

# Temporal turnover of common species in avian assemblages in North America

Frank A. La Sorte\* and William J. Boecklen

Department of Biology, New Mexico State University, Las Cruces, NM, USA

## ABSTRACT

**Aim** We examine patterns of temporal turnover of common species in avian assemblages in North America to test the hypothesis that changes in avian diversity structure observed in these assemblages were associated with the colonization of common species.

**Location** The contiguous United States and southern Canada.

**Methods** We measured temporal turnover from 1968 to 2003 for 547 avian species at 1673 North American Breeding Bird Survey (BBS) routes. We used the Euclidian distance between expected and observed presence/absence vectors and randomization tests to place species into two categories, common and not-common, and into three categories for common species: (1) always common, (2) common and colonizing, and (3) common and extirpated. We used these categories to identify species experiencing extreme colonization and extirpation events and to examine changes in species composition at BBS routes. We also determined how these patterns were associated with changes in species richness and changes in similarity in species composition.

**Results** Nine of the 547 species represented outliers, where the number of BBS routes colonized greatly exceeded the number extirpated; no species showed extreme values for extirpation. The nine species colonized BBS routes primarily in the upper Midwest and north-eastern United States. Presence of the nine species at BBS routes was correlated with increasing net gain in common species (difference between common colonized and common extirpated), higher levels of species richness and increasing species richness over time, more similar species compositions and increasing similarity over time, and a greater prevalence of common species over not-common species. The literature indicates that all nine species experienced some form of geographical range expansion during the time of the survey involving four elements: (1) introduction and invasion; (2) the ability to use human-altered environments, including habitats associated with agricultural, suburban, or urban areas; (3) intensive management activities, including habitat improvements and reintroductions and (4) the ability to use habitats formed through forest regeneration. These factors in combination point to anthropogenic activities and related land use histories as the primary drivers of change. One of the nine species colonized regions well outside its historic geographical range and the remaining eight species were native within the regions they colonized.

**Main conclusions** Our results suggest that a combination of anthropogenic activities promoted, within certain regions of North America, the geographical expansion of a limited number of common species that were native to those regions. These colonization events were correlated with changes in diversity structure, implying that large-scale diversity patterns were being influenced by anthropogenic activities. These changes can be characterized primarily by gains in

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

species richness, an increased prevalence of common species, and more similar species compositions. Thus, using simple large-scale measures of diversity could be problematic if recent biogeographical patterns of species diversity are not considered. Specifically, using species richness or an indicator species to assess diversity could bias assessments towards common species whose populations have recently benefited through anthropogenic activities.

### Keywords

Anthropogenic activities, avian assemblages, common species, homogenization, North American Breeding Bird Survey, species turnover, temporal turnover.

## INTRODUCTION

Turnover in biological communities is defined as the pattern of change in species composition that occurs over space and time. Understanding turnover, its patterns and processes, has been a major goal in ecology and conservation biology with attention focused primarily on two perspectives: temporal turnover in insular communities (island biogeography theory; MacArthur & Wilson, 1963, 1967) and spatial turnover in non-insular communities ( $\beta$ -diversity; Whittaker, 1972). A third perspective that has received little attention is temporal turnover occurring in non-insular communities. This is due, at least in part, to the challenge of documenting and modelling patterns of temporal turnover in biological communities not confined within biogeographical barriers. In general, biological communities typically have high rates of temporal turnover (Rice *et al.*, 1983; Schoener & Spiller, 1987; Arnott *et al.*, 1999; Brown *et al.*, 2001) and a predominance of rare species (Preston, 1948; May, 1975; Gray, 1987; Tokeshi, 1993; Gaston, 1994; Brown *et al.*, 1995; Russell *et al.*, 1995) which, in a non-insular system, adds a tremendous amount of complexity to temporal turnover patterns. These difficulties can, nonetheless, be avoided to a large degree by focusing on patterns associated with common species. Common species have received limited attention but, in general, contain better properties with regards to temporal turnover. The presence or absence of a common species can be known with a high level of accuracy and, consequently, inferences based on an analysis of temporal turnover of common species in non-insular communities can be quite strong. Further, analysing patterns associated with common species inevitably generates insights into patterns associated with not-common species, i.e. those species not identified as common and thus including rare species.

A second goal in ecology and conservation biology has been to understand the ecological patterns and the evolutionary causes associated with differences in rare and common species (Gaston, 1994; Kunin & Gaston, 1997). The level of rareness or commonness of a species has traditionally been defined by differences in abundance level or differences in geographical range size (Gaston, 1994). However, these measures do not

always provide a distinct or consistent demarcation between the two categories. In this study we provide a different perspective on the rare/common dichotomy. We use presence/absence temporal patterns to provide an objective procedure to demarcate common from not-common species. Our approach avoids some of the difficulties associated with the use of abundance or geographical range in selecting a demarcation point; specifically, issues associated with subjectivity, spatial scale, and estimation of abundance or geographical range size (Gaston, 1994). In addition, there is ample evidence that abundance and occupancy are positively correlated; i.e. for an individual species, the population size at sites where that species occurs is related to the species' extent of occurrence in that region (reviews: Gaston, 1999; Holt *et al.*, 2002). Therefore, our use of presence/absence patterns will likely be correlated with patterns associated with abundance and geographical range size. Furthermore, the addition of time in our assessment provides a more comprehensive and realistic ecological representation of commonality and temporal turnover.

A recent study using data from the North American Breeding Bird Survey (BBS) reported a trend from 1968 to 2003 of increasing species richness at the local scale in North America (La Sorte & Boecklen, 2005). In the present study, we test a possible explanation for this pattern: common species whose populations have recently benefited from anthropogenic activities are responsible, at least in part, for the pattern of increasing species richness at the local scale.

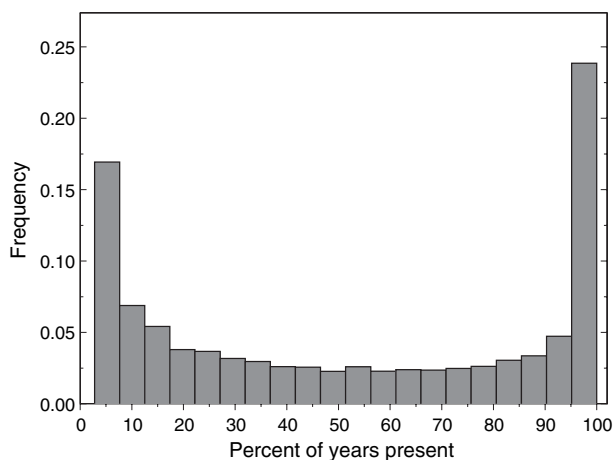
Much effort in conservation biology has been directed towards measuring biological diversity for conservation planning. However, little attention has been paid to temporal turnover, the role of common species, or the impacts of anthropogenic activities on natural communities at large spatial scales and its effect on conservation planning. Our approach expands our understanding of the patterns and processes associated with temporal turnover, the differences between common and not-common species and how anthropogenic activities are differentially impacting these two groups. In addition, our approach benefits conservation efforts by providing a technique that can be used to incorporate this critical information into ecological assessments.

## METHODS

We used data from the North American BBS from 1968 to 2003, a 36-year period, for our analysis (USGS, 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-min point counts are conducted. BBS routes are located in non-urban areas characterized by low night-time light activity and moderately low human population densities (La Sorte & Boecklen, 2005). Surveys are conducted during the breeding season (between May and July) and take approximately 5 h to complete. Our analysis contained 547 species, including native and introduced terrestrial and aquatic species and excluding accidental and vagrant species. We selected 1673 BBS routes for analysis. These routes met BBS quality standards and were sampled at least once during each of four 9-year time periods (1968–76, 1977–85, 1986–94, 1995–2003) and were sampled a minimum of nine times [see La Sorte & Boecklen (2005) for a map of route locations].

The frequency distribution of species occurrence at BBS routes indicated the presence of a bimodal distribution partitioned between common species that were observed nearly every year and rare species that were observed quite infrequently (Fig. 1). We divided this distribution into several categories. The first division separated common species that were very common, observed nearly every year, from the remainder of the species which we designated as not-common. We then divided common species into three categories: (1) species that were present every year surveyed, (2) common species that colonized the assemblage during the time of the survey and (3) common species that were extirpated from the assemblage during the time of the survey.

We used binary presence/absence vectors (a vector of 1's and 0's, respectively) to determine a species membership within the



**Figure 1** Frequency distribution representing, for the 547 species examined in the study, the per cent of years each species was present from the total number of years surveyed for 1673 Breeding Bird Survey routes from 1968 to 2003.

three common categories. For each of the 1673 routes examined, 547 presence/absence vectors were identified, indicating the presence or absence of each species for each year surveyed. We placed each of the 547 species into one of the three categories by contrasting the observed presence/absence vectors with three expected presence/absence vectors that represented ideal states for the three categories. For the first category (a species was present every year surveyed) we defined the expected vector as [1,1,...,1], for the second category (a species colonized the route and was observed every year after the colonization event) we defined the expected vector as [0,0,...,0,1,1,...,1], and for the third category (a common species that was extirpated from the route) we defined the expected vector as [1,1,...,1,0,0,...,0]. For BBS routes that were sampled an even number of years, the expected vector contained an equal number of 1's and 0's. For BBS routes that were sampled an odd number of years, the number of 0's was one less than the number of 1's.

This technique sampled colonization and extirpation events of common species that occurred at or near the halfway point of the survey, in this case, between 1984 and 1987. Common species that colonized routes or were extirpated from routes early or late during the length of the survey were not captured by this technique. This created several sources of bias in our estimates of the number of species identified as common and not-common. Species that were extirpated late or colonized early could possibly be categorized as common and species that were extirpated early or colonized late could possibly be categorized as not-common. The primary consequence of these biases would be inflated estimates for the number of species identified as common and not-common at a BBS route. We dealt with this discrepancy by examining the ratio of common to not-common species at each BBS route. This procedure is described in detail below.

To determine the level of similarity between the expected and observed vectors, we measured the Euclidian distance between the two vectors in the space defined by the vector's dimension (i.e. vector length). If  $n$  represented the number of years the survey was conducted and  $x$  the entries of 0's and 1's in the observed vector  $\mathbf{x}$  and  $y$  the entries of 0's and 1's in the expected vector  $\mathbf{y}$ , the Euclidian distance would be of the form:

$$\|\mathbf{x} - \mathbf{y}\| = \left[ \sum_{i=1}^n (x_i - y_i)^2 \right]^{1/2}.$$

We applied a randomization test to each combination of observed and expected vectors to determine the probability of getting the observed distance by chance alone (Manly, 1997). The procedure for the randomization test consisted of sampling with replacement the entries in the observed vector and recalculating the Euclidian distance from the expected vector 10,000 times. Where the observed distance occurred within this sample space of resampled distances provided an estimate of the probability of getting the observed distance by chance alone. We selected an  $\alpha$ -level = 0.1 to demarcate a region of 'significance' within the sample space for each expected vector; i.e. any observed vector located within this

region approximated the expected vector well enough to be placed into that category. From the *P*-values estimated for each of the three common categories, we placed each species into the category that had the smallest *P*-value below 0.1. If none of the *P*-values were below 0.1, the species was identified as not-common. This procedure contains mathematical tools typically used in inferential statistics which, in this case, are used not to generate inference but to estimate the level of similarity of vector pairs within an objective analytical framework.

We used this procedure to estimate for each species the number of BBS routes where the species was common, common and extirpated, common and colonized, and the number where the species was not-common. We then used this information to examine three relative patterns. The first examined associations among species based on an analysis of outliers, the second examined associations within BBS routes based on the ratio of two categories, and the third examined associations within species and BBS routes based on the difference between two categories. First, we identified species that represented extreme colonization or extirpation events based on an examination of outliers. In a plot of the number of BBS route colonized vs. extirpated for each species, we identified species that did not follow an 'equilibrium' pattern, i.e. species whose values for colonization and extirpation were not equivalent and close to zero. Two possible 'non-equilibrium' scenarios were possible: (1) the number of BBS routes colonized exceeded the number extirpated, indicating geographical expansion and (2) the number of BBS routes extirpated exceeded the number colonized, indicating a geographical contraction. Secondly, for each BBS route, we calculated the ratio of common to not-common species. Values above one indicate a dominance of common species and values below one indicate a dominance of not-common species for a BBS route. Thirdly, for each species, we calculated the difference between the number of BBS routes colonized and the number extirpated. This provided an estimate of the net gain in the number of BBS routes colonized for each species. Finally, for each BBS route, we calculated the difference between the number of species that colonized the route and the number extirpated from the route. This provided an estimate of the net gain in the number of common species for each BBS route.

We used linear least squares regression (lm: S-PLUS 6.2, Insightful) in combination with locally weighted regression (loess: S-PLUS 6.2, Insightful) to examine patterns of change in species composition at BBS routes. The LOESS model was used to indicate the appropriateness of the linear regression model based on how well the LOESS curve followed the 99% confidence intervals of the linear regression model. We compared means of samples and determined the significance of correlation coefficients using randomization tests with 100,000 permutations and two-sided *P*-values (permutation-Test: S-PLUS 6.2, Insightful).

Lastly, we examined how species richness and similarity in species composition had changed over time at BBS routes using linear regression least squares. We estimated for each

BBS route the rate of change in species richness over time, based on the slope of the regression line with year as the explanatory variable and the number of species at the BBS route as the response variable. Our analysis of similarity in species composition was based on the application of the  $\beta_{sim}$  dissimilarity index (Lennon *et al.*, 2001; Koleff *et al.*, 2003) to 470,731 BBS route pairs containing 1052 of the 1673 original BBS routes. The BBS route pairs were selected because they were sampled a minimum of four times during each of four 9-year time periods (1968–76, 1977–85, 1986–94, 1995–2003) and had a minimum of 16 total samples. This index ranges from 0, high similarity, to 1.0, low similarity. We applied the same regression procedure to estimate the rate of change in similarity of species composition for BBS route pairs over time. See La Sorte & Boecklen (2005) for more details on these procedures.

## RESULTS

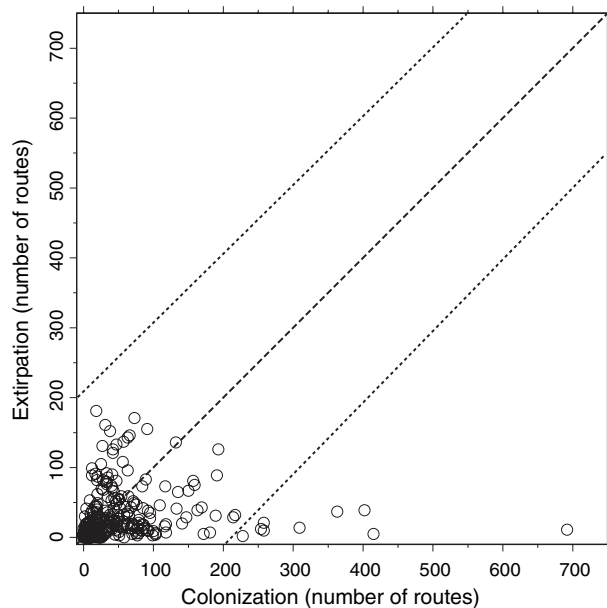
The analysis of the presence/absence vectors estimated the number of the 1673 BBS routes where, for each of the 547 species, the species was identified as common, the number where the species was identified as common and colonized, the number where the species was identified as common and extirpated, and the number where the species did not fall into any of these three categories and was considered not-common (Table 1 contains 14 species identified as most common; Appendix S1 contains the results for all 547 species). Examining the number of BBS routes each species colonized vs. the

**Table 1** The 14 most common species, with the number of Breeding Bird Survey (BBS) routes where the species was identified as common (COM), common and extirpated (EXT), common and colonized (COL) and not-common (NCOM), based on an analysis of observed and expected presence/absence vectors for 547 species from 1968 to 2003 at 1673 BBS routes. Appendix S1 contains the results for all 547 species

Common name	Scientific name	COM	EXT	COL	NCOM
Red-winged blackbird	<i>Agelaius phoeniceus</i>	1502	44	16	82
Mourning dove	<i>Zenaid macroura</i>	1469	16	78	78
Brown-headed cowbird	<i>Molothrus ater</i>	1460	52	46	105
European starling	<i>Sturnus vulgaris</i>	1421	48	47	131
Barn swallow	<i>Hirundo rustica</i>	1394	35	95	113
American crow	<i>Corvus brachyrhynchos</i>	1392	21	39	120
American robin	<i>Turdus migratorius</i>	1392	8	51	96
House sparrow	<i>Passer domesticus</i>	1305	105	25	145
Common grackle	<i>Quiscalus quiscula</i>	1234	18	43	77
Common yellowthroat	<i>Geothlypis trichas</i>	1192	34	62	193
Killdeer	<i>Charadrius vociferus</i>	1167	96	63	306
Blue jay	<i>Cyanocitta cristata</i>	1165	4	30	99
Eastern kingbird	<i>Tyrannus tyrannus</i>	1066	80	32	241
Chipping sparrow	<i>Spizella passerina</i>	1060	46	109	239

number where they were extirpated, the majority of species were clustered around zero and the line of perfect equality where the number of routes colonized equalled the number extirpated (Fig. 2). Based on where the majority of species were clustered, nine species showed evidence towards greater colonization and no species showed evidence towards greater extirpation (Fig. 2; Table 2). Based on the net gain in the number of BBS routes colonized (for each species, the number of BBS routes where the species was extirpated, subtracted from the number where the species colonized), these nine species also ranked the highest (Table 2).

The location of BBS routes where the nine species colonized indicated that the eastern section of the continent experienced the greatest number of colonization events, with the densest clusters located in the upper Midwest and north-eastern United States (Fig. 3). The average net gain in common species (for each BBS route, the number of common species that were extirpated subtracted from the number of common species that colonized) was positively correlated with the presence of the nine colonizing species, with an average gain of approximately 1.8 common species for each additional colonizing species (Fig. 4a; slope = 1.75,  $t_{1,671} = 18.71$ ,  $P \leq 0.001$ ). Hence, the number of common colonizing species at BBS routes exceeded the number based exclusively on the presence of the nine colonizing species. The ratio of common to not-



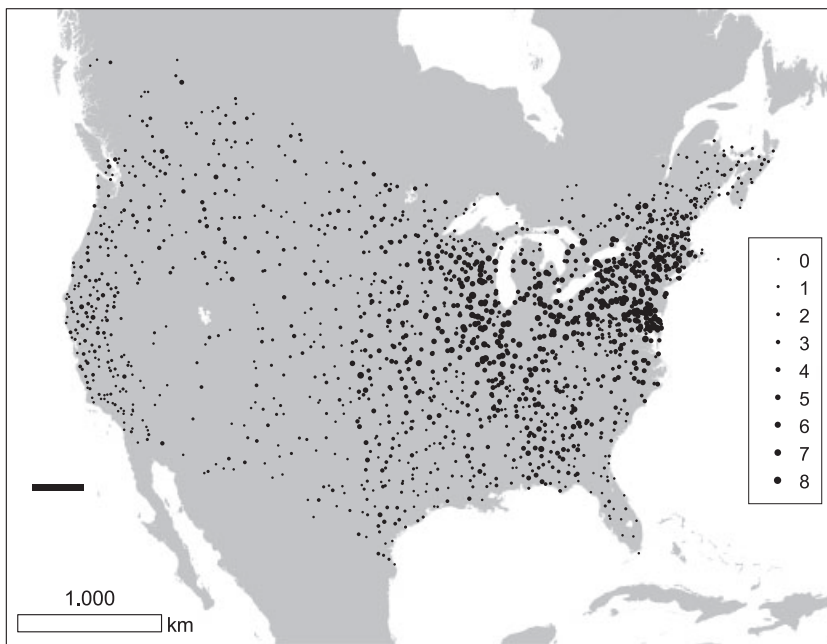
**Figure 2** Plot of the 547 species and the number of Breeding Bird Survey (BBS) routes where the species was documented as common and colonized by the number of routes where the species was documented as common and extirpated. These values were estimated from an analysis of observed and expected presence/absence vectors using randomization tests for 1673 BBS routes from 1968 to 2003. The dashed line is the line of perfect equality where the number of BBS routes colonized equals the number extirpated. The two dotted lines are parallel and equidistant to the line of perfect equality and contain approximately 98% of the 547 species.

**Table 2** Nine colonizing species, with the number of Breeding Bird Survey (BBS) routes where the species was identified as common (COM), common and extirpated (EXT), common and colonized (COL), and not-common (NCOM), based on an analysis of observed and expected presence/absence vectors for 547 species from 1968 to 2003 at 1673 BBS routes. The rank of each species shown in parenthesis is based on the net gain in common species, defined as COL – EXT

Common name	Scientific name	COM	EXT	COL	NCOM
House finch (1)	<i>Carpodacus mexicanus</i>	225	11	692	354
Canada goose (2)	<i>Branta canadensis</i>	36	5	415	633
Great blue heron (3)	<i>Ardea herodias</i>	277	39	402	773
Red-tailed hawk (4)	<i>Buteo jamaicensis</i>	327	37	363	833
Eastern bluebird (5)	<i>Sialia sialis</i>	513	14	309	343
Cedar waxwing (6)	<i>Bombycilla cedrorum</i>	512	10	258	369
Mallard (8)	<i>Anas platyrhynchos</i>	335	21	258	686
Turkey vulture (7)	<i>Cathartes aura</i>	357	12	254	659
Wild turkey (9)	<i>Meleagris gallopavo</i>	5	2	228	624

common species at BBS routes was also positively correlated with the presence of the nine colonizing species (Fig. 4b). As more of the colonizing species were identified at a BBS route, the ratio rose above one, indicating greater dominance of common species, and remained consistently above one. In other words, for BBS routes where none of the nine colonizing species were present, the average number of species identified as not-common ( $\bar{X} = 46.3$ ) exceeded the number identified as common ( $\bar{X} = 36.6$ ) by approximately 10 ( $P \leq 0.001$ ). In contrast, if any of the nine species were present, the average number of species identified as not-common ( $\bar{X} = 43.7$ ) was less than but statistically equivalent to the average number identified as common ( $\bar{X} = 44.2$ ;  $P = 0.289$ ).

Average species richness at BBS routes was greater for routes that contained these nine species (Fig. 5a). For BBS routes that lacked these species, species richness averaged 48.0 ( $n = 366$ ; SD = 13.6); for BBS routes that contained these species, species richness averaged 55.5 ( $n = 1,307$ ; SD = 10.4;  $P \leq 0.001$ ). In addition, the average change in species richness over time at BBS routes was positively correlated with the presence of the nine colonizing species (Fig. 5b; slope = 0.061,  $t_{1,671} = 13.53$ ,  $P \leq 0.001$ ). That is, as the number of the nine colonizing species at a BBS route increased, the average rate of increase in species richness over time increased by approximately 0.06 species per year for each gain of a colonizing species. The average level of similarity in species composition for BBS routes pairs increased on average as the number of the nine colonizing species found at BBS route pairs increased (Fig. 6a; slope =  $-0.0334$ ,  $t_{470,714} = -353.2$ ,  $P \leq 0.001$ ). In addition, change in similarity of species composition over time increased as the number of the nine colonizing species found at BBS route pairs increased (Fig. 6b; slope =  $-0.0001$ ,  $t_{470,714} = -89.67$ ,  $P \leq 0.001$ ). That is, as the number of the nine colonizing species shared between BBS route pairs increased, the composition of species became more similar



**Figure 3** Map of the southern portion of North America with the locations of 1673 Breeding Bird Survey (BBS) routes and the number of nine colonizing species found at each route from 1968 to 2003. The number of the nine colonizing species for each BBS route is represented by a gradient of increasing point size.

between BBS route pairs over time. However, the magnitude was weak, with an approximate loss of 0.0001 in the dissimilarity index per year for each gain of a colonizing species.

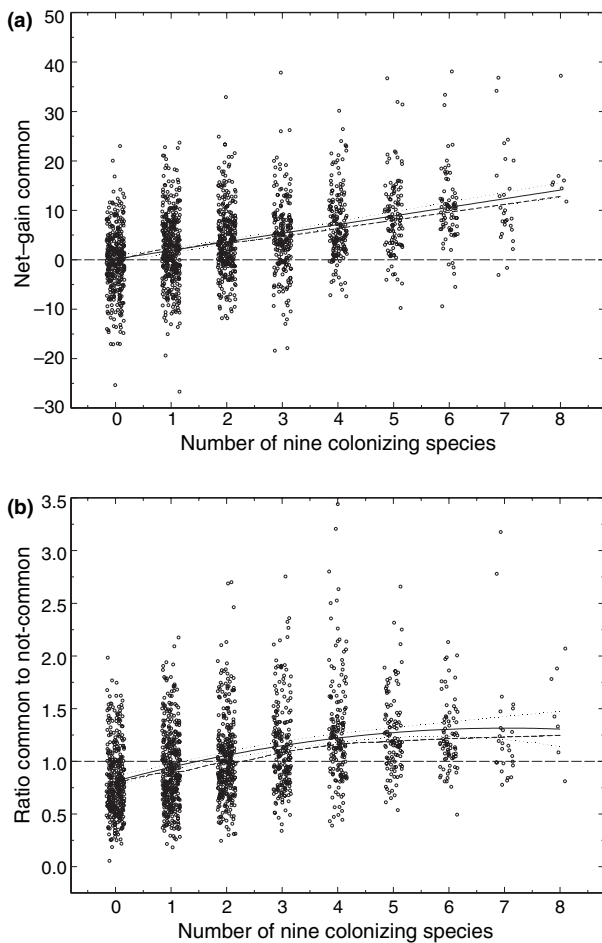
## DISCUSSION

Our analysis suggests that the majority of common species observed at BBS routes from 1968 to 2003 experienced ‘equilibrium’ patterns of colonization and extirpation, with the exception of nine species that colonized many more routes than from which they were extirpated. Our analysis further indicates that these colonization events were correlated with changes in the composition and structure of avian assemblages. Our findings, therefore, provide evidence that the geographical expansion of a limited number of common species played a role in altering avian diversity structure. Moreover, native species were the dominate colonizers, with the presence of only one species that could be labelled as exotic and invasive.

Several relevant spatial and temporal patterns were associated with the colonization of the nine species. Two regions in North America experienced the majority of colonization events. As a consequence, these regions also experienced changes in species composition and diversity structure associated with these colonizations. These changes include gains in species richness and increased similarity in species composition. The association with species richness was ecologically significant, but the association with similarity in species composition was much weaker, indicating that the presence of the nine colonizing species was possibly the only homogenizing factor. However, independent of the rate of homogenization, BBS routes where these species colonized contained, on average, more species and species compositions that were more similar. Our results also suggest that the ratio of common to not-common species changed from a dominance

of not-common species to a dominance of common species. The timing for this pattern, however, cannot be directly determined from our analysis; it could represent changes that occurred during the survey or patterns that existed before the survey, or a combination of both, i.e. pre-existing patterns that either persisted or were strengthened during the time of the survey. In addition, our results suggest that the net gain in common species at BBS routes exceeded the gains due exclusively to the colonization of the nine species. That is, for each of the nine colonizing species at a BBS route, there was an approximate net gain of two common species at that route. Overall, we can characterize these patterns as indicating that, where these nine species colonized, species richness was greater and increased over time, species composition was more similar and became more similar over time, additional common species colonized these routes, and the number of common species exceeded the number of not-common species independent of the colonization-extirpation events.

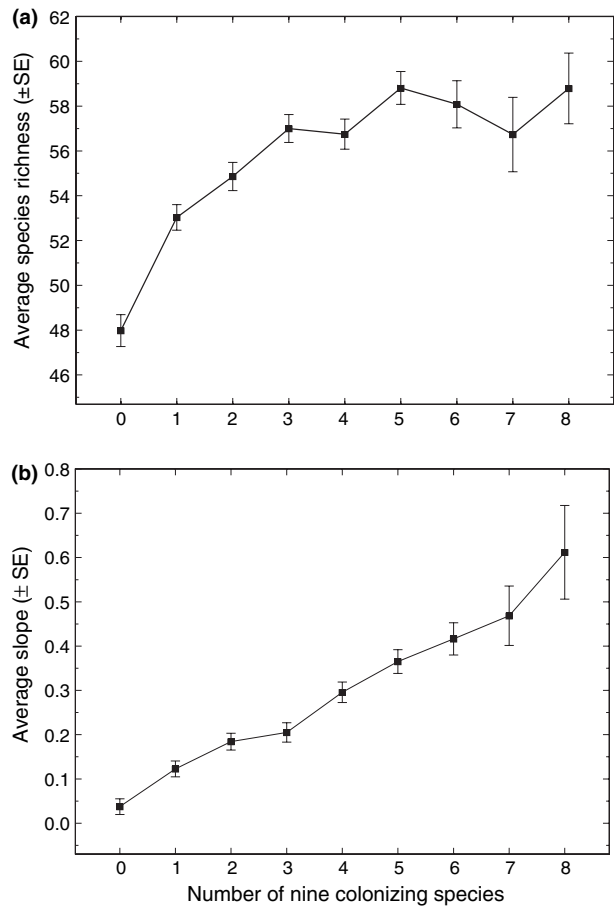
Mechanisms associated with these patterns can be inferred by examining the natural history of the nine colonizing species during the later half of the 20th Century. Evidence from the literature suggests that all nine species underwent some form of geographical range expansion during this time period (Table 3). These accounts contain similarities that can be summarized by four factors: (1) introduction and invasion; (2) the ability to use human-altered environments, including habitats associated with agricultural, suburban, or urban areas; (3) intensive management activities, including habitat improvements and reintroductions and (4) the ability to use habitats created through forest regeneration of abandoned agricultural lands in the upper Midwest and north-eastern United States (Whitney, 1994; Foster, 1995; DeGraaf & Miller, 1996; Parody *et al.*, 2001). These factors in combination point to anthropogenic activities and related land use histories as the primary drivers of change – factors of growing importance in



**Figure 4** Plot of the number of the nine colonizing species found at Breeding Bird Survey (BBS) routes by (a) the net gain in common species (number colonized minus number extirpated for each BBS route) and (b) the ratio of the number of species identified as common to the number identified as not-common. The horizontal dashed line indicates in (a) a net gain of zero and an equilibrium pattern of turnover and in (b) a ratio of one and an equivalent quantity of common and not-common species. For both plots, the solid line is the linear least squares regression fit and the two dotted lines the 99% confidence intervals. The dashed line represents the locally weighted regression fit (LOESS).

recent patterns of environmental and ecological change (Vitousek *et al.*, 1997; Foster *et al.*, 2003).

Several conclusions can be drawn from the results of this study. First, management activities have had a powerful influence in manipulating target avian species if the species is common and, in some cases, if the species is able to establish itself in human altered environments. Secondly, if an avian species is a habitat generalist and a human commensalist, i.e. can adapt to anthropogenic activities and can use a wide variety of habitats including ones located in human altered environments, it will have opportunities to become established in new regions regardless of management activities. Finally, our results suggest that native species can play a significant role in changing the composition and structure of avian assem-

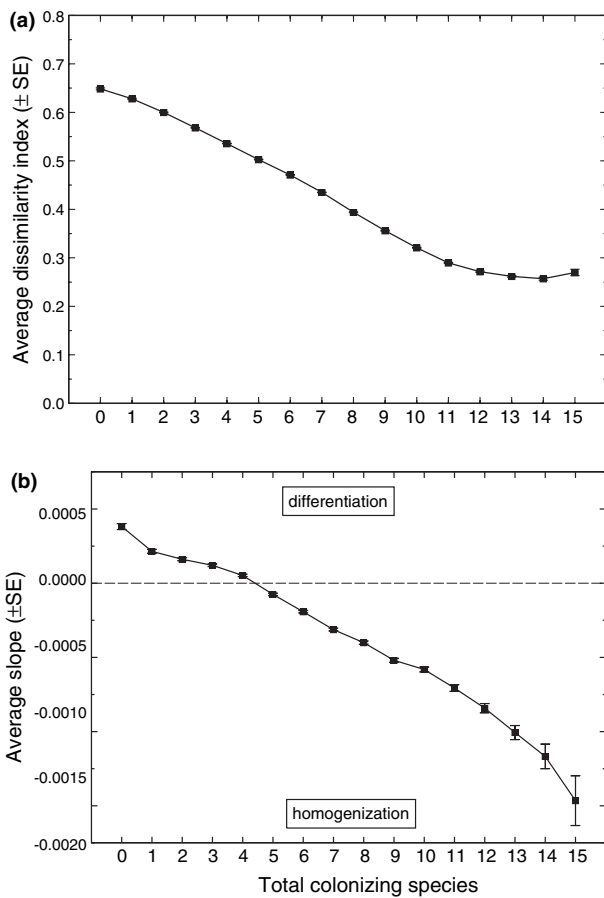


**Figure 5** Plot of the total number of the nine colonizing species present at 1673 Breeding Bird Survey routes from 1968 to 2003 by (a) average species richness at those routes during the time of the survey and (b) the average slope coefficient estimated from the linear least squares regression of species richness by year for each route.

blages. Only the house finch invaded regions well beyond its historic geographical range during the time of the survey. It was introduced to the north-eastern United States from the west in 1940 and invaded much of the east after 1985 (Elliott & Arbib, 1953; Hill, 1993).

In addition, these four factors appear to have created the opportunity for increased species richness at the local scale for avian assemblages in North America. This phenomenon could be temporary and species richness could return to its original level if ecosystem processes remain consistent (Brown *et al.*, 2001). This appears unlikely because ecosystem processes will likely continue to change with the growing prevalence of anthropogenic activities within the biosphere. In addition, gains in species richness did not occur uniformly across species but favoured common species whose populations benefited from anthropogenic activities. Alternatively, species richness could fall below its original level if habitat in North America continues to be altered through anthropogenic activities and an extinction debt is extracted (Tilman *et al.*, 1994). Our results suggest that, for regions sampled by BBS routes, the





**Figure 6** Plot of the total number of the nine colonizing species shared by 470,731 Breeding Bird Survey (BBS) route pairs by (a) the average value of the  $\beta_{sim}$  dissimilarity index averaged over the years surveyed for each BBS route pair and (b) the average slope coefficient estimated from linear least squares regression of the  $\beta_{sim}$  dissimilarity index by year for each BBS route pair. The average slope estimated the rate of change in species composition over time. Positive values above the dashed line indicating decreasing similarity over time (differentiation) and negative values below the dashed line indicates increasing similarity in species composition over time (homogenization).

extinction debt is absent or operating at a relatively slow rate. However, this could change if the level of anthropogenic activity at BBS routes increased.

Understanding the ecological differences between rare and common species has gained in importance for ecology and conservation biology as investigators have tried to understand the spatiotemporal dynamics of biological diversity. Because of the difficulty in documenting diversity patterns for conservation planning, a wide variety of surrogate measures have been forwarded that attempt to capture diversity, with the majority focused on patterns of species richness or patterns associated with rare, endemic, or threatened species. As a consequence, common species and their role in diversity patterns have received limited attention. In some avian communities, the spatial distribution of common species are positively correlated

**Table 3** Summary of factors associated with each of the nine colonizing species' geographical range expansion during the second half of the 20th Century. The factors include (I) introduction and invasion, (H) the ability to use human modified environments, (M) the application of intensive management activities and (F) the ability to use habitats formed from the regeneration of forests in the upper Midwest and north-eastern United States from abandoned agricultural lands

Species	I	H	M	F	Author (year)
House finch	*	*			Elliott & Arbib (1953), Hill (1993), Veit & Lewis (1996), Able & Belthoff (1998), Mauer <i>et al.</i> (2001), Gammon & Mauer (2002)
Canada goose	*	*			Mowbray <i>et al.</i> (2002)
Great blue heron	*				Butler (1992)
Red-tailed hawk	*			*	Preston & Beane (1993)
Eastern bluebird		*		*	Gowaty & Plissner (1998)
Cedar waxwing	*			*	Witmer <i>et al.</i> (1997)
Mallard	*	*			Drilling <i>et al.</i> (2002)
Turkey vulture	*				Kirk & Mossman (1998)
Wild turkey		*			Eaton (1992)

with the distribution of species richness and poorly correlated with distribution of rare species (Prendergast *et al.*, 1993; Williams *et al.*, 1996; Lennon *et al.*, 2004). Our results suggest that this pattern is being strengthened through anthropogenic activities, i.e. species richness is increasing as a function of the establishment of common species. Furthermore, using simple, large-scale measures of diversity could be problematic if recent biogeographical patterns of species diversity within those regions are not considered. Specifically, high species richness or high abundance of an indicator species could represent species compositions biased towards the presence of native common species that have recently benefited from anthropogenic activities. Overall, our results show the importance of considering the role of anthropogenic activities in biogeographical patterns. Some authors argue that historical, environmental and (natural) ecological processes still play a primary role in determining large-scale biogeographical patterns (e.g. Van Rensburg *et al.*, 2004). However, if the present trend continues, it is likely that anthropogenic activities will play a greater role in shaping these patterns.

In summary, using presence/absence information to demarcate common species from not-common species and to model temporal turnover provides a robust, objective and consistent method to capture this dynamic process. This is particularly true with surveys of limited duration that sample communities over long time periods where communities have relatively high levels of temporal turnover. As the biosphere continues its present course of human induced alterations, biological communities will continue to change due either to direct manipulations or as the product of secondary consequences. Empirical information on common species for other taxonomic groups would contribute considerably to our understanding of this process and will, in total, support an informed debate on the



consequences of anthropogenic activities on the biosphere. However, rare and endemic species are of considerable importance and efforts to clarify their contributions to the turnover process would also deepen our understanding of how temporal turnover proceeds and, more importantly, how biological communities are responding to environmental change.

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## SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1271/JBI1271sm.htm>

**Appendix S1** Results from the analysis of observed and expected presence/absence vectors for all 547 species.

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## BIOSKETCHES

**Frank A. La Sorte** has research interests in the fields of community ecology, biogeography and numerical ecology, with an interest in combining aspects of these fields to examine how patterns of biological diversity are changing over space and time due to the influence of anthropogenic activities.

**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.

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