

Identification and conservation application of signal, noise, and taxonomic effects in diversity patterns

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Abstract

Identification and conservation application of signal, noise, and taxonomic effects in diversity patterns.— Ongoing research on butterflies and birds in the Great Basin has identified biogeographic patterns while elucidating how dynamic measures of diversity (species richness and turnover) affect inferences for conservation planning and adaptive management. Nested subsets analyses suggested that processes influencing predictability of assemblage composition differ among taxonomic groups, and the relative importance of those processes may vary spatially within a taxonomic group. There may be a time lag between deterministic environmental changes and a detectable faunal response, even for taxonomic groups that are known to be sensitive to changes in climate and land cover. Measures of beta diversity were sensitive to correlations between sampling resolution and local environmental heterogeneity. Temporal and spatial variation in species composition indicated that spatially extensive sampling is more effective for drawing inferences about biodiversity responses to environmental change than intensive sampling at relatively few, smaller sites.

Key words: Adaptive management, Beta diversity, Great Basin, Monitoring, Nestedness, Species richness.

Resumen

Identificación y aplicación en la conservación de los efectos señal, ruido y taxonómicos en patrones de diversidad.— Los estudios de mariposas y aves en el Great Basin han identificado patrones biogeográficos que permiten evaluar cómo las medidas dinámicas de biodiversidad (riqueza específica y renovación de especies) pueden afectar la planificación y la gestión adaptativa de la conservación. El análisis de subgrupos anidados sugiere que los procesos que influyen en la predicibilidad de la composición de los grupos difieren entre los distintos grupos taxonómicos. Asimismo la importancia relativa de estos procesos puede variar espacialmente dentro de un grupo taxonómico. Puede haber un retraso en el tiempo entre los cambios ambientales deterministas y una respuesta faunística detectable, incluso para los grupos taxonómicos que se sabe que son sensibles a los cambios del clima y de la cubierta del suelo. Las medidas de diversidad beta eran sensibles a las correlaciones entre la resolución del muestreo y la heterogeneidad ambiental local. La variación espacial y temporal en la composición de especies indicó que el muestreo extensivo en el espacio es más efectivo, para obtener inferencias sobre cómo responde la biodiversidad a cambios ambientales, que el muestreo intensivo, en relativamente pocos sitios y más pequeños.

Palabras clave: Gestión adaptativa, Diversidad beta, Great Basin, Control, Anidamiento, Riqueza específica.

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Introduction

Conservation planning is motivated and directed by evidence that native species, assemblages, and ecological functions are responding to deterministic environmental change (Scott et al., 1987, 1993; Stein et al., 2000). Human land uses such as urbanization and agriculture frequently drive the environmental changes of greatest concern to conservation biologists (Czech et al., 2000; Lockwood & McKinney, 2001). In order to implement adaptive management, we also must evaluate the biological effects of landscape reconstruction, restoration, and directed efforts to conserve species and ecosystems (Meretsky et al., 2000; Lake, 2001). Meanwhile, in the decision-making arena, credible data on ecological responses to climate change have proven essential for influencing environmental policy (Easterling et al., 2000; Schär et al., 2004).

Survey and monitoring data sometimes reveal substantial changes in measures of biodiversity and ecosystem function across space or time, but those changes may reflect dynamic processes rather than observational or experimental treatments *per se*. Diversity metrics (including species richness, abundance, evenness, and so forth) are infamously dependent on the spatial and temporal scale of measurement and on life history. For example, the size of each sampling unit (sampling resolution), the configuration of sampling units across the landscape, and the spatial extent of the area from which samples are drawn affect inferences regarding number of species (henceforth, species richness) and identity of species (henceforth, species composition) (Noss, 1983; Wilson & Shmida, 1984; Conroy & Noon, 1996). Geographic coordinates and context also matter. For instance, species richness often increases along ecotones (Risser, 1995), at intermediate levels of disturbance (Petraitis et al., 1989), and at intermediate points along abiotic environmental gradients (Fleishman et al., 1998; Colwell & Lees, 2000). Scale dependencies in diversity patterns bear on a wide range of conservation applications, from identification of mechanisms that generate and maintain species richness to exploration of relationships between species diversity and ecological function (Waide et al., 1999; Willis & Whittaker, 2002).

Scaling issues related to species richness and composition also have a taxonomic component. Species perceive and react to their environment as a function of life-history characteristics including resource requirements, mobility, and body size (Addicott et al., 1987; Kotliar & Wiens, 1990; Mac Nally, 2005). In theory, therefore, the spatial and temporal resolution and extent of sampling should be dictated by the ecology of the taxa under investigation. In reality, however, sampling designs frequently reflect logistic constraints. The resolution and extent of sampling for multi-taxonomic studies commonly is established using a single survey design bounded by human conventions, such as administrative boundaries or land-use types. But a

uniform sampling framework is unlikely to be meaningful for understanding diversity patterns in all taxonomic groups of interest because it confounds the components of diversity. For some species a given sampling resolution will estimate only the alpha component of richness (the mean number of species within a local community) while for other species it will estimate both the alpha and beta (between-habitat diversity) components.

Nonetheless, empirical ecological and biogeographical research can be designed to quantify effects of scale and life history in addition to effects of environmental change. For the past decade, my colleagues and I have quantified diversity patterns in assemblages of butterflies and birds in the Great Basin and Mojave Desert in order to elucidate deterministic and stochastic influences on patterns of species richness and composition, dependence of those patterns on temporal and spatial scale and life history, and practical sampling approaches most likely to provide valid inferences about ecological responses to an array of environmental changes. Butterflies and birds also are well-known ecologically, relatively easy to study and monitor, and popular with the general public. In addition, various measures of the species diversity or occurrence of butterflies and birds frequently have been proposed as a surrogate measure of the status of each other, of other taxonomic groups, and of environmental variables (Temple & Wiens, 1989; New et al., 1995; Chase et al., 1998; Blair, 1999; Swengel & Swengel, 1999; O'Connell et al., 2000).

The Great Basin and Mojave are well suited for examining issues of scale and sampling associated with many types of diversity patterns. Desert ecosystems are thought to be highly responsive to major environmental changes including shifts in temperature and precipitation, invasion by non-native species, and altered disturbance regimes (Sala et al., 2000; Smith et al., 2000). In addition, approximately 75% of the Great Basin and Mojave is managed by federal and state resource agencies for sustained multiple uses ranging from conservation to recreation to production of renewable and non-renewable commodities. In this paper, I present a synopsis of several approaches we have taken to identify biogeographic patterns and trends in the fauna of the Great Basin while elucidating how dynamic measures of diversity affect interpretation of ecological data in the context of conservation and management. First, I describe our use of nested subsets analyses to determine whether the composition of local assemblages is predictable and to identify abiotic and biotic factors that may be associated with the order in which species are likely to appear and disappear. Second, I summarize how we have addressed the probability of detecting faunal responses to deterministic environmental changes over time. Third, I review our work on the effects of sampling resolution and proximity of sampling locations on inferences about species richness and turnover.

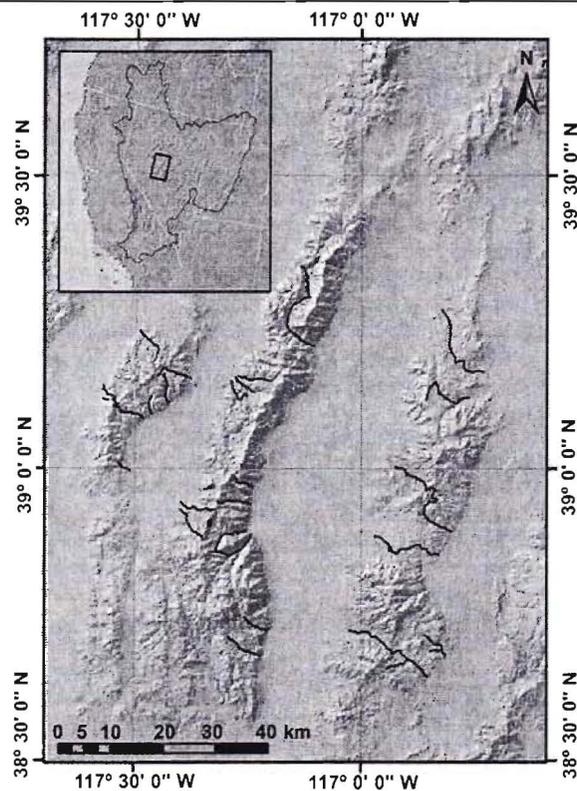


Fig. 1. Location of (west to east) the Shoshone Mountains, Toiyabe Range, and Toiquima Range in the Great Basin (black rectangle, see inset) and inventory canyons in the three mountain ranges (thick black lines). Two pairs of canyons in the Toiyabe Range and three pairs of canyons in the Toiquima Range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

Fig. 1. Localización (de oeste a este) de los montes Shoshone, de la cordillera Toiyabe, y de la cordillera Toiquima en el Great Basin (rectángulo negro, ver el recuadro) y la relación de cañones de las tres cordilleras montañosas (líneas negras finas). Dos pares de cañones de la cordillera Toiyabe y tres pares de cañones de la cordillera Toiquima conectan en la cima de la cordillera.

Methods

Our data collection incorporates well-established techniques that reliably detect species presence and permit assessment of distributional trends across space and time. Because these methods have been described in considerable detail in previous publications, along with discussion of sampling adequacy (e.g., Fleishman et al., 1998; Mac Nally et al., 2004), I provide just a brief overview here.

Data for our analyses in the Great Basin were collected from 1996–2003 in three adjacent mountain ranges in central Nevada, the Shoshone Mountains, Toiyabe Range, and Toiquima Range (Lander and Nye counties) (fig. 1). These mountain ranges have similar regional climate, biogeographic past and ancestral biota, and human land-use histo-

ries (Grayson, 1993). Inventories for breeding birds were conducted in five canyons in the Shoshone Mountains, five canyons in the Toiyabe Range, and six canyons in the Toiquima 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 Toiquima 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 resident butterflies (Fleishman et al., 1997) and birds during the breeding season (Ryser, 1985; Dobkin & Wilcox, 1986). We have collected data on both species occurrence (presence / absence) and abundance; only the occurrence data are presented in this paper.

We divided canyons into multiple contiguous sites (segments) from base to crest. Each site was 100–150 m wide and long enough to span a 100–m change in elevation (Fleishman et al., 1998, 2001b). Mean site length was 1.5 km; more than two-thirds of the sites were longer than 1 km. Inventories for butterflies were conducted from 1995–2003 in 39 sites in the Shoshone Mountains, 102 in the Toiyabe Range, and 54 in the Toquima Range. Inventories for birds were conducted from 2001–2003 in 24 sites in the Shoshone Mountains, 31 in the Toiyabe Range, and 28 in the Toquima Range.

Our sampling locations covered an elevational range of 1872–3272 m and areas from 1.5' ha to 44.4 ha. Using walking transects, a standard, dependable method for temperate regions (Pollard Yates, 1993; Harding et al., 1995), we recorded 65 resident species of butterflies from our study sites. Birds were sampled using point counts (three per season) that spanned the range of dominant vegetation types (Bibby et al., 2000; Siegel et al., 2001; Poulson, 2002). Point counts have been shown to be an effective method of sampling birds in riparian areas in the Great Basin (Dobkin & Rich, 1998; Betrus, 2002). We recorded 79 species of breeding birds from our study sites. Lists of species are available on request.

We partitioned the landscape into three hierarchical spatial levels: sites within canyons, canyons, and mountain ranges. Our finest sampling resolution (smallest sampling grain) was the site. A given site was located within a particular canyon within one of the three mountain ranges. To produce species lists at the whole canyon level, our intermediate sampling resolution or 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. To produce species lists at the mountain range level, our coarsest sampling resolution or largest grain, we compiled species lists for all canyons that were visited in a given mountain range.

Predictability of assemblage composition

Nestedness analyses have greatly expanded our capacity to understand biotic patterns across networks of terrestrial or aquatic "islands" of resources or habitat (Wright et al., 1998). A nested biota is one in which the species present in relatively depauperate locations are subsets of the species present in locations that are richer in species (Patterson & Atmar, 1986). Nestedness is a property of assemblages or communities, not of individual species (Wright et al., 1998), and has been interpreted as a measure of biogeographic order in the distribution of species (Atmar & Patterson, 1993). Numerous studies have demonstrated that nested distributional patterns are common across taxonomic groups and ecosystems.

Biotas rarely are perfectly nested. Nestedness analyses often cannot identify critical thresholds

of environmental variables with respect to system state or reliably predict the order of species extirpation or colonization. Nonetheless, nestedness analyses are useful as conservation tools because they quantify a widespread ecological pattern and—more importantly—highlight processes, including nonrandom extinction, differential colonization, and nestedness of critical resources, that affect not only species richness but also species composition (Patterson & Atmar, 1986; Simberloff & Martin, 1991; Cook & Quinn, 1995; Lomolino, 1996; Baber et al., 2004). Although even strong correlations between mechanisms or variables and distributional patterns cannot be interpreted as cause-and-effect relationships, those correlations can, at minimum, help refine hypotheses that can be tested with further observations or manipulative experiments (Cook & Quinn, 1995; Kadmon, 1995; Fleishman & Mac Nally, 2002). This aspect of nestedness analysis is especially pertinent to conservation planning because it may help to elucidate whether certain land uses may be responsible for local extinction or colonization events (Hecnar & M'Closkey, 1997; Fleishman & Murphy, 1999; Jonsson & Jonsell, 1999).

Presence/absence matrices for nestedness analysis typically are assembled by listing locations as rows in order of decreasing species richness and species as columns in order of decreasing ubiquity. This ordering provides a description of assemblage composition but contributes little toward understanding agents that drive assemblage structure and help us predict species composition across space and time. If one wishes to test whether a particular environmental variable may be related to a nested distributional pattern, then rows instead may be ordered with respect to that variable (Fleishman & Mac Nally, 2002). For example, listing rows in order of decreasing area quantifies the degree to which faunas are nested by area. If an assemblage is nested with respect to a selected environmental variable—or if an assemblage is more nested with respect to one environmental variable than another—it suggests that the variable in question has a non-trivial influence on species occurrence in the assemblage.

To test whether assemblages were nested with respect to alternative ordering variables, we computed the relative nestedness index *C* (Wright & Reeves, 1992) with the program NESTCALC (Wright et al., 1990). We estimated statistical significance using Cochran's *Q* statistic (Wright & Reeves, 1992). Values of *C* vary between 0 and 1.0, approaching 1.0 for perfectly nested matrices. A key advantage of this metric is that it allows for statistical comparison of degree of nestedness among matrices or data sets. Moreover, *C* is not highly sensitive to matrix size (Wright & Reeves, 1992; Bird & Boecklen, 1998), although nestedness may be more variable when matrices are relatively small (Wright et al., 1998). We used *Z* scores (standard-Normal variates) to test whether significant differences existed in relative nestedness among matrices (Wright & Reeves, 1992).

Table 1. Relative nestedness of butterflies. Values are one-tailed Z-scores for matrices ordered by different criteria: area and topographic heterogeneity (topo). Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness. For example, the Shoshone Mountains matrix ordered by area was significantly less nested than the Toiyabe Range matrix ordered by area: SH. Shoshone Mountains; TY. Toiyabe Range; TQ. Toquima Range; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Tabla 1. Anidamiento relativo en mariposas. Los valores son puntuaciones-Z de una sola cola para matrices ordenadas con distintos criterios: área y heterogeneidad topográfica (topo). Los valores representan el anidamiento relativo de filas respecto a columnas; valores positivos indican un mayor anidamiento y los negativos, menor anidamiento. Por ejemplo la matriz de los montes Shoshone ordenada por áreas fue significativamente menos anidada que la matriz de la Cordillera Toiyabe ordenada por áreas: SH. Montañas Shoshone; TY. Cordillera Toiyabe; TQ. Cordillera Toquima; * $P \leq 0,05$; ** $P \leq 0,01$; *** $P \leq 0,001$.

	SH area	TY area	TQ area	SH topo	TY topo	TQ topo
SH area		-4.68***	3.27***	1.31		
TY area	4.68***		9.12***		9.03***	
TQ area	-3.27***	-9.12***				-6.67***
SH topo	1.31				3.89***	-1.51
TY topo	-9.03***		-3.89***		-6.12***	
TQ topo			6.67***	1.51	6.12***	

Initially, we tested whether nestedness of butterflies and birds in the Shoshone Mountains, Toiyabe Range, and Toquima Range appeared to be influenced by the same environmental variables and whether those patterns were consistent in space. Although the distributional pattern of both taxonomic groups was strongly nested, the environmental variables most closely associated with the nested pattern differed between butterflies and birds (Fleishman et al., 2002a). For example, topography (elevation and local topographic heterogeneity) may help generate nested distributions of butterflies (Fleishman & Mac Nally, 2002). Varied topography tends to create a full gradient of microclimatic conditions, which in turn promotes high species richness of plants that serve as resources for larval and adult butterflies. Varied topography also provide numerous locations for seeking mates (Scott, 1975, 1986) and shelter from extreme weather events. However, topography did not appear to be a reliable correlate of assemblage structure of birds. This result may reflect differences in the specific resource requirements of birds and butterflies in the montane Great Basin. For instance, species richness of birds frequently corresponds to vegetation structure, whereas species richness of butterflies may be more closely associated with vegetation composition (but see Rotenberry, 1985; Mac Nally, 1990). Comparative resource requirements of butterflies and birds in this landscape are addressed in greater detail in the section on beta diversity.

Contrary to widespread biogeographic assumptions (Doak & Mills, 1994; Boecklen, 1997), the association between area and nestedness of both butterflies and birds was relatively slight. If area is positively correlated with species richness and a biota is perfectly nested, then species richness should be greater in an extensive, contiguous site than in a collection of smaller sites. Virtually all real biotas have presences and absences that deviate from perfect nestedness, however, and area may or may not be an important correlate of species richness of a nested system (Brown, 1978; Doak & Mills, 1994; Kadmon, 1995; Rosenzweig, 1995; Ricklefs & Lovette, 1999). In a region as climatically erratic and topographically heterogeneous as the Great Basin, critical resources for both butterflies and birds may not be strongly correlated with area.

Also contrary to fundamental biogeographic assumptions, we found limited evidence that nestedness of either group was affected by selective dispersal (Fleishman et al., 2002a; see also Bird & Boecklen, 1998). If colonization tends to decrease nestedness (i.e., counter the effects of selective extinction), then less vagile taxonomic groups should be more nested than comparatively vagile groups. But if colonization tends to generate nestedness (Loo et al., 2002), then the more vagile taxonomic groups should be more nested. Results of the relatively few previous comparisons have been mixed (Cook & Quinn, 1995; Wright et al., 1998). There are several potential explanations why

correlations between nestedness and dispersal ability were weak. One possibility is that the spatial resolution of our bird analyses was too small. Limited dispersal of birds between study sites would dilute the effect of differential colonization in generating nestedness in our analyses. Analyses at a larger spatial resolution (full canyons rather than sites), however, produced virtually identical results (Fleishman et al., 2002a). Another possibility is that most resources used by butterflies and birds are present in the majority of the locations that we inventoried, at least during their peak periods of activity.

For butterflies (but not for birds), the rank order of mountain ranges with respect to nestedness was sensitive to which environmental variable was used to order the matrices (Fleishman et al., 2002a) (table 1). Order of species occurrence in the Shoshone Mountains and Toquima Range was more closely associated with topography than with area per se, whereas nestedness of butterflies in the Toiyabe Range was better explained by area than as a function of topography. Ecologically, this suggests that the influence of area and topography on species composition of butterflies varies among mountain ranges. The importance of local microclimatic conditions may increase as the availability of water decreases and vegetational resources become less widespread and abundant.

We also tested whether distribution patterns of butterfly and bird assemblages appeared to be sensitive to human use of riparian areas, a dominant anthropogenic stressor in the Great Basin (Kauffman & Krueger, 1984; Armour et al., 1991; Dobkin & Rich, 1998). Livestock grazing, recreation, and other activities that reduce water availability and degrade riparian vegetation had little detectable effect on nestedness of butterflies and birds (Fleishman et al., 2002a). At least three explanations seem plausible (Fleishman & Murphy, 1999). First, human modification of riparian areas may not be sufficiently severe to cause local extirpations. Second, species with high vulnerability to changes in the structure and composition of riparian vegetation may already have disappeared. Third, the magnitude of riparian disturbance may not be arranged in a predictable (nested) manner across the region (Hecnar & M'Closkey, 1997).

Few studies of nestedness explicitly have compared data on multiple taxonomic groups at the same locations. Our results suggest that the processes influencing even such prevalent assemblage-level distribution patterns as nestedness vary among taxonomic groups. We also found that the relative importance of selected processes can vary spatially, both within and among taxonomic groups. These conclusions serve as a reminder that taxonomic groups are not interchangeable for conservation planning, for monitoring the biological effects of known environmental changes, or for assessing the relative influence of natural and anthropogenic disturbances on native species (Niemi et al., 1997; Simberloff, 1998; Andelman & Fagan, 2000; Fleishman et al., 2001a; Rubinoff, 2001).

Signal and noise in longitudinal measures of biodiversity

Contemporary climate change, invasion of non-native species, and biotic homogenization are motivating efforts to understand the resilience of ecological systems (Easterling et al., 2000; Olden & Poff, 2003). Detection of faunal responses to known environmental changes on the order of years to decades typically is based on longitudinal field surveys in which selected taxonomic groups are monitored across large areas; data on temporal trends are used to guide and adjust land management. Because time and money for biological surveys and monitoring inevitably are limited, it is important to examine whether short-term measures or "snapshots" of species richness and occurrence accurately reflect longer-term patterns (Hanski, 1999; Moilanen, 2000).

We used up to six years of survey data from two mountain ranges, the Toquima Range and Shoshone Mountains, to examine whether annual variation in butterfly assemblages over consecutive years reflected an ecologically meaningful trend as opposed to stochastic system dynamics (Fleishman & Mac Nally, 2003). In essence, we aimed to document the apparent signal-to-noise ratio in these assemblages over time. Because our study area did not encompass species' full geographic ranges, we did not attempt to determine whether the ranges of individual species had expanded or contracted (e.g., Parmesan et al., 1999; Thomas et al., 2001). Instead, we focused on among-site and among-year variation in species richness and species composition, two measures that likely will remain the focus of much biological monitoring on public and private land.

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 sites and a and b are the number of species in sites A and B , respectively. C_j approaches 1.0 when species composition is identical between sites and 0.0 when two sites have no species in common (Magurran, 1988). A "time lag" refers to the number of years that elapsed between inventories. We calculated similarity of species composition for time lags of one to six years in the Toquima Range and of one or two years in the Shoshone Mountains. For a more detailed description of methods and analyses, see Fleishman & Mac Nally (2003).

Mean similarity of species composition of butterflies (i.e., the mean of the site-level values for each mountain range) varied little as a function of time lag (fig. 2). In the Toquima Range, for example, mean similarity of species composition varied by only 0.06 (range 0.43 to 0.49) among time lags of one to six years. Much less of the difference in species composition of butterflies was attributable to turnover of species composition within sites over time than to spatial differences among sites. This pattern was illustrated most clearly in the Shoshone Mountains, where 3% of the difference in species composition was attributable to turnover of species

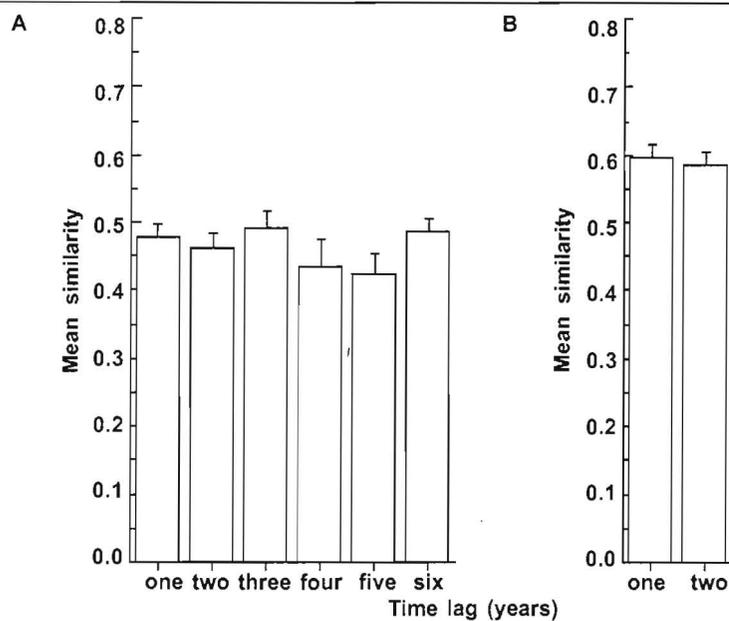


Fig. 2. Mean similarity of species composition of butterflies in the Toquima Range (a) and Shoshone Mountains (b) among time lags of one to six years. Error bars are standard error.

Fig. 2. Similitud media de la composición específica de mariposas en la cordillera Toquima (a) y los montes Shoshone (b) entre periodos de tiempo de uno a seis años. Las barras de error indican los errores estándar.

composition within sites whereas 74% was attributable to spatial differences among sites.

Our results demonstrate that extraction of biotic "signals" from the "noise" of background variation in arid ecosystems is complicated by the severity and unpredictability of weather patterns and various environmental disturbances (Houghton et al., 1975; Rood et al., 2003). Whether measurements of biodiversity at two or more points in time are likely to reflect a bona fide temporal trend as opposed to stochasticity largely depends on two related factors: the extent of deterministic environmental change and the degree of variability characteristic of the biotic assemblage. One potential explanation for the lack of a detectable temporal trend in our data on species composition and species richness of butterflies (despite considerable variability, especially in species composition, between any two given years, Fleishman et al., 2003a) is that during the relatively short duration of our study, there were few if any ecologically significant changes in climate or land cover. For example, in five of the six years of our study, annual precipitation was 20% to 60% below the mean for the past century. However, precipitation from year to year was erratic. For instance, precipitation in 2000 was nearly double that in 1999, despite the fact that both years were relatively dry.

Further, although information on species richness and species composition are among the most practical data to collect in managed landscapes, these measures may not be highly sensitive to environmental changes over years to decades as compared with demographic parameters like abundance and reproduction (Parmesan et al., 1999; Thomas et al., 2001). Population-level measures, however, may be even more prone to random fluctuations than assemblage-level variables.

By 2100, substantial environmental changes in the Great Basin are anticipated, ranging from anthropogenic climate change to modified disturbance regimes to expansion of non-native invasive species (Chambers & Miller, 2004). But detection of faunal responses to such changes is likely to be complicated by high background levels of local turnover in species composition. Moreover, biological responses to environmental change may depend in part on the speed at which those changes occur (Grayson, 2000) and whether variance in environmental conditions also increases (McLaughlin et al., 2002). Our work emphasizes that at minimum, there may be a time lag between deterministic changes in climate or land cover and a detectable faunal response that can be used to guide management.

Response of beta diversity to spatial scale

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., 1987; Myers et al., 2000) and to measure biological responses to natural disturbance processes, human land use, and alternative management actions at numerous spatial extents (Chapin 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, 1966; Whittaker, 1977; Lande, 1996). For example, the technique of additive partitioning uses a hierarchical model of landscape organization (Allen & Starr, 1982) to represent species richness at each nested level of a landscape as the sum of alpha diversity (the mean number of species within a local community) and beta diversity at the next lower level (Lande, 1996; Wagner et al., 2000; Gering et al., 2003).

After discovering 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), we decided it would be useful to explore relationships between beta diversity and spatial scale more thoroughly. Accordingly, we focused directly on whether beta diversity of butterflies and birds in the Great Basin depended on sampling resolution and the proximity of sampling units across the landscape (Mac Nally et al., 2004). We also examined the taxonomic component of scaling issues by comparing how species composition of butterflies and birds responded to sampling resolution and proximity. We calculated mean similarity of species composition, using the Jaccard index, for each sampling grain in turn—sites, canyons, and mountain ranges.

We found that variation in species composition of butterflies and of birds could be explained as functions of both spatial resolution of sampling and relative distances among sampling units across the landscape (Mac Nally et al., 2004). Similarity of species composition increased as the sampling resolution decreased (i.e., as grain increased), with more than 85% of the variation in similarity values for both taxonomic groups attributable to sampling resolution. This result almost certainly reflects the effect of local environmental heterogeneity on species composition. High-resolution sampling in a relatively heterogeneous landscape tends to emphasize differences in species composition along gradients of resource availability, topography, or microclimate. As sampling resolution increases, species composition may reflect emerging similari-

ties in terms of regional climate, land cover, and land use, and biotic assemblages will appear more homogeneous.

Irrespective of sampling resolution or taxonomic group, similarity of species composition decreased as the biogeographic separation between sampling units increased. Although the effect of relative proximity was statistically substantial, however, the absolute difference in species composition in response to relative proximity was modest. For example, 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 probably reflect the extraordinarily high variability in topography in our study system. Although there are relatively few major land cover types in the Great Basin, they are distributed in a remarkable array of local vegetational mosaics. 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.

The effects of relative proximity of sampling units across the landscape were not uniformly greater for either butterflies or birds (Mac Nally et al., 2004). As we compared the effects of spatial grain on beta diversity of butterflies and birds, however, two differences immediately were apparent (fig. 3). First, at all sampling resolutions, species composition of butterflies was more similar than species composition of birds. Second, the effect of sampling resolution was greater for birds than for butterflies, especially when the intermediate sampling resolution was compared to the smallest sampling resolution. In other words, the difference in mean similarity values at the resolution of mountain ranges versus sites, and at the resolution of canyons versus sites, was greater for birds than for butterflies.

Birds in our study system typically have territory sizes or home ranges about an order of magnitude larger than those of butterflies. If home range size is the primary influence on species composition, then we would expect beta diversity of birds in our study system to be lower than beta diversity of butterflies. But previous work suggested, to the contrary, that resource specialization was more strongly associated with structure of bird assemblages than territory size (Fleishman et al., 2002a). If ecological specialization and geographic distribution are negatively correlated (Rabinowitz, 1981; Kunin & Gaston, 1997), then beta diversity of taxonomic groups with relatively general resource needs should be lower than beta diversity of groups with more specialized needs. Although in many instances one might assume that birds have more general requirements than butterflies, this may not be the case in the Great Basin. Butterflies often are considered "specialists" because as larvae

they are restricted to one or a few closely related host plants (Ehrlich & Raven, 1964; Scott, 1986). In many ecosystems, however, the resource requirements of adult butterflies are fairly general (Holl, 1995; Pullin, 1995), and species composition of butterflies may be more closely associated with distribution of an array of potential nectar sources than with distribution of specific larval host plants. Availability of nectar is positively correlated with spatial distribution of adults and larvae (Gilbert & Singer, 1973; Murphy, 1983; Murphy et al., 1984) and may reduce the probability of local emigration (Kuussaari et al., 1996; Moilanen & Hanski, 1998). Many adult butterflies in the Great Basin can exploit virtually any source of nectar, from flowering shrubs to native forbs to non-native invasive species. Thus, it may be appropriate to classify butterflies in our study system as relative generalists.

Species composition of birds traditionally was thought to be more closely associated with vegetation structure (physiognomy) than with vegetation composition (floristics) (MacArthur et al., 1966; Rotenberry & Wiens, 1980). However, some evidence suggests that vegetation composition is more influential than vegetation structure (Tomoff, 1974; Wiens & Rotenberry, 1981), especially at relatively fine spatial resolution (Rotenberry, 1985; Wiens et al., 1987). In the Great Basin, species composition of breeding birds may be affected by the patchy distribution of various species of trees, which provide nesting sites that differ in their suitability for particular species or guilds (Fleishman et al., 2003a). In particular, Neotropical migrant birds, which account for about one-third the assemblage in our study system (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). Two of the most common trees in our study system, piñon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*), are relatively widespread and sometimes form large stands, especially in drier areas. However, dominant riparian trees and shrubs such as cottonwood and aspen (*Populus* spp.), willow (*Salix* spp.), birch (*Betula occidentalis*), and rose (*Rosa woodsii*) have comparatively patchy distributions.

Ecologists are well aware that measures of biodiversity, and inferences about diversity patterns, depend on spatial and temporal scale. Our results, which did not support the assumption that species turnover largely is a function of relative home range size, emphasize the relevance of empirical tests of diversity theories to conservation and management. Further, as our understanding of relationships between species diversity and various components of "scale" increases, so should our ability to recognize underlying mechanisms and to maintain native biodiversity and ecological processes.

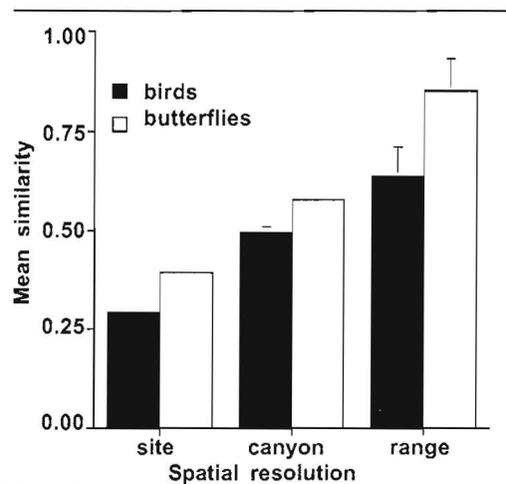


Fig. 3. Beta diversity (mean community similarity) of butterflies and birds at different spatial resolutions of sampling. Spatial extent of sampling was constant. Error bars are one standard deviation. Values are parameter means.

Fig. 3. Diversidad beta (similitud media en la comunidad) de mariposas y aves de muestreos realizados a distintas resoluciones espaciales. La extensión espacial de la muestra fue constante. Las barras de errores son una desviación estándar. Los valores son medias paramétricas.

Discussion

Around the world, climate change, urbanization and other land uses, and invasive species are modifying ecosystem processes, species distributions, and population dynamics of native species. Understanding how assemblages of native plants and animals respond and evolve to these environmental changes is critical to development of effective, practical strategies for ecological restoration and maintenance. Yet the trinity of time, money, and information is elusive for conservation biologists and practitioners. Knowledge of the extent to which measures of biological diversity vary in space and time in the absence of deterministic "treatments" is essential for making accurate inferences and taking appropriate conservation action, especially when the consequences of those actions may be irreversible.

In virtually all of our work in the Great Basin, irrespective of geographic location or taxonomic group, we have been struck by the considerable variation in species composition across space and time. At our finest sampling resolution (site level), for example, mean similarities of species composi-

tion of butterflies and birds were 0.397 and 0.295; at the mountain range level, mean similarities were 0.875 for butterflies and 0.662 for birds (Mac Nally et al., 2004). As a consequence, our work suggests strongly that spatially extensive sampling may be a more effective strategy for drawing inferences about regional species composition than sampling small areas scattered across the landscape. Similarly, recent work has shown that even after accounting for differences in detection probability, annual site-level turnover rates of many species of butterflies and birds in the Great Basin are as high as 50%. Despite considerable turnover in species composition, however, species richness of butterflies and birds in our study system has tended to be relatively consistent between years, especially at the landscape level (Fleishman & Mac Nally, 2003; Fleishman et al., 2003b). Brown et al. (2001) likewise found that species richness of birds in northern Michigan and rodents in the Chihuahuan Desert remained fairly constant over the long term (22 years and 50 years, respectively) notwithstanding substantial changes in species composition, climate, and other environmental conditions.

In related work, we examined whether relatively limited spatial and temporal sampling can provide valid inferences about biological responses to variables that are affected by conservation and restoration actions, including dominance of non-native invasive plants (Mac Nally et al., 2004; Fleishman et al., 2005). In the Mojave Desert, both invasion of salt-cedar (*Tamarix ramosissima*) and human efforts to eradicate salt-cedar have altered vegetational communities and some measures of faunal diversity. We examined whether similar inferences about relationships between plants and butterflies in the Muddy River drainage could have been obtained by using data from a subset of the 85 locations included in the study, by sampling less intensively in time (fewer visits per site), or by sampling over a shorter period of time. We found that similar inferences about the importance of six vegetation-based predictor variables on species richness of butterflies, and about occurrence rates of individual species of butterflies, could be obtained by sampling as few as 10% of sites and by sampling less intensively or extensively in time.

Collectively, our ongoing research in arid environments in the western United States suggests that relatively limited data sets may allow us to draw reliable inferences for adaptive management in the context of ecological restoration and rehabilitation. Integrating studies of biogeographic patterns with examination of how study design itself affects ecological inferences may be one of the most productive avenues for developing adaptive management strategies that will conserve both biodiversity and the processes that sustain it.

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