

Linking global turnover of species and environments

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Patterns of species turnover are central to the geography of biodiversity and resulting challenges for conservation, but at broad scales remain relatively little understood. Here, we take a first spatially-explicitly and global perspective to link the spatial turnover of species and environments. We compare how major groups of vertebrate ectotherms (amphibians) and endotherms (birds) respond to spatial environmental gradients. We find that high levels of species turnover occur regardless of environmental turnover rates, but environmental turnover provides a lower bound for species turnover. This lower bound increases more steeply with environmental turnover in tropical realms. While bird and amphibian turnover rates are correlated, the rate of amphibian turnover is four times steeper than bird rates. This is the same factor by which average geographic ranges of birds are larger than those of amphibians. Narrow-ranged birds exhibit rapid rates of species turnover similar to those for amphibians, while wide-ranged birds largely drive the aggregate patterns of avian turnover. We confirm a strong influence of the environment on species turnover that is mediated by range sizes and regional history. In contrast to geographic patterns of species richness, we find that the turnover in one group (amphibians) is a much better predictor for the turnover in another (birds) than is environment. This result confirms the role of amphibian sensitivity to environmental conditions for patterns of turnover and supports their value as a surrogate group. This spatially-explicit analysis of environmental turnover provides understanding for conservation planning in changing environments.

beta diversity | biodiversity | distance decay | environmental gradients | spatial turnover

Understanding patterns of species turnover is central to both applied issues of conservation planning (1, 2) and to long-standing conceptual questions on the origin and distribution of biodiversity (3, 4). Linking these species turnover patterns to changes in environmental conditions is crucial to addressing how the edges of species' ranges are delineated (5). Both environmental dissimilarity and geographic distance are central causes of species turnover (6). Along local environmental gradients, species distributions often represent the outcome of competitive sorting (7, 8). At broader scales, evolutionary histories of speciation and extinction, along with environmental conditions, constrain the richness and distribution of species (9–11). We examine how both the environment and species composition change over geographic space to disentangle the influence of environmental conditions and space on species turnover. This extends Whittaker's studies (8) of species turnover along environmental gradients to global scales.

We term our examination of changes in species composition along spatial and environmental gradients species turnover (8, 12). While beta diversity is often used synonymously with species turnover (13), beta diversity can also refer to mathematical partitioning of diversity into components (14, 15) and dissimilarity between paired sites (reviewed in 16, 17). Dissimilarity studies based on distance between paired sites lack spatial continuity and a link to a particular location with given environmental conditions. This limits their value in linking environmental and species turnover. For this reason, very few maps of

species turnover have been produced compared with the numerous maps of species richness.

Gaston *et al.* (18) recently produced a map of global species turnover for birds. Species turnover was calculated between pairs of neighboring cells and then related to mean environmental conditions. Using a neighborhood to examine species turnover departs from Whittaker's (8) notion of species turnover along environmental gradients. Other authors have used distance decay in species similarity to examine spatial turnover patterns (1, 19). Qian and Ricklefs (20) calculate plant turnover as the decay of species similarity over either geographic or environmental space. While the decay of species similarity over environmental space is ecologically informative, we chose to relate the decay in species similarity over geographic space to the corresponding decay in environmental similarity. This maintains the importance of geography in both the environment and species composition.

We can then ask how the relationship between turnover in species composition and turnover in the environment varies (*i*) between our focal groups of vertebrate ectotherms and endotherms; (*ii*) with the geographic extent considered; and (*iii*) between biogeographical realms with distinct regional histories. Amphibians tend to have narrow ranges and to be tightly constrained by environmental conditions, particularly the water-temperature balance (21, 22). Amphibians also respond sharply to spatial differences in environmental conditions because of limited dispersal ability (23). We thus expect that amphibian turnover will occur more rapidly than bird turnover. Broad-scale diversity patterns have been found previously to be contingent on the geographic range sizes of species (11). Given the direct link between size of ranges and their average turnover in space (24), much of the cross-taxon variation in turnover may be because of this component. We investigate whether the approximately fourfold difference in geographic range sizes between amphibians and birds can account for differential rates of turnover.

We examine constraints in the relationship between species and environmental turnover. Is a high degree of environmental turnover necessary to observe a high degree of species turnover? Is a high degree of environmental turnover always accompanied by a high degree of species turnover? How does the relationship change with the distance over which decay is examined? We expect differences in range sizes between taxa to become less important at larger scales of analysis. Whether the relationship between environmental and species turnover varies between temperate and tropical realms is central to understanding the distribution and origin of diversity. Such variation would be expected if differential rates of speciation lead to differences in

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niche specialization and sizes of regional species pools (10). The relationship between environmental and species turnover addresses Janzen's (3) notion that "mountain passes are higher in the tropics"—that less variable tropical climates lead to specialization and high rates of species turnover.

Congruence between taxa for areas of high species richness can facilitate conservation planning (25). Designing conservation reserves to include areas of high species turnover is a less frequently implemented conservation strategy (2), and less is known regarding congruence in patterns of species turnover between taxa (but see 1). Amphibians with their acute sensitivity to environmental conditions may be viable surrogates for species turnover of other taxa (26). Here, we provide an explicit test of this notion and examine across spatial scale whether environment or amphibian turnover is a better surrogate and predictor of geographic turnover in bird species.

Results and Discussion

We first examined the increase in environmental distance and decay in avian and amphibian species similarity with spatial distance (km) for an example location in central Africa (Fig. 1). Environmental distance (the absolute difference in the environment principle component values) increased steadily with spatial distance. The (ln) Jaccard similarity of amphibian species composition declined more rapidly than that for birds, consistent with the tendency for amphibians to have smaller range sizes (slope \pm 95% CI for 1,000 km spatial window = $-2.80 \times 10^{-3} \pm 2.9 \times 10^{-4}$ amphibians; $-1.44 \times 10^{-3} \pm 1.0 \times 10^{-4}$ birds). The slopes of these relationships were reasonably stable over choices of spatial distances. For the majority of the analyses that follow, we examined an intermediate spatial distance of 1,000 km. Slopes can shallow at distances of 2,000 km because of complete dissimilarity posing a lower bound on species turnover.

We used the slopes of these site-specific relationships to consider global patterns of turnover in the environment and species composition. The steeper distance decay in compositional similarity for amphibians was globally consistent (mean slope \pm 95% CI = $-1.90 \times 10^{-3} \pm 1.2 \times 10^{-5}$ for amphibians, $-1.16 \times 10^{-3} \pm 5.1 \times 10^{-6}$ for birds, $n = 10,529$; $t_{13128} = 74.3$, $P < 1.0 \times 10^{-15}$). While the spatial decay relationships accounted for 89% (median) of the variation in bird species similarity, the relationship accounted for only 74% (median) of the relationship for amphibians [supporting information (SI) Fig. S1]. Over 99% of the relationships were significant ($P < 0.01$) for both taxa as well as for environmental turnover.

Regions with the highest rates of species turnover were largely congruent for amphibians and birds, and corresponded closely to regions of high environmental turnover rates (Fig. 2; coefficients of determination in Fig. S1). These regions of high species and environmental turnover include the Andes, Northern Africa, and Himalayas. Individual environmental variables turned over in a similar pattern to that when the four variables were combined in the principal component analysis (temperature, net primary productivity (NPP), annual evapotranspiration (AET), and precipitation, Fig. S2).

When we related environmental turnover to amphibian species turnover (Fig. 3), we found that high levels of species turnover can occur regardless of the degree of environmental turnover. However, a high degree of environmental turnover tends to correspond to a high degree of species turnover. This triangular relationship between environmental and species turnover is particularly clear for birds. We used quantile (10%) regression to examine the lower bound on species turnover with increasing environmental turnover. The slope of this lower bound on avian turnover ranged from 0.18 to 0.31 and increased slightly with increasing spatial scale (Table 1). The analogous slope for amphibians was substantially steeper with a range from

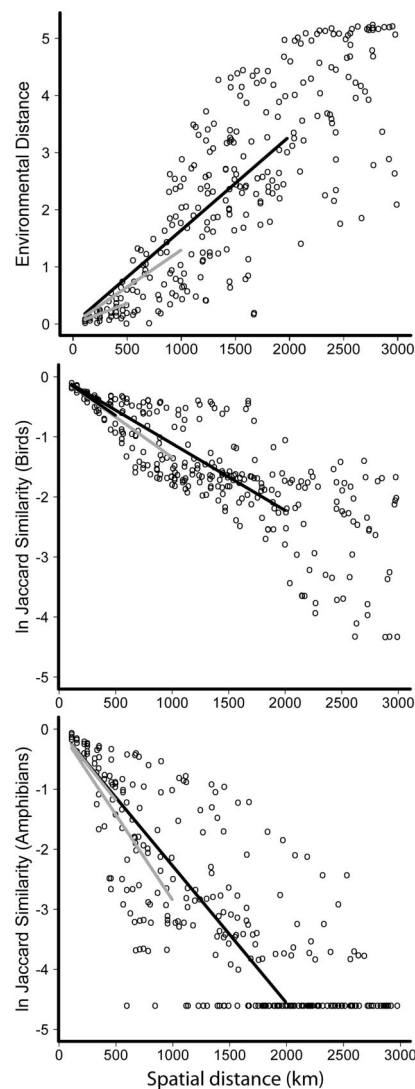


Fig. 1. Turnover of environment and species with spatial distance (km) for an example location in central Africa (depicted in Fig. 2). Environmental distance is the absolute difference in the environment principal component between locations (1,000 km slope \pm 95% CI = $1.6 \times 10^{-3} \pm 1.7 \times 10^{-4}$, $F_{1,871} = 320$, $P < 1.0 \times 10^{-15}$, $r^2 = 0.78$). Species turnover for birds and amphibians is measured as the natural log of Jaccard Similarity in species composition between sites. Distance decay in similarity occurs more rapidly for amphibians (1,000 km slope \pm 95% CI = $-2.80 \times 10^{-3} \pm 2.9 \times 10^{-4}$, $F_{1,1021} = 360.7$, $P < 1.0 \times 10^{-15}$, $r^2 = 0.78$) than for birds (1,000 km slope \pm 95% CI = $-1.44 \times 10^{-3} \pm 1.0 \times 10^{-4}$, $F_{1,921} = 764.4$, $P < 1.0 \times 10^{-15}$, $r^2 = 0.89$), and the slope of the decay varies with the spatial distances examined (500 km, 1,000 km, and 2,000 km). These slopes formed the basis for the maps of Fig. 2.

0.53 to 0.69. High species turnover in homogenous environments may result from histories of vicariant evolution.

Despite the differences in turnover rates between groups, rates of amphibian and avian turnover highly correlated across grid cells (see Fig. 3). The association was much tighter for amphibian predicting bird turnover (Table 1; Spearman correlations: 500 km $r_s = 0.63$, 1,000 km $r_s = 0.73$, 2,000 km $r_s = 0.74$) than for environment predicting bird turnover (Table 1; Spearman correlations: 500 km $r_s = 0.33$, 1,000 km $r_s = 0.37$, 2,000 km $r_s = 0.48$). These results were confirmed when we accounted for spatial autocorrelation (Table 1). We note that for every increment of amphibian turnover birds turned over by a smaller increment, allowing more precise predictions by the former for the latter than vice versa. Amphibians, with their high sensitivity

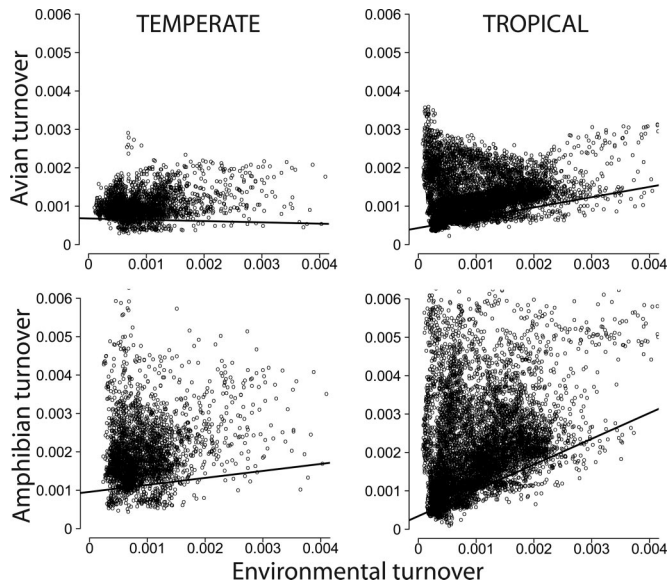


Fig. 5. The increase in avian and amphibian turnover with increasing environmental turnover is steeper in tropical realms than in temperate realms. The 10% quantiles of species turnover depict the lower bounds on this relationship for a focal distance of 1000 km.

birds 1,000 km slope \pm 95% CI = -0.02 ± 0.04 , $F_{[1, 3020]} = 1.3$, $P = 0.2$; temperate amphibians 1,000 km slope \pm 95% CI = 0.21 ± 0.09 , $F_{[1, 2787]} = 22.3$, $P < 1.0 \times 10^{-5}$). Among tropical realms, the slope of the relationship between species and environmental turnover was substantially steeper for amphibians than for birds as was observed when considering all realms together (tropical birds 1,000 km slope \pm 95% CI = 0.30 ± 0.02 , $F_{[1, 17504]} = 1032.6$, $P < 1.0 \times 10^{-15}$; tropical amphibians 1,000 km slope \pm 95% CI = 0.75 ± 0.04 , $F_{[1, 6879]} = 1527.0$, $P < 1.0 \times 10^{-15}$).

The differential relationship between species and environmental turnover in temperate and tropical realms provides evidence that environmental conditions and regional histories jointly constrain species turnover as has been extensively documented for species richness (6, 10). Our results are consistent with Janzen's (3) hypothesis that mountain passes are "higher" in the tropics. Tropical mountains, with more constant climates potentially resulting in limited acclimation potential, narrow climatic tolerances, and ultimately greater genetic divergence and rates of speciation, may pose substantial physiological barriers. This should favor narrower distributions and increased species turnover along altitudinal gradients (3). Janzen's assumptions have received substantial empirical support (reviewed in 21, 32). Ranges do tend to be narrower in the tropics for amphibians (33, 34) and birds (32, 35, 36).

The tight linking of environmental and species turnover in the tropics suggests that tropical communities may be particularly susceptible to climate change. Tropical organisms with narrow thermal tolerances may be closer to their thermal limits and may, thus, be more severely impacted by climate change despite the lesser projected temperature changes in tropical areas (37). Differential rates of species turnover between taxa are likely to have repercussions for species' interactions within communities following climate-induced range shifts. Our analysis provides a framework for linking spatial patterns of environmental and species turnover to understand how environmental and historical processes constrain diversity in current and potential future environments.

Methods

Distribution Data. Species presence was established by using extent of occurrence maps for 5,634 of the \approx 6,000 known amphibian species (Global Amphibian Assessment, 38) and 8,750 breeding ranges of the \approx 9,713 known land birds (excluding water birds and endemics on small islands, 39). We used an equal area cylindrical projection and equal area grid cells of 12,364 km² (approximately equivalent to 1° x 1° latitude-longitude near the equator) to examine species and environmental turnover. Following Gaston *et al.* (18), we emphasized equal area and a globally comparable count of species per grid cell, but acknowledged the shorter grid cell distances at high compared with low latitudes caused by the equal-area projection. We also acknowledged that range maps have the potential to overestimate species' occurrence and that this overestimation may be more severe for amphibians because of their small range sizes. We feel that 1° grid cells both accommodate amphibian's small range sizes and minimize range map overestimation. While this overestimation can influence species richness patterns for grid cells smaller than 2° (40), amphibian species richness patterns are robust to grid cell size (22).

Environmental Data. We selected four environmental variables known to constrain amphibian and bird distributions (11, 22) and extracted them across the same grid used to assess species turnover. We used mean annual temperature and precipitation data from 1961 to 1990 with 10' resolution (41). As estimates of energy availability, we used consensus mean annual NPP estimates compiled from numerous models by the Potsdam institute (gC m⁻², 30' resolution, 42) and AET, which is closely tied to the water-temperature balance (30' resolution, 43). We then combined the data in a principal component analysis to define the environmental gradient. Principal component analysis transforms a number of (possibly) correlated variables into a smaller number of uncorrelated variables (principal components, PC). The first principal component accounts for as much of the variability in the data as possible. In our analysis, this first PC axis accounted for a very large amount (76.2%) of the variance in environmental space and loaded the variables approximately equally (loadings: temperature = 0.33, NPP = 0.54, AET = 0.56, and precipitation = 0.54). This variable then enabled us to examine the combined environmental turnover along a single gradient. This allowed us to calculate the environmental distance between a focal site *i* and a compared site *j* as the absolute difference between the values of the PC variable at those two points, i.e., as $abs(PC_i - PC_j)$. Results are qualitatively similar when temperature was omitted despite the strong latitudinal temperature gradient.

Species Turnover. Species similarity metrics are a function of the species shared by two areas, *a*; the species gained by an area relative to the focal area, *b*; and the species loss by an area relative to a focal area, *c*. We employed the Jaccard similarity index, which reflects the compositional dissimilarity between two sites as the likelihood that a species occurs in just one site: $\beta_j = (b+c)/(a+b+c)$ (44). We used distance decay relationships to assess rates of decline in species similarity and increases in environmental distance as a function of geographic distance (reviewed in 19, 20, 45, 46). The absolute value of the slope (linear least-squares) of the relationship between environmental distance or (ln transformed) species similarity and distance was used as the metric for species and environmental turnover (19). This approach produced similar species turnover rate maps to that of McKnight *et al.* (1), but we feel it allows for a more straightforward comparison of environmental and species turnover rates. The regression intercept was fixed at zero (complete similarity at 0 km). We used the R function `spDistsN1` to calculate the great circle distance (km) between the centers of grid cells. We examine distance decay within three spatial windows (500, 1,000, and 2,000 km). Grid cells were subsampled by using a probability of selection inverse to distance to maintain a constant sample density as a function of distance. The total number of grid cells selected was set to four times the number of grid cells within a distance radius of 500 km. All coefficients are reported in the text with 95% confidence intervals (CI). We accounted for spatial autocorrelation in error terms by using maximum-likelihood spatial autoregressive models with 1,000-km neighborhoods and row standardization (R package `spdep`; Bivand 2005).

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1. McKnight MW, et al. (2007) Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biol* 5:2424–2432.
2. Pimm SL, Gittleman JL (1992) Biological Diversity: Where is it? *Science* 255:940.
3. Janzen DH (1967) Why mountain passes are higher in the tropics. *Am Nat* 101:233–249.
4. Whittaker RH (1972) Evolution and measurement of diversity. *Taxon* 21:213–251.
5. Holt RD, et al. (2005) Theoretical models of species' borders: Single species approaches. *Oikos* 108:18–27.
6. Ricklefs RE (2007) History and diversity: Explorations at the intersection of ecology and evolution. *Am Nat* 170:S56–S70.
7. Cody ML (1975) in *Ecology and Evolution of Communities*, eds Cody ML, Diamond JM (Belknap Press of Harvard Univ Press, Cambridge), pp 214–257.
8. Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol Monographs* 30:279–338.
9. Currie DJ, et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol Lett* 7:1121–1134.
10. Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. *Ecol Lett* 7:1–15.
11. Jetz W, Rahbek C (2002) Geographic range size and determinants of avian species richness. *Science* 297:1548–1551.
12. Harrison S, Ross S J, Lawton JH (1992) Beta diversity on geographic gradients in Britain. *J Anim Ecol* 61:151–158.
13. Vellend M (2001) Do commonly used indices of β -Diversity measure species turnover? *J Veg Sci* 12:545–552.
14. Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of species diversity: Recent revival of an old idea. *Oikos* 99:3–9.
15. Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
16. Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. *J Anim Ecol* 72:367–382.
17. Tuomisto H, Ruokolainen K (2006) Analyzing or explaining beta diversity? understanding the targets of different methods of analysis. *Ecology* 87:2697–2708.
18. Gaston KJ, et al. (2007) Spatial turnover in the global avifauna. *Proc Roy Soc B* 274:1567–1574.
19. Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. *J Biogeogr* 26:867–878.
20. Qian H, Ricklefs RE (2007) A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecol Lett* 10:737–744.
21. Feder ME, Burggren WW (1992) *Environmental physiology of the amphibians* (University of Chicago Press, Chicago).
22. Buckley LB, Jetz W (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proc Roy Soc B* 274:1167–1173.
23. Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: Are all amphibian populations metapopulations? *Ecography* 28:110–128.
24. Arita HT, Rodriguez P (2002) Geographic range, turnover rate and the scaling of species diversity. *Ecography* 25:541–550.
25. Lamoreux JF, et al. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature* 440:212–214.
26. Stuart SN, et al. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
27. Qian H, Ricklefs RE (2008) Global concordance in diversity patterns of vascular plants and terrestrial vertebrates. *Ecol Lett* 11:547–553.
28. Hawkins BA, Porter EE (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *Am Nat* 161:40–49.
29. Jetz W, Kreft H, Ceballos G, Mutke J (2008) Global associations between terrestrial producer and vertebrate consumer diversity. *Proc R Soc* 10.1098/rspb.2008.1005
30. Mittelbach GG, et al. (2007) Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol Lett* 10:315–331.
31. Harrison S, Cornell H (2008) Toward a better understanding of the regional causes of local community richness. *Ecol Lett* 11:969–979.
32. Ghalambor CK, et al. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Int Comp Biol* 46:5–17.
33. Huey RB (1978) Latitudinal pattern of between-altitude faunal similarity—Mountains might be higher in the tropics. *Am Nat* 112:225–229.
34. Navas CA (2006) Patterns of distribution of anurans in high Andean tropical elevations: Insights from integrating biogeography and evolutionary physiology. *Int Comp Biol* 46:82.
35. Orme CDL, et al. (2006) Global Patterns of Geographic Range Size in Birds. *PLoS Biol* 4:e208.
36. Stevens GC (1989) The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am Nat* 133:240.
37. Deutsch CA, et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672.
38. IUCN, Conservation International, and NatureServe (2006) *Global Amphibian Assessment*, www.globalamphibians.org.
39. Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol* 5:e157.
40. Hurlbert AH, Jetz W (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc Natl Acad Sci USA* 104:13384–13389.
41. New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. *Climate Res* 21:1–25.
42. Cramer W, et al. (1999) Comparing global models of terrestrial net primary productivity (NPP): Overview and key results. *Glob Change Biol* 5:1–15.
43. Ahn CH, Tateishi R (1994) Development of a global 30-minute grid potential evapotranspiration data set. *J Jpn Soc Photogrammetry and Remote Sensing* 33:12–21.
44. Jaccard P (1912) The distribution of the flora in the alpine zone. *New Phytol* 11:37–50.
45. Morlon H, et al. (2008) A general framework for the distance-decay of similarity in ecological communities. *Ecol Lett* 11:904–917.
46. Ferrier S, Manion G, Elith J, Richardson K (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers Distrib* 13:252–264.