

Research article

Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin, USA

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Abstract

Different taxonomic groups perceive and respond to the environment at different scales. We examined the effects of spatial scale on diversity patterns of butterflies and birds in the central Great Basin of the western USA. We partitioned the landscape into three hierarchical spatial levels: mountain ranges, canyons, and sites within canyons. We evaluated the relative contribution of each level to species richness and quantified changes in species composition at each level. Using additive partitioning, we calculated the contribution of spatial level to overall species diversity. Both canyon and mountain range had significant effects on landscape-level species richness of butterflies and birds. Species composition of butterflies was more similar in space than species composition of birds, but assemblages of both groups that were closer together in space were less similar than assemblages that were further apart. These results likely reflect differences in resource specificity and the distribution of resources for each group. Additive partitioning showed that alpha diversity within canyon segments was the dominant component of overall species richness of butterflies but not of birds. As the size of a sampling unit increased, its contribution to overall species richness of birds increased monotonically, but the relationship between spatial scale and species richness of butterflies was not linear. Our work emphasizes that the most appropriate scales for studying and conserving different taxonomic groups are not the same. The ability of butterflies and birds to serve as surrogate measures of each other's diversity appears to be scale-dependent.

Introduction

Landscapes can be partitioned in many alternative ways. For example, a landscape may be represented as a relatively static mosaic of non-overlapping 'patches' or of vegetation types. Landscapes also may be partitioned in a nested spatial or temporal hierarchy (Allen and Starr 1982; Kotliar and Wiens 1990; Underwood and Chapman 1996; Willis and Whittaker 2002). Partitioning of countries into states or provinces, and further partitioning of states into counties or townships, is a familiar illustration of a spatial hi-

erarchy. Months, weeks, and days provide a classic example of a nested temporal hierarchy.

Regardless of how a landscape is partitioned, different components of a landscape typically vary in their contribution to the species diversity of the landscape as a whole. For example, some locations may have relatively high species richness (number of species) or relatively high concentrations of rare species, while other locations may have relatively low species richness or be inhabited mostly by ubiquitous species. The fact that landscape components vary in their contribution to species diversity has important consequences for efforts to understand and conserve bio-

logical diversity (Underwood and Chapman 1996; Willis and Whittaker 2002). If we can determine how each component influences species diversity of the landscape, then we may be able to predict how perturbations to one component—positive or negative—will affect diversity of the system as a whole.

Relationships between landscape components and species diversity also bear on selection of the most appropriate design for a particular research study or land-use plan. Interpretation of how ecological systems are structured often depends on the spatial and temporal scale at which an experimental or observational study is conducted, and the results of studies carried out at different scales may not be comparable (Osenberg et al. 1999; Waide et al. 1999; Gross et al. 2000; Scheiner et al. 2000; Mittelbach et al. 2001; Mac Nally 2002). Testing explicitly whether certain biodiversity patterns are scale-dependent helps to identify relevant spatial and temporal boundaries for studying mechanisms that underly those patterns (Kolasa 1989; Underwood and Chapman 1996; Gering et al. 2003). It is increasingly apparent that different mechanisms may explain diversity patterns at different scales (Willis and Whittaker 2002).

Landscape and diversity partitioning

Organisms vary in their perception of and reaction to their environment as a function of life-history characteristics including resource requirements, mobility, and lifespan (Addicott et al. 1987; Kotliar and Wiens 1990; Mac Nally 2002). Therefore, taxonomic variation adds an additional layer of complexity to deciding how a landscape should be partitioned for research or management purposes. One option is to partition the landscape in terms of the ecology of the focal organism (Kotliar and Wiens 1990; Mac Nally 2002). From the perspective of an insectivorous bat, for example, a landscape may be several square km in spatial extent, consisting of patches suitable for roosting, foraging, and movement, interspersed with areas that the animal cannot exploit (M. Evelyn, personal communication). Another option is to partition the landscape using a convenient human perspective (e.g., administrative boundaries or land-use types), then test whether the latter framework is meaningful for understanding diversity patterns in the taxonomic groups of interest (Addicott et al. 1987; Kolasa 1989).

Under a hierarchical model of landscape organization, such as patches nested within a vegetation type and vegetation types nested within an ecoregion,

measures of species diversity including species richness (number of species) and evenness (the extent to which individuals are distributed equally among species) can be partitioned into within-sampling unit diversity (e.g., diversity of each patch or each vegetation type) and among-sampling unit diversity (e.g., diversity among patches or among vegetation types). Within-sampling unit diversity is roughly equivalent to mean alpha diversity of each sampling unit, and among-sampling unit diversity is roughly equivalent to beta diversity, the degree of change (turnover) in species diversity among the sampling units (MacArthur 1965; Whittaker 1977; Magurran 1988). Using an additive partitioning framework (Allan 1975; Lande 1996; Wagner et al. 2000; Fournier and Loreau 2001; Gering et al. 2003), diversity of each nested component of the landscape can be represented as the sum of alpha and beta diversity at the next lower level. Thus, in the example outlined above, diversity of the landscape would be the sum of mean alpha diversity within vegetation types and beta diversity among vegetation types. Likewise, the diversity of each vegetation type would be the sum of mean alpha diversity within patches and beta diversity among patches. The additive partitioning framework is useful because it allows workers to explore simultaneously the contribution of each nested level to total diversity of the landscape.

In this paper, we use the definitions of grain and extent presented in King (1991) and Morrison and Hall (2001). 'Grain' is the smallest resolvable unit of study (e.g., a 100-m² quadrat), and 'extent' is the area over which observations are made (e.g., 100 km²). The relatively large extent of our study area as compared with many previous examinations of nested or additive measures of species diversity reflects the typical size of land-management units in our focal landscape. Indeed, Loreau (2000) noted the lack of correspondence between most theoretical and experimental studies of biotic diversity and ecosystem function, which have been conducted at relatively small grains and extents, and the much larger extents over which management decisions frequently are made.

Study system and objectives

The Great Basin of western North America includes more than 425,000 km² of internal drainage extending from the Sierra Nevada in the west to the Wasatch Range in the east (Grayson 1993). More than 75% of

Level	Within-level richness (alpha diversity)	Among-level richness (beta diversity)
Landscape	Additive species richness of the mountain ranges	
Mountain range	Species richness of each mountain range	Turnover in species richness among mountain ranges
Canyon	Species richness of each canyon	Turnover in species richness among canyons
Canyon segment	Species richness of each canyon segment	Turnover in species richness among segments within a canyon

Figure 1. Hierarchical model of species richness. Richness at each spatial level derives from the sum of alpha and beta diversity at the next lower level.

the ecoregion is federally owned and is managed for multiple, and often competing, land uses, but implementation of scientifically-informed management plans is hampered in part by lack of information on species distributions and diversity patterns. The topography of the Great Basin is dominated by more than 200 north-south oriented mountain ranges. Plants and animals in these ranges largely were isolated from the surrounding valleys as the regional climate became warmer and drier after the Pleistocene (Brown 1978; Grayson 1993). The climate is arid. Summers are hot, except at high elevations. Winters are mild. Numerous canyons incise the east and west slopes of the ranges. Resource agencies generally develop separate management plans for individual mountain ranges under their jurisdiction. Within mountain ranges, land uses commonly are delineated at the extent of individual or several adjacent canyons.

Our study landscape is contained within ~4000 km² of the Toiyabe Subregion of the Great Basin (Austin and Murphy 1987). Because the Great Basin is so extensive, most taxonomic groups have some biogeographic segregation within the ecoregion (Behle 1978; Harper 1978). Each subregion represents an approximate center of faunal differentiation (Austin and Murphy 1987). We partitioned the study landscape into three nested spatial levels: mountain ranges, canyons within mountain ranges, and segments of canyons (Figure 1). Canyon segments were the smallest grain at which we measured species diversity. By aggregating segments within a canyon (i.e., changing the 'focus' sensu Scheiner et al. 2000), we could measure species diversity at the grain of canyons – or, by aggregating canyons within a mountain range, at the grain of mountain ranges. We evaluated diversity patterns at two spatial extents, landscape and

mountain range, because the functional response of species richness to major environmental gradients sometimes varies among mountain ranges (Fleishman et al. 2000; Fleishman et al. 2001b).

Our partitioning of the landscape certainly reflects human perceptions of topography and land use. The extent to which the levels we designated also reflect faunal perspectives depends on the taxonomic group in question (Addicott et al. 1987; Kolasa 1989). In this study we examined diversity patterns of two taxonomic groups, butterflies and birds. Individual mountain ranges within the Great Basin 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 (McDonald and Brown 1992; Murphy and Weiss 1992). For many species, canyons also represent archipelagos of habitat islands (Fleishman et al. 1997; Fleishman and Murphy 1999; Fleishman and 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. Few of the resident butterflies in our study system regularly disperse more than a few hundred m from where they eclosed (Fleishman et al. 1997; Fleishman et al. 2000). Many of the breeding birds in our study system, however, have territory sizes ranging from 4 ha–40 ha (AOU 1992). Thus, movement among segments within a canyon probably is rare for butterflies but more common for birds.

Our first objective was to determine how butterfly and bird diversity were partitioned within the landscape and to compare patterns between the taxonomic groups. Second, by evaluating the relative contribution of each hierarchical spatial level to over-

all diversity, we aimed to elucidate the most appropriate scales for (1) testing hypotheses about mechanisms underlying distributions of butterflies and birds and (2) sampling and conserving butterflies and birds in the Great Basin.

Methods

Data collection

Data for our analyses were collected in three adjacent mountain ranges in the Great Basin: the Shoshone Mountains, Toiyabe Range, and Toquima Range (Lander and Nye counties, Nevada, USA). The ranges are similar in terms of their regional climate, biogeographic past and ancestral biota, and human land-use histories (Wilcox et al. 1986; Austin and Murphy 1987; Grayson 1993; Fleishman et al. 2000). Inventories for both butterflies and birds were conducted in five canyons each in the Shoshone Mountains and Toiyabe Range and six canyons in the Toquima Range. We divided canyons into multiple segments from base to crest. Each segment was 100 m wide and long enough to span a 100-m change in elevation (Fleishman et al. 1998; Fleishman et al. 2001a). Mean segment length was 1.5 km; more than two-thirds of the segments were > 1 km long. Inventories for both taxonomic groups were conducted in 25 canyon segments in the Shoshone Mountains, 31 segments in the Toiyabe Range, and 28 segments in the Toquima Range.

Our inventories followed standard methods for butterflies and birds in temperate regions (Shapiro 1975; Thomas and Mallorie 1985; Swengel 1990; Kremen 1992; Pollard and Yates 1993; Harding et al. 1995; Bibby et al. 2000). We inventoried resident butterflies using walking transects, an established technique that reliably detects species presence and permits assessment of distributional trends across space and time (e.g., Pollard and Yates 1993; Harding et al. 1995). Approximately every two weeks throughout the majority of the adult flight season (approximately late May through August), we walked the length of each segment at a constant pace (thus, sampling effort was equal per unit area) and recorded the presence of all butterfly species seen. Methods for butterflies are described in more detail in Fleishman et al. (1998). 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).

Breeding birds were sampled three times for five minutes each during the breeding season (May and June) using two or three 75-m fixed-radius point counts in each segment. Within a segment, points were located in each of the dominant vegetation types. Each time a point was surveyed, we recorded all birds actively using terrestrial habitat within the circle. 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 the Great Basin (Dobkin and Rich 1998).

Diversity analyses

As described above, we partitioned our study landscape into three nested spatial levels: mountain ranges, canyons, and canyon segments (Figure 1). Canyon segments were the smallest grain at which we measured species diversity.

Alpha diversity

We used species richness S as our measure of alpha diversity. There are two main reasons why we restricted our analyses to presence-absence data. First, in the Great Basin, abundances of butterflies and, to a lesser extent, birds vary both within and between years in response to variation in temperature and precipitation (Shapiro 1975; Kremen 1992; Pollard and Yates 1993; DeVries et al. 1997; Belthoff et al. 1998; Pollard et al. 1998). Second, variation in faunal abundance is somewhat sensitive to observer bias and its causes can be difficult to attribute (Droege et al. 1998; Link and Sauer 1998).

We analyzed the contribution of canyons and mountain ranges to landscape-level species richness of birds and butterflies using nested analysis of variance (canyon nested into mountain range).

Species composition

To examine spatial variation in species composition, we calculated dissimilarity of species composition between pairs of sampling units (segments within a canyon or canyons within a mountain range) using Bray-Curtis distances. We used non-parametric multivariate analysis of variance (NPMANOVA, Ander-

son 2001; McArdle and Anderson 2001) to test whether community dissimilarity differed (1) among mountain ranges within the landscape and (2) among canyons within a mountain range.

Additive partitioning

The relationship between species diversity and an environmental variable can differ depending on the grain and extent of analysis (e.g., Waide et al. 1999; Gross et al. 2000; Scheiner et al. 2000; Fleishman et al. 2001b). Therefore, we calculated the contribution of each nested spatial level of the landscape to species richness of butterflies and birds at two extents, landscape and mountain range. Species richness of the landscape is the sum of mean alpha diversity within canyon segments, beta diversity (turnover in species richness) among canyon segments, beta diversity among canyons, and beta diversity among mountain ranges. Species richness of each mountain range is the sum of mean alpha diversity within canyon segments, beta diversity among canyon segments, and beta diversity among canyons.

Results

We recorded a total of 64 species of resident butterflies and 67 species of breeding birds from our study locations. Complete species lists are available from the corresponding author upon request.

Alpha diversity

Both canyon and mountain range had significant effects on landscape-level species richness of butterflies (Table 1a) and birds (Table 1b). Mean species richness of both taxonomic groups was highest in the Toiyabe Range and lowest in the Toquima Range. However, species richness of butterflies and birds was not significantly rank-correlated at the level of canyon segments in any of the three mountain ranges.

Species composition

At the landscape extent, variation in species composition was significantly different among mountain ranges (butterflies: $F_{2,15} = 4.99$, $P < 0.001$; birds: $F_{2,15} = 4.46$, $P < 0.001$, Table 2a). Pairwise a posteriori tests showed that species composition of butterflies and of birds was significantly ($P < 0.05$) less

similar among canyons in the Toquima Range than in either the Shoshone Mountains or Toiyabe Range, and that species composition was significantly less similar among canyons in the Shoshone Mountains than in the Toiyabe Range.

At the mountain range extent, variation in species composition of butterflies and birds was significantly different among canyons within all three mountain ranges (Table 2b). In the Shoshone Mountains (butterflies: $F_{4,24} = 2.64$, $P < 0.01$; birds: $F_{4,24} = 2.08$, $P < 0.01$) and Toquima Range (butterflies: $F_{5,27} = 3.40$, $P < 0.001$; birds: $F_{5,27} = 2.05$, $P < 0.01$), the canyon in which species composition was least similar was the same for both taxonomic groups (Underdown in the Shoshone Mountains, Petes West in the Toquima Range), but the rank order of the remaining canyons with respect to community dissimilarity varied between taxonomic groups. In the Toiyabe Range (butterflies: $F_{4,30} = 1.84$, $P < 0.05$; birds: $F_{4,30} = 1.81$, $P < 0.05$), species composition of both butterflies and birds was most similar among segments in the same canyon (Washington), but the rank order of the remaining four canyons with respect to community dissimilarity again varied between taxonomic groups.

Contrary to the expectation that assemblages closer together in space should be more similar to each other than assemblages that are further apart (Underwood and Chapman 1996, but see Underwood and Chapman 1998), variation in species composition of butterflies and birds tended to be greater among segments within a canyon than among canyons within a mountain range. For both taxonomic groups, the latter pattern was violated in only three of 16 canyons (two of which were the same for both butterflies and birds).

Additive partitioning of species richness

At both the landscape extent and the mountain range extent, mean alpha diversity of butterflies at every spatial level – canyon segments, canyons, and mountain ranges – was considerably greater than beta diversity at that level. Mean alpha diversity of birds within mountain ranges also was much greater than beta diversity among mountain ranges. However, beta diversity of birds among canyons and among canyon segments was greater than alpha diversity within canyons and within canyon segments.

For butterflies, the relationship between the size of a landscape level and its contribution to overall spe-

Table 1. Effects of canyon and mountain range on alpha diversity (mean species richness, \bar{S}) of butterflies and birds. Effects were analyzed using nested analysis of variance.

effect	df	F	P		\bar{S} (mean \pm SE)
1a. Butterflies					
canyon	13	2.22	0.02	Moores East	19.3(2.5)
				Moores West	21.0(4.5)
				Northumberland East	20.8(2.2)
				Northumberland West	27.5(1.7)
				Petes East	18.7(1.9)
				Petes West	9.2(2.4)
				Big Creek	29.3(4.5)
				Birch	37.7(3.4)
				Kingston	34.9(3.8)
				San Juan	28.0(2.4)
				Washington	35.6(2.9)
				Barrett	27.8(1.7)
				Becker	24.0(1.5)
				Riley	10.4(1.4)
				Schoonover	16.5(1.6)
				Underdown	20.7(2.1)
mountain range	2	25.08	< 0.0001	Toquima	21.7(1.6)
				Toiyabe	35.9(1.5)
				Shoshone	25.1(1.7)
1b. Birds					
canyon	13	1.81	0.0551	Moores East	7.8(1.4)
				Moores West	5.8(0.5)
				Northumberland East	5.2(0.5)
				Northumberland West	9.0(0.7)
				Petes East	10.3(1.9)
				Petes West	7.4(1.3)
				Big Creek	8.4(1.0)
				Birch	9.9(2.2)
				Kingston	9.4(0.6)
				San Juan	9.4(3.2)
				Washington	15.2(0.8)
				Barrett	8.3(1.1)
				Becker	7.7(0.3)
				Riley	10.4(1.4)
				Schoonover	16.8(2.1)
				Underdown	6.6(1.2)
mountain range	2	3.73	0.03	Toquima	9.0(1.0)
				Toiyabe	12.5(1.0)
				Shoshone	11.7(1.1)

cies richness was not monotonic (Figure 2). At the landscape extent, mean alpha diversity within canyon segments contributed the most to overall species richness (40%), followed by beta diversity among canyons (25%), among canyon segments (21%), and among mountain ranges (14%). The rank order in which different levels contributed to overall species richness of the Shoshone Mountains and Toquima Range was the same as at the landscape extent: mean alpha diversity within-canyon segments > beta di-

versity among canyons > beta diversity among canyon segments. In the Toiyabe Range, alpha diversity within-canyon segments again contributed the most to overall species richness, but beta diversity among canyon segments was greater than beta diversity among canyons.

For birds, in contrast to butterflies, the contribution of each landscape level to overall species richness tended to increase as its size increased (one exception: at the landscape extent, beta diversity among

Table 2. Dissimilarity of species composition of butterflies and birds at different spatial extents. At the landscape extent (Table 2a), mountain ranges are the sampling grain; at the mountain range extent (Table 2b), canyons are the sampling grain. Values are Bray-Curtis distances.

mountain range	butterflies	birds
2a. Average within-mountain range dissimilarities		
Toquima Range	28.766	43.881
Toiyabe Range	10.880	33.810
Shoshone Mountains	21.009	39.428
2b. Average within-canyon dissimilarities		
Toquima Range		
Moores East	28.497	43.961
Moores West	38.825	47.569
Northumberland East	27.023	43.404
Northumberland West	28.167	41.602
Petes East	37.991	43.928
Petes West	51.992	71.250
Toiyabe Range		
Big Creek	34.796	54.344
Birch	23.389	67.062
Kingston	30.787	48.800
San Juan	34.346	72.353
Washington	21.549	41.442
Shoshone Mountains		
Barrett	25.585	55.343
Becker	23.625	52.500
Riley	29.652	54.931
Schoonover	25.724	35.176
Underdown	37.354	68.209

canyons was greater than beta diversity among mountain ranges) (Figure 3). Accordingly, at the landscape extent and for all three mountain ranges, beta diversity among canyons > beta diversity among canyon segments > alpha diversity of canyon segments. Thus, we noted that although beta diversity tended to be greater among canyons than among canyon segments in both taxonomic groups, alpha diversity was the most important component with respect to overall species richness of butterflies and the least important with respect to overall species richness of birds. We also found that beta diversity among canyons relative to beta diversity among canyon segments tended to be much greater for birds than for butterflies.

Discussion

Our results contribute empirical evidence that bears upon two central issues in biogeography and ecoregional land-use planning. First, as an increasing num-

ber of studies suggest, at least some patterns or measures of species diversity vary among mountain ranges in the Great Basin.

Second, diversity patterns vary among taxonomic groups, especially as spatial scale decreases. Thus, the ability of butterflies and birds to serve as surrogate measures of the status of each other's diversity appears to be scale-dependent.

Alpha diversity

We found that both mountain range and canyon had significant effects on landscape-level species richness of butterflies and birds. This probably reflects differences among mountain ranges – some relatively obvious, others more subtle – in topography, microclimate, and vegetation structure and composition. In a mountain range that is relatively dry, for example, even the most species-rich canyons may be more depauperate than the 'average' canyon in a comparatively mesic range.

Species composition: resource distribution vs availability of particular resources

At all spatial levels, species composition of butterflies was more similar than species composition of birds. This result initially was surprising because birds are more mobile than butterflies. Hence, we might expect species composition of birds to be more uniform in space than species composition of butterflies. A likely explanation for the pattern we observed is that in our study system, the resource requirements of adult butterflies tend to be more general than those of birds. For example, most species of butterflies will exploit virtually any nectar source, from shrubs to native forbs to non-native weeds. Thus, shifting composition of key resources along an environmental gradient may not directly affect species composition of butterflies. Species composition of birds, by contrast, may be more markedly affected by shifting availability of resources. Trees such as willow (*Salix* spp.), aspen (*Populus* spp.), and piñon (*Pinus monophylla*) provide different types of nesting sites, which may constrain the distribution of particular species or guilds of birds. Another possibility is that either competitive exclusion or niche availability affects local species composition of birds to a greater extent than butterflies.

Although the magnitude of variation in species composition was greater for birds than for butterflies

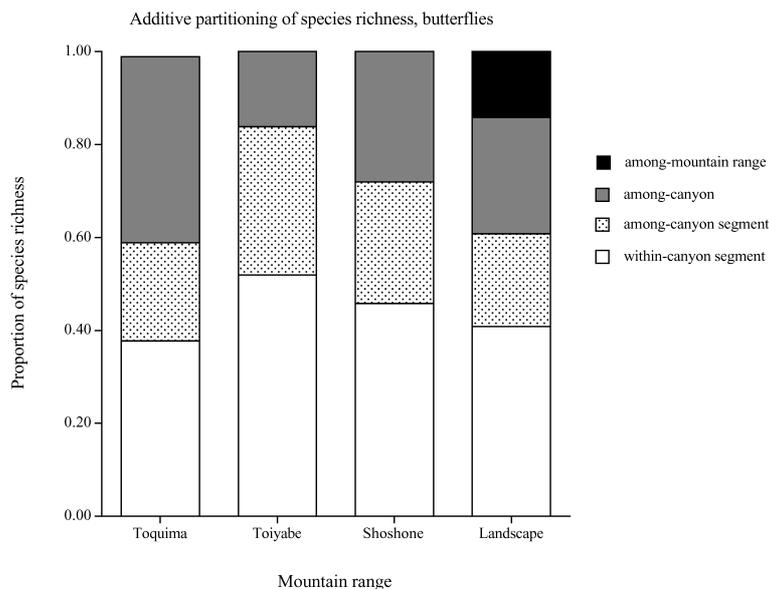


Figure 2. Additive partition of butterfly diversity at the mountain range extent and landscape extent. Bars show the proportion of total species richness explained by alpha and beta components of diversity at three spatial levels: canyon segments, canyons, and mountain ranges (see text for details).

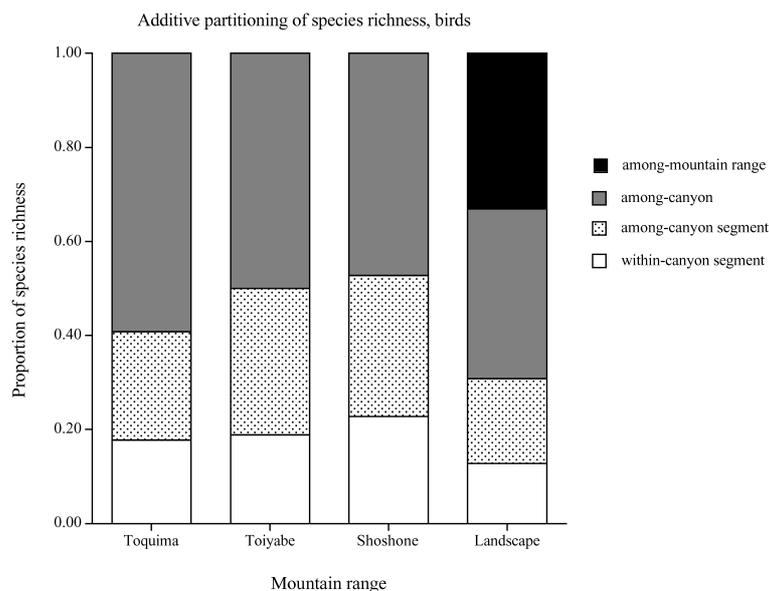


Figure 3. Additive partition of bird diversity at the mountain range extent and landscape extent. Bars show the proportion of total species richness explained by alpha and beta components of diversity at three spatial levels: canyon segments, canyons, and mountain ranges (see text for details).

at all spatial levels, the two taxonomic groups had the same pattern of variation in species composition across the landscape. Species composition of butterflies and birds was most similar among canyons in the

Toiyabe Range and least similar among canyons in the Toquima Range. This may reflect the fact that the Toiyabe Range is somewhat larger and less arid than many other mountain ranges in its biogeographic

subregion (Fleishman et al. 1999; Fleishman et al. 2000). A majority of the canyons that incise its slopes have ephemeral, if not permanent, streams. A regular supply of water helps to support an unusually diverse vegetational community in terms of both species richness and structure. As a result, a high proportion of the butterflies and birds present in the Toiyabe Range may be able to persist in the 'average' Toiyabe Range canyon. In the Toquima Range, by contrast, resources for butterflies and birds (e.g., larval host plants, fruiting trees) are both more limited and more patchily distributed than in the Toiyabe Range. While the diversity of resources in the Shoshone Mountains does not appear to be particularly high, the distribution of those resources may be relatively homogenous among canyons (Tausch and Tueller 1990). Patterns of variation in species composition of butterflies and birds among canyons within a mountain range may have similar explanations. Species composition is likely to be more variable within a canyon that has relatively heterogeneous topography or resource distributions than within a comparatively homogenous canyon.

Species composition of both taxonomic groups tended to be less similar among segments within a canyon than among canyons within a mountain range. Variation in species composition within a canyon may reflect shifting distributions of resources or microclimatic features along an elevational gradient. But, at least within a mountain range, the distribution of resources along an elevational gradient may be similar among canyons. This may explain why species composition was more similar among canyon segments than among canyons.

Additive partitioning of species richness

There were two noteworthy differences in the diversity partitions of butterflies and birds. First, alpha diversity within canyon segments was the dominant component of overall species richness of butterflies but was not an important contributor to overall species richness of birds. Second, as the size of a landscape level increased, its contribution to overall species richness of birds increased monotonically; the relationship between size of a landscape level and its contribution to overall species richness of butterflies was not linear (Figure 2, Figure 3).

The difference in the relative contribution of alpha diversity between taxonomic groups suggests that the most appropriate grain for studying and conserving

butterflies and birds in the Great Basin may not be the same. Clearly, birds tend to have larger home ranges than butterflies, so more extensive areas may be necessary to protect population viability of birds than of butterflies. More importantly, our results indicate that turnover of bird species richness within canyons is relatively high. Because adult butterflies have relatively general resource requirements, most canyon segments that are not extremely dry or floristically depauperate are likely to be inhabited by a high proportion of the species present in the canyon. But even if plant diversity is high at the canyon level, vegetation composition and structure tends to shift along an elevational gradient. Species richness of birds may be closely associated with such changes in plant assemblages within a canyon. Conservation of a representative sample of the bird fauna requires a larger area than conservation of a representative sample of butterflies. The point is not only that birds have larger home ranges than butterflies but also that home ranges of different bird species, reflecting the distribution of their critical resources, may not overlap.

Scale-dependence in species diversity of birds may reflect a relatively straightforward species-area relationship. By contrast, several studies have shown that species diversity of butterflies in the Great Basin is not monotonically correlated with area (Fleishman et al. 2001b; Fleishman et al. 2002; Fleishman and Mac Nally 2002; Mac Nally et al. 2003). In our study system, area is variably correlated with some environmental variables that appear to drive species richness of butterflies, such as topographic heterogeneity and water availability. The latter discrepancy is more pronounced at smaller scales—i.e., topographic heterogeneity and area are more closely linked at the level of canyons or mountain ranges than at the level of canyon segments. This may explain why beta diversity of butterflies among canyons was greater than beta diversity among canyon segments in the Toquima Range and Shoshone Mountains. Indeed, the Toiyabe Range is one of few mountain ranges in which species richness of butterflies does appear to be positively correlated with area (Fleishman et al. 2001a).

Taxonomic groups vary in their perception of and response to environmental patterning, including the spatial and temporal distribution of biotic and abiotic resources. This can make it difficult to compare results of ecological studies from different taxonomic groups in the same landscape (Addicott et al. 1987).

Differences in diversity patterns among taxonomic groups also confound holistic efforts to sample and to effectively conserve representatives of multiple floras and faunas. Our work emphasizes that both scale-dependence in biodiversity patterns within a taxonomic group and differences in scale dependence among taxonomic groups constrain the application of surrogate species concepts such as 'indicators' of species richness or ecosystem integrity. Shifts in resource abundance and the distribution of critical resources for individual guilds or taxonomic groups appear to be the most prevalent mechanisms underlying scale dependence in diversity patterns.

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