

LETTER

Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications

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Abstract

Species richness patterns are characterized either by overlaying species range maps or by compiling geographically extensive survey data for multiple local communities. Although, these two approaches are clearly related, they need not produce identical richness patterns because species do not occur everywhere in their geographical range. Using North American breeding birds, we present the first continent-wide comparison of survey and range map data. On average, bird species were detected on 40.5% of the surveys within their range. As a result of this range porosity, the geographical richness patterns differed markedly, with the greatest disparity in arid regions and at higher elevations. Environmental productivity was a stronger predictor of survey richness, while elevational heterogeneity was more important in determining range map richness. In addition, range map richness exhibited greater spatial autocorrelation and lower estimates of spatial turnover in species composition. Our results highlight the fact that range map richness represents species coexistence at a much coarser scale than survey data, and demonstrate that the conclusions drawn from species richness studies may depend on the data type used for analyses.

Keywords

Geographical range, range map, spatial scale, species richness, survey data.

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INTRODUCTION

Understanding the determinants of species richness is a central focus of ecology and biogeography. Determining the location of peaks in species richness is essential for prioritizing conservation efforts (Prendergast *et al.* 1993; Myers *et al.* 2000), and understanding why these peaks occur at their current locations may be necessary to predict how ongoing global change will influence biodiversity (Midgley *et al.* 2002; Burns *et al.* 2003). Major factors proposed to influence species richness include productivity (Waide *et al.* 1999; Hawkins *et al.* 2003a), temperature (Rohde 1992; Allen *et al.* 2002), habitat heterogeneity (MacArthur 1964; Rahbek & Graves 2001), geometric constraints (Jetz & Rahbek 2001; Colwell *et al.* 2004) and historical factors (Ricklefs *et al.* 1999; Qian & Ricklefs 2000). These and other variables have received varying degrees of support in different taxonomic groups and locations and there is currently vigorous debate as to the most important underlying processes. However, the first

step in understanding the determinants of species richness is to accurately characterize the geographical patterns themselves, and little attention has been paid to how the different types of data used to generate these patterns might influence the observed results.

Richness patterns in the ecological literature are constructed from one of two possible data sources: (i) species range maps, which are overlaid to estimate the number of species expected to occur at a given point locality or within a quadrat of some fixed size; and (ii) survey data, where standardized field samples are used to estimate richness at each of numerous points distributed across geographical space. Because standardized data collection is only rarely conducted over broad spatial scales, most continental and global patterns of species richness have been generated using range maps. Hawkins *et al.* (2003a) recently reviewed 85 analyses of species richness. Of these, richness patterns based on range maps made up 69% of the total analyses, and 80% of the analyses conducted at continental to global scales (Hawkins *et al.* 2003a).

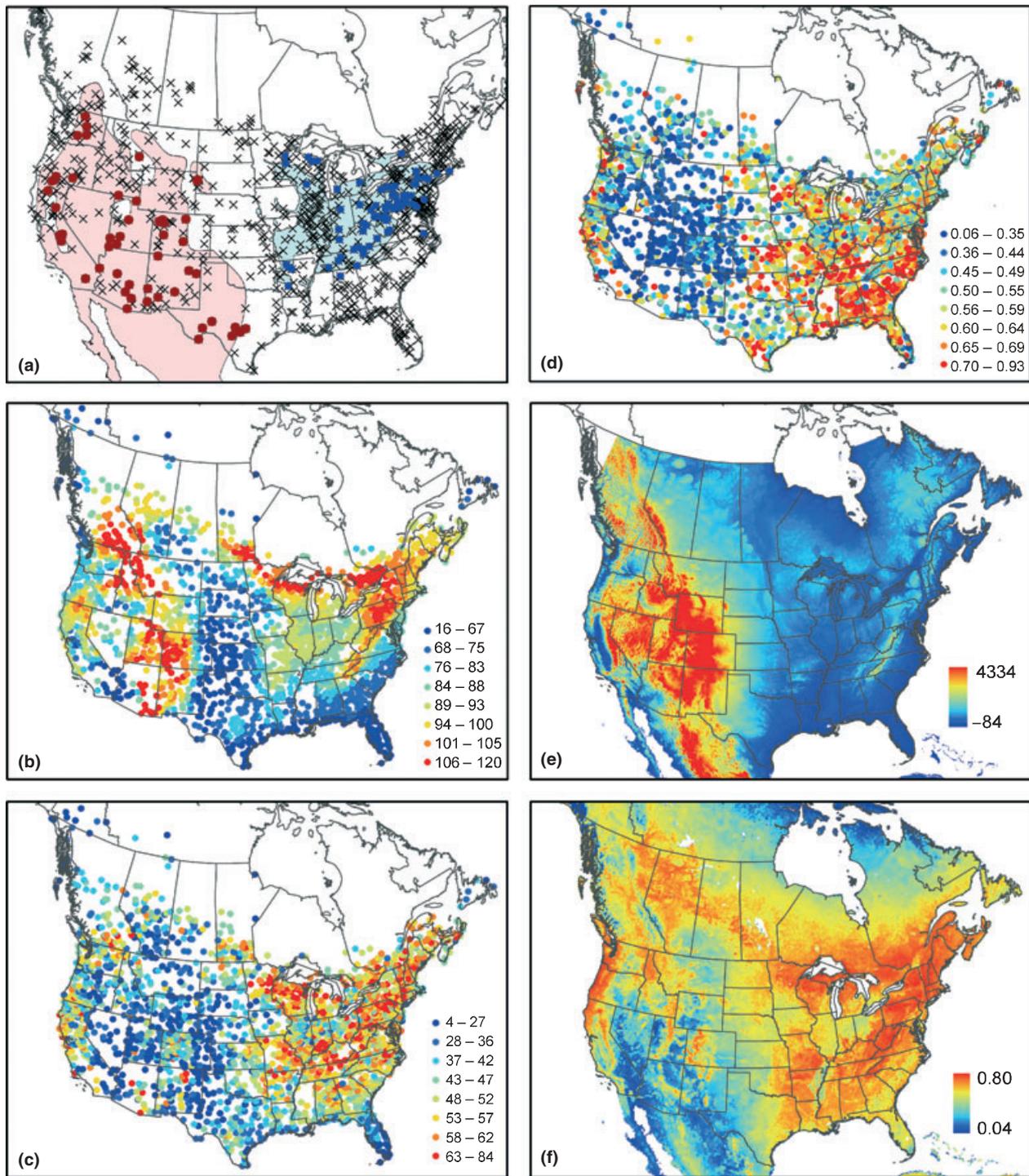


Figure 1 (a) Geographical ranges of the canyon wren (red) and cerulean warbler (blue) from Ridgely *et al.* (2003). Symbols represent Breeding Bird Survey (BBS) routes that have been surveyed every year from 1993 to 2002. X's denote surveys on which the focal species were never detected over this period, while filled circles indicate where the focal species were detected. (b) Geographical pattern of avian richness based on the number of species ranges overlapping each point. (c) Geographical pattern of avian richness based on the number of species observed on each BBS route in 2002. (d) Geographical pattern of the ratio of survey to range map richness, showing the greatest concordance in the south-east and the greatest disparity in the west. Richness and concordance values in (b)–(d) are binned into quantiles. (e) Digital elevation model of North America at 1-km resolution. (f) Mean values for the normalized difference vegetation index in the month of June at 1-km resolution (see text).

As a representation of the spatial distribution of individuals, a species geographical range is necessarily a scale-dependent abstraction (Rapoport 1982; Brown *et al.* 1996; Gaston 2003). The exact location of a range boundary, and the degree to which gaps within the range are identified, depend upon the spatial resolution and temporal window over which the range is mapped. At all but the coarsest resolutions, gaps within the range will typically be present, and thus species ranges have been likened to slices of Swiss cheese (Rapoport 1982). However, range maps are typically constructed by drawing a smoothed outline around records of occurrence, producing an irregular, contiguous surface that ignores much of this internal structure (Brown & Lomolino 1998). With this in mind, any amateur naturalist realizes that a species is not guaranteed to be present at every point within the range delimited by a field guide. For example, the two species ranges depicted in Fig. 1a appear to be drawn with some degree of precision. However, even after aggregating over 10 years of bird surveys, the species were observed on fewer than 30% of the sites within their mapped ranges. A species may fail to be detected over parts of its range because of (i) inadequate sampling and/or low overall levels of abundance (MacKenzie *et al.* 2003), (ii) discontinuities in suitable habitat (Lawton & Woodroffe 1991), and (iii) naturally patchy distributions of individuals caused by factors such as dispersal limitation (Hubbell 2001; Svenning & Skov 2004). While the consequences of this 'range porosity' have been considered for the interpretation and analysis of geographical range size (Gaston 1991, 1994; Brown *et al.* 1996), the consequences for continental patterns of species richness have yet to be assessed (but see Freitag & van Jaarsveld 1995).

For the estimation of richness at a given locality, surveys and range maps will typically provide under- and over-estimates, respectively. On the one hand, the sampling of a community may fail to detect rare species that are actually present (MacKenzie *et al.* 2003), resulting in underestimation. Conversely, because overlaid range maps provide an approximate characterization of the total pool of species that could conceivably occur at a particular site, the species richness derived from range maps provides an upper bound on the total number of species that actually coexist in a local community.

As long as the location of range gaps is uncorrelated among species, then survey richness should be a well-correlated proportion of range richness, and the resulting geographical patterns should be very similar. If, however, range gaps tend to coincide in space across species, then survey and range map richness will be more weakly correlated and the geographical patterns more disparate. A substantial discrepancy between survey- and range map-based richness patterns would have important implications for geographical ecology and conservation biology. First, the

relative ranking and explanatory power of various predictor variables might differ between the two types of data, leading to different conclusions about the determinants of species richness. This would complicate attempts to derive general principles governing species richness patterns. Second, such a discrepancy would raise difficult questions for conservation groups and policy makers attempting to determine the location of diversity hotspots for prioritized conservation.

Here, we use a detailed quantitative analysis to compare the patterns and determinants of avian species richness across North America using range map and survey data. Birds are one of only a handful of taxa for which there are sufficiently intensive survey data at the continental scale to perform these comparisons. We begin by quantifying the degree to which North American bird species fill their geographical ranges. We then compare survey- and range map-based patterns of species richness, and evaluate differences in the extent to which key environmental factors explain these patterns. Finally, we examine how range map and survey data differ with regard to spatial patterns of turnover in species composition and spatial autocorrelation of richness values.

METHODS

Data sources

We examined the distribution of 372 species of North American landbirds, excluding nocturnal, crepuscular, and otherwise difficult to survey groups (e.g., raptors) from analyses. Digital range maps of the breeding distributions of these species were obtained from Ridgely *et al.* (2003). Survey data were taken from the North American Breeding Bird Survey (BBS; Bystrak 1981), an annual continent-wide standardized survey effort. For constructing the geographical pattern of survey-based richness, we used data from the 2405 survey routes meeting BBS data quality standards that were conducted on a single morning in May or June 2002. Each BBS route is a roadside survey consisting of 50 points separated at 800 m intervals, and at each point a single observer records all birds seen or heard within 400 m and over a 3-min period. For some analyses, we also used data from the subset of these routes ($n = 837$) that were surveyed every year between 1993 and 2002. For these survey routes, we estimated species richness and proportional range occupancy (see below) for a single year (2002), a 5-year period (1998–2002), and a 10-year period (1993–2002). Longer time spans can be used to reduce the influence of inadequate sampling on species richness (e.g. McGill 2003), but may also introduce real temporal turnover and thus exaggerate the number of co-occurring species. In the BBS, sampling ceases to be the predominant factor governing the increase in species richness with time span

after 2–3 years (White 2004), suggesting that our 5- and 10-year periods provide conservatively high estimates of local species richness.

We determined the values of three environmental variables over a circular spatial neighbourhood, 40 km in radius, centred on the starting coordinates of each BBS route. The neighbourhood size was chosen to ensure the complete inclusion of the 40-km long survey route. Using a 1-km resolution digital elevation model of North America, we calculated both the mean elevation and elevational range within the spatial neighbourhood of each survey route. We also calculated the mean value of the normalized difference vegetation index (NDVI) for the month of June. The NDVI is a remotely sensed measure of greenness, calculated from reflectance in the infrared and near infrared portions of the electromagnetic spectrum. The data resolution is at 0.1 decimal degrees, and the value in each pixel represents the mean value for the month of June based on composite images from 1982 to 2000, excluding 1994. The NDVI is correlated with net primary productivity and total green biomass (Chong *et al.* 1993; Paruelo *et al.* 1997). Recent work has shown that a seasonal rather than annual estimate of productivity is more appropriate for predicting the seasonal richness of bird communities (H-Acevedo & Currie 2003; Hurlbert & Haskell 2003; Hawkins 2004).

Analyses

For each species with a geographical range encompassing at least 10 BBS survey routes, we calculated the fraction of routes within the species range on which the species was actually recorded on BBS surveys. This ‘proportional range occupancy’ was calculated for each species based on the 1-, 5- and 10-year survey periods described above.

We used ordinary least squares univariate and stepwise multiple regressions to model survey richness, range map richness, and the ratio of survey richness to range richness as a function of mean elevation, elevational range and NDVI. We were unable to obtain both NDVI and elevational data for \approx 4% of BBS routes, and so these routes were excluded from the relevant regression analyses.

For every pairwise combination of BBS routes, we calculated spatial turnover in species composition as the number of species unique to either BBS route divided by the sum of richness values for the two routes (Wilson & Shmida 1984). This measure of turnover is also equal to one minus the Dice similarity index (Dice 1945). Turnover values were binned into 100-km distance classes and mean turnover was plotted as a function of distance. We also calculated Moran’s I (Legendre & Legendre 1998) over the same distance classes to examine spatial autocorrelation of raw survey- and range map-based species richness values, and we performed the same

analysis on residual species richness after taking into account NDVI, mean elevation and elevational range (i.e. the residuals from a multiple regression of the three environmental variables on species richness; see Diniz-Filho *et al.* 2003).

RESULTS

For a single-year survey, species were detected on average at only 40.5% of the sites within their mapped ranges, and 83% of species were detected on less than two-thirds of the surveys within their range (Fig. 2). After accumulating species records on survey routes over 5- and 10-year periods, mean occupancy increased to 53.8 and 59.8%, respectively. Still, using 10 years of aggregated survey data, more than half (55%) of North American landbird species were detected on less than two-thirds of the surveys within their range (Fig. 2).

The geographical patterns of species richness are strikingly different when compiled from range maps and survey

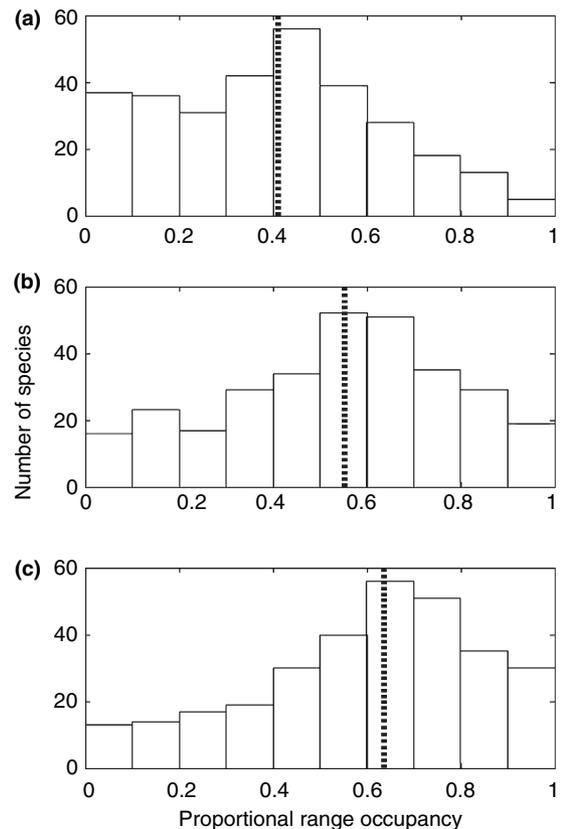


Figure 2 Frequency distributions of proportional range occupancy (number of sites observed/number of sites within the species range) for 306 landbird species based on Breeding Bird Survey data aggregated over 1-year (a), 5-year (b) and 10-year (c) periods. Dotted line indicates median values. Only species that were expected to occur on at least 10 survey routes were used for analyses.

data (Fig. 1b,c). According to range map overlays, the most species rich regions of North America include the Rocky Mountain West down into south-eastern Arizona, the eastern boreal-deciduous forest transition zone, and the Appalachian Mountains. The richness pattern based on the 2002 survey data is roughly congruent with the range map pattern for eastern North America. However, only a handful of sites in the western half of the continent have high levels of species richness, and these occur in California and the Pacific Northwest. Although range richness and survey richness are positively correlated, the relationship accounts for only 21% of the variation ($r = 0.46$). This magnitude of variation means that the survey richness of a site in a single year could potentially include any value less than or equal to the range richness at that site (Fig. 3). Using 5- and 10-year

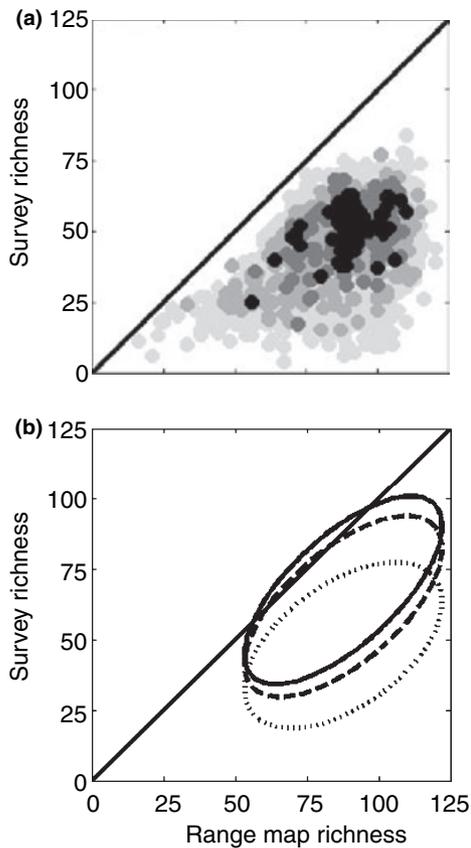


Figure 3 The relationship between survey- and range map-based estimates of species richness. Heavy line denotes the 1 : 1 line. (a) Plot of 1-year survey richness vs. range map richness. From lightest to darkest, the four shades denote 1, 2, 3 and > 3 sites with identical survey and range map richness values. (b) 95% confidence ellipses representing the relationship between survey and range map richness for 1-year (dotted line), 5-year (dashed line), and 10-year (solid line) aggregations of survey data. As the observed data do not satisfy bivariate normality these ellipses are used merely to indicate the location of the majority of data points.

estimates of survey richness shifts the distribution of points closer to the one-to-one line, and reduces some of this variation (Fig. 3). However, even after 10 years of surveys range map richness still only explained 40% of the variation in survey richness.

Survey richness is closest to range richness along the south-eastern coastal plain, and most disparate in the Rocky Mountain West and desert south-west (Fig. 1d). Mean elevation explains 33% of the variation in the survey to range richness ratio, and adding NDVI to the model raises the r^2 to 40% ($y = -0.10 \times \text{Elevation (km)} + 0.29 \times \text{NDVI} + 0.43$). Thus, the disparity between survey and range richness is greatest in high elevation regions with low NDVI (Fig. 1d-f).

In regressions predicting species richness from environmental variables, the relative importance of different predictor variables, and the magnitude and even sign of any given predictor variable varied with data source (Fig. 4). In univariate analyses NDVI explained more than 40% of 1-, 5-, and 10-year survey richness, while mean elevation was negatively correlated with survey richness and explained 3.9–12.6% of the variation. Elevational range explained almost none of the variation in survey richness at any temporal scale. In contrast, both mean elevation ($r^2 = 7.7\%$) and elevational range ($r^2 = 11.5\%$) were positively correlated with range map richness, and NDVI explained only 14.5% of the variation in range richness (Fig. 4). In addition, the slope of the NDVI–richness relationship was significantly greater for survey data than for range map data (ANCOVA, $F_{1,1610} > 26.23$, $P < 0.0005$), and parameter estimates for both elevation variables were significantly lower for survey data than for range map data (ANCOVA, $F_{1,1610} > 34.93$, $P < 0.0005$). Multiple regressions produced qualitatively similar results with both elevation variables

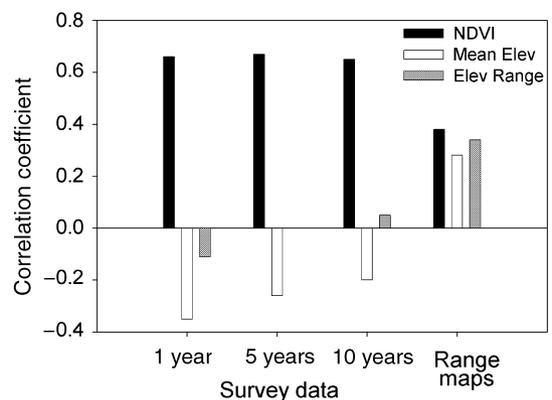


Figure 4 Univariate correlation coefficients between three predictor variables and four measures of species richness: range map richness and survey richness aggregated over 1-, 5- and 10-year periods.

positively related to range map richness. For survey data, only one of the two elevation variables entered a given regression and the total effect of elevational variables was either negative (1 year data) or much less positive than for the range map analyses (see Table S1).

Both survey- and range map-derived richness values exhibited significant spatial autocorrelation (Fig. 5). At distances < 400 km, range map richness was more positively autocorrelated than survey richness, while between 400 and 1600 km survey richness was more positively autocorrelated. At distances > 2000 km, survey richness was typically more negatively autocorrelated than

range richness. Spatial autocorrelation in predictor variables accounted for most of the autocorrelation in survey richness (Fig. 5a). Conversely, range map richness remained strongly spatially autocorrelated up to 900 km, with autocorrelation in the predictor variables explaining very little of the autocorrelation in range richness over that spatial scale.

Species turnover was consistently lower for range map data than for survey data across all distance classes (Fig. 5b). At distances of < 100 km, average survey turnover was five times greater than range map turnover. Even at distances up to 1000 km, survey-estimated turnover was at least 50% greater than range map turnover (Fig. 5b inset).

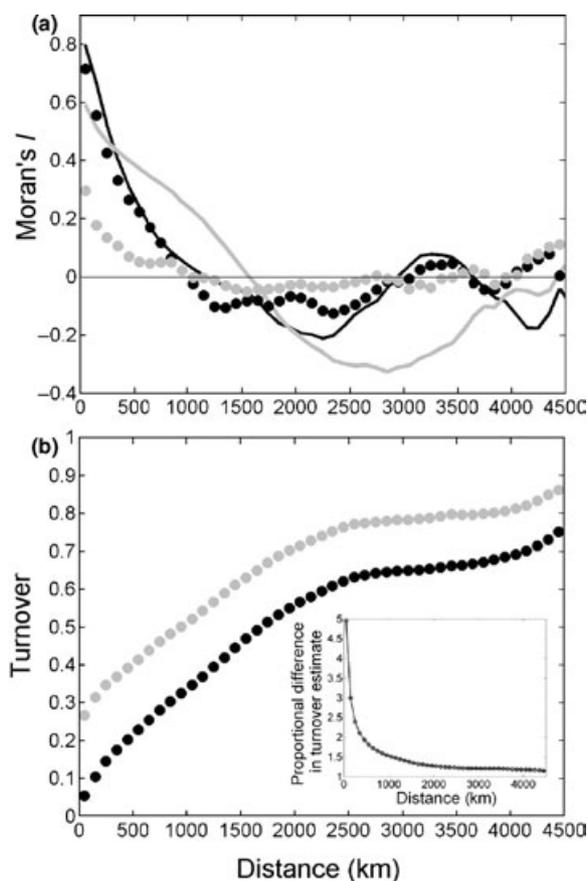


Figure 5 (a) Spatial correlogram across 100-km distance classes for raw range map richness (black line), raw 1-year survey richness (grey line), and residual range map and survey richness (black and grey symbols, respectively) after fitting NDVI, mean elevation and elevational range in a multiple regression model. (b) Mean spatial turnover in species composition between sites as a function of distance for range map data (black symbols) and 1-year survey data (grey symbols). Five- and 10-year data (not shown) are intermediate. Inset shows relative difference in turnover estimates as survey turnover divided by range map turnover for each distance class.

DISCUSSION

It is generally accepted that species geographical ranges are inherently porous despite the continuous occurrence implied by most range maps (Rapoport 1982; Brown *et al.* 1996; Gaston 2003). As cautioned in a popular North American field guide, '[b]ear in mind that within the mapped range, each species occurs only in appropriate habitat and at variable density' (Sibley 2000: ii). While data from a single-year survey likely overestimates range porosity due to inadequate sampling, even after aggregating species presence over a 10-year period, the majority of species still exhibit a high degree of range porosity. Although we discuss correlates of range porosity in detail elsewhere (Hurlbert and White, unpublished data), species in decline [e.g. red-cockaded woodpecker (*Picoides borealis*), black-capped vireo (*Vireo atricapillus*)], species with low average densities [e.g. spruce grouse (*Falcapennis canadensis*), Swainson's warbler (*Limnothlypis swainsonii*)], and species with narrow habitat requirements [e.g. canyon wren (*Catherpes mexicanus*), marsh wren (*Cistothorus palustris*)] tend to be those with the lowest values of range occupancy.

Geographical variability in the porosity of species ranges can lead to substantial differences in observed species richness patterns between survey and range map data. The range map-based pattern of richness presented in Fig. 1b is similar to that of previously published patterns of avian species richness in North America (MacArthur & Wilson 1967; Cook 1969; Hawkins *et al.* 2003b), with a pronounced peak in the mountainous and arid regions of the western half of the continent. The conspicuous absence of this broad richness peak from the survey-based pattern (Fig. 1c) makes a critical point about the comparability of the two data sources. Because habitats in mountainous areas are often delimited by elevational zones, they are typically distributed more patchily than in regions with less topographic relief. Similarly, habitats in arid regions are often patchily distributed along riparian corridors and other water sources. The patchy distribution of habitat in mountainous

and arid regions occurs at a finer resolution than is captured by most range maps. Thus, range maps tend to overestimate the occurrence of species, and hence local species richness, in areas where habitat diversity is highest (Fig. 1d).

This disparity leads to differences in the observed richness–environment relationships because using different data types effectively alters the scale of analysis and thus the contributions of environmental factors that operate at different scales (Huston 1999; Gaston 2000; Willis & Whittaker 2002). Although we generated point estimates of species richness from our two data sources, they represent two fundamentally different scales of coexistence. Species observed on a single survey tend to occur within the same habitat, or at least within a relatively narrow range of environmental conditions, whereas species with overlapping ranges may exhibit strong habitat differentiation such that they rarely coexist at all at the local scale (Rodman 1991; Bullock *et al.* 2000). As such, range map-based estimates of species richness include both within- and between-habitat diversity components causing variables related to beta diversity, such as topographic and biome heterogeneity, to explain a greater proportion of the variation in range map richness compared to survey richness. This result is consistent with other studies showing an increase in the explanatory power of habitat heterogeneity variables as richness data is determined for progressively larger quadrats (Rahbek & Graves 2001; van Rensburg *et al.* 2002; Hurlbert & Haskell 2003). What is particularly surprising about our results is that not only did the magnitude of the effect of the heterogeneity variables on species richness vary between data types, but the sign of the effect changed as well. This difference is due to the negative correlation between NDVI and both mean elevation ($r = -0.45$) and elevational range ($r = -0.19$). Because NDVI decreases along the elevational gradient, at the finer spatial scale of surveys, the negative effect of lost resource availability on richness overwhelms the positive effect of increased habitat heterogeneity. These results emphasize the importance of considering the implicit scale of the data when evaluating richness patterns and the mechanisms proposed to explain them.

Another important way that range map and survey data differ is in the inherent spatial autocorrelation of species occurrences. When species are assumed to be present at every point within their geographical range, adjacent sites will tend to have similar richness values and low values of spatial turnover in species composition. However, the survey data suggest that most species ranges are fairly porous and thus species occurrences are less tightly correlated among adjacent sites. Consequently, at short distances, spatial autocorrelation is weaker for survey richness than for range richness. In addition, the correlogram reveals that most of the spatial structure in survey richness is explained by the spatial structure of underlying environmental variables. With

the inclusion of additional environmental variables this autocorrelation would likely be further reduced (Diniz-Filho *et al.* 2003). In contrast, range map richness is inherently spatially autocorrelated by virtue of the assumption that each species occurs everywhere within its range (Diniz-Filho *et al.* 2003). Thus, even when the spatial structure in predictor variables is accounted for, range map residual richness remains highly autocorrelated. This finding is consistent with patterns observed in African birds (Jetz & Rahbek 2001, but see Diniz-Filho *et al.* 2003), and suggests that spatial autocorrelation has a greater influence on range map-based analyses than on survey-based analyses.

We have shown that survey and range map data can produce markedly different results with regards to: (i) the geographical patterns and spatial autocorrelation of species richness, (ii) the magnitude and direction of influence of different determinants of species richness, and (iii) the partitioning of diversity into within- and between-habitat components. We emphasize that our intention is not to condemn one data type or to advocate the other. At present, the debate over which kind of data to use is largely academic, as very few geographically extensive survey datasets exist. Rather, we hope to emphasize the fact that range maps describe inherently coarse-grained patterns of species richness and must be interpreted as such, regardless of the grain at which range maps are analysed. This can lead to results that are remarkably different from those of surveys in many types of community-level analyses. Explicitly considering the scale of both species richness and environmental data will greatly facilitate the search for generality in the determinants of richness across disparate regions, time scales and taxonomic groups.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE726/ELE726sm.htm>

Table S1 Stepwise multiple regression models for survey- and range map-based measures of species richness of North American land birds

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