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## Nestedness analysis and conservation planning: the importance of place, environment, and life history across taxonomic groups

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**Abstract** We used nested subsets analysis to examine distribution patterns of birds and butterflies in the same set of 83 locations in canyons of three mountain ranges in the Great Basin of western North America. We tested whether the same environmental variables influenced nestedness among taxonomic groups and among mountain ranges within taxonomic groups. We also examined whether nestedness of birds and butterflies appeared to be sensitive to human use of riparian areas in the ecoregion. Site area and topography did not appear to differ in their influence on nestedness of birds. By contrast, area and topography differed in how strongly they affected nestedness of butterflies, but their respective influence varied among mountain ranges. Riparian dependence had little discernible effect on nested distribution patterns of either taxonomic group. Because processes influencing distribution patterns can differ among taxonomic groups, and the relative importance of those processes may vary spatially even within a taxonomic group, we urge restraint in using birds and butterflies as surrogates of other taxa for conservation planning.

**Keywords** Birds · Butterflies · Conservation · Indicator species · Nestedness

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### Introduction

Ecologists seek generalizations about patterns and processes among geographic locations and taxonomic groups (Huston 1994; Rosenzweig 1995). If patterns and processes have sufficiently broad ecological relevance, we can use them both as heuristic tools and as guidelines for making land-use decisions.

Species–area relationships have been widely observed for many decades. However, recent developments taking into account species composition through “nestedness” analyses have greatly expanded ecologists’ capacities to deal with complex biotic patterns within archipelagos or “islands” of terrestrial or aquatic habitat (Wright et al. 1998). A nested biota is one in which the species present in depauperate locations are subsets of species present in locations that are richer in species (Patterson and Atmar 1986). Nestedness is a property of communities or assemblages, not of individual species (Wright et al. 1998). Diverse biotic and abiotic processes are believed to generate nested distributions, including non-random extinction, differential colonization, and nestedness of critical resources (Cody 1983; Patterson and Atmar 1986; Rabinowitz et al. 1986; Patterson 1990; Simberloff and Martin 1991; Atmar and Patterson 1993; Cook and Quinn 1995; Kadmon 1995; Worthen and Rhode 1996; Wright et al. 1998; Calmé and Desrochers 1999; Honnay et al. 1999; Ricklefs and Lovette 1999; Loo et al. 2002).

As studies of nestedness have shifted away from mere documentation of pattern to exploring factors that may produce the pattern (e.g., Lomolino 1996), the relationship between habitat features and nested distributions increasingly has attracted attention. Nestedness analyses can suggest, albeit via correlation, whether a given environmental variable is likely to affect local species composition (Cook and Quinn 1995; Kadmon 1995; Mac Nally et al. 2002a). This aspect of nestedness analysis is pertinent to conservation planning because it may help to elucidate whether certain human land uses are responsible for local extinctions (Hecnar and M’Closkey 1997; Fleishman and Murphy 1999; Jonsson and Jonsell 1999).

Although it may not be possible to establish a causal relationship between habitat variables and nestedness, significant correlations can suggest mechanistic hypotheses and help to prioritize more detailed observations or experimental manipulations (Fleishman and Mac Nally 2002).

Understanding distribution patterns and their degree of generality is particularly important among taxonomic groups that have been suggested as surrogate measurements or "indicators" of species richness or ecological condition (e.g., Noss 1990; Prendergast 1997; Carroll and Pearson 1998; Turak et al. 1999; Mac Nally and Fleishman 2002). The concept of indicator species is appealing, and reliable indicators would offer several practical benefits (Niemi et al. 1997; Scott 1998). For example, if the indicators are easier to detect, especially by inexperienced observers, than other species of interest, it may be considerably faster and cheaper to monitor the indicators than to conduct comprehensive surveys (Gustafsson 2000). Although indicator-species concepts are popular, they rarely have been tested empirically. Few species have proven to be efficient correlates of community-level or ecosystem-level variables (Scott 1998; Watt 1998; Andersen 1999; Caro and O'Doherty 1999; Lindenmayer 1999; Gustafsson 2000).

Various measures of the species diversity or occurrence of birds and butterflies frequently have been proposed as a surrogate measure of the status of each other, of other taxonomic groups, or of environmental variables (Pyle et al. 1981; Erhardt 1985; Temple and Wiens 1989; Kremen 1994; Hooson 1995; New et al. 1995; Blair and Launer 1997; Mac Nally 1997; Chase et al. 1998; Blair 1999; Swengel and Swengel 1999; O'Connell et al. 2000). Birds and butterflies also are well-known ecologically, relatively easy to study and monitor, and popular with the general public. To evaluate the ecological information that the distribution of birds and butterflies can convey, it is helpful to test whether the distribution of each group reflects dominant environmental gradients or habitat features, whether species-environment relationships are consistent in space, and whether the two groups have similar responses to selected environmental features. Assessments of consistency of responses to environmental structures among different taxonomic groups are critical, and there is a need to build on a limited number of existing published works (e.g., Howard et al. 1998; Ricketts et al. 1999; Mac Nally et al. 2002b).

Previously, we found that elevation and local topographic heterogeneity (henceforth, "topography") may be responsible for generating nested species distributions among resident butterflies in the Toquima Range, a mountain range in the Great Basin of western North America (Fleishman and Mac Nally 2002). Not only species richness but also relative degree of nestedness was better explained by a function of topography than as a function of area. Here, we take advantage of a more extensive data set on both bird and butterfly occurrence in three neighboring mountain ranges to test whether assemblage-level distribution patterns are similar among mountain ranges, which often are treated as separate manage-

ment planning units, and among taxonomic groups. Specifically, we test whether species composition of birds and butterflies appears to be influenced by the same environmental variables and whether those patterns are consistent in space. We also test whether distribution patterns of bird and butterfly assemblages across the landscape appear to be sensitive to human use of riparian areas.

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## Materials and methods

### Study system

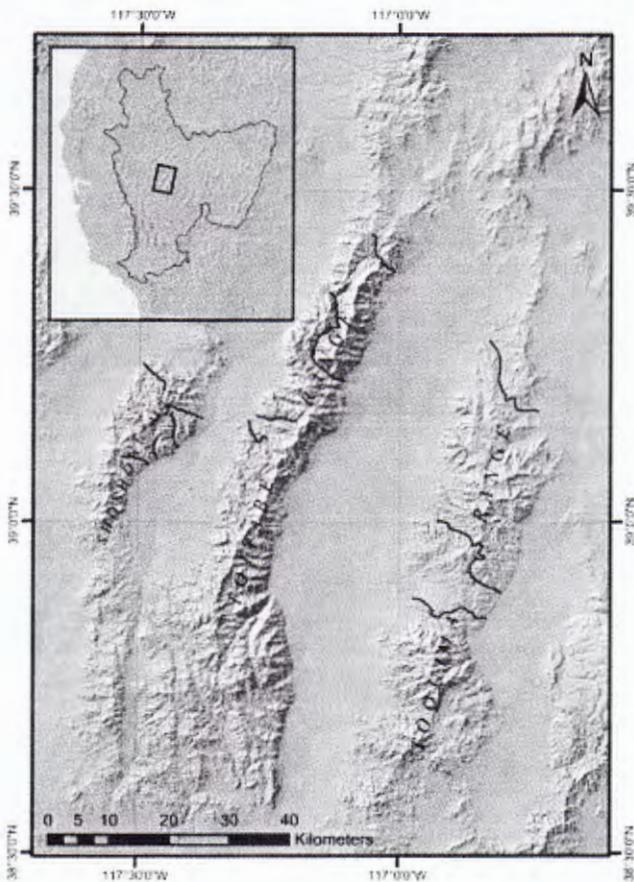
The Great Basin of western North America includes more than 200 mountain ranges. These ranges were isolated from each other and from the surrounding lower-elevation valleys as the regional climate became warmer and drier following the Pleistocene (Brown 1978; Wells 1983; Grayson 1993). The United States Forest Service generally develops separate management plans for individual mountain ranges under its jurisdiction and is seeking ecological data to contribute to these plans. Individual mountain ranges function as discrete habitat islands for many taxa that either are restricted to montane habitats or have relatively low mobility (McDonald and Brown 1992; Murphy and Weiss 1992, but see Skaggs and Boecklen 1996; Lawlor 1998). For many resident butterflies (taxa that complete their entire life cycle in the mountain range), canyons or segments of canyons within mountain ranges also represent archipelagos of habitat islands (Fleishman et al. 1997; Fleishman and Murphy 1999; Fleishman and Mac Nally 2002). Movement of birds among canyons similarly is restricted by canyon topography (frequently narrow and steeply-walled) and the dearth of resources and shelter from predators in the intervening uplands. Distances between canyons – particularly between the canyons we sampled – usually are much greater than the territory or home range sizes during the breeding season of many of the birds in our study system (AOU 1992; Ryser 1985; Dobkin and Wilcox 1986).

Our study system met three key assumptions of most of the common nestedness analyses (Patterson and Atmar 1986; Patterson 1987; Wright and Reeves 1992; Atmar and Patterson 1993; Wright et al. 1998). First, locations had a common biogeographic history. Second, locations shared an ancestral pool of species. Third, relatively complete species inventories were available.

### Data collection

Data for our analyses were collected from 1995 to 2001 in three adjacent mountain ranges in the central Great Basin (Lander and Nye counties, Nevada, U.S.A.). Inventories for both birds and butterflies were conducted in five canyons in the Shoshone Mountains, five canyons in the Toiyabe Range, and six canyons in the Toquima Range (Fig. 1). 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, 2001c). 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 24 segments in the Shoshone Mountains, 31 in the Toiyabe Range, and 28 in the Toquima Range.

Our inventories covered an elevational range of 1,921–2,691 m and an area span of 1.5–44.4 ha. Our inventories followed standard methods for birds and butterflies 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). Birds were sampled 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. Each point was visited 3 times during the breeding season. Three surveys are considered sufficient to determine which spe-



**Fig. 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). One pair of canyons in the Toiyabe Range and three pairs of canyons in the Toquima Range connect at the crest of the range

cies 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 and Rich 1998).

We inventoried 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 2 weeks throughout the majority of the flight season (late May through August – i.e., the period during which adult butterflies are present), 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). Although multiple segments within a canyon were not “independent”, spatially or faunally, this is not critical because nestedness analyses, especially differential-colonization models, assume that dispersal between locations occurs (Darlington 1957; Worthen 1996). In addition, the short-term presence of bird and butterfly species in each segment was independent (i.e., an individual was not recorded in >1 segment during a canyon inventory). While the dynamics of some populations may be linked (Brown and Kodric-Brown 1977; Hanski and Gilpin 1997), measurement of species occurrence should not be confounded by movement among canyon segments. Moreover,

our focus is on relative nestedness of different matrix-ordering criteria, so absolute independence is less critical.

We recorded 67 species of breeding birds and 56 resident species of butterflies from our study locations. Presence/absence matrices are available from the corresponding author upon request. We categorized species according to their residency status, riparian dependence, and typical movement distance (estimated using breeding territory size for birds, vagility for butterflies). In desert ecoregions like the Great Basin, riparian areas tend to receive disproportionately heavy use from numerous faunal groups and from humans. Riparian-obligate plants and animals may be particularly vulnerable to human land uses and are of special concern to land managers (Kauffman and Krueger 1984; Armour et al. 1991; Dawson 1992; Chaney et al. 1993). Birds were categorized as year-round residents, short-distance migrants (some individuals winter north of the neotropics, others may migrate to the neotropics), or neotropical migrants (winter in the neotropics) (Gough et al. 1998). Riparian dependence of birds was categorized as obligate, intermediate, or non-riparian (Dobkin and Wilcox 1986). Territory size of birds during the breeding season was classed as low (<4 ha), moderate (4–40 ha), or high (>40 ha) (AOU 1992). Butterfly species that rarely if ever are found in the valleys that separate Great Basin mountain ranges were categorized as montane residents (Fleishman et al. 1997). Species whose larval host-plants rarely if ever occur away from permanent water were classified as riparian obligates (Fleishman et al. 1997). We categorized the vagility of each butterfly species as low (10s of m), moderate (100s of m), or high (1,000s of m) (Fleishman et al. 1997).

For both birds and butterflies, residency status is roughly analogous to resource or habitat specificity. Neotropical migrant birds, for instance, 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. Similarly, because valleys in the Great Basin typically have lower plant diversity, are drier, and have less topographic heterogeneity than the mountains, butterflies that can breed in the valleys tend to have less specific resource requirements with respect to larval hostplants, water availability, and sites for finding mates than montane residents (Fleishman et al. 1997).

We computed the relative nestedness (C) of each species-by-locations matrix with the program NESTCALC (Wright et al. 1990). We chose to use this metric because it allows for statistical comparison of degree of nestedness among matrices or data sets. To test whether matrices were significantly nested, we used Cochran's *Q* statistic (Wright and Reeves 1992). We used Z-scores (standard-Normal variates) to test whether significant differences existed in relative nestedness among matrices (Wright and Reeves 1992).

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 or incidence (number of presences). This phenomenological ordering provides a description of assemblage composition (cf. Worthen 1996). To test whether a particular environmental variable may be related to a nested distributional pattern (at least by correlation), rows instead may be ordered with respect to that variable (Lomolino 1996; Lomolino and Davis 1997; Deacon and Mac Nally 1998; Honnay et al. 1999; Mac Nally and Lake 1999; Patterson and Atmar 2000; Fleishman and Mac Nally 2002; Mac Nally et al. 2002a). 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 help elucidate factors that may influence assemblage structure, we computed the relative nestedness of six matrices (birds and butterflies in each mountain range) ordered using different criteria.

**Table 1** Matrix size and values of the relative nestedness index *C*. See text for more complete descriptions of row ordering criteria and life history categories. Degrees of freedom are (number of species-1). *P*-values are all <0.0001 (exceptions noted)

Row order	Life history category	Locations	Species	<i>C</i>
Shoshone Mountains, birds				
Species richness		24	44	0.353
Area		24	44	0.268
Topography		24	44	0.218
	Resident	18	9	0.444
	Short-distance migrant	23	19	0.255
	Neotropical migrant	24	16	0.478
	Riparian-obligate	20	13	0.491
	Intermediate	21	11	0.316
	Nonriparian	24	20	0.389
	Small territory	24	29	0.399
	Moderate territory	21	8	0.375
	Large territory	12	7	0.030
Shoshone Mountains, butterflies				
Species richness		24	48	0.544
Area		24	48	0.392
Topography		24	48	0.432
	Montane resident	24	28	0.449
	Resident	24	20	0.753
	Riparian obligate	19	9	0.406
	Not riparian-obligate	24	39	0.581
	Low vagility	24	14	0.511
	Moderate vagility	24	23	0.626
	High vagility	24	11	0.567
Toiyabe Range, birds				
Species richness		31	52	0.415
Area		31	52	0.344
Topography		31	52	0.334
	Resident	16	9	0.195
	Short-distance migrant	30	23	0.323
	Neotropical migrant	31	20	0.453
	Riparian obligate	26	14	0.549
	Intermediate	23	14	0.324
	Nonriparian	31	23	0.390
	Small territory	31	32	0.397
	Moderate territory	25	10	0.497
	Large territory	11	10	-0.074***
Toiyabe Range, butterflies				
Species richness		31	63	0.577
Area		31	63	0.512
Topography		31	63	0.332
	Montane resident	31	39	0.582
	Resident	31	24	0.604
	Riparian obligate	30	13	0.604
	Not riparian-obligate	31	50	0.603
	Low vagility	31	19	0.304
	Moderate vagility	31	28	0.547
	High vagility	31	16	0.650
Toquima Range, birds				
Species richness		28	40	0.444
Area		28	40	0.332
Topography		28	40	0.334
	Resident	19	6	0.512
	Short-distance migrant	27	18	0.362
	Neotropical migrant	28	16	0.625
	Riparian obligate	6	6	-0.138**
	Intermediate	19	11	0.375
	Nonriparian	28	23	0.502
	Small territory	28	25	0.516
	Moderate territory	20	10	0.256
	Large territory	12	5	-0.047*

**Table 1** (continued)

Row order	Life history category	Locations	Species	C
Toquima Range, butterflies				
Species richness		28	52	0.556
Area		28	52	0.299
Topography		28	52	0.475
	Montane resident	27	30	0.430
	Resident	28	22	0.727
	Riparian obligate	11	8	0.126
	Not riparian-obligate	28	44	0.532
	Low vagility	27	15	0.592
	Moderate vagility	28	25	0.570
	High vagility	23	21	0.487

\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ ,  
\*  $P < 0.05$

First, we listed rows in order of decreasing species richness and columns in order of decreasing incidence. Second, we listed rows in order of decreasing area of the canyon segment. Third, we ordered rows according to "topography," a simple function that explained significant deviance (57%,  $P < 0.0001$ ) in the species richness of butterflies in the Toquima Range (Mac Nally et al. 2002c) and also appeared to play a role in generating nested distributions of butterflies in that range (Fleishman and Mac Nally 2002). The variables included in this model are mean elevation of the canyon segment and the standard deviation of topographic exposure within a 150-m radius. Exposure is calculated by comparing the elevation of the canyon segment with the elevation of a specified neighborhood around that segment, thus is analogous to local topographic heterogeneity.

Given the potentially large number of comparisons that could be made based on the limited number of data matrices, we were selective in choosing the comparisons presented here. We chose not to use Bonferroni-like corrections because of their inherent conservatism and their tendency to reduce statistical power (Swager 1984; Levin 1996). Moreover, the less-conservative (and hence more powerful) sequential approaches, such as Holm's (1979), treat  $P$ -values of multiple tests as 'orderable' (i.e. 'least probable' to 'most probable' given the null hypothesis). This implies that  $P$ -values are orderable, monotonic measures of evidence against the null hypothesis, which has been contested (Hilborn and Mangel 1997). Thus, we deliberately restricted the number of comparisons in lieu of undertaking type-I error rate corrections (for a discussion, see Quinn and Keough 2002).

To examine whether distribution patterns of single taxonomic assemblages were similar across space, we tested whether relative nestedness varied among mountain ranges. We also explored whether relative nestedness differed between birds and butterflies. Within each taxonomic group, we examined whether area and topography might be responsible for producing nestedness, and whether those species-environment relationships were consistent across space.

Both among and within taxonomic groups, nestedness that varies in relation to life history can suggest natural and anthropogenic phenomena that affect diversity patterns (e.g., Blake 1991; Hecnar and M'Closkey 1997; Bird and Boecklen 1998). Therefore, for both birds and butterflies, we tested whether groups of species with different residency status, riparian dependence, and territory size or vagility had different degrees of nestedness. For these analyses, matrix rows were ordered by species richness; we compared nestedness values for matrices that included species with different life history characteristics. Because not all species categories were represented in all locations, we culled the data sets to include only those species fitting into various categories. Thus, the number of locations included in some analyses was smaller than the total number of study locations (Table 1).

## Results

The number of species of birds and butterflies in each life-history category in each mountain range is presented

**Table 2** Relative nestedness of birds. Values are one-tailed  $Z$ -scores for matrices ordered by different criteria. 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 (*SH* area) was significantly less nested than the Toiyabe Range matrix ordered by area (*TY* area). *SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range. *Topo* refers to matrices ordered by topography (see text for more complete description)

	SH area	TY area	TQ area	SH topo	TY topo	TQ topo
SH area		-1.81*	-1.49	0.98		
TY area	1.81*		0.38		0.33	
TQ area	1.49	0.38				-0.05
SH topo	-0.98				-2.75**	-2.68**
TY topo		-0.33		2.75**		0.01
TQ topo			0.05	2.68**	-0.01	

\*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$

in Table 1. Five species of birds were found only in the Shoshone Mountains; 13 species of birds and 8 species of butterflies were restricted to the Toiyabe Range, and 7 species of birds and 1 butterfly species were recorded only from the Toquima Range. No species is endemic to one mountain range.

With three exceptions, regardless of how matrices were ordered or faunas subdivided with respect to life history characteristics, assemblages were significantly more nested than expected by chance (Table 1). The exceptions were riparian birds in the Toquima Range and birds with the largest territories in the Toiyabe and Toquima ranges, which were significantly less nested than expected by chance (i.e., anti-nested, sensu Wright et al. 1998; Poulin and Guégan 2000). Apparent anti-nestedness of the three matrices may have resulted in part from their small size (see Table 1). Although  $C$  is not sensitive to matrix size (Wright and Reeves 1992; Bird and Boecklen 1998), nestedness may be more variable when matrices are relatively small (Wright et al. 1998).

Using values of the relative nestedness index  $C$  for mountain-range level matrices ranked by species richness, we compared nestedness between our focal groups and other bird and butterfly assemblages. Our  $C$ -values for birds (0.353–0.444) were lower than the mean  $C$  computed for birds on habitat islands by Boecklen

**Table 3** Relative nestedness of butterflies. Values are one-tailed Z-scores for matrices ordered by different criteria. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate

lower nestedness. *SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range. *Topo* refers to matrices ordered by topography heterogeneity (see text for more complete description)

	SH area	TY area	TQ area	SH topo	TY topo	TQ topo
SH area						
TY area	4.68***	-4.68***	3.27***	1.31		
TQ area	-3.27***	-9.12***	9.12***		9.03***	-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***	

\*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$

**Table 4** Relative nestedness as a function of residency status of birds. Values are one-tailed Z-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness.

*SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range; *res* resident; *sdm* short-distance migrant; *ntm* neotropical migrant (see text for more detailed definitions)

	SH res	SH sdm	SH ntm	TY res	TY sdm	TY ntm	TQ res	TQ sdm	TQ ntm
SH.res		1.55	-0.34						
SH.sdm	-1.55		-2.30**						
SH.ntm	0.34	2.30**							
TY.res					-0.57	-1.15			
TY.sdm				0.57		-2.22**			
TY.ntm				1.15	2.22**				
TQ.res								1.41	-1.14
TQ.sdm							-1.41		-4.71***
TQ.ntm							1.14	4.71***	

\*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$

**Table 5** Relative nestedness as a function of residency status of butterflies. Values are one-tailed Z-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness. *SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range; *mres* montane resident; *res* resident (see text for more detailed definitions)

	SH mres	SH res	TY mres	TY res	TQ mres	TQ res
SH.mres		-6.92***				
SH.res	6.92***					
TY.mres				-0.71		
TY.res		0.71				
TQ.mres						-7.36***
TQ.res					7.36***	

\*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$

(1997) or for birds in the Great Basin using mountain ranges as the sampling unit (Brown 1978), but within the range of reported values for other bird communities on habitat islands (Cook and Quinn 1995; Boecklen 1997). *C*-values for butterflies (0.544–0.577) were higher than the mean *C* computed either for invertebrates on habitat islands or for terrestrial invertebrates on habitat islands by Boecklen (1997), but within the range of reported values for other lepidopteran assemblages (Cook and Quinn 1995; Boecklen 1997).

### Spatial patterns

Birds in the Shoshone Mountains consistently appeared to have low nestedness – i.e., less ordered composition – relative to the other two mountain ranges (Table 2). When matrices were ordered with respect to area, birds were more nested in the Toiyabe Range than the Shoshone Mountains. When matrices were ordered with respect to topography, birds in both the Toiyabe and Toquima ranges were more nested than birds in the Shoshone Mountains.

Nestedness of butterflies varied in space and relative nestedness rankings were sensitive to how the matrices were ordered (Table 3). When matrices were ordered by area, relative nestedness of butterflies decreased from the Toiyabe Range to the Shoshone Mountains to the Toquima Range. By contrast, matrices ordered by topography indicated that butterflies in the Shoshone Mountains and Toquima Range were more nested than butterflies in the Toiyabe Range. In all three mountain ranges, regardless of how matrices were ordered, butterflies were more nested than birds. This suggests that at the spatial grain and extent of our study, local species composition of butterflies may be more ordered than local species composition of birds.

**Table 6** Relative nestedness as a function of riparian obligacy of birds. Values are one-tailed Z-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness.

	SH obl	SH int	SH non	TY obl	TY int	TY non	TQ obl	TQ int	TQ non
SH.obl		1.36	1.25						
SH.int	-1.36		-0.61						
SH.non	-1.25	0.61							
TY.obl					2.52**	3.19***			
TY.int				-2.52**		-0.75			
TY.non				-3.19***	0.75				
TQ.obl								-0.40	-0.49
TQ.int							0.40		-1.25
TQ.non							0.49	1.25	

\*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$

**Table 7** Relative nestedness as a function of riparian obligacy of butterflies. Values are one-tailed Z-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness. *SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range; *rip* riparian obligate; *non* non-obligate (see text for more detailed definitions)

	SH rip	SH non	TY rip	TY non	TQ rip	TQ non
SH.rip		-1.82*				
SH.non	1.82*					
TY.rip				0.03		
TY.non			-0.03			
TQ.rip						-0.63
TQ.non					0.63	

\*  $P \leq 0.05$

#### Species–environment relationships

To test whether area and topography affected nestedness to an equal extent, we considered each location (mountain range) separately and compared results of different ordering criteria. Area and topography did not appear to differ in their influence on bird distributions: in none of the three mountain ranges was relative nestedness of

*SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range; *obl* riparian obligate; *int* intermediate; *non* non-riparian (see text for more detailed definitions)

birds affected by which environmental variable was used to order the matrix (Table 2). By contrast, area and topography differed in how strongly they affected species composition of butterflies, but the comparative importance of the gradients varied among ranges (Table 3). In the Toquima Range, nestedness (and species richness; Mac Nally et al. 2002c) was better explained as a function of topography than of area per se (see also Fleishman and Mac Nally 2002). The Toiyabe Range showed the opposite relationship – nestedness of butterflies was better explained by area than as a function of topography. Relative nestedness of butterflies did not differ as a function of either environmental variable in the Shoshone Mountains.

#### Life history and nestedness

We found limited evidence that life history affected relative nestedness. Relative nestedness of both taxonomic groups differed according to residency status, but the trends for birds and butterflies were opposite and neither was strong (Table 4). For birds, species with more specific nesting and food requirements tended to be more nested. In each of the three mountain ranges, neotropical

**Table 8** Relative nestedness as a function of territory size of birds. Values are one-tailed Z-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher

	SH sm	SH mod	SH lg	TY sm	TY mod	TY lg	TQ sm	TQ mod	TQ lg
SH.sm		0.21	0.18						
SH.mod	-0.21		0.17						
SH.lg	-0.18	-0.17							
TY.sm					-1.58	0.67			
TY.mod				1.58		0.81			
TY.lg				-0.67	-0.81				
TQ.sm								2.13*	0.40
TQ.mod							-2.13*		0.21
TQ.lg							-0.40	-0.21	

\*  $P \leq 0.05$

nestedness and negative values indicate lower nestedness. *SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range; *sm* small; *mod* moderate; *lg* large (see text for more detailed definitions)

**Table 9** Relative nestedness as a function of vagility of butterflies. Values are one-tailed Z-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher

nestedness and negative values indicate lower nestedness. *SH* Shoshone Mountains; *TY* Toiyabe Range; *TQ* Toquima Range; *lo* low; *mod* moderate; *hi* high (see text for more detailed definitions)

	SH lo	SH mod	SH hi	TY lo	TY mod	TY hi	TQ lo	TQ mod	TQ hi
SH.lo		-2.08**	-0.83						
SH.mod	2.08**		1.08						
SH.hi	0.83	-1.08							
TY.lo					-4.37***	-5.99***			
TY.mod				4.37***		-2.87**			
TY.hi				5.99***	2.87**				
TQ.lo								0.52	1.45
TQ.mod							-0.52		1.20
TQ.hi							-1.45	-1.20	

\*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$

migrant birds were significantly more nested than short-distance migrants. For butterflies, species with less specific requirements with respect to food, water, and topographic heterogeneity generally were more nested. In the Shoshone Mountains and Toquima Range, resident butterflies (species that sometimes are found in the valleys) were more nested than montane residents (Table 5).

There were few significant differences in the relative nestedness of species grouped according to riparian dependence (Tables 6, 7). Riparian-obligate birds in the Toiyabe Range were significantly more nested than either intermediate or non-riparian birds (Table 6). Non-riparian butterflies were significantly more nested than riparian-obligate butterflies in the Shoshone Mountains (Table 7).

The only significant difference in nestedness among birds grouped according to territory size was in the Toquima Range, where birds with small territories were more nested than birds with moderately-sized territories (Table 8). Butterflies showed the opposite trend (Table 9). In the Shoshone Mountains, butterflies with moderate vagility were more nested than species with low vagility. In the Toiyabe Range, relative nestedness of butterflies increased as vagility increased: species with moderate vagility were more nested than species with low vagility, and species with high vagility were more nested than species with moderate or low vagility (see also Fleishman et al. 2001a).

## Discussion

The work presented here was motivated by our desire to address questions about assemblage-level distribution patterns and underlying processes over large areas while simultaneously responding to conservation needs. In particular, our objective was to examine whether generalizations about species composition can be drawn across taxonomic groups and landscape planning units (in this case, mountain ranges).

Regardless of how matrices were ordered or species categorized, significant nesting was almost ubiquitous.

## Spatial patterns

Birds in the Shoshone Mountains appeared to be less nested than birds in other nearby mountain ranges. If faunal nestedness partly reflects habitat nestedness, then we would expect relatively low nestedness in systems with relatively homogenous (or otherwise non-nested) habitat. We suspect that the distribution of critical resources for birds indeed may be less nested in the Shoshone Mountains than in the Toiyabe and Toquima ranges. Piñon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) woodlands in the Shoshone Mountains are believed to have increased substantially in area and density over the past 150 years at the expense of native shrubs and grasses (Tausch and Tueller 1990). More recently, non-native grasses have begun to invade the understory. As a result, vegetation in the Shoshone Mountains may be more homogenous and less diverse in both structure and composition than vegetation in the Toiyabe and Toquima ranges.

Site area and topography may not be the most influential environmental drivers of assemblage structure of birds in our study system. We would not expect relative nestedness to vary significantly among matrices ordered according to different environmental variables if none of those variables was strongly associated with species occurrence. Although the general resource requirements of birds and butterflies in the montane Great Basin overlap (e.g., both groups exploit riparian areas for food and shelter), some of their specific needs differ. For instance, species richness of birds frequently corresponds to vegetation structure, while species richness of butterflies may be more closely associated with vegetation composition (but see Rotenberry 1985; Mac Nally 1990). We note that the association between nestedness of birds and area was relatively slight (Mac Nally et al., unpublished data). The latter result echoes previous work on butterflies across the Great Basin (Fleishman et al. 2001a). In an ecoregion as climatically erratic and topographically heterogeneous as the Great Basin, critical resources for both birds and butterflies may not be strongly correlated with area.

Conclusions about relative nestedness of butterflies among mountain ranges were sensitive to how matrices were ordered. Ecologically, this suggests that the influence of area and topography on species composition of butterflies varies in space. Our results indicate that local species composition in one mountain range (landscape planning unit) is no more predictable than local species composition in other mountain ranges. However, by ordering matrices according to a series of variables, it may be possible to rank like assemblages in different planning units by their sensitivity to various environmental gradients.

### Life history

Several workers have recognized the value of comparing patterns of nestedness among taxonomic groups at the same locations (Patterson and Brown 1991; Cook and Quinn 1995; Wright et al. 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 and Quinn (1995) found that more vagile groups often were more highly nested than less vagile taxonomic groups, but Wright et al. (1998) did not find significant differences in mean nestedness rank by taxonomic group. Butterflies were more nested than birds on an archipelago of four islands in the Greater Antilles, but, in the same archipelago, birds were more nested than ground beetles (Wright et al. 1998).

We found that butterflies were more nested than birds in all mountain ranges regardless of how matrices were ordered. Our results do not necessarily imply that extinction is a more important contemporary process than colonization in our study system. Instead, our results may indicate that, as suggested by earlier zoogeographers in the montane Great Basin, extinction has been more influential in driving assemblage structure of groups with limited migration among mountain ranges (e.g., butterflies) and colonization has been more influential in determining assemblage structure of more efficient dispersers (e.g., birds) (Cutler 1991; McDonald and Brown 1992; Cook and Quinn 1995).

Examining relationships between nestedness, residency status, and territory size or vagility within taxonomic groups could shed more light on processes affecting species composition (Cook and Quinn 1995). Among birds, similar to results reported from remnant woodlands in the midwestern United States (Blake 1991), we discovered that increasing habitat selectivity with respect to nesting sites and food sources was associated with greater nestedness, but overall, we found limited evidence that nestedness of birds and butterflies was affected by selective dispersal (see also Bird and Boecklen 1998; Fleishman et al. 2001a). Several factors may explain

why these correlations were weak. One possibility is that the spatial grain of our bird analyses was too small. Limited dispersal of birds between canyon segments would dilute the effect of differential colonization in generating nestedness in our analyses. To explore that possibility, we compared nestedness at the grain of canyons (pooled among ranges in order to increase sample size) as opposed to canyon segments. Using a larger spatial grain produced virtually identical results: neotropical migrants were significantly more nested than short-distance migrants ( $Z=-3.39$ ,  $P<0.001$ ). Another possibility is that most resources used by birds and butterflies are present in the majority of the locations that we inventoried, at least during peak activity periods for both groups.

Although there is considerable human use of riparian areas in the Great Basin, riparian dependence had little detectable effect on nestedness of birds and butterflies. At least three explanations seem plausible (Fleishman and Murphy 1999). First, it is possible that modification of riparian areas has not been severe enough to cause local extirpations. Second, species with high vulnerability to loss of riparian habitat may already have disappeared (an extinction "sieve"). Third, the magnitude of riparian disturbance may not be arranged in a predictable (nested) manner among study locations (Hecnar and M'Closkey 1997). In this system, more detailed autecological studies may be necessary to reveal ecological mechanisms underlying nested distributional patterns of assemblages of conservation interest.

### Generality of distributional patterns

Few studies of nestedness have explicitly compared data on multiple taxonomic groups at the same locations (e.g., Howard et al. 1998; Ricketts et al. 1999; Mac Nally et al. 2002b). Spatially extensive documentation of distribution patterns of bird and butterfly assemblages should prove useful in ecoregions where even basic information on species occurrence is lacking. Potential mechanisms underlying the distribution patterns are numerous, ranging from vegetation structure and composition to topography and climate. Although we recognize the potential of land-cover type to explain patterns of species composition, we chose to focus on variables that can be derived efficiently from remotely sensed data and geographic information systems (Fleishman et al. 2001c; Mac Nally et al. 2002c). Our choice partly reflects the financial and logistic obstacles to obtaining relatively fine-grained, validated data on land cover for a large area. Several land-cover classifications for North America, based on different aggregations of remotely sensed seasonal land cover regions, are currently available online from the United States Geological Survey. Unfortunately, these classifications are not sufficiently detailed (or ground-truthed) to shed light on distribution patterns of birds and butterflies in our study area.

Our results suggest that the abiotic and biotic processes influencing even such prevalent assemblage-level dis-

tribution patterns as nestedness vary among taxonomic groups. The relative importance of those processes varies spatially, even within a taxonomic group. As a result, we urge caution in using birds and butterflies as surrogate measures of the status of each other or of other taxonomic groups. Our results also reinforce that a "one-size-fits-all" approach to sampling (e.g., measuring diversity of multiple taxonomic groups at the same grain) may be misleading. These conclusions do not invalidate the use of birds and butterflies as focal species for monitoring the biological effects of known environmental changes, but they are a reminder that taxonomic groups are not interchangeable for conservation planning (Stohlgren et al. 1995; Niemi et al. 1997; Simberloff 1998; Caro and O'Doherty 1999; Andelman and Fagan 2000; Fleishman et al. 2001b; Rubinoff 2001).

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