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Geographic range structure in North American landbirds: variation with migratory strategy, trophic level, and breeding habitat

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We investigated the relationship between abundance and geographic range structure of 258 North American landbirds. For this purpose we used six measures of range structure based upon fractal geometry and geostatistics, and three ecological characteristics that can influence avian distribution. Permanent residents (PRs) that were abundant showed little fragmentation of their abundance surface at the periphery of their breeding range. Conversely, common Neotropical migrants (NTMs) exhibited low fragmentation of their central populations. The abundance surface was smoother for PRs than NTMs or short-distance migrants (SDMs), indicating that changes in abundance occurred more gradually across space for this group. The areas of high abundance for grassland species had little demographic fragmentation, but other populations showed little spatial autocorrelation in abundance. Species that bred in late-successional forests were relatively rare compared to species breeding in other habitat types. Among carnivores, PRs had a higher average abundance than either NTMs or SDMs. Although carnivores had more distributional gaps within their ranges than other trophic groups, the number of gaps did not differ between rare and abundant species, indicating that increased abundance did not change their presence/absence distribution maps. Knowledge of patterns and variations of geographic range structure among species may provide insights into processes that shape and maintain the biodiversity of a continent.

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Understanding the distributional processes is a fundamental objective if we are to understand continental-scale variations in biodiversity (Gaston and Lawton 1990, Maurer 1999). The increasing availability of long-term data sets documenting species abundance over national or continental scales and the development of powerful tools to analyze these data sets have created new opportunities for research on species distributions. Previously researchers could only ask questions pertaining to general differences among the geographic ranges of species (e.g. local abundance vs range size). Now we can address questions con-

cerning the spatial variation in abundance of species or guilds, thereby allowing inferences to be made about population dynamics at the continental-scale. The study of large-scale patterns and the processes underlying these patterns has direct applications in community ecology (Brown 1995, Gaston 1996, Stone et al. 1996, Maurer 1999), conservation biology (McDonald and Brown 1992, Lawton 1993, Gaston 1994, Lawton et al. 1994, Maurer 1994, Gaston and Blackburn 1996), biogeography, the evolution of biodiversity (Maurer and Nott 1998) and phylogenetics (Gaston 1996).

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Two important ecological relationships were documented in 1922, but remained relatively unexplored for the next half century. Firstly, Willis (1922) suggested that there is a general positive relationship between local abundance and range size. A renewed interest in Willis' idea has generated numerous hypotheses attempting to provide a mechanistic explanation for this pattern (Gaston et al. 1997a, b, 1998). However, no single hypothesis appears to adequately explain exceptions to the relationship. While many hypotheses require testing, others have already been refuted. Whatever the mechanism(s) underlying this relationship, it appears that it is consistent across scales and applicable to many taxa (see Gaston and Lawton 1990 for a review).

Secondly, Grinnell (1922) noted that many species of birds exhibit areas of high and low abundance within their ranges. However, he probably did not surmise the generality of this observation nor the magnitude at which the variation exists. Brown (1984) expanded upon this notion and suggested the distribution of abundance of a given species is generally characterized by a single peak, with decreasing abundance toward the periphery of the range. Subsequent analyses supported Brown's findings, but it appeared that most species have multiple peaks of abundance centrally located within a species range (Maurer and Villard 1994, Price et al. 1995). These central populations do not only contain more individuals, but they may produce an excess of individuals, thereby acting as sources that subsidize peripheral populations (Maurer and Villard 1994, Curnutt et al. 1996). Thus, for many species, we may see source-sink dynamics occurring at scales much larger than previously suggested (Pulliam 1988).

The spatial variation in abundance across geographic ranges, referred to as the abundance surface or abundance texture (Maurer 1994), can be described by a variety of methods (Rossi et al. 1992, Maurer and Heywood 1993, Maurer 1994, Villard and Maurer 1996). Ecologists have begun to use tools from other disciplines to describe several aspects of a species abundance texture. Two of the most widely used tools include fractal analysis (Palmer 1988, Sugihara and May 1990, Milne 1991, 1992, Virkkala 1993, Maurer and Heywood 1993, Maurer 1994) and geostatistics (Maurer 1994, Villard and Maurer 1996). Each metric corresponds to a different aspect of the distribution; hence, to different aspects of the population processes.

In this paper, we examine various aspects of the abundance surface for a large group of North American landbirds using measures of fractal geometry and geostatistics. Since the abundance surface of any species is neither even nor continuous, it can be considered fragmented. We will address two general types of fragmentation in this study: areographic and demographic (Maurer and Heywood 1993). Areographic fragmentation measures the physical properties (e.g. area and

perimeter) of the geographic range boundary based upon the simple presence or absence of individuals. Variation in the amount of areographic fragmentation is related to migratory strategy and breeding habitat, and though not explicitly tested, possibly to trophic level (Virkkala 1993, Maurer and Heywood 1993 but see Gautestad and Mysterud 1994). Demographic fragmentation is related to the spatial variation of abundance and it corresponds to the intra- and inter-population dynamics across the landscape (Maurer and Heywood 1993). Demographic fragmentation has been shown to vary with migratory status and breeding habitat (Maurer and Heywood 1993).

While many factors influence the distribution of abundance of landbirds, we restrict our analysis to three potential sources of variation: migratory strategy, trophic level, and breeding habitat. By examining a large group of related species we may gain insight into the processes that influence the distribution of abundance (Brown and Maurer 1989, Maurer and Heywood 1993, Brown et al. 1995). It is also useful when attempting to determine how species may react to dramatic environmental change, such as global warming or habitat fragmentation (Maurer 1994, Flather and Sauer 1996, Boulinier et al. 1998).

Previous studies suggest that Neotropical and Palearctic bird species (those that migrate from temperate habitats in the northern hemisphere to more tropical latitudes) tend to have a higher degree of areographic fragmentation than species that remain in temperate latitudes during the winter (Virkkala 1993, Maurer and Heywood 1993, Gautestad and Mysterud 1994). It has also been suggested that migratory strategy affects how a species "fills" its range (Maurer and Heywood 1993). The filling of a range describes how and where increases in abundance occur for a given species. Assuming we can generalize from the findings of Maurer and Heywood (1993), which pertained to four passerine families, we would expect that the ranges of Neotropical migrants (hereafter NTMs) should be characterized by smooth abundance textures and lower average abundances than temperate residents/migrants. Maurer and Heywood also found a negative relationship between abundance texture and average abundance for NTMs. No relationship existed for temperate residents/migrants. Virkkala (1993) distinguished between temperate migrants and residents in his analysis of the areographic fragmentation of Finnish birds. He determined that short-distance migrants (SDMs) had a higher average abundance than tropical migrants or permanent residents (PRs). Consequently, we will include three migratory groups in our analysis.

The production and distribution of available energy vary greatly across a landscape and species vary in their metabolic requirements. As energy flows through a system (e.g. energy pyramid), the majority is lost, leaving less available for those species occupying higher

trophic levels. It follows that geographic range structure should vary with trophic level. Specifically, species at progressively higher trophic levels should be less abundant, while their distributions become more fragmented, reflecting the discontinuous distribution of resources.

Brown (1984) suggested that the driving mechanism for the abundance-range size relationship stems from the differences among species in their ability to use resources. He argued that generalists (whether habitat generalists or omnivores) will occupy one end of the spectrum, being both numerous and widespread. If this pattern is true, we would expect that on average, omnivores and habitat generalists should exhibit lower levels of demographic and areographic fragmentation than dietary or habitat specialists. Among species that predominantly breed within a single habitat type, susceptibility to demographic fragmentation may be correlated with historical levels of areographic fragmentation. For example, since the distribution of desert/scrub habitat is patchy by nature, the demographic fragmentation of species associated with this habitat type may be lower than that of species breeding in habitat that has become fragmented due to recent anthropogenic stresses.

Methods

Data on geographic patterns of abundance were obtained from the Breeding Bird Survey (BBS), a series of censuses conducted annually by the U.S. National Survey and the Canadian Wildlife Service. Each annual census consists of ca 3000 40-km census routes. There are some observer and species-specific biases in this data set (Bystrak 1981, Robbins et al. 1986), but it represents one of the few data sets that are continental in scope and that allow estimation of geographic range fragmentation and texture. Maurer (1994) further discusses issues related to using the BBS in analyses of the distribution of abundance.

Data from the BBS were obtained for 202 species of passerines (Passformes), 21 woodpeckers (Piciformes), 14 species of Gallinaceous birds (Galliformes) and 21 raptor/vultures (Falconiformes and possibly Ciconiiformes). We classified all birds among three migratory strategies: Neotropical migrants ($N = 101$), short-distance migrants ($N = 57$) or temperate residents ($N = 100$), following Partners in Flight Research Working Group (Gauthreaux 1992). Temperate residents include those species that are either permanent residents or winter extensively within the area covered by the BBS (Canada and the U.S.). Classifications of breeding habitat and trophic group were obtained from Ehrlich et al. (1988). The bird species were classified according to their breeding habitat; we used the following five categories: arid (desert and scrub), early- and late-succes-

sional forests, grassland, and habitat generalist. Only species that have the majority of their geographic distribution north of U.S.–Mexico border were included. Original trophic classification included four levels: omnivore, insectivores, herbivores, and carnivores. However, due to small sample size and the recognition that most herbivores feed insects to their young, we combined that group with omnivores. The resulting classifications are available from the authors upon request.

For each species, a map describing the variation in abundance across the North American continent north of the Mexican border was obtained using the following procedure. We selected 3017 BBS routes on which censuses were conducted between 1967 and 1989. Using the UNSBC/CWS classification of route reliability (Sauer et al. 1977), we removed sites deemed unreliable. On each route, the abundance of each species was averaged across all years that the route had been run. To estimate the distribution of abundances across the North American continent, a grid of 40×40 km cells was created. Abundances for each cell were obtained using ordinary kriging (Burrough 1986, Maurer and Heywood 1993, Maurer 1994). Ordinary kriging is a procedure that obtains interpolated values across a regular grid from irregularly spaced points by using information on the spatial autocovariation among randomly sampled locations. All values resulting from kriging were > 0 since they are based upon averages. Subsequent analyses were performed upon log-transformed values of abundance.

The geographic range boundary was determined by estimating the zero-abundance contour line of the abundance map for each species. We estimated the fractal dimension of this contour by calculating the box dimension (Williamson and Lawton 1991, Peitgen et al. 1992, Virkkala 1993, Gautestad and Myrsterud 1994) of the contour. The box dimension is related to the jaggedness of the zero-abundance contour line and represents the range boundary as well as distributional gaps within the range where individuals do not occur. A species whose range has relatively more gaps will have a lower box dimension value.

Within the boundaries of a geographic range, abundance may change gradually or abruptly, depending on how sensitive a species is to changes in environmental conditions. The degree to which such changes occur is related to the spatial autocorrelation in abundance (Burrough 1983, Palmer 1988, Kendal 1992, Maurer 1994). For this we used the semivariance dimension (hereafter semivariance), which can be thought of as the spatial variability of a species across its geographic range. Higher values of the semivariance are related to rougher abundance textures, and hence, increased demographic fragmentation.

Another approach for measuring the roughness of the abundance texture is to examine complexity of abundance contours of the map with changes in inter-

val used to draw them. One such measure is the volume dimension (Maurer 1994). The volume dimension expresses the relative degree of fragmentation for the areas of high abundance. (Maurer 1994). For most species, areas of high abundance are those populations that are centrally located within a species geographic range (Brown 1984, Maurer and Villard 1994). Higher volume dimensions are related to higher degrees of fragmentation of central populations. We also considered the perimeter/area (P/A) ratio for each geographic range. The justification for using this measure is based on the assumption that the boundary of the geographic range represents the limit to ecological conditions for the species reach a limit beyond which viable populations cannot be maintained. The higher this ratio is, the greater the proportion of local populations that are in contact with the extreme ecological conditions for the

species. Finally, we considered the size of the geographic range itself.

Statistical analysis of variation in the abundance surface among species

The first test we conducted on the six metrics describing the geographic range was a principal component analysis (PCA). PCA allows one to determine to what extent, if any, these metrics covary. Results indicated that none of the metrics considered in this study were strongly correlated with one another. As such, each metric may provide unique insight into the geographic range structure of a particular group of species.

Next, we performed analyses of variance (proc GLM; Anon. 1988) on each of the six range metrics of the abundance surface: average abundance, geographic range size, P/A ratio, box dimension, semivariance dimension, and volume dimension. Initially, each model contained all main factors (trophic level, migratory status, and breeding habitat) and their interactions. However, due to missing cells in our full model, we used a stepwise procedure, sequentially eliminating the least significant, highest order interaction in the model until we obtained a significant interaction ($p < 0.05$) or until only main effects remained. We also used Tukey's pairwise or multiple pairwise comparisons to determine if means were different between models that approached significance (Zar 1984).

Regression analysis (proc REG; Anon. 1988) was conducted to determine the relationship between abundance and each of the measures of range fragmentation. Each species represented a single point and analyses were conducted on ecologically similar groups. Examining the relationship between range fragmentation and abundance revealed how species fill their geographic ranges and if differences occur among groups. Because we were examining ecologically similar groups, changes in range fragmentation within a group may be similar to those experienced by a species as it becomes more or less abundant.

Results

The average abundance of SDMs and NTMs did not differ in any of the trophic groups, but this was not true for PRs ($F_{4,228} = 6.23, p < 0.001$). Resident omnivores were less abundant and resident carnivores were more abundant than their migratory counterparts (Fig. 1A). The average geographic range size differed among trophic groups according to migratory strategy ($F_{6,236} = 7.26, p < 0.001$). Among carnivores, SDMs had larger ranges than NTMs or PRs, while PRs had significantly smaller ranges among insectivores and omnivores (Fig. 1B).

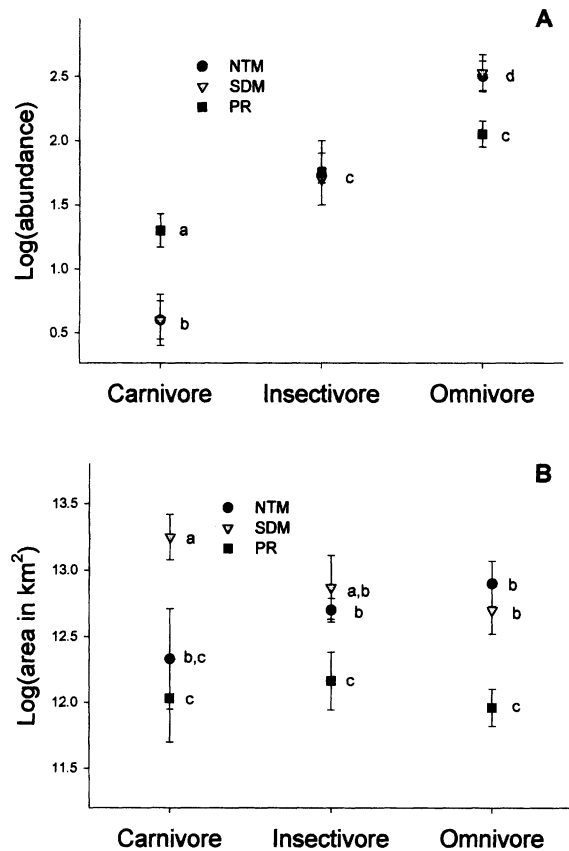


Fig. 1. The relationship between migratory strategy and trophic group for abundance and range size. Migratory include Neotropical migrants (NTMs), short-distance migrants (SDMs), and permanent residents (PRs). Different letters represent significant differences ($p < 0.05$) between means (Tukey's multiple pairwise comparison). A) Mean (± 1 SE) abundance, log-transformed, of resident carnivores was greater than other carnivores, while resident omnivores were less common than other omnivores. B) Mean (± 1 SE) geographic range size, log-transformed, of PRs was smaller than that of SDMs or NTMs.

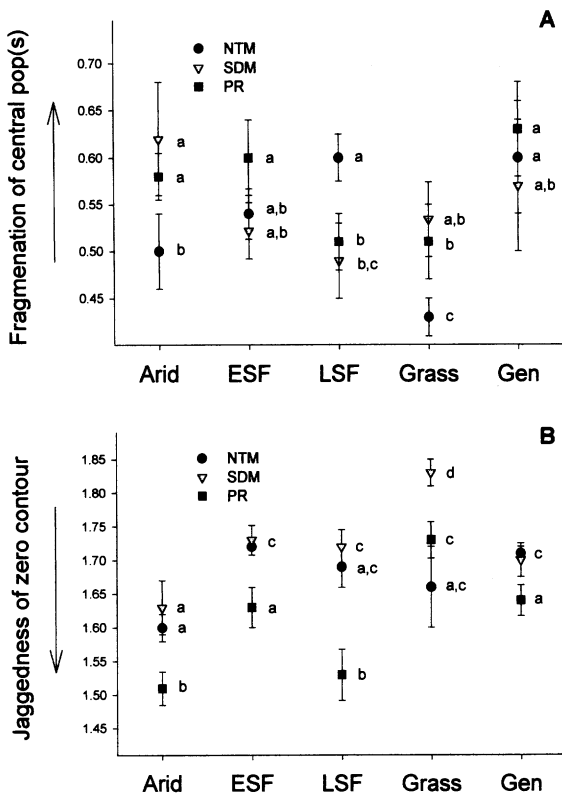


Fig. 2. The relationship between migratory strategy and breeding habitat for the volume and box dimension. Migratory groups include Neotropical migrants (NTMs), short-distance migrants (SDMs), and permanent residents (PRs). Breeding habitat groupings include desert/scrub (Arid), early-successional forest (ESF), late-successional forest (LSF), grassland (Grass), and habitat generalist (Gen). Different letters represent significant differences ($p < 0.05$) between means (Tukey's multiple pairwise comparison). A) Mean (± 1 SE) volume dimension is lower for NTMs in arid and grassland habitat, indicating greater demographic fragmentation, but not so in late-successional forests. B) PRs typically have a more jagged zero abundance contour, based upon the mean (± 1 SE) box dimension, than SDMs or NTMs.

The structure of geographic ranges varied among species according to their migratory strategy, but not consistently among habitats. Central populations of each migratory group were not similarly fragmented across habitats ($F_{8,226} = 1.76$, $p < 0.085$). Pairwise comparisons revealed that central populations of NTMs were less fragmented than central populations of SDMs or PRs in arid and grassland habitats (Fig. 2A). However, this pattern was reversed for species breeding in late-successional forests, where the central populations of NTMs had greater fragmentation than SDMs or PRs. The zero abundance contour of PRs was more jagged (indicated by the box dimension) than that of NTMs or SDMs in all habitats except grassland habitats (Fig. 2B).

The interaction between breeding habitat and trophic level also revealed some general patterns. The abun-

dance surface did not have a similar texture among the trophic groups ($F_{13,242} = 6.40$, $p > 0.001$). Omnivores typically had the smoothest abundance surface, but not in grassland habitats (Fig. 3A). There was little spatial autocorrelation between populations for most grassland species, but relatively more so for carnivores. Central populations of omnivores were fragmented less than that of insectivores in all habitats except arid habitats (Fig. 3B).

Due to the large number of significant interactions, there were only a few models in which any of the main effects were found to be significantly different. Spatial variation in abundance appeared to be relatively less for PRs than NTMs or SDMs, which were not different from another ($F_{2,225} = 5.74$, $p < 0.001$). We found that the average abundance of species breeding in late-suc-

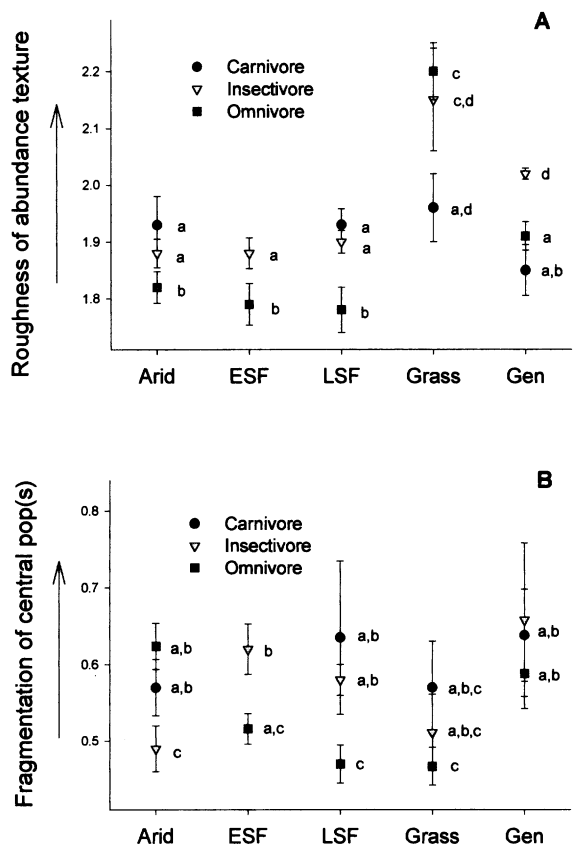


Fig. 3. The relationship between trophic group and breeding habitat for two measures of demographic fragmentation. Breeding habitat groupings include desert/scrub (Arid), early-successional forest (ESF), late-successional forest (LSF), grassland (Grass), and habitat generalist (Gen). Different letters represent significant differences ($p < 0.05$) between means (Tukey's multiple pairwise comparison). A) Mean (± 1 SE) semivariance, measuring spatial variation in abundance, is typically lower for omnivores than other trophic groups. Note the relatively rough texture of all grassland birds. B) Mean (± 1 SE) volume dimension is typically lower for omnivores, thereby indicating greater fragmentation of high abundance populations.

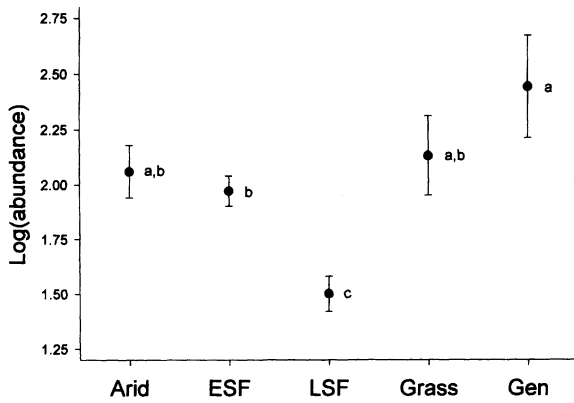


Fig. 4. Mean (± 1 SE) abundance, log-transformed, is lower for species breeding in late-successional forests (LSF) than other habitats, including desert/scrub (Arid), early-successional forest (ESF), grassland (Grass) and habitat generalists (Gen). Different letters represent significant differences ($p < 0.05$) between means (Tukey's multiple pairwise comparison).

cessional forests was substantially less than that of species in other habitats (Fig. 4). Finally, we found species breeding in arid habitats had significantly smaller geographic ranges than species utilizing other habitats. However, this may be in part due to our inability to measure range size below the U.S.–Mexico border.

Regression analyses

Regression models indicated that within NTMs, abundant species had relatively smoother abundance textures than uncommon or rare species. This was not true

for SDMs or PRs (Table 1). Similarly, central populations of abundant species of NTMs were less fragmented than rare species but not for SDMs or PRs (Table 1). For PRs, there was a trend for more abundant species to actually have more fragmentation of their central populations, although this was not significant (Table 1). There was neither a positive nor a negative trend for SDMs. While there was a positive correlation between range size and abundance in all migratory groupings, the only significant correlation was found among NTMs. Conversely, PRs were characterized by two distinct relationships. Firstly, there was a significant negative correlation between abundance and the P/A ratio for PRs, which did not hold for NTMs or SDMs. Secondly, there was a positive relationship between abundance and the box dimension, but this was only significant for PRs (Table 1).

The relationship between abundance and measures of areographic fragmentation was not consistent among trophic groups. For omnivores and insectivores, species that were more abundant had fewer gaps within or at the edge of their geographic ranges (indicated by the box dimension and P/A ratio, respectively). While this trend existed for carnivores, it is not significant (Table 2). Another interesting result suggested that while abundant omnivores and insectivores have larger geographical ranges than their less abundant counterparts, this pattern is reversed in carnivores, although not significant (Table 2).

When results of regression analysis among breeding habitats were analyzed, it found trends were similar for the five groups. Thus more abundant species do not appear to have any intrinsic differences in their geographic range structure than less abundant species, irrespective of breeding habitat.

Table 1. Relationship between the logarithm of average abundance and two measures of demographic fragmentation (semivariance and volume dimension) and two measures of areographic fragmentation (perimeter/area ratio and box dimension) for Neotropical migrants (NTMs), short-distance migrants (SDMs) and permanent residents (PRs) using least squares regression.

	Number of species	Estimated slope	Standard error	t-test for $H_0: b = 0$
Semivariance				
NTM	100	-0.05474	0.02704	-2.024*
SDM	56	-0.00165	0.02582	-0.064
PR	99	-0.01202	0.02991	-0.483
Volume dimension				
NTM	99	-0.07738	0.02043	-3.789**
SDM	56	-0.02317	0.02054	-1.128
PR	98	0.00435	0.02056	-0.212
P/A ratio				
NTM	100	-0.00693	0.00444	-1.563
SDM	56	-0.00505	0.00476	-1.061
PR	99	-0.01137	0.00454	-2.508*
Box dimension				
NTM	100	0.02043	0.01224	1.449
SDM	56	0.01778	0.01428	1.248
PR	98	0.04770	0.01596	2.989**

* $|T| < 0.05$.

** $|T| < 0.01$.

Table 2. Relationship between the logarithm of average abundance and three measures of range fragmentation for three trophic groups using least squares regression. Note differences in the abundance of carnivores were not related to either fractal measure.

	Number of species	Estimated slope	Standard error	t-test for $H_0: b = 0$
Box dimension				
Carnivore	25	0.00796	0.03171	0.251
Insectivore	103	0.04619	0.01643	2.812**
Omnivore	127	0.04781	0.01352	0.537**
P/A ratio				
Carnivore	25	-0.00498	0.00586	-0.849
Insectivore	103	-0.01303	0.00449	-2.930**
Omnivore	127	-0.00748	0.00451	-1.959*
Range size				
Carnivore	25	-0.23634	0.23635	-1.000
Insectivore	103	0.34986	0.14291	2.448**
Omnivore	127	0.39325	0.11988	3.280**

* $|T| < 0.05$.

** $|T| < 0.01$.

Discussion

The general objective of this study was to examine the relationships between the geographic range fragmentation and several ecological characteristics of North American landbirds. The ecological needs of a species and the geographic distribution of these needs would be expected to result in a specific geographic pattern of population dynamics for each species or ecologically related group of species (Maurer and Brown 1989). Our results suggest that fundamental differences exist among species, in both how they are distributed across space and how they fill that geographic space.

One of the most glaring contradictions among migrant groups is how abundant species are distributed across their ranges compared to species with lower abundances. If these interspecific abundance patterns hold for intraspecific changes in abundance, then what we expect to see are different processes through which individuals disperse themselves through the species' geographic range. For example, despite changes in abundance the periphery of the abundance surface does not differ between abundant and rare NTMs. Instead, increased abundance results in continued smoothing of the abundance surface at the center, where populations of high abundance typically occur. The opposite pattern occurs with PRs, as increased abundance corresponds to a smoothing of the abundance surface at the periphery and not at the center. Another way to view these results is that NTMs are more prone to demographic fragmentation or local population extinctions, while PRs are more sensitive to areographic fragmentation that results from local environmental variation.

We also found that trophic level also contributed to the variation in geographic range structure. Not surprisingly, average abundance decreased with increasing energetic requirements. Average abundances were quite similar within trophic groups except for resident carnivores, which were much more numerous than SDM or

NTM carnivores. This may be attributable to some of the members of this group, e.g. black vulture *Coragyps altratus* and Mississippi kite *Ictinia mississippiensis*, which had small geographic ranges but were relatively abundant.

The differing trophic groups also appear to have distinctive range-filling characteristics. For example, abundant species of omnivores and insectivores had a smoother range boundary and had fewer distributional gaps compared to uncommon omnivores and insectivores. Conversely, the abundance surface at the periphery of the range did not differ between abundant and rare carnivores. Gaps within the range of a species may reflect the distribution of one or more limiting resources. Lawton and Woodroffe (1991) concluded that gaps in the distribution of the water vole *Arvicola terrestris* were due to habitat unsuitability, isolation, or high predation rates. For avian carnivores, gaps may be due to a lack of suitable nesting sites or to areas where prey density is too low to allow successful reproduction (Newton 1979).

Another interesting pattern that emerged was the negative relationship, although not significant, between geographic range size and average abundance for carnivores (Table 2). The trend was significant and positive among insectivores and omnivores, which is typical of most taxa (Gaston and Lawton 1990). This pattern suggests there may be ecological constraints imposed upon carnivore abundance that operate independently of geographic range size that do not operate for species occupying lower trophic levels. Virkkala (1993) suggested that the success, defined as widespread and abundant, of bird species in Finland was attributable to a more varied diet. Our results partly support Virkkala's conclusion, with omnivores having a higher average abundance than carnivores or insectivores, but no difference in range size.

For most species, there is a positive relationship between demographic or areographic parameters. For example, the abundance texture of omnivores was typi-

cally smooth and with low levels of fragmentation among populations of high abundance (Fig. 3A, B). This was not the case for species breeding in grassland habitats. Grassland species had relatively cohesive populations of high abundance (Fig. 3B), but extremely dramatic population changes across their respective ranges (Fig. 3A). Demographic fragmentation is strongly correlated with the long-term persistence of populations. Central populations may be of particular importance as they tend to be characterized by greater densities and less relative variability (Curnutt et al. 1996) and as such, may have a lower likelihood of going extinct (Pimm 1991, 1993). Consequently, all else being equal, central populations would be expected to have a greater influence on the global persistence of species. However, in a recent study of species that have seen dramatic range collapse, many species (68%) continue to occupy a greater than expected portion of their historical distribution in the periphery and for some species (37%), the periphery holds all remnant populations (Channell and Lomolimo 2000). It is important to note that this pattern of range collapse was largely attributable to anthropogenic stressors, thereby distorting the historical dynamics of the abundance texture.

Although we predicted that habitat generalists would be more abundant than species that have a preference for a single habitat, the considerably lower average abundance of species breeding in late-successional forests was somewhat surprising. It is unclear whether the lower density of species in late-successional forests is the result of recent decline (Whitcomb et al. 1981, Askins et al. 1990, Hagan and Johnston 1992) or if this group has always existed at lower numbers. It is also possible that the lower densities of individual species in late-successional forests may be a result of the greater species richness found there.

Although our data indicated that the ecological factors considered in this study all contributed to the observed variability in the abundance surface, there was also residual variation not explained by these effects. Clearly other factors may potentially affect the abundance surface or range properties of a species. Chief among these factors are the phylogenetic relationships among species. Species that are more closely related would tend to have similar ecological requirements (Brooks and McLennan 1991), and hence, would be expected to have more similar abundance surfaces than distantly related species. There are no comprehensive phylogenies of birds that can be used to examine the importance, and the subsequent magnitude, of the phylogenetic component to variation of the abundance surface. Differences in the relationship between demographic fragmentation and abundance have been documented among four families of passerines, but it was suggested that migratory strategy explained a greater proportion of the variation found (Maurer and Heywood 1993).

It is important that we understand patterns of geographic and demographic fragmentation and the processes that generate them if we are to perform large-scale conservation planning on a sound basis (Pimm 1991, Maurer 1994). Most of the processes leading to the global extinction of a species do not pertain to the viability of a single population. Consequently, it is crucial that we study how populations vary spatially and temporally across their geographic range. Understanding the variation across the abundance surface may help us discover which species may be more susceptible to large-scale habitat alteration and what makes them so (Lawton 1993, Maurer and Heywood 1993, Maurer 1994, Brown 1995, Curnutt et al. 1996). We suggest that future conservation plans for North American birds include information regarding the abundance surface of a species.

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References

- Anon. 1988. SAS/STAT user's guide, ver. 6 (3rd ed.). – Cary, N.C.
- Askins, R. A., Lynch, J. F. and Greenberg, R. S. 1990. Population declines in migratory birds in eastern North America. – *Curr. Ornithol.* 7: 1–57.
- Boulinier, T. et al. 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. – *Proc. Natl. Acad. Sci.* 95: 7497–7501.
- Brooks, D. R. and McLennan, D. A. 1991. Phylogeny, ecology, and behavior. – Univ. of Chicago Press.
- Brown, J. H. 1984. On the relationship between distribution and abundance. – *Am. Nat.* 124: 255–279.
- Brown, J. H. 1995. Macroecology. – Univ. of Chicago Press.
- Brown, J. H. and Maurer, B. A. 1989. Macroecology: the division of food and space among species on continents. – *Science* 243: 1145–1150.
- Brown, J. H., Melhmen, D. W. and Stevens, G. C. 1995. Spatial variation in abundance. – *Ecology* 76: 2028–2043.
- Burrough, P. A. 1983. Multiscale sources of spatial variation in soil. I. The application of fractal concepts to nested levels of soil variation. – *J. Soil Sci.* 34: 577–597.
- Burrough, P. A. 1986. Principles of geographical information systems for land resources assessment. – Oxford Univ. Press.
- Bystrak, D. 1981. The North American breeding bird survey. – *Stud. Avian Biol.* 6: 34–41.
- Channell, R. and Lomolimo, M. V. 2000. Dynamic biogeography and conservation of endangered species. – *Nature* 403: 84–86.
- Curnutt, J. L., Pimm, S. L. and Maurer, B. A. 1996. Population variability of sparrows in space and time. – *Oikos* 76: 131–144.
- Ehrlich, P. R., Dobkin, D. S. and Wheye, D. 1988. The birder's handbook: a field guide to the natural history of North American birds. – Simon and Schuster, New York.
- Flather, C. H. and Sauer, J. R. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. – *Ecology* 77: 28–35.

- Gaston, K. J. 1994. Rarity. – Chapman and Hall.
- Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms, and implications. – *Trends Ecol. Evol.* 11: 197–201.
- Gaston, K. J. and Lawton, J. H. 1990. Effects of scale and habitat on the relationship between regional distribution and local abundance. – *Oikos* 58: 329–335.
- Gaston, K. J. and Blackburn, T. M. 1996. Conservation implications of geographic range size-body size relationships. – *Conserv. Biol.* 10: 638–646.
- Gaston, K. J., Blackburn, T. M. and Gregory, R. D. 1997a. Interspecific abundance-range size relationships: range position and phylogeny. – *Ecography* 20: 390–399.
- Gaston, K. J., Blackburn, T. M. and Lawton, J. H. 1997b. Interspecific abundance-range size relationships: an appraisal of mechanisms. – *J. Anim. Ecol.* 66: 579–601.
- Gaston, K. J., Blackburn, T. M. and Gregory, R. D. 1998. Interspecific abundance-range size relationships of British breeding birds. – *Ecography* 21: 149–158.
- Gautestad, A. O. and Myrnerud, I. 1994. Fractal analysis of population ranges: methodological problems and challenges. – *Oikos* 69: 154–157.
- Gauthreaux, S. A. Jr 1992. A preliminary list of migrants for Partners in Flight migratory bird conservation program. – *Partners in Flight* 2: 30.
- Grinnell, J. 1922. The role of the “accidental”. – *Auk* 39: 373–380.
- Hagan, J. H. and Johnston, D. W. (eds) 1992. Ecology and conservation of Neotropical migrant landbirds. – Smithsonian Inst. Press, Washington, DC.
- Kendal, W. S. 1992. Fractal scaling in the geographic distribution of populations. – *Ecol. Model.* 64: 65–69.
- Lawton, J. H. III 1993. Range, population abundance, and conservation. – *Trends Ecol. Evol.* 8: 409–413.
- Lawton, J. H. III and Woodroffe, G. L. 1991. Why are there gaps in a species’ range? – *J. Animal Ecol.* 60: 79–91.
- Lawton, J. H. III et al. 1994. Animal distributions: patterns and processes. – In: Edwards, P. J., May, R. M. and Webb, N. R. (eds), *Large-scale ecology and conservation biology*. Blackwell, pp. 41–58.
- Maurer, B. A. 1994. Geographical population analysis. – Blackwell.
- Maurer, B. A. 1999. Untangling ecological complexity. – Univ. of Chicago Press.
- Maurer, B. A. and Brown, J. H. 1989. Distributional consequences of spatial variation in local demographic processes. – *Ann. Zool. Fenn.* 26: 121–131.
- Maurer, B. A. and Heywood, S. G. 1993. Geographic range fragmentation and abundance of neotropical migratory birds. – *Conserv. Biol.* 7: 501–509.
- Maurer, B. A. and Villard, M.-A. 1994. Geographic variation in abundance of North American birds. – *Research and Exploration* 10: 306–317.
- Maurer, B. A. and Nott, M. P. 1998. Geographic range fragmentation and the evolution of biological diversity. – In: McKinney, M. L. (ed.), *Biodiversity dynamics: turnover of populations, species, higher taxa, and communities*. Columbia Univ. Press.
- McDonald, K. A. and Brown, J. H. 1992. Using montane mammals to model extinctions due to global change. – *Conserv. Biol.* 6: 409–415.
- Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. – In: Turner, M. G. and Gardner, R. H. (eds), *Quantitative methods in landscape ecology – the analysis and interpretation of landscape heterogeneity*. Springer, pp. 199–235.
- Milne, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. – *Am. Nat.* 139: 32–57.
- Newton, I. 1979. Population ecology of raptors. – Buteo Books, Vermillion, SD.
- Palmer, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. – *Vegetatio* 75: 91–102.
- Peitgen, H.-O., Jurgens, H. and Saupe, D. 1992. Chaos and fractals. – Springer.
- Pimm, S. L. 1991. The balance of nature? – Univ. of Chicago Press.
- Pimm, S. L. 1993. Life on the intermittent edge. – *Trends Ecol. Evol.* 8: 45–46.
- Price, J., Droege, S. and Price, A. 1995. The summer atlas of North American birds. – Academic Press.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. – *Am. Nat.* 132: 652–661.
- Robbins, C. S., Bystrak, D. and Geissler, P. H. 1986. The Breeding Bird Survey: its first fifteen years. – Resour. Publ. 157, US Dept Interior, Fish Wildl. Serv., Washington, D.C.
- Rossi, R. E. et al. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. – *Ecol. Monogr.* 62: 277–314.
- Sauer, J. R. et al. 1977. The North American Breeding Bird Survey Results and analysis. Ver. 96.3. – Patuxent Wildl. Res. Cent. Laurel, Maryland.
- Stone, L., Dayan, T. and Simberloff, D. 1996. Community-wide assembly patterns unmasked: the importance of species’ differing geographical ranges. – *Am. Nat.* 148: 997–1015.
- Sugihara, G. and May, R. M. 1990. Applications of fractals in ecology. – *Trends Ecol. Evol.* 5: 79–86.
- Villard, M.-A. and Maurer, B. A. 1996. Geostatistics as a tool for examining hypothesized declines in migratory songbirds. – *Ecology* 77: 59–68.
- Virkkala, R. 1993. Ranges of northern forest passerines: a fractal analysis. – *Oikos* 67: 218–226.
- Whitcomb, R. F. et al. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. – In: Burgress, R. L. and Sharpe, D. M. (eds), *Forest island dynamics in man-dominated landscapes*. Springer, pp. 125–205.
- Williamson, M. H. and Lawton, J. H. 1991. Fractal geometry of habitats. – In: Bell, S. S., McCoy, E. D. and Mushinsky, H. R. (eds), *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, pp. 69–86.
- Willis, J. C. 1922. Age and area. – Cambridge Univ. Press.
- Zar, J. H. 1984. Biostatistical analysis. – Prentice-Hall.