results). Because the weighting of the individual trait axes with respect to ecological niche dimensions cannot be quantified and because the combination of multiple trait axes may mask processes acting on separate axes (Spasojevic and Suding 2012; Chapter 1 of this thesis), each trait axis PC was analysed separately (Ricklefs 2012; Claramunt 2010). Following recent studies using intraspecific trait variability as a proxy for species niche width (Hulshof et al. 2013; Le Bagousse-Pinguet et al. 2013), intraspecific variation was calculated for species with ≥ 5 individuals (19% of the species pool for Wayqecha and 20% for CICRA). For species with more than 5 individuals sampled, 5 individuals were selected at random to ensure equal sampling effort among species. The total trait variance for a site was calculated as the variance in trait values among all individuals of all species at the site (81% of the species pool for Wayqecha and 98% for CICRA). Both species intraspecific trait variation as a proxy for species niche width, and the ratio of intraspecific trait variation to total trait variation as a measure of niche packing and niche overlap were compared between sites. I used t-tests to test for differences between sites because there was no phylogenetic signal in either intraspecific trait variance or the ratio of intraspecific to total trait variance. All statistical analyses were conducted in R v. 3.0.1 (R Core Team 2013).

RESULTS

The two bird communities did not overlap in isotope space; species in the high elevation, low species richness cloud forest community had higher mean $\partial^{13}C$ and lower mean $\partial^{15}N$ values than those in the low elevation, high species richness Amazonian forest community (Fig. 1). Total community isotope space was also greater for the high species richness community (Fig. 1). Individual species dietary niche widths were wider in the high species richness [2.03 ± 0.12 SE, n = 21] compared to the low species richness community [1.13 ± 0.07 SE, n = 8] ($t = 6.33$, $df = 27$, $p<0.001$; Fig. 2a). However, when comparing species niche widths as a proportion of their community niche width, species occupied a smaller proportion of community niche space (total community isotope space) at high species richness [0.04 ± 0.002 SE, n = 21] than at low species richness [0.12 ± 0.01 SE, n = 8] ($t = -2.64$, $df = 27$, $p<0.001$; Fig. 2b), suggesting reduced dietary niche overlap at high species richness, and proportionately tighter packing of species in niche space. Furthermore, the proportion of variance in isotope signatures explained by species identity was greater at high ($F_{78,820} = 23.05$, $p<0.005$, $\Lambda = 0.098$, partial $\eta^2 = 0.69$) than at low ($F_{22,256} = 14.08$, $p<0.005$, $\Lambda = 0.205$, partial $\eta^2 = 0.55$) species richness, providing additional evidence for reduced dietary niche overlap in the high species richness community. Nevertheless, the form of niche partitioning among species was similar for both the high and low species richness communities, with greater variance among species at each site due to species partitioning in $\partial^{13}C$ (partial $\eta^2_{\text{high species richness}} = 0.83$, $p<0.005$; partial $\eta^2_{\text{low species richness}} = 0.71$, $p<0.005$) versus $\partial^{15}N$ (partial $\eta^2_{\text{high species richness}} = 0.41$, $p<0.005$; partial $\eta^2_{\text{low species richness}} = 0.36$, $p<0.005$).

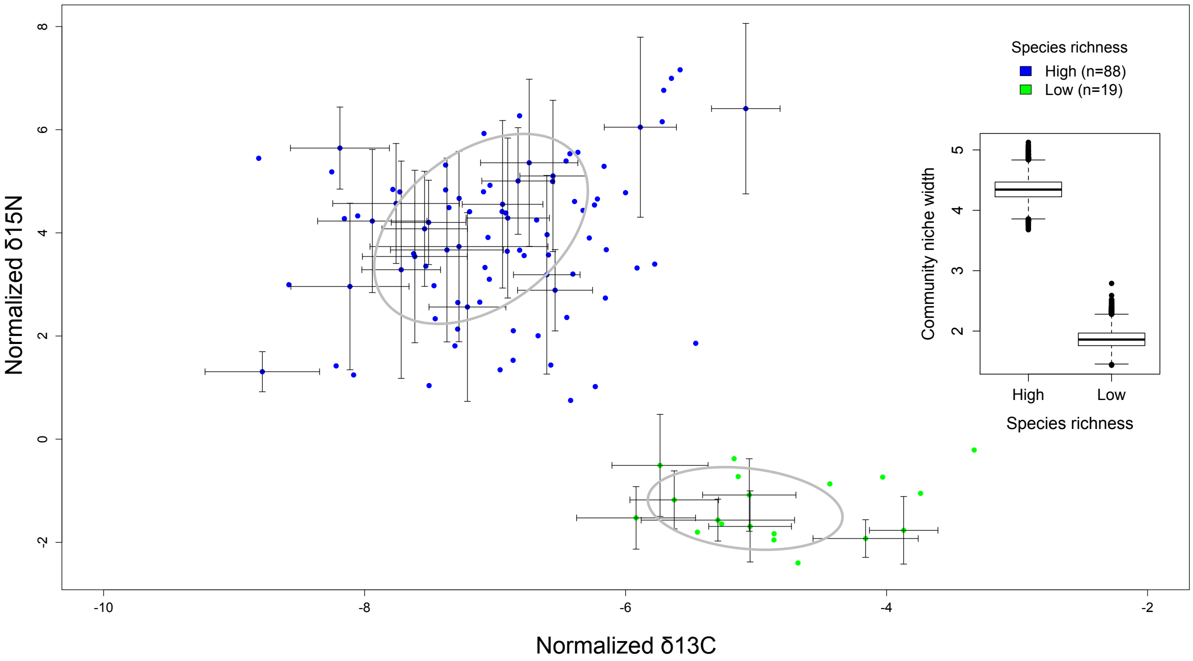

Figure 1. The mean isotopic values for each species in the high and low species richness sites. Error bars show the standard deviation for the species from each community with 10 or more individuals sampled. Grey lines trace the median standard ellipse area estimates of community isotopic variance (community niche width) based on all individuals sampled from all species for the given community. The inset figure shows boxplots of the Bayesian posterior distribution of standard ellipse area estimates for the high and low species richness communities.

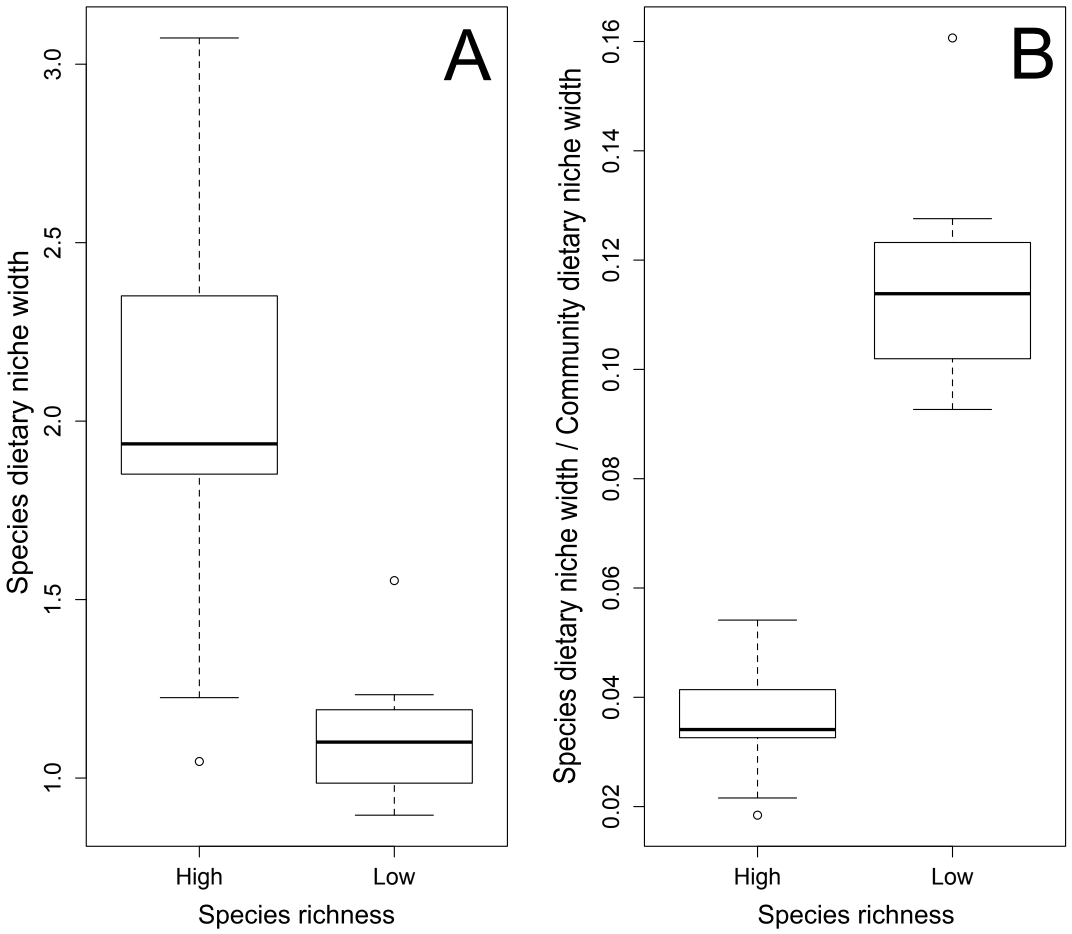

Figure 2. Boxplots of species dietary niche widths in the high and low species richness communities. (A) Species dietary niche widths estimated as the median Bayesian standard ellipse area for all the sampled individuals of a species. Only species with more than 10 individuals sampled were used to estimate species-level dietary niche widths (N=21 for high species richness and N=8 for low species richness). (B) Species dietary niche estimated the same as in (A), but as a proportion of the community niche width (the standard ellipse area for all individuals sampled in the high or low species richness community).

Although median intraspecific trait variance—a proxy for niche width—was greater at low than at high species richness, there were no significant differences in intraspecific trait variation between communities for any of the four functional trait axes (Table 1; Fig. 3a-d), suggesting no difference in species trait-based niche widths between high and low species richness. The median ratio of intraspecific to total community trait variation was higher at low than at high species richness for all four functional trait axes (Fig. 3e-f). However, size was the only trait axis for which this ratio showed a significant difference between high and low species richness (Fig. 3e; Table 2), indicating reduced overlap among species in size at high species richness.

Table 1. Species intraspecific trait variation: Results of two sample t-tests for differences in the mean intraspecific trait variance between high and low species rich insectivorous forest bird communities.

Trait	Species richness	Mean	SE	T	d.f.	p
Size	High	0.061	0.012	–1.32	48	0.20
Size	Low	0.074	0.016			
Beak size: Body size	High	0.027	0.005	–0.02	48	0.98
Beak size: Body size	Low	0.033	0.005			
Beak shape	High	0.026	0.004	–1.37	10.4§	0.20
Beak shape	Low	0.031	0.004			
Tarsus:Tail	High	0.020	0.004	0.83	46.4§	0.40
Tarsus:Tail	Low	0.016	0.003			

§ Welch approximation to degrees of freedom used when the variance of the two samples was not equal.

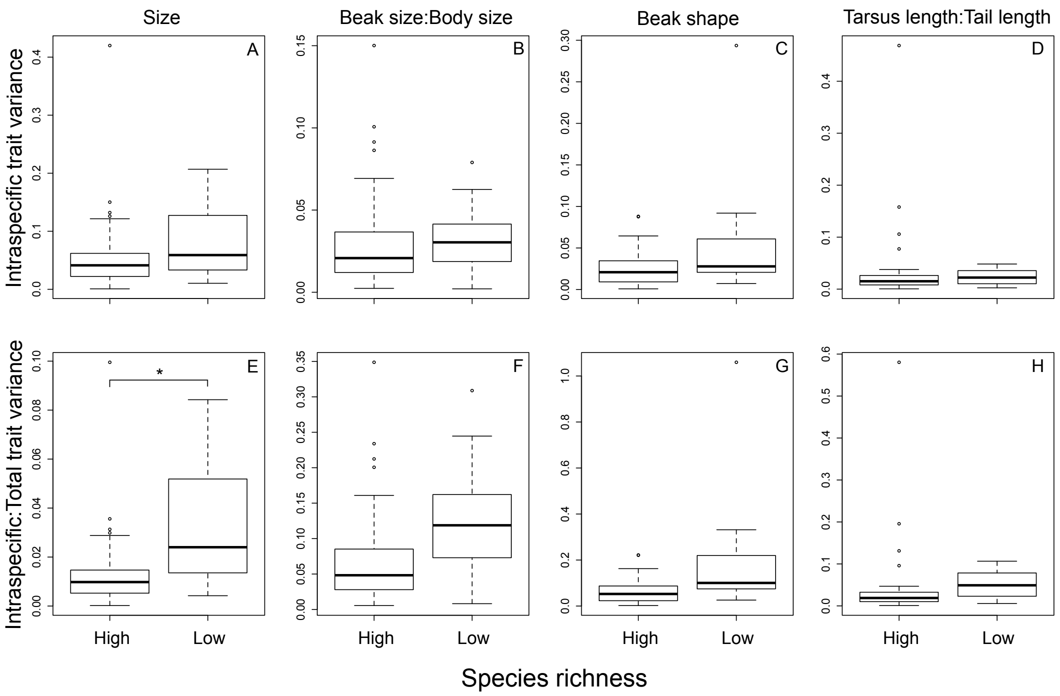

Figure 3. (A–E) Boxplots of intraspecific trait variance for high (n = 39 species sampled) and low (n = 11 species sampled) species richness communities. (E–F) Species intraspecific trait variance as a proportion of total trait variance. * denotes significant difference ($P < 0.05$)

Table 2. Ratio of intraspecific to total community trait variance: Results of two sample t-tests for differences in the mean ratio of intraspecific to total community trait variation between high and low species rich insectivorous forest bird communities.

Trait	Species richness	Mean	SE	T	d.f.	p
Size	High	0.015	0.003	–2.61	12.2§	0.02*
Size	Low	0.030	0.007			
Beak size: Body size	High	0.064	0.011	–1.93	48	0.06
Beak size: Body size	Low	0.128	0.019			
Beak shape	High	0.066	0.010	–1.68	10.2§	0.12
Beak shape	Low	0.111	0.017			
Tarsus:Tail	High	0.024	0.005	–0.47	44.3§	0.64
Tarsus:Tail	Low	0.034	0.007			

§ Welch approximation to degrees of freedom used when the variance of the two samples was not equal.

DISCUSSION

Here, using variance in species stable isotope ratios and functional traits, I tested whether species niche widths and niche overlap differed between communities showing a threefold difference in species richness across an elevation gradient. I found that species niche widths, based on intraspecific trait variance in key foraging traits, showed no significant difference between high species richness (low elevation) and low species richness (high elevation) communities (Table 1 and Fig. 3a-d). Thus contrary to the key prediction of the ecological specialisation model, increased species-level ecological specialisation (i.e. narrower niches) was not associated with higher species richness (Hutchinson 1959; MacArthur 1972). Furthermore, in the species rich lowland community, both species dietary niches and intraspecific variation in size occupied a smaller proportion of total community niche space (Figs 2b and 3e), and species identity explained a greater proportion of the total community isotopic variance in the lowland site (Table 2). Thus, my analyses also provide strong evidence that greater species richness is associated with reduced overlap in species niches. This does not support the hypothesis that increased species richness is driven by species requiring lower levels of resource partitioning to coexist, allowing for increased niche overlap and therefore the tighter packing of species into available niche space (Klopfer and MacArthur 1961; May and MacArthur 1972).

My finding of reduced niche overlap at higher species richness agrees with previous work across a bird latitudinal diversity gradient that showed tropical understory insectivores overlapped less in foraging behaviours and substrate use than temperate forest species (Marra and van Remsen 1997). Accordingly, reduced niche overlap may be a more general feature of high insectivorous bird diversity. In addition, my results showed that isotopic niche partitioning among species was greater in $\partial^{13}C$, typically more indicative of habitat use, than in $\partial^{15}N$, indicative of trophic position (Matthews and Mazumder 2004; Olsson et al. 2008). This is consistent with greater niche partitioning in foraging substrate than in diet for four sympatric Amazonian ovenbird species, based on stomach contents analysis and behavioural observations (Chapman and Rosenberg 1991). These findings support the suggestion for insectivorous birds of greater partitioning in foraging microhabitat and foraging behaviour than in prey item selection (MacArthur 1958). They also lend some support to the prediction that this pattern will be more pronounced where the number of potentially competing species is increased, due to the supposed greater evolutionary lability of foraging microhabitat use than prey item selection (Schoener 1965). However, while there was evidence of reduced niche overlap in size—a trait related to prey item selection in birds (Schoener 1965)—with increased species richness, there was no change in niche overlap along the other trait-based niche axes. This suggests that, with respect to microhabitat use, measures of foraging behaviour and resource use may provide better estimates of fine-scale species niche partitioning than trait-based approaches for this group.

The absence of increased ecological specialisation at higher species richness contradicts findings from global bird diversity gradients (Belmaker et al. 2011) and tropical versus temperate comparisons of greater ecological specialisation in species rich assemblages (Marra and van Remsen 1997). Specialisation is predicted to evolve in more stable environments that allow for narrower species tolerances (Klopfer and MacArthur 1960; MacArthur 1972; Jocque et al. 2010). Thus, one potential explanation for these findings is that elevation gradients do not show the same changes in climatic variability (e.g. seasonality of solar energy flux) as latitudinal gradients (Brown 2001; Körner 2007), and therefore do not provide the gradient in environmental stability required for differences in ecological specialisation to evolve. Contrasts with previous studies may also result from differences in the scale at which specialisation was assessed. Belmaker et al. (2011) quantified diet specialisation at the species-level, based on the use of eight diet categories (e.g. fruit, invertebrates), and did not consider intraspecific variability. In contrast, I focussed within a dietary category—a scale at which further ecological specialisation may not be a key mechanism driving increased species richness. This agrees with Ghosh-Harihar and Price (2013), who showed that

Old World leaf warblers in high species richness assemblages exhibited narrower niches in elevation range and foraging movement, associated with lower arthropod abundance and reduced vegetation resource diversity, respectively, suggesting a resource-influenced cap on species richness. It also agrees with a recent global analysis showing that both animal pollinators and seed dispersal were more specialized in higher latitude, species poor assemblages (Schleuning et al. 2012).

There is no clear 'correct' level at which to assess ecological specialisation, and fine-scale assessments of resource use are difficult. The use of variance in species isotopic signatures to estimate species niche width is a promising approach. However, the variance in a population's $\partial^{13}C$ and $\partial^{15}N$ values will in part be driven by the range and variance of the prey, and accounting for this is required in order to make robust comparisons of niche width between sites (Mazumder and Matthews 2004; Syvaranta et al. 2013). Therefore, the increased species dietary niche widths at high species richness may be the result of greater isotopic variability of prey at the lowland Amazonian site. The approach used in this study of dividing the isotopic niche width estimate of each species by the niche width estimate for the entire community to which it belongs is unsatisfactory because although this allows for a comparison among sites of the *proportion* of the community niche width occupied by the species it does not allow for tests of differences in the absolute niche widths among species at different sites: the metric value will decrease due to both narrower species niche widths or wider community niche widths and thus provides an inexact test of niche packing. An alternative approach is to divide each species' isotope values by the isotopic range of its prey to account for differences in prey isotopic range and thus make direct comparisons of niche widths among species, but this requires knowledge of the range of prey items used by each species. Simple standardisation by the full range of prey isotope values available at a site will lead to the underestimation of niche width for species that consume only a subset of this range. One potential solution is the use of isotope mixing models to assign prey item dietary proportions to each species, but their usefulness is limited when the number of potential prey groups is high and the isotopic distance among some of these groups relatively small (Inger et al. 2009), as was the case in this study. Thus, while isotope-based approaches to niche overlap are often robust (e.g. Bodey et al. 2013), further progress in the use of isotopes to compare niche width across sites requires more detailed observation of the range of prey groups used by each species (Cummings et al. 2012). Alternatively, the use of intraspecific trait variance as a proxy for niche width has recently received renewed attention in community ecology (Violle et al. 2012; Bolnick et al. 2011), especially in plants (e.g. Hulshof et al. 2013; Le Bagousse-Pinguet et al. 2013). In birds, there is some evidence for an association between trait variation and dietary niche width (Hsu et al. 2013), increasing confidence in the finding of no reduction in niche width with increased species richness in this study. However, the link between morphological variance and niche width needs to be better established for many animal groups, such as birds, where behaviour can play a large role in ecological specialisation (Bolnick et al. 2007).

In conclusion, my results showed that higher species richness at low elevations was associated with neither increased ecological specialisation nor greater niche overlap. Taken together, these results suggest that, although at high species richness species occupied a smaller fraction of niche space, there is no increase in niche packing from low to high species richness. This implies that insectivorous bird species richness across this elevation gradient is limited by available niche space, lending tentative support to an equilibrial model of species richness for this system (MacArthur 1965; Tilman 1982; Wiens 2011). This is consistent with insectivorous bird species richness showing a strong positive association with forest habitat complexity along an Andean elevation gradient (Terborgh 1977), and with evidence for resource-limited species richness in other insectivorous bird groups (MacArthur 1965; Ghosh-Harihar and Price 2013). It is also consistent with increased net primary productivity at lower elevation along this gradient (Girardin et al. 2010), and with bird species richness more generally being correlated with increased productivity (Hurlbert and Jetz 2010). However, a resource-influenced limit to species richness is not mutually exclusive of increased niche packing (Belmaker et al. 2011; Cornell 2013), and this study has only examined a limited set of niche dimensions. Thus, further work characterising species resource use and site-specific resource diversity is needed to more confidently assess the relative importance of niche packing and total niche space in explaining diversity gradients in this group.

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CHAPTER 6

General Discussion

6.1 Community assembly in Neotropical birds

In this thesis I have tested hypotheses about the mechanisms shaping patterns of species diversity and composition in Neotropical birds. My research was carried out using both local community data from a pristine elevation gradient in the Peruvian Andes, which has among the highest bird diversities in the world, and data on regional-scale species occurrence across South America. In the General Introduction (Chapter 1), I gave a broad overview of the development of past research into the processes thought to influence community assembly: speciation, demographic stochasticity, niche-based fitness trade-offs and dispersal. I highlighted that, despite emerging consensus on the relevance of this set of processes for community assembly, intense debate remains over the relative importance of any particular process. I then outlined three areas in which our understanding of how community assembly processes influence patterns of species diversity and composition is most limited. First, how the importance of assembly processes, especially niche-based processes such as habitat filtering and interspecific competition, changes across spatial scales, remains unclear. Second, despite strong theoretical support for the interaction of assembly processes, few studies have tested empirically for the importance of interactions among processes in shaping species occurrence, especially at regional spatial scales. Third, if niche-based interspecific competition is important in shaping community composition, it is unclear how resource partitioning among species explains patterns in species richness.

6.2 Interspecific competition and habitat filtering across small spatial scales

In the first data chapter, I found patterns of trait overdispersion and clustering within communities that suggest that both interspecific competition and habitat filtering structure insectivorous bird communities at the scale of individual territories (~1–2 ha). This is contrary to the expectation that habitat filtering dominates at larger and interspecific competition dominates at smaller spatial scales (Weiher and Keddy 1995; Weiher et al. 2011). Instead, these results suggest that the action of both these processes can be highly localized. Importantly, these patterns were only apparent when using single-trait-axis metrics, which revealed that although both habitat filtering and interspecific competition acted on locomotory traits, only interspecific competition acted on body size and beak shape. This separation of processes across trait axes is consistent with longstanding ideas that while habitat filtering constrains foraging substrate use, resource partitioning of both substrate use and prey item selection is important for promoting co-occurrence in birds (MacArthur 1958; Hutchinson 1959).

One implication of these results is that when multiple niche-based processes influence community assembly, single-trait-axis metrics, which do not integrate processes operating on separate trait axes, may be more suitable than multi-trait-axis metrics for detecting the full set of niche-based processes influencing community assembly. There is a growing sense that linking traits to niche-based coexistence mechanisms should provide greater generality and predictability to community ecology, as well as to related applications, such as the ecological forecasting of how species distributions will be impacted by climate change (McGill et al. 2006; Adler et al. 2013). Single-trait-axis metrics would seem to have a clear advantage in this case. However, the robustness of these metrics for detecting a particular niche-based process when multiple processes act on a trait axis can be low (see Chapter 3; Aiba et al. 2013). In addition, finding overdispersion or clustering in community trait or phylogenetic structure does not necessarily provide evidence for the higher relative importance of a given coexistence mechanism (Adler et al. 2013; Chapter 3). For example, significant divergences from the random assembly null model for the bird communities studied in this chapter were associated with relatively weak effect sizes. Thus while niche-based processes are important, demographic stochasticity also likely plays a significant role in shaping species composition at these small spatial scales (Vellend 2010). Improved understanding of the capacity for trait and phylogenetic metrics to identify not just the presence, but also the relative importance of different community assembly processes, would advance our ability to accurately incorporate them into predictive models of community composition.

6.3 Robustness of trait and phylogenetic metrics for detecting niche-based assembly processes

In Chapter 3, I explored the robustness of trait and phylogeny-based metrics of community structure to detect the influence of either interspecific competition or habitat filtering on community assembly across a wide range in the relative importance of these processes. I found that trait-based metrics outperformed phylogenetic metrics, but that both classes of metric often failed to reject random assembly when a combination of habitat filtering and interspecific competition was important for community assembly. In addition, I found that many multi- and single-trait-axis metrics detected habitat filtering over interspecific competition, even when competition was the dominant process in community assembly. Finally, the power of multi-trait-axis metrics to detect a particular process increased, often dramatically, when the proportion of independent traits exposed to that process was increased in the set of traits sampled for metric calculation.

One implication of these results is that the use of functionally relevant traits should be preferred over phylogenetic proxies of ecological similarity among species, even when niche conservatism is relatively strong (see also Mason and Pavoine 2013). That morphology reflects diet and foraging ecology more generally is a cornerstone of evolutionary ecology (Losos 1990; Ricklefs and Travis 1980; Schluter 2000). However, considerable variation in bird functional traits, such as tarsus and midtoe length, is unrelated to the foraging variables that characterize species' ecological relationships (Miles and Ricklefs 1984). This simulation study and others like it may overstate the effectiveness of trait-based metrics for detecting niche-based processes because they assume too close a link between morphology and ecology. Thus, in addition to the low power of trait-based metrics when a combination of processes is important for community assembly, this variance in the link between traits and ecology may contribute to the low percentage of trait-based studies (18%) that have rejected random assembly in plant communities (Götzenberger et al. 2012).

One possibility for improving metric performance suggested by my results is to group independent traits into sets according to the niche-based processes for which they are hypothesized to be important and then apply the appropriate multi-trait-axis metric to each trait set. However, to do this will often require an improved understanding of the mechanistic links between particular functional traits and resource use. In addition, while the use of a relatively small number of independent functional traits has been shown to yield high predictive power for plant community composition (Laughlin 2014), the ability of morphological traits to reflect resource use may be expected to asymptote well below explaining the full spectrum of resource partitioning among species, especially in animals (Blaum et al. 2011; Ricklefs 2012). Therefore, improved approaches to estimating resource partitioning across large numbers of species are needed (see Chapter 5).

Finally, while trait-based metrics of community structure may be able to detect the full set of niche-based processes active in community assembly, the results of this chapter show that they usually do not allow for the inference of the relative importance of a particular niche-based process. However, when traits can be linked to specific niche-based processes, the use of phylogenetic mixed-modelling approaches (e.g. Ives and Helmus 2011) in combination with trait metrics may offer a solution by allowing estimation of the variance in species occurrence associated with a particular trait.

6.4 Interactions among assembly processes at regional scales

In Chapter 4 I used a phylogenetic generalised linear mixed-modelling approach to test for the effects of interactions among assembly processes on ovenbird species occurrence at the regional scale. The effects of interspecific competition and habitat filtering on species occurrence probability were greater for species with greater dispersal ability. These results suggest that, at regional scales, the occurrence of a species is closer to equilibrium with the spatial extent of the species's ecological niche for species with greater dispersal ability. Although for plants there is evidence that more dispersive species are closer to range equilibrium with their ecological niche (Moore and Elmendorf 2006, Sexton et al. 2009), this has not been shown before for a vertebrate group, and when considering both biotic and abiotic components of the ecological niche. Furthermore, in combination with the results of Chapter 2, the results of this chapter show that interspecific competition and habitat filtering play an important role in shaping species occurrence for Neotropical insectivorous birds at scales from individual territories to regional assemblages. This result challenges the common assumption that interspecific competition affects species composition at small spatial scales only, while habitat filtering dominates at larger scales.

Importantly, the effect of interspecific competition on species occurrence was only detected when interaction effects among assembly processes were considered. Thus, previous studies that failed to detect any effects of interspecific competition and dispersal ability on species occurrence at regional scales may have done so because they did not consider the potential for the interaction of these processes. Furthermore, this result also implies that species distribution models should incorporate differences in dispersal ability among species and the interactions among assembly processes. Indeed, recent simulation studies suggest that ecological forecasting models that do not consider interspecific differences in dispersal ability may greatly underestimate the impact of environmental change on species diversity (Urban et al. 2012; Urban et al. 2013).

However, the type of interaction between dispersal ability and either habitat filtering or interspecific competition is likely to be scale-dependent. For example, contrary to the findings of this chapter, ecological limits to species occurrence may be less important for more dispersive species when high dispersal distributes species into sites regardless of their ecological suitability (Holyoak et al. 2005; Urban et al. 2008). This alternative interaction between dispersal ability and the ecological limits to species occurrence may be prevalent at small spatial scales where large barriers to dispersal are absent. To test for this predicted scale-dependency in the interactions among assembly processes, the approach taken to modelling species occurrence probability in this chapter could be applied to data on species occurrence for local communities within the range of each ovenbird species. Across these smaller spatial scales, I would expect the interaction effects between dispersal ability and interspecific competition and dispersal ability and habitat filtering to be opposite those observed among regional assemblages.

Another opportunity for future research within the analysis framework used in this chapter is the consideration of competitive exclusion due to interspecific competition based on relative fitness differences among species (Chesson 2000; HilleRisLambers et al. 2012). Instead of competitive exclusion based on niche differentiation driving overdispersion within a community, a competitive hierarchy based on relative fitness differences may result in the clustering of species' trait values related to competitive ability (Mayfield and Levine 2010). Experiments with song playback to provoke interspecific territory defence suggest the existence of this type of a competitive hierarchy, based on body size, for insectivorous bird species in Amazonia (Robinson and Terborgh 1995). Thus, the use of raw as opposed to absolute distance measures to quantify body size differences among species should capture some of the structure of this competitive hierarchy. If a competitive hierarchy is important in shaping regional-scale species composition, then the occurrence of smaller-bodied species within a region may be driven by compensation of lower relative fitness with a higher relative niche difference (Chesson 2000; Adler et al. 2007). Accordingly, the effect on species occurrence probability of nearest neighbour trait distances in body size should be greater for smaller-bodied species.

6.5 Resource partitioning and species richness

In my final data chapter, I used a combination of trait- and isotope-based approaches to compare insectivorous bird species niches between two communities at opposite ends of an Andes–Amazon gradient, which shows a threefold decrease in species diversity with elevation. Although stable isotope analysis has a long history of use for quantifying resource partitioning in avian systems (Inger and Bearhop 2008), its utility for quantifying niche dynamics in species rich systems has not previously been tested. I found that species niche widths did not differ significantly between high and low species richness communities. This does not support the hypothesis that increased ecological specialisation (i.e. narrower niche widths) contributes to the maintenance of increased species richness (MacArthur 1972; Belmaker et al. 2011). I also showed that niche overlap among species was lower in the high compared to the low species richness community. This result is inconsistent with the prediction that increased species richness results from an increase in species' tolerance of reduced resource partitioning (Klopfer and MacArthur 1961; May and MacArthur 1972). Taken together, these results suggest that differences in species richness between the two communities are not explained by increased niche packing, but rather by differences in the breadth of available niche space between high and low elevation communities.

This result is relevant to the current intense debate over the extent to which species richness at large spatial scales, such as continents, is set by ecological limits (Ricklefs 2012; Cornell 2013; Rabosky 2013). If interspecific competition results in diversity dependent diversification, both niche packing and limited resource space may result in a steady-state level of species richness within a system (Rabosky 2013). However, diversity dependent diversification due to interspecific competition and diversity maintenance based on niche packing does not place an absolute limit on species richness (Jablonski et al. 2006; Rabosky 2013). Instead, species richness and resource space are decoupled in this model. In contrast, the evidence against niche packing from this chapter supports a model in which diversity dependent diversification due to interspecific competition is coupled with the maintenance of diversity being restricted by the extent of the resource space. Therefore, this chapter lends tentative support to there being an ecological limit on the absolute number of species and to predictions that species richness will be positively correlated with resource diversity (Currie 1991; Rabosky 2013).

The use of stable isotope analysis to quantify species' niche widths also offers the potential for more detailed tests of the influence of interspecific competition on diversity maintenance. To the extent that the position of a species in morphological space reflects its position in ecological space, niche theory predicts that to coexist, species in relatively clustered parts of morphological space should have narrower niches (MacArthur and Levins 1967). Combining data on species' functional traits and stable isotope ratios allows for improved testing of this hypothesis by incorporating data on species resource use obtained independently from species morphology. Species that have smaller nearest neighbour trait distances or smaller mean trait distances to other species within an assemblage should have narrower isotopic niche widths.

6.6 Applied significance

Given the prospect of rapid global environmental change, understanding how ecological and evolutionary processes influence species occurrence and community composition is a major concern for conservation and management (Walther et al. 2002; Parmesan 2006). This thesis demonstrates that habitat filtering, interspecific competition and dispersal ability are important determinants of community composition for insectivorous birds across large spatial scales. This result adds to the growing evidence base for incorporating both species interactions and differences in dispersal ability among species into models that seek to inform conservation management strategies and policy debates through assessments of species extinction risk and community turnover in response to environmental change (Araújo and Luoto 2007; Urban et al. 2013). Although some species distribution modelling approaches have begun to include proxy measures for interspecific competition (e.g. Laube et al. 2013), the results of this thesis suggest that future models need also to account for interactions between dispersal ability and interspecific competition, and dispersal ability and habitat filtering, as well as species evolutionary relationships. One promising approach for doing this across a large number of species that is supported by the results of this thesis is the use of trait-based proxies for interspecific competition, habitat filtering and dispersal ability. The increasing availability of both trait and phylogenetic information coupled with an improved understanding of the interaction of community assembly processes across spatial scales should promote the development of more nuanced models of the impact of environmental change on biological communities, and thus improve the ability of policymakers and managers to mitigate and adapt to changes in biological diversity. For example, improved models of extinction risk and community dynamics for frugivorous birds are essential for anticipating the impact of changes in seed dispersal on the demographics of rain forest trees and could use trait-based approaches (Galetti et al. 2013). More generally, by quantifying functional diversity, the trait-based approaches used in this thesis also offer the possibility of linking models of the influence of community assembly processes on biological diversity with models of how biological diversity influences ecosystem functioning, an advance that would have wide application for predicting impacts to human welfare as a result of environmental change (Naeem et al. 2012).

Conclusion

Overall I tested how interspecific competition, habitat filtering and dispersal ability shape patterns of neotropical bird diversity and species composition. I found support for the influence of interspecific competition and habitat filtering on species composition at both local (individual territory) and regional (~75000 km^2) scales. This finding contests the widely held perception that interspecific competition influences species composition only at small spatial scales, whereas habitat filtering dominates at larger scales. The prevalence of this perception may be due in part to the demonstrated low power of many trait and phylogenetic metrics of community structure to detect habitat filtering and especially interspecific competition, when both of these processes shape community composition. In addition, the effect of interspecific competition on species occurrence at regional scales was only apparent when analyses included interactions between dispersal ability and interspecific competition and dispersal ability and habitat filtering. Thus, previous studies at regional scales may have failed to detect an effect of interspecific competition because they did not include the potential for interactions among assembly processes. That interspecific competition and habitat filtering were more important for limiting regional-scale species occurrence in species with higher dispersal ability suggests that more dispersive species are closer to range equilibrium with their ecological niches. This emphasizes the need for ecological forecasting models to include interspecific differences in dispersal ability, as well as the interaction of dispersal ability with competition and habitat filtering to improve predictions of how environmental change will alter species distribution patterns. Finally, I found that species' niche widths did not differ significantly between a high species richness (low elevation) and low species richness (high elevation) community and that niche overlap among species was less at high species richness. This result does not support the hypothesis that increased niche packing due to narrower niches or increased niche overlap explains the difference in species richness between these communities. Taken together, the results from this thesis provide support for the importance of interspecific competition, habitat filtering and dispersal ability in shaping species composition in neotropical birds. Given the evidence for the influence of interspecific competition on community composition in this system, they also suggest that rather than niche packing, differences in the size of resource space (i.e. the breadth of niche space) among sites play an important role in explaining patterns in species richness.

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APPENDIX S1

Unravelling the complex interplay of community assembly processes acting on multiple niche axes across spatial scales

Survey methods

Surveys were focused at 72 survey points arranged in a grid of 6 by 12 points. All points were visited six times during the first three hours after dawn. No survey point was visited twice on the same day, and the order in which points were visited on each survey round was randomized to reduce bias from sampling a survey point at the same time after dawn in multiple survey rounds (Buckland 2006). During each survey period, one observer recorded all birds detected within a 50m radius of the survey point. The distance from the observer to individual birds was estimated using a laser range finder (Nikon Laser 550).

To overcome the fact that many bird species are difficult to detect, particularly in forested habitats, I identified individuals on the basis of acoustic signals. This survey technique is standard, and particularly effective in this study because most Neotropical forest birds vocalise regularly year-round with distinctive territorial songs (Parker 1991). Vocalisations were recorded using an Edirol R-09 (Roland, Nakagawa, Japan) sound recorder and identifications were verified retrospectively by an expert (JAT) with reference to sound archives (e.g. www.xeno-canto.com). To produce communities spanning a variety of spatial scales I pooled each ‘point community’ (0.8 ha) with neighbouring communities as shown in Fig. 1 to produce communities of 1.6, 3.2 and 6.4 ha. The gaps between communities were not surveyed and are not included in estimations of community size.

Diet and habitat classification

To focus within a distinct trophic level, I only included species whose primary diet is insects or other arthropods in my analyses. Diet was determined from the literature (see Table S8), and confirmed through field observations. Species were also assigned to one of two primary habitat types—forest or non-forest—using key literature (see Table S8), with classifications verified at the study site using field observations.

Funtional trait measurements

Variation in beak design has profound impacts on the ability of birds to forage and survive in the wild (Mallarino et al. 2011), and beak morphology is a classic trait for the study of foraging ecology and competition in birds (Hutchinson 1959; Schoener 1965; Grant and Grant 2006). Tarsus length is also related to foraging niche and substrate (Claramunt et al. 2012), and represents the best univariate index of overall body size in birds. Wing length and tail length contribute to indices of foraging niche related to dispersal ability (Dawideit et al. 2009) and locomotion (Claramunt et al. 2012), respectively. Such indices apply particularly well to insectivorous species, with larger bodied and larger beaked birds taking larger insect prey (Hespenheide 1971), beak shape correlated with trophic niche (Fitzpatrick 1985), and tarsus, wing and tail length related to foraging substrate use and foraging manoeuvre (Miles and Ricklefs 1984; Miles et al. 1987).

Beaks were measured (to the nearest 0.01 mm) in three ways: (1) length from the anterior edge of the nostrils to the tip; (2) depth (vertical height) at the anterior edge of nostrils; and (3) width at the anterior edge of the nostrils. Tarsus length was measured down the back of the leg from the middle of the ankle joint (i.e. the notch between the tibia and tarsus) to the end of the last scale of the acrotarsium (usually the last undivided scale). Wing length was measured as the distance from the carpal joint (i.e. wing bend) to the tip of the unflattened wing, and tail length as the distance from the tip of the longest rectrix to the point at which the two central rectrices protrude from the skin.

As intra- and interspecific differences in trait values may be driven by local adaptation (Badyaev et al. 2008) or geographical variation (Milá et al. 2009), I maximized sampling of biometric data from within the study site. This ensured that trait measurements were relevant to the community structure I detected during field surveys. My approach contrasts with most previous studies of vertebrates that have included trait measures from museum specimens collected across a wide environmental range.

Sequencing methods and phylogeny estimation

I constructed a phylogeny (Fig. S4) for all species detected during surveys based on two mtDNA genes: NADH dehydrogenase subunit 2 (ND2) and Cytochrome B (Cyt *b*). I downloaded existing sequences from Genbank and—for species lacking existing data—produced 35 novel gene sequences (19 Cyt *b* and 16 ND2) by extracting DNA from blood samples collected in the field (Table S8).

I extracted whole genomic DNA from blood samples using the DNeasy Blood and Tissue Kit (250) (Qiagen), then used PCR to amplify both genes in two units, following published protocols (McCracken and Sorenson 2005). I used primers from (Sorenson et al. 1999) for ND2 and the primer pairs L14996-H15646 and L15413-H16064.B for Cyt *b* (primer sequences listed in Table S1). Automated sequencing was performed using the EZ-Seq service (Macrogen Europe).

When downloading sequence data from Genbank I selected from the closest geographical locality to my Peruvian field site (see Table S8 for accession numbers). In two cases where tissues or Genbank sequences were not available (*Grallaria erythroleuca* and *Myiodynastes chrysocephalus*), I downloaded relevant sequences from the most closely related species (*Grallaria ruficapilla* and *Megarynchus pitangua*, respectively). This should not affect the branch lengths calculated in my analyses because the substitute species are far more closely related to the missing species than to any other species in the observed communities (Ohlson et al. 2008; Tello et al. 2009). Thus, the pattern of community phylogenetic structure should be insensitive to the use of these substitutes.

I edited sequences using *Sequencher 4.2* (Gene Codes Corporation) and sequence alignment was done using *ClustalW* (Thompson et al. 1994) and by eye in *MEGA* v5.05 (Tamura et al. 2011). I estimated phylogeny and branch lengths simultaneously using a relaxed clock Bayesian method in *BEAST* v1.6.2 (Drummond and Rambaut 2007). I used a GTR + G model of nucleotide substitution and a pure birth prior on branching rates. I conducted two runs of ten million generations each. I used *Tracer* v1.5 (Rambaut and Drummond 2009) to assess that the two runs were sampling from the same posterior distribution and that the estimated sample size was sufficiently high to obtain good parameter estimates. I discarded the first 500 of 5000 trees of each run as burn-in before combining the trees from both runs.

Finally, tissues of wild birds and ND2 or Cyt *b* sequence data from close relatives were not available for two lineages (*Myiotheretes striaticollis* and *Pyrrhomias cinnamomeus*), so I inserted them into the MCC tree as sister species to their closest relative in my study based on published phylogenies (Ohlson et al. 2008; Tello et al. 2009). To account for uncertainty in the branch lengths from the node where *Myiotheretes striaticollis* and *Pyrrhomias cinnamomeus* were inserted, I generated 50 trees varying the relevant node heights at random from a range between zero and the height of the node below the insertion. I performed community phylogenetic tests on all 50 trees and found no significant difference in the results among them. Thus, I report results for a single randomly selected tree.

Functional Diversity (FD) calculations

I calculated FD by converting the matrix of trait comparisons between all 41 study species into a distance matrix, and then clustering this to produce a dendrogram depicting functional relationships (Petchey and Gaston 2002). I used Euclidean distance and UPGMA clustering (Pielou 1984) because these produced a dendrogram with the highest cophenetic correlation (Petchey et al. 2007). The FD of the total species pool is the total branch length of the dendrogram; the FD of a given community is the total branch length required to connect all of the species in the community (Petchey and Gaston 2006).

Further tests of habitat filtering

I assessed the scale at which spatial autocorrelation was present in vegetation structure using a correlogram (Fig. S5) and a Mantel test, with 1000 permutations, of the correlation between survey point locations and vegetation structure (Venables and Ripley 2002). This showed there to be spatial autocorrelation, i.e. homogeneity, in habitat over distances separating survey sites at the 0.8 ha scale, but not at larger spatial scales. I then used ordinary least squares regression to test, at the 0.8 ha scale for a relationship between a site's vegetation structure and the rank of the mean trait value of the bird community at the site, relative to the 999 null communities for the site. A significant relationship would show that more forested sites, at the 0.8 ha scale, have communities with mean trait values that are either greater or smaller than those expected by chance. If so, the increase in habitat heterogeneity at spatial scales above 0.8 ha will weaken any trait clustering signal for the trait, as communities with both higher and lower than expected mean trait values are grouped into a single community at larger scales. I restricted these tests to trait axes showing habitat filtering in the main analyses.

Statistical analyses and R code sources

All analyses were performed in R (R Core Team 2013). Calculation of Blomberg's K statistic, Mean Phylogenetic Distance (MPD) and Mean Nearest Taxon Distance (MNTD) and all independent swap null model simulations were performed using the *Picante* package (Kembel et al. 2010). Estimation of the phylogenetic signal in habitat type, using D (Fritz and Purvis 2012), was performed in the *Caper* package (Orme et al. 2012).

R code used in my analyses are available online from the following sources:

1) Calculations of convex hull volume used code developed by Villeger et al. (2008):

http://www.ecolag.univ-montp2.fr/software/F_RED.R

2) Calculations of functional diversity (FD) used code developed by Petchey and Gaston (2002) and Petchey and Gaston (2006):

http://www.ieu.uzh.ch/petchey/Code/Code/calculatingfd.html

3) Calculations of SDNDr and community assembly simulations used code developed by Kraft and Ackerly (2010):

http://life.umd.edu/biology/kraftlab/Code_files/trait_tests.R

http://life.umd.edu/biology/kraftlab/Code_files/community_assembly.R

4) Code for calculating functional diversity and convex hull volume in combination with null model simulations using the *Picante* package was written for this study and is available online [link to be added when accepted for publication].

Supplementary Tables

Table S1 Primer sequences used for amplification of Cytochrome *b*

Primer	Sequence
L14996	AAYATYTCWGYHTGATGAAAYTTYGG
H15646	GGNGTRAAGTTTTCTGGGTCNCC
L15413	GGGGGWTTYTCMGTNGAYAAYCC
H16064.B	CTTCANTYTTTGGYTTACAAGRCC

Table S2 Variance components analysis of the variation in functional trait values attributable to species and individuals (residuals) for well-sampled species ($N = 21$ species, with > 5 individuals sampled per species).

Trait	Variance component (%)	
	Species	Residuals
Tarsus	89.8	10.2
Bill depth	94.7	5.3
Bill width	84.5	15.5
Bill length	91.4	8.6
Wing length	89.9	10.1
Tail length	91.8	8.2

Table S3 Factor loadings (eigenvectors) and percentage of total variance explained for principal components (PCs) from the PCA including all six functional traits.

	PCs					
Functional traits	1	2	3	4	5	6
Wing length	0.45	–0.14	0.18	–0.06	0.80	0.33
Tail length	0.37	–0.43	–0.75	–0.30	–0.11	–0.08
Tarsus length	0.25	0.86	–0.28	–0.23	0.14	–0.23
Beak length	0.44	–0.02	–0.06	0.82	–0.04	–0.35
Beak width	0.43	–0.16	0.56	–0.42	–0.22	–0.50
Beak depth	0.46	0.18	0.11	0.03	–0.53	0.68
% variance	0.70	0.15	0.07	0.04	0.02	0.01

Table S4 Factor loadings (eigenvectors) and percentage of total variance explained for retained principal components (PCs) from trophic trait, locomotory trait, and body size PCAs in the two-step PCA process

PCA	PC	% variance	Loadings		
Trophic			Beak length	Beak width	Beak depth
	1*	0.85	0.61	0.55	0.57
	2	0.10	0.75	–0.63	–0.19
Locomotory			Tail length	Tarsus length	Wing length
	1*	0.62	0.60	0.44	0.66
	2	0.28	–0.49	0.86	–0.13
Body size			Beak traits 1*	Locomotory traits 1*	
	1	0.94	0.71	0.71	

*Denotes principal component axes used in the body size PCA (see Fig. S2).

Table S5 Results of phylogenetic signal tests using Blomberg's K statistic

Trait	K	*P**
Body size (PC1)	0.67	<0.001
Trophic trait (PC2; beak shape)	0.61	<0.001
Locomotory trait (PC2; tarsus to tail-length ratio)	0.76	<0.001

A K value of zero corresponds to a random, non-phylogenetic model of trait evolution; a K value of 1 corresponds to a Brownian motion model of trait evolution. A null distribution of K values for each trait was generated by shuffling the observed trait values across the tips of the phylogeny 999 times, estimating K each time. P-values were calculated by dividing the number of all null model values greater than the observed K by 999. P values <0.05 indicate traits with non-random phylogenetic signal.

Table S6 Factor loadings (eigenvectors) and percentage of total variance explained for principal components (PCs)

Component	% Variance	Canopy height	% Tree cover	% Shrub cover	% Grass cover
PC1	0.71	0.56	0.55	–0.42	–0.46
PC2	0.16	–0.05	-0.04	–0.79	0.61
PC3	0.09	0.38	0.49	0.45	0.64
PC4	0.05	–0.73	0.67	–0.03	-0.05

Note: PC data are from a PCA on habitat variables for 0.8-ha survey points.

Table S7 Results of ‘multi-pattern, multi-niche-axis’, trait-based tests for habitat filtering and interspecific competition on unstandardized trait axes.

Spatial scale (ha)	FD	*P*	CHV	*P*
0.8	0.0103 ± 0.12	0.91	–0.023 ± 0.11	0.05
1.6	–0.003 ± 0.17	0.96	–0.137 ± 0.12	0.15
3.2	0.008 ± 0.23	0.67	–0.163 ± 0.20	0.27
6.4	–0.060 ± 0.42	1.00	–0.003 ± 0.37	0.65

Note: FD = functional diversity; CHV = convex hull volume

Values are Mean SES ± SE (SES = standard effect sizes, calculated as observed value – null model mean, divided by sd of the null model distribution, averaged across all observed communities at each spatial scale). Positive SES indicates overdispersion (higher than expected trait spacing of community members) and negative SES indicates clustering (lower than expected trait spacing of community members).

P-values are for two-tailed Wilcoxon signed-ranks tests of the hypothesis that observed metric values are not significantly different from null model expectation.

Figure S1 Map of the study site based on a satellite image from Google Earth. Black dots show the distribution of 72 survey point locations across the cloudforest/grassland ecotone. The pale line is a road.

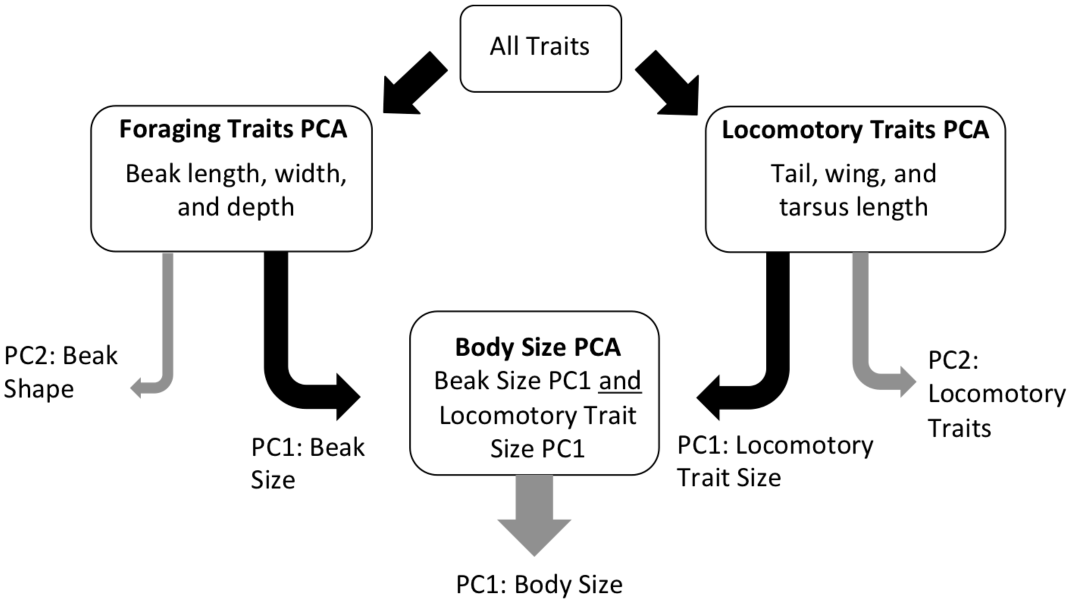

Figure S2. Diagram of a two-stage PCA of functional traits used to generate indices of trophic traits, locomotory traits, and body size for all species. Traits used in each PCA are listed in the boxes. Arrow width represents the relative proportion of trait variation explained by a principal component; black arrows represent principal components used in the body size PCA and gray arrows depict principal components retained for trait-spacing analyses. I found that this approach outperformed a simple PCA pooling all traits in separating candidate niche axes.

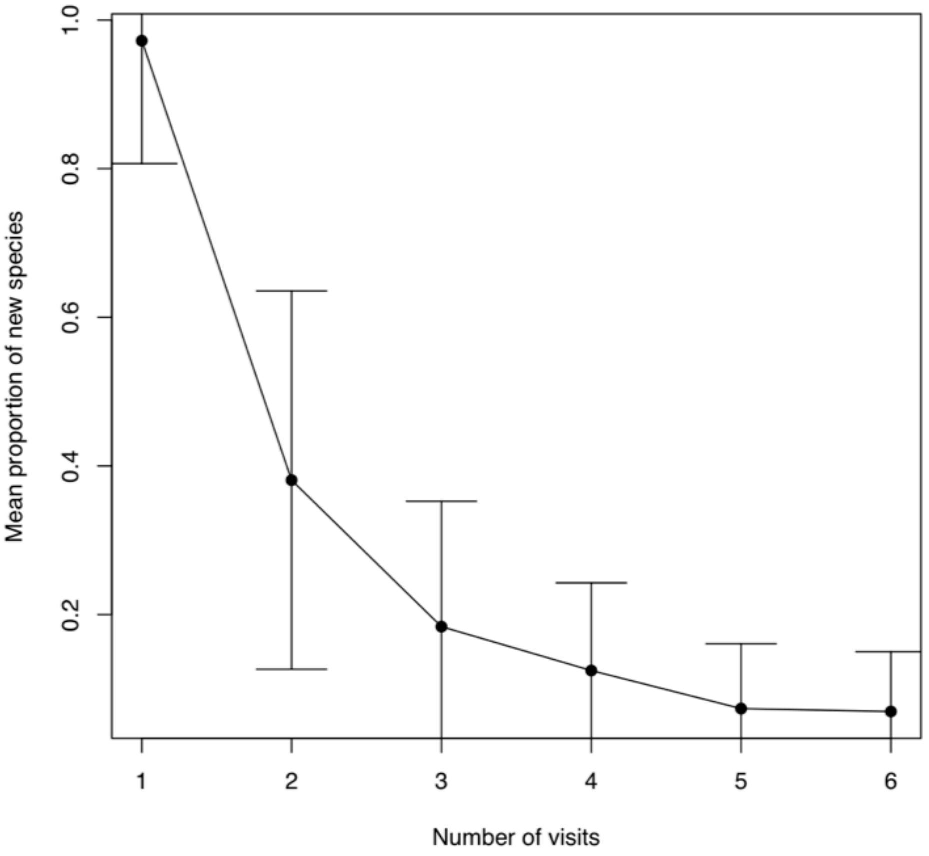

Figure S3 The mean (± SD) proportion of new insectivorous bird species detected per survey visit decreases with increasing number of visits.

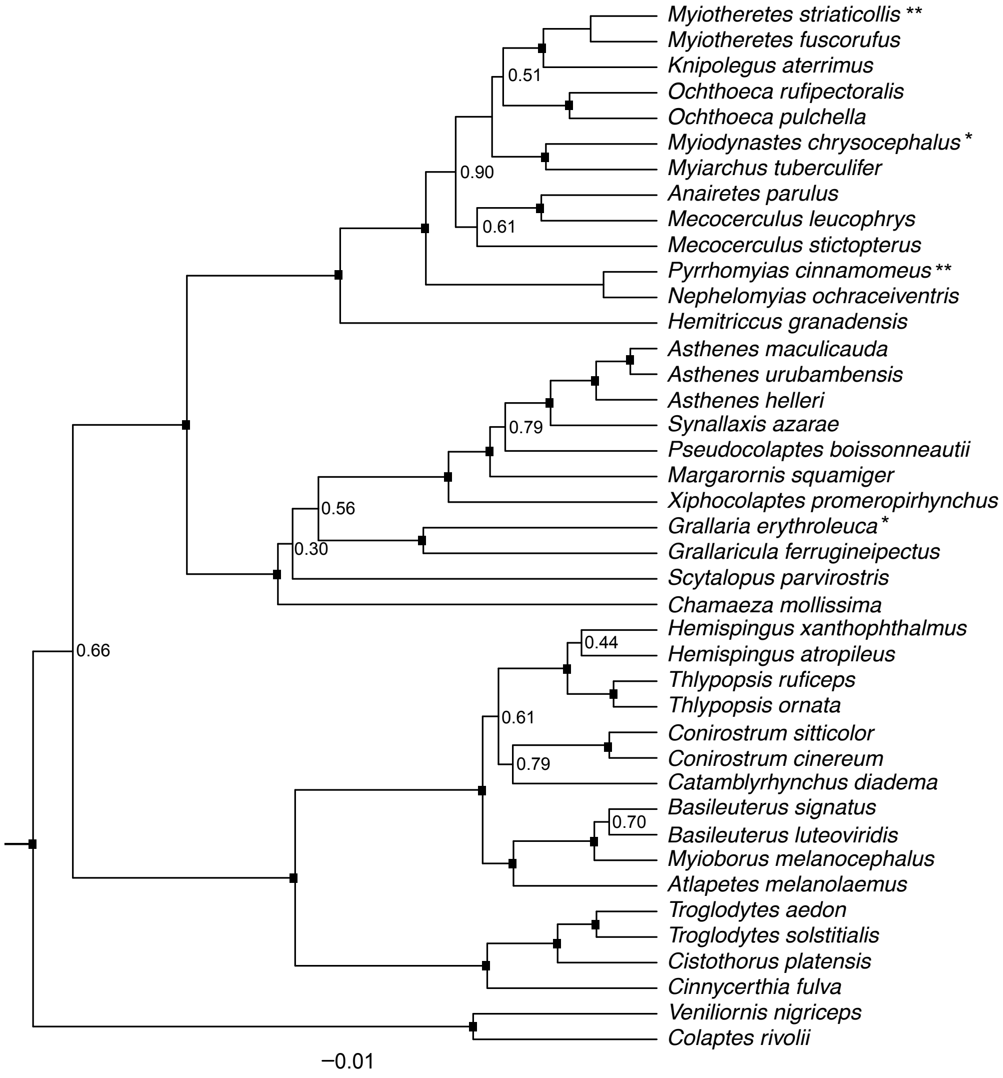

Figure S4 Maximum clade credibility tree of phylogenetic relationships among species at the survey site inferred from analysis of two mitochondrial DNA regions. Nodes with black circles indicate posterior probability support > 95%. Other posterior probability values are written above nodes. Single asterisk (*) denotes species used as substitutes for *Grallaria erythroleuca* and *Myiodynastes chrysocephalus*, respectively. Double asterisk (**) denotes species lacking sequence data that were inserted on the basis of published phylogenies, with varying node heights (see methods). Scale bar indicates sequence divergence.

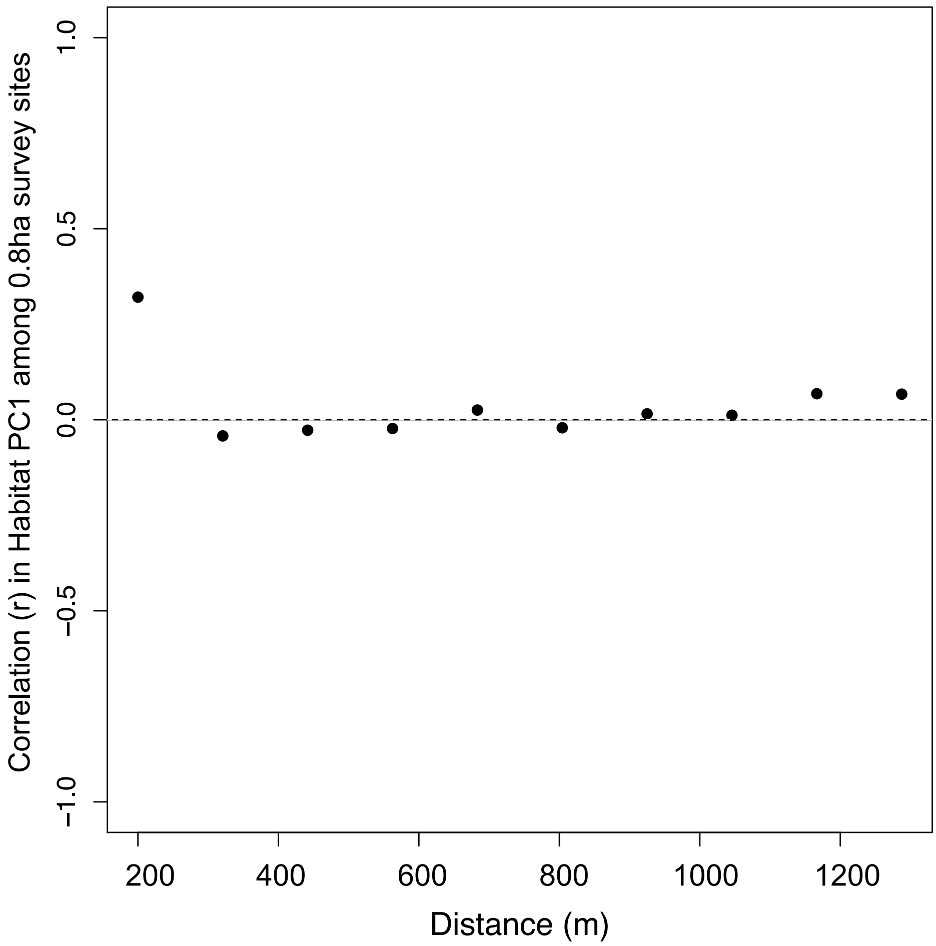

Figure S5 Autocorrelation coefficients in vegetation structure (Habitat PC1) among survey points in 10 distance bins. The distance between two neighbouring survey point vegetation plots at the 0.8 ha scale was 120 m. The figure shows a steep decline to around zero of spatial autocorrelation in vegetation structure at distances greater than those joining neighbouring survey points at the 0.8 ha scale.

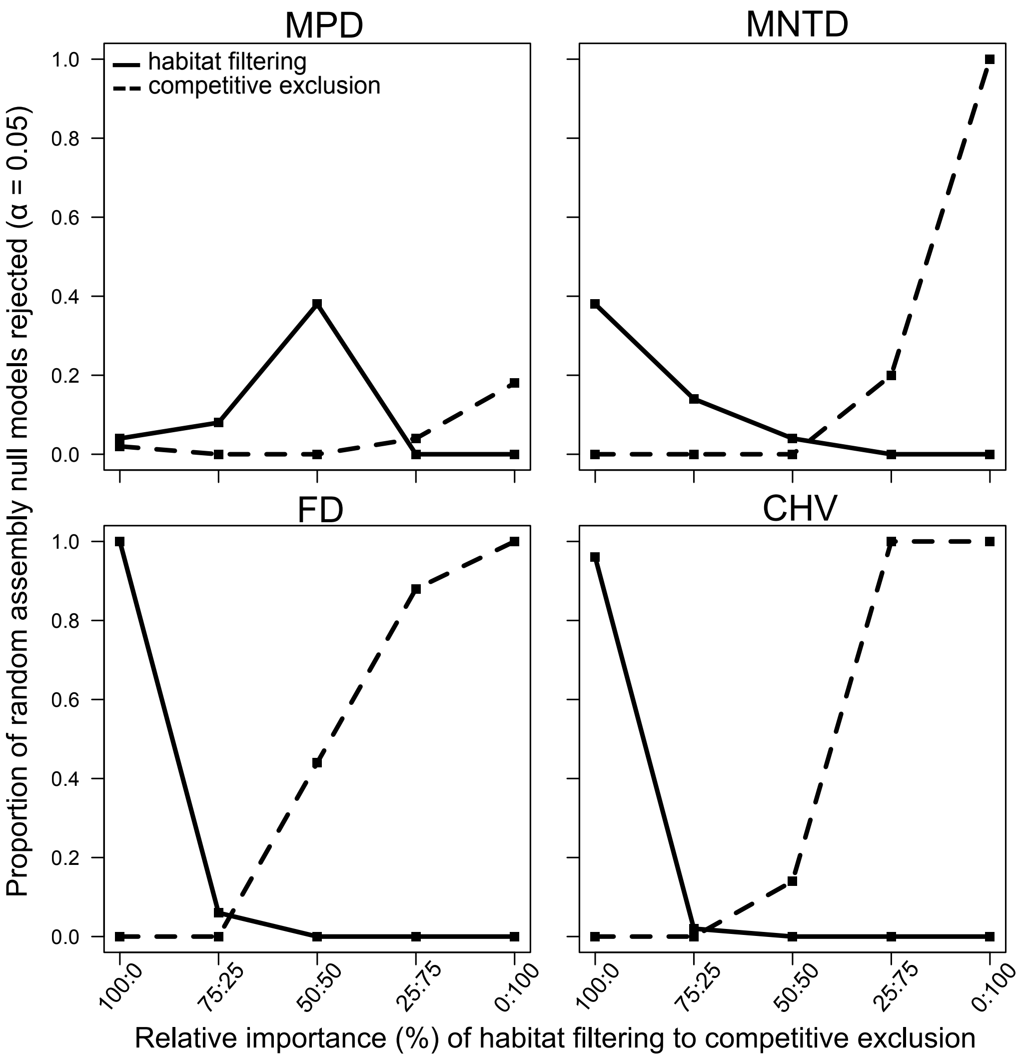

Figure S6. The power of multi-pattern, phylogenetic and functional trait metrics— mean phylogenetic distance [MPD]; mean nearest taxon distance [MNTD]; Functional diversity [FD]; Convex hull volume [CHV]—to reject correctly the random community assembly null model in favor of either habitat filtering or competitive exclusion across five assembly scenarios, ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. Each metric is calculated using multiple niche axes; each species is a composite of three such axes: body size, trophic traits and locomotory traits. The locomotry trait axis was subjected directly to habitat filtering and competitive exclusion, body size to habitat filtering only, and beak shape to competitive exclusion only. See methods for further details of trait and community simulations, null models, and statistical tests.

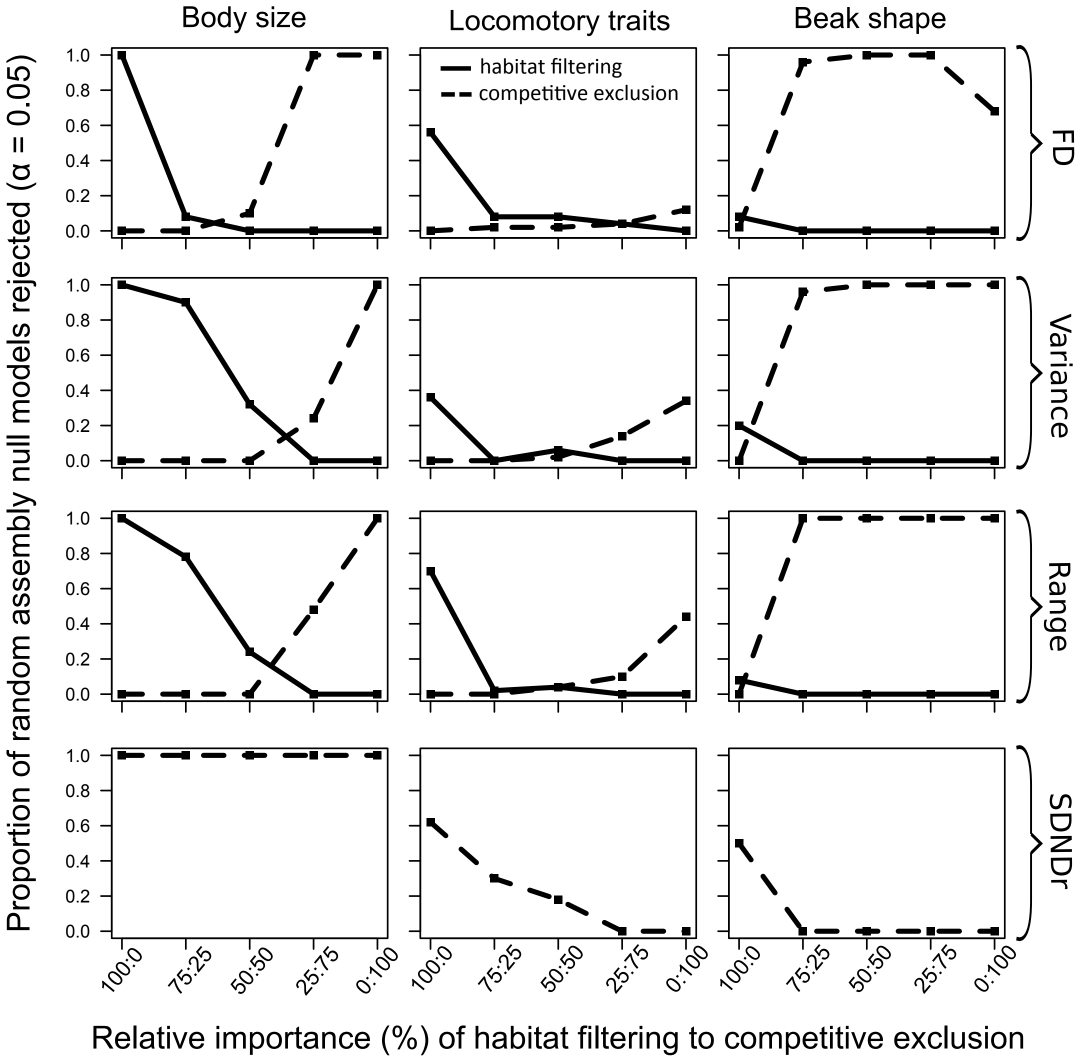

Figure S7. The power of multi-pattern and single-pattern trait metrics, calculated using only a single niche axis, to reject the random assembly null model in favour of either habitat filtering or competitive exclusion. Assembly models were tested under five scenarios ranging in the relative importance of habitat filtering and competitive exclusion from the sole action of one process to a 50:50 mixing of both processes. Each metric was calculated using only a single niche axis; each species is a composite of three traits: body size, trophic traits and locomotory traits. Body size was subjected directly to habitat filtering and competitive exclusion, locomotory traits to habitat filtering only, and trophic traits to competitive exclusion only. SDNDr is a single-pattern metric focused only on the detection of competitive exclusion and so a one-tailed test was used. See methods for further details of trait and community simulations, null models, and statistical tests.

Table S8 List of all insectivorous bird species recorded in communities, with sample sizes for biometric measurements and accession details for sequences used in phylogenetic tree building. Taxonomy follows Remsen et al. (2011). Sources for dietary information and primary habitat are given below*.

Species	**Sample**	**Genbank Accession Numbers**	
		Cyt *b*	ND2
Colaptes rivolii	3	AY940812	DQ361278
Veniliornis nigriceps	2	AF389337	DQ361287
Troglodytes solstitialis	19	-	AY460232
Troglodytes aedon	13	DQ415711	AY460233
Cistothorus platensis	10	AY352526	AY460236
Cinnycerthia fulva	27	-	KM065785
Basileuterus luteoviridus	25	AF100530	AY039288
Basileuterus signatus	22	AF100532	GU932070
Myioborus melanocephalus	14	AY968852	AY968900
Atlapetes melanolaemus	71	AF310061	AF015827
Thlypopsis ornata	1	KM065778	-
Thlypopsis ruficeps	4	EF529968	EF529856
Hemispingus atropileus	16	AF383019	AF383135
Hemispingus xanthopthalmus	1**	-	AY039295
Catamblyrhynchus diadema	13	KM065783	AF447271
Conirostrum cinereum	9	KM065779	-
Conirostrum sitticolor	2	AF383000	AF383116
Hemitriccus granadensis	8	KM065777	KM065786
Nephelomyias ochraceiventris	2	KM065776	KM065791
Pyrrhomyias cinnamomeus	1	-	-
Knipolegus aterrimus	2	KM065774	KM065787
Myiotheretes fuscorufus	1	KM065780	-
Myiotheretes striaticollis	5**	-	-

Octhoeca pulchella	50	KM065772	KM065792
Octhoeca rufipectoralis	30	KM065773	KM065793
Myiarchis tuberculifer	1	KM065775	EF501913
Myiodynastes chrysocephalus	5**		
Mecocerculus stictopterus	8	KM065782	KM065790
Mecocerculus leucophrys	1	KM065781	KM065789
Anairetes parulus	1	AF067002	AF066993
Scytalopus parvirostris	9	KM065770	KM065794
Margarornis squamiger	14	AY065703	KM065788
Pseudocolaptes boissonneautii	1	AY998198	HM125585
Synallaxis azarae	53	KM065769	KM065795
Asthenes urubambensis	1	AY998195	HM125590
Asthenes maculicauda	1**	-	JF975251
Asthenes helleri	11	KM065768	KM065784
Xiphocolaptes promeropirhynchus	8**	AY089798	AY089872
Grallaricula ferrugineipectus	6	KM065771	-
Grallaria erythroleuca	1**	-	-
Chamaeza mollissima	1**	AY370537	AY370574
Grallaria ruficapilla[1]	-	AY370544	AY370544
Megarynchus pitangua[2]	-	-	FJ175975

*Ecological data were extracted from specialized literature sources (Bello et al. 2013; Belmaker et al. 2012; Bennett et al. 2013; Mason and Pavoine 2013; Pavoine et al. 2013)

**Measurements taken from museum specimens

[1] Substitute sequence for *Grallaria erythroleuca*

[2] Substitute sequence for *Myiodynastes chrysocephalus*

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APPENDIX S2

Detecting the influence of niche-based processes on community assembly: an evaluation of functional and phylogenetic metrics

Figures

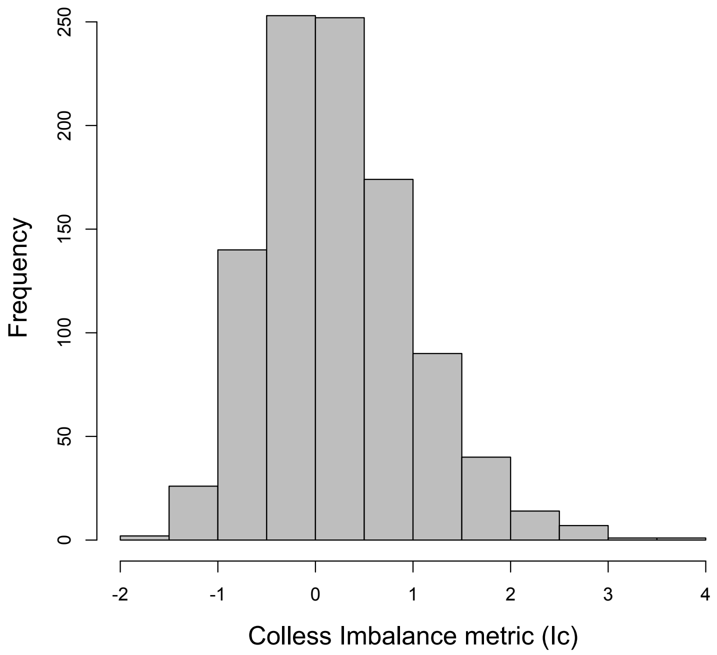

Figure S1. Colless' index (Blum et al. 2006) for the 1000 regional pool phylogenies. The index has an expected value of zero under a constant rate pure birth model. Values of I_c <0 indicate phylogenies that are more balanced than expected from a null model where all lineages have an equal probability of speciating.

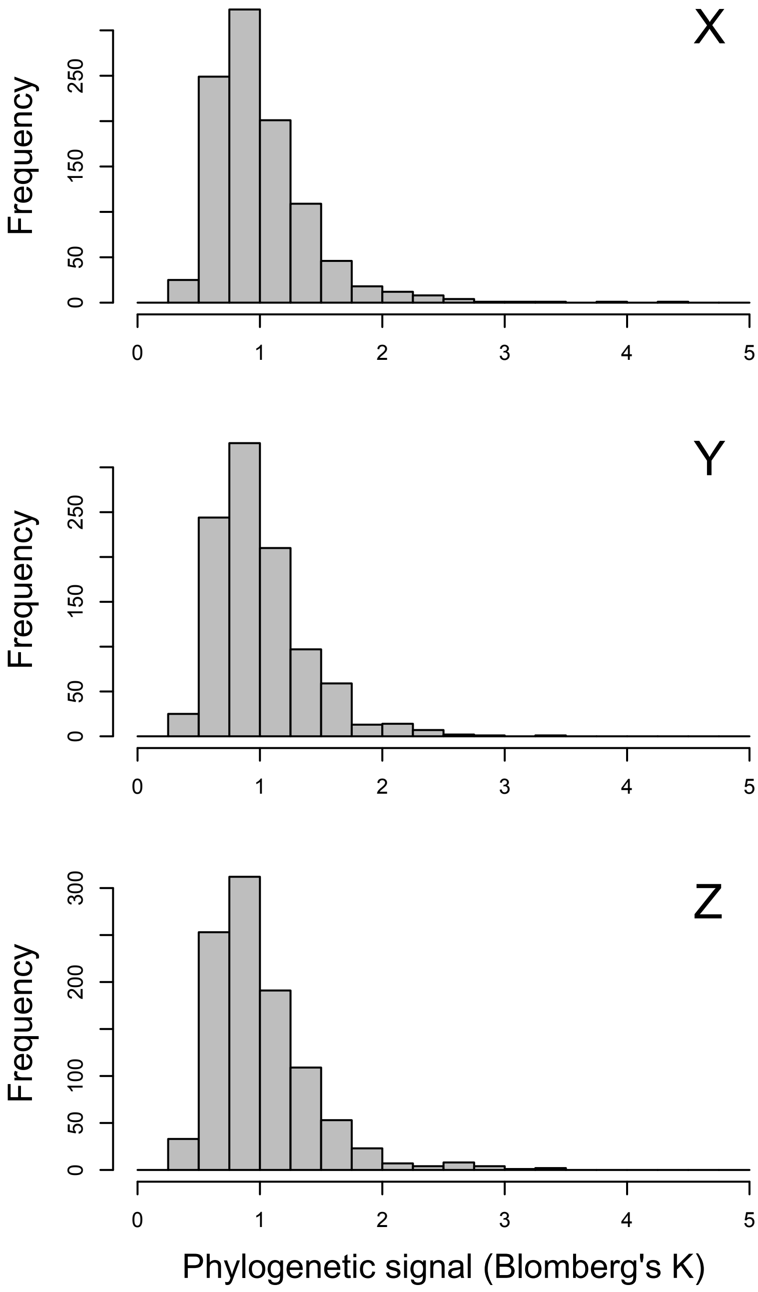

Figure S2. Phylogenetic signal in species traits X, Y and Z. K is expected to equal one under Brownian motion evolution of traits.

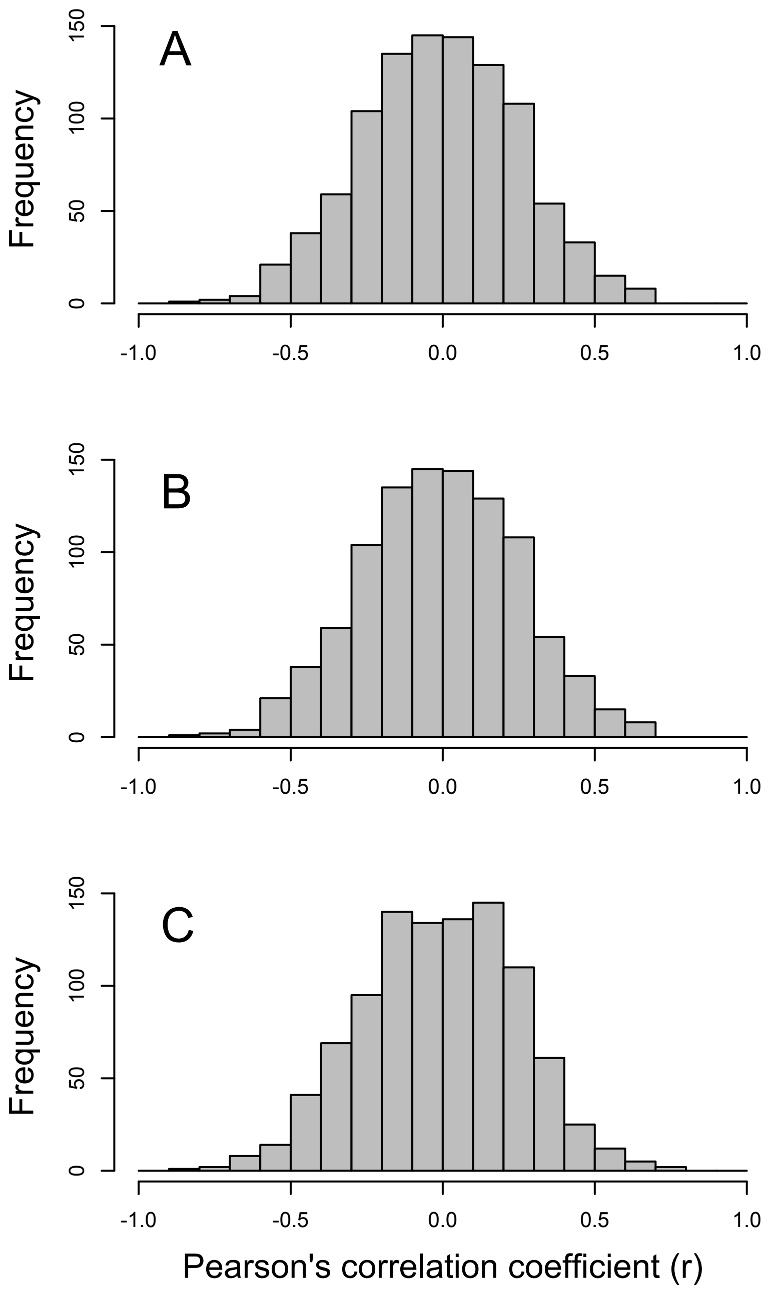

Figure S3. Correlations between species traits for the 100 species in each of the 1000 regional pools (A) traits X and Y, (B) X and Z, (C) Y and Z).

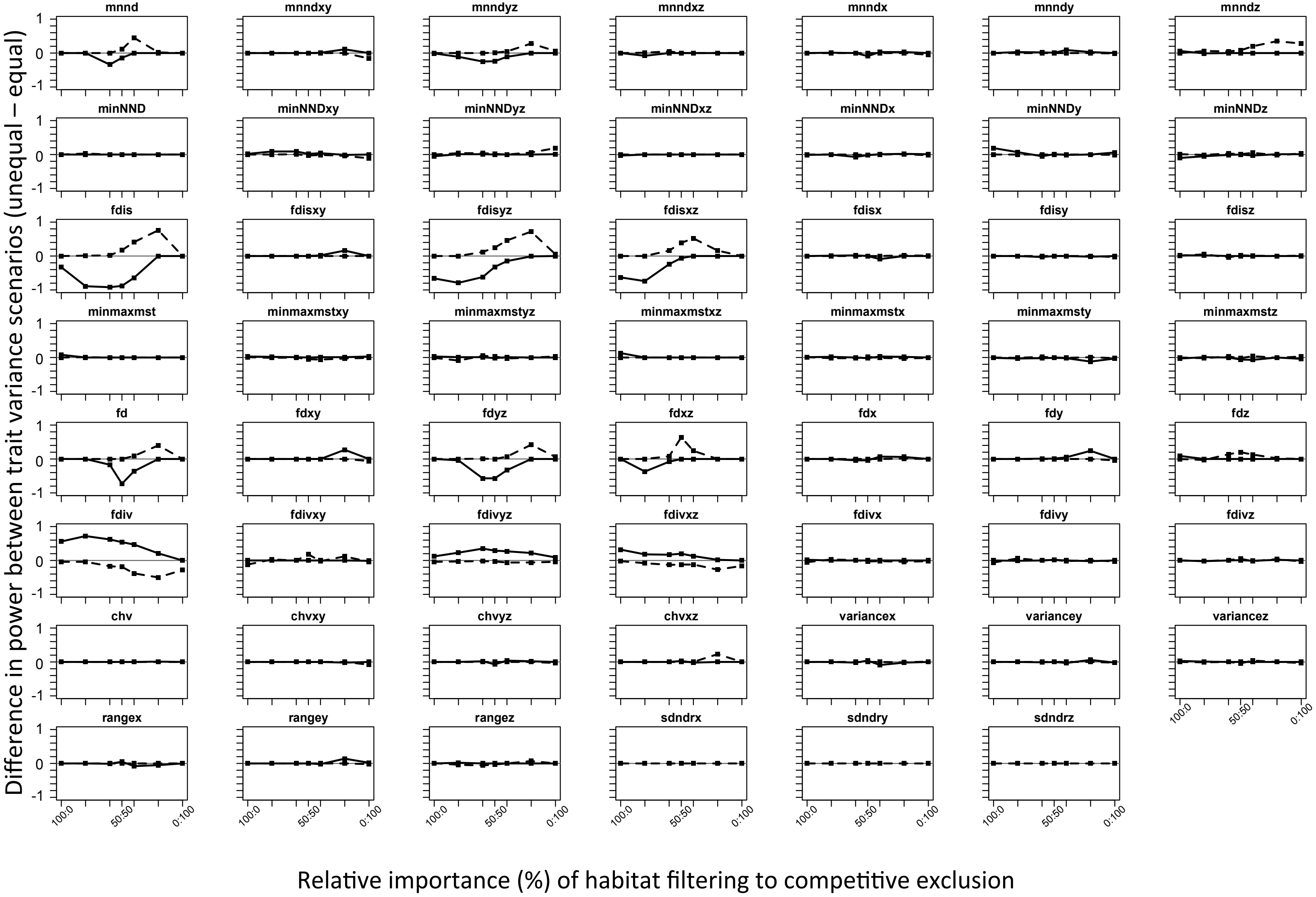

Figure S4. The difference in the power (proportion of random assembly null models rejected) of the metrics to detect habitat filtering and competitive exclusion between the community assembly model in which trait Z had increased variance, and therefore increased importance for competition, and that in which every trait had equal variance. Here, traits were not scaled before analysis. See figures 2 and 3 for metric abbreviations.

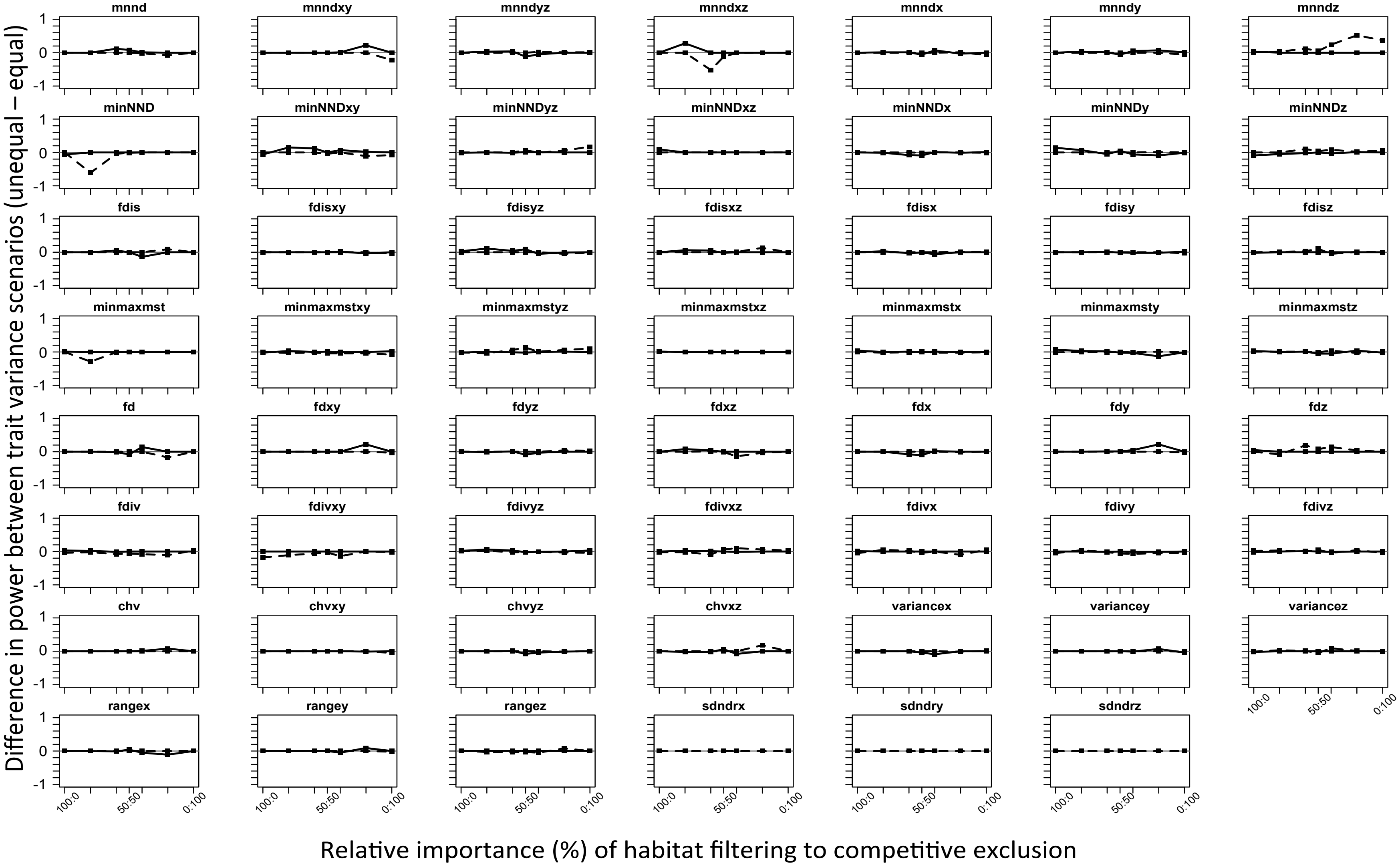

Figure S5. The difference in the power (proportion of random assembly null models rejected) of the metrics to detect habitat filtering and competitive exclusion between the community assembly model in which trait Z had increased variance, and therefore increased importance for competition, and that in which every trait had equal variance. Here, traits were scaled before analysis. See figures 2 and 3 for metric abbreviations.

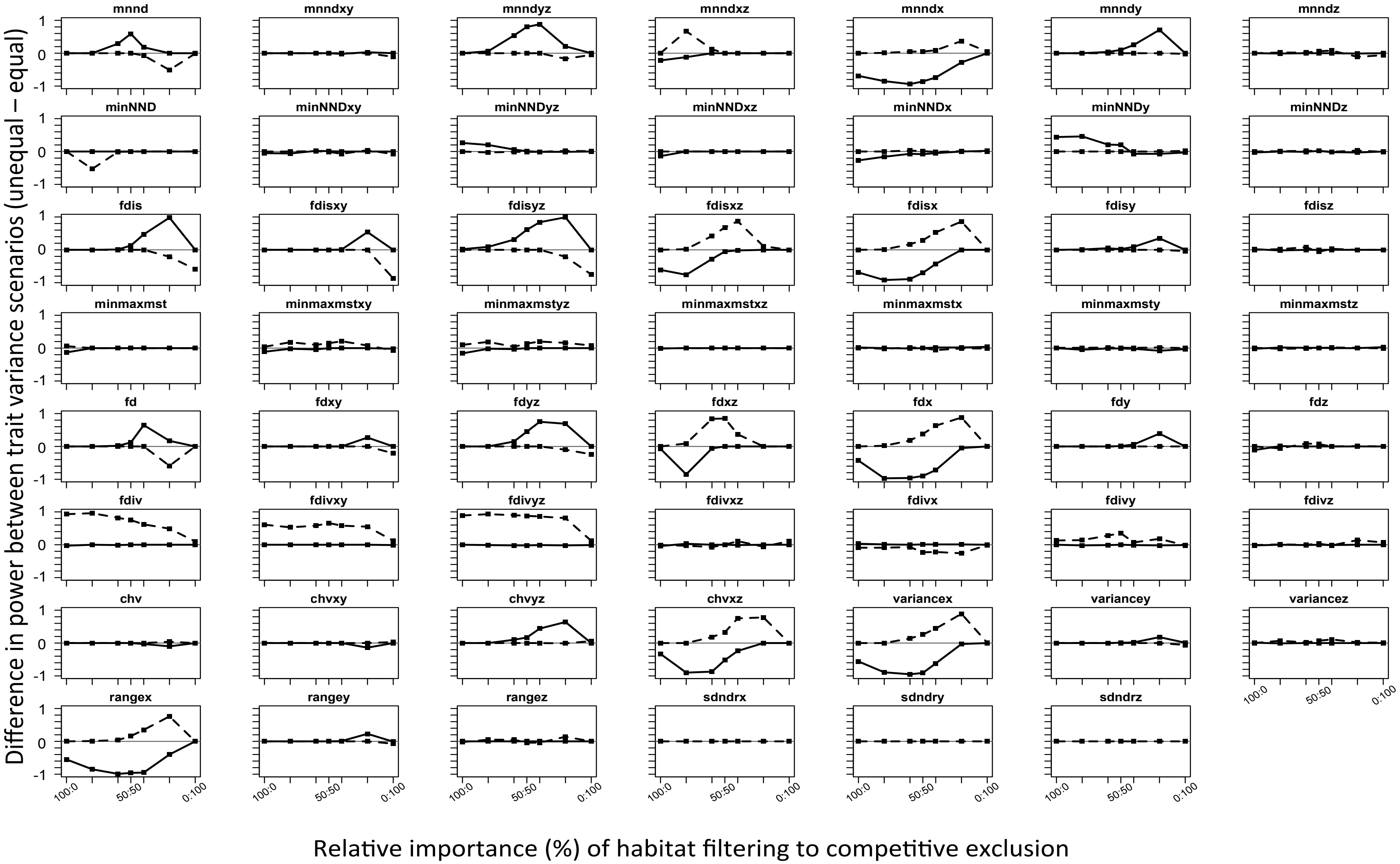

Figure S6. The difference in the power (proportion of random assembly null models rejected) of the metrics to detect habitat filtering and competitive exclusion between the community assembly model in which trait Y had increased variance, and therefore increased importance for habitat filtering, and that in which every trait had equal variance. Here, traits were not scaled before analysis. See figures 2 and 3 for metric abbreviations.

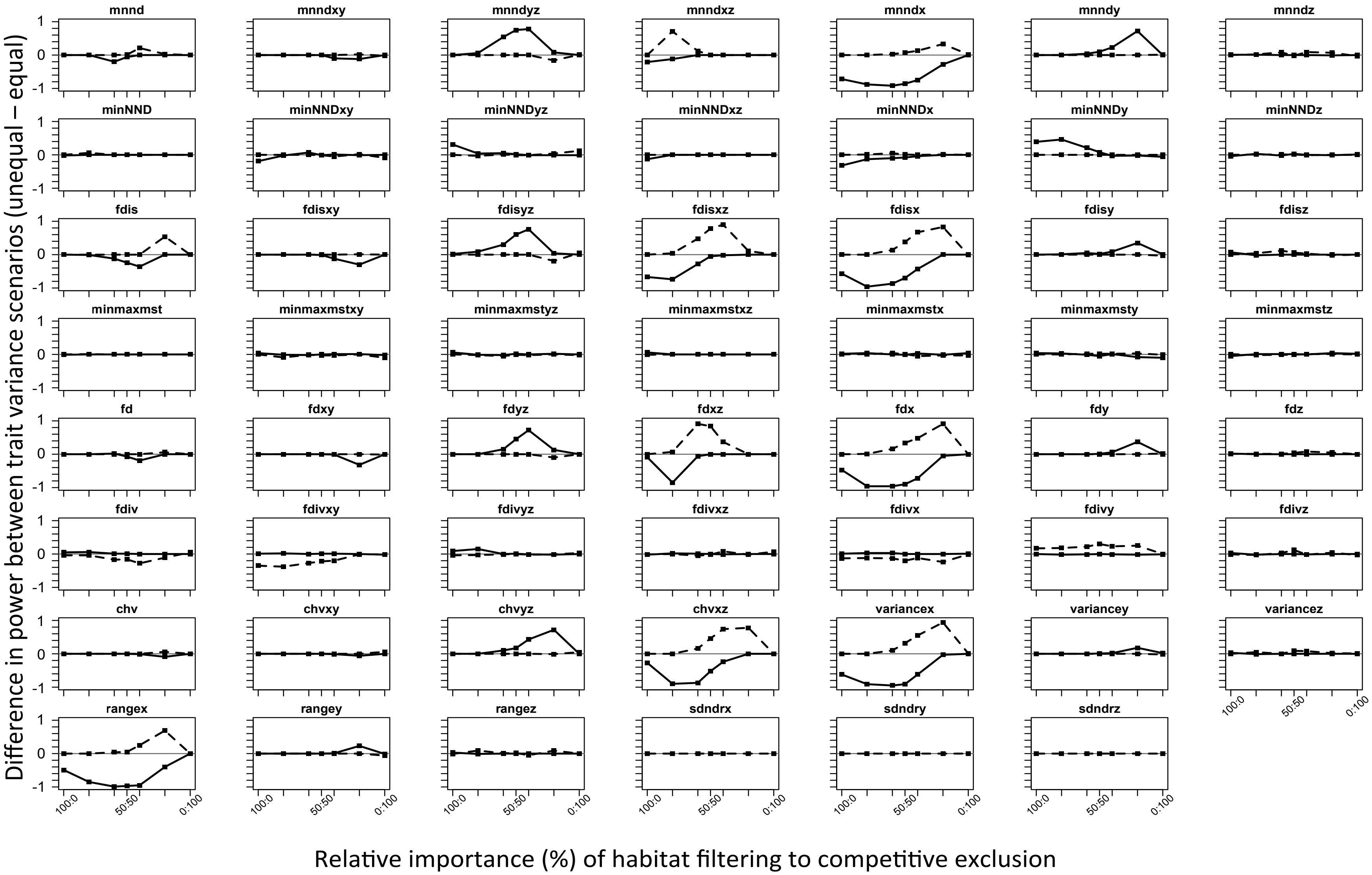

Figure S7. The difference in the power (proportion of random assembly null models rejected) of the metrics to detect habitat filtering and competitive exclusion between the community assembly model in which trait Y had increased variance, and therefore increased importance for habitat filtering, and that in which every trait had equal variance. Here, traits were scaled before analysis. See figures 2 and 3 for metric abbreviations.

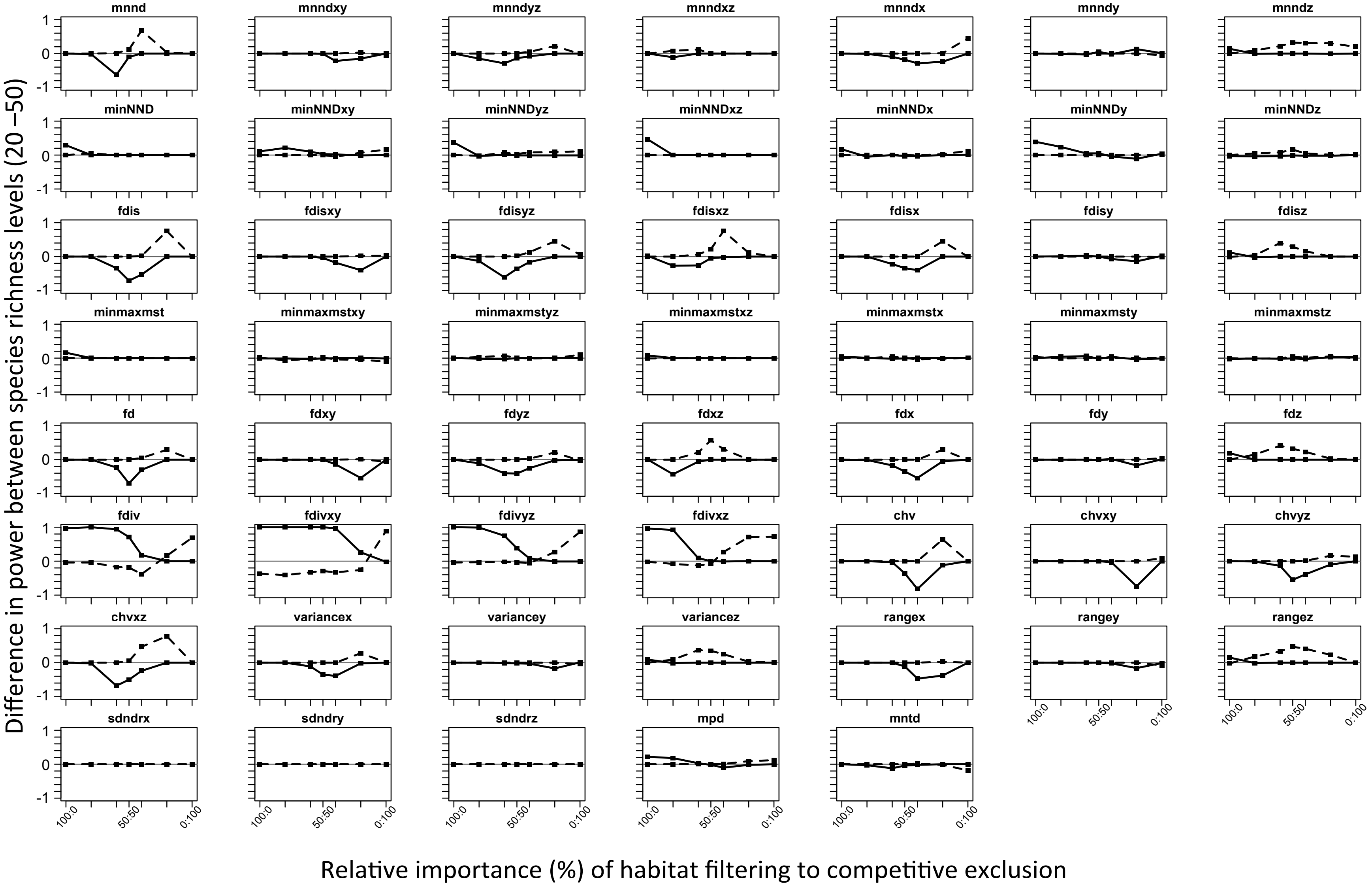

Figure S8. The difference in the power (proportion of random assembly null models rejected) of the metrics to detect habitat filtering and competitive exclusion between the community assembly model with local species richness 20, and that with local species richness of 50. See figures 2 and 3 for metric abbreviations.

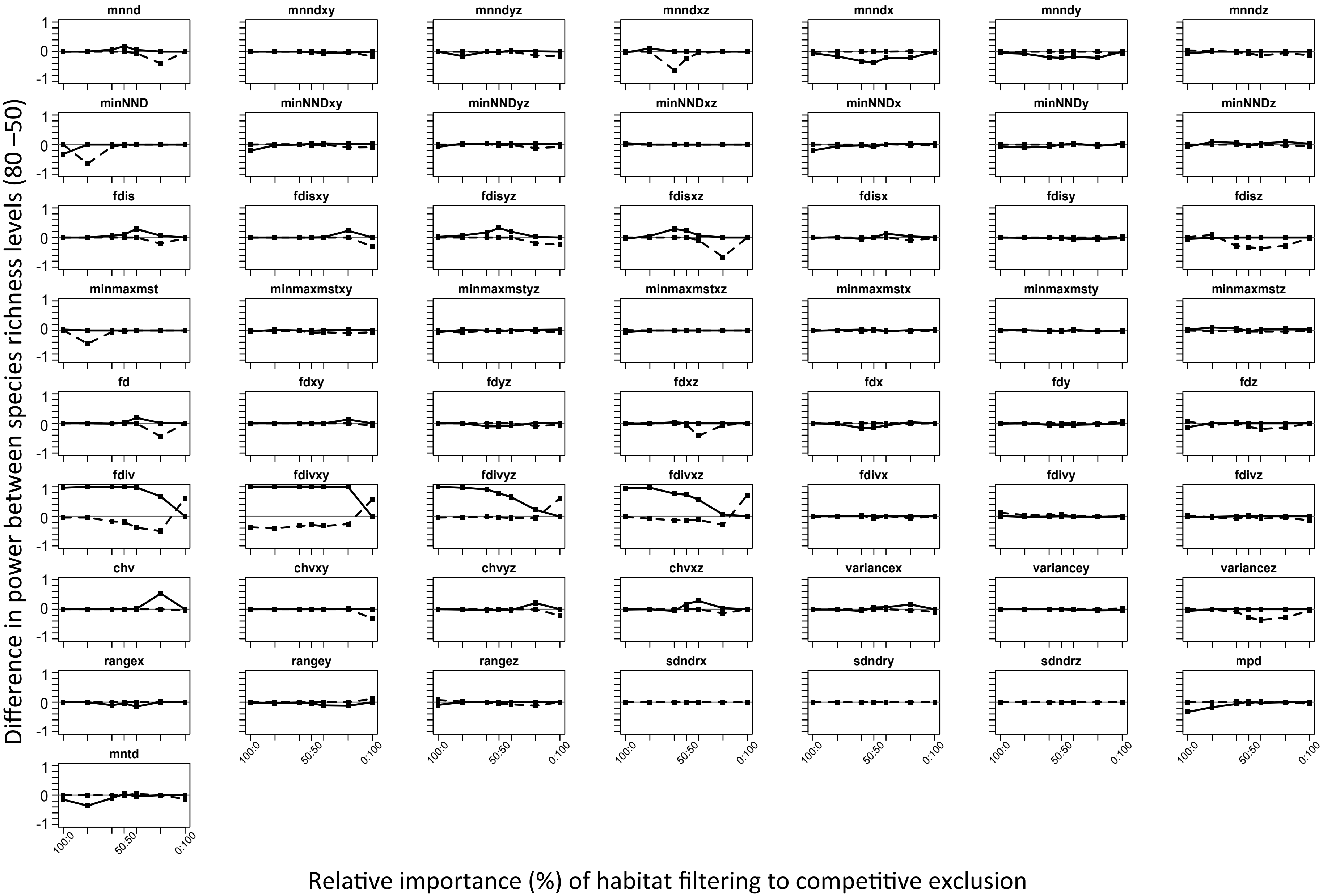

Figure S9. The difference in the power (proportion of random assembly null models rejected) of the metrics to detect habitat filtering and competitive exclusion between the community assembly model with local species richness 20, and that with local species richness of 80. See figures 2 and 3 for metric abbreviations.

Appendix S2: R code for community simulations

```
## Nathan Kraft functions (modified for use in Chapter 2 of this thesis)
## University of California, Berkeley
## and currently
## Biodiversity Research Centre, University of British Columbia
## nkraft@biodiversity.ubc.ca

## Trait-based community assembly simulation functions in R

## Supplemental code from
## Nathan J. B. Kraft and Davd D. Ackerly, 2010, Functional trait and
 phylogenetic tests of community assembly across spatial scales in an
 Amazonian forest, Ecological Monographs 80:401-422.

## Functions here are based on the EVELYN community assembly
 model(which was originally written in JAVA) from:
## Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait
 evolution, community assembly, and the phylogenetic structure of ecological
 communities. American Naturalist 170:271-283.

## for the original verbal description of the competition algorithm used here
 and general inspiration see:
## Colwell, R. K., and D. W. Winkler. 1984. A null model for null models in
 biogeography., Pages 344-359 in D. R. Strong, D. S. Simberloff, L. G. Abele,
 and A. B. Thistle, eds. Ecological communities: conceptual issues and the
 evidence. Princeton, NJ, Princeton University Press.



## File begins with a set of functions
## run the functions in the R terminal window to enter them into memory
## the end of the file contains a brief demonstration of the functions with
 commentary

## the key functions are: random_assembly(), compete_until() and
 filter_until().  Everything else supports these three assembly functions.


########################
### GENERAL FUNCTIONS ##
########################

#check for duplicate species names in a community vector
validate_community=function(community=community){
        community[,1]->spnames
        if(length(spnames)>length(unique(spnames))){
                print("warning- duplicate species names")
                return(FALSE)
                }
```

```
		return(TRUE)
 }

#remove a species from the community (general function used in all models)
zap=function(target, community=community){
 #target can be either a species name (letters) or a column number(numeric). Can also be a vector of names
 #defaults to looking for a vector called community with two columns (first for name and second for trait value)

 ##currently no error is given if some targets match species in the community and others do not- only matching species removed

 if(!is.numeric(target)){
		target<-which(target==community[,1])

		if(length(target)<1){
			print("target does not match anyone in community- can not zap")
			return(community)
			}

		}

 community<-community[-target,]
 return(community)

 }

####################
## RANDOM ASSEMBLY #
####################

## Randomly removes species, weighted by abundance, from the species pool until a final_richness value is reached
random_assembly=function(pool=pool, final_richness, abund=NULL){
 size<-nrow(pool)
 n_victim<-size-final_richness
 if(n_victim<1){
		print("pool has equal or lesser richness to final size- can't do random assembly")
		return(pool)
		}


 if(is.null(abund)){
		alive<-sample(1:size, final_richness)
		return(pool[alive,])
 }
```

```
 merge(pool, abund)->poolPlus

 alive<-sample((1:nrow(poolPlus)), final_richness, prob=poolPlus$abund)

 return(poolPlus[alive,c(1,2)])



 }


######################
## COMPETITION MODEL #
######################

#find the most similar taxa within the community:
find_most_similar_taxa=function(community=community,
 speciesNamesCol1=TRUE){
 if(speciesNamesCol1!=TRUE){
           print("first col needs to be species names for now")
           return(community)
           }
 ##somewhat of an awkward fix here:
 labels<-community[,1]
 traits<-community[,-1]
 dist(traits)->m
 as.matrix(m)->m2
 which(m2==min(m), arr.ind=TRUE)->m3
 as.vector(m3[,1])->a
 as.vector(m3[,2])->b
 ##will contain multiples but this is good- more weight to a "sandwiched" taxa
 being removed
 taxa_indices<-c(a[which(a!=b)], b[which(a!=b)])
 return(labels[taxa_indices])
 }


## find most similar species and remove it from a community
one_round_competition=function(community=community){
 threatened_list<-find_most_similar_taxa(community)
 n<-length(threatened_list)
 if(n<2){
           print("couldn't find most similar taxa for competition")
           return(community)
           }
 return(zap(sample(threatened_list, 1), community=community))
 }

## remove species via competition from the community until a specified
```

```
 number of taxa are left (nfinal)

compete_until=function(nfinal, community=community){
 nrow(community)->start
 if(nfinal>start){
           print("community is already smaller than target- can't compete")
           return(community)
           }

 if(nfinal<1){
           print("target for competition is too small- can't compete")
           return(community)
           }

 start-nfinal->to_kill

 for(i in 1:to_kill){
           one_round_competition(community)->community

           }

 if(nrow(community)!=nfinal){
           print('error- competition ended with incorrect number of species')
           }
 return(community)

 }

######################
## Habitat Filtering #
######################

#Used to identify which species in a community is farthest from the trait
 optima used for habitat filtering- farthest species are removed first.

find_farthest_from_optima=function(optima=optima, community=community,
 speciesNamesCol1=TRUE){
 if(speciesNamesCol1!=TRUE){
           print("first col needs to be species names for now")
           return(community)
           }

 if( (length(optima)!=(ncol(community)-1))){
           print("error- filtering optima is not right dimension for community")
           return(community)
           }

 ##cludgy- will generate warnings- not sure how to avoid (Fixed by C Trisos)
 paste(community[,1])->start
 labels<-c(start,"optima")
```

```
 com<-community[,-1]
 traits<-rbind(com,optima)
 #traits<-suppressWarnings(rbind(community, optima)[,-1]) Kraft's original
 code

 dist(traits)->m
 as.matrix(m)->m2
 ##get last row, which is the distance of each taxa from optimum
 m2[,nrow(m2)]->comp
 which(comp==max(comp))->index
 return(labels[index])

 }


##identify farthest species from optima and remove it
one_round_filtering_optima=function(community=community,
 optima=optima){

 threatened_list<-find_farthest_from_optima(optima, community)
 n<-length(threatened_list)
 if(n<1){
		print("couldn't find farthest taxa for filtering")
		return(community)
		}
 return(zap(sample(threatened_list, 1), community=community))

 }


##run filtering model until only nfinal number of taxa are left in the community
filter_until=function(nfinal, community=community, optima=optima){
 nrow(community)->start
 if(nfinal>start){
		print("community is already smaller than target- can't filter")
		return(community)
		}

 if(nfinal<1){
		print("target for filtering is too small- can't filter")
		return(community)
		}

 start-nfinal->to_kill

 for(i in 1:to_kill){
		one_round_filtering_optima(community, optima)->community

		}
```

```
 if(nrow(community)!=nfinal){
        print('error- filtering ended with incorrect number of species')
        }
 return(community)

 }

##############################################################
 ###
##############################################################
 ###


##############################################################
 #########################
# Community trait-based assembly simulations from Christopher Trisos DPhil
 thesis, Chapter 2)
##############################################################
 #########################

#1. load Kraft functions from above section
#2. run script below
rm(list=ls())
library(geiger)
library(picante)


# Generate metacommunity phylogeny and calculate trait correlation and K.

Kdata<-as.list(rep,NA,100)
cordata<-as.list(rep,NA,100)
for (i in 1:100){

mcom.numsp<-100

# simulate pure birth tree
phylo<-sim.bdtree(b=0.1,d=0,stop="taxa",n=mcom.numsp)

# simulate coalescent tree and then transform branch lengths
phylo<-rcoal(mcom.numsp)
stretch<-runif(1,0.1,100)
phylo<-transform(phylo,"delta",stretch)

# Set correlation among traits

corr=0

# create var-covar matrix for traits
q<-cbind(c(1,corr,corr),c(corr,1,corr),c(corr,corr,1))
colnames(q) <- rownames(q) <- c("trait_x","trait_y", "trait_z")
```

```
# simulate trait evolution according to brownian motion model
traits<-sim.char(phylo,q,nsim=1,model="BM")

traits<-as.matrix(traits[,1:3,])
colnames(traits)<-c("trait_x","trait_y", "trait_z")

# Estimate phylogenetic signal in the traits
psignaltraits<-traits[phylo$tip.label,]
K<-multiPhylosignal(psignaltraits, phylo, reps=999)

# calculate trait correlations
cortrait<-cor(traits)
cortrait<-cortrait[lower.tri(cortrait)]

Kdata[[i]]<-K
cordata[[i]]<-cortrait
}
cors<-unlist(cordata)
mean(cors)
sd(cors)
Allkdata<-do.call("rbind",Kdata)
mean(Allkdata$K)
sd(Allkdata$K)
par(mfrow=c(1,2))
hist(cors)
hist(Allkdata$K)



###########################
### Community simulations
###########################



# If I make 1000 metacommunities, I need to save the phylogeny, regional
 community with species traits, and local comunity compositions for each one.

## Kraft style

# Simulation parameters

Restrict=FALSE # if TRUE, then habitat filtering local trait optima are selected
 from only the central 60% of the regional species pool trait range.

num.sims<-1000

mcom.numspecies<-100
```

```
local.com.numsp.to.remove<-80

trait.correlations<-0

Proportions.HabitatFiltering<-c(100,80,60,50,40,20,0)

# List to store results
Metacommunities<-as.list(rep(NA,num.sims))

for (i in 1:num.sims){

 mcom.numsp<-mcom.numspecies
 # simulate pure birth tree
 phylo<-sim.bdtree(b=0.1,d=0,stop="taxa",n=mcom.numsp)

 # simulate coalescent tree and then transform branch lengths
 #phylo<-rcoal(mcom.numsp)
 #stretch<-runif(1,0.1,100)
 #phylo<-transform(phylo,"delta",stretch)

 # Set correlation among traits

 corr=trait.correlations

 # create var-covar matrix for traits
 q<-cbind(c(1,corr,corr),c(corr,1,corr),c(corr,corr,1))
 colnames(q) <- rownames(q) <- c("trait_x","trait_y", "trait_z")

 # simulate trait evolution according to brownian motion model
 traits<-sim.char(phylo,q,nsim=1,model="BM")

 traits<-as.matrix(traits[,1:3,])
 colnames(traits)<-c("trait_x","trait_y", "trait_z")

 # Make regional community data frame
 regional.com<-as.data.frame(traits)
 regional.com<-cbind(rownames(regional.com),regional.com)
 colnames(regional.com)[1]<-c("species")

 # Set the different proportions of HF and LS
 proportionHF<-Proportions.HabitatFiltering

 # List to store local community results
 Localcommunities<-as.list(rep(NA,10))

         for (j in 1:7){
         # Generate regional phylogeny and traits evolved via brownian
 motion

         local.com.sp.richness<-local.com.numsp.to.remove
```

```
	# set % species removed due to HF
	Prophf=proportionHF[j]

	Phf=mcom.numsp-(local.com.sp.richness/mcom.numsp)*Prophf

	# set % species removed due to LS
	Propls=100-Prophf
	Pls=mcom.numsp-(mcom.numsp-Phf)-(local.com.sp.richness/mcom.numsp)*Propls

	# Habitat filter

	local.community.hf<-regional.com[,-4] # remove trait z from having any direct involvement in filtering

	# Habitat filtering trait optima: selected from uniform random distribution with min and max set by simulated trait axes.

	if (Restrict==TRUE){
	## Using restricted trait space to select local optimum trait values
	minx<-min(local.community.hf$trait_x)
	maxx<-max(local.community.hf$trait_x)
	miny<-min(local.community.hf$trait_y)
	maxy<-max(local.community.hf$trait_y)
	rangex<-maxx-minx
	rangey<-maxy-miny
	upperx<-maxx-rangex*0.2
	lowerx<-minx+rangex*0.2
	uppery<-maxy-rangey*0.2
	lowery<-miny+rangey*0.2

	new.x<-local.community.hf$trait_x[which(local.community.hf$trait_x < upperx & local.community.hf$trait_x > lowerx )]

	new.y<-local.community.hf$trait_y[which(local.community.hf$trait_y < uppery & local.community.hf$trait_y > lowery )]

	x<-runif(1,min(new.x),max(new.x))

	y<-runif(1,min(new.y),max(new.y))
							}else{## Using all of trait space to select local optimum trait values
	x<-runif(1,min(local.community.hf$trait_x),max(local.community.hf$trait_x))

	y<-runif(1,min(local.community.hf$trait_y),max(local.community.hf$trait_y))}

	if(Phf==mcom.numsp){
```

```
                local.community.hf<-local.community.hf
                }else{local.community.hf<-
 filter_until(Phf,local.community.hf,optima=c(x,y))
        }

        # Competitive exclusion based on limiting similarity

        outfiltered<-
 which(is.na(match(regional.com$species,local.community.hf$species)))
        if(Phf==mcom.numsp){
                local.community.comp<-regional.com
                }else{local.community.comp<-regional.com[-outfiltered,]
        }


        # remove trait y from having any direct involvement in ls based
 competition
        local.community.comp<-local.community.comp[,-3]

        if(Pls==Phf){
                local.community.comp<-local.community.comp
                }else{local.community.comp<-
 compete_until(Pls,local.community.comp)
         }

        # make the local community
        if(Pls==Phf){
                local.community<-regional.com[-outfiltered,]
        }else{outcompeted<-
 which(is.na(match(regional.com$species,local.community.comp$species)))
        local.community<-regional.com[-outcompeted,]
        }

        local.community$species<-as.character(local.community$species)
        local.community$PropHF<-Prophf
        local.community$PropLS<-Propls

        Localcommunities[[j]]<-local.community
}
#save phylogeny
Localcommunities[[8]]<-phylo

# Save regional community
regional.com$trait.correlation<-corr
regional.com$species<-as.character(regional.com$species)
Localcommunities[[9]]<-regional.com

# Calculate simulated trait correlations and Phylogenetic signal

# Estimate phylogenetic signal in the traits
```

```
psignaltraits<-traits[phylo$tip.label,]
K<-multiPhylosignal(psignaltraits, phylo, reps=999)

# calculate trait correlations
cortrait<-cor(traits)
cortrait<-cortrait[lower.tri(cortrait)]
K$cor.xy<-cortrait[1]
K$cor.xz<-cortrait[2]
K$cor.yz<-cortrait[3]

Localcommunities[[10]]<-K

Metacommunities[[i]]<-Localcommunities
print(i)
}
```

APPENDIX S3

Dispersal ability and ecological similarity interact to shape species occurrence in a diverse radiation of birds

Table S1 Loadings for principal components analysis of morphological traits.

Traits	PC1	PC2	PC3	PC4	PC5
Bill length	–0.747	0.607	0.270	0.023	–0.020
Bill depth	–0.874	–0.316	0.249	–0.132	–0.237
Bill width	–0.908	–0.236	0.196	–0.037	0.282
Wing length	–0.823	0.117	–0.472	–0.293	0.004
Tarsus length	–0.865	–0.069	–0.241	0.433	–0.044
% variance explained	71	11	9	6	3

Results are from a phylogenetic principal components analysis (Revell et al. 2009) based on the correlation matrix, following log-transformation of species trait values.

Table S2 Trait-based model of species-level occurrence probability at the ecoregion scale without interactions. Species assignment to biomes used the 5% percent range overlap threshold.

Parameter	Estimate*	CI	ESS	P
(Intercept)	–0.572	(–2.324, 1.269)	731	
NNTD	0.088	(–0.056, 0.241)	1000	0.226
MTD	–0.977	(–1.219, –0.761)	1000	<0.001
HWI	0.551	(0.139, 0.974)	904	0.012
Species age	0.387	(–0.050, 0.755)	1000	0.066
Divergence time	–0.061	(–0.231, 0.130)	1000	0.534
Ecoregion area	0.764	(0.418, 1.114)	1000	<0.001

* Parameter estimates are effect sizes standardized on 2 SD following Gelman (2008).

Table S3 Trait-based model of species-level occurrence probability at the ecoregion scale, considering interactions among dispersal ability, a species' trait-based similarity to the ecoregion and species age. Species assignment to biomes used the 20% percent range overlap threshold.

Parameter	Estimate*	CI	ESS	P
(Intercept)	–0.879	(–2.994, 1.125)	712	
NNTD	0.277	(0.080, 0.448)	1000	<0.001
Species age	0.458	(–0.178, 0.980)	746	0.116
MTD	–1.065	(–1.325, –0.788)	1000	<0.001
HWI	0.492	(–0.066, 1.085)	1000	0.084
Divergence time	0.465	(0.204, 0.680)	1000	<0.001
Ecoregion area	0.988	(0.587, 1.458)	1000	<0.001
NNTD x Species age	–1.251	(–1.586, –0.880)	1000	<0.001
NNTD x HWI	0.559	(0.127, 0.952)	977	0.012
MTD x HWI	–0.371	(–0.855, 0.195)	897	0.164
HWI x Species age	–0.375	(–0.990, 0.352)	1000	0.284

*Parameter estimates are effect sizes standardized on 2 SD following Gelman (2008).

Table S4 Trait-based model using maximum likelihood estimation of species-level occurrence probability at the ecoregion scale, considering interactions among dispersal ability, a species' trait-based similarity to the ecoregion and species age. Species assignment to biomes used the 5% percent range overlap threshold.

Parameter	Estimate*	SE	P**
(Intercept)	–0.855	0.529	
NNTD	0.101	0.065	0.118
MTD	–0.766	0.098	<0.001
HWI	0.486	0.211	0.021
Species age	0.564	0.194	0.004
Divergence time	–0.180	0.083	0.031
Ecoregion area	0.662	0.161	<0.001
NNTD x Species age	–0.974	0.125	<0.001
NNTD x HWI	0.715	0.144	<0.001
MTD x HWI	–0.604	0.200	0.003
HWI x Species age	–0.259	0.243	0.286

*Parameter estimates are effect sizes standardized on 2 SD following Gelman (2008).

** Wald Z-statistic

APPENDIX S4

Niche space constrains species richness in Andean birds: insights from dietary niches and functional traits

Table S1 Factor loadings (eigenvectors) and percentage of total variance explained for retained principal components (PCs) from prey item (beak length, beak width, beak depth), foraging movement (wing length, tail length and tarsus length), and size PCAs from the two-step PCA process.

PCA	PC	% variance	Loadings		
Prey item selection			Beak length	Beak width	Beak depth
	1*	83	0.57	0.56	0.60
	2	10	0.69	0.72	–0.02
Foraging movement			Tail length	Tarsus length	Wing length
	1*	70	0.61	0.45	0.65
	2	24	–0.43	0.88	–0.21
Size			Beak trait PC1*	Foraging movement trait PC1*	
	1	87	0.75	0.66	
	2	13	–0.66	0.75	

*Denotes principal component axes used in the body size PCA (see Chapter 1 of this thesis for full methodological details of two-step PCA).