

Regional Pools and Environmental Controls of Vertebrate Richness

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ABSTRACT: The species richness of local communities depends on the richness of the regional pool and the filtering processes that preclude some regional species from occurring locally. These filters may include absolute attributes of the local environment and also how representative the local environment is of the surrounding region. The latter is consistent with a species-sorting perspective, in which regional species only occupy the local habitats to which they are adapted. Here we evaluate the relative effects of local environmental conditions, environmental representativeness, and environment-independent processes on the probability of local species occurrence, given their regional presence, of birds, mammals, and amphibians worldwide. In multipredictor models, environmental representativeness is a strong independent predictor of local species occurrence probability, with a relative contribution greater than that of absolute local environmental conditions. Furthermore, we find that local occurrence probability diminishes with increased regional richness independent of the local environment. This is consistent with reduced local occupancy in richer regions, which is a pattern that could stem from a largely neutral community assembly process. Our results support the importance of both environment-independent and species-sorting processes and suggest that regional richness and environmental representativeness should be jointly used for understanding richness gradients across scales.

Keywords: species richness, scale, regional enrichment, environmental similarity, terrestrial vertebrates, species pool, range maps, biological inventories.

Introduction

The composition of local communities is intertwined with that of assemblages at broader spatial scales. It is striking that locations with similar conditions that are situated in separate regions frequently exhibit highly discrepant local species richness (Harrison and Cornell 2008). This attests to the influence of broadscale processes on local diversity (Ricklefs 2007; Cavender-Bares et al. 2009). Broadscale and

fine-scale processes may be reconciled by a hierarchical perspective of abiotic and biotic filters that control which species existing in the regional species pools appear in local assemblages (Zobel 1997; Rajaniemi et al. 2006; Algar et al. 2011). In this view, a combination of filtering strength and the size of the regional species pool ultimately determines local diversity.

Broadscale diversity patterns are increasingly being documented and analyzed using expert opinion range maps (Jetz and Rahbek 2002; Baillie et al. 2004; Schipper et al. 2008). However, range map reliability dramatically deteriorates below spatial grains of approximately 10,000 km² (Hurlbert and White 2005; Hurlbert and Jetz 2007). Therefore, substantial uncertainty remains for diversity estimates at finer grains where resources for surveys are often limited. An understanding of how regional richness combines with environmental filters to shape the occurrence of local species may provide critical help in advancing our geographic biodiversity knowledge.

Considerable effort has already been directed to understanding the contribution of regional processes to local richness by studying the shape of the association between local and regional richness (Cornell and Lawton 1992; Srivastava 1999; Hillebrand and Blenckner 2002; Karlson et al. 2004). A linear relationship was considered an indication of an overriding importance of regional processes, whereas a curvilinear relationship was interpreted as the outcome of strong local interactions. This interpretation has come under question, because curvilinear associations may form with no biotic interactions, whereas strong local interaction may not prevent a linear association (Arita and Rodriguez 2004; He et al. 2005; Hillebrand 2005; Belmaker et al. 2008). Therefore, recent studies have focused on understanding how environmental filters combine with the regional species pool to jointly determine finer-grained richness (Karlson and Cornell 1998; Harrison et al. 2006; White and Hurlbert 2010; Grace et al. 2011). Four major classes of hypotheses are currently put forward to explain

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the formation of local assemblages on the basis of their regional species pool and environmental filters.

The first view emphasizes local environmental conditions as regulators of community structure. In this case, the local environment determines what proportion of the regional species will appear at fine scales by altering the number of species that can locally coexist. In this view, habitat preferences of species in the pool are irrelevant for understanding filtering strength, which instead is limited by the capacity of the local environment to support species. For example, net primary productivity (NPP), which is an important correlate of terrestrial vertebrate richness (Hawkins et al. 2003; Storch et al. 2006; Belmaker and Jetz 2011), has been shown to remain an influential predictor of local richness of birds in North America even after accounting for regional richness (White and Hurlbert 2010). Higher productivity may increase overall local resources by increasing occupancy (Bonn et al. 2004), total density (the more individuals hypothesis; Hurlbert 2004; Evans et al. 2005), or local habitat heterogeneity (see view three below), thereby increasing the probability that a given species that is present regionally will also be present locally.

A second view on local-regional richness associations is that of species sorting (Leibold et al. 2004). This view is also at the heart of the species pool hypothesis (Zobel 1997), which states that the number of local species may largely reflect the regional availability of species capable of existing within the local habitat. To the extent that environmental niches are conserved (Wiens et al. 2010) and the spatial configuration of habitats within a region is heterogeneous, local species diversity might be determined more by the makeup of regional habitats and the large-scale processes that shape the habitat preferences of regional species than by any specific local environmental conditions (Harrison and Grace 2007; Partel et al. 2007; Ricklefs 2007). The role of species sorting in affecting the species diversity of a given location may be quantified by how representative local environmental conditions are for the whole region or, in other words, by the similarity between local environmental conditions (e.g., habitats and climatic niches) and the broader regional environments. A larger proportion of regional species may colonize a location if the location contains habitats that are similar to those found in much of the surrounding region. Conversely, fewer regional species may be able to colonize a local site if it is environmentally distinct from many other portions of the region (Herzog and Kessler 2006). To our knowledge, despite the strong connection between local-regional richness relationships and species turnover (Srivastava 1999; Loreau 2000; Sojininen et al. 2007), the usefulness of environmental representativeness (i.e., habitat turnover) for understanding cross-scale gradients of species richness has not been quantitatively assessed.

A third view emphasizes the importance of local habitat heterogeneity for increasing the probability that a species that is present regionally will also be present locally. Heterogeneity at the local scale combines elements from both the local environmental conditions and the species-sorting perspectives. On the one hand, increased local heterogeneity can increase the capacity of locations to support multiple species and is thus in line with the local environmental conditions perspective (Hillebrand and Blenckner 2002; Freestone and Harrison 2006; Questad and Foster 2008; Myers and Harms 2009). However, this increase is strongly related to the niche preferences among species in the regional pool and is thus in line with a species-sorting perspective (Questad and Foster 2008). We will therefore treat local heterogeneity separately, with its effect supporting both local environmental filtering and a species-sorting perspective.

The final hypothesis assumes environment-independent community assembly processes. A major environment-independent theory is the neutral theory of biodiversity, which downplays any difference between species in habitat preferences or competitive abilities (Hubbell 2001). Under the neutral view, the total regional number of individuals of all species is limited (the zero-sum assumption), and hence larger regional richness must be associated with a decrease in range size or local occupancy of constituent species. This will cause a curvilinear relationship between local and regional richness (Arita and Rodriguez 2004). Consequently, a decrease in local species occurrence probabilities towards higher regional richness may support neutral community assembly or other processes that cause smaller ranges in richer regions (Stevens 1989) as well as local interactions that limit local richness.

In this study, we use worldwide data from 294 extensively sampled terrestrial vertebrate assemblages and their broader surrounding areas to evaluate the relative importance of local environmental conditions (productivity and heterogeneity), local environmental representativeness, and regional richness to the probability of species' local occurrence given their presence in the regional pool. The global scale of the analysis ensures maximal biological independence of study units and generality of results. This novel framework allows us to estimate the contribution of local environmental filters, species sorting, and environment-independent processes to community assembly. The importance of different community assembly processes may be context dependent. For example, local assemblages may display anomalous patterns of impoverishment relative to the species pool for unique local reasons, such as local disturbance, fine-scale habitat degradation, or extreme isolation. We assess this context dependence by examining how the relationships between specific predictors and local occurrence probability change

across regression percentiles (i.e., how they are different between assemblages with low vs. high occurrence probability). The study's integrative approach and broad scope aim to help bridge between macroecological and finer-grain perspectives on community assembly.

Methods

Local and Regional Species Lists

We use species inventories to assess local richness and expert opinion range maps to estimate regional richness (Stevens and Willig 2002; Hortal et al. 2008; White and Hurlbert 2010; Belmaker and Jetz 2011). Regional richness was estimated from the intersection of extent-of-occurrence range maps with 100-km radius circles around assemblage location centroids, a scale at which diversification and historical processes are likely to be prominent. We considered a 100-km radius (i.e., a 31,400-km² area) as a methodologically necessary minimum area to define regional richness, because global expert range maps for vertebrates have been shown to be prone to increasing levels of false presence at grain sizes below 200-km quadratic grids (Hurlbert and Jetz 2007). We repeated the analyses for regions with a 200-km radius, but results were extremely similar (fig. A1, available online), and for brevity, only 100-km results are presented. We included all birds (breeding ranges only), all terrestrial nonvolant mammals, and all amphibians (resulting in a total of 7,241, 3,573, and 2,881 species at a 100-km radius grain, respectively). Range maps were based on the International Union for Conservation of Nature assessment (<http://www.iucnredlist.org/>) for mammals (Schipper et al. 2008) and amphibians (Baillie et al. 2004; Buckley and Jetz 2008). Distributions for birds were compiled from the best available sources for a given broad geographical region or taxonomic group (Jetz et al. 2007).

The determination of what spatial extent may represent an actual local assemblage or community is dependent on the preferred definition of these terms (Ricklefs 2008). Without knowledge about the spatial scale of the interactions of its members, the threshold areal extent of a "local" community is hard to define. For the purpose of this study, and in line with other recent work analyzing the North American Breeding Bird Survey data at the scale of a circle with a radius of 40 km (White and Hurlbert 2010), we consider the median size of 411 km² (equivalent to a circle with ~11.5-km radius or 20-km quadratic grid cell grain) as local for terrestrial vertebrates. It is at these scales that the knowledge gap between actual community composition and macroecological data occurs (Hurlbert and White 2005; Hurlbert and Jetz 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 which were protected areas (Meese 2005; Belmaker and Jetz 2011). 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 that were not found at the regional scale. For birds, this procedure was indispensable, because inventories include many vagrant and even pure fly-over nonbreeding species. For mammals and amphibians, a large proportion of the species were retained (mean proportion \pm SE, 0.82 ± 0.01 for mammals and 0.86 ± 0.01 for amphibians), and results were similar when these species were not excluded. We identified the geographic boundaries of these locations on the basis of the 2009 annual release of the World Database on Protected Areas (<http://www.wdpa.org>) or digital gazetteers, and we manually checked and edited placement. We only used assemblages covering areas between 10 and 7,875 km² (median area, 411 km²), with four additional larger assemblages (8,283–21,577 km²) added in underrepresented regions (including two in Amazonia, three in Siberia, and one in West Africa). In the absence of globally standardized vertebrate inventories, varying area sizes are the only way to ensure environmentally and geographically representative coverage. In total, we used 294 assemblages with data on all three taxa (data deposited at Dryad; doi:10.5061/dryad.cr5751br).

Variation in the area of local assemblages was partially addressed by including area as a covariate in analyses (see "Statistical Analyses"). Although this is a common procedure, it implicitly assumes that the influence of area does not vary substantially along geographical and environmental gradients. In support, we found no interactions between area and other environmental variables when explaining the ratio of local to regional richness ($P > .05$ for all variables and taxa). Moreover, local assemblage area did not differ substantially among realms (fig. A2, available online), and we found low correlation between local area and productivity ($r = -0.12$, $P = .19$), negating the possibility that analyses are confounded by large localities being restricted to low-productivity regions. Importantly, the results remained qualitatively unchanged when the analysis was restricted to the middle 50% of assemblage area quantiles (108–1,429 km²; fig. A1, available online).

Local Environmental Conditions

We quantified two aspects of the local environment that are strongly related to a location's capacity to support coexisting species: productivity and habitat heterogeneity.

Productivity has been commonly used as a proxy for local carrying capacity and is used here as a sole local environmental filter. Annual NPP ($\text{kg C} \times \text{m}^{-2} \times \text{year}^{-1} \times 0.0001$) at 1-km resolution, averaged over the years 2000 through 2006, was obtained from <http://www.ntsg.emt.edu> on the basis of the National Air and Space Administration Earth Observatory System Moderate Resolution Imaging Spectroradiometer and calculated using the MOD17 algorithm. As measures of location-wide potential habitat heterogeneity, we used its area (*Area*, measured in km^2), the number of distinct land cover types (*HabVar*), and the elevation range (*ElRange*, maximum–minimum elevation in meters). Land cover types were extracted from the United States Geological Survey Global Land Cover Characterization (<http://edc2.usgs.gov/glcc/>), which separates vegetation globally into 96 classes at 1-km resolution. A global 30" digital elevation model was used to calculate elevation range.

Local Environmental Representativeness

The proportion of the regional area that contains the values found at the local scale was used to estimate how extensively environmental conditions at a given location represent those of a region. The larger the discrepancy, the higher the proportion of species that may not occur locally because of mismatch between environmental affinity and local habitat availability. Representativeness in habitat (*simHab*), elevation (*simElv*), and productivity (*simNPP*) intuitively quantifies the relative area within the region that contains habitats from which species can potentially invade a local assemblage. For *simElv* and *simNPP*, both local and regional data were binned into 100-unit groups before the proportion was calculated (the effect of different groupings on results was negligible). Conventional symmetric distance or (dis)similarity indices are not appropriate for calculating environmental representativeness between scales because (1) the local and regional environments are nested, (2) the discrepancy in size between the local and regional scales is large, and (3) we a priori assume asymmetry (i.e., species from the regional pool dispersing into local assemblages). Circumventing these problems, we also calculated the multivariate Mahalanobis environmental distance between the local scale and equal area grids (27-km quadratic grid cell grain at the equator) at the regional scale using a suite of environmental predictors (elevation, productivity, annual precipitation, temperature, coefficient of variation in precipitation, and proportional habitat categories). Because this did not increase the total predictive power of the models and necessitated a loss of information on individual predictors, we do not present these results.

Data Subsetting

The local assemblages captured a reasonable amount of global climate space but were not distributed evenly and tended to undersample extreme environmental combinations (Belmaker and Jetz 2011). To minimize potential bias caused by uneven sampling, we subset the data before all analysis by randomly selecting a maximum of two points within a 5° cell (approximately 550 × 550 km near the equator).

Statistical Analyses

When assemblages are small enough to enable abundance estimates, the observed local-regional relationship can be compared to predictions derived from null models (e.g., randomly sampling individuals from the regional pool; Rajaniemi et al. 2006; Belmaker et al. 2008; Chase and Myers 2011; Kraft et al. 2011) or more mechanistic models in which the relationship between local and regional richness is estimated from local scale parameters (Harte et al. 2009; O'Dwyer and Green 2010). However, at broader scales, abundance estimates are lacking, making these approaches currently nonfeasible for large taxonomic groups and broad extents. Hence, we focus on quantifying the strength of effects driving the empirical association between local and regional richness (Karlson and Cornell 1998; Harrison et al. 2006; Qian et al. 2007; Passy 2009; White and Hurlbert 2010).

We used quasi-binomial generalized linear models (GLMs) with a logit link function to quantify the degree to which local richness deviated from that expected on the basis of the regional species pool. Thus, the response was composed of local richness (successes) and regional-local richness (failures). By using the quasi-binomial model, we essentially model the probability of local species occurrence given their regional presence. This procedure remedies the statistical problems associated with local-regional regressions in which the bounded nature of local richness (it is limited by regional richness) may invalidate the assumptions of GLMs. Moreover, this framework provides a formal statistical means to estimate curvature (i.e., deviations from proportional sampling) in the local-regional relationship by using regional richness as an additional predictor. A negative effect for regional richness corresponds to lower local occurrence probabilities in richer regions and hence to a curvilinear local-to-regional relationship.

Productivity, heterogeneity, and regional richness (SR) were \log_{10} transformed before analyses, because this was found to improve the normality of the residuals and reduce heteroscedasticity. Environmental representativeness predictors were bound between 0 and 1 and were therefore

logit transformed. To account for nonlinear associations with NPP even after appropriate transformation, NPP^2 ($[\log_{10} \text{untransformed NPP}]^2$) was used as an additional predictor. No evidence for nonlinearity was detected in any other predictor (including regional richness).

We divided all predictors into one of the following four groups: (1) regional richness (*SR*), (2) productivity (*NPP* and NPP^2), (3) heterogeneity (*Area*, *HabVar*, and *ElRange*), and (4) environmental representativeness (*SimHab*, *SimElv*, and *SimNPP*). We first selected the combination of predictors within each of the last three groups (productivity, heterogeneity, and representativeness) that, together with regional richness, provided the lowest quasi Akaike Information Criterion (qAIC) value (Burnham and Anderson 2002; table A1, available online). Because of the anticipated strong effect of *Area*, we always retained this predictor in the heterogeneity group. When $\Delta qAIC < 1$, we retained the fuller model (i.e., the model with more predictors). After establishing the best model within each group, we combined all groups to create an additive model that considered all three predictor groups. For each taxon, a limited number of assemblages (<8) were excluded at this stage if they demonstrated high leverage (Cook statistic >1). However, the results were similar when these assemblages were retained.

We used hierarchical partitioning to assess the relative importance of predictors (Murray and Conner 2009). Here, the average contribution of regional richness, heterogeneity, productivity, and representativeness predictors to the variance in the response is assessed over all possible models, thus allowing the variance shared by correlated predictors to be partitioned into the variance attributable to each predictor group. Null expectations were generated by randomizing all elements within each predictor and calculating relative importance values. This procedure was repeated 200 times to obtain a population of null values. All analyses were performed in the computer program R (R Development Core Team 2008). For hierarchical partitioning, we modified the code present in the R package “hier.part” to accommodate quasi-binomial models.

To quantify context dependence in local occurrence probabilities, we use quantile regressions, which examine how predictor estimates change as a function of the specific percentiles in the response variable. Quantile regressions estimate multiple associations between the predictors and the response variable (a relationship for each percentile of the response variable). We consider the upper percentiles of the response variable, where the effect of unmeasured limiting factors is minimal (Cade and Noon 2003), to be particularly revealing. Specifically, in our analyses, quantile regressions allow us to examine whether assemblages with high local occurrence probabilities (high regression percentiles) display distinct associations, compared with as-

semblages with low occurrence probabilities (low regression percentiles), which may be species-poor because of unique unmeasured local processes. We use quantile binomial regression, which is similar to ordinary quantile regression but is designed to operate with binomial response variables. Quantile binomial regressions were performed using asymmetric likelihood in the package “VGAM.”

Results

Despite ~10-fold variation in local and regional richness, all taxa display qualitatively similar local-to-regional richness associations (fig. 1). We first examine the contribution of regional richness, local environmental conditions (productivity and heterogeneity), and local environmental representativeness to the local species occurrence probabilities using quasi-binomial multipredictor regression models (table 1). Regional richness emerges as a prime predictor with large negative coefficients, indicating that the proportion of regional species locally present decreases toward regions with more species. As predicted, productivity is positively related to local occurrence probabilities. Among the heterogeneity predictors, *ElRange* displays negative coefficients for all taxa. Hence, more topographically complex localities contain a lower proportion of the regional

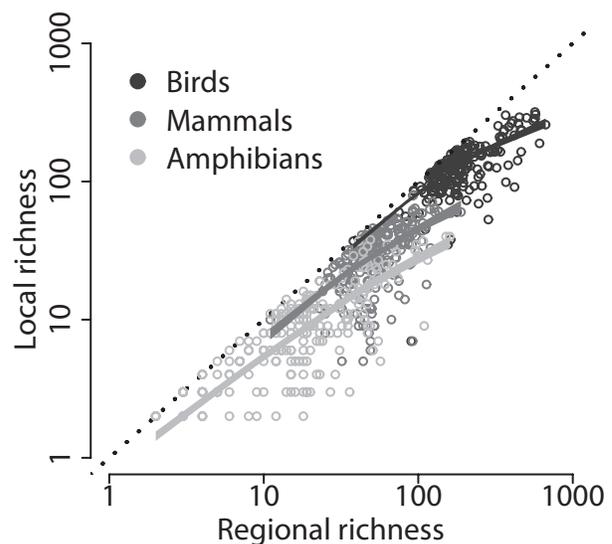


Figure 1: The observed relationship between local and regional richness for the 3×294 assemblages analyzed. Solid polygons are best-fit predictions ± 1 SE, derived from quasi-binomial generalized linear models including all selected predictors (see table 1). The dotted line represents richness equivalency. Note the log transformation of the axes. In this study, we analyze this relationship using the ratio of local to regional species richness as response.

Table 1: Multipredictor quasi-binomial generalized linear models with regional richness and three sets of environmental variables as predictors of the probability of local occurrence given regional presence

Group, predictor	Birds		Mammals		Amphibians	
	Coefficient (SE)	<i>t</i> value (<i>P</i>)	Coefficient (SE)	<i>t</i> value (<i>P</i>)	Coefficient (SE)	<i>t</i> value (<i>P</i>)
Regional richness:						
<i>Intercept</i>	-1.36 (5.13)	-.3 (.79)	-11.6 (4.2)	-2.7 (<.01)	-4.91 (5.10)	-.1 (.33)
<i>SR</i>	-2.12 (.32)	-6.6 (<.001)	-1.20 (.32)	-3.8 (<.001)	-1.26 (.21)	-5.8 (<.001)
Heterogeneity:						
<i>Area</i>	.00 (.11)	.0 (.98)	-.04 (.12)	-.3 (.76)	.11 (.11)	1.1 (.29)
<i>ElRange</i>	-.24 (.08)	-2.8 (<.01)	-.04 (.08)	-.5(.62)	-.22 (.07)	-3.0 (<.01)
<i>HabVar</i>	.32 (.32)	.1 (.32)	.21 (.30)	.7 (.48)	NA	NA
Productivity:						
<i>NPP</i>	4.32 (2.82)	1.5 (.12)	7.70 (2.37)	3.2 (<.01)	3.43 (2.78)	1.2 (.22)
<i>NPP</i> ²	-.63 (.40)	-1.6 (.11)	-1.01 (0.34)	-3.3 (<.01)	-.45 (.39)	-1.2 (.24)
Representativeness:						
<i>simElv</i>	.07 (.03)	2.7 (<.01)	.07 (.03)	2.9 (<.01)	.08 (.03)	2.9 (<.01)
<i>simHab</i>	NA	NA	NA	NA	.03 (.04)	.8 (.41)
<i>simNPP</i>	NA	NA	.06 (.04)	1.7 (.09)	NA	NA
Summary	<i>R</i> ² = .41		<i>R</i> ² = .26		<i>R</i> ² = .32	

Note: For each predictor group (regional richness, heterogeneity, productivity, and representativeness), we chose the best combination of variables based on the quasi Akaike Information Criterion values (see text for details). Models include all selected predictors (those not selected are marked as not applicable [NA]). Significant ($P < .05$) relationships are shown in boldface type. *Area* = area in km²; *ElRange* = elevation range in meters; *HabVar* = number of distinct land cover types; *NPP* = net primary productivity; *simElv* = similarity in elevation; *simHab* = similarity in habitat; *simNPP* = similarity in productivity; *SR*, regional richness.

richness. Somewhat surprisingly, the coefficients for *Area* are very close to zero in all three taxa. Local environmental representativeness exhibits consistently positive coefficients on local occurrence probability. This means localities that contain habitats similar to those found in the region tend to capture relatively more of the regional richness. The total amount of variance explained by combining all predictors was generally reasonable to good ($R^2 = 0.41$ for birds, $R^2 = 0.26$ for mammals, and $R^2 = 0.32$ for amphibians; table 1). Nevertheless, for all three taxa, substantial variation in the local occurrence probability remains unexplained.

We use hierarchical partitioning of these quasi-binomial multipredictor models to further quantify the relative importance of regional richness, productivity, heterogeneity, and environmental representativeness (fig. 2). For all taxa, regional richness emerges as a prime independent predictor ($R^2 = 0.24$ for birds, $R^2 = 0.07$ for mammals, and $R^2 = 0.14$ for amphibians). However, environmental representativeness explains a substantial independent portion of the variance, especially for mammals and amphibians ($R^2 = 0.06$ for birds, $R^2 = 0.09$ for mammals, and $R^2 = 0.09$ for amphibians). Local heterogeneity ($R^2 = 0.07$ for birds, $R^2 = 0.03$ for mammals, and $R^2 = 0.05$ for amphibians), and productivity ($R^2 = 0.06$ for birds, $R^2 = 0.05$ for mammals, and $R^2 = 0.05$ for amphibians) explain only a small amount of variance for all taxa.

Finally, within multipredictor models, we examine how

predictor strengths change across regression percentiles, examining assemblages with increasingly high local occurrence probabilities (fig. 3). We find that the effect of regional richness becomes increasingly negative at high regression percentiles. Thus, although local occurrence probabilities decrease with regional richness at all percentiles, this effect is strongest for assemblages that have high residual local occurrence probabilities. Coefficients for heterogeneity and productivity generally increase towards higher percentiles. In contrast, environmental representativeness coefficients change in an inconsistent manner across percentiles. The total predictive power of the model increased substantially with increased percentiles (fig. 3). This means that the ability to correctly predict local richness given regional richness is greatest in assemblages that have high probabilities of local occurrence.

Discussion

Ecologists have long desired to quantify how processes at various scales combine to affect species diversity. The local-regional richness relationship has provided a powerful framework for demonstrating the local-scale importance of regional processes (Harrison and Cornell 2008). However, the direct use of the local-regional regression alone for understanding community assembly is limited, because the shape of this relationship is influenced by many processes (Hillebrand and Blenckner 2002; Arita and Rodri-

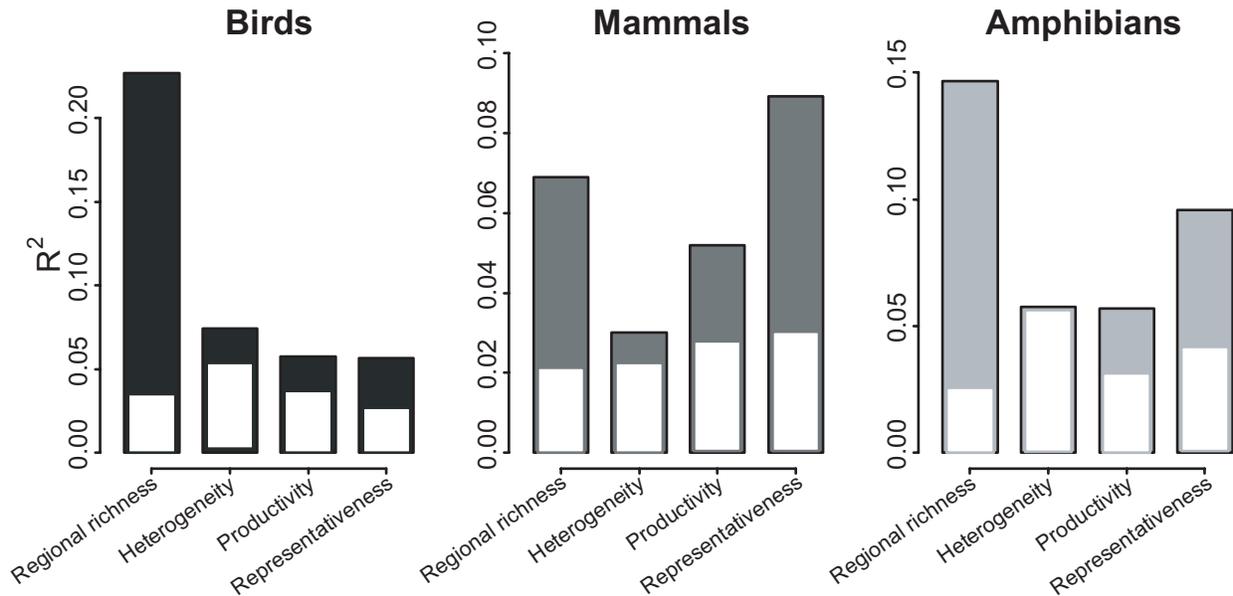


Figure 2: The relative importance of environmental predictor groups in quasi-binomial generalized linear models predicting local occurrence given regional presence (i.e., the ratio of local to regional species richness). Term R^2 is decomposed using hierarchical partitioning to the independent contributions of regional richness, heterogeneity (*Area*, *HabVar*, and *ElRange*), productivity (*NPP* and *NPP²*), and representativeness (*simHab*, *simElv*, and *simNPP*). The identity of the predictors used within each predictor group varies slightly among taxa according to the results of the model selection procedure (see table 1). Empty bars encompass 95% of the null relative importance values estimated from random permutation of all elements within each predictor. Thus, observed values (shaded bars) higher than the null expectation (empty bars) represent relative importance significantly larger than random.

guez 2004; He et al. 2005; Hillebrand 2005; Belmaker et al. 2008). To circumvent this problem, we here focus on identifying the relative importance of regional richness, local environmental conditions, and environmental representativeness to the probability of species' local occurrence, given their regional presence.

Focusing on local occurrence probabilities with a quasi-binomial GLM approach, instead of directly regressing local on regional richness, remedies the statistical problems associated with the bounded nature of local richness and provides a formal statistical method to estimate deviations from proportional sampling (i.e., to detect curvilinear local-regional relationships). Large influences of local environmental conditions would indicate a strong response to environmental gradients that is shared by many species. Prominence of environmental representativeness would point to the importance of relative rather than absolute environment and thus to species sorting as a major determinant of local community structure. Finally, a large and negative contribution of regional richness would suggest a curvilinear local-regional relationship and environment-independent community assembly. Our findings reveal strong support for the latter two hypotheses, because we find strong influences of both regional

richness and environmental representativeness on local occurrence probabilities.

The relationship between local and regional richness is directly connected to species turnover, because lower local richness with similar values of regional richness necessitates higher spatial species turnover (Srivastava 1999; Loreau 2000). Because species turnover is tied to species identity, the relationship between local and regional richness transcends hypotheses pertaining to richness gradients alone and is closely associated with understanding spatial patterns of species composition (Qian et al. 2005; Buckley and Jetz 2008). Thus, in this study, we essentially use richness gradients to address questions related to community composition, bearing in mind that determinants of species richness and species composition may be different (Algar et al. 2009).

We find that regional richness was a strong predictor of local occurrence probability in all three taxa (birds, mammals, and amphibians; fig. 2). The coefficients are negative, indicating curvilinear local-regional relationships with relatively lower levels of local richness in high-richness regions. The dependence of local occurrence probability on regional richness is consistent with a decrease in range sizes or local occupancy with increased regional richness.

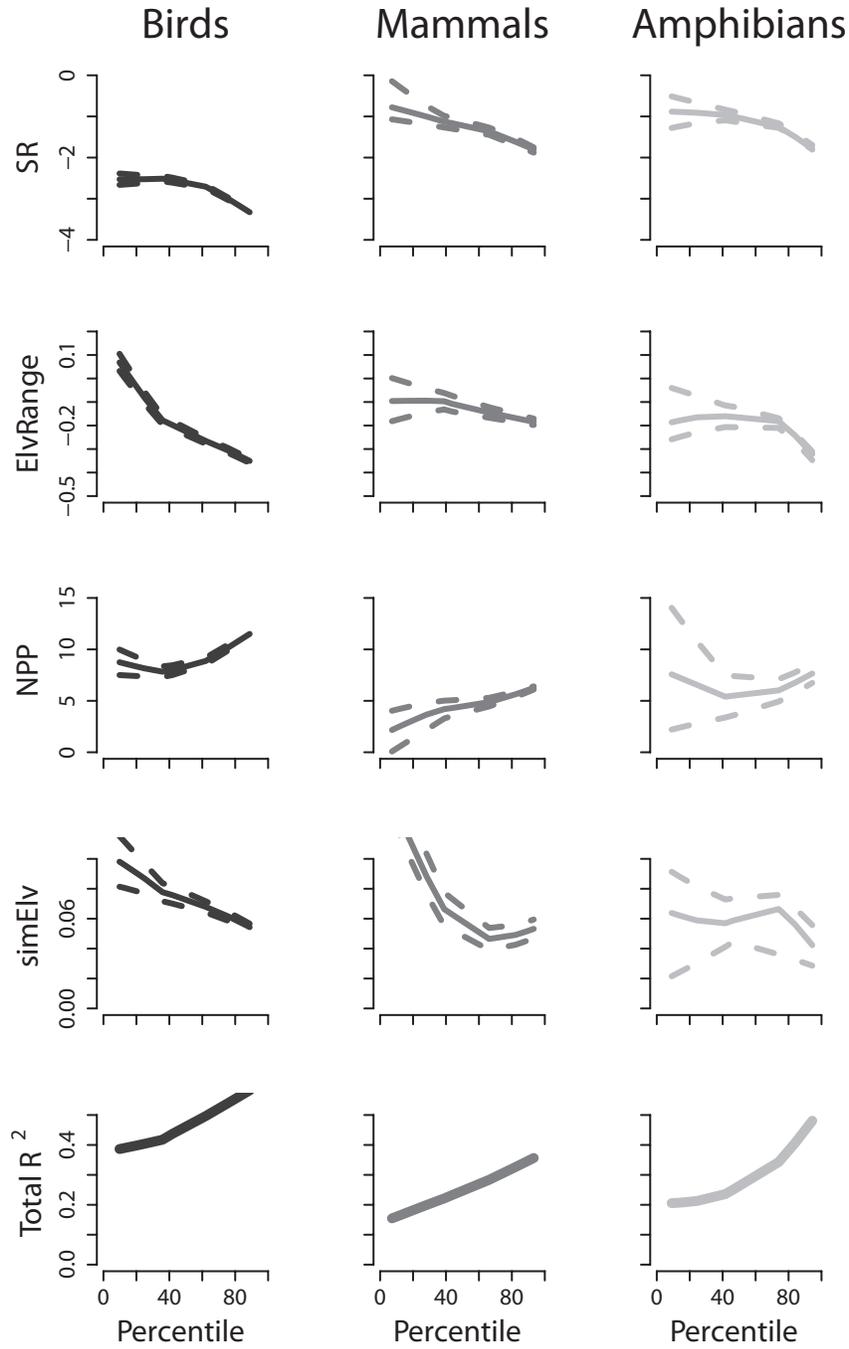


Figure 3: The change in the estimated relationships between environmental predictors and local occurrence probability (the ratio of local to regional species richness) as a function of regression percentile. A binomial quantile regression was used with a logit link function. The multipredictor models were constructed with all selected variables (see table 1), but only one predictor within each group (regional richness [SR], heterogeneity, productivity, and representativeness; based on the highest relative importance) is shown. The solid line represents estimated coefficients, and dashed lines encompass the coefficients ± 1 SE. The bottom panels depict the total R^2 of the models as a function of the percentile examined.

This supports the general observation of smaller species ranges in tropical regions (which are usually more species-rich) than in temperate regions (Stevens 1989), accompanied by lower local-to-regional richness ratios (Soininen et al. 2007; Freestone and Osman 2011) and higher species turnover (Stevens and Willig 2002; Buckley and Jetz 2008; Qian et al. 2009). Importantly, because the contribution of regional richness was independent of environment, this pattern cannot be explained by higher habitat heterogeneity in richer regions. Thus, we find patterns that are consistent with a largely environmentally independent community assembly process.

Several underlying processes can lead to environmentally independent reduced local occurrence probabilities in richer regions, including local limitation on richness or abundance (e.g., by species interactions; Cornell and Lawton 1992) and dispersal limitation (He et al. 2005). For example, ecological specialization often positively covaries with regional richness (MacArthur 1972; Jocque et al. 2010; Belmaker et al. 2012). Because specialization may be associated with reduced range size and lower local occupancy (Jetz et al. 2008; Jocque et al. 2010), an overall latitudinal gradient in range size may be produced (Stevens 1989). Here, dispersal limitation, which causes the reduced local occurrence probabilities in richer regions, is introduced through the limitation on range size (Arita and Rodriguez 2004). Although causes of the possible covariance between regional richness and range-size or occupancy were not examined here, our results suggest that much of this relationship is generally independent of productivity, heterogeneity, and environmental representativeness. As with all observational data, these conclusions are contingent on the quality of the underlying data. It is possible that the incorporation of better environmental variables may boost model performance. Such improvements are likely to reduce the unexplained variance, but they may also reduce the amount of the environmentally independent variance attributed to regional richness.

We find that local environmental representativeness strongly influences local occurrence probabilities, particularly for amphibians and mammals (fig. 2). In contrast, local productivity or heterogeneity predictors explained relatively little. This supports the additional operation of species sorting, in which habitat suitability determines the local presence of species (Leibold et al. 2004). Because of the close connection between local-regional richness relationship and turnover (Srivastava 1999; Loreau 2000; Belmaker et al. 2008), it is somewhat surprising that environmental representativeness has not been directly assessed in this context. We suggest that cross-scale measures of environmental representativeness are hitherto underappreciated yet critical predictors of fine-scale community structure, given regional pools.

We note that, with the presented approach, it is difficult to distinguish regional-to-local from local-to-regional influences. For example, when environmental representativeness is high, regional species will be adapted to the prevailing conditions in the region, thus allowing them to occupy local habitats. However, an equally plausible explanation may be that the region is composed of many communities that are similar to the local one, so that the local species also dominate the regional species pool. Although all local-regional patterns can be interpreted from both a bottom-up and top-down perspective, this does not impede the use of this conceptual framework.

Productivity can influence patterns of diversity both at regional (Hawkins et al. 2003; Storch et al. 2006; Belmaker and Jetz 2011) and local (Chase 2010) scales. If similar mechanisms influence local and regional richness, we would expect local occurrence probabilities to be independent of productivity. On the other hand, increased occurrence probabilities with increased local productivity will suggest a distinct mechanism by which productivity influences richness at local scales. In this study, productivity does not emerge as an important environmental filter (fig. 2). Thus, it seems that local productivity does not have a strong influence on local richness that is independent of regional richness gradients. This contrasts with a previous study of North American birds (White and Hurlbert 2010). A likely explanation for this discrepancy is that, in our study, local assemblages are a product of long-term compilation efforts and careful exclusion of transient species, both of which will tend to accentuate regional influence at the expense of local environmental gradients (Belmaker 2009; White et al. 2010). This emphasizes that the perceived importance of different community assembly processes may depend on both the temporal scale and the taxonomic scope (i.e., which species are included) of the study.

The generally weak influence of productivity and heterogeneity on local occurrence probabilities is consistent with other observational studies (Karlson et al. 2004; Freestone and Harrison 2006) but seems to clash with predictions that regional influences should depend on the local environmental conditions (Huston 1999). How are our results reconciled with smaller-scale and experimental studies that often find community assembly processes to be moderated by local habitat attributes (Chase 2007; Starzomski et al. 2008; Myers and Harms 2009; Chase 2010)? Our findings suggest that the key may lie in the degree of similarity between the local and regional scales. When environmental representativeness is high, more of the regional species will be adapted to a particular local environment (or, conversely, the region may be composed of many communities that are similar to the local one, so those local species dominate the regional pool). Here,

community assembly processes will depend on local environmental conditions (Huston 1999), which will tend to influence all species in a similar way. However, when the local environment is decoupled from the prevailing regional conditions (i.e., when environmental representativeness is low), community assembly will depend more strongly on the particular habitat affinities of species in the pool (Belmaker 2009). Species will respond idiosyncratically to habitats and environmental gradients, and consequently local environmental conditions will have little explanatory power. A decoupling of local and regional environments is much less likely in small-scale manipulated experiments, compared with broadscale observational studies in which high levels of environmental heterogeneity prevail. As a consequence, environmental representativeness, rather than local conditions per se, may be expected to emerge as the more dominant predictor of community assembly in observational studies.

To quantify possible context dependence in the determinants of local occurrence probability, we examine how patterns change across regression percentiles, thus examining assemblages with different local-regional richness associations. We find that, for all taxa, coefficients for regional richness become more negative at higher percentiles (fig. 3). This suggests that the decrease in occurrence probabilities towards increased regional richness is not simply a product of undersampling local richness (Cornell et al. 2008). Such undersampling would result in more negative coefficients (higher curvature of the local-regional regression) in assemblages that are sampled less intensively and hence belong to lower occurrence probability percentiles. In contrast, the observed decrease in the strength of regional richness at lower percentiles, and hence relatively low local-regional richness ratios, can result from unique local processes obscuring the strong influence of regional richness. These processes may include local disturbances (e.g., hunting and emergent pathogens) or extreme isolation (which reduces immigration rates). At high regression percentiles, which focus on assemblages with higher local occurrence probabilities and thus may not be limited by these local processes, the strong influence of regional richness becomes more apparent.

In addition, we find an increase in the total variance explained by the models at higher regression percentiles (fig. 3). Thus, it is possible to better predict the local richness of assemblages of higher local occurrence probabilities. If our above interpretation is true and local processes tend to depress the predictive power at lower regression percentiles, then focusing on assemblages with higher occurrence probabilities will allow prediction of richness values independent of local dampening effects. Therefore, given regional richness values and environmental conditions, even models with moderate explana-

tory power (in this study, total R^2 varies between 0.26 and 0.41) may provide valuable estimates of maximum local richness when focusing on high regression percentiles.

The relative importance of regional richness, local environment, and environmental representativeness will be contingent on the method for quantifying regional richness (Lessard et al. 2011). Some have argued that regional species pools should be based only on the species that can inhabit the study site (Zobel 1997). From a practical perspective, constructing a restricted species pool is challenging, because it requires explicit knowledge as to whether each species in the region can or cannot inhabit a particular local site. Our approach avoids such categorization of species by using environmental representativeness in a way that does not require data on individual species. More importantly, restricting the species pool does not allow for the quantification of the processes that shape the size of the restricted species pool relative to all species capable of dispersing into a local site. Naturally, for restricted species pools, the importance of environmental representativeness, and thus species sorting, will be minimal, because most species will be able to occupy the local habitat. Broad-scale habitat preferences are increasingly evoked as major determinants of local richness patterns (Harrison and Grace 2007; Partel et al. 2007). Thus, to understand the relative importance of broad-scale and local processes for a given group, we find it necessary to include all species that can potentially disperse into the local assemblage, regardless of their habitat preference.

Understanding the relative influences of regional richness and environment on local occurrence probabilities has direct applied implications (e.g., for attempts to estimate local diversity of yet unsurveyed locations of conservation concern). We here demonstrate how well regional estimates of richness, based on expert range maps that are only accurate at coarse grains, may provide useful estimates of local richness. Our findings quantify the uncertainty of such predictions across taxa and highlight how simple environmental models may improve estimates. Regional richness combined with measure of environmental representativeness enables reasonably useful probabilistic estimates of local richness. These estimates are substantially improved when examining assemblage with higher local occurrence probabilities (fig. 3). We expect that future work making use of ever more detailed global remote sensing data will enable yet stronger fine-scale predictions of richness. In the face of rapid environmental change and limited biodiversity knowledge, we see a vital use for extending local-regional studies in ecology to broader scales where abundance data is usually lacking and the scope for manipulations is limited, yet conservation needs are strong.

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Literature Cited

- Algar, A. C., J. T. Kerr, and D. J. Currie. 2009. Evolutionary constraints on regional faunas: whom, but not how many. *Ecology Letters* 12: 57–65.
- . 2011. Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. *Ecology* 92:903–914.
- Arita, H. T., and P. Rodriguez. 2004. Local-regional relationships and the geographical distribution of species. *Global Ecology and Biogeography* 13:15–21.
- Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart. 2004. IUCN Red List of threatened species: a global species assessment. IUCN, Cambridge.
- Belmaker, J. 2009. Species richness of resident and transient coral-dwelling fish responds differentially to regional diversity. *Global Ecology and Biogeography* 18:426–436.
- Belmaker, J., and W. Jetz. 2011. Cross-scale variation in species richness-environment associations. *Global Ecology and Biogeography* 20:464–474.
- Belmaker, J., Y. Ziv, N. Shashar, and S. R. Connolly. 2008. Regional variation in the hierarchical partitioning of diversity in coral-dwelling fishes. *Ecology* 89:2829–2840.
- Belmaker, J., C. H. Sekercioglu, and W. Jetz. 2012. Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography* 39:193–203.
- Bonn, A., D. Storch, and K. J. Gaston. 2004. Structure of the species-energy relationship. *Proceedings of the Royal Society B: Biological Sciences* 271:1685–1691.
- Buckley, L. B., and W. Jetz. 2008. Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences of the USA* 105:17836–17841.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer, New York.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12:693–715.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the USA* 104:17430–17434.
- . 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388–1391.
- Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351–2363.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61: 1–12.
- Cornell, H. V., R. H. Karlson, and T. P. Hughes. 2008. Local-regional species richness relationships are linear at very small to large scales in west-central Pacific corals. *Coral Reefs* 27:145–151.
- Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* 80:1–25.
- Freestone, A. L., and S. Harrison. 2006. Regional enrichment of local assemblages is robust to variation in local productivity, abiotic gradients, and heterogeneity. *Ecology Letters* 9:95–102.
- Freestone, A. L., and R. W. Osman. 2011. Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. *Ecology* 92:208–217.
- Grace, J. B., S. Harrison, and E. I. Damschen. 2011. Local richness along gradients in the Siskiyou herb flora: R. H. Whittaker revisited. *Ecology* 92:108–120.
- Harrison, S., and H. Cornell. 2008. Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11: 969–979.
- Harrison, S., and J. B. Grace. 2007. Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *American Naturalist* 170(suppl.):S5–S15.
- Harrison, S., H. D. Safford, J. B. Grace, J. H. Viers, and K. F. Davies. 2006. Regional and local species richness in an insular environment: serpentine plants in California. *Ecological Monographs* 76:41–56.
- Harte, J., A. B. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species-area curve. *Ecology Letters* 12:789–797.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guegan, D. M. Kaufman, J. T. Kerr, et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- He, F. L., K. J. Gaston, E. F. Connor, and D. S. Srivastava. 2005. The local-regional relationship: Immigration, extinction, and scale. *Ecology* 86:360–365.
- Herzog, S. K., and M. Kessler. 2006. Local vs. regional control on species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography* 15:163–172.
- Hillebrand, H. 2005. Regressions of local on regional diversity do not reflect the importance of local interactions or saturation of local diversity. *Oikos* 110:195–198.
- Hillebrand, H., and T. Blenckner. 2002. Regional and local impact on species diversity: from pattern to processes. *Oecologia (Berlin)* 132: 479–491.
- Hortal, J., J. Rodriguez, M. Nieto-Diaz, and J. M. Lobo. 2008. Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography* 35:1202–1214.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- Hurlbert, A. H. 2004. Species-energy relationships and habitat complexity in bird communities. *Ecology Letters* 7:714–720.
- Hurlbert, A. H., and W. Jetz. 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the USA* 104:13384–13389.
- Hurlbert, A. H., and E. P. White. 2005. Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters* 8:319–327.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate

- scales for understanding variation in the diversity of plants and animals. *Oikos* 86:393–401.
- Jetz, W., and C. Rahbek. 2002. Geographic range size and determinants of avian species richness. *Science* 297:1548–1551.
- Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211–1219.
- Jetz, W., C. H. Sekercioglu, and J. E. M. Watson. 2008. Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology* 22:110–119.
- Jocque, M., R. Field, L. Brendonck, and L. De Meester. 2010. Climatic control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography* 19:244–252.
- Karlson, R. H., and H. V. Cornell. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecological Monographs* 68:259–274.
- Karlson, R. H., H. V. Cornell, and T. P. Hughes. 2004. Coral communities are regionally enriched along an oceanic biodiversity gradient. *Nature* 429:867–870.
- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, et al. 2011. Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science* 333:1755–1758.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Lessard, J. P., M. K. Borregaard, J. A. Fordyce, C. Rahbek, M. D. Weiser, R. R. Dunn, and N. J. Sanders. 2012. Strong influence of regional species pools on continent-wide structuring of local communities. *Proceedings of the Royal Society B: Biological Sciences* 279:266–274.
- Loreau, M. 2000. Are communities saturated? on the relationship between alpha, beta and gamma diversity. *Ecology Letters* 3:73–76.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.
- Meese, R. J. 2005. *Biological inventory databases*. Information Center for the Environment, Davis, CA.
- Murray, K., and M. M. Conner. 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology* 90:348–355.
- Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters* 12:1250–1260.
- O'Dwyer, J. P., and J. L. Green. 2010. Field theory for biogeography: a spatially explicit model for predicting patterns of biodiversity. *Ecology Letters* 13:87–95.
- Partel, M., L. Laanisto, and M. Zobel. 2007. Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history. *Ecology* 88:1091–1097.
- Passy, S. I. 2009. The relationship between local and regional diatom richness is mediated by the local and regional environment. *Global Ecology and Biogeography* 18:383–391.
- Qian, H., R. E. Ricklefs, and P. S. White. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8:15–22.
- Qian, H., P. S. White, and J. S. Song. 2007. Effects of regional vs. ecological factors on plant species richness: an intercontinental analysis. *Ecology* 88:1440–1453.
- Qian, H., C. Badgley, and D. L. Fox. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography* 18:111–122.
- Questad, E. J., and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* 11:717–726.
- R Development Core Team. 2008. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rajaniemi, T. K., D. E. Goldberg, R. Turkington, and A. R. Dyer. 2006. Quantitative partitioning of regional and local processes shaping regional diversity patterns. *Ecology Letters* 9:121–128.
- Ricklefs, R. E. 2007. History and diversity: explorations at the intersection of ecology and evolution. *American Naturalist* 170(suppl.):S56–S70.
- . 2008. Disintegration of the ecological community. *American Naturalist* 172:741–750.
- Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322:225–230.
- Soininen, J., J. J. Lennon, and H. Hillebrand. 2007. A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88:2830–2838.
- Srivastava, D. S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* 68:1–16.
- Starzomski, B. M., R. L. Parker, and D. S. Srivastava. 2008. On the relationship between regional and local species richness: a test of saturation theory. *Ecology* 89:1921–1930.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133:240–256.
- Stevens, R. D., and M. R. Willig. 2002. Geographical ecology at the community level: perspectives on the diversity of new world bats. *Ecology* 83:545–560.
- Storch, D., R. G. Davies, S. Zajicek, C. D. L. Orme, V. Olson, G. H. Thomas, T. S. Ding, et al. 2006. Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity. *Ecology Letters* 9:1308–1320.
- White, E. P., and A. H. Hurlbert. 2010. The combined influence of the local environment and regional enrichment on bird species richness. *American Naturalist* 175:E35–E43.
- White, E. P., S. K. M. Ernest, P. B. Adler, A. H. Hurlbert, and S. K. Lyons. 2010. Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3633–3643.
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution* 12:266–269.