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Changes in the diversity structure of avian assemblages in North America

Frank A. La Sorte* and William J. Boecklen

New Mexico State University, Department of Biology, PO Box 30001 MSC 3AF, Las Cruces, NM 88003–8001, USA

ABSTRACT

Aim To determine the major patterns of change in avian diversity structure over space and time at a local resolution and continental extent in non-urban areas in North America.

Location The contiguous United States and southern Canada.

Methods We used 1673 North American Breeding Bird Survey (BBS) routes containing 547 terrestrial and aquatic species to estimate four diversity components: species richness, individual abundance, taxonomic distinctness and species evenness. We implemented three levels of analysis to examine changes in diversity structure on a yearly basis from 1968 to 2003: (1) a canonical analysis of discriminance, (2) a univariate analysis across BBS routes, and (3) a univariate analysis at individual BBS routes. We estimated changes in similarity in species composition over time between 470,730 BBS route pairs. We also estimated the level of human activity at BBS routes using three spatial anthropogenic databases.

Results BBS routes were located in non-urban areas in association with low nighttime light activity and moderately low human population densities. The analysis of diversity structure indicated the presence of two independent patterns: (1) a temporally consistent pattern defined by increasing species richness (12% increase from 1968 to 2003) associated with limited gains in taxonomic distinctness, and (2) an association between species abundance and evenness related to variability in abundance associated with the most abundant species. The similarity analysis indicated that BBS routes located closer to the Atlantic and the Pacific coasts of the United States experienced the strongest patterns of homogenization of species composition.

Main conclusions Our results suggest that avian diversity structure has changed at the local scale in non-urban areas in North America. However, there was no evidence for a consistent continent-wide pattern. Instead, the evidence pointed to the presence of regional factors influencing diversity patterns. This study provides a foundation for more detailed investigations of the spatiotemporal and taxonomic details of these general patterns.

Keywords

Anthropogenic activity, avian diversity, biological diversity, evenness, homogenization, North American Breeding Bird Survey (BBS), similarity, species richness, taxonomic distinctness.

*Correspondence: Frank A. La Sorte, New Mexico State University, Department of Biology, PO Box 30001 MSC 3AF, Las Cruces, NM 88003–8001, USA.
E-mail: flasorte@nmsu.edu

Present address: Department of Fisheries and Wildlife Sciences, 302 Natural Resources, University of Missouri, Columbia, MO, 65211, USA.
E-mail: lasortef@missouri.edu

INTRODUCTION

As the human population grows in density and extent, the biosphere is increasingly being impacted by anthropogenic activities resulting in changes in the diversity structure of biological communities (Wilson, 1992; Vitousek, 1994; Pimm *et al.*, 1995;

Maurer, 1996; Vitousek *et al.*, 1997; Swanson, 1998; Chapin *et al.*, 2000). We define diversity structure as the biological diversity of an assemblage of species in its entirety; that is, the complete representation of all possible measures of biological diversity across space and time. Anthropogenic activities promote changes in diversity structure primarily through two processes: the

alteration of habitat and the alteration of colonization opportunities. These two factors, acting independently or in concert, favour certain species by promoting their immigration and establishment, and disfavour others by degrading their habitat and limiting their dispersal opportunities (Diamond, 1989; Wilcove *et al.*, 1998; Mack *et al.*, 2000; Novacek & Cleland, 2001). To expand our understanding of the nature and consequences of these changes, we require empirical information from a variety of research perspectives including contrasting spatiotemporal scales.

How we perceive changes in diversity structure is dictated by our spatial frame of reference, that is, the resolution and extent of our observations (Preston, 1960; Huston, 1999; Whittaker *et al.*, 2001; Adler & Lauenroth, 2003). Globally, species richness is decreasing as extinction outpaces speciation. In contrast, at local and regional scales, species richness is increasing as colonization of new species outpaces extirpation (Sax & Gaines, 2003). Evidence for increasing species richness at local and regional spatial scales has been documented for a variety of taxa but primarily for vascular plants that, in contrast with vertebrates, have experienced higher levels of biotic mixing and fewer extinctions (Sax & Gaines, 2003, and references therein).

The most prominent anthropogenic activity that generates long-term changes in the diversity structure of biological communities is urbanization. Typically, urban development transforms native environments into human-specific environments resulting in the extirpation of native species and the establishment of non-native, human-commensal species (McKinney, 2002, and references therein). Another factor associated with urbanization is the long-term loss of area containing native habitat. The species–area relationship indicates that the number of species supported within a region will inevitably decrease as areas containing suitable habitat diminishes (Simberloff, 1986; Boecklen, 1991; May *et al.*, 1995). However, this outcome is countered by the loss of biogeographical barriers through human-mediated transport, which creates greater opportunities for biotic mixing that, effectively, increases area and thus increases the number of species that can be supported within a region (Rosenzweig, 2001). These contrasting interpretations of the species–area relationship as it applies to habitat loss and biotic mixing are tempered by the limited explanatory and predictive power of the relationship and the uncertainty regarding its underlying mechanisms (Boecklen & Gotelli, 1984; Boecklen & Simberloff, 1986; Collins *et al.*, 2002).

In this study, we examine how the diversity structure of avian assemblages has changed over time at a local resolution and on a continental extent in North America. Since European settlement, avian species richness in the contiguous United States has increased, with the number of introduced species exceeding the number of extirpated species (Case, 1996). Evidence at local and regional scales is equivocal, with avian species richness remaining the same in some cases and increasing in others (Hobbs & Mooney, 1998; Parody *et al.*, 2001). Investigations in non-urban areas in North America have documented changes in species composition in avian assemblages and have also provided evidence that species richness has remained unchanged over time (Brown *et al.*, 2001; Holmes & Sherry, 2001; Parody *et al.*,

2001). Overall, inferences generated from these studies are limited to relatively small regions. We will overcome this limitation by examining avian diversity structure across a continental extent.

The impact of anthropogenic activities on biological diversity has typically been examined with two measures: extinction rates and changes in species richness. To clarify how diversity is changing over space and time, however, requires measures that capture other aspects of diversity's multifaceted nature (May, 1994; Purvis & Hector, 2000; Balmford *et al.*, 2003). In this study, we will present a procedure to quantify diversity structure and to test for general patterns of change in that structure over time. This procedure can be used as an omnibus test to identify the presence of significant general trends. Following the application of this procedure, hypotheses can be formulated to address questions raised by the outcome of the analysis. In other words, the application of this procedure provides an inferential foundation for the development and testing of hypotheses in a robust manner. This study will focus on the outcome of this procedure and aspects related to the second step will be presented in future investigations.

METHODS

For the analysis, we used data from the North American Breeding Bird Survey (BBS) from 1968 to 2003, a 36-year period (United States Geological Survey, Patuxent Wildlife Research Center). We designated the BBS route as the sample unit, a 39.4-km roadside survey on secondary roads with 50 stops at 0.8-km intervals where 3-minute point counts are conducted. Surveys are conducted during the breeding season (between May and July) and start one-half hour before sunrise and take approximately 5 hours to complete. We included 547 bird species in our analysis as designated in the 2003 American Ornithological Union's checklist of North American birds. Our analysis included both native and introduced terrestrial and aquatic species, and excluded accidental and vagrant species. Aquatic species were included after it was determined that their exclusion did not alter the quantitative results.

Anthropogenic activity analysis

We used three spatial databases to estimate the level of anthropogenic activity at BBS routes. The first was a grid of the nighttime lights of North America estimated from satellite data collected during 1996 and 1997 and modelled at 1-km² resolution (USGS, National Geophysical Data Center). This database has unitless values on a linear scale ranging from 1 to 72, high nighttime light intensity to low nighttime light intensity, respectively. The second spatial database was a grid of the land cover characteristics of North America classified using 1-km² resolution advanced very high resolution radiometer (AVHRR) satellite data from April 1992 to March 1993 (USGS, EROS Data Center). We used the urban class from this grid to estimate the Euclidian distance from each BBS route to the nearest urban area. The third spatial database was a grid of population density per US county estimated from the 2000 US census. The resolution of this database was dependent on the idiosyncratic and highly variable size and

shape of US counties. However, to aid in the analysis, we represented the resolution of this database as 1 km². Therefore, the resolutions of the land cover and nighttime light databases are accurate and the inferences based on these databases are sound. However, the inference based on the population density database is site-specific – depending on the US county and how well the census represents its population density – and the results of the analysis using this database should be interpreted cautiously.

We represented each BBS route by collecting the values from 1-km² grid cells that defined the 39.4-km route (USGS, Patuxent Wildlife Research Center). For this analysis, we used all 3229 BBS routes located within the contiguous United States. We estimated nighttime light, distance to urban areas, and population density for each BBS route by averaging the values from the three grids that fell on the 1-km² grid cells delineating each BBS route. The BBS routes selected for this analysis did not match the routes selected for the diversity and similarity analyses (see below). Therefore, inference from the anthropogenic activity analysis is restricted to BBS routes located within the contiguous United States. However, the analysis is complete for this region, that is, all BBS routes in this region were sampled and the results represent the status for the entire population. We used ARC/INFO version 8.3 (ESRI, Redlands, CA) to implement this analysis.

Diversity analysis

For the diversity analysis we used BBS routes that met BBS quality standards and were sampled a minimum of nine times and at least once during each of four nine-year time periods (1968–76, 1977–85, 1986–94, 1995–2003). This limited the number of routes eligible for the analysis to 1673 and our study area to the contiguous United States and southern Canada (Fig. 1). We defined diversity structure as the complete representation of the biological diversity of an assemblage of species over space and

time or, quantitatively, as the parameter space containing all possible measures of biological diversity over space and time. In general, this can be estimated by taking a collection of independent measures that describe some general aspect of this overall structure. We selected four diversity components for our analysis that were found to be reasonably independent: species richness, individual abundance, taxonomic distinctness and species evenness (Fig. 2). Using these components, we conducted three analyses to examine changes in diversity structure over time: (1) a multivariate analysis of all four components combined across all 1673 BBS routes combined, (2) a univariate analysis of each component individually across all 1673 BBS routes combined, and (3) a univariate analysis of each component individually at each of the 1673 BBS routes individually.

We defined species richness (Richness) as the number of species documented at a BBS route during each survey and individual abundance (Abundance) as the total number of individual birds documented at a BBS route during each survey. We defined taxonomic distinctness (Distinctness) as the average taxonomic relatedness of the assemblage of species documented at a BBS route during each survey (Δ^+ in Clarke & Warwick, 1998a). We estimated the distance between taxonomic levels using Sibley and Monroe (1990, 1993) in a fashion similar to Von Euler and Svensson (2001): 1.1 between congeneric species, 3.35 between species in different genera, 8 between species in different subfamilies, 10 between species in different families, and 21 between species in different orders. These values represent an estimate of evolutionary distance corresponding to the level of DNA incompatibility between species (Sibley & Ahlquist, 1990, p. 254). This particular weighting scheme was selected because it provided a biological interpretation for values derived from the index. Moreover, the use of different weighing schemes has been found not to significantly alter the qualitative results (Clarke & Warwick, 1998b, 1999). Small values for taxonomic

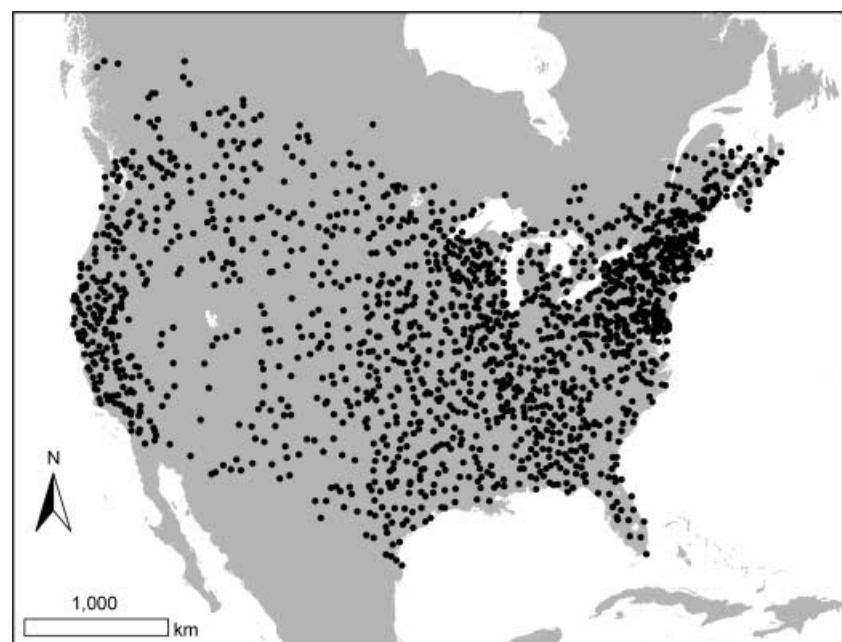


Figure 1 Map of the southern portion of North America with the locations of 1673 BBS routes used in the analysis.

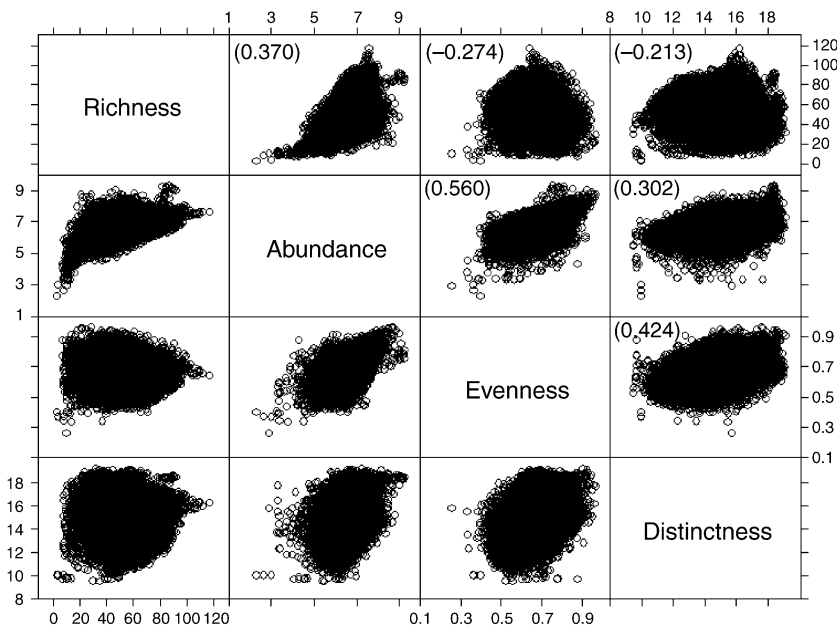


Figure 2 Scatterplot matrix of the four diversity components. The correlation coefficients are displayed in parentheses in the upper left-hand corners. Abundance is log-transformed.

distinctness indicate that on average, the assemblage of species is taxonomically more closely related and less distinct. Large values indicate that on average, they are taxonomically less closely related and more distinct. The final diversity component (Evenness) estimated how evenly the individuals were distributed among species at a BBS route during each survey. We estimated Evenness using the Lorenz curve (relative species abundance curve) and the Gini coefficient (Lorenz, 1905; Nijssen *et al.*, 1998). We used the formula from Glasser (1962) to calculate the Gini coefficients. The Gini coefficient has a minimum of 0 and a theoretical maximum of 1.0 and is defined as two times the area contained between the Lorenz curve and the line of perfect equality. Values close to 0 for the Gini coefficient indicate high evenness (i.e. all species have nearly equal abundance) and values close to 1.0 indicate low evenness (i.e. some species are considerably more abundant than others).

For the multivariate analysis, we performed a canonical analysis of discriminance to examine how the diversity structure represented by the four components had changed over time (discriminance: s-PLUS version 6.2, Insightful, Seattle; McGarigal *et al.*, 2000, pp. 129–187). This is a dimension-reducing procedure that determined the linear combination of the four diversity components (i.e. canonical functions) that best distinguishes the 36 years. Because we used large sample sizes ($n > 900$ for each year) and did not predict group membership (i.e. classification), inference generated from this procedure was robust to violation of the assumptions of normality and homogeneity of the variance–covariance matrices. This procedure provided a comprehensive examination of changes in diversity structure by incorporating the correlation structure of the four diversity components into the analysis. More specifically, this procedure increased our ability to detect general trends by combining all of the information, both unique and redundant, contained in the four diversity components.

To estimate the role of each diversity component in the discriminant analysis, we used the structure coefficients which

estimate the full correlation of each component with each canonical function. To provide an objective measure of the significance of the four diversity components within the discrimination, we used randomization tests to generate one-sided *P*-values using the original structure coefficients as test values (McGarigal *et al.*, 2000, p. 175). The resampling procedure shuffled the years within each of the 1673 BBS routes individually 10,000 times without replacement and recalculated the structure coefficients. The integrity of the diversity vectors and route–year combinations were retained; that is, each BBS route retained the years that were sampled at that route and the diversity vectors associated with these years were shuffled. The significance of each structure coefficient for each canonical function was based on the location of the observed coefficient within the distribution of coefficients estimated from 10,000 permutations. Two consequences of eigenanalysis that could interfere with this resampling procedure — axis reflection and axis reordering of the canonical axes within the resampled data space (Peres-Neto *et al.*, 2003) — were treated as legitimate results of the resampling procedure.

To determine if the arrangement of years was sequentially meaningful within the canonical space, we developed a metric to measure the probability of getting the observed temporal sequence of centroids by chance. Specifically, this metric tested the hypothesis that the diversity structure had changed in a temporally consistent manner over the 36 years against the null that the diversity structure had changed randomly over time. We defined the metric as the ratio of the Euclidian distances between the 1968 and 2003 centroids in the canonical space divided by the sum of the Euclidian distances between all the centroids sequentially from 1968 to 2003 in the canonical space. For two canonical functions, the metric has the form:

$$D = \frac{[(x_{2003} - x_{1968})^2 + (y_{2003} - y_{1968})^2]^{1/2}}{\sum_{i=1968}^{2002} [(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2]^{1/2}}$$

where x represents values with canonical function 1 and y represents values with canonical function 2 for each year's centroid. Values of D approaching 1.0 indicate that years are arranged sequentially in the canonical space (i.e. the Euclidian distance between the first and last year is equivalent to the sum of distances between the consecutive years) and values < 1.0 indicate deviation from a linear temporal sequence (i.e. the distance between the first and last year is less than the sum of distances between the consecutive years). The location of the observed value of this metric within the distribution of values generated from the 10,000 permutations, using the same resampling design for the diversity vectors described previously, was used to estimate a P -value.

To complement the multivariate analysis, we implemented two univariate procedures. For the first procedure, we used least-squares simple linear regression (lm: s-PLUS version 6.2, Insightful) to examine how each diversity component had changed over time for all 1673 BBS routes combined. For the second procedure, we applied the same regression model to each of the 1673 BBS routes individually. The second procedure allowed us to estimate, at the level of individual BBS routes, the patterns of change over time for each diversity component and the level of correlation between patterns of change for pairs of diversity components at each BBS route. To determine the significance of the correlation coefficients from the second procedure, we used randomization tests with 100,000 permutations and two-sided P -values (permutationTest: s-PLUS version 6.2, Insightful) and we also used the Moran's index (I) to determine if BBS routes were clustered or dispersed in space based upon the spatial location of BBS routes and the value of the slope coefficients from the second procedure (ARC/GIS version 8.3, ESRI).

Similarity analysis

From the 1673 BBS routes selected for the diversity analysis, we selected BBS route pairs that were sampled a minimum of four times during each of four 9-year time periods (1968–76, 1977–85, 1986–94, 1995–03) that contained a minimum of 16 total samples. This limited the analysis to 470,731 unique BBS route pairs containing 1052 BBS routes. To estimate the level of similarity in species composition between BBS route pairs for each year surveyed, we used the dissimilarity index:

$$\frac{\min(b, c)}{\min(b, c) + a}$$

where a was the total number of species common to both BBS routes, and b and c the number of species unique to the first and second BBS routes, respectively (β_{sim} : Lennon *et al.*, 2001; Koleff *et al.*, 2003). This index has a range from 0, high similarity, to 1.0, low similarity. We chose this index because it reduced the influence of species richness on our estimates of change in similarity in species composition over time. We applied least-squares simple linear regression (lm: s-PLUS version 6.2, Insightful) to each of the 470,731 BBS route pairs where the dissimilarity index was the dependent variable and year was the independent variable to estimate how similarity in species composition had

changed over time. We used the sign of the slope coefficients to divide the BBS route pairs into two groups: (1) positive slope indicating decreasing similarity (differentiation) over time, and (2) negative slope indicating increasing similarity (homogenization) over time. We measured the distance between BBS route pairs using ARC/INFO version 8.3 (ESRI) and we compared means using randomization tests with 100,000 permutations and two-sided P -values (permutationTest: s-PLUS version 6.2, Insightful).

RESULTS

The level of anthropogenic activity across the 3229 BBS routes located in the contiguous United States was, on average, moderately low. BBS routes were located in regions with low levels of nighttime light activity ($\bar{X} = 70$, $SD = 5$; range = 1–72; bright light to dim light, respectively). BBS routes were located in counties with moderately low human population densities ($\bar{X} = 335$ people per km^2 , $SD = 868$; range = 0.3–173,402); and BBS routes were located 24 km on average from urban areas ($SD = 21$; range = 0–158).

Abundance was positively skewed and was log-transformed to achieve normality. The three remaining diversity components fell within the assumptions for multivariate analysis and all four presented no evidence for multicollinearity or singularity (Fig. 2). The first two canonical functions were the most significant in their ability to distinguish years. After removal of the first canonical function, the association between years and the four diversity components persisted ($\chi^2 = 151.81$, $df = 102$, $P = 0.001$). After removal of the second canonical function, the association disappeared ($\chi^2 = 63.15$, $df = 66$, $P = 0.577$). The first two canonical functions accounted for 95% and 4%, respectively, of the between-year variability. The centroids for the 36 years formed a linear pattern when plotted on the first two canonical functions in a fashion that was temporally consistent (Fig. 3). The probability of this temporal pattern occurring by chance alone was low (observed $D = 0.4218$, $P \leq 0.001$). We developed interpretations for the first two canonical functions based on the structure coefficients and P -values generated from randomization tests (Table 1). The first canonical function was positively correlated with Richness and Distinctness, with Richness playing a stronger role. Abundance and Evenness were negatively correlated with the first canonical function but there was no evidence that they played a significant role in distinguishing years. The second canonical function was positively correlated with all four diversity components with only Abundance playing a significant role in distinguishing years. Overall, the multivariate analysis suggested that a temporal trend was evident, characterized by increasing species richness followed by increasing taxonomic distinctness. There was evidence that individual abundance had decreased and the distribution of individuals across species had become more even; however, these two factors did not play a significant role in the temporal trend. Abundance played the dominant role explaining the variability about this temporal trend.

The first univariate procedure corroborated aspects of the multivariate analysis and also provided additional details for

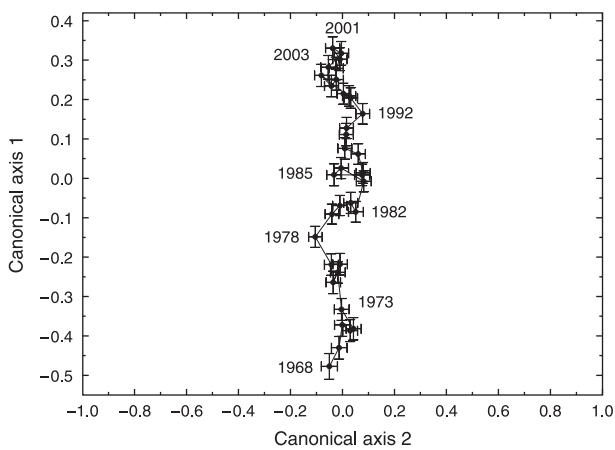


Figure 3 Plot of the centroids (\pm SE) for each of 36 years on the first two standardized canonical functions from a canonical analysis of discriminance of four diversity components by year (1968–2003) for 1673 BBS routes and 547 species. The line connects consecutive years and several centroids are labelled by their respective years. The first two canonical functions accounted for 95% and 4%, respectively, of the between-year variability.

consideration. Richness presented a linear pattern of increasing species richness over time with a gain of approximately 12% on average from 1968 to 2003 and a rate of change of approximately 0.2 species per year (Fig. 4a; $r^2 = 0.022$, slope = 0.189, $t_{44,976} = 31.44$, $P \leq 0.001$). Distinctness presented a non-linear but monotonic pattern with a gain of approximately 2% on average from 1968 to 2003 (Fig. 4b; $r^2 = 0.001$, slope = 0.005, $t_{44,976} = 7.90$, $P \leq 0.001$). Abundance followed a highly variable pattern with an overall loss of approximately 6% on average from 1968 to 2003 (Fig. 4c; $r^2 = 0.002$, slope = 1.85, $t_{44,976} = -8.73$, $P \leq 0.001$). Evenness decreased in a linear fashion with a loss of approximately 3% on average from 1968 to 2003 (Fig. 4d; $r^2 = 0.011$, slope = -0.0008 , $t_{44,976} = -22.47$, $P \leq 0.001$).

The second univariate analysis provided additional details for consideration. Species richness increased at more BBS routes (71%) and the spatial distribution of slope coefficients was not distributed randomly among BBS routes but was clustered spatially ($I = 0.0234$, $P \leq 0.001$), and more BBS routes experienced increasing taxonomic distinctness (61%) and the spatial

distribution of slope coefficients tended to be clustered in space ($I = 0.0170$, $P \leq 0.001$). Change in Distinctness over time at individual BBS routes was weakly correlated with Richness (Fig. 5; $r = 0.177$, $P \leq 0.001$). More BBS routes experienced declines in Abundance (55%) and the correlation between changes in Abundance over time at individual BBS routes with changes in Richness was relatively strong (Fig. 5; $r = 0.489$, $P \leq 0.001$). More BBS routes experienced declines in Evenness (66%) and the correlation between changes in Abundance and in Evenness at individual BBS routes was also strong (Fig. 5; $r = 0.479$, $P \leq 0.001$). In contrast, the correlation between changes in Abundance and in Distinctness at individual BBS routes was weak (Fig. 5; $r = 0.164$, $P \leq 0.001$) and there was no relationship between changes in Richness and changes in Evenness at individual BBS routes (Fig. 5; $r = 0.002$, $P = 0.966$).

The similarity analysis displayed several relevant patterns. The average slope coefficient was negative but small, providing limited evidence that similarity in species composition was increasing across all of the BBS routes combined ($\bar{X} = -0.0001$, $P \leq 0.001$). When the slope coefficients were subsampled based on the sign of the coefficient and five α levels, the number of BBS route pairs with negative slope was always greater than the number with positive slope and the percentage increased with decreasing P -values for the slope coefficients (Table 2). When the slope coefficients were averaged based on 50 distance categories (0–5000 km at 100-km intervals), the trend as a function of distance presented a pattern that indicated BBS routes separated by approximately 3200–4200 km experienced the most significant increases in similarity of species composition over time (Fig. 6).

DISCUSSION

Our study provides quantitative evidence that changes have occurred within the diversity structure of avian assemblages at the local scale in non-urban areas in North America from 1968 to 2003. The most significant pattern suggests species richness increased for avian assemblages at the local scale; patterns associated with the three remaining diversity components and with the similarity analysis were, in contrast, much weaker. Nevertheless, our results outline the presence of an assortment of trends and relationships of varying magnitudes and levels of

Table 1 Standardized canonical and structural coefficients from the first two canonical functions with their associated Eigenvalues (λ) from a canonical analysis of discriminance of four diversity components at 1673 BBS routes by year (1968–2003). P -values were generated from randomization tests using structure coefficients as test values and 10,000 permutations. Abundance is log transformed

Variable	Canonical function 1 ($\lambda = 0.054$)			Canonical function 2 ($\lambda = 0.002$)		
	Standardized coefficients	Structure coefficients	P -value	Standardized coefficients	Structure coefficients	P -value
Richness	1.122	0.642	≤ 0.001	-0.143	0.488	0.207
Abundance	-0.856	-0.212	0.994	1.265	0.866	≤ 0.001
Evenness	0.027	-0.461	0.794	-0.714	0.108	0.443
Distinctness	0.664	0.167	0.003	0.178	0.288	0.327

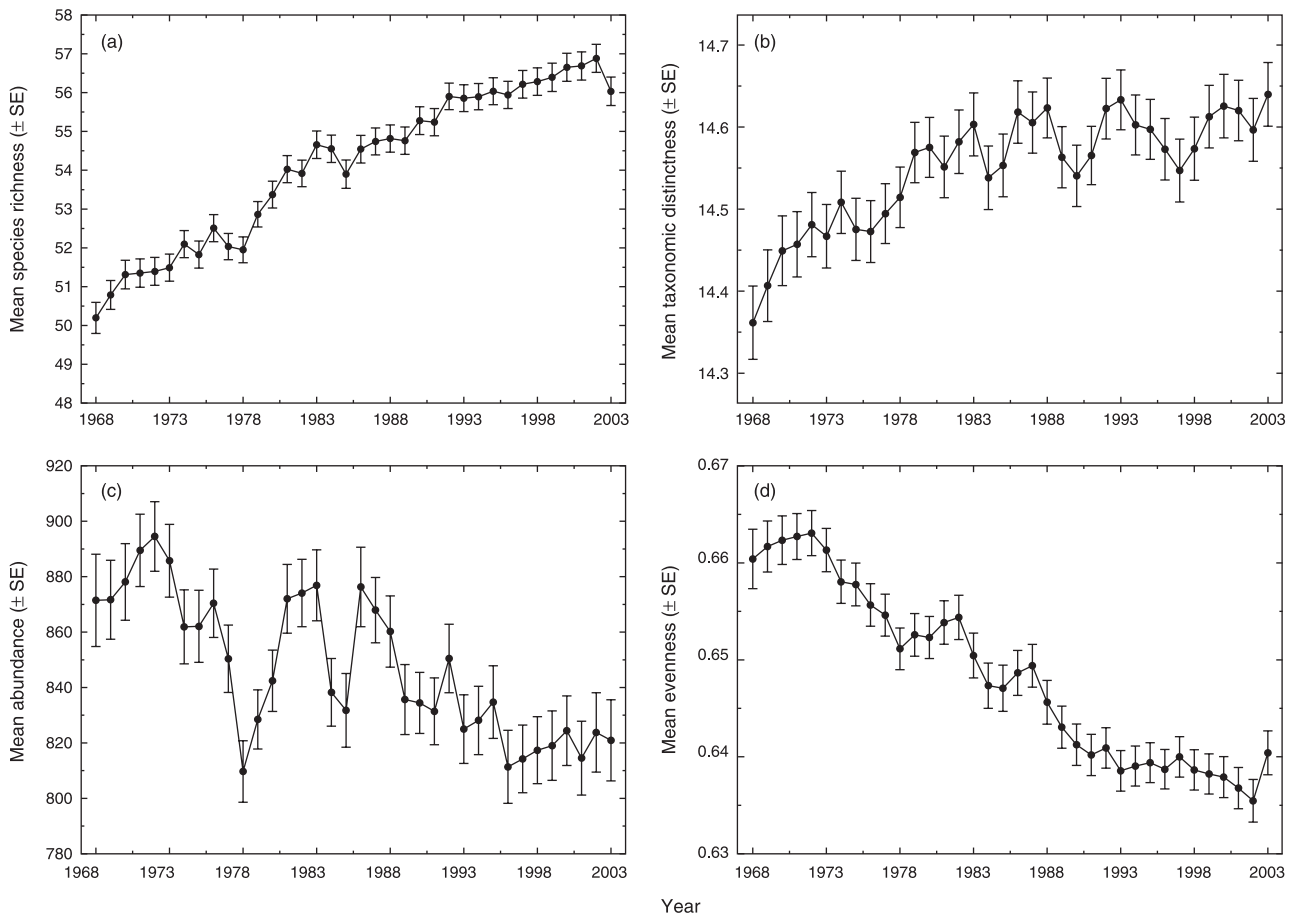


Figure 4 Plots of means (\pm SE) by year for the four diversity components (1968–2003). The diversity components include: (a) Richness, (b) Distinctness, (c) Abundance and (d) Evenness. The components were measured at 1673 BBS routes and include 547 species. Abundance is not log-transformed.

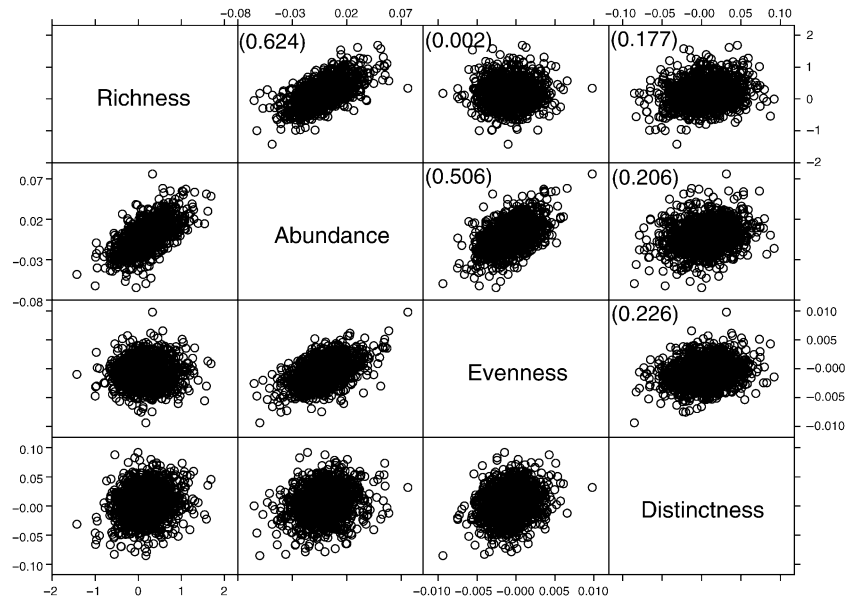


Figure 5 Scatterplot matrix of the slope coefficients from the least-squares simple linear regression of the four diversity components by year for each of the 1673 BBS routes individually. The correlation coefficients are displayed in parentheses in the upper left-hand corners. Abundance is log-transformed.

significance. This work provides an initial assessment of these general patterns; future investigations will need to examine the spatiotemporal details of these patterns to determine their ecological legitimacy, causal structure, and their generality.

Numerous research and conservation efforts have been directed towards understanding the ecological consequences of decreasing species richness at local and regional scales. As our results indicate, species loss at these scales might not be

Table 2 Summary of the least-squares simple linear regression of the dissimilarity index by year for 470,731 BBS route pairs with the average slope and standard deviation of the slope coefficients for two groups, positive and negative slopes, and six categories. The first category contains all of the BBS route pairs. The remaining five categories are subsets of this category distinguished by the significance of their slope coefficients at five α levels

Category	Positive slope (differentiation)			Negative slope (homogenization)			Percent negative
	<i>n</i>	\bar{X}	SD	<i>n</i>	\bar{X}	SD	
All route pairs	224,764	0.0016	0.0013	245,966	-0.0016	0.0013	52%
$\alpha = 0.1$	50,024	0.0020	0.0006	55,471	-0.0019	0.0006	52%
$\alpha = 0.01$	24,513	0.0028	0.0008	28,608	-0.0028	0.0008	54%
$\alpha = 0.001$	11,952	0.0035	0.0009	15,299	-0.0034	0.0009	56%
$\alpha = 0.0001$	5,709	0.0042	0.0011	7,707	-0.0040	0.0011	57%
$\alpha = 0.00001$	4,258	0.0052	0.0015	7,295	-0.0049	0.0014	63%

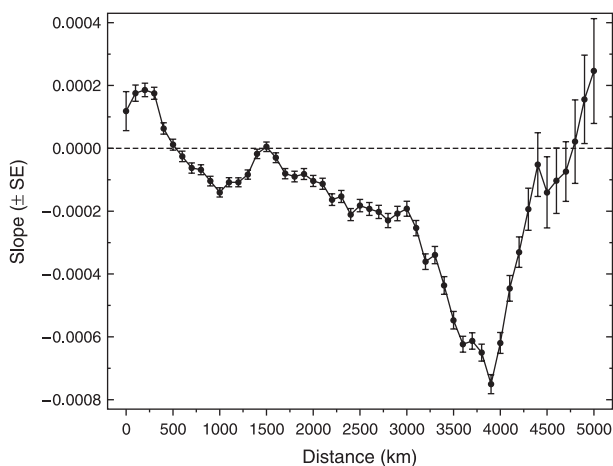


Figure 6 Plot of average slope coefficients (\pm SE) for 50 distance categories (0–5000 km at 100-km intervals) from the least-squares simple linear regression of the dissimilarity index by year for 470,731 BBS route pairs. Values located above zero indicate positive slope and decreasing similarity in species composition over time (differentiation), and points located below zero indicate negative slope and increasing similarity in species composition over time (homogenization).

occurring for all taxonomic groups. Therefore, issues associated with the ecological consequence of increasing species richness need to be addressed as well. However, if we consider the extinction debt theory (Tilman *et al.*, 1994), increasing species richness at local scales could represent a temporary phenomenon, particularly if patterns of habitat destruction continue. However, it is unclear to which spatial scale the extinction debt theory best applies and the quantity of empirical evidence for the theory is quite limited (Tilman *et al.*, 1994; Hanski & Ovaskainen, 2002; Malanson, 2002). Ignoring circumstances where species richness has increased based on assumptions originating from the extinction debt theory, therefore, could be detrimental for both scientific progress and the achievement of conservation objectives. In addition, biological diversity is more complex than simply the number of species observed at different spatial scales. Other components are involved and how they change over time in asso-

ciation with changes in species richness will also determine the structure of biological diversity.

Our results provide evidence that taxonomic distinctness increased at some BBS routes resulting in avian assemblages that were, on average, more unique taxonomically and possibly evolutionarily. However, the general pattern of change in taxonomic distinctness was weak and the positive association with gains in species richness was limited. Both Richness and Distinctness presented non-random spatial patterns indicating the presence of regional factors that could be influencing these two components. However, these two components appear to be changing independently of each other indicating the presence of separate regional influences. Therefore, future investigations need to determine the ecological importance of the changes associated with taxonomic distinctness, how these are related to changes in species richness and the role of regional processes in shaping these patterns.

Variation in Abundance over time, a pattern found throughout our analysis, is a well-known characteristic of population data and BBS data in particular and originates from a variety of sources (Link *et al.*, 1994; Thomas, 1996; Link & Sauer, 1998). The primary factor is environmental change and the abundance levels of individual species tracking these changes over time (Taper *et al.*, 1995; Holmes & Sherry, 2001). Another factor is related to heterogeneity in species detectability (Boulinier *et al.*, 1998) and differences within and among BBS observers in their ability to detect species within and across years and environments (Sauer *et al.*, 1994; Kendall *et al.*, 1996). These factors are compounded by the short sampling period used by the BBS which limits the total number of species that can be observed during the time of the survey (species–time relationship; Rosenzweig, 1995) and the accuracy of abundance estimates.

Overall, our analysis suggests that Abundance declined significantly from 1968 to 2003 and the distribution of individuals across species became more even. However, the high variability displayed by Abundance and the weak pattern presented by Evenness limit the ecological legitimacy of these patterns. The evidence for declining Abundance is supported, nonetheless, by evidence of a global decline in avian abundance in association with increasing anthropogenic activities (Gaston

et al., 2003). Abundance did provide significant positive associations with Richness and Evenness at individual BBS routes even though Richness and Evenness did not display a strong relationship. These associations suggest that the relationship between Richness and Abundance and between Abundance and Evenness were independent of one another. This is in contrast to an investigation of 90 avian communities where abundance distributions were found to be more even for communities containing greater species richness (Cotgreave & Harvey, 1994). Our findings lead to two conclusions. First, the pattern of increasing species richness at BBS routes was not associated with significant changes in the distribution of individuals across species, and the association between Richness and Abundance appears to be related to the fact that when more species are present there will likely be more individuals. Second, the relationship between Abundance and Evenness was related to the high variability displayed by Abundance and how that variability was expressed in the species–abundance distribution when species richness remained unchanged. BBS routes had highly uneven distributions on average ($\bar{X} = 0.65$, $SD = 0.079$), with a few species containing the majority of individuals reflecting the well-established species–abundance relationship (Preston, 1948; Gray, 1987; Tokeshi, 1993). Therefore, when species richness remained consistent, variability in abundance was associated with the most abundant species. Thus, as our results indicate, BBS routes with high individual abundance or increasing abundance over time would be associated with less even distributions of individuals among species and with decreasing evenness over time. Conversely, BBS routes with low individual abundance or decreasing abundance over time would be associated with more even distributions of individuals among species or with increasing evenness over time. This represents the most parsimonious explanation; however, these patterns need to be explored in greater detail.

Across the four diversity components, a uniform pattern of change in diversity structure was not evident. However, we can summarize two general patterns that our analysis supports. First, we have evidence for a temporally consistent pattern that appears to be regionally localized, characterized by increasing species richness with limited gains in taxonomic distinctness. Second, our results provide evidence for an association between Abundance and Evenness related primarily to the species–abundance relationship. Our analysis supports the first pattern as a legitimate temporal trend, thus the details of this pattern are likely worth pursuing in future investigations. The second pattern, on the other hand, reflects a well-known ecological relationship. However, decreasing Abundance contains important ecological implications (see Gaston *et al.*, 2003 for discussion) and if the variability in Abundance associated with the BBS database could be accounted for, the details of this pattern and its association with Evenness might be worth pursuing.

The similarity analysis provided little evidence that avian species composition changed in a consistent manner over time and space at the local scale in North America. Our results did indicate that changes in species composition were defined largely by distance between BBS routes, with the most significant patterns concentrated within a limited range of distances. An examina-

tion of BBS route pairs separated by these distances indicates that these routes were located primarily within several hundred kilometres of the Pacific and Atlantic coasts of the United States. Increasing similarity in species composition is a pattern of growing prevalence in association with anthropogenic activities (McKinney & Lockwood, 1999; McKinney & Lockwood, 2001), and coastal regions generally have higher human population densities. This suggests that species involved with these patterns could represent species that have benefited directly from anthropogenic activities. Examining the spatial and taxonomic details of these patterns in association with an analysis of anthropogenic activities would add much to clarifying how species composition has changed in North America and the role of anthropogenic activities and human-altered environments as a homogenizing force.

In general, mechanisms responsible for the patterns observed in this study must summarize the dominant processes occurring at BBS routes. Our results indicate that BBS routes are located in non-urban areas containing moderately low levels of anthropogenic activities. This agreed with the survey's intent – to sample secondary roads disassociated from urban areas. Therefore, BBS routes are associated with environments that have not been altered by urbanization or through other extreme anthropogenic-based environmental transformations. However, the intimate association with roads and the relatively close proximity to urban areas provide a constant and direct source of anthropogenic activities that must be considered in any interpretation of BBS data (Bart *et al.*, 1995; Keller & Scallan, 1999).

Several studies provide evidence that successional patterns of vegetation at BBS routes, as a result of either anthropogenic or natural processes, might play a role in altering avian diversity structure (Brown *et al.*, 2001; Holmes & Sherry, 2001; Parody *et al.*, 2001). Several scenarios have been forwarded: (1) vegetation associated with BBS routes could be returning to states that existed prior to European settlement (e.g. closed-forest structure in the Upper Midwest and Northeast; Parody *et al.*, 2001), (2) vegetation could be following natural successional pathways apart from human influence leading to changes in vegetation structure and/or composition (Holmes & Sherry, 2001), and (3) anthropogenic activities (e.g. agriculture, silviculture, livestock grazing, or urban development) could be directly altering habitat and associated successional patterns and disturbance regimes. All of these scenarios are likely operating to some degree within the study area. However, as indicated above, anthropogenic activities cannot be totally excluded, thus scenarios that include this factor should have greater significance. Another consideration is that some of the scenarios might create an 'intermediate' level of disturbance which, in some cases, has been associated with higher levels of species richness, a pattern documented in this study (intermediate disturbance hypothesis: Levin & Paine, 1974; Connell, 1978). Investigations examining avian assemblages along urban gradients have found higher species richness at intermediate levels of human habitation (Vale & Vale, 1976; Jokimäki & Suhonen, 1993; Blair, 1996; Crooks *et al.*, 2004) and it has been proposed that these patterns are due to increased habitat diversity generated by anthropogenic activities in these regions (Lancaster & Rees, 1979; Andr n, 1994).

In addition to local processes, our results indicate the presence of regional patterns which suggest that regional or global processes that encompass or are peripheral to local sites could be influencing local patterns (Cornell & Lawton, 1992; Cornell, 1999; Huston, 1999; Cam *et al.*, 2000). Climate change is a major factor operating at a global scale that drives broadscale changes in the environment, including changes in vegetation structure and composition, successional patterns, and disturbance regimes (Graves & Reavey, 1996; Harvey, 1999). Other factors that could influence local patterns at BBS routes include habitat alterations peripheral to BBS routes, the primary example being urbanization. Urban avian assemblies are characterized by lower species richness and the presence of non-native, human-commensal species (Batten, 1972; Emlen, 1974; Lancaster & Rees, 1979; Beissinger & Osborne, 1982; Clergeau *et al.*, 1998; Germaine *et al.*, 1998). These urban species pools could potentially provide a continuous source of migrants for peripheral, non-urban areas. If local conditions at BBS routes included intermediate levels of anthropogenic activity, these source pools of non-native, human-commensal species could create a significant colonizing (possibly homogenizing) force for BBS routes.

As the biosphere responds to anthropogenic activities, we are witnessing changes within biological communities. To understand these patterns well enough to generate models and predictions for sound planning and management, we must examine biological communities in a variety of environments, from urban to pristine, and from a variety of spatiotemporal perspectives. Moreover, non-urban and seminatural regions, which in North America are more abundant and contain more species than nature reserves (Scott *et al.*, 2001), will likely take on greater importance as a source of preserved or semi-preserved habitats for the conservation of biological diversity and ecosystem services. Therefore, understanding how biological diversity is being impacted in these regions will be critical in the development of comprehensive conservation plans. In addition, as the global impact of anthropogenic activities expands and intensifies, studying biological communities at continental and global scales will take on greater importance. Future research, therefore, needs to explore how biological communities are being impacted in regions with varying levels of anthropogenic activities and how local, regional and global processes are operating to influence patterns of biological diversity. With the BBS database, future research needs to address how species composition has changed at BBS routes and the role of non-native, human-commensal species in these changes. In addition, future research needs to determine if the level of anthropogenic activity at BBS routes represents an intermediate level of disturbance promoting greater species richness. Lastly, these factors need to be examined at a regional scale as evidenced by the spatial clustering of BBS routes with similar patterns of change in diversity structure and species composition.

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BIOSKETCHES

Frank A. La Sorte has research interests in developing methods for quantifying patterns of biological diversity over space and time, documenting how and why these patterns have changed as a result of anthropogenic activities, studying the dynamics of temporal turnover as they apply to changes in biological diversity, and exploring the spatiotemporal dynamics of geographical ranges.

William J. Boecklen has research interests in statistical ecology, conservation biology, community ecology and insect–plant interactions, with particular emphasis on the role of endophytic fungi in mediating tri-trophic interactions involving plants, herbivores and natural enemies.