Interactive effects of land use and other factors on regional bird distributions

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Abstract

Aim We assessed the independent and interactive effects of land use and other factors on regional distributions of lake shore bird assemblages.

Location Analyses were restricted to lakes of the northeastern United States (New England, New York, New Jersey).

Methods Lake shore bird and habitat data were collected from a regional sample of 186 lakes between 1991 and 1995. Local and regional gradients in environmental attributes of the lakes and their watersheds, and in bird species composition, were characterized using detrended correspondence analysis. Bird assemblages were also characterized with respect to species diversity, total bird abundance, and absolute and proportional abundance for neotropical migrants, omnivores and tree foragers. The assemblage measures were compared with the environmental gradients and with the environmental variables from which those gradients were derived using correlations, linear regression and bivariate plots.

Results Anthropogenic variables (e.g. human density) and nonanthropogenic variables (e.g. climate, forest composition, lake productivity) were highly confounded regionally, reflecting the influence of climate and geomorphology on land use and, in turn, the influence of land use on the environment. Moving south along the regional gradient to watersheds with more intensive land use, changes in bird assemblage structure were consistent with anthropogenic effects on the avifauna attributable to forest fragmentation: total bird abundance increased, fragmentation-tolerant species were encountered more frequently, the proportional abundance of omnivores increased and the proportional abundances of tree foragers and neotropical migrants decreased. Bird diversity, as assayed using rarefaction, peaked at an intermediate position along the regional gradient, as did the absolute abundances of tree foragers and migrants.

Main conclusions We propose that some community attributes peaked at an intermediate position along the regional gradient as a result of the interactive effects of land use and other factors on this region's avifauna, with broad-scale anthropogenic factors constraining assemblages on the urbanized lakes, and climate or other nonanthropogenic factors constraining assemblages on the pristine lakes. Anthropogenic and nonanthropogenic factors of similar scale and magnitude thus acted in concert to shape regional bird distributions.

Keywords
Avian abundance, biodiversity, forest fragmentation, lake, land use, riparian habitat, urbanization.

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INTRODUCTION

Many populations of neotropical migrants appear to be declining in portions of the eastern United States (US) (Robbins *et al.*, 1989b; Askins, 1995). Contributing factors may include the loss of wintering and migratory stopover habitat, but recent attention has focused on the negative effects of forest fragmentation on breeding success (Robinson *et al.*, 1995). Replacement of forests by agriculture and residential–urban development reduces, subdivides and isolates breeding habitat required by forest interior birds. Species requiring contiguous forest tracts above some minimum size therefore tend to disappear from highly fragmented landscapes (Whitcomb *et al.*, 1981; Robbins *et al.*, 1989a). Even if forest tracts of sufficient size are present in the landscape, their numbers may be too small to maintain species metapopulations over the long-term to the extent that habitat isolation impedes dispersal (Matthysen & Currie, 1996).

Expansion and intensification of land use also creates habitat for non-native species and native omnivores and granivores capable of exploiting resources associated with forest edges and human-built environments (Mills *et al.*, 1989; Blair, 1996). The favourable influence that forest fragmentation has on human-tolerant species exacerbates the negative effects on forest interior specialists (Ambuel & Temple, 1983). Many neotropical migrants nest near the ground, have relatively low reproductive potential, or have limited defences with which to counter brood parasites (Whitcomb *et al.*, 1981). This may render migrants, as a group, more vulnerable than residents to increased rates of nest predation and brood parasitism (Whitcomb *et al.*, 1981; Askins, 1995) which often accompany forest fragmentation (Andren, 1992; Robinson *et al.*, 1995).

Landscape-level studies have been crucial in identifying the mechanisms through which forest fragmentation restructures the avifauna and in documenting forest fragmentation effects over small spatial extents (e.g. Whitcomb *et al.*, 1981; Lynch & Whigham, 1984; Askins *et al.*, 1987). However, these studies do not address the cumulative effects of forest fragmentation on regional bird distributions. Far less is known about the extent to which forest fragmentation restructures the avifauna regionally (Flather & Sauer, 1996). This is because it is difficult to extrapolate regional patterns from the results of independent small-scale studies unless those studies can be shown to be a sample representative of the region (Brown & Maurer, 1989).

Landscape-level forest fragmentation effects may be mediated, to a large extent, by the regional availability of forest (Robinson *et al.*, 1995; Donovan *et al.*, 1997; Rosenberg *et al.*, 1999). Moreover, populations situated in highly fragmented landscapes, with insufficient reproduction to be self-sustaining (sink populations; Pulliam, 1988), may be maintained by a distant source population (Trine, 1998) owing to the high vagility of bird species. A regional perspective is therefore called for to compliment and provide a context for landscape-level studies (Flather & Sauer, 1996). To this end, we analysed lake shore bird assemblage data collected from 186 lakes in New England, New York and New Jersey in order to assess the cumulative effects of land use on the avifauna of the northeastern US. The broad extent of this study required that we give explicit consideration to anthropogenic and non-anthropogenic factors, and their interactive effects on the avifauna, because climate and geomorphology influence not only bird distributions, but also the potentials and capacities of the land for different human uses (Omernik, 1987).

METHODS

Lakes analysed and field methods

Data were collected between 1991 and 1995 from 186 lakes in New England, New York and New Jersey by the US Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP; Paulsen & Linthurst, 1994). The lakes analysed were a representative sample of all lakes in the region, permitting results of this study to be extrapolated to all lake shore bird assemblages of the northeastern US with known statistical confidence (Larsen *et al.*, 1994). We analysed bird and habitat data collected during a single visit to each lake.

Surveys were conducted between 0.5 h before sunrise and 4 h after sunrise on days with minimal wind and precipitation between late May and early July (Baker *et al.*, 1997). Bird and habitat data were collected by canoe every 200 m along a transect 10 m from and parallel to the lake shore. All birds seen or heard within a 100-m radius during a 5-min period were recorded to species at each sampling location using the fixed radius point count method (Hutto *et al.*, 1986). Habitats present in the 100-m radius plots were also recorded. For lakes with perimeters >4.8 km, 24 point counts were established based on the relative occurrence of habitats along the lake shore.

Analytical approach

We analysed four aspects of assemblage structure: species composition, functional group composition, species diversity and total bird abundance. Species compositional measures were analysed to resolve site-to-site changes in species co-occurrence. Functional group measures were analysed to identify factors constraining the use of particular foraging, dietary and migratory strategies by birds. Species diversity and total bird abundance measures were analysed to resolve habitat characteristics influencing multiple species populations regardless of species identity and functional group designation. We compared the assemblage measures with the environmental variables to gain insight into the factors structuring this region's avifauna.

Assemblage measures

Species composition
The site-by-species matrix was submitted to detrended correspondence analysis (DCA) in PC-ORD (McCune & Medford, 1995) to derive site and species scores representing gradients in species composition (ter Braak, 1987). DCA assigns scores

to sites and species such that similarly scored sites are more similar in species composition than sites located further apart in the DCA coordinate space, and similarly scored species are more likely to co-occur at sites. The first DCA axis captures the most variation possible in the community matrix, with subsequent axes then partitioning successively smaller portions of the remaining variability. The presence of many zeros in a data matrix can adversely affect ordinations (Legendre & Legendre, 1983). Therefore, species present on <10% of the lakes were dropped prior to DCA (92 species of 171 total), leaving a matrix of 186 lakes and 79 species (Appendix) for analysis. These 79 species comprised 95% of all individuals surveyed.

Species differ in their detectability when surveyed using the fixed-radius point-count method (Hutto *et al.*, 1986). To ensure that our results were robust to this sampling artefact, we compared DCA ordinations derived from the original data matrix, which contained species abundances, with ordinations derived from a presence–absence matrix (abundance of 0 or 1). Scores on the first DCA axis of the original data correlated highly with those of the presence–absence matrix for both sites and species ($r > 0.96$), indicating that our results are robust to differences in species detectability.

Functional groups
Each of the 79 species was classified in three ways: to a functional group defined by its foraging technique, to one defined by its dietary preference and to one defined by its migratory status (Appendix). For each lake's assemblage we examined the absolute abundance (individuals count^{-1}) and proportional abundance of tree foragers (bark gleaners, foliage gleaners and hover-and-gleaners combined; Ehrlich *et al.*, 1988), omnivores (Ehrlich *et al.*, 1988) and migrants (Finch, 1991).

Species diversity
Species richness was significantly correlated with the number of individuals counted at the lake ($r = 0.83$, $P < 0.0001$), indicating that richness variation was partly a function of sample size (Allen *et al.*, 1999a). To characterize diversity while controlling for differences in individual counts among samples, we used rarefaction (Hurlbert, 1971) to determine the number of species that would be encountered in random draws (without replacement) of 30 individuals from the bird samples. Rarefaction measures were computed using data for all bird species, not just the 79 listed in the Appendix. The 30 individual cut-off was chosen as a compromise between the number of lakes for which rarefaction measures could be computed and the number of individuals used to estimate diversity. While arbitrary, this rarefaction measure was highly correlated with another determined using quadruple the numbers of individuals ($r = 0.93$). For the 10 lakes with samples <30 individuals, a 10 individual rarefaction measure was extrapolated up to 30 individuals using a locally weighted regression model (Cleveland & Devlin, 1988) fitted to data for the 176 other lakes (model d.f. = 3.6, $r = 0.98$, $P < 0.0001$).

Abundance
Individual totals were summed across the 79 species and then divided by the number of point counts conducted at the lake (individuals count^{-1}).

Environmental measures
We selected 35 environmental variables for analysis (Table 1) based on results of previous EMAP investigations (Allen *et al.*, 1999a,b; Dixit *et al.*, 1999; Allen & O'Connor 2000). These variables characterized: (i) the lake (morphology, water quality, riparian-littoral zone structure), (ii) its watershed and (iii) the surrounding landscape. Data on lake water quality and riparian–littoral zone structure were collected by EMAP (Baker *et al.*, 1997). The riparian habitat data were used to determine the proportions of the 100-m radius sample plots with various habitats present. The land use-land cover (LULC) classification of Anderson *et al.* (1976) was used to determine the proportions of the watersheds in various land uses. Human and road densities within each watershed were estimated using the 1990 US Census data and the TIGER file database, respectively (US Bureau of Census, 1990). LULC land use, road density, human population density and point-source pollution density were determined for each watershed by EMAP. Landscape compositional measures derived from AVHRR satellite imagery and the Digital Chart of the World, and a seasonal climatic index (seasonality, difference between July and January mean temperature) derived from the historical climate database, were spatially registered to a 640-km^2 grid of hexagons whose centres were 27 km apart by O'Connor *et al.* (1996). Values for climatic and landscape compositional measures were assigned as attributes to lakes present in each hexagon. The hexagon data classified lands somewhat differently than LULC and at a coarser resolution. Environmental variables were transformed as necessary to normalize their distributions prior to analysis.

We performed DCA on the environmental data to characterize environmental gradients for this region's lakes and watersheds, and to quantify covariation between land use and other factors. The 35 environmental variables were standardized to equal mean and variance prior to DCA so that all variables would be given equal weight in the analysis. DCA site scores were correlated with the 35 environmental variables from which the gradients were derived (Table 1). These correlations cannot be assigned statistical significance, but are useful for interpretation because the square of the correlation coefficient is equal to the proportion of each variable's variance shared with the DCA axis. Results of environmental DCA (presented below) were similar to those of Allen *et al.* (1999b), who derived environmental gradients from these same data using principal components analysis (PCA). DCA was used here to correct for gradient distortions (the 'arch' effect; ter Braak, 1987) introduced when performing PCA on data with long gradients. The assemblage measures were compared with the DCA environmental gradients and with the 35 environmental variables from which those gradients were derived using Pearson product–moment correlations, Spearman rank correlations, linear regression and bivariate plots.

Table 1 Correlation (r) of site scores on the first two environmental DCA axes (ENV1, ENV2) with the 35 variables from which they were derived, and correlations of the first two bird DCA axes (DCA1, DCA2) with those same variables. Land use measures are underlined. Environmental variables are successively grouped and sorted on the axes where their influence appears most prominent (denoted in bold type), but the cut-off used for assessing influence ($|r| \geq 0.40$) is arbitrary.

Variable		Environmental gradients		Bird gradients	
Feature	Attribute	ENV1	ENV2	DCA1	DCA2
Watershed	Human density†	**−0.92**	0.10	**−0.86**	−0.11
Water chemistry	Chloride‡	**−0.86**	0.19	**−0.81**	−0.10
Landscape	Seasonality§	**0.80**	0.05	**0.76**	0.11
Landscape	Mixed-conifer§	**0.79**	0.06	**0.69**	0.08
Watershed	Point-source pollution††	**−0.72**	0.05	**−0.61**	−0.07
Watershed	Urban¶	**−0.71**	0.10	**−0.64**	−0.07
Landscape	Urban§	**−0.69**	−0.01	**−0.60**	−0.09
Watershed	Road density‡‡	**−0.69**	0.11	**−0.68**	−0.13
Landscape	Elevation	**0.61**	0.08	**0.52**	−0.09
Landscape	Deciduous§	**−0.59**	0.12	**−0.54**	−0.17
Shoreline	Conifer‡	**0.59**	−0.30	**0.59**	0.20
Water chemistry	Sulphate‡	**−0.53**	0.34	**−0.51**	−0.06
Water chemistry	Total phosphorus‡	**−0.49**	−0.59	−0.39	0.27
Shoreline	Deciduous‡	**−0.48**	0.06	−0.39	0.08
Shoreline	Residential‡	**−0.47**	0.28	**−0.56**	−0.22
Water chemistry	Calcium‡	**−0.45**	0.23	**−0.40**	0.21
Watershed	Agriculture¶	**−0.44**	0.05	−0.39	0.22
Water chemistry	Turbidity‡	**−0.44**	−0.43	−0.39	0.28
Water chemistry	Aluminium‡	**0.42**	−0.43	0.37	0.13
Shoreline	Mixed‡	**0.41**	0.22	0.32	−0.26
Water chemistry	Chlorophyll a‡	**−0.40**	−0.54	−0.32	0.19
Lake morphology	Depth‡	0.22	**0.84**	0.12	**−0.43**
Water chemistry	Dissolved organic carbon‡	0.19	**−0.71**	0.21	**0.45**
Water chemistry	Min. water temp.‡	−0.28	**−0.69**	−0.22	0.30
Water chemistry	Total nitrogen‡	−0.37	**−0.60**	−0.31	0.36
Shoreline	Wetland‡	0.08	**−0.59**	0.08	**0.51**
Littoral zone	Substrate size‡	0.20	**0.57**	0.16	−0.39
Water chemistry	pH‡	−0.24	**0.47**	−0.18	0.04
Lake morphology	Area	0.37	**0.43**	0.26	−0.21
Littoral zone	Macrophyte cover‡	−0.08	−0.30	−0.04	0.24
Watershed	Wetland¶	0.30	−0.28	0.19	0.12
Water chemistry	Min. dissolved oxygen‡	0.23	−0.23	0.23	0.01
Landscape	Agriculture§	−0.37	−0.21	−0.31	0.09
Shoreline	Agriculture‡	−0.38	−0.07	−0.32	0.20
Water chemistry	Silica‡	0.00	0.03	−0.04	0.16
% Variance in data accounted for by axis		24	14	13	5

Data source: † US Bureau of Census (1990), ‡ Baker *et al.* (1997), § O'Connor *et al.* (1996), ¶ Anderson *et al.* (1976), †† Abramovitz *et al.* (1990), ‡‡ TIGER file database.

RESULTS

Environmental gradients

The first two environmental DCA axes captured 38% of the variance (Table 1), indicating considerable covariation among the 35 environmental variables. The first DCA axis of the environmental data (ENV1) distinguished between relatively unproductive lakes at high elevations in landscapes with few people, extensive conifer forests and severe climate to the north, and more productive lakes at lower elevations in landscapes with greater human densities, deciduous forests and milder climates to the south (Fig. 1a). All nine land-use measures were negatively correlated with ENV1 ($r \leq -0.37$, Table 1). Human

density in the watershed and chloride showed the strongest correlations ($r = -0.92$ and −0.86, respectively). Variables whose values increase with lake trophic state (phosphorus, turbidity, chlorophyll a, nitrogen) were also negatively correlated with ENV1 ($-0.37 \geq r \geq -0.49$), as were the two deciduous forest measures ($r \leq -0.48$) and calcium ($r = -0.45$). This contrasted with positive correlations for other nonanthropogenic measures (shoreline mixed and coniferous forest, landscape mixed-coniferous forest, seasonality, elevation; $r \geq 0.41$).

The second DCA axis of the environmental data (ENV2) largely reflected lake morphology and related factors judging from its positive correlations with lake depth ($r = 0.84$) and area ($r = 0.43$), and its negative correlation with minimum temperature ($r = -0.69$; Table 1), i.e. smaller, shallower lakes
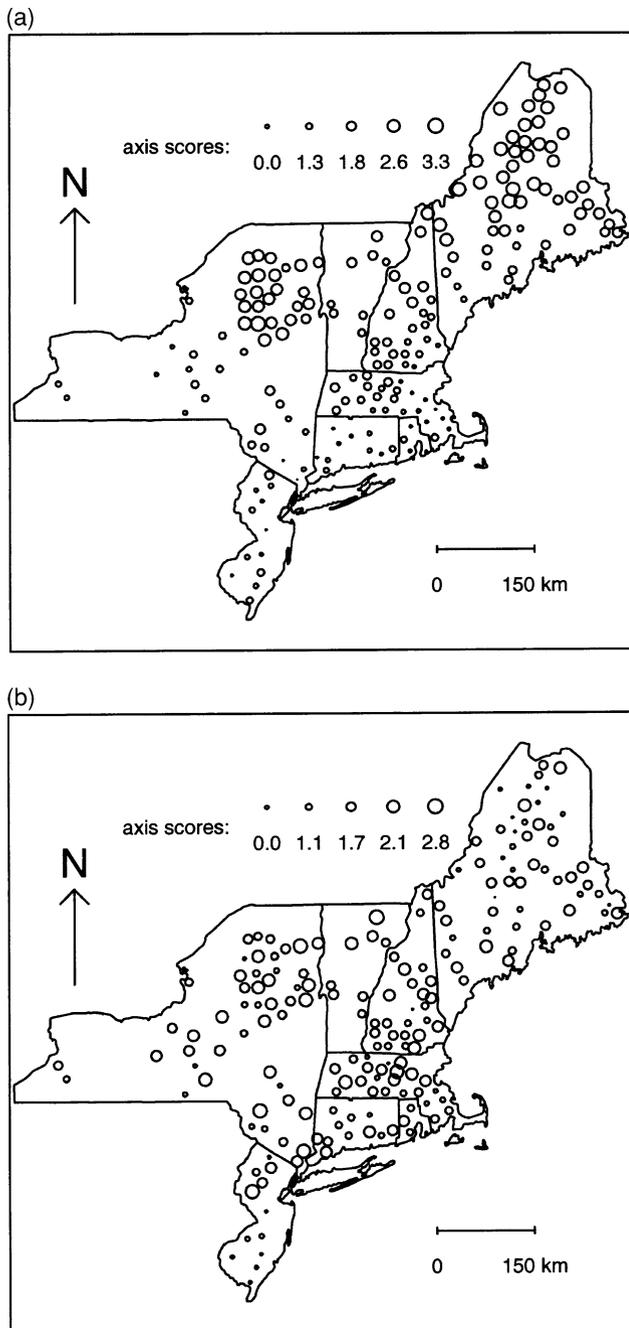
(a)

(b)

Figure 1 Spatial distribution of DCA site scores for the first (a) and second (b) axes derived from 35 environmental variables (Table 1). Circle size increases continuously with the magnitude of the score.

Figure 2 Relationship between lake and species scores for bird DCA1 (a) and DCA2 (b). Means (notch centres), standard errors (notch widths), interquartile ranges (boxes) and 95% confidence intervals (whiskers) of species scores are given for species occurring at lakes grouped on the basis of site scores. Box width is proportional to the number of lakes in the group.

are generally warmer. Correlations of ENV2 with the lake productivity indicators (phosphorus, turbidity, chlorophyll a, nitrogen; $r \leq -0.43$), lake shore wetland ($r = -0.59$), dissolved organic carbon ($r = -0.71$) and substrate size ($r = 0.57$) were also consistent with an influence of lake morphology because shallower lakes tend to have more extensive littoral zones, higher productivity, higher concentrations of dissolved organic
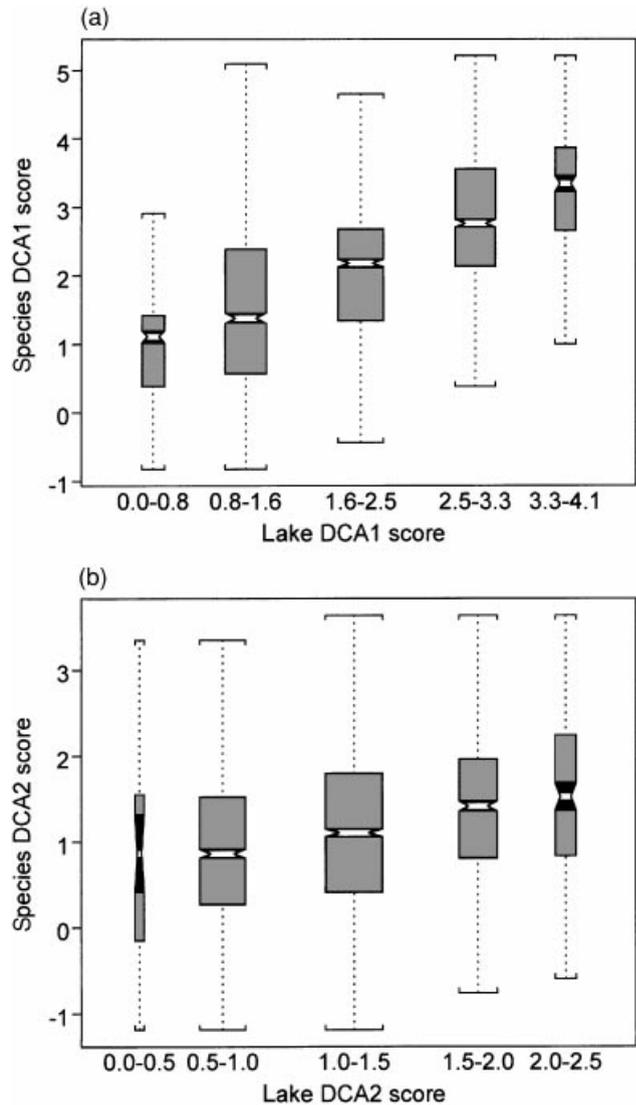
carbon and finer littoral sediment particle sizes. pH tended to increase ($r = 0.47$) and aluminium tended to decrease ($r = -0.43$) with increasing lake depth and decreasing productivity on this gradient. Scores for ENV2 (Fig. 1b) varied at a more local scale than those for ENV1 (Fig. 1a).

Species composition

DCA assigned scores to species to correspond with the scores of lakes where they occurred as illustrated by the fact that lakes with higher site scores had, on average, higher scoring species present (Fig. 2). There was, however, considerable

Figure 3 Scores of the 79 species on the first two bird DCA axes. Some species have been moved slightly to minimize overlap. Refer to the Appendix for species codes.

overlap in the 95% confidence intervals (whiskers) of species scores for disparately scored lakes. Overlap was greater for bird DCA2 than DCA1, reflecting the fact that bird DCA2 accounted for less variation in the community matrix (5%) than DCA1 (13%).

Bird DCA1 lake scores showed a stronger correlation with ENV1 ($r = 0.90$, $P < 0.0001$) than with ENV2 ($r = -0.07$, $P = 0.29$) or with the 35 environmental variables from which the two environmental gradients were derived (Table 1). Bird DCA1 thus represented an integrated response of the avifauna to multiple environmental attributes. Lake and species scores on bird DCA1 increased moving north along this region's dominant environmental gradient (ENV1) to less productive lakes situated in higher elevation landscapes with more severe climates, fewer people, and more extensive conifer relative to deciduous forest (Table 1, Fig. 1a).

A multiple linear regression analysis showed that characteristics of individual lakes and watersheds made little independent contribution to the dominant gradient in bird composition: addition of shoreline residential development to the one-term regression model predicting bird DCA1 lake scores using ENV1 increased the total explained variance by <3%. Addition of any other variable from Table 1 to the one-term regression model increased the total explained variance by even less. This region's dominant gradient in bird

composition was thus most strongly associated with regionally confounded anthropogenic and nonanthropogenic variables (ENV1), although watersheds with relatively high levels of residential development locally tended to have somewhat lower bird DCA1 scores.

As expected given the relationship between lake and species scores (Fig. 2), species with lower scores on bird DCA1 tended to be more tolerant of humans and to have more southern ranges (Fig. 3). Among the species with the lowest scores were four species non-native to the Northeast (European starling, house sparrow, house finch, house wren) that often occur in suburban and urban areas (Peterson, 1980; Whitcomb *et al.*, 1981; DeGraaf & Rudis, 1986; Ehrlich *et al.*, 1988). Other species with low scores on this axis occupy southern forests (tufted titmouse), forest edges and residential areas (northern cardinal, northern oriole, gray catbird, mourning dove, rufous-sided towhee, common grackle) and human-altered wetlands (Canada goose, mallard). Species with intermediate scores were more varied in their habitat requirements and included deciduous and mixed forest interior specialists (American redstart, red-eyed vireo, ovenbird, scarlet tanager, black-and-white warbler), species that use forests and forested residential areas (brown creeper, northern flicker, black-capped chickadee, cedar waxwing, hairy woodpecker, pine warbler, great-crested flycatcher, eastern wood-pewee, eastern phoebe),

and ubiquitous species (American crow, American robin). The highest scoring species were predominantly mixed and coniferous forest interior specialists (golden-crowned kinglet, Swainson's thrush, winter wren, magnolia warbler, bay-breasted warbler, northern parula warbler, red-breasted nuthatch, black-burnian warbler).

Bird DCA2 lake scores were correlated most strongly with shoreline wetland ($r = 0.51$, $P < 0.0001$; Table 1) and ENV2 ($r = -0.50$, $P < 0.0001$); their association with ENV1 was not significant ($r = 0.02$, $P = 0.80$). Bird DCA2 thus reflected local responses of bird assemblages to the presence of wetlands along the lake shore which, in turn, was partly a function of lake morphology (ENV2, Table 1). Habitat affinity varied with DCA2 species scores in the manner expected, although more equivocally than for DCA1. Species with low and intermediate DCA2 scores varied considerably in their habitat requirements, but the four species with the highest scores on this axis (Nashville warbler, swamp sparrow, red-winged blackbird, alder flycatcher) are often associated with wetlands (Peterson, 1980; DeGraaf & Rudis, 1986).

Other assemblage measures

All assemblage measures were significantly correlated with ENV1 ($P < 0.0001$) except migrant abundance ($P = 0.72$) (Fig. 4). Bird diversity showed an overall increase moving north along the dominant environmental gradient (ENV1), but a bivariate plot indicated a unimodal response (Fig. 4a). Both linear and quadratic terms for ENV1 were found to be significant predictors of bird diversity in a multiple regression model (both $P < 0.0001$) whether variables were expressed on a rank scale or in their original units. Bird diversity thus peaked at an intermediate position along the regional environmental gradient (ENV1) on lakes with moderate levels of human settlement and a mix of deciduous and coniferous forest. Total bird abundance declined moving north (Fig. 4b), as did omnivore abundance (Fig. 4e). Migrants showed no linear response (Fig. 4g), but their numbers appeared constrained at either extreme of the gradient judging from the triangular pattern for the points. Tree forager abundance generally increased moving north, but was also constrained on the most pristine lakes (Fig. 4c). Tree foragers and migrants increased proportionally moving north along the entire regional gradient (Fig. 4d,h, respectively), whereas omnivores proportionally decreased (Fig. 4f). The high total bird abundance for southern urbanized lakes (Fig. 4b) was therefore attributable to omnivorous resident species that did not use trees as foraging substrates. Our most human-tolerant species (i.e. those with the lowest scores on bird DCA1; Fig. 3) met these criteria (Appendix).

Product–moment correlation analysis showed that diversity, abundance and functional group measures were only weakly associated with ENV2 ($|r| \leq 0.24$). Bird diversity decreased with increasing wetlands and productivity on ENV2 ($r = 0.24$, $P < 0.01$), whereas total bird abundance increased ($r = -0.21$, $P < 0.01$). None of the other assemblage measures showed significant associations with ENV2 ($P > 0.05$).

DISCUSSION

The northeastern US was characterized by a marked regional gradient involving many anthropogenic and nonanthropogenic variables (ENV1; Fig. 1a, Table 1). The close correspondence of human population density with this region's dominant environmental gradient (ENV1) reflected the constraints imposed by climate and geomorphology on land use (Omernik, 1987) and, in turn, the influence of land use on other aspects of the environment. The climate and soils of northern New England and the Adirondacks of northeastern New York are better suited to forestry than to agriculture and other intensive land uses. Private ownership of land in northern Maine by paper and timber companies and public ownership of land in the Adirondacks has served to limit human densities in these areas compared with the rest of the region (Allen *et al.*, 1999b). Climatic and geomorphological influences on land use thus explain the close correspondence of land-use measures with climate, forest composition, elevation and calcium on ENV1. Land use has, in turn, introduced nutrients, chloride and other chemicals into lakes of the north-east (Dixit *et al.*, 1999), linking lakes to broader scale human systems and increasing the correspondence between land use and lake water chemistry measures along the regional environmental gradient (Allen *et al.*, 1999b).

Relationships that exist between land use and other environmental factors complicate the task of assessing anthropogenic effects on the biota at broad spatial scales. Using the same data analysed here, Allen *et al.* (1999b) showed that 68% of the variance in bird species composition that was associated with land use could equally well be attributed to nonanthropogenic factors (e.g. climate, forest composition). This 'ambiguous' variance could reflect human effects on bird assemblages, commonality in the environmental gradients integrated by humans and birds, or some combination thereof. Disentangling these confounded associations requires extending the analysis into the temporal dimension. Where antecedent data are unavailable, the only recourse is to infer process from patterns based on ecological understanding.

Despite the large magnitudes of the confounded associations observed in this study, we argue that anthropogenic factors have been similar in scale and magnitude to nonanthropogenic factors in structuring bird assemblages of this region. We observed a diversity peak at an intermediate position along the regional gradient (Fig. 4a). At a more local scale, Blair (1996) observed a similar pattern which he attributed to increases in environmental heterogeneity induced by moderate human disturbances. Similar mechanisms related to habitat heterogeneity may also hold true here at the regional scale, but the broader extent of our study allows for other explanations (Bohning-Gaese, 1997).

We propose that anthropogenic factors account for the decline to one side of the bird diversity peak (Rapport *et al.*, 1985), and that climatic severity accounts for the decline to the other side (Currie, 1991). Our diversity peak would then have evolved from interactions between broad-scale anthropogenic and nonanthropogenic factors because climate influenced land use across the region. Using data collected
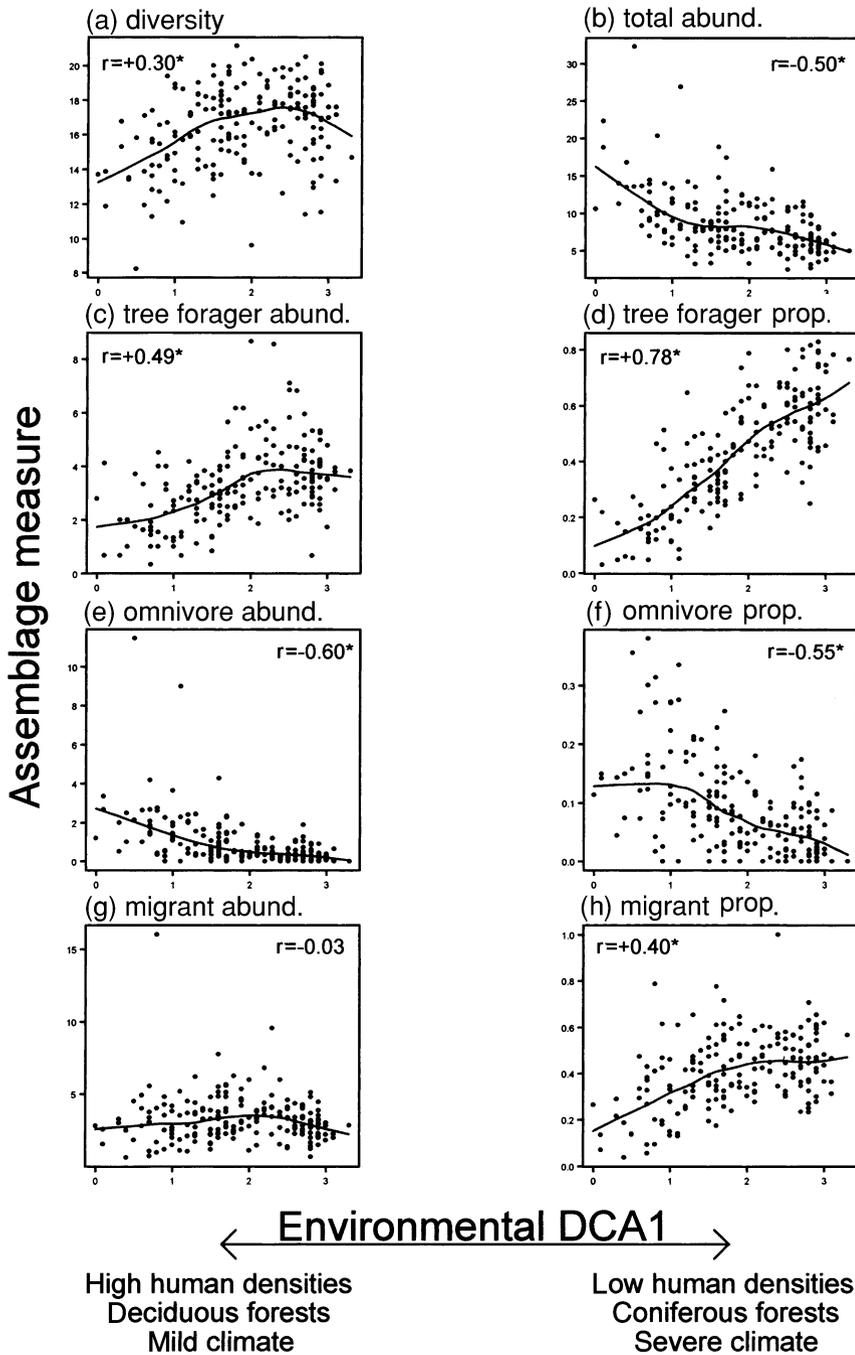
Figure 4 Plots comparing site scores on the first DCA axis of the environmental data (ENV1) with: (a) bird diversity, (b) total bird abundance, (c) tree forager abundance, (d) the tree forager individual proportion, (e) omnivore abundance, (f) the omnivore individual proportion, (g) migrant abundance and (h) the migrant individual proportion. Locally weighted regression curves and Spearman rank correlations (asterisks indicating a significance level of $P < 0.0001$) have been added to the plots. Spearman rank correlations were used instead of product-moment correlations to control for nonlinearity and heterogeneous variance.

on breeding birds from a variety of forests in North America, James & Wamer (1982) showed that rarefaction richness measures based on 40 individuals (similar to the 30 used here) were higher for deciduous forests than for mixed and coniferous forests. They attributed this pattern to the greater numbers of niches provided by deciduous forests owing to their taller canopies and greater diversity of trees. Based on their results, we would expect lake shore bird assemblages to become increasingly diverse moving south from coniferous

to deciduous forested watersheds, not less diverse, as observed in this study. Their results are thus consistent with our hypothesis that the relatively low bird diversity on pristine northern lakes was attributable to natural causes, but that the relatively low diversity on the southern urbanized lakes was attributable to humans.

Human-induced declines in diversity are thought to occur in part because expansion of intensive land use homogenizes the environment and thereby facilitates the replacement

of a relatively diverse group of human-intolerant species with a smaller number of opportunistic, human-tolerant species (Rapport *et al.*, 1985). Our findings were consistent with this explanation: land use was associated with proportional increases in omnivores (opportunists) and proportional declines in migrants and tree foragers along the entire regional gradient (Fig. 4f, h and d, respectively).

The relatively low numbers of migrants and tree foragers observed at either extreme of the regional gradient (Fig. 4g and c, respectively) appear to also reflect shifts from anthropogenic to nonanthropogenic environmental constraints. Neotropical migrants are detrimentally affected by fragmentation of forests regionally (Robinson *et al.*, 1995) and by human encroachment of riparian habitats locally (Croonquist & Brooks, 1993). We would therefore expect migrant numbers to be low in the southern part of this region where human densities are highest. We would also expect the abundance of tree foragers to be relatively low to the south, regardless of their migratory status, because intensive land use entails removal of the forest canopy. Migrant and tree forager numbers were also low at the opposite extreme of the gradient on the most pristine lakes. However, total bird abundance was also low (Fig. 4b), indicating that other factors related to climate and lake productivity constrained the abundance of all birds in the far north.

The observed changes in species composition on bird DCA1 were also consistent with broad-scale anthropogenic effects attributable to forest fragmentation (Fig. 3). As observed in our study, Croonquist & Brooks (1993) found that non-native species increased in number with human encroachment of riparian habitats, presumably because they utilize resources the native avifauna has not yet evolved to exploit. Our results were also concordant with those of Whitcomb *et al.* (1981): their measure of fragmentation tolerance, based on species occupancy of small deciduous forest patches relative to large patches in Maryland, was significantly correlated with our DCA1 species scores for the 21 forest bird species analysed in both investigations ($r = 0.67$, $P = 0.009$). Their study was conducted over a much smaller spatial extent than ours, so it is unlikely that their fragmentation index was confounded with nonanthropogenic correlates of land use.

Superimposed on the broad-scale bird–environment patterns were much weaker associations attributable to local mechanisms. After accounting for the region's dominant environmental gradient (ENV1), lake morphology induced local-scale differences between lakes (Fig. 1b) with respect to riparian–littoral zone structure and water quality (ENV2, Table 1). Lake morphology also induced changes in the species composition of bird assemblages (DCA2, Fig. 3) through its influence on the presence of wetlands along the lake shore. Increased wetland development was associated with reduced bird diversity, presumably because wetlands offer fewer trees and so support a less diverse avifauna than forested lake shores with greater vegetation structure. Total bird abundance increased with wetlands, as would be expected if lakes of higher productivity supported greater numbers of birds.

CONCLUSIONS

Land use and other aspects of the environment were interrelated to such an extent that we could not quantify their independent associations with regional bird distributions. Nevertheless, the consistency of our results with those of other investigations studying the effects of forest fragmentation over smaller spatial extents suggests that human activities have resulted in cumulative effects on this region's avifauna that are of similar scale and magnitude to those of climate and geomorphology. Despite the fact that migrant abundance failed to exhibit a linear relationship to the level of forest fragmentation (Fig. 4g), we argue that forest fragmentation has strongly suppressed migrant numbers in the southern part of the region, and that no clear relationship was found because of the interplay between land use and its natural determinants. These results emphasize the importance of analysing interrelationships among anthropogenic and nonanthropogenic variables as part of ecological studies at the regional scale.

Within the context of this region, relationships that exist between land use and other aspects of the environment have resulted in the systematic removal of some bird habitats at broad spatial scales while leaving others relatively intact. Species restricted to the interiors of deciduous forests in the northeastern US, including many neotropical migrants, have been reduced by agriculture and urbanization because their former habitat is well suited to these intensive forms of land use. Species requiring northern coniferous forests appear less severely affected by comparison because they inhabit lands that are currently used for forestry rather than more intensive land uses. However, the true 'winners' in this massive unplanned experiment appear to be the non-native species, native omnivores and other resident species that have been favourably affected by forest fragmentation at the expense of other species. The end result of this experiment has likely been a reduction in the local diversity of lake shore bird assemblages across much of the northeastern US.

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Appendix Listing of the 79 species analysed, their four-letter codes, and their functional group designations as to foraging technique (For), dietary preference (Diet) and migratory status (Mig). Foraging and dietary group assignments are those of Ehrlich *et al.* (1988), and migratory assignments are those of Finch (1991).

Code	Common name	Scientific name	For†	Diet‡	Mig§
ALFL	Alder flycatcher	*Empidonax alnorum*	HA	IN	MI
AMCR	American crow	*Corvus brachyrhynchos*	GG	OM	RE
AMGO	American goldfinch	*Carduelis tristis*	FG	GR	RE
AMRE	American redstart	*Setophaga ruticilla*	HG	IN	MI
AMRO	American robin	*Turdus migratorius*	GG	IN	RE
BAOR	Northern oriole	*Icterus galbula*	FG	IN	MI
BBWA	Bay-breasted warbler	*Dendroica castanea*	FG	IN	MI
BCCH	Black-capped chickadee	*Parus atricapillus*	FG	IN	RE
BEKI	Belted kingfisher	*Ceryle alcyon*	HD	PI	RE
BHCO	Brown-headed cowbird	*Molothrus ater*	GG	IN	RE
BKSW	Bank swallow	*Riparia riparia*	AF	IN	MI
BLJA	Blue jay	*Cyanocitta cristata*	GG	OM	RE
BLWA	Blackburnian warbler	*Dendroica fusca*	FG	IN	MI
BRCR	Brown creeper	*Certhia americana*	BG	IN	RE
BRSW	Barn swallow	*Hirundo rustica*	AF	IN	MI
BTBW	Black-throated blue warbler	*Dendroica caerulescens*	HG	IN	MI
BTGW	Black-throated green warbler	*Dendroica virens*	FG	IN	MI
BWWA	Black-and-white warbler	*Mniotilta varia*	BG	IN	MI
CAGO	Canada goose	*Branta canadensis*	SU	FO	RE
CAWA	Canada warbler	*Wilsonia canadensis*	HG	IN	MI
CEWA	Cedar waxwing	*Bombycilla cedrorum*	FG	FR	RE
CHSP	Chipping sparrow	*Spizella passerina*	GG	IN	MI
CHSW	Chimney swift	*Chaetura pelagica*	AF	IN	MI
COGR	Common grackle	*Quiscalus quiscula*	GG	OM	RE
COLO	Common loon	*Gavia immer*	SD	PI	RE
COME	Common merganser	*Mergus merganser*	SD	PI	RE
COYE	Common yellowthroat	*Geothlypis trichas*	FG	IN	MI
CSWA	Chestnut-sided warbler	*Dendroica pensylvanica*	FG	IN	MI

Appendix *continued*

Code	Common name	Scientific name	For†	Diet‡	Mig§
DEJU	Dark-eyed junco	*Junco hyemalis*	GG	GR	RE
DOWO	Downy woodpecker	*Picoides pubescens*	BG	IN	RE
EAKI	Eastern kingbird	*Tyrannus tyrannus*	HA	IN	MI
EAPH	Eastern phoebe	*Sayornis phoebe*	HA	IN	RE
EAWO	Eastern wood-pewee	*Contopus virens*	HA	IN	MI
EUST	European starling	*Sturnus vulgaris*	GG	IN	RE
EVGR	Evening grosbeak	*Coccothraustes vespertinus*	GG	GR	RE
GBHE	Great blue heron	*Ardea herodias*	SS	PI	RE
GCFL	Great crested flycatcher	*Myiarchus crinitus*	HA	IN	MI
GCKI	Golden-crowned kinglet	*Regulus satrapa*	FG	IN	RE
GRCA	Gray catbird	*Dumetella carolinensis*	GG	IN	MI
HAWO	Hairy woodpecker	*Picoides villosus*	BG	IN	RE
HEGU	Herring gull	*Larus argentatus*	GG	OM	RE
HETH	Hermit thrush	*Catharus guttatus*	GG	IN	RE
HOFI	House finch	*Carpodacus mexicanus*	GG	GR	RE
HOSP	House sparrow	*Passer domesticus*	GG	GR	RE
HOWR	House wren	*Troglodytes aedon*	GG	IN	MI
LEFL	Least flycatcher	*Empidonax minimus*	HG	IN	MI
MADU	Mallard	*Anas platyrhynchos*	DA	GR	RE
MAWA	Magnolia warbler	*Dendroica magnolia*	HG	IN	MI
MODO	Mourning dove	*Zenaida macroura*	GG	GR	RE
NAWA	Nashville warbler	*Vermivora ruficapilla*	FG	IN	MI
NOCA	Northern cardinal	*Cardinalis cardinalis*	GG	IN	RE
NOFL	Northern flicker	*Colaptes auratus*	GG	IN	RE
NOPA	Northern parula	*Parula americana*	FG	IN	MI
NOWA	Northern waterthrush	*Seiurus noveboracensis*	GG	AI	MI
OVEN	Ovenbird	*Seiurus aurocapillus*	GG	IN	MI
PIWA	Pine warbler	*Dendroica pinus*	BG	IN	RE
PUFI	Purple finch	*Carpodacus purpureus*	GG	GR	RE
RBGR	Rose-breasted grosbeak	*Pheucticus ludovicianus*	FG	IN	MI
RBNU	Red-breasted nuthatch	*Sitta canadensis*	BG	IN	RE
REVI	Red-eyed vireo	*Vireo olivaceus*	HG	IN	MI
RSTO	Rufous-sided towhee	*Pipilo erythrophthalmus*	GG	IN	RE
RWBB	Red-winged blackbird	*Agelaius phoeniceus*	GG	IN	RE
SCTA	Scarlet tanager	*Piranga olivacea*	HG	IN	MI
SOSP	Song sparrow	*Melospiza melodia*	GG	IN	RE
SOVI	Solitary vireo	*Vireo solitarius*	FG	IN	MI
SPSA	Spotted sandpiper	*Actitis macularia*	GG	IN	RE
SWSP	Swamp sparrow	*Melospiza georgiana*	GG	IN	RE
SWTH	Swainson's thrush	*Catharus ustulatus*	FG	IN	MI
TRSW	Tree swallow	*Tachycineta bicolor*	AF	IN	RE
TUTI	Tufted titmouse	*Parus bicolor*	FG	IN	RE
VEER	Veery	*Catharus fuscescens*	GG	IN	MI
WAVI	Warbling vireo	*Vireo gilvus*	HG	IN	MI
WBNU	White-breasted nuthatch	*Sitta carolinensis*	BG	IN	RE
WIWR	Winter wren	*Troglodytes troglodytes*	GG	IN	RE
WOTH	Wood thrush	*Hylocichla mustelina*	GG	IN	MI
WTSP	White-throated sparrow	*Zonotrichia albicollis*	GG	IN	RE
YBSA	Yellow-bellied sapsucker	*Sphyrapicus varius*	BG	IN	RE
YEWA	Yellow warbler	*Dendroica petechia*	FG	IN	MI
YRWA	Yellow-rumped warbler	*Dendroica coronata*	FG	IN	RE

† Foraging groups: AF, aerial forager; BG, bark gleaner; DA, dabbler; FG, foliage gleaner; GG, ground gleaner; HA, hawker; HD, high diver; HG, hover-and-gleaner; SD, surface diver; SS, stalk-and-striker; SU, surface dipper.
‡ Dietary groups: AI aquatic invertivore; FO, folivore; FR, frugivore; GR, granivore; IN, insectivore; OM, omnivore; PI, piscivore.
§ Migratory groups: MI, neotropical migrant; RE, resident.