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# Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions

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## ABSTRACT

**Aim** Habitat and climate heterogeneity may affect patterns of species diversity from the relatively local scale of communities to the broad biogeographical scale of continents. However, the effects of heterogeneity on species diversity have not been studied as widely at intermediate scales although differences among landscapes in local climate and habitat should maintain beta-diversity.

**Location** Bailey ecoregions in the USA.

**Methods** Using a geographically extensive dataset on bird distribution and abundance in 35 ecoregions, we tested for the effects of habitat and climate heterogeneity on beta-diversity at two discrete spatial scales: among sample points within landscapes, and among landscapes within ecoregions.

**Results** Landscape-level beta-diversity typically accounted for 50% or more of gamma-diversity and was significantly and positively related to habitat heterogeneity (elevational range within an ecoregion) and climate heterogeneity (variation in potential evapotranspiration). Contrary to predictions, point-level beta-diversity was negatively related to habitat and climate heterogeneity, perhaps because heterogeneity constrains alpha-diversity at the landscape level. The geographical spatial separation of landscapes within an ecoregion did not significantly affect beta-diversity at either scale.

**Main conclusions** Our results suggest that habitat selection and adaptation to local climate may be the primary processes structuring bird diversity among landscapes within ecoregions, and that dispersal limitation has a lesser role in influencing beta-diversity among landscapes.

## Keywords

Bailey ecoregions, Breeding Bird Survey, distance decay of similarity, diversity partitioning, environmental heterogeneity, randomization.

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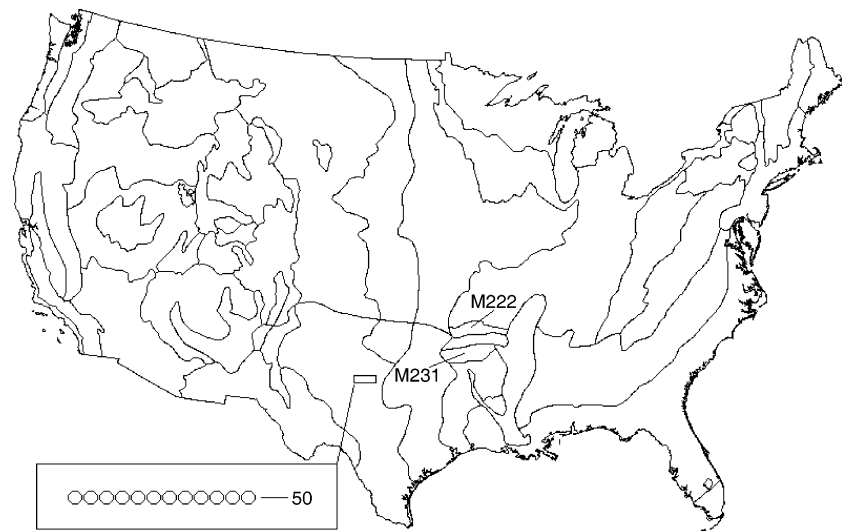
## INTRODUCTION

Both individualistic and interactive factors may be involved in maintaining beta-diversity. That is, differences in species richness and composition among localities within a landscape and among landscapes may be due to species interactions as well as the interaction of each species with the abiotic environment. Environmental heterogeneity in the form of spatial variation in habitat and local climate can affect species distributions and hence influence beta-diversity. There are many studies of the effects of habitat and climate heterogeneity on species diversity, particularly with respect to explaining the latitudinal gradient of

species diversity and other continental-scale patterns (Wright, 1983; Currie, 1991; Kerr & Packer, 1997; Hawkins *et al.*, 2003a, Tews *et al.*, 2004). As for smaller scales, ecologists have recognized the importance of habitat on beta-diversity among ecological communities as far back as the pioneering research of Whittaker (1956, 1960) and MacArthur *et al.* (1966). Indeed, the original notion of beta-diversity was diversity among habitats (Whittaker, 1956). There are fewer studies of beta-diversity at scales between those of local communities and continents.

Because species are differentially adapted to local habitat and climate, any spatial variation in habitat and climate within a relatively large region (e.g. an ecoregion or any area of 10,000s to

**Figure 1** Map of the 35 Bailey ecoregional provinces within the continental United States. Within each province or ecoregion, there are 6 to 263 BBS routes or landscapes that are approximately linear (rectangular). There are 50 points (circular areas with radius = 400 m) along each 39.2-km route. Landscape is not drawn to scale.



100,000s of km<sup>2</sup>) may produce and maintain beta-diversity among landscapes (areas of hundreds of km<sup>2</sup>) within the region. In addition, the spatial separation of landscapes within a region could maintain beta-diversity through dispersal limitation (Condit *et al.*, 2002; Nekola & Kraft, 2002) and produce the pattern of 'distance decay of similarity' (Nekola & White, 1999). However, within landscapes, some of these factors are predicted not to affect beta-diversity. Climate should not affect beta-diversity among localities (sample points) within a landscape as variation in climate from point to point is minimal or non-existent. Habitat heterogeneity may occur even in areas of relatively small size, such that habitat heterogeneity should have a positive effect on beta-diversity within landscapes as well as among them. Using extensive data sets of the distribution and abundance of breeding birds within 35 ecoregions of the United States, we tested for the effects of habitat and climate heterogeneity, as well as distance-decay, on gamma-diversity (total species richness within an ecoregion) and beta-diversity among landscapes and points within landscapes.

## METHODS

### Bird diversity data

We obtained data on bird diversity, distribution and abundance from the North American Breeding Bird Survey (BBS). The BBS is conducted annually in May and June along more than 3000 established survey routes in the United States. An observer records the abundance of bird species seen or heard (for 3-min periods) within 400 m of each of 50 'stops' equally spaced along each 39.2-km route (Robbins *et al.*, 1986; Sauer *et al.*, 2003). Although the survey has been conducted since 1966, we used only data for a 9-year period between 1997 and 2005 because data at the stop level were not available for the previous years. The study thus included 2395 routes. Most of these routes (74%) had data for most ( $\geq 5$ ) of the 9 years. Because we were interested in spatial patterns of diversity, instead of temporal

patterns, we pooled data from all 9 years and conducted all subsequent analyses on summed abundances of each species at each stop. Using summed abundance was preferable to using mean abundance because summed abundances recognize differences in sampling effort (number of years the route was surveyed) and our method of analysing diversity (see below) controls for sampling effort.

The Patuxent Wildlife Research Center (Laurel, MD, USA) of the United States Geological Survey has assigned each BBS route to the Bailey ecoregional classification system (Bailey, 1996). This is a hierarchical system of describing and classifying ecoregions within North America on the basis of climate, topography, geology and vegetation. The Bailey system is widely recognized and used by various government agencies and environmental conservation organizations. The system recognizes 35 'provinces' within the continental United States (Fig. 1). We analysed species richness at the stop and route levels separately for each province. Compared with smaller Bailey hierarchical units (e.g. sections), provinces contain a sufficient number of routes ( $\geq 10$ ) for analysis of diversity patterns, and compared with larger units (e.g. divisions) there is a sufficient sample size ( $n = 35$ ) for provinces. An alternative approach would have divided the continental USA into a grid of cells of an arbitrary size. However, by using the Bailey system, we subdivide continental-level diversity into smaller units based on natural climatic and physiographic boundaries that are manageable and suitable for analysis. Our use of Bailey provinces does not imply that each province has a unique bird fauna. Hereafter, we refer to BBS routes as 'landscapes' and stops as 'points' within the landscapes (Fig. 1); provinces are referred to as 'ecoregions'. There were 577 bird species distributed among the 35 ecoregions (see Appendix S1 in Supplementary Material). We did not exclude any particular species from the analysis even though the BBS survey protocol does not assess some species (e.g. nocturnal and very small bodied birds) as well as others. Inclusion of these species should not affect our results as there is no reason to believe that the occurrence of such species is biased towards any particular routes or ecoregions.

### Analysis of alpha- and beta-diversity

For each ecoregion, we used additive diversity partitioning to calculate alpha-diversity at the point level and beta-diversity at the point and landscape levels:  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$ . This statistical technique involves the decomposition of total (gamma) diversity into the additive components of alpha- and beta-diversity (Lande, 1996; Veech *et al.*, 2002; Crist *et al.*, 2003). When applied to hierarchical data in which samples at one level are nested within the samples at the next highest level (e.g. points within landscapes), the alpha-diversity at the higher level is the sum of the alpha- and beta-diversities at the next lowest level (Wagner *et al.*, 2000; Veech *et al.*, 2002; Crist *et al.*, 2003); e.g.  $\alpha_{\text{land}} = \alpha_{\text{point}} + \beta_{\text{point}}$ . That is, samples at lower levels are pooled to form samples at higher levels. The alpha-diversity at the lowest level and the beta-diversities at each level sum to give gamma-diversity (Crist *et al.*, 2003):  $\gamma = \alpha_{\text{point}} + \beta_{\text{point}} + \beta_{\text{land}}$ .

We used the software program *PARTITION* (Veech & Crist, 2005) and selected the individual-based randomization routine (Crist *et al.*, 2003) to test the significance of observed  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  and to obtain expected values of each diversity component. With individual-based randomization, the total number of individuals of all species (sample size) is conserved, but the individuals of each species are randomly assigned to samples at each level. Therefore, this type of randomization assumes that any species could exist in any sample and thus gives diversity estimates that might exist in the absence of dispersal limitation. This is a biologically reasonable null hypothesis test for these data because randomization tests were conducted separately for each region, and most bird species found within a given ecoregion have geographical ranges that are larger than a single ecoregion. Individual-based randomization is essentially equivalent to the random placement model (Coleman *et al.*, 1982; Crist *et al.*, 2003; Crist & Veech, 2006). Thus, departures from random placement suggest that there is intraspecific aggregation within preferred habitats or dispersal limitation between habitats.

For each ecoregion, *PARTITION* created null statistical distributions of  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  using 10,000 iterations of the randomization routine. The means of the null distributions are the values of  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$ ,  $\alpha_{\text{land}}$  and  $\beta_{\text{land}}$  expected when there is a random spatial distribution of individuals at the point and landscape levels. The difference between the observed and expected values, expressed as a percentage of the expected value, is an estimate of either the increase or decrease in diversity due to non-random spatial distributions of individuals at the point and landscape levels. The statistical significance of each diversity component was assessed as the proportion of null values greater than (or less than) the observed diversity value. This proportion is a *P*-value that indicates the probability of obtaining a diversity value as great as (or as small as) the observed value by chance.

### Effects of environmental heterogeneity and space on gamma- and beta-diversity

We examined the effects of environmental heterogeneity (habitat and climate) and space on gamma-diversity and beta-diversity

within each ecoregion. The elevational range (ER) within an ecoregion served as a proxy variable for habitat heterogeneity in each ecoregion. In their recent study of Caribbean bird diversity, Ricklefs & Bermingham (2004) used elevational range as a proxy for habitat heterogeneity on islands of the Lesser Antilles. Kerr & Packer (1997) also used elevational range as a surrogate measure of habitat heterogeneity in  $2.5^\circ \times 2.5^\circ$  quadrats within North America. In a broader context, vegetation changes with elevation such that there is a greater variety of habitats in areas with substantial topographic variation (Rosenzweig, 1995; Brown & Lomolino, 1998). We obtained estimates of the highest and lowest elevations in each ecoregion from McNab & Avers (1994). Elevational range along individual routes (landscapes) was not assessed.

We assessed spatial heterogeneity in local climate by obtaining an estimate of annual potential evapotranspiration (PET) for each landscape. PET is widely used in studies of the effects of climate and atmospheric energy on species diversity (Hawkins *et al.*, 2003a); it is a combination of annual precipitation, temperature, solar radiation and other biophysical variables. In contrast, actual evapotranspiration (AET) is more indicative of plant productivity rather than the ambient climate measured by PET. Although AET and other variables have been used to test the productivity version of the species–energy theory (Hawkins *et al.*, 2003b; Hawkins, 2004), we were primarily interested in the direct role of climate rather than the role of productivity and trophic cascades. We obtained PET data from the United Nations Environment Programme (<http://www.grid.unep.ch/data/index.php>, data set GNV183). Hawkins *et al.* (2003b) also used these data in their study of the latitudinal diversity gradient. The PET data set contained > 4000 point estimates of PET on a grid within the continental USA. For each landscape or BBS route, we found the closest point to the centre of the route and assigned that PET estimate to the landscape (the mean distance between route centre and PET point estimate was 17.7 km, the maximum distance was 79.4 km). Hence, the number of PET estimates for each ecoregion equalled the number of landscapes and had a similar spatial distribution. For each ecoregion, we calculated the mean and standard deviation of the PET estimates and used the coefficient of variation (PETcv) as a measure of spatial heterogeneity in local (landscape to landscape) climate. We measured the spatial separation of landscapes within each ecoregion as the mean linear distance between all BBS routes within the ecoregion (MDL). Locations of BBS routes were defined as the centres or midway points of the routes; these data are available on the BBS website. Appendix S1 provides the values for ER, PETcv and MDL for each ecoregion.

We used multiple regression to test for significant effects of habitat heterogeneity, climate heterogeneity and space on gamma-diversity (total species richness in an ecoregion =  $\gamma_{\text{ecoreg}}$ ) and beta-diversity at the point and landscape levels ( $\beta_{\text{point}}$  and  $\beta_{\text{land}}$ ). Because  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  may be positively correlated with  $\gamma_{\text{ecoreg}}$ , we converted  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  to percentages of the total richness. In addition,  $\beta_{\text{point}}$ ,  $\beta_{\text{land}}$  and  $\gamma_{\text{ecoreg}}$  were correlated with ecoregion area ( $r = -0.81, 0.77$  and  $0.83$ , respectively). Therefore, prior to conducting the multiple regression models, we removed

the effect of ecoregion area on  $\beta_{\text{point}}$ ,  $\beta_{\text{land}}$  and  $\gamma_{\text{ecoreg}}$  by using the residuals obtained from regressions of each of the three against  $\log(\text{area})$ . There was a multiple regression model for each response variable ( $\beta_{\text{point}}$ ,  $\beta_{\text{land}}$ ,  $\gamma_{\text{ecoreg}}$ ) and each model included the three predictor variables: ER, PETcv and MDL. Because data from each of the 35 ecoregions were used in each model, the *F*-tests had 3 and 31 degrees of freedom.

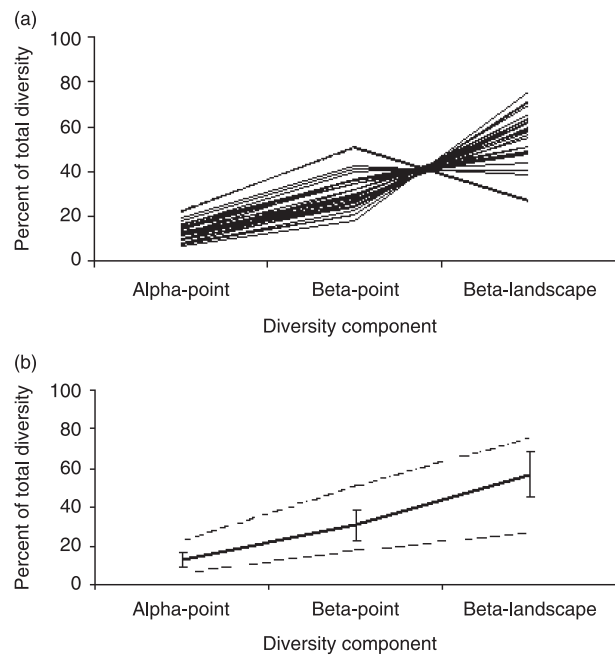
A major advantage of using multiple regression is that it provides the standardized partial regression coefficient (for each predictor variable), which represents the effect of that predictor variable while the other predictor variables are held constant (Sokal & Rohlf, 1995). The effects of the predictor variables can be assessed by comparing these coefficients and their *P*-values (Quinn & Keough, 2002). Regression coefficients may sometimes be affected by substantial correlations among the predictor variables (i.e. multicollinearity). PETcv and MDL were correlated ( $r = 0.51$ ), but this correlation did not affect the regression coefficients as the coefficients from the full regression models (with all three predictor variables) were very similar to those obtained from models that omitted either PETcv or MDL.

## RESULTS

### Analysis of alpha- and beta-diversity

In all 35 ecoregions,  $\alpha_{\text{point}}$  was the smallest component of total diversity, on average accounting for 13% of the total, followed by  $\beta_{\text{point}}$  with an average of 30% and  $\beta_{\text{land}}$  with an average of 57% (Fig. 2b). The randomization test, implemented by PARTITION, indicated that  $\alpha_{\text{point}}$  was significantly low ( $P < 0.001$ ) in all 35 ecoregions,  $\beta_{\text{point}}$  was significantly low ( $P < 0.001$ ) in all but one ecoregion, and  $\beta_{\text{land}}$  was significantly high ( $P < 0.001$ ) in all ecoregions. The mean percentage difference between observed and expected  $\alpha_{\text{point}}$  was  $-113.9\%$  with a range of  $-214\%$  to  $-37.4\%$ . For  $\beta_{\text{point}}$  the mean percentage difference was  $-58.9\%$  with a range of  $-141.4\%$  to  $1.9\%$ . For  $\beta_{\text{land}}$  the mean percentage difference was  $51.0\%$  with a range of  $34.1\%$  to  $66.8\%$ .

There was consistency among the 35 ecoregions in the decomposition of total diversity into observed  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  (Fig. 2a). All but four of the ecoregions exhibited the relationship of  $\alpha_{\text{point}} < \beta_{\text{point}} < \beta_{\text{land}}$ , which is also the mean relationship depicted in Fig. 2(b). The other four exhibited  $\alpha_{\text{point}} < \beta_{\text{point}} > \beta_{\text{land}}$ .



**Figure 2** (a) The decomposition of total diversity into observed  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  for each of the 35 ecoregions. (b) Mean values over all ecoregions are shown for observed  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$ . Dashed lines represent minimum and maximum values. Error bars represent  $\pm 1$  SD.

### Effects of environmental heterogeneity and space on gamma- and beta-diversity

Each of the three multiple regression models fit the data well ( $\gamma_{\text{ecoreg}}$ , adj.  $R^2 = 0.33$ ,  $F_{3,31} = 6.70$ ,  $P = 0.001$ ;  $\beta_{\text{point}}$ , adj.  $R^2 = 0.27$ ,  $F_{3,31} = 5.12$ ,  $P = 0.005$ ; and  $\beta_{\text{land}}$ , adj.  $R^2 = 0.30$ ,  $F_{3,31} = 5.88$ ,  $P = 0.003$ ). The models revealed that habitat and climate heterogeneity significantly affected gamma-diversity and landscape-level beta-diversity in the predicted way as evidenced by positive standardized partial regression coefficients (Table 1). However, point-level beta-diversity was negatively correlated with habitat and climate heterogeneity, contrary to the predictions of a positive correlation with habitat and no correlation with climate. Spatial separation or the mean distance between routes had no significant effect on gamma-diversity or beta-diversity at either level (Table 1).

**Table 1** Standardized partial regression coefficients for the effects of habitat heterogeneity, climate heterogeneity and spatial separation on total bird species richness within ecoregions and beta-diversity at the point and landscape levels. *P*-values are in parentheses.

Factor	Variable*	$\gamma_{\text{ecoreg}}$	$\beta_{\text{point}}$	$\beta_{\text{land}}$
Habitat heterogeneity	ER	0.41 (0.007)	-0.35 (0.024)	0.43 (0.005)
Climate heterogeneity	PETcv	0.49 (0.006)	-0.47 (0.011)	0.41 (0.021)
Spatial separation	MDL	-0.19 (0.245)	0.29 (0.102)	-0.27 (0.119)

\*Variable abbreviations represent elevational range (ER), the coefficient of variation for potential evapotranspiration (PETcv) and the mean distance between all landscapes within an ecoregion (MDL).

## DISCUSSION

Environmental heterogeneity appears to increase the overall species richness of birds within ecoregions. Even after controlling for ecoregion area, gamma-diversity is positively related to elevational range and variation in potential evapotranspiration. Presumably, a greater range of elevation within an ecoregion equates to a greater range of habitat or vegetation types and hence more bird species. Greater spatial variation in PET among landscapes indicates a greater range of local climate, which could also contribute to differences in vegetation, and thus greater gamma-diversity. To some extent, the positive effects of habitat and climate heterogeneity on gamma-diversity operate through their effects on beta-diversity.

Habitat and climate heterogeneity contributed to substantial variation in species composition among landscapes. In most ecoregions, landscape-level beta-diversity was the largest component of gamma-diversity (Fig. 2). Ecoregions that had greater variation in local climate and habitat tended to have greater beta-diversity among landscapes regardless of the spatial separation of the landscapes. Thus, our study reveals support for the habitat heterogeneity and climate heterogeneity hypotheses, but not dispersal limitation and distance decay (Nekola & White, 1999). The relationship between spatial separation of landscapes and beta-diversity was not significant, suggesting that dispersal limitation and a distance-decay pattern may not hold for highly vagile vertebrates (e.g. birds) within these ecoregions. Alternatively, some form of distance-decay effect might exist in the data (e.g. two most widely separated landscapes in each ecoregion may be most dissimilar) and was not revealed.

The positive effects of habitat and climate heterogeneity on beta-diversity could be grounded in the same general mechanism: adaptation to local environmental conditions. In this scenario, the interaction of each species with the biotic and abiotic environment determines whether it exists in a particular landscape. Within a given ecoregion, if landscapes differ enough in habitat and climate then most species will be found within a subset of landscapes; only a few generalist species will be found in all landscapes. Of course, this individualistic explanation of beta-diversity does not preclude the potential importance of species interactions and their influence in determining local community assembly and the patterns of beta-diversity among local assemblages.

Habitat and climate heterogeneity both had negative effects on beta-diversity *within* landscapes (or point-level beta-diversity). The variable that we used to measure heterogeneity (elevational range within an ecoregion) was probably too coarse to measure the heterogeneity within landscapes (i.e. along BBS routes). BBS routes are < 40 km in length; most probably do not traverse much of an elevational gradient, hence any habitat heterogeneity is due to other unexamined factors rather than to elevation. As for climate heterogeneity, we predicted the absence of a significant effect of PETcv on point-level beta-diversity. Again, PETcv is probably assessing climate at a scale that is too coarse to have much relevance for diversity patterns within landscapes. Moreover, the landscapes were small enough that there was

probably very little internal spatial variation in climate anyway. In retrospect, the negative effects of habitat and climate heterogeneity on point-level beta-diversity could arise through their negative effects on landscape-level alpha-diversity. Because  $\beta_{\text{point}} = \alpha_{\text{land}} - \alpha_{\text{point}}$ , any factors that decrease  $\alpha_{\text{land}}$  will also decrease  $\beta_{\text{point}}$ , assuming  $\alpha_{\text{point}}$  is relatively stable. Landscape-level alpha-diversity was negatively correlated with habitat and climate heterogeneity, as revealed by regressions of area-corrected  $\alpha_{\text{land}}$  against ER (slope = -0.003) and PETcv (slope = -0.54) while  $\alpha_{\text{point}}$  was relatively stable when regressed against ER and PETcv (slopes = -0.001 and -0.16, respectively). In other words, constraints on alpha-diversity at the landscape level limit the scope of beta-diversity at the point level.

Although we found significant effects of a climate variable (PETcv) on gamma-diversity of ecoregions and landscape-level beta-diversity within ecoregions, our study is not a direct test of the species–energy hypothesis (Hawkins *et al.*, 2003a). We examined the effects of *variation* in PET on species diversity and not the effects of *mean* PET. In fact, the mean PET of an ecoregion had a slightly negative effect on gamma-diversity (slope = -0.08,  $R^2 = 0.11$ ,  $P = 0.04$ ) and no significant effects on any of the components of gamma-diversity. There are two versions of the species–energy hypothesis. The ambient energy version suggests that physiological adaptations to climate constrain gamma-diversity, whereas the plant productivity version states that diversity is constrained by plant biomass and bottom-up trophic cascades (Hawkins *et al.*, 2003a). Hawkins (2004) found that the large-scale richness of birds in eastern North America was strongly influenced by plant biomass during the summer breeding season. Gamma-diversity increased linearly with plant biomass, thus supporting the productivity version of the species–energy hypothesis. Our study did not examine the effect of plant productivity on either beta- or gamma-diversity, although presumably differences in plant productivity among landscapes and ecoregions could affect patterns of bird diversity at both levels.

Although the total bird diversity within the ecoregions varied from 109 to 296 species and some ecoregions had greater habitat and climate heterogeneity than others, there was some consistency in the way that the diversity components contributed to total diversity (Fig. 2a). Thus, the same general pattern of diversity within points, among points and among landscapes is repeated over and over among the ecoregions. In 25 of 35 ecoregions, diversity among landscapes contributed more than half of the total diversity. There were two small ecoregions (M222 and M231; Fig. 1) where beta-diversity among landscapes made up only about 25% of total diversity, whereas beta-diversity among points made up about 50% of the total (Fig. 2a). Despite these two exceptions and the variation in  $\alpha_{\text{point}}$ ,  $\beta_{\text{point}}$  and  $\beta_{\text{land}}$  among all ecoregions, the general pattern of  $\alpha_{\text{point}} < \beta_{\text{point}} < \beta_{\text{land}}$  suggests that there may be common ecological processes, such as habitat selection and adaptation to local climate, that are operating in response to environmental heterogeneity and that spatially structure bird diversity within ecoregions.

In an earlier study using BBS data, Brown *et al.* (1995) found substantial intraspecific aggregation at the landscape level (i.e.

BBS route) for most of the 90 bird species included in their study. Most species were very common in a few landscapes, less common in others and completely absent in many. Brown *et al.* (1995) concluded that intraspecific aggregation might result from variation in local environmental conditions among sites and the extent to which those conditions meet the niche requirements of the species. Brown *et al.* (1995) did not directly link this intraspecific aggregation to beta-diversity; however, substantial beta-diversity among landscapes would be expected from intraspecific aggregation at the landscape level (Veech, 2005; Crist & Veech, 2006). In their study of Great Basin birds and butterflies, Mac Nally *et al.* (2004) found that beta-diversity at the site level (as measured by percentage dissimilarity in species composition) increased with increasing geographical separation of the sites in different canyons and mountain ranges. They attributed this pattern of diversity to environmental heterogeneity in the form of differences among the canyons in vegetation, elevational range, precipitation and food resources. A study conducted in Israel revealed an increase in beta-diversity of birds due to the separate effects of geographical distance and a gradient in precipitation (Steinitz *et al.*, 2006). Summerville *et al.* (2006) examined the effect of dispersal ability (body size) and habitat selection (host plant use) on beta-diversity of moths. They concluded that the body size of moths did not affect beta-diversity in that small-bodied and large-bodied moths exhibited remarkably similar patterns of beta-diversity. Instead, habitat selection had a strong influence: generalist species exhibited much less beta-diversity than specialists. These studies demonstrate that environmental heterogeneity can influence patterns of beta-diversity even in highly vagile organisms.

Historically, the study of ecological species diversity emerges from community ecology at one scale (MacArthur, 1958, 1972; Hutchinson, 1959; Elton, 1966; Paine, 1966) and biogeography at another much larger scale (Darlington, 1957; Simpson, 1964; MacArthur & Wilson, 1963, 1967; Paine, 1966; MacArthur, 1972). To the extent that studying species diversity is a search for repeated patterns and underlying mechanisms, analyses of diversity in landscapes and regions is very worthwhile. Landscapes of several hundred to thousands of hectares may be the ideal unit for measuring alpha- and beta-diversity, at least for vagile vertebrates such as birds. Units of this size are often small enough to be replicated in different ecoregions such that relatively distinct but repeated patterns of diversity can be uncovered. Moreover, at the landscape level of analysis, local and regional factors come together to influence species composition (Ricklefs, 2004), whereas the scale of most ecological communities is often too small for the study of regional processes and the scale of biogeographical realms is too large for local processes. We uncovered distinct and somewhat repetitive patterns in the decomposition of gamma-diversity into beta-diversity at within-landscape and among-landscape scales. Of most importance, beta-diversity in birds appeared to be influenced by factors, habitat and climate heterogeneity, that could affect beta-diversity in other types of organisms. Further study may establish the generality of these effects.

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#### BIOSKETCHES

**Joseph Veech** is interested in landscape-level patterns of species diversity and the ecological factors that affect the patterns. He has also developed various statistical methods for analysing species diversity.

**Tom Crist** is interested in habitat fragmentation and species diversity within landscapes. His research methods include field experiments, sampling of insect diversity and modelling.

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#### SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Ecoregion characteristics.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2007.00315.x>

(This link will take you to the article abstract).

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