

SPECIAL  
FEATURE

# Patterns of spatial autocorrelation of assemblages of birds, floristics, physiognomy, and primary productivity in the central Great Basin, USA

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## ABSTRACT

We fitted spatial autocorrelation functions to distance-based data for assemblages of birds and for three attributes of birds' habitats at 140 locations, separated by up to 65 km, in the Great Basin (Nevada, USA). The three habitat characteristics were taxonomic composition of the vegetation, physical structure of the vegetation, and a measure of primary productivity, the normalized difference vegetation index, estimated from satellite imagery. We found that a spherical model was the best fit to data for avifaunal composition, vegetation composition, and primary productivity, but the distance at which spatial correlation effectively was zero differed substantially among data sets (c. 30 km for birds, 20 km for vegetation composition, and 60 km for primary productivity). A power-law function was the best fit to data for vegetation structure, indicating that the structure of vegetation differed by similar amounts irrespective of distance between locations (up to the maximum distance measured). Our results suggested that the spatial structure of bird assemblages is more similar to vegetation composition than to either vegetation structure or primary productivity, but is autocorrelated over larger distances. We believe that the greater mobility of birds compared with plants may be responsible for this difference.

## Keywords

Bayesian analysis, biodiversity patterns, dissimilarity measures, Great Basin, semivariograms, spatial scale.

## INTRODUCTION

Ecologists arguably often have been remiss in not quantifying spatial (and temporal) relationships among both response and predictor variables. As a result, conventional statistical inferences have less reliability and power (Legendre, 1993; Selmi & Boulinier, 2001; Dale *et al.*, 2002; although see Diniz-Filho *et al.*, 2003). Spatial structure often is treated as a nuisance that must be accounted for to improve the statistical properties of tests. Nevertheless, spatial structure potentially offers many insights into ecological patterns and processes (Tobin, 2004). Because many distributional patterns are not spatially independent, it is useful to identify the lag (difference in space) over which a pattern is autocorrelated and to characterize the functional form of the autocorrelation. If a response variable and a potential predictor variable have similar patterns of autocorrelation, it may be reasonable to infer either a causal relationship or that both variables are responding similarly to another phenomenon (Matérn, 1986; Diniz-Filho *et al.*, 2003; Tobin, 2004). Note that the term 'autocorrelation' can be used to describe a spatial pattern, as we

do in this paper, or to refer to the generation of an autocorrelated spatial pattern by endogenous processes related to a variable of interest (e.g. correlations in species abundances that are linked to dispersal).

Birds are used widely as targets for management strategies, ecological assessments, and monitoring programs. They are biologically and taxonomically well known, relatively easy to study and monitor and are responsive to natural and anthropogenic environmental change. Many studies have addressed spatial autocorrelation in species richness, abundance, or assemblage composition of birds (e.g. Linder *et al.*, 2000; Koenig, 2001; Fairbanks *et al.*, 2002). At relatively large spatial extents, measurements associated with mechanisms potentially driving the spatial distribution of species often have been derived from geographical information systems (GIS) and remote sensing (e.g. van Rensburg *et al.*, 2002; Storch *et al.*, 2003; Marzluff *et al.*, 2004). Here, we focus on spatial autocorrelation of avian composition and three aspects of birds' habitats: floristics (taxonomic composition of the vegetation), physiognomy (physical structure of the vegetation), and an estimate of primary productivity. Floristics

and physiognomy were characterized on the basis of field measurements. Productivity was estimated from a satellite image on the basis of the normalized difference vegetation index (NDVI), a measure of 'greenness' (Tucker, 1979). The primary objective of our work was to examine whether the pattern of spatial autocorrelation for birds was concordant with, and hence might in part be explained by, patterns of spatial autocorrelation of floristics, vegetation structure, and estimated productivity. We do not regard spatial autocorrelation as a factor that is detrimental to understanding, but as an underutilized source of information that can elucidate influences on assemblage composition across space.

There has been an enduring ecological debate about the relative roles of floristics and physiognomy in structuring assemblages of birds (MacArthur & MacArthur, 1961; Robinson & Holmes, 1984; Rotenberry, 1985; Mac Nally, 1990). Data on the respective influence of these factors on species composition of birds may be helpful for development and implementation of conservation and land-use plans. Evidence on whether species composition of birds is more closely associated with floristics or vegetation structure is equivocal (MacArthur *et al.*, 1966; Anderson & Shugart, 1974; Tomoff, 1974; Wiens & Rotenberry, 1981). Some authors have suggested that as spatial lag increases, the importance of floristics decreases and the role of vegetation structure increases (Rotenberry, 1985; Wiens *et al.*, 1987). There also may be correlations between floristic similarities and structural similarities across relatively large areas (Mac Nally *et al.*, 2002). Various estimates of primary productivity have been shown to explain spatial patterns in species richness and species composition of birds in many systems, especially at subcontinental to global scales (van Rensburg *et al.*, 2002; Hawkins *et al.*, 2003; Hurlbert & Haskell, 2003).

Geostatistical analyses usually model spatial autocorrelation with semivariograms, which are representations of variances in a variable (e.g. mineral concentration) as a function of distance (also called spatial lag) (Cressie, 1993; Carr, 1995). Geospatial analyses have at least two major advantages over techniques such as multiple regression. First, one need not assume that variation in the response variable is linearly related to variation in the predictor variables, which is a basic assumption of multiple regression. Although nonlinear versions of multiple regression are possible (e.g. quadratic terms of predictors), the exact choice of functional form is potentially complicated by interactions among predictor variables (including nonlinear terms) and different spatial patterns. The latter point underlies our decision to use geospatial methods. Second, it is unclear how to gauge the importance of correlations among similarities in conventional regression analysis; for example, how many degrees of freedom are reasonable? Geospatial analysis, however, offers a variety of semivariogram models to characterize different types of spatial phenomena and is designed to work on data arising from pairs of points. In many cases, prior knowledge about the model most likely to fit a given phenomenon does not exist, or there may be valid alternative hypotheses. We fitted a set of the most commonly used semivariogram models to measures of the similarity of bird assemblages, floristics, vegetation structure,

and estimated productivity at 140 sites in the mountains of the central Great Basin (Lander and Nye counties, Nevada, USA).

## METHODS

### Field methods

Data for our analyses were collected from 2001 to 2004 in three adjacent mountain ranges in the central Great Basin, the Shoshone Mountains (1850 km<sup>2</sup>, approximate north–south boundaries 39°14' to 38°57'), Toiyabe Range (3100 km<sup>2</sup>, 39°54' to 38°30'), and Toquima Range (1750 km<sup>2</sup>, 39°17' to 38°29'). The mountain ranges are in the same biogeographical subregion and contain similar assemblages of plants and animals. Relatively dry canyons in all of the ranges are dominated by pinyon (*Pinus monophylla* Torr. & Frém.), juniper (*Juniperus osteosperma* (Torr.) Little, *Juniperus occidentalis* Hook.), sagebrush (*Artemisia tridentata* ssp. (Rydb.) B. Boivin), and rabbitbrush (*Chrysothamnus nauseosus* spp. (Pall.) Britt.). Riparian vegetation in canyons with permanent or ephemeral streams can include aspen (*Populus tremuloides* Michx.), cottonwood (*Populus* spp.), willow (*Salix* spp.), water birch (*Betula occidentalis* Hook.), rose (*Rosa woodsii* (S. Wats.) Jepson), and a diverse understorey of grasses and forbs.

Data for birds were collected using established techniques that detect species presence reliably. These methods have been described in detail and tested for sampling adequacy in previous work (e.g. Betrus, 2002). We sampled birds during the breeding season (late May through June) using 75-m variable-radius point counts, an effective method for sampling birds in riparian areas and uplands in the Great Basin (Dobkin & Rich, 1998). Before selecting sampling points, we divided each of our study canyons into multiple segments from base to crest. Each segment was long enough to span a 100-m change in elevation. Within a segment, points were located in each of the dominant vegetation types (usually two or three points per segment). Most points were established > 200 m apart (i.e. 350 m between point centres); territory sizes of birds during the breeding season typically are smaller than distances between neighbouring sampling points. Point counts were conducted only in calm weather, and none were conducted > 3.5 h after dawn. Each point was visited three times per year (Siegel *et al.*, 2001; Betrus, 2002). Geographical coordinates at the centre of the point were measured with a global positioning system.

To characterize floristics and vegetation structure (Table 1), we established three vegetation sampling plots at each bird point. We measured three radial 30-m lines, separated by 120°, from the centre of the point count location. The end of each line served as the centre of a circular vegetation sampling plot with 11.3 m radius (0.04 ha). Each plot was divided into four quadrants. Within each quadrant, we recorded the size of all live trees (either diameter at breast height (d.b.h.) or basal diameter, depending on plant morphology) and the identity of all live trees. Trees generally were defined as woody vegetation > 1 m in height and ≥ 5 cm d.b.h. We also recorded the size and, where possible, the identity of standing or fallen dead trees.

**Table 1** Variables used to define floristics and vegetation structure at each sampling point

Variable	Estimated frequency or proportion cover	
	Minimum	Maximum
<b>Floristics</b>		
<i>Populus tremuloides</i>	0	0.630
<i>Pinus monophylla</i>	0	0.651
<i>Juniperus</i> spp.	0	0.897
<i>Cercocarpus ledifolius</i>	0	0.685
<i>Betula occidentalis</i>	0	0.112
<i>Prunus virginiana</i>	0	0.112
<i>Salix</i> spp.	0	0.674
<i>Ephedra</i> sp.	0	0.155
<i>Rosa woodsii</i>	0	0.333
<i>Ribes</i> spp.	0	0.713
<i>Artemisia tridentata</i> ssp.	0	0.952
<i>Chrysothamnus</i> spp.	0	0.630
Grasses	0	1.000
Forbs	0	0.810
<b>Vegetation structure</b>		
Canopy cover	0	0.857
Shrub cover	0	0.952
Ground cover	0	1.000
Bare ground	0	0.952
Number of live trees	0	145
Average diameter of live trees (cm)	6.56	200
Number of dead trees	0	64
Average diameter of dead trees (cm)	8	75.4

We used a concave spherical densiometer to estimate proportion of canopy cover. To estimate cover of shrubs, ground vegetation, litter, and bare ground, we used an ocular tube (Noon, 1981). Ocular tube measurements were taken at a 45° angle downward from the line of sight. When vegetation was present, we recorded the occurrence of dominant species (approximately 25 different taxa; most grasses and forbs were not treated separately). We collected 21 densiometer and ocular tube readings at each bird point: one each at 8 m, 16 m, and 24 m along the 30-m line from the centre of the bird point to the perimeter of each circular vegetation plot; and one while facing in each of the four cardinal directions from the centre of each circular plot. Cover values for each structural layer (canopy, shrubs, ground vegetation, and bare ground) were averaged at each bird point. Occurrence data for individual species or taxonomic groups of plants were aggregated into a relative measure of frequency at each bird point. Taxa detected in very few points were not included in our analyses.

To estimate primary productivity in a 30 × 30 m pixel at the centre of each point, we calculated the normalized difference vegetation index (Rouse *et al.*, 1973), a measure of 'greenness' that is an extensively used vegetation ratio in remote sensing (Tucker, 1979). We derived NDVI measures from a single cloud-free, geocorrected Landsat 7 EMT + image (WRS 41/33)

acquired in June 2002, coincident with the peak growing season and the most active period for breeding birds in the Great Basin.

### Dissimilarity measures

We used data on geographical coordinates, abundances of 79 species of birds, floristics, vegetation structure, and NDVI at 140 sampling points to build a matrix of dissimilarities for each response variable. This process generated geographical separations (linear distances) and dissimilarity values for each response variable at 9730 pairs of points. We used the Canberra distance as our measure of dissimilarity for bird assemblages, floristics, and vegetation structure because its structure internally scales within variables. Accordingly, calculations on matrices that include variables with substantially different ranges are not strongly influenced by variables with large numerical ranges (Lance & Williams, 1967). Although abundances of most species of birds did not differ widely in numerical range, measures of floristics and vegetation structure often spanned broader ranges (see Table 1). NDVI is measured on a scale from -1.0 to 1.0, where increasing positive values indicate increasing concentrations of green vegetation and negative values indicate non-vegetated surface features such as water, bare ground, or rock. Values at our sampled points ranged from -0.313 to 0.170. Our measure of dissimilarity for NDVI was mean difference.

### Semivariogram models

For each of the four response variables, we calculated eight of the most commonly used (isotropic) semivariogram models: (1) linear, (2) spherical, (3) exponential, (4) Gaussian, (5) wave (or sine-hole), (6) cubic, (7) Matérn ( $\nu = 3/2$ ), and (8) power-law. Formulae for these models are given by Banerjee *et al.* (2004; Table 3.2). Diagrams of many of these models are provided in Cressie (1993; Fig. 2.13).

Different semivariogram models characterize ecological associations that have different types of spatial relationships. For example, many spatially autocorrelated phenomena follow a spherical model — spatial autocorrelation decreases linearly to a certain lag and reaches an asymptote (Carr, 1995), beyond which the locations are statistically uncorrelated and can be regarded as 'independent'. Exponential models are similar to spherical models, but the spatial autocorrelation approaches its maximum value asymptotically (Carr, 1995).

Three parameters describe most semivariogram models (Dale, 1999). The first parameter, the range, is the geographical separation at which semivariogram values become constant (i.e. the distance at which the response variable no longer is spatially autocorrelated). The second parameter, the nugget, is the estimated dissimilarity as the geographical separation approaches zero. The third parameter, the sill, is the dissimilarity value at the range. Linear and power-law models have nugget parameters but neither has a range or a sill; both have a slope parameter. The power-law model also has an exponent parameter.

We used Bayesian model-fitting to compute semivariograms (Congdon, 2003: Chapter 7). We first grouped values for each

response variable into bins with lag distances of 1 km. For each bin, we computed the mean dissimilarity ( $\gamma_d$ ) and the variance of the dissimilarity ( $V_d = 1/\text{precision}$ , Congdon, 2003). We grouped all site-pairs with geographical separations  $> 62$  km into one bin, because sample sizes ( $N_d$ ) were relatively low for kilometre-wide bins at those lags. Among all bins,  $77 \leq N_d \leq 260$ , which far exceeded the minimum of 30 recommended by Journel and Huijbregts (1978).

For the range, we used a uniform prior with a minimum of 0.05 km and a maximum of 150 km. For all semivariogram models except the linear and power-law models, we used a uniform prior for the ratio of the nugget to the sum of the nugget and sill (minimum = 0.05, maximum = 0.95; Congdon, 2003). For the linear and power-law models, we gave the nugget a gamma prior with parameters of 1.0 and 0.001 and the slope a normal prior (mean = 0, precision =  $10^{-6}$ ). For the exponent in the power-law model, the prior was a uniform distribution with minimum of 0 and a maximum of 10.

We used the WINBUGS software package (version 1.4, Spiegelhalter *et al.*, 2003) for all modelling. WINBUGS uses Markov chain Monte Carlo methods to iteratively estimate model parameters by repeatedly 'sampling' from posterior probability distributions specified in the model (Gilks *et al.*, 1996).

### Semivariogram discrimination

We used criterion-based methods (Akaike, 1973; Schwarz, 1978) to identify the best semivariogram model for each of the four response variables. Model complexity for the different semivariogram formulae is similar. The linear model requires estimates for two parameters (nugget and slope), whereas the other seven models require estimates for three parameters (nugget, slope, and exponent for the power-law model; range, nugget, and sill for the remaining models). We computed the Bayesian information criterion (BIC; Schwarz, 1978). Note that criterion-based approaches seek the smallest value (i.e. most negative BIC) for the criterion because the goal is to minimize a function of a weighted sum of model fit and model complexity. Models with BIC values that differ by less than three are held to have similar statistical support (Burnham & Anderson, 1998).

## RESULTS

We calculated the fit (BIC) of the eight models for birds, floristics, vegetation structure, and NDVI (Table 2). We also calculated  $\Delta$ -BIC values, which refer to differences in BIC values between the best (lowest BIC) model and the other seven models.

The best fit for avifaunal composition was a spherical model. Fits for cubic and exponential semivariogram models were within three BIC units of the fit of the spherical model (Table 2). Based on the parameters for the spherical model, avifaunal composition was spatially autocorrelated at lag distances from 0 to 29.6 km (Table 3a); mean Canberra dissimilarities increased rapidly from a mean of 0.38 for lag distances of 0–1 km to 0.53 at the range (Fig. 1a). The plot of observed dissimilarities also revealed decreases in mean dissimilarity (increases in spatial autocorrela-

**Table 2** Bayesian information criterion (BIC) and  $\Delta$ -BIC values for semivariogram models for species composition of birds, floristics, vegetation structure, and NDVI.  $\Delta$ -BIC values refer to differences in BIC values between the 'best' (lowest BIC) model and the other seven models

Model	Variable	BIC	$\Delta$ -BIC
Linear	Birds	-86.5	18.2
*Spherical	Birds	-104.7	0.0
Exponential	Birds	-102.1	2.6
Gaussian	Birds	-99.3	5.4
Sine-hole	Birds	-101.7	3.0
Cubic	Birds	-103.5	1.2
Matérn (3/2)	Birds	-95.9	8.8
Power-law	Birds	-97.7	7.0
Linear	Floristics	-114.5	19.7
*Spherical	Floristics	-134.2	0.0
Exponential	Floristics	-133.7	0.5
Gaussian	Floristics	-127.3	6.9
Cubic	Floristics	-132.0	2.2
Matérn (3/2)	Floristics	-125.8	8.4
Power law	Floristics	-128.1	6.1
Sine-hole	Floristics	-119.7	14.5
Linear	Structure	-115.7	10.0
Spherical	Structure	-121.7	4.0
Exponential	Structure	-121.8	3.9
Gaussian	Structure	-117.8	7.9
Sine-hole	Structure	-114.4	11.3
Cubic	Structure	-122.2	3.5
Matérn (3/2)	Structure	-118.8	6.9
*Power law	Structure	-125.7	0.0
Linear	NDVI	-224.4	32.4
*Spherical	NDVI	-256.8	0.0
Exponential	NDVI	-209.8	47.0
Gaussian	NDVI	-214.1	42.7
Sine-hole	NDVI	-218.5	38.3
Cubic	NDVI	-204.1	52.7
Matérn (3/2)	NDVI	-220.8	36.0
Power law	NDVI	-222.2	34.6

\*model of best fit as assessed by minimum BIC value.

tion) at lag distances near 12 km and 52 km (Fig. 1a). The parameters for the cubic model were similar to those for the spherical model (range = 32.4 km, nugget = 0.39, sill = 0.53). The exponential model, which has a different shape to the spherical and cubic semivariograms because the sill is reached at infinite spatial lag, had a range of 12.9 km, a nugget of 0.35, and a sill of 0.54.

Floristics data were spatially autocorrelated at lag distances from 0 to 20.1 km (Table 3a). A spherical semivariogram model was the best fit to the data (Fig. 1b). Modelled dissimilarity values increased from 0.40 at lag distances 0–1 km to an asymptotic value of 0.53 (Table 3b). The dissimilarity curve was relatively smooth up to the sill. Again, the exponential and cubic models had fits within three BIC units of the best model (Table 2). The exponential model had a range of 9.5 km, nugget of 0.36, and sill

**Table 3** Parameter values for the best-fitting semivariogram models for (a) species composition of birds, (b) floristics, (c) vegetation structure, and (d) estimated productivity (NDVI)

	Mean	SD	95% credible interval	
			Lower	Upper
(a) Bird assemblages: spherical model				
Range (km)	29.6	13.5	4.2	55.7
Nugget	0.37	0.07	0.23	0.48
Sill	0.53	0.02	0.49	0.58
(b) Floristics: spherical model				
Range (km)	20.1	15.2	0.8	54.8
Nugget	0.40	0.13	0.10	0.59
Sill	0.53	0.02	0.49	0.57
(c) Vegetation structure: power-law model				
Exponent	0.18	0.13	0.05	0.53
Nugget	0.30	0.13	0.04	0.48
Slope	0.13	0.10	0.01	0.35
(d) NDVI: spherical model				
Range (km)	58.1	1.6	54.1	60.0
Nugget	0.08	0.002	0.08	0.09
Sill	0.13	0.001	0.13	0.13

SD, standard deviation.

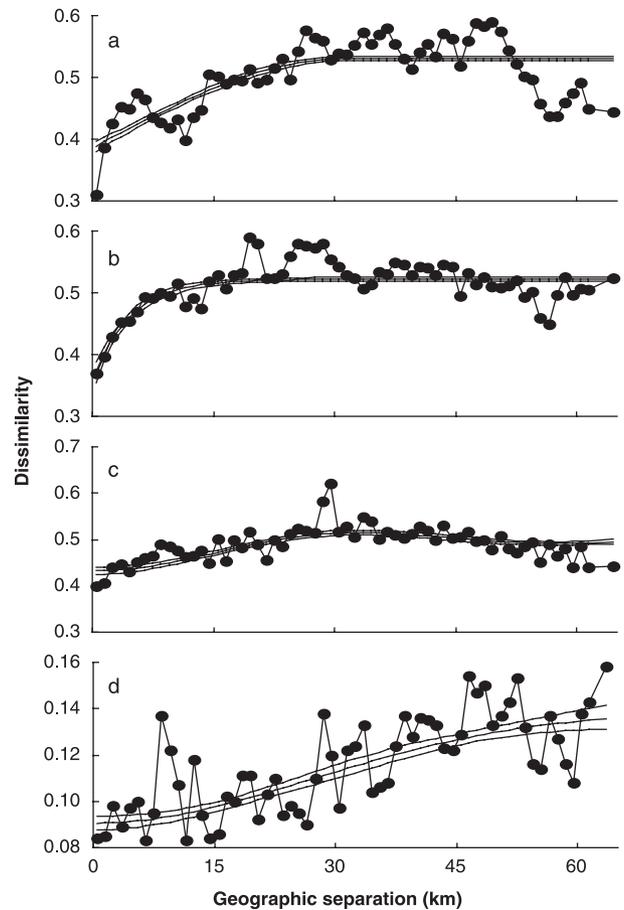
of 0.53. Range, nugget, and sill values for the cubic model were 20.6 km, 0.39, and 0.53, respectively.

The best-fitting semivariogram model for vegetation structure was the power-law (Table 2); because the BIC for the next best-fitting model, the cubic, was three BIC units greater, the power-law was deemed superior to all other modelled semivariogram forms. Although the semivariogram did not attain an asymptote (by definition), the semivariogram was relatively flat, suggesting that vegetation structure was fairly homogenous regardless of lag distance (Fig. 1c).

Estimated productivity (NDVI) was spatially autocorrelated at lag distances from 0 to 58.1 km, with a nugget of 0.08 and a sill of 0.13 (Table 3d). A spherical model was the best fit to the NDVI data (Fig. 1d). The next best was a linear model, with BIC greater than 30 units more than the spherical model (Table 2), so there is little doubt that the spherical model fit data on NDVI much better than any of the other seven models.

## DISCUSSION

We determined the best statistical representations of spatial variation in avian composition and three major components of birds' habitats, identified whether a threshold distance existed beyond which each response variable effectively was not autocorrelated, and examined whether the pattern of spatial autocorrelation for birds was concordant with, and thus might in part reflect, patterns of spatial autocorrelation of habitat variables. We found that species composition of birds was spatially auto-



**Figure 1** Best-fit semivariograms for (a) species composition of birds (spherical), (b) floristics (spherical), (c) vegetation structure (power-law), and (d) estimated productivity (NDVI) (spherical). Points for (a–c) are mean Canberra dissimilarities, points for (d) are mean differences. Lines indicate the mean and 95% credible intervals.

correlated over a larger lag distance than floristics, but over a much smaller distance than NDVI or vegetation structure, which did not attain an asymptote over the range of measured lag distances.

Dissimilarity values for birds were relatively high at all distances measured. This is consistent with previous work in our study system that found considerable spatial variation in species composition of birds, averaged across all lag distances, regardless of sampling resolution (Mac Nally *et al.*, 2004). The range value for birds (*c.* 30 km) was lower than the greatest lag distance for points within a mountain range (*c.* 35 km). Thus, at least some key influences on spatial autocorrelation of avifaunal composition appear to be operating within mountain ranges rather than across larger spatial extents. There is substantial evidence that individual mountain ranges function as permeable but distinct islands of habitat for many taxa whose resources in the arid valleys separating the mountain ranges are scarce (McDonald & Brown, 1992; Murphy & Weiss, 1992). In addition, although the mountain ranges we surveyed are in the same ecological province, differences in elevation and precipitation at the mountain-range level lead to some differences in land cover (Grayson,

1993). The observed increase in spatial autocorrelation at *c.* 12 km may reflect similarities in avifaunal composition at points with similar elevation (especially points at relatively low elevation or relatively high elevation) but in different canyons.

Species composition of both birds and plants was both described best by a spherical model. Dissimilarity values for avifaunal composition were slightly lower than values for floristics at very small lag distances, but were similar at the asymptotic maximum. These results suggest that the spatial pattern of avifaunal composition in the montane central Great Basin, as distinct from species composition at any one point in space, is more consistent with spatial variation in floristic composition than with spatial patterns of variation in vegetation structure. This does not imply that the structure of vegetation plays no role in where different species of birds occur, but spatial dissimilarities in species composition were not concordant with our measures of vegetation structure. It is possible that one or more variables associated with vegetation structure (e.g. canopy cover or number of live trees) would be more closely associated with avifaunal composition than our aggregate assessment of vegetation structure.

It is possible that species composition of birds and species composition of plants have similar responses to abiotic environmental gradients (Hawkins *et al.*, 2003). These relationships may be fairly common in desert ecosystems across south-western North America (Fleishman *et al.*, 2003), where availability of water is a primary driver of biodiversity patterns and ecological processes (Huxman *et al.*, 2004). Although we did not measure spatial autocorrelation of temperature or precipitation, these gradients often influence spatial patterns in avifaunal richness and composition (Root *et al.*, 2003; Storch *et al.*, 2003), floristic composition, and primary productivity across a range of scales. Climate affects the distribution of birds both directly, in terms of physiological responses, and indirectly, by mediating availability of food and other resources (Jones *et al.*, 2003). Unfortunately, few weather stations are located in our study area, and, in part because of the lack of field data, the accuracy of most existing climate models in heterogeneous montane terrain is limited. In particular, spatial comparisons based on absolute climatic values generated by such models, rather than rank orderings, may be unreliable.

Another possibility is that avifaunal composition is responding in part to attributes of bird habitat that we did not characterize. We did not measure several resources, such as availability of insect prey, which may have different spatial patterns to vegetation. The scales at which we measured avifaunal composition and habitat may have been mismatched. Furthermore, we did not examine potential differences in spatial autocorrelation among groups of bird species that differed with respect to functional traits such as migratory status, diet, or dependence on water (Koenig, 2001; Selmi & Boulinier, 2001; Lockwood *et al.*, 2002). Such an analysis is to be reported in a subsequent paper.

Lack of correspondence between spatial patterns of bird composition and vegetation structure also may suggest that avifaunal assembly in our study system is influenced by population dynamics or dispersal history (Storch *et al.*, 2003; Hawkins *et al.*, 2003). Many of the species we recorded are not residents; they

breed but do not winter in the study system. If availability of nesting sites is not strongly limited, individuals may select territories from a suite of potentially suitable locations. On the basis of which territories are occupied in a given year, there may be substantial variation in the attributes that are inferred to be important in birds' use of habitats. Another explanation, not mutually exclusive, is that some birds may select territories on the basis of 'greenness' rather than a certain vegetational profile. The differences in models for the three vegetation variables suggest that estimated productivity in this system cannot be predicted as a simple function of floristics and vegetation structure.

In a temporally variable system such as the Great Basin, certain vegetation variables may fail to explain distributional patterns if species exhibit site fidelity, natal philopatry, and attraction to assemblies of conspecific individuals (Wiens, 1985; Lichstein *et al.*, 2002). Distributions of birds may be affected more by the presence or quantity of different resources in the landscape than by the structural arrangement of those habitat types (Mac Nally, 2005). Indeed, the difference between autocorrelation ranges for birds and floristics probably reflects differences in dispersal ability between birds and plants. As the lag distance over which spatial autocorrelation is present decreases, it implies that spatial variation increasingly is structured in patches (Diniz-Filho *et al.*, 2003). This suggests that in our study system, the distributions of plant species are more patchy than the distributions of birds.

Spatial autocorrelation often is seen in a negative light by ecologists because it reduces statistical independence among sites, and hence, in frequentist inference, also reduces power. However, explicitly modelling spatial autocorrelation increases the reliability of inferences about relationships between distributional patterns and potential predictor variables. A rich statistical toolset for analyses of spatial autocorrelation has been developed by geospatial modellers, and the availability of Bayesian (Congdon, 2003) and smoothing (Tobin, 2004) methods provides even greater flexibility than existing frequentist estimation had allowed. We agree with Reyers *et al.* (2002) and Tobin (2004) that ecologists should embrace spatial autocorrelation modelling for its potential to provide insights about the potential causes of distributional patterns of focal taxa and to help to ensure that ecological processes supporting biodiversity patterns are managed appropriately.

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