Spatial Scaling of Functional Structure in Bird and Mammal Assemblages

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ABSTRACT: Differences in trait composition, or functional structure, of assemblages across spatial scales may stem from the ability to tolerate local conditions (environmental filters) and from assembly rules (biological filters). However, disentangling their respective roles has proven difficult, and limited generalities have emerged from research on the spatial scaling of functional structure. Here we quantify differences in trait composition among 679 spatially nested (i.e., paired regional pool and local community) bird and mammal assemblages worldwide. Among the regional pool, we identify species with trait combinations within the range observed locally as the ecological species pool. The ecological species pool has a trait structure that is generally different from that of the regional pool, consistent with the operation of environmental filters. In contrast, local species trait structure generally shows little difference from that of the ecological pool. We find notable deviations from expectations based on equiprobable draws from the ecological pool. However, these deviations vary little across scales and broad environmental gradients. For mammals, but not birds, this is consistent with assembly rules. Thus, by conceptualizing ecological pools, we demonstrate that functional structure is jointly determined by processes causing both low and high functional differences between scales and are able to quantify their relative importance.

Keywords: functional traits, community assembly, scale, functional turnover, species pool, terrestrial vertebrates.

Introduction

The trait, or functional, structure of species assemblages is increasingly being used to understand community assembly processes (Kraft et al. 2008; Mason et al. 2008; Prinzing et al. 2008; Cornwell and Ackerly 2009) and how they may affect ecosystem function (Loreau et al. 2001). Typically, two types of processes are believed to influence the trait composition of assemblages. On the one hand,

local occurrence may be limited to species in the region with trait combinations conferring the ability to tolerate local conditions. These environmental filters will cause trait clustering compared to the range of traits represented in the regional pool. On the other hand, certain assembly rules, such as competition among functionally similar co-occurring species, may lead to patterns of trait overdispersion (Silvertown et al. 2006; Swenson et al. 2007; Kraft et al. 2008). While this framework is alluring in its simplicity, it is becoming clear that the link between pattern and process is not straightforward, as several different processes might result in similar patterns of trait overdispersion or clustering (Cavender-Bares et al. 2009; Mayfield and Levine 2010; Pausas and Verdu 2010; Pavoine and Bonsall 2011).

Synthesis, and especially broader-scale extensions, may benefit from the consideration of three major issues. First, processes causing divergent functional patterns (e.g., environmental filters causing clustering and assembly rules causing overdispersion) may occur simultaneously (Helmus et al. 2007; Pillar et al. 2009; Pausas and Verdu 2010). Thus, equally strong processes acting in opposing directions may result in a community assembly that is random with regard to species traits. This issue can be addressed by explicitly defining an ecological pool as the group of species with trait combinations that are suitable for the local environment (Kraft et al. 2008; Pausas and Verdu 2010). This definition of the ecological pool results in disregarding the species that are clearly not adapted to local conditions and thus identifying functional effects beyond those imposed by environmental filters. We present a novel method for defining the ecological pool that can be used with very limited data on the actual habitat affinity of individual species.

A second concern is that when measuring functional patterns, the actual regional availability of species with particular traits is not always explicitly taken into account. Most current methods focus on quantifying patterns of

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trait distribution within an assemblage (e.g., trait richness and trait dispersion; Schleuter et al. 2010), while regional availability is only indirectly taken into account using null models. However, when the goal is to understand functional community assembly (i.e., what differentiates species that are found in a local assemblage from species that are found in the species pool but locally absent), a direct quantification of functional differences across spatial scales (i.e., area of assemblages) may be more revealing. In this study, we focus on directly measuring the functional difference between regional and local assemblages. Instead of comparing geographically or temporally separate assemblages (Graham and Fine 2008; Devictor et al. 2010; Swenson et al. 2011; Villeger et al. 2011), we assess functional differences between nested subsets to elucidate the mechanisms structuring assemblages across scales.

Finally, it is clear that the dominant drivers of community assembly may change with spatial scale (Cavender-Bares et al. 2006; Swenson et al. 2006; Emerson and Gillespie 2008). The most commonly held view is that environmental filters dominate at coarse spatial scales, while species interactions influence community assembly predominantly at finer scales. However, most analyses to date have focused on a single scale, usually within a single region (but see Messier et al. 2010; Freschet et al. 2011; de Bello et al., forthcoming). For generalities to emerge, it may be necessary to explicitly examine how functional structure varies over a wide range of scales and over broad extents.

In this study, we address all three of these concerns and assess the scaling of functional structure for 679 spatially nested bird and mammal assemblages worldwide. We ask three interrelated questions: (1) Are functional differences between assemblages at regional and local spatial scales higher, lower, or similar to those expected from equiprobable draws from the species pool? (2) How do patterns of functional difference between assemblages depend on the definition of the species pool? (3) How do patterns of functional difference between assemblages vary across scales, between taxa, and across geographical gradients? We expect that evaluating the scaling of assemblage functional structure within this framework will enhance the generality and depth of our understanding of the processes structuring vertebrate communities worldwide.

Methods

Conceptual Framework: Scaling of Functional Difference

There are potential limitations associated with using local assemblage trait structure for understanding community assembly. Environmental filtering is frequently inferred from a reduction in the range of traits within an assem-

blage, which can be quantified using a convex hull approach (Cornwell et al. 2006). Two assemblages of similar "trait volumes" (fig. 1A, 1B) might thus suggest that the same filtering processes have operated on both assemblages. However, in this example, assemblage B has undergone a larger change compared to the species pool than assemblage A. Similarly, trait overdispersion, often quantified as variation among local species in nearest-neighbor distances (Kraft and Ackerly 2010) or minimum spanning tree branch lengths (Villeger et al. 2008), may be very different between assemblages (fig. 1C, 1D), even when differences in trait composition across scales are small. Consequently, methods that can provide a direct quantification of functional differences across scales will offer more reliable inference about community assembly compared to methods that characterize local trait distribution alone.

We here adopt such an approach and concentrate on the functional difference (i.e., multivariate trait dissimilarity) between regional and local assemblages (fig. 2). Instead of calculating indexes of assemblage functional diversity (Graham and Fine 2008; Devictor et al. 2010; Swenson et al. 2011; Villeger et al. 2011; de Bello et al., forthcoming), we directly assess functional differences be-
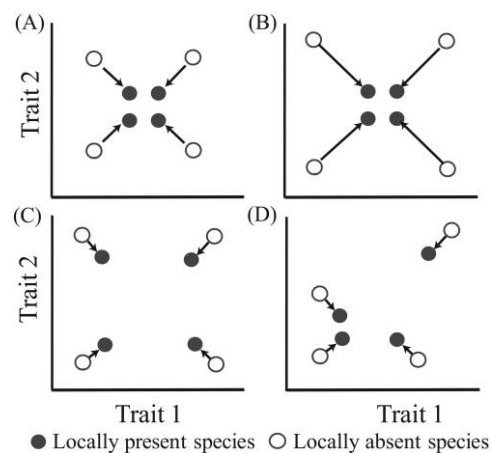

Figure 1: Functional difference among nested assemblages and its relationship to trait clustering and overdispersion. Note that the species present locally are always part of the regional pool. Each circle represents the trait combination of a single species (for simplicity, only two traits are shown). Functional difference is calculated as the average minimum distance (arrows) between species at the regional scale (species pool) and the species present within the local assemblage. *Top*, although local trait richness, as quantified by the convex hull approach, is similar in *A* and *B*, local trait combinations are more distinct from the regional pool (higher difference) in assemblage B. *Bottom*, trait combinations are similar across scales, resulting in low functional difference in *C* and *D*, both when local traits show high (*C*) and low (*D*) overdispersion, as quantified by the variance in the nearest-neighbor distance between species at the local scale.
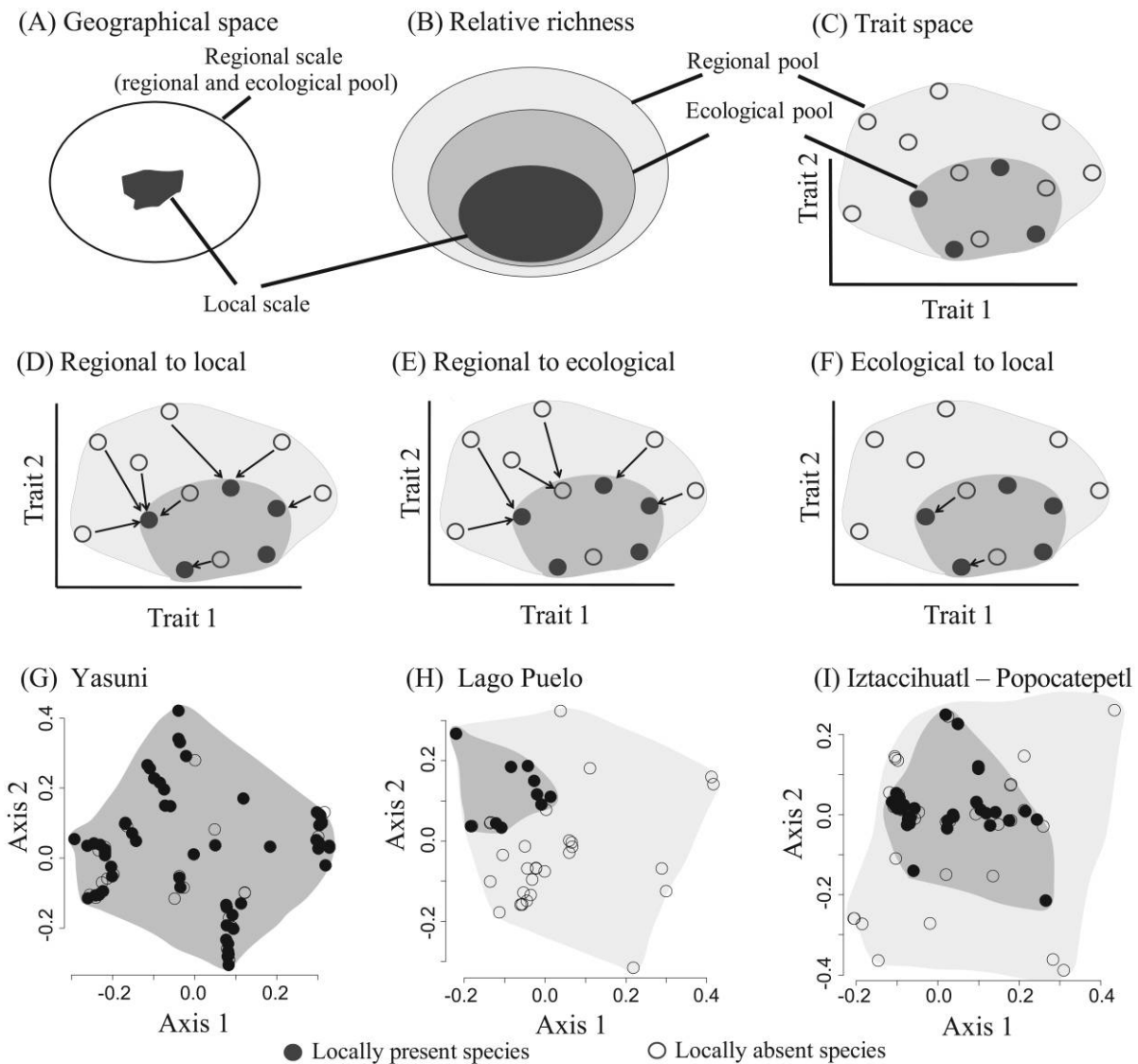
Figure 2: The different types of assemblages and species pools used to calculate functional difference. Each circle represents a single species, and therefore adjacent dots represent species that have similar trait values (for simplicity, only two are shown). Only a subset of the regional species (light gray) may have trait combinations that enable them to potentially inhabit a particular local environment. These species delimit the ecological species pool (intermediate gray). However, only part of the ecological pool is actually observed at the local scale (dark gray). Consequently, local assemblages are nested within ecological pools, which are in turn nested within the entire regional pool (*A–C*). Functional difference can thus be calculated in three ways: between the regional pool and the local assemblage (*D*), between the regional pool and the ecological pool (*E*), and between the ecological pool and the local assemblage (*F*). In *D–F*, arrows represent the minimum trait distance between the assemblages compared. While the functional difference depicted in *D* is the most straightforward to calculate (as it does not require estimating the ecological pool), the results are hard to interpret as they represent the effect of two opposing patterns. *G–I* depict functional differences for three empirical mammalian assemblages (between scales of 200-km diameter and biological inventory): *G*, Yasuni National Park (00°56′S, 75°24′W); *F*, Lago Puelo National Park (42°04′S, 71°37′W); *I*, Iztaccihuatl-Popocatepetl National Park (19°10′N, 98°38′W).

tween spatially nested subsets to elucidate the mechanisms structuring assemblages across scales (see also de Bello et al. 2009). Measures of functional difference between spatially nested assemblages explicitly take into account the trait combinations available in the regional species pool and provide a way of quantifying changes in trait composition across scales. Moving from regional to local scales, a high functional difference implies that certain trait com-

binations that exist in the region do not appear at the local assemblage. If this difference is associated with environmental differences, it may point to the importance of environmental filters in community assembly. As environmental filters result in species exclusion from the local assemblage, we predict a reduction of local richness relative to the species pool in regions with high functional differences.

In contrast, low functional difference suggests that many trait combinations at the broader scales also occur locally. This trait conservatism indicates that when moving from regional to local scales, the loss of species is not associated with the loss of unique trait combinations. At least three distinct sets of processes can cause differences in trait composition between scales to be lower than expected from a random community assembly model.

First, "restrictive" assembly rules may depress the co-occurrence of species with similar, or "clustered," traits. An obvious example of such assembly rules is competitive exclusion, where functionally similar species tend not to co-occur in the same area (Armstrong and McGehee 1980; Webb et al. 2002). Over broader taxonomic definitions (e.g., all mammals), such competition may result in guild assembly rules (sensu Fox 1999), such as a roughly constant ratio of consumers to producers across assemblages (Cohen 1977). These processes will cause overdispersion of traits and low functional difference between scales relative to equiprobable draws from the species pool.

Second, and closely related, low cross scale functional difference may be due to "facilitative" assembly rules, where functionally different yet codependent species have high co-occurrence probabilities (Cavender-Bares et al. 2009). For example, the trophic structure of assemblages may be conserved because of the trophic dependence of predators on the occurrence of prey. Thus, species within assemblages may occupy more diverse guilds than expected from their regional availability, causing low functional difference across scales. Similar to restrictive assembly rules, facilitative assembly rules seem particularly relevant for broadly defined taxa.

There are as yet few clear hypotheses regarding the strength of these two types of assembly rules across broad environmental gradients. However, one prominent theory suggests greater intensity of biotic interactions in the more species-rich tropics, compared to temperate regions where abiotic environment might be more limiting (Schemske et al. 2009). This gradient in the intensity of biotic interactions will lead to a lower difference in trait structure between scales toward lower latitudes and more productive environments.

Third, higher-than-expected cross scale trait similarity and, thus, low functional difference may also arise due to within-region geographic barriers and dispersal limitation (Kembel 2009). When species with similar traits occupy geographically separate parts of a region (e.g., following allopatric speciation), we may find high spatial turnover of species accompanied by little functional difference across scales.

Therefore, three different processes may all lead to patterns of low cross scale functional difference, making them difficult to disentangle (Kembel 2009). However, we propose that they may be separated by their different influence on local-to-regional richness. Competition and other restrictive assembly processes impose constraints on fine-scale co-occurrence of species and thus will also limit local richness in relation to the regional pool. Thus, low functional difference would be associated with low local richness (given regional richness) and result in a positive correlation between functional difference and local-to-regional richness ratios. In contrast, facilitative assembly processes are expected to increase local richness, causing the correlation to be negative. Finally, geographic separation and dispersal limitation will also cause lower local-to-regional richness ratios as fewer regional species can reach a local assemblage (Belmaker and Jetz 2012). However, as opposed to restrictive assembly processes, under dispersal limitation the relationship between local-to-regional richness ratios and functional difference will be weak. This is because low functional difference between scales can be found both when dispersal limitation is strong, resulting in a small local assemblage with trait structure similar to the regional pool, and when it is weak, resulting in a large local assemblage that is also similar to the regional pool. Hence, under dispersal limitation alone we do not predict a strong directional association between local-to-regional richness ratios and functional difference across scales, while for restrictive and facilitative assembly rules we predict a positive and negative correlation, respectively.

Conceptual Framework: Species Pool Definitions

We aim to separate environmental limitation from other processes that may cause the exclusion of regional species from local communities. We thus define the regional pool as all species that belong to a specific taxa from a specific region. We define an ecological pool, part of the regional pool but at the same spatial scale, as the group of species with trait combinations that appear suitable for the local environment (fig. 2A–2C). The environmental filtering effect is then given by the differences in trait composition between the regional pool and the ecological pool (fig. 2E). In turn, trait differences between the ecological pool and the local assemblage capture processes that exclude species suited to local conditions from entering the local assemblage (e.g., Partel et al. 2011; fig. 2F). This use of the ecological pool allows us to disregard the species that

are clearly not adapted to local conditions and thus to identify processes beyond those imposed by environmental filters (fig. 2*G*–2*I*). We expect explicit consideration of the ecological species pool to increase the ability to tease apart the relative importance of these largely opposing processes causing trait variation between scales.

Appropriately defining the set of species that inhabit a given environmental setting requires experimental evidence or, in its absence, detailed species-specific knowledge about environmental requirements, for example, data derived from extensive fine-scale species distribution models. In practice, this is not feasible for all but very taxonomically and geographically limited cases. To allow a first-order distinction between regional and ecological pools at coarse scales, we utilize the multivariate trait composition of the local assemblage. We define as belonging to the ecological pool the set of all regional species that are bounded within the trait combinations of locally occurring species (fig. 2). Thus, species with trait combinations that are outside the range of traits found within the local scale are excluded from the regional assemblage, thereby defining the smaller ecological pool. The ability of this ecological pool to reproduce the true environmental limitation on local occurrence depends on the assumption that the traits considered are relevant for survival in the local environment.

As a simple example, consider two trait axes, diet and foraging height, across two distinct locations, say, a savanna and a forest. We may find that the diets of savanna dwellers are distinct from the pooled dietary makeup of species in both habitats but that no canopy dwellers are found in the savanna. Excluding canopy dwellers from the combined pool to form the more restricted ecological pool provides a more realistic representation of the set of species able to enter a local community, thus exposing novel patterns, such as an unusually diverse or homogeneous makeup of the savanna community.

Species Composition

Quantifying functional difference across spatial scales requires the paired comparison between regional and local assemblages. For data on local assemblages, we use global biological inventories at a median grain of ∼400 km^2 (see below). We then quantify species composition at coarser scales using the intersection of extent-of-occurrence range maps with concentric circles around each of these inventory geographical location centroids. Circle sections overlapping no ranges (such as those in the ocean) were disregarded. We initially focus on differences between 200-km diameter (∼31,000 km^2) and the inventory scales as regional and local scales, respectively. We then quantify how patterns of functional difference vary with scale by (1)

maintaining the local assemblages as biological inventories but increasing the size of the regional assemblages from 200-km diameters to 400, 1,000, and 2,000 km (fig. A1, available online) and (2) using the 2,000-km diameters (∼3,140,000 km^2) as a fixed regional scale and decreasing the size of the local assemblages to diameters of 1,000, 400, and 200 km and the biological inventory scales.

Data selection procedures followed Belmaker and Jetz (2011, 2012). We included all nonmarine birds (breeding ranges only) and all terrestrial nonvolant mammals. Range maps were based on the International Union for Conservation of Nature (IUCN) assessment (http://www.iucnredlist.org/) for mammals (Schipper et al. 2008), while range maps for birds were compiled from the best available sources for a given broad geographical region or taxonomic group (Jetz et al. 2007). Species inventories were compiled through an extensive survey of the literature, including only well-sampled and thoroughly documented terrestrial vertebrate assemblages over clearly defined small extents, most of them protected areas (Meese 2005; Belmaker and Jetz 2011; data deposited in the Dryad repository, doi:10.5061/dryad.78sr6). To ensure data quality, we were careful to retain for analyses only inventories that were considered to be complete by the original source. We addressed the occurrence of migrants, vagrants, and observational errors in inventories by excluding records of species not found at the regional scale. This procedure was indispensible, especially for birds, as inventories include many vagrant and nonbreeding species. We used only assemblages covering areas between 10 and 7,875 km^2 (median: 411 km^2). In the absence of globally standardized vertebrate inventories, varying area size is the only way to ensure environmentally and geographically representative coverage. Variation in area of local assemblages was partially addressed by including area as a covariate in analyses that incorporate environmental predictors (see app. B, available online). Importantly, the results remained qualitatively unchanged when the analysis was restricted to the middle 50% of assemblage area quantiles (98–1,359 km^2; results not shown). In total, we used 370 assemblages for birds and 309 for mammals, for a total of 6,060 and 1,612 species, respectively (see the Dryad repository, doi: 10.5061/dryad.78sr6).

Species Traits

To calculate functional difference, we compiled extensive data on ecologically important traits that describe the ecological roles species play within a community. As these traits describe species-level attributes, they do not accommodate intraspecific variation, which is likely to be low relative to interspecific differences. For both birds and mammals, we used five trait categories: diet, body size,

activity time, and two measures of foraging niche. These traits quantify important information about the likelihood of species to occupy similar ecological niches (and thus potentially to compete for similar resources).

Diet. Diet included estimates of the proportional use of each of seven dietary categories for mammals (seeds, fleshy fruits, nectar and pollen, other plant material, invertebrates, fish, vertebrates) and eight dietary categories for birds (seeds, fleshy fruits, nectar and pollen, other plant material, invertebrates, fish, carrion, other vertebrates; Belmaker et al. 2012). For the mammal diets, we use *Walker's Mammals of the World* (Nowak 1999) as our main reference. For species, or groups of species, where *Walker's Mammals* was lacking in useful data, we use numerous other sources, both books and primary literature. These sources are referenced in Wilman (2011). The majority of avian diets are taken from *Handbook of the Birds of the World* (del Hoyo et al. 2008), which covers the majority of the world's bird species. Additional sources were used for missing species (Wilman 2011). Species that are data deficient were given genus and family averages (this was done for 816 and 210 mammal species and 655 and 113 bird species, respectively). Specific proportions of various foods making up the diet were used if available. If not, text-based descriptions of species' diets were translated into estimates of diet percentage (rounded to closest 10%), following a standardized rule set connecting terms indicating food preference to numerical quantities. For a given diet category, for example, "almost exclusively" indicated 90%, "mostly" at least 60%, "sometimes" 10% or 20%, "occasionally" 10% or less, and so on. Values for less frequent diet categories were adjusted by the number of additional diet types used. For a full description of this data extraction, see Wilman (2011). In cases where comparative words were not used in the description, we gave higher weight to diet items that were listed first, then decreasing proportions to those coming later. We further categorized species according to uncertainty associated with their diet estimates, but these data were not used in the final analyses.

Body Mass. For birds, body mass ($\log_{10}$ transformed) was based on Dunning (2007). For mammals, data on body mass ($\log_{10}$ transformed) were obtained from the PanTHERIA database (Jones et al. 2009). For both groups, data-deficient species were given the average value within their genus or, when unavailable, within their family. This procedure was necessary for 34% of all terrestrial nonvolant mammals (4,152 species) and 9% of all nonmarine birds (8,973 species).

Activity Time. Activity time included five ordinal variables (1 = nocturnal, 2 = nocturnal and crepuscular, 3 = crepuscular or cathemeral, 4 = diurnal and crepuscular, 5 = diurnal). While crepuscular and cathemeral (irregularly active at any time of night or day) represent very different activity patterns, they are both intermediate between diurnal and nocturnal patterns and hence were given an intermediate score. Each activity pattern was defined by the time of foraging or hunting as related to local light levels: nocturnal as foraging between the end of sunset and the beginning of sunrise, diurnal as foraging between the end of sunrise and the beginning of sunset, crepuscular as foraging during dawn and/or dusk, and cathemeral as foraging at any time. Because species can vary in activity patterns during different seasons or at different locations, species exhibiting such patterns were assigned the activity patterns in breeding season/location, if known. For example, in the absence of precise breeding information, a species with both diurnal and crepuscular populations, a species that is diurnal and crepuscular at different times of year, or one that is always active at dawn, dusk, and the middle of the day would be marked as both "diurnal" and "crepuscular." For birds, data were collected from *Handbook of the Birds of the World*, with some supplementary data taken from the International Union for Conservation of Nature (IUCN Red List, http://www.iucnredlist.org/) as needed. Data-deficient species were flagged and marked with the activity levels of congeners, with diet and habitat taken into account in cases of ambiguity. For mammals, activity time was originally based on the PanTHERIA database, which contains only three categories. These data were expanded using mostly genus-level information from Nowak (1999) to include information for missing species and to extend to the five ordinal levels used for birds.

Foraging Niche. For both birds and mammals, two foraging niches were used. For birds, the first foraging niche trait reflects proportional use of each of seven categories (in water below surface, in water on surface, terrestrial ground level, understory, mid canopy, upper canopy, aerial). The second foraging niche trait separates species according to their broad habitat affinity to freshwater or land. Proportional use was extracted from the same literature sources and translated into percentages (in 10% intervals) in the same way as diet (see above). For mammals, the first foraging niche trait includes foraging height categories on an ordinal scale (1 = fully arboreal, 2 = scansorial, 3 = terrestrial). Categorization was based on major foraging habitat, and thus species that forage solely on the ground but rest on trees were considered terrestrial. Species were categorized as scansorial if they often forage both on the ground and on trees. Data-deficient species with climbing adaptations such as a prehensile tail were categorized as scansorial. The second

mammalian foraging niche trait is the degree to which a species is fossorial on an ordinal scale (1 = not fossorial, 2 = semifossorial, 3 = fully fossorial). Again, these categories pertain to the major foraging habitats. Species were considered semifossorial if they forage both below- and aboveground or if they were data deficient but possess distinct digging adaptations. Species that dig to extract food from belowground but do not tunnel into it were not considered fossorial. Data for both foraging traits was based on Nowak (1999), and species were given genus values when specific reference to a species was missing.

Estimating Functional Difference

To estimate functional difference between scales, we first quantify the multivariate trait dissimilarity between species. The dissimilarity between species at the regional and local scales was then summarized to capture the total functional difference between spatial scales (see below). We constructed separate trait distance matrices for birds and mammals. We used Gower's dissimilarity index, which allows the use of categorical, ordinal, and continuous variables (Podani 1999; Pavoine et al. 2009), using the function "gowdis" in the R package "FD" (Laliberte and Legendre 2010). Trait distance matrices were produced using equal weighting of the variables (each trait was given a weight of 0.2, except for composite traits such as diet, for which each category was given a weight proportional to the total number of categories). However, results were robust to changes in weighting of traits up to a factor of 3. For composite traits that must sum to 1, a category was excluded to represent the correct degrees of freedom.

We were interested in quantifying how different local species traits are from traits of species at the regional scale. As all local species are nested within the regional species pool, we used the asymmetric average nearest-neighbor dissimilarity index proposed by Ricotta and Burrascano (2009):

$$ \mathrm{FD} = \frac{\sum_{j=1}^{S_\gamma} \min\, \delta_{jn}}{S_\gamma}, \tag{1} $$

where FD is functional difference, S_γ is species richness in the regional scale, and $\min\, \delta_{jn}$ is the minimum functional distance between each species j at the regional scale and any local species. This index measures the average minimum ecological distance between species in the region and the nested local assemblage and for Gower distance varies between 0 and 1. High functional difference means that the local assemblage contains only a small number of the trait combinations used by species in the region. Low functional difference means that species at the fine scale possess most of the trait combination in the regional species pool.

Defining the Ecological Pool

To ask whether species qualify for the ecological pool, we examine whether these species are bounded within the trait combinations of local species. For this we used nonmetric multidimensional scaling (nMDS) to represent the distance among species in ordination space (using "metaMDS" in the R package "vegan"). A unique nMDS was applied to each paired regional and local assemblage. We then recorded the species scores along the nMDS axes. We used four axes, but results were similar when using higher and lower values (note that computation time increases substantially with increased dimensionality). After excluding one mammalian assemblage and one bird assemblage with stress values >0.25, stress values were low (range 0.04–0.10 and 0.002–0.08 for mammals and birds, respectively), indicating that the nMDS represents the original dissimilarity well. We considered as belonging to the ecological pool all species in the region that are bounded within the convex hull computed around the set of species observed within the local assemblages (Cornwell et al. 2006; Laliberte and Legendre 2010). We also assessed as an alternative selection criteria scores that appear within the minimum and maximum scores of local species (Cornwell and Ackerly 2009), which produced similar results.

Null Model

Patterns of functional difference are naturally expected to be affected by richness as richer local assemblages will contain more trait combinations and hence tend to show lower functional difference. We used an equiprobable draw null model to correct for this bias (Cornwell et al. 2006; Villeger et al. 2008). First, we sampled (without replacement) from the regional species pool the same number of species observed in the local assemblage. These random assemblages were used to calculate functional difference between the regional and local assemblages. Second, a convex hull was computed around these randomly selected species to define the null ecological pool. This was used to calculate the functional difference between the regional pool and the ecological pool. Finally, we sampled from the ecological pool the same number of species observed in the local assemblage to calculate functional difference between the ecological pool and local assemblages. This procedure was repeated 1,000 times, and the percentile of observed values in relation to the null distribution was recorded. This percentile was then converted to a z-score using the normal quantile function to be used as a measure of functional difference standardized effect size (SES; i.e., the value of a random variable from a standard normal distribution that will give values at, or below, the observed percentile). We did not use the more common approach

(using the (observed − null mean)/null SD), as some assemblages displayed skewed null distributions and could not use the percentiles themselves as they are nonstationary (i.e., the difference between 0.1 and 0.2 is not comparable to the difference between 0.5 and 0.6).

Statistical Analyses

Functional difference SESs were related to environmental predictors (see app. B) using generalized linear models (GLMs). We used hierarchical partitioning (using the metric "lmg" in the R package "relaimpo") to assess the relative importance of predictors (Gromping 2006). To assess the degree to which relative local to regional richness is predicted by functional difference SES, we used quasi-binomial GLMs, with the response composed of local richness (success) and regional-local richness (failures), using a logit link function. The quasi-binomial approach models the probability of local species occurrence given regional presence (Belmaker and Jetz 2012). All analyses were performed using the computer program R (R Development Core Team 2008).

Results

Functional Difference and Species Pool Definitions

Comparing 200-km-diameter regions with biological inventories, we find that functional difference is generally higher than that expected based on equiprobable draws from the regional pool (fig. 3; Wilcoxon test: $P < .001$ for birds, $N = 370$; $P < .05$ for mammals, $N = 309$). Thus, local trait combinations are distinct from those available at the regional pool. However, when separating functional difference into that between regional and ecological pools and that between ecological pools and the local assemblages, two distinct patterns emerge: while regional and ecological pools are more different than expected based on equiprobable draws from the regional pool (regional to ecological pool SES is higher than 0; $P < .001$ for birds, $P < .05$ for mammals), the ecological pool is more similar to local assemblages than expected based on equiprobable draws from the ecological pool (fig. 3; ecological to local SES is substantially lower than 0; $P < .001$ for both taxa). These patterns were robust to the definition of the scale over which the regional pool was defined (increasing the regional scale from 200- to 2,000-km diameter; fig. A1). We further find that regional pool to ecological pool SES and ecological pool to local SES are positively correlated with regional SES to local SES (fig. A2, available online). However, regional to ecological and ecological pool to local SESs are only very weakly correlated (fig. A2). This suggests
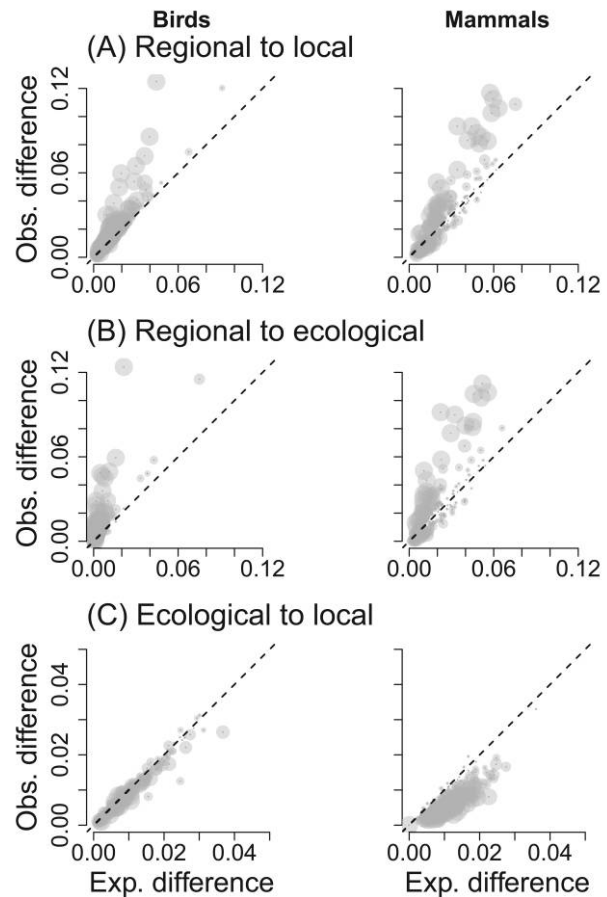

Figure 3: Observed (obs.) versus expected (exp.) functional difference between assemblages at the 200-km-diameter scale (regional) and the biological inventories (local) for three comparisons: regional pool to local assemblage, regional pool to ecological pool, and ecological pool to local assemblage. Expected values are based on equiprobable draw null models (see text for details). Points below the dashed black 1 : 1 line indicate low functional difference between scales, while points above the line indicate high functional difference. Point size is proportional to functional difference SES.

that these latter two types of functional difference capture distinct aspects of the scaling of functional structure.

We examined the relative magnitude of regional to ecological and ecological pool to local SESs using their log ratios (the ratios were log transformed to obtain a symmetric and normally distributed measure). Stronger regional to ecological pool functional difference will result in positive log ratios, while stronger ecological pool to local functional difference will result in negative log ratios. We find the mean log ratio to be slightly positive for birds (0.19 ± 0.09 [SE], $P < .05$ [*t*-test]; corresponding to regional to ecological SES being 1.2-fold stronger than ecological pool to local SES) but strongly negative for mammals (-0.53 ± 0.08, $P < .001$; corresponding to ecological

pool to local SES being 1.7-fold stronger than regional to ecological SES).

If functional difference between regional and ecological pools is associated with environmental filters, trait differences should be correlated with environmental gradients. In contrast, trait differences between ecological pools and local assemblages, trait differences that are expected to become smaller when assembly rules operate, may be only weakly associated with the environment. This prediction is largely upheld, as the total R^2 explained by environmental predictors is larger for regional to local functional difference SES and for regional to ecological SES than for ecological pool to local SES (fig. 4). Specifically, the R^2_{adj} for the relationship between functional difference SES and the environmental predictors for the 200 km to biological inventory comparison is 0.14 and 0.09 for regional to ecological SES (for mammals and birds, respectively), 0.11 and 0.14 for regional to local SES, but only 0.06 and 0.04 for ecological pool to local SES. This low explanatory power results in ecological pool to local functional difference SES showing no clear response to geographical or latitudinal gradients (fig. A3, available online).

In accordance with regional to ecological pool functional difference caused by processes of species exclusion such as environmental filters, we find that higher SESs are associated with lower ecological pool richness given regional richness (table 1). We further predicted that ecological to local SES will be positively or negatively related to the ratio of local assemblage to ecological pool richness if restrictive or facilitative assembly rules operate but show no directional association if the pattern is produced predominantly by dispersal limitation. We find mixed support for these predictions, as there is a positive association in mammals and no directional association in birds (table 1).

The Scaling of Assemblage Functional Difference

To assess the generality of the identified relationships for variable spatial scales, we use 2,000-km-diameter regional assemblages and successively decrease the area over which the local assemblages are defined. As expected for spatially nested assemblages, we find a decrease in richness toward finer scales accompanied by an increase in functional difference between the regional pool and local assemblages (fig. 5). Importantly, we find scale dependence in functional difference SES: regional to local SES is negative for coarser-scale comparisons (for birds at the 2,000 to 1,000 km comparison, Wilcoxon test, $P < .05$; for mammals at the 2,000 to 1,000, 400, and 200 km comparison, $P < .001$, .001, and .05, respectively) but positive for finer-scale comparisons (2,000 km to biological inventory comparison, $P < .001$ for both birds and mammals). This suggests that assemblages tend to be functionally similar to their
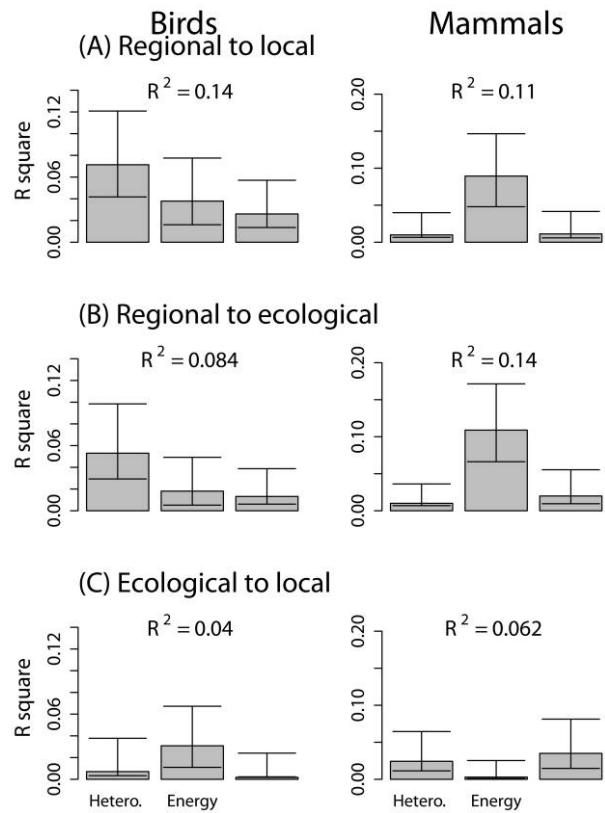

Figure 4: Relative importance of major environmental predictor groups for the 200-km diameter to biological inventory comparison (see fig. 3). We separate functional difference into three comparisons: regional pool to local assemblage, regional pool to ecological pool, and ecological pool to local assemblage. Hetero. = heterogeneity predictors ("Area," "HabVar," "ElRange"); energy = energetic predictors ("TEMP," "NPP"); similarity = environmental similarity between the regional and local scales ("simHab," "simElv," "simNPP"). Error bars represent bootstrapped 95% confidence intervals. The total R^2 for the models is presented in each panel.

corresponding regional pool when the respective local assemblages are defined over large extents and become increasingly functionally different toward smaller areas. This makes the perceived patterns of functional community assembly contingent on the precise scales chosen for analyses.

When invoking the ecological pool and separately analyzing regional to ecological pool and ecological pool to local assemblage comparisons, we find very different scaling patterns. While the ecological pool to local assemblage richness ratio decreases substantially toward finer scales, closely resembling the pattern for the regional to local comparisons, the decrease is very small between the regional and ecological pools (fig. 5). However, the effects of using the ecological pool on patterns of functional difference SES are substantial. We find that the regional to

Table 1: Functional difference standardized effect size (SES) as a predictor of the ratio of local to regional species richness

Scale, functional difference SES	Birds			Mammals		
	Slope (SE)	t value	R^2	Slope (SE)	t value	R^2
200 km to biological inventories:						
Regional pool to ecological pool	−.35 (.04)	−8.3***	.24	−.41 (.05)	−13.3***	.39
Ecological pool to local assemblage	−.02 (.03)	−.8	.00	.11 (.03)	3.4***	.03
2,000 km to 200 km:						
Regional pool to ecological pool	−.26 (.03)	−7.7***	.16	−.09 (.05)	−1.8	.11
Ecological pool to local assemblage	.01 (.02)	.5	.00	.23 (.03)	7.4***	.13

Note: Two types of functional difference SES (regional pool to ecological pool and ecological pool to local assemblages) are assessed. At both spatial scales, local to regional richness ratios decrease as the functional difference between regional and ecological pool increases (negative coefficients). However, in mammals, the converse is true for the functional difference between the ecological pool and local assemblage, as local assemblages that are functionally different from their ecological pool also have relatively higher local richness (positive coefficients). Results are based on quasi-binomial generalized linear models, where the response is the number of local species (success) and regional − local richness (failures). The asterisks indicate $P < .001$.

ecological SESs are slightly higher than the regional to local SESs (for mammals: positive at the 2,000 to 200 km and biological inventory comparison, Wilcoxon test, $P < .05$, .001, respectively; for birds: negative at the 2,000 to 1,000 km comparison but positive at the 2,000 km to biological inventory comparison, $P < .001$). However, ecological to local SESs are consistently negative ($P < .001$ for all scale comparisons and for both taxa). This scale independence is corroborated by a shallow slope of the relationship between ecological to local functional difference SES and $\log_{10}$ area of the local assemblage (mammals: slope = -0.21 ± 0.65 (SD); birds: slope = -0.13 ± 060; $P > .05$ in both cases). Therefore, using the ecological pool uncovers consistent and scale-invariant patterns of trait structure. We find low correlations of functional difference SES between two independent comparisons: 2,000 to 200 km diameter and 200 km diameter to biological inventories (fig. A4, available online).

Discussion

We find strong evidence that difference in assemblage functional structure between scales is composed of two patterns operating in opposing directions. Comparing 679 assemblages across multiple scales from areas of 3,140,000 to ~400 km², we find that functional difference between all species in the region and the ecological pool, that is, the set of species with trait combinations that appear suitable for the local environment, is generally high but scale dependent. Simultaneously, functional difference between the ecological pool and local assemblage is lower than predicted by null models. Therefore, the subset of regional species that possess traits suitable for the local environment have a functional structure very similar to the observed local species. Moreover, contrary to our expectations, functional difference SES between ecological pools

and local assemblages seems to be scale invariant. Thus, using the ecological pool allows us to detect formerly unappreciated patterns of consistently low functional difference from very coarse to fine scales. Several studies have found evidence for both environmental filters and assembly rules when studying functional or phylogenetic community assembly of plants (Kraft et al. 2008; Kraft and Ackerly 2010; Pillar and Duarte 2010) and fish (Helmus et al. 2007). This study shows that patterns of high and low functional difference jointly appear globally and over a large range of spatial scales.

Functional Difference between Scales and Species Pool Definition

Environmental filtering is hypothesized to be the dominant force structuring assemblages over coarse scales, where species are sorted into local habitats based on their trait combination (Emerson and Gillespie 2008; Cavender-Bares et al. 2009). In support, we find functional difference between the regional pool and local assemblages to be higher than predicted by equiprobable draw null models when scale discrepancy between the local and regional scales is high (fig. 5). However, this pattern is hard to interpret as it represents the total effect of processes causing both high and low functional differences. We disentangle these effects using the ecological pool and find that between the regional and ecological pools functional difference deviation from equiprobable draw null predictions increases toward finer scales of the nested assemblage (fig. 5). A considerable portion of the variance in this functional difference is predicted by environmental variables (fig. 4). This is consistent with filters limiting the regional trait combinations that can appear in the local environment.

Further support for the presence of environmental filters can be found in the strong negative correlation be-
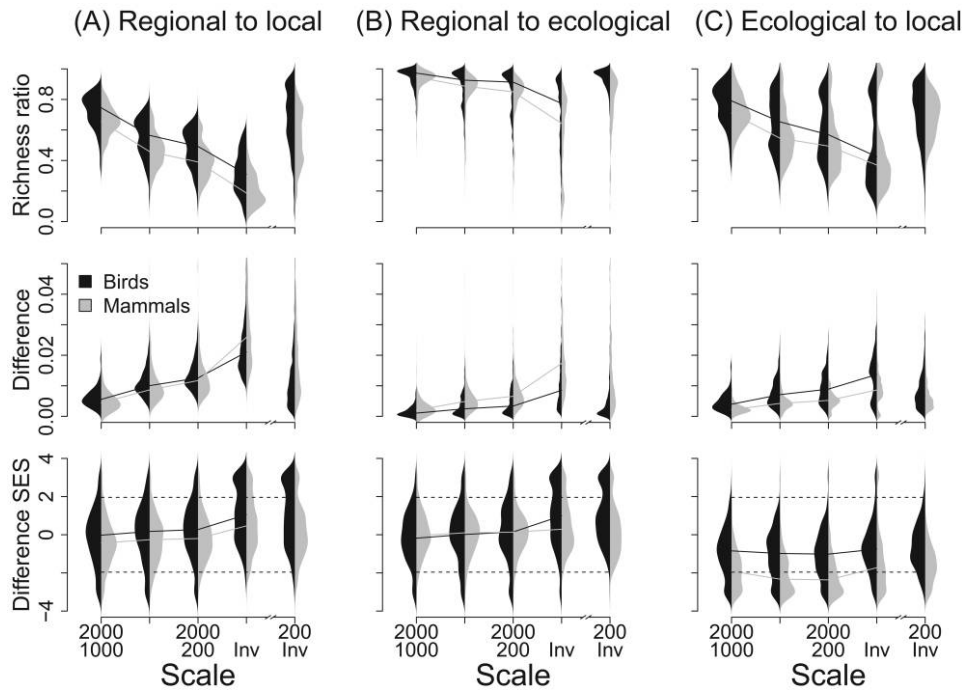
Figure 5: Violin plots depicting the scaling of richness, functional difference, and functional difference SES for bird (black) and mammal (gray) assemblages for the three comparisons: regional pool to local assemblage, regional pool to ecological pool, and ecological pool to local assemblage. We compare the 2,000-km-diameter scale with scales of 1,000, 400, and 200 km and biological inventories (Inv). We also included a comparison between the scale of 200-km diameter and the biological inventories (see fig. 3). *Top*, the ratio between richness of the local assemblage and the regional species pool. *Middle*, functional difference. *Bottom*, functional difference SES. Assemblages beyond the horizontal dashed lines are significantly different from random at $\alpha = 0.05$. Solid lines connect median values across scales.

tween regional to ecological pool functional difference SES and local to regional richness ratios (table 1). This negative association indicates that increased functional difference between scales is associated with reduced richness of the ecological pool, as expected under the operation of environmental filters. Together, our results corroborate the notion that, for both taxa, environmental trait filtering is an important process structuring community assembly from very coarse to fine scales.

We note, however, that much of the variance in functional difference SES remains unaccounted for by environmental variables. This leaves additional room for the operation of environment-independent processes in producing the high functional difference between scales. For example, low historical dispersal rates or dispersal barriers within regions may prevent unique regional trait combinations from reaching particular finer-scale assemblages. This will result in trait differences between the regional and ecological pool that cannot be directly predicted by the environment.

We further find that species in the local assemblage have trait combinations much closer to the species in the ecological pool than predicted by equiprobable draws from

the ecological pool (fig. 3). This means that despite large richness differences many of the trait combinations that can be found within the ecological pool over coarse spatial scales are also observed at finer scales. It has been postulated that competition among functionally similar species will lead to patterns of functional overdispersion, or low functional difference, especially at fine scales (Silvertown et al. 2006; Swenson et al. 2007; Kraft et al. 2008). However, it is becoming clear that the link between pattern and process is not straightforward and that several processes may result in similar community assembly patterns (Cavender-Bares et al. 2009; Mayfield and Levine 2010; Pausas and Verdu 2010). For example, trait overdispersion can be caused by competition, facilitation, and dispersal limitation (Emerson and Gillespie 2008; Kembel 2009). This ambiguity requires applying further tests to link patterns to processes.

We predicted that, between the ecological pool and local assemblage, restrictive assembly rules would result in a positive correlation between functional difference and local-regional richness ratios, facilitative assembly rules would cause a negative correlation, and dispersal limitation would not lead to a directional relationship. For birds,

functional difference SES between the ecological pool and local assemblage was not directionally associated with local-regional richness ratio at both scales examined (table 1). This suggests that for birds the low functional difference across scales may be mostly attributed to dispersal limitation restricting local richness with little turnover in species trait composition. Alternatively, it may indicate equal strengths of assembly processes causing exclusion of similar-trait species (e.g., competition) and the addition of species with divergent traits (facilitation). In contrast, in mammals we find a significant positive association between functional difference SES and richness ratios from ecological pool to local assemblages (table 1). Hence, assemblages with lower functional difference also contain fewer local species given the ecological pool. This implies that competition or other restrictive assembly rules, such as those maintaining similar trophic or guild structure across scales, may constrain local richness in these mammalian assemblages.

It has been suggested that biological structuring processes might be more important at low latitudes than at high latitudes (Schemske et al. 2009; Freestone and Osman 2011). In this study we find little geographic variation in functional difference SES from ecological pool to local assemblage, a measure that we expected to capture the strength of biological structuring processes such as assembly rules (at least in mammals). This would suggest that strength of biological structuring processes varies little along broad-scale environmental gradients. Further work, for example, including other clades or more detailed trait data, is needed to determine the generality of this pattern.

The directionality of the relationship between functional difference SES and local-to-regional richness ratios is not the only difference between birds and mammals. While both taxa have similar functional difference SES between regional to ecological pool, functional difference SES going from ecological pool to local assemblage is lower (more negative) in mammals (figs. 3, 5). Ecologically, this indicates that while both groups may respond similarly strongly to environmental filters, avian trait assemblage structure is much less conserved across scales. These results are supported by studies that found evidence for competitively structured mammalian assemblages at large scale (Davies et al. 2007; Cooper et al. 2008) while more variable and context-dependent patterns in bird assemblages (Graham et al. 2009; Gomez et al. 2010). The weaker structuring of bird assemblages may be partly explained by the birds' higher mobility, which allows for functionally more heterogeneous local assemblages.

The Scaling of Functional Difference

Regional-local functional difference increases with increased scale discrepancy. However, when using the eco-

logical species pool as an intermediate step, we find that the SES of the ecological pool to local functional difference is consistently negative across scales (fig. 5). Previous analyses of functional and phylogenetic patterns over similar spatial scales have found conflicting results. Studies for birds, mammals, insects, and plants have uncovered assemblages that are functionally or phylogenetically overdispersed relative to the species pool (Cooper et al. 2008), are clustered (Freschet et al. 2011; Lessard et al. 2012), show no consistent pattern (Kamilar and Guidi 2010; Kooyman et al. 2011), or show both patterns (Graham et al. 2009; Gomez et al. 2010). Most of these studies do not separate the regional from constituent ecological pools, and hence the patterns represent the total effect of processes causing clustering and overdispersion. We show that this total effect, functional difference between the regional pool and local assemblage, is sensitive to the scales over which assemblages are defined (fig. 5). Hence, the lack of a general pattern emerging from these studies may reflect not only heterogeneous processes across studies and organisms but also the sensitivity of overall patterns to changes in spatial scale. By separately comparing the patterns between ecological pools and local assemblages, we here demonstrate that, for both birds and mammals, finescale assemblages form a predictable, nonrandom subset of assemblages at broader scales.

Estimating the Ecological Pool

We estimate the ecological pool by using the locally present trait combination of species. An alternative definition would use species preference for locally available type of habitat (Gerhold et al. 2008; Bartish et al. 2010), which has the advantage of directly accounting for environmental requirements. However, in practice, the required detailed environmental information and objective delineation of habitats make this approach challenging. In contrast, ecological pool estimation via locally present trait combinations is easy to implement and requires no environmental information.

Nevertheless, the utility of our approach as a proxy of the "true" ecological pool rests on several assumptions. First, the traits used should be relevant to the local survival of the species. When the traits selected are irrelevant to local environmental suitability, there should be no difference between locally and regionally present traits and the ecological pool will be overestimated. The more closely the traits quantify true axes of environmental limitation, the closer the estimated ecological pool will be to the true ecological pool. Thus, traits that quantify the physiological tolerance of species may capture the ecological pool more closely than the ecological traits used here.

Second, when using the convex hull approach to delin-

eate the ecological pool, we assume trait combinations suited to the local environment are clustered within the regional trait combinations and thus occupy a clearly defined portion of the regional trait space. However, there may be cases in which extreme trait combinations are suitable for the local environment, while intermediate trait combinations are not. This would also result in an overestimation of the ecological pool by the inclusion of species that would not persist locally. Gross overestimation of the ecological pool will result in little difference in richness and functional structure between the regional and ecological pools, as well as in patterns of ecological pool to local assemblage functional differences resembling those observed for regional to local comparisons. The strong trait differences observed here between the regional and ecological pools would suggest that even if some overestimation of the ecological pool has occurred, this was not enough to blur the ecological signals we were trying to detect.

Finally, when using the locally present species to define the ecological pool, we might exclude species with extreme trait combinations that could use the local environment but have been locally absent due to external processes or chance. This may spuriously increase patterns of functional difference between the regional and ecological pools. However, this should not bias patterns of functional difference between the ecological pool and local assemblages, as the estimated ecological pool is used as the basis for comparisons.

Conclusions

Our findings illustrate the differences in the trait makeup of communities from regional to local assemblages. We find that processes that result in high and low functional difference occur simultaneously over a wide range of scales. As these patterns may cancel each other out, estimating the total functional difference between regional and "local" assemblages may prevent the detection of strong trait filters. The recognition of these divergent community assembly processes requires the estimation of the appropriate ecological pool. In this study, we provide a readily implementable method to do so by using the observed species to define the locally suitable trait combinations. A similar approach could be applied to measures of functional diversity (e.g., Laliberte and Legendre 2010; Schleuter et al. 2010). By using this approach, we are able to show that functional difference between the regional pool and the ecological pool is similar in magnitude for birds and mammals and covaries with environmental conditions (fig. 4). In contrast, functional difference between the ecological pool and local assemblage is stronger in mammals than in birds. While this pattern, at least in mammals,

may be associated with restrictive assembly rules, we do not find evidence that its strength varies along environmental or latitudinal gradients. Future work will likely benefit from ecological pool estimates that invoke additional detailed data on, for example, species habitat preferences and habitat availability. This study supports the growing call for more ecological realism in the definition of regional pools (Lessard et al. 2012), which can then be used to better understand the influence of the regional functional and phylogenetic structure on local assemblages.
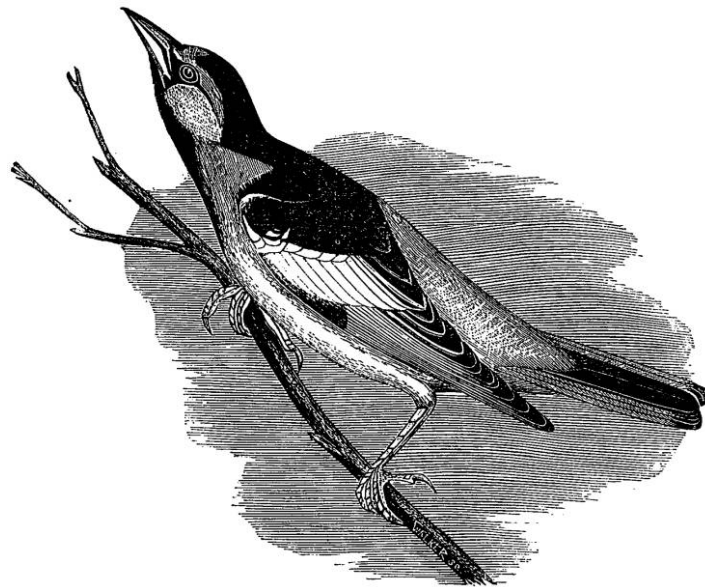
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Editor: Judith L. Bronstein

Bullock's Oriole.

"All the orioles are wonderful architects, weaving pensile nests of soft pliable fibrous substances with a nicety and beauty of finish that human art would vainly attempt to rival." From "Bullock's Oriole" by Elliott Coues (*American Naturalist*, 1871, 5:678–682).