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ORIGINAL ARTICLE

Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies

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ABSTRACT

Aim We examined whether variation in species composition of breeding birds and resident butterflies in the Great Basin of North America depended on sampling grain (the smallest resolvable unit of study) and on the relative proximity of sampling units across the landscape. We also compared patterns between the two taxonomic groups with reference to their life-history characteristics.

Location Data for our analyses were collected from 1996 to 2003 in three adjacent mountain ranges in the central Great Basin (Lander and Nye counties, Nevada, USA): the Shoshone Mountains, Toiyabe Range and Toquima Range.

Methods Data on species composition for both taxonomic groups were collecting using standard inventory methods for birds and butterflies in temperate regions. Data were compiled at three sampling grains, sites (average 12 ha), canyons (average 74 ha) and mountain ranges. For each sampling grain in turn, we calculated similarity of species composition using the Jaccard index. First, we investigated whether mean similarity of species composition among the three ranges differed as a function of the grain size at which data were compiled. Secondly, we explored whether mean similarity of species composition was greater for canyons within the same mountain range than for canyons within different mountain ranges. Thirdly, we examined whether mean similarity of species composition at the site level was different for sites within the same canyon, sites within different canyons in the same mountain range, and sites within canyons in different mountain ranges. We used a Bayesian model to analyse these comparisons.

Results For both taxonomic groups, mean similarity of species composition increased as the sampling grain increased. The effect of spatial grain was somewhat greater for birds than for butterflies, especially when the intermediate sampling grain was compared with the smallest sampling grain. Similarity of species composition of butterflies at each sampling grain was greater than similarity of species composition of birds at the same grain. Mean similarity of species composition of both birds and butterflies at the canyon level and site level was affected by relative proximity of sampling locations; beta diversity increased as the relative isolation of sampling locations increased.

Main conclusions The sensitivity of beta diversity to sampling grain likely reflects the effect of local environmental heterogeneity: as sampling grain increases, biotic assemblages appear more homogeneous. Although breeding birds in our study system have larger home ranges than resident butterflies, birds may have more specialized resource requirements related to vegetation structure and composition, especially at small sampling scales. The degree of variation in species composition of both taxonomic groups suggests that spatially extensive sampling

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will be more effective for drawing inferences about regional patterns of species diversity than intensive sampling at relatively few, smaller sites.

Keywords

Bayesian analyses, diversity patterns, Great Basin, Jaccard similarities, Nevada, proximity of samples, riparian areas, sampling grain, spatial scale, species composition.

INTRODUCTION

Measures of species diversity are dependent on spatial and temporal scale. For example, the size of each sampling unit, the spatial configuration or relative proximity of sampling units across the landscape, and the spatial extent of the area from which samples are drawn affect inferences about species richness and composition (Noss, 1983; Wilson & Shmida, 1984; Ricklefs & Schluter, 1993; Conroy & Noon, 1996; Reaka-Kudla *et al.*, 1997). Knowledge of relationships between species diversity and scale has wide-ranging application, from identification of appropriate boundaries for studying mechanisms that generate and maintain biological diversity (Kolasa, 1989, Rosenzweig, 1995, Underwood & Chapman, 1996; Willis & Whittaker, 2002), to prediction of how local and regional environmental changes will affect diversity at multiple levels of organization (Huston, 1994; Lockwood & McKinney, 2001; Scott *et al.*, 2002), to examination of relationships between species richness and ecological function (Waide *et al.*, 1999).

Most work on scaling issues associated with diversity patterns has concentrated on species richness. In part because counting species is logistically more feasible than collecting detailed demographic data, species richness has been used as a variable to help prioritize conservation efforts (Scott *et al.*, 1993; Environment Conservation Council, 2000; Pimm *et al.*, 2001; Roberts *et al.*, 2002) and to measure biological responses to natural disturbance processes, human land use, and alternative management actions at numerous spatial extents (Chapin *et al.*, 2000; Pressey *et al.*, 2000). Beta diversity (between-habitat diversity), which increases as a function of turnover in species composition among communities, most often has been considered in terms of its contribution to species richness of a heterogeneous landscape (MacArthur, 1965; Whittaker, 1977; Lande, 1996). For example, the method of additive partitioning uses a hierarchical model of landscape organization (Allen & Starr, 1982) to represent diversity at each nested level of a landscape as the sum of alpha (within-habitat) and beta diversity at the next lower level (Allan, 1975; Lande, 1996; Wagner *et al.*, 2000; Fournier & Loreau, 2001; Gering *et al.*, 2003). In other words, additive partitioning calculates the relative contributions of alpha and beta diversity to overall species richness at multiple spatial levels. In this paper, by contrast, we focus directly on whether beta diversity depends on sampling grain (the smallest resolvable unit of study, King, 1991; Morrison & Hall, 2002) and the proximity of sampling units across the landscape.

We also examine the taxonomic component of scaling issues. Species perceive and react to their environment as a function of their resource requirements, mobility, and other life-history characteristics (Addicott *et al.*, 1987; Kotliar & Wiens, 1990; Mac Nally, 2004). In theory, the grain of sampling and the extent of sampling (the area over which observations are made) should be dictated by the ecology of the species under investigation (Kotliar & Wiens, 1990; Mac Nally, 2004). In reality, however, sampling designs frequently reflect logistic constraints. Even if the optimal sampling regime for each major guild in a landscape has been identified, the grain and extent of sampling for multi-taxonomic studies commonly is established using a single convenient human perspective, such as administrative boundaries or land-use types. But a uniform sampling framework may not be meaningful for understanding diversity patterns in all taxonomic groups of interest (Addicott *et al.*, 1987; Kolasa, 1989), and sampling schemes can affect practical decisions about allocation of conservation funds and protected areas (Bassett & Edwards, 2003). Several studies have found low correlation in species richness among taxonomic groups at scales associated with local management (Prendergast *et al.*, 1993; Rubinoff, 2001). However, evidence on correlation in species richness among taxonomic groups at scales associated with ecoregional assessment is more equivocal (Olson & Dinerstein, 1998; Ricketts *et al.*, 1999; Stein *et al.*, 2000). Correlations between species richness of different taxonomic groups often increase as the spatial grain and extent of sampling increase (e.g. Swengel & Swengel, 1999).

The Great Basin of western North America is an excellent study system for exploring simultaneously the effects of spatial scale and taxonomic group on beta diversity. The Great Basin includes more than 425,000 km^2 of internal drainage extending from the Sierra Nevada in the west to the Wasatch Range in the east (Grayson, 1993). The topography of the region is dominated by more than 200 major mountain ranges, most with a north–south orientation, that were isolated from each other and from the surrounding lower-elevation valleys as the regional climate became warmer and drier following the Pleistocene (Brown, 1978; Wells, 1983; Grayson, 1993). Individual mountain ranges function as discrete habitat islands for many taxa that have relatively low mobility or cannot survive in the arid valleys (tens of km wide) separating the

ranges, including birds and butterflies (McDonald & Brown, 1992; Murphy & Weiss, 1992). We recently found that turnover of species composition within sites over time accounted for much less of the difference in species composition of butterflies in the Great Basin than did spatial differences among sites (Fleishman & Mac Nally, 2003). Therefore, we decided it would be useful to explore relationships between beta diversity and spatial scale more thoroughly.

Numerous canyons incise the eastern and western slopes of mountain ranges in the Great Basin. For many species of birds and butterflies, canyons also represent archipelagos of habitat islands (Fleishman *et al.*, 1997; Fleishman & Murphy, 1999; Fleishman & Mac Nally, 2002). Although some animals may be physically capable of dispersing among canyons, movement often is deterred by canyon topography (frequently narrow and steeply-walled) and the dearth of resources and shelter from predators in the intervening uplands. Many of the breeding birds in our study system have territory sizes ranging from 4 to 40 ha (American Ornithologists' Union, 1992). By contrast, few of the resident butterflies regularly disperse more than a few hundred metres from where they eclosed (Fleishman *et al.*, 1997). Thus, movement within canyons probably is somewhat more common for birds than for butterflies. As a result, one might expect species composition of birds to be less variable in space than species composition of butterflies.

If one assumes that ecological specialization and geographical distribution are correlated (Rabinowitz, 1981; Kunin & Gaston, 1997), then one also might expect beta diversity to be greater among species with relatively specialized resource requirements than among relative generalists. Although birds initially might seem to have more general requirements than butterflies, this may not be the case in the Great Basin. In fact, previous work suggested that resource specialization was more strongly associated with structure of bird assemblages than was territory size (Fleishman *et al.*, 2002). Species composition of breeding birds in our study system may be affected by the patchy distribution of trees such as willow (*Salix* spp.), aspen (*Populus tremuloides*), and piñon (*Pinus monophylla*), which provide nesting sites that differ in their suitability for particular species or guilds (Fleishman *et al.*, 2003). Butterflies often are considered 'specialists' because they are restricted to one or a few closely related larval host plants (Ehrlich & Raven, 1965; Scott, 1986; Kremen, 1992; Blair & Launer, 1997). However, in many ecosystems, the resource requirements of adult butterflies are fairly general (Holl, 1995; Pullin, 1995). Many adult butterflies can exploit virtually any source of nectar, from flowering shrubs to native forbs to non-native invasive species. Previous work has shown that availability of nectar is positively correlated with spatial distribution of adults and larvae (Gilbert & Singer, 1973; Murphy, 1983; Murphy *et al.*, 1984) and may lessen local emigration (Kuussaari *et al.*, 1996; Moilanen & Hanski, 1998). Thus, species composition of butterflies in the Great Basin may be more closely associated with distribution of an array of potential nectar sources than with distribution of specific larval host plants.

In this paper, we examine whether variation in species composition of birds and of butterflies in the Great Basin depended on sampling grain (the smallest resolvable unit of study) and on the proximity of sampling units across the landscape. We also compare response of species composition to sampling grain and proximity between the two taxonomic groups with reference to their life-history characteristics.

METHODS

Field methods

Data for our analyses were collected from 1996 to 2003 in three adjacent mountain ranges in the central Great Basin, the Shoshone Mountains (1850 km^2, approximate north–south boundaries 39°14′19″ to 38°57′32″), Toiyabe Range (3100 km^2, approximate north–south boundaries 39°54′ to 38°30′), and Toquima Range (1750 km^2, approximate north–south boundaries 39°17′50″ to 38°29′9″) (Lander and Nye counties, Nevada, USA) (Fig. 1). These mountain ranges have similar regional climate, biogeographical past and ancestral biota, and human land-use histories (Wilcox *et al.*, 1986; Austin & Murphy, 1987; Grayson, 1993; Fleishman *et al.*, 2000).

Inventories for breeding birds were conducted in five canyons in the Shoshone Mountains, five canyons in the Toiyabe Range and six canyons in the Toquima Range. Inventories for resident butterflies were conducted in eight canyons in the Shoshone Mountains, 15 canyons in the Toiyabe Range and 11 canyons in the Toquima Range. Distances between canyons in these three mountain ranges, and particularly between the canyons we sampled, usually were much greater than the territory or home range sizes of birds (at least during the breeding season) (Ryser, 1985; Dobkin & Wilcox, 1986; American Ornithologists' Union, 1992) and resident butterflies (Fleishman *et al.*, 1997) in our study system.

We divided canyons into multiple contiguous sites (segments) from base to crest. Each site was 100 m wide and long enough to span a 100-m change in elevation (Fleishman *et al.*, 1998, 2001). Mean site length was 1.5 km; more than two-thirds of the sites were >1 km long. Inventories for birds were conducted from 2001 to 2003 in 24 sites in the Shoshone Mountains, 31 in the Toiyabe Range and 28 in the Toquima Range. Inventories for butterflies were conducted from 1995 to 2003 in 39 sites in the Shoshone Mountains, 102 in the Toiyabe Range and 54 in the Toquima Range.

Our sampling locations covered an elevational range of 1872–3272 m and areas from 1.5 to 44.4 ha. We followed standard inventory methods for birds and butterflies in temperate regions (Shapiro, 1975; Swengel, 1990; Pollard & Yates, 1993; Harding *et al.*, 1995; Bibby *et al.*, 2000). Birds were sampled during the breeding season (late May to June) using two or three 75-m fixed-radius point counts in each site.

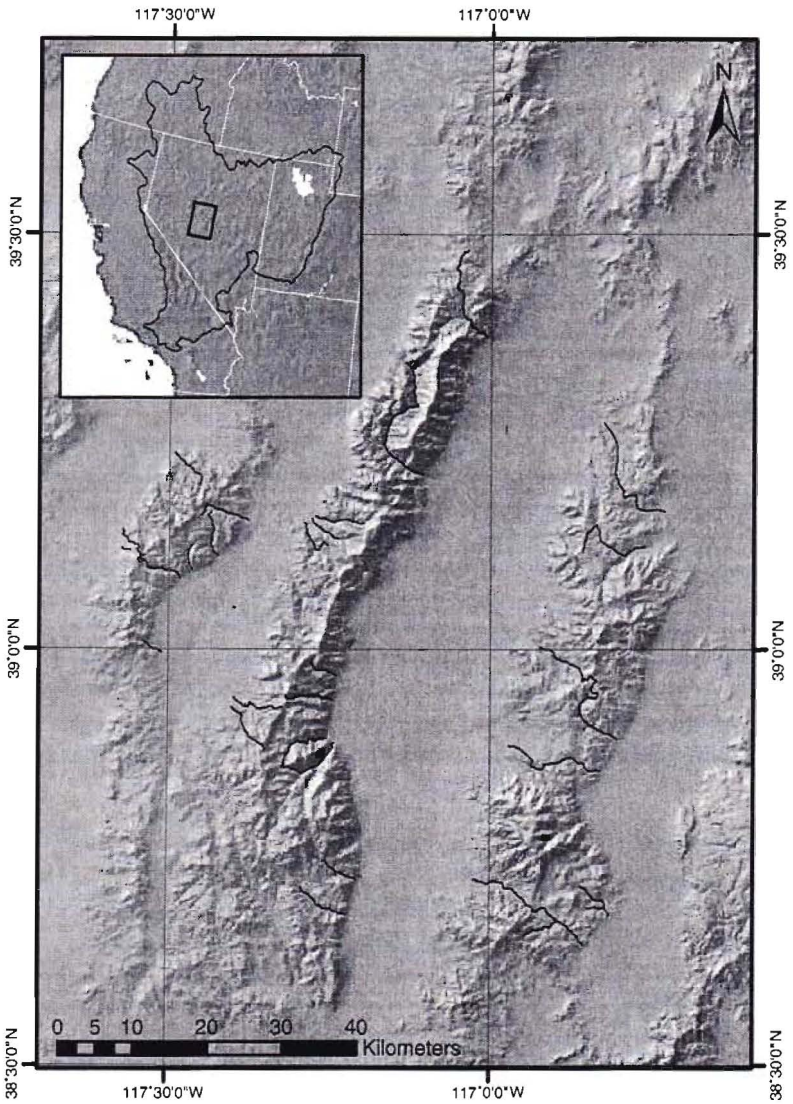

Figure 1 Location of the Shoshone Mountains, Toiyabe Range and Toquima Range in the Great Basin (black rectangle, see inset) and inventory canyons in the three mountain ranges (thick black lines). Two pairs of canyons in the Toiyabe Range and three pairs of canyons in the Toquima Range connect at the crest of the range.

Within a site, points were located in each of the dominant vegetation types (e.g. aspen, willow, piñon-juniper, wet meadow and sagebrush) to account for the influence of variables such as tree species composition, tree size, and water availability on avian species richness and composition (Betrus, 2002; Poulson, 2002). Each site included at least two point-count locations even if there was only one major vegetation type. Sites included three point-count locations when there were three different vegetation types within the site. Point count locations were at least 200 m apart.

Each time a point was surveyed, we recorded all birds actively using terrestrial habitat within the circle. During our inventories, birds displayed a variety of breeding behaviours including frequent song repetition by males, collection of nest material, nest building, incubation, parental care and territorial defence. Each point was visited three times during the breeding season. Point counts were conducted only under fair skies. Each point received at least one count within 2 h of dawn and at least one count between 2 and $3\frac{1}{2}$ h after dawn. No counts were conducted more than $3\frac{1}{2}$ h after dawn. Three surveys are considered sufficient to determine which species of birds are present at point count locations (Siegel *et al.*, 2001). In addition, point counts have been shown to be an effective method of sampling birds in riparian areas in the Great Basin (Dobkin & Rich, 1998). In our work, species accumulation curves for birds at the site and canyon levels generally approached an asymptote by the third round of surveys (Betrus, 2002). We recorded 79 species of breeding birds from our study sites. Complete data are available from the corresponding author on request.

We inventoried butterflies using walking transects, an established technique for temperate regions that reliably detects species presence and permits assessment of distributional trends across space and time (Pollard & Yates, 1993; Harding *et al.*, 1995). These methods have been described in considerable detail in previous publications (e.g. Fleishman

et al., 1998, 2000, 2001), so we present just a brief overview here. Approximately every 2 weeks throughout the majority of the flight season (late May to August – i.e. the period during which adult butterflies are present), using equal sampling effort per unit area, we recorded the presence of all butterfly species seen in each site. It is reasonable to interpret that a given butterfly species is absent if the area has been searched using these methods during the appropriate season and weather conditions (Pullin, 1995; Reed, 1996). In the Toiyabe Range, for example, we recorded 98% of the theoretical number of species expected under a Michaelis–Menten model (Clench, 1979; Raguso & Llorente-Bousquets, 1990; Soberón & Llorente, 1993; Fleishman *et al.*, 1998). Sites were sufficiently large relative to the home ranges of resident butterflies in the region that the short-term presence of butterfly species in each site was independent (i.e. an individual was not recorded in >1 site during an inventory round) (Fleishman *et al.*, 1997). We recorded 65 resident species of butterflies from our study sites. Complete data are available from the corresponding author on request.

Analyses

Our smallest sampling grain was the site. A given site was located within a particular canyon within one of the three mountain ranges. In assessing faunal similarity, we could compare the species composition of birds or butterflies in any one site with the species composition in any other site. There were three possibilities with respect to the relative proximity of two sites. First, both sites could be located within the same canyon ($\pi_{\text{within-canyons}}$). Secondly, the two sites could be in different canyons within the same mountain range ($\pi_{\text{among-canyons}}$). Thirdly, the sites could be located in canyons in different mountain ranges ($\pi_{\text{among-ranges}}$). The number of species was the same for all spatial arrangements (79 species of birds, 65 species of butterflies).

To produce species lists at the whole canyon level, our intermediate sampling grain, we compiled species lists for all contiguous sites within a given canyon. On average, the area of a canyon was six times larger than the area of a site. There were two possibilities with respect to the relative proximity of two canyons. First, two canyons might be located within the same mountain range ($\chi_{\text{within-ranges}}$). Secondly, the canyons could be in different mountain ranges ($\chi_{\text{among-ranges}}$). To produce species lists at the mountain range level, our largest sampling grain, we compiled species lists for all canyons that were visited in a given mountain range. We could then calculate similarity of species composition among mountain ranges ($\rho_{\text{among-ranges}}$). Data at the mountain range level were less exhaustive than data for canyons or sites. Although we included the majority of accessible canyons in our inventories, especially for butterflies, some canyons in each mountain range were too remote or impenetrable to be visited on a regular basis. Inventories for birds were constrained by the number of locations that could be visited in the early morning hours during the breeding season.

For each sampling grain in turn – sites, canyons and mountain ranges – we calculated similarity of species composition using the Jaccard index, $C_J = j/(a+b-j)$, where j is the number of species found in all locations and a and b are the number of species in locations A and B, respectively. C_J is 1.0 when species composition is identical between locations and 0.0 when two locations have no species in common (Magurran, 1988).

We conducted three analyses on the sets of similarity values for sites, canyons and mountain ranges. First, we investigated whether mean similarity of species composition among the three ranges differed as a function of the grain size at which data were compiled:

$$\pi_{\text{among-ranges}} \text{ vs. } \chi_{\text{among-ranges}} \text{ vs. } \rho_{\text{among-ranges}}.$$

Secondly, we explored whether mean similarity of species composition was greater for canyons within the same mountain range than for canyons within different mountain ranges:

$$\chi_{\text{among-ranges}} \text{ vs. } \chi_{\text{within-ranges}}.$$

Thirdly, we examined whether mean similarity of species composition at the site level was different for sites within the same canyon, sites within different canyons in the same mountain range, and sites within canyons in different mountain ranges:

$$\pi_{\text{within-canyons}} \text{ vs. } \pi_{\text{among-canyons}} \text{ vs. } \pi_{\text{among-ranges}}.$$

We used a simple Bayesian approach to quantify these comparisons. One of the advantages of this approach was that it provided credible intervals for differences between mean similarities of species composition. Credible intervals summarize the state of uncertainty concerning the value of the fixed constant – the parameter's true value – about which our sample provides information. Thus, one often uses '95% Bayesian credible intervals' (Lee, 1989) to characterize the range of values for the parameter that encompasses 95% of the probability mass for that parameter. Credible intervals are conceptually distinct from the frequentist confidence interval, the interpretation of which depends on the theoretical possibility of repeating an experiment or survey many times, which is rarely possible in biogeographical studies (e.g. there is only one Shoshone Mountains, one Toiyabe Range and one Toquima Range).

The basic model we used was

$$Y_{ij} = \mu_0 + \zeta_i, \quad Y_{ij} \sim \text{Norm}(\mu_i, \sigma^2_{\text{within}}); \quad \mu_i \sim \text{Norm}(\mu_i, \sigma^2_{\text{between}}).$$

In this model, the Y_{ij} are the similarities of species composition between a pair of sampling units at any spatial grain (sites, canyons or mountain ranges), μ_0 is the intercept, and ζ_i is the effect of 'treatment' i. Treatments were alternative proximities of locations, e.g. sampling units within the same mountain range vs. sampling units in different mountain ranges, and there were either two or three treatments depending on which spatial grain was being examined (two for mountain ranges and canyons, three for

sites; see above). The intercept was 'aliased' with the first treatment, so that the ζ_i for the second (and, in some cases, third) treatment(s) was expressed relative to the first treatment (i.e. $\zeta_1 \equiv 0$). For example, if $\mu_0 = 0.3$ and $\zeta_2 = 0.2$, then the mean of the first treatment was estimated to be 0.3 and the mean of the second treatment was $\mu_0 + \zeta_2 = 0.3 + 0.2 = 0.5$.

The Y_{ij}s are imperfect measurements assumed to represent Normally distributed unknown fixed means μ_i with a common variance. We computed variance components for between treatments ($\sigma^2_{\text{between}}$) and within treatments (σ^2_{within}).

Software and statistical decision criteria

We used the WinBUGS Bayesian analysis program (version 1.4, Spiegelhalter *et al.*, 2003). The Bayesian approach to estimating parameters formally incorporates prior knowledge about the values of a parameter and produces a probability statement about the interval within which the parameter value lies. This means that each regression coefficient will have a distribution of values rather than a single value. If one has no prior knowledge about the values of a parameter, then it is appropriate to use a 'non-informative' prior distribution for that parameter. One might use a flat uniform distribution (between two endpoints, ±1000 perhaps) or a Normal distribution with high variance (mean = 0, variance = 200, perhaps). Use of non-informative priors when there is little or no prior information means that the posterior probability distributions are dictated by the newly collected data (Lee, 1989). In this study, we used non-informative, Normal priors for all parameters because we had no prior information about how mean similarity of species composition of birds and butterflies varied as a function of spatial grain or relative proximity of sampling units. In all analyses, means and medians of posterior distributions of parameters were similar, indicating symmetric probability distributions.

Bayesians eschew significance tests using the null-hypothesis–*P*-value framework. Nevertheless, there is a sophisticated field of Bayesian decision-making using Bayes factors (Spiegelhalter & Smith, 1982; Gelman *et al.*, 1995) and decision theory (Bernardo & Smith, 1994; Jaynes, 2003). We took a simple approach in which our decision criterion for whether there were 'substantial' differences among treatments was whether differences in model coefficients had a high (> 90%) posterior probability of being greater than or less than zero. Bayesian calculations provide a probability distribution for each model parameter (and combinations thereof, such as differences between any two parameters), and one can compute how much of this distribution lies above or below zero. For example, for a parameter with a negative mean, 78% of the probability mass might lie below zero and 22% above zero. Because 78% < 90%, we regarded the values as providing only limited evidence that the parameter was sufficiently 'far' from zero to be an important effect. However, if 93% of the probability mass were below zero, then this provided stronger evidence that the effect associated with the parameter indeed was important. For parameters (or functions of parameters) with positive means, the fraction of the probability mass above zero was used as the criterion. Note that use of a decision criterion, as with a significance level, is arbitrary. However, because our data were Normally distributed, readers can select a different decision criterion, such as > 75% or > 95%, that they believe to be more appropriate.

RESULTS

To avoid potential confusion, note that the mean ± SD values cited in the text are the sample means and SDs computed from the Jaccard similarities, without reference to the Bayes model. Sample means are not expressed relative to the first treatment (see Methods). Values in the accompanying tables are parameter means (±SDs) from the Bayes model, and are expressed relative to the first treatment. Percentages in the text were calculated using parameter means.

Similarity of species composition among mountain ranges as a function of sampling grain: $\pi_{\text{among-ranges}}$ vs. $\chi_{\text{among-ranges}}$ vs. $\rho_{\text{among-ranges}}$

Birds

First, we explored whether similarity of species composition of birds among mountain ranges differed as a function of sampling grain. We found that mean similarity of species composition increased as the sampling grain increased: $\pi_{\text{among-ranges}} < \chi_{\text{among-ranges}} < \rho_{\text{among-ranges}}$. Mean similarity of species composition of birds among mountain ranges was 117% higher when measured at the spatial grain of mountain ranges (ρ) (0.662 ± 0.068 SD) than at the spatial grain of sites (π) (0.295 ± 0.126 SD) (percentage calculated using parameter means in Table 1). Likewise, mean similarity of species composition of birds among mountain ranges was 69% higher when measured at the spatial grain of canyons (χ) (0.498 ± 0.088 SD) than at the spatial grain of sites (π). These differences were deemed substantial using our Bayesian decision criterion [posterior probability mass (PPM) column in Table 1]. About 85% (median 88%) of the variation in the similarity values was attributable to differences in sampling grain; we provide median estimates for these variance proportions because of their asymmetric (Gamma) probability distributions (Table 1).

Butterflies

Similarity of species composition of butterflies among mountain ranges, like birds, differed as a function of sampling grain, with mean similarity of species composition increasing as the sampling grain increased. However, similarity of species composition of butterflies at each sampling grain was greater than similarity of species composition of birds at the same grain (Tables 1 & 2). At the smallest grain,

Table 1 Bayesian comparisons of differences in mean similarity of species composition of birds at three sampling grains in increasing order of size: sites, canyons, and mountain ranges. μ_0 is the intercept, and ζ_i is the effect of each 'treatment' i – an alternative spatial configuration (relative proximity) of sampling units. ζ_i for the second and third treatments are expressed relative to the first treatment. Thus, the mean of the second treatment was 0.295 + 0.203 = 0.498, and the mean of the third treatment was 0.295 + 0.344 = 0.639. $\sigma^2_{between}$ is the variance component between treatments and σ^2_{within} is the variance component within treatments. Values for the lowest 2.5% of the posterior probability distribution of each quantity fell below the 2.5% credible interval, and values for the upper 2.5% of the probability distribution of each quantity fell above the 97.5% credible interval. The posterior probability mass (PPM) shows the fraction of the probability distribution that lay above zero. PPM > 0.9 (for positive means) or < 0.1 (for negative means) were considered substantial – i.e. evidence that the effect was important

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: sites (n = 3486)	0.295 ± 0.002	0.291	0.299	–
ζ_2: canyons (n = 120)	0.203 ± 0.012	0.179	0.227	1
ζ_3: ranges (n = 3)	0.344 ± 0.074	0.204	0.492	1
$\zeta_2 - \zeta_3$	−0.142 ± 0.075	−0.288	0.006	0.03
$\sigma^2_{between}$ (proportion)	0.846 ± 0.122*	0.570	0.994	–
σ^2_{within} (proportion)	0.154 ± 0.122†	0.008	0.442	–

Medians: *0.876, †0.125.
Values in the text are sample means rather than means obtained from the Bayes model.

sites (π), mean similarity of species composition of butterflies was 0.397 ± 0.132 SD. At the intermediate grain, canyons (χ), mean similarity of species composition of butterflies was 0.581 ± 0.136 SD. At the largest sampling grain, mountain ranges (ρ), mean similarity of species composition of butterflies was 0.875 ± 0.079 SD. The difference in values among spatial grains was substantial on the basis of our Bayesian decision criterion (Table 2). More than 88% of the variance in mean similarity of species composition was attributable to difference in relative proximity of sampling units (Table 2).

Similarity of species composition among canyons as a function of relative proximity: $\chi_{among\text{-}ranges}$ vs. $\chi_{within\text{-}ranges}$

Birds

We investigated whether similarity of species composition of birds among canyons differed as a function of relative proximity – whether mean similarity of species composition was greater for canyons within the same mountain range than for canyons within different mountain ranges. Mean similarity of species composition of birds among pairs of canyons within the same mountain range (0.554 ± 0.074 SD) was 14% greater than mean similarity of species composition of birds among pairs of canyons in different mountain ranges (0.474 ± 0.082 SD); this difference was substantial using our Bayesian decision criterion (Table 3). The majority of the variance in mean similarity of species composition (69%) was associated with relative proximity (the treatment difference) (Table 3).

Butterflies

Results for butterflies were similar to those for birds. Similarity of species composition of butterflies among canyons differed as a function of relative proximity. Mean similarity of species composition of butterflies among pairs of canyons within the same mountain range (0.615 ± 0.137 SD) was about 8% greater than mean similarity of species composition among pairs of canyons in different mountain ranges (0.564 ± 0.132 SD); this difference was substantial (Table 4). However, in this analysis, unlike previous analyses, less than 50% of the variance

Table 2 Bayesian comparisons of differences in mean similarity of species composition of butterflies at three sampling grains in increasing order of size: sites, canyons and mountain ranges

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: sites (n = 18,916)	0.397 ± 0.001	0.396	0.399	–
ζ_2: canyons (n = 561)	0.184 ± 0.005	0.173	0.195	1
ζ_3: ranges (n = 3)	0.457 ± 0.078	0.306	0.613	1
$\zeta_2 - \zeta_3$	−0.273 ± 0.078	−0.425	−0.117	0
$\sigma^2_{between}$ (proportion)	0.881 ± 0.103*	0.630	0.997	–
σ^2_{within} (proportion)	0.119 ± 0.103†	0.003	0.375	–

PPM, posterior probability mass.
Medians: *0.907, †0.093.

Table 3 Bayesian comparisons of differences in mean similarity of species composition of birds at the intermediate sampling grain (canyons), with two different relative proximities: canyons within the same mountain range and canyons in different mountain ranges

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: within ranges (n = 35)	0.553 ± 0.014	0.525	0.580	–
ζ_2: among ranges (n = 85)	−0.078 ± 0.017	−0.110	−0.045	0
$\sigma^2_{between}$ (proportion)	0.692 ± 0.255*	0.183	1.000	–
σ^2_{within} (proportion)	0.308 ± 0.255†	0.001	0.821	–

PPM, posterior probability mass.
Medians: *0.752, †0.250.

Table 4 Bayesian comparisons of differences in mean similarity of species composition of butterflies at the intermediate sampling grain (canyons), with two different relative proximities: canyons within the same mountain range and canyons in different mountain ranges

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: within ranges (n = 187)	0.616 ± 0.010	0.596	0.636	–
ζ_2: among ranges (n = 374)	−0.051 ± 0.013	−0.076	−0.026	0
$\sigma^2_{between}$ (proportion)	0.438 ± 0.311*	0.042	0.996	–
σ^2_{within} (proportion)	0.562 ± 0.311†	0.004	0.958	–

PPM, posterior probability mass.
Medians: *0.358, †0.643.

in mean similarity of species composition (44%, median 36%) was attributable to relative proximity or 'treatment' (Table 4).

Similarities of species composition among sites as a function of relative proximity: $\pi_{within\text{-}canyons}$ vs. $\pi_{among\text{-}canyons}$ vs. $\pi_{among\text{-}ranges}$

Birds

Mean similarity of species composition of birds among sites varied as a function of the relative proximity of those sites: $\pi_{within\text{-}canyons} > \pi_{among\text{-}canyons} > \pi_{among\text{-}ranges}$. Mean similarity of species composition of birds among pairs of sites within the same canyon (0.379 ± 0.156 SD) was about 8% greater than mean similarity of species composition among pairs of sites in different canyons in the same mountain range (0.348 ± 0.138 SD). The greatest difference in species composition of birds occurred among sites in different mountain ranges (0.267 ± 0.107 SD). Similarity of species composition of birds among sites in different mountain ranges was 30% less than similarity among sites within the same canyon. Differences in relative proximity were substantial (Table 5). About 38% of the variance in similarities was attributable to relative proximity of sampling units (Table 5).

Butterflies

Results for butterflies were similar to results for birds: $\pi_{within\text{-}canyons} > \pi_{among\text{-}canyons} > \pi_{among\text{-}ranges}$. Mean similarity of species composition of butterflies among pairs of sites within the same canyon (0.523 ± 0.156 SD) was *c.* 20% greater than mean similarity of species composition among pairs of sites in different canyons in the same mountain range (0.419 ± 0.140 SD) and *c.* 28% greater than mean similarity of species composition among pairs of sites in different mountain ranges (0.379 ± 0.120 SD). Both differences were substantial using our Bayesian decision criterion (Table 6). About 42% of the variation in similarity of species composition was attributable to relative proximity (Table 6).

Table 5 Bayesian comparisons of differences in mean similarity of species composition of birds at the smallest sampling grain (sites), with three different relative proximities: sites in different canyons in the same mountain range, sites in different mountain ranges, and sites within the same canyon

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: among canyons (n = 951)	0.347 ± 0.004	0.340	0.354	–
ζ_2: among ranges (n = 2343)	−0.080 ± 0.005	−0.098	−0.072	0
ζ_3: within canyons (n = 192)	0.031 ± 0.009	0.012	0.050	1
$\zeta_2 - \zeta_3$	−0.112 ± 0.009	−0.128	−0.092	0
$\sigma^2_{between}$ (proportion)	0.377 ± 0.237*	0.080	0.923	–
σ^2_{within} (proportion)	0.624 ± 0.237†	0.080	0.920	–

PPM, posterior probability mass.
Medians: *0.306, †0.695.

Table 6 Bayesian comparisons of differences in mean similarity of species composition of butterflies at the smallest sampling grain (sites), with three different relative proximities: sites in different canyons in the same mountain range, sites in different mountain ranges, and sites within the same canyon

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: among canyons (n = 6772)	0.419 ± 0.002	0.415	0.422	–
ζ_2: among ranges (n = 11,592)	−0.040 ± 0.002	−0.043	−0.036	0
ζ_3: within canyons (n = 555)	0.104 ± 0.006	0.093	0.115	1
$\zeta_2 - \zeta_3$	−0.143 ± 0.006	−0.155	−0.132	0
$\sigma^2_{between}$ (proportion)	0.419 ± 0.232*	0.107	0.938	–
σ^2_{within} (proportion)	0.581 ± 0.232†	0.063	0.893	–

PPM, posterior probability mass.
Medians: *0.366, †0.664.

DISCUSSION

We found that variation in species composition of birds and of butterflies in the Great Basin depended on both sampling grain (the smallest resolvable unit of study) and on the relative proximity of sampling units across the landscape. At all three sampling grains, species composition of butterflies was more similar than species composition of birds. The effect of spatial grain was greater for birds than for butterflies, especially when the intermediate sampling grain was compared with the smallest sampling grain. The effects of relative proximity of sampling units across the landscape were not uniformly greater for either taxonomic group.

Sampling grain

Species composition of both birds and butterflies varied as a function of sampling grain (the smallest resolvable unit of study). Similarity of species composition increased as the sampling grain increased, and the majority of variation in similarity values (*c.* 85% for birds, 88% for butterflies) was attributable to sampling grain. This result almost certainly reflects the effect of local environmental heterogeneity on species composition. Species composition within a canyon may respond to differing distributions of resources or microclimatic features along an elevational gradient. As sampling resolution increases, biotic assemblages appear more homogeneous (i.e. similarity of species composition between two assemblages increases). Within a mountain range, the distribution of resources along an elevational gradient may be similar among canyons (Fleishman *et al.*, 2003). At the mountain range level, species composition may reflect emerging similarities in terms of regional climate, land cover and land use.

Relative proximity

We examined the effects of relative proximity of sampling units at two different grains – canyons and sites. Irrespective of grain size or taxonomic group, similarity of species composition decreased as the biogeographical separation between sampling units increased. At the canyon grain, the effect of relative proximity was considered substantial using the Bayesian decision criterion. However, the absolute difference in species composition in response to relative proximity was modest – assemblages of birds were 14% more similar, and assemblages of butterflies were 8% more similar, when canyons were located in the same mountain range than when canyons were located in different mountain ranges. These results and our personal observations concur with the remarks of previous workers (e.g. Dobkin & Wilcox, 1986) that even within the same mountain range, canyon physiography is extremely variable. Although there are relatively few major land cover types in the Great Basin, they are distributed in a remarkable array of local vegetational mosaics. Canyons in relatively dry mountain ranges usually have more depauperate assemblages of plants and animals than canyons in relatively mesic mountain ranges, yet almost every canyon remains an 'island' with a distinct character. Thus, a randomly selected pair of canyons within the same mountain range may not be much more similar than a randomly selected pair of canyons from two nearby mountain ranges.

At the smallest grain (sites), the effect of relative proximity was again (statistically) substantial but less than expected, especially within a mountain range. Mean similarity of species composition of birds among sites within the same canyon was only *c.* 8% greater than among sites in different canyons in the same mountain range. Relative proximity had a stronger effect on similarity of butterfly assemblages (20% greater among sites within the same canyon than among sites in different canyons in the same mountain range). A likely explanation may be, as noted above, that species composition within a canyon reflects local environmental heterogeneity – the distribution of resources for birds and butterflies often shifts along an elevational gradient (Fleishman *et al.*, 1998, 2000). Two sites within the same canyon are more similar than two sites within different canyons, but the resemblance is not necessarily close. The magnitude of the difference in species composition increased as we compared sites within a canyon to sites in different ranges. The latter result may be associated with broad, mountain range-level differences in moisture and associated resource availability.

Taxonomic group

As we compare the effects of spatial grain and relative proximity on beta diversity of birds and butterflies, two differences immediately are apparent. First, at all spatial grains (sites, canyons and mountain ranges), species composition of butterflies was more similar than species composition of birds. At the smallest grain (sites), mean similarity of species composition of butterflies was 10% higher than that of birds. The difference was 8% at the intermediate grain (canyons) and 21% at the largest grain (mountain ranges). Secondly, although the difference in species composition at the largest vs. intermediate grains was very similar for both taxonomic groups, there was noticeably (23%) more difference in species composition of birds than of butterflies at the intermediate grain vs. the smallest grain.

Breeding birds in our study system typically have territory sizes or home ranges about an order of magnitude larger than resident butterflies (American Ornithologists' Union, 1992; Fleishman *et al.*, 1997). If home range size is the primary influence on species composition, then beta diversity of birds should be lower than beta diversity of butterflies. If resource requirements are influential, then beta diversity of taxonomic groups with relatively general needs should be lower than beta diversity of groups with more specialized needs.

Species composition of birds has been thought to be more closely associated with vegetation structure (physiognomy) than with vegetation composition (floristics) (MacArthur *et al.*, 1966; Anderson & Shugart, 1974; Rotenberry & Wiens, 1980). However, some evidence suggested that vegetation composition is more influential than vegetation structure (Tomoff, 1974; Power, 1975; Wiens & Rotenberry, 1981), especially at relatively small spatial grains and extents (Rotenberry, 1985; Wiens *et al.*, 1987). As we noted in the Introduction, most species of trees in our study system have heterogeneous distributions. Piñon (*P. monophylla*) and juniper (*Juniperus osteosperma*) are relatively widespread and sometimes form large stands, especially in drier areas. However, riparian trees and shrubs such as cottonwood and aspen (*Populus* spp.), willow (*Salix* spp.), chokecherry (*Prunus virginiana*), elderberry (*Sambuca* spp.), birch (*Betula occidentalis*), and rose (*Rosa woodsii*) have relatively patchy distributions, even in canyons with permanent sources of running or

standing water. Neotropical migrant birds in particular (about one-third of the species of birds we recorded winter in the neotropics, Gough *et al.*, 1998) are thought to be relatively selective in choosing nesting sites because of the physical stress they undergo during migration and the limited temporal window available for establishing a breeding territory and reproducing (Robbins *et al.*, 1989; Martin, 1992, 1995). Year-round residents tend to be less selective. Most Neotropical migrants are insectivores, for example, while most year-round residents must exploit a greater range of food sources because insects are not available during the winter.

As spatial scale increases, the strength of the correlation between floristics and physiognomy may also increase (Mac Nally *et al.*, 2002). In addition, at larger spatial scales, species composition of birds, butterflies, and their resources may exhibit similar responses to abiotic environmental gradients (Hawkins & Porter, 2003). It is possible that for birds, the scale at which species distributions reflect sensitivity to floristics, vegetational heterogeneity, or both that lies somewhere between the site (canyon segment) level and the canyon level.

A similarity in the response of beta diversity of birds and butterflies to sampling grain also stands out: at small spatial grains, and even at intermediate sampling grains, variation in species composition was considerable. At the smallest grain, mean similarities of species composition of birds and butterflies were 0.295 and 0.397, respectively; at the intermediate grain, mean similarities were 0.498 for birds and 0.581 for butterflies. At the largest grain, mean similarities were 0.662 for birds and 0.875 for butterflies. In ecosystems with appreciable heterogeneity in physiography and land cover, turnover in species composition across a range of spatial scales is an important component of diversity patterns. Our results suggest that spatially extensive sampling may be a more effective strategy than sampling small areas scattered across the landscape for drawing inferences about regional species composition.

Ecologists are well aware that measures of species diversity, and inferences about diversity patterns, depend on spatial and temporal scale. Our work examined alternative hypotheses about sensitivity of birds and butterflies to the size of sampling units (spatial grain or resolution) and to the relative proximity of sampling units across the landscape. Contrary to expectations based on relative home range size of taxonomic groups, we found that assemblages of birds were more variable in space than assemblages of butterflies. Our results suggest that nesting and food resources may have considerable influence on beta diversity of birds, while the distribution of adult food resources appears to have a strong influence on beta diversity patterns of butterflies. Although the species composition of potential nectar sources varies in space, those resources often are relatively widespread. Field tests of diversity theories have great value for ecology and conservation. As our understanding of relationships between species diversity and various components of 'scale' increases, so should our ability to recognize underlying mechanisms. Such knowledge also increases our ability to make decisions about land use and land management that will allow us to maximize native biological diversity and ecological integrity.

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