LANDSCAPE CORRELATES OF BREEDING BIRD RICHNESS ACROSS THE UNITED STATES MID-ATLANTIC REGION

K. BRUCE JONES[1], ANNE C. NEALE[1], MALIHA S. NASH[1], KURT H. RIITTERS[2], JAMES D. WICKHAM[3], ROBERT V. O'NEILL[4] and RICK D. VAN REMORTEL[5]

[1]U.S. Environmental Protection Agency, Las Vegas, NV USA; [2]U.S. Geological Survey, Biological Resources Division, Raleigh, NC VU; [3]US Environmental Protection Agency, Research Triangle Park, NC USA; [4]Oak Ridge National Laboratory, Oak Ridge. TN USA; [5]Lockheed-Martin, Las Vegas, NV USA

Abstract Using a new set of landscape indicator data generated by the U.S.EPA, and a comprehensive breeding bird database from the National Breeding Bird Survey, we evaluated associations between breeding bird richness and landscape characteristics across the entire mid-Atlantic region of the United States. We evaluated how these relationships varied among different groupings (guilds) of bids based on functional, structural, and compositional aspects of individual species demographics, Forest edge was by far the most important landscape attribute affecting the richness of the lumped specialist and generalist guilds; specialist species richness was negatively associated with forest edge and generalist richness was positively associated with forest edge. Landscape variables (indicators) explained a greater proportion of specialist species richness than the generalist guild (46% and 31%, respectively). The lower value in generalists may reflect finer-scale distributions of open habitat that go undetected by the Landsat satellite, open habitats created by roads (the areas from which breeding bird data are obtained), and the lumping of a wide variety of species into the generalist category. A further breakdown of species into 16 guilds showed considerable variation in the response of breeding bii to landscape conditions; forest obligate species had the strongest association With landscape indicators measured in this study (55% of the total variation explained) and forest generalists and open ground nesters the lowest (17% of the total variation explained). The variable response of guild species richness to landscape pattern suggests that one must consider species' demographics when assessing the consequences of landscape change on breeding bii.

1. Introduction

Scientists and environmental managers alike are concerned about large-scale changes in land use and landscape pattern and their cumulative impact on biodiversity, extinction, and biotic potential over a variety of scales (Schlesinger et al. 1990, Lubchenco et al. 1991, UNEP 1992, Woodley et al. 1993, Noss and Cooperrider 1994, Houghton 1994, Ojima et al. 1994, Noss et al. 1995). Fragmentation and simplification of natural habitats are primary factors influencing the decline of biological diversity at regional and continental scales (Turner et al. 1989, 1991, Saunders et al. 1991). Fragmentation results in decreased sizes of continuous habitat (e.g., interior forests) and decreased connectivity among metapopulations (Verboom et al. 1991). As distances between patches of suitable habitat increase, the probability of extinction increases for individual populations, and the probability of recolonization by surviving populations decreases (Verboom et al. 1991). The result of habitat loss and fragmentation is the loss of

Environmental Monitoring and Assessment 63: 159–174, 2000.

populations and species over time (Kattan et al. 1994, Koopowitz et al. 1994, Short and Turner 1994, Knick and Rotenberry 1995).

Traditionally, within-site habitat characteristics have been used to evaluate habitat suitability (Short and Hesbeck 1995). Additionally, the spatial distribution of suitable habitats has been modeled by linking certain species with biophysical attributes, including soils, vegetation, elevation, geology, and land form (Scott et al. 1993, Short and Hesbeck 1995). The relationship between species and biophysical attributes are determined and then applied to maps representing the spatial distribution of the attributes; this results in a spatial representation of suitable habitat (Short and Hesbeck 1995). But spatial pattern, including shapes of habitat, distances among habitats (connectivity), and habitat size also determine the suitability of habitat for and survivorship of many species (Whitcomb et al. 198 1, Cutler 1991, Danielson 1992, McCollin 1993, Kattan et al. 1994, Koopowitz et al. 1994, Short and Turner 1994, Wilson et al. 1994, Blackstock et al. 1995, Lacy and Lindenmayer 1995, McIntyre 1995, Flather et al. 1992, Riitters et al. 1997), and these are often excluded from habitat assessments. Only recently have we begun to understand the importance of spatial pattern of habitats on individual species and species richness.

Within a geographic region, species respond differently to habitat changes because of differences in habitat requirements and the scales at whichthey interact with the environment (Hansen and Urban 1992, Holling 1992, Pulliam et al. 1992, Kattan et al. 1994, Koopowitz et al. 1994, Lacy and Lindenmayer 1995). In recognition of these potential differences, a number of species guild classifications have been developed (MacMahon 1976, Szaro 1986, Croonquist and Brooks 199 1, Peterjohn 1994, O'Connell et al. 1998ab). Some guildclassifications are limited to species' uses of habitats (e.g., interior forest, woodland, and grassland, Van Home and Wiens 1991), whereas others consider species demographic characteristics, including functional (e.g., feeding behavior), structural (e.g., nesting sub&ate), and composition attributes (O'Connell et al. 1998ab).

The lack of wall-to-wall landscape data at relatively fine scales has precluded an assessment of the spatial pattern ofwildlife habitat across regional scales. However, in 1996, a regional-scale land cover database was developed for the five-state area of the United States mid-Atlantic region, and this database along with other regional landscape coverages (e.g., topography, soils, road networks, stream networks, and human population density) was used to assess landscape conditions across the entire region down to a scale of 30 meters (Jones et al. 1997). The assessment used a set of landscape indicators (O'Neill et al. 1988, 1997) to evaluate the spatial patterns of forest, forest-edge, and riparian habitats. A national-scale land cover database similar to that in the mid-Atlantic will be available by the spring of 2000 (Vogelmann et al. 1998), and these new data offer the potential to conduct a national-scale assessment of wildlife habitat.

The National Breeding Bird Survey (BBS) is the only biological database that permits a comparison of species richness and landscape pattern across regional scales (Peterjohn 1994). The BBS consists of approximately 3,700 routes nationally, and the samples are taken in a consistent manner from year to year; some routes date back to 1967.

Using these two databases, we assessed quantitative relationships between breeding bird richness and landscape pattern across the mid-Atlantic region. The mid-Atlantic region was an excellent area to assess these relationships because it possesses considerable environmental variability, including variability in human populations and uses of the landscape. This research was conducted as part of the Environmental Monitoring and Assessment Program (EMAP) with the ultimate goal of improving our ability to assess ecological conditions at multiple scales across entire regions.

2. Methods

We acquired breeding bird data from the BBS (Peterjohn 1994) and landscape indicator data from the U.S. Environmental Protection Agency's Landscape Ecology Program. We used 181 routes from the mid-Atlantic region in our analysis (Figure 1); these sites had at least 4 out of 5 years of data between 1990-94 and known locations for their center points. BBS data collection methods can be found in Peterjohn (1994). Known geographic coordinates were necessary to evaluate landscape conditions associated with each route.

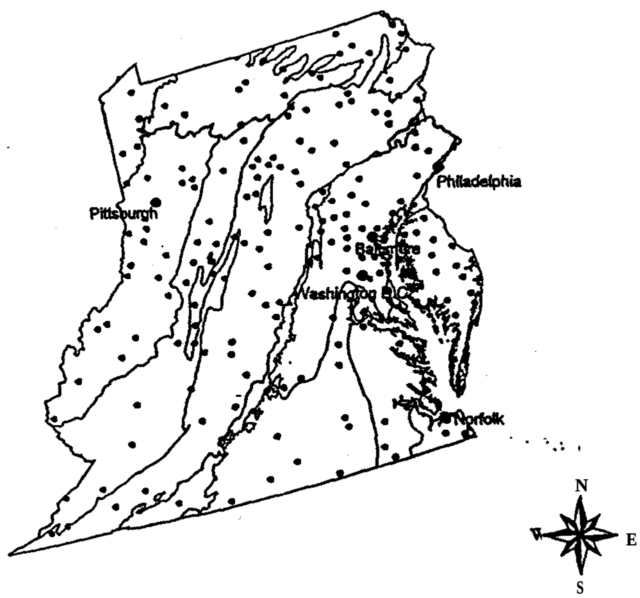

Figure 1. Study area and center locations of breeding bird routes used in the study.

We established circular landscape analysis areas around each BBS route center point (18 1 total) using Arc/Info GIS software (ESRI 1996). We used circles because only the center point of each route was known. Circles were 19.7 km in radius, encompassing the entire route. We acquired digital coverages Of landscape indicators generated by Jones et al. (1997) and calculated values for each of the circular analysis areas in Arc/Info (Table I). The landscape indicators selected in this study measured characteristics of the landscape that were known or hypothesized to affect breeding bird richness. Because differences in the ranges of indica-

Table I

List of landscape indicators compared to breeding bird richness. Calculation methods and details of each indicator can be found in Jones et al. (1997). Spatial filtering to estimate forest habitat suitability can be found in Riitters et al. (1997). Indicators were calculated on circular landscape support areas (19.7 km radius).

Name of Indicator	Explanation
Riparian agriculture (ripa)	Percent of support area with agricultural land cover adjacent to stream edge.
Riparian forest (ripf)	Percent of support area with forest land cover adjacent to stream edge.
Forest fragmentation (ffrg)	Forest fragmentation index for support area. Of all edges in the support area involving at least one forested pixel, the percent that joins a forested pixel to a non-forested pixel. Higher values indicate higher fragmentation.
Forest extent (density) (fd)	Percent of support area with suitable interior forest habitat Estimated by using a 9 × 9 pixel (approximately 7 hectares) sliding window as a spatial filter. Ninety percent or greater of the pixels in the window had to be forest in order to be suitable.
Forest (Interior) at 3 scales (fsc3)	Percent of support area with three scales of interior forest habitat Estimated by using 3 sliding windows (approximately 7, 65, and 600 hectares) as spatial filters where each different-sized window had to have 90% or more of the pixels as forest to be considered interior forest.
Forest edge habitat (fe)	Percent of support area with suitable forest edge. Forest edge is defined as the literal edge between contrasting forest and non-forested land. Estimated by using a 9 × 9 (approximately 7 hectares) sliding window as a spatial filter.
Road density (rd)	Road density for support area expressed as an average number of kilometers of roads per square kilometer of support area.
Forest land cover (flc)	Percent of support area that had forest land cover.
Agricultural land cover (alc)	Percent of support area that had agricultural land cover (pasture/crops).

tor values can affect multivariate analyses, we transformed certain landscape indicators into ranges of values similar to other indieators.

We calculated species richness by guild using a classification that incorporates functional, structural, and compositional aspects of individual species demographic characteristics (Table II, O'Connell et al. 1998a). As the classification reflects different aspects of bird behavior, each species can belong simultaneously to different guilds. Our data set was limited to those songbird species and guild assignments included in O'Connell's Bird Community Index (O'Connell et al. 1998a). Guild richness was expressed as the proportion of the total number of species observed from each guild to the total number of species observed from each site. Proportions were calculated for each year and then averaged for the five years. We ranked each individual site from 1-181 for each guild (7 generalist and 9 specialist guilds). We then calculated specialist and generalist metrics by summing the individual guild ranks that fell into specialist and generalist guild classes,

We examined the data, both visually and statistically, and concluded that the data fit a linear model better than a non-linear one. We ran a backwards linear multiple regression in SAS (SAS 1990) to determine relationships between breeding bird metrics (dependent variables) and landscape indicators (independent variables). We also ran a principal components analysis on the landscape variables to

Table II

Breeding bird guild classifications used in the study (from O'Connell et al. 1998b).

Generalists	
	omnivore
	Nest Predator/Brood Parasite
	Exotic
	Resident
	Temperate Migrant
	Shrub Nester
	Forest Generalist
specialists	
	Bark-Prober
	Ground Gleaner
	Upper-Canopy Forager
	Lower-Canopy Forager
	Single-Brooded
	Canopy Nester
	Open-Ground Nester
	Forest-Ground Nester
	Interior Forest Obligate

determine how the individual sites tended to cluster in multidimensional landscape indicator space. We then plotted breeding bird richness onto the graph to evaluate how richness varied across landscape indicator space.

3. Results

3.1 PRINCIPAL COMPONENTS ANALYSIS

From the principle components analysis (PCA) of the 9 landscape indicators, we used the first three dimensions (eigenvectors) of landscape indicator space: the first (PC1) captured a gradient of landscape modification, the second (PC2) captured a gradient of urban forests, and the third (PC3) captured a gradient of agriculture and forested riparian zones (Table III). These three dimensions explained 91 percent of the variation in the landscape indicators (Table III). Of these, overall

Table III

Results of a principal **components analysis** of landscape indicators. Loadings of **landscape** indicators on orthogonal **axes (Eigenvectors)** are given along with the proportion of **variance** in the landscape indicator database explained by **the** first **three** principal components. Landscape indicator abbreviations are given in Table I.

Landscape Indicator	PC1	PC2	PC3
flc	-0.37	0.04	**0.25**
fd	-039	0.03	0.10
fe	039	0.06	0.06
fsc3	**-0.32**	-0.27	0.03
alc	036	-0.30	0.18
ffrg	037	0.22	0.12
rd	**0.25**	0.64	0.15
ripa	**0.25**	-0.52	0.60
ripf	-026	033	0.70
Variation Explained	0.72	**0.11**	0.08

Cumulative Proportion of Variation Explained = 91%

Vector (PC) Interpretation

PC1 - **Human use gradient**
PC2 - Urban and residential **forest**
PC3 - **Riparian agriculture** / forest mosaics / coastal areas

disturbance (PC1) was by far the most important dimension (72% of the variation explained).

3.2 BREEDING BIRD/LANDSCAPE ASSOCIATIONS

Landscape variables explained a greater proportion of the overall variance in the specialist guild richness than in the generalist guild (46% versus 3 1% of the variation, respectively, Table IV). Specialist species richness was negatively associated with forest edge and positively associated with the presence of all three scales of forests measured (Table IV). Generalist species richness was positively associated with forest edge and negatively associated with forest fragmentation (Table IV). Forest edge was by far the most important landscape variable in determining both specialist and generalist species richness (Table IV). The relationships between landscape indicators and each of the 16 individual guilds was highly variable among generalists and specialists alike (Table V). Interior forest obligates had a relatively high proportion of their variability explained by landscape variables (53%), including the presence of all three forest scales (positive association), and to a lesser degree the overall amount of forest (positive association) and forest

Table IV

Results of backward regression analysis relating generalist and specialist breedii bid richness (dependent variable) to landscape indicators (independent variables, Table I). Landscape indicators included in the model were significant at $p < .05$. Landscape indicator abbreviations are given in Table I.

Equation: Sum of Ranks for Generalists = 41202 + 15.57 (fe) - 11.72 (ffrg)

Variables:
fe - 30 % of variation explained (positive association)
ffrg - 2 % of variation explained (negative association)

Total Variation Explained by Model: 3 1.9 %

Equation: Sum of Ranks for Specialists = 1023.8 - 10.03 (fe) + 266 (fsc3)

Variables:
fe - 44 % of variation explained (negative association)
fsc3 - 2 % of variation explained (positive association)

Total Variation Explained by Model: 462 %

fragmentation (negative association) (Table V). Exotic species also had a relatively high proportion of their variability explained by landscape variables (46%), including a positive association with the amount of forest edge and density of roads (Table V). However, landscape variables explained only small amounts of the total variation in richness for many of the specialist and generalist guilds (Table V).

In some cases, the signs of the slopes of individual variables in the regression models did not follow our expectations. For example, certain generalist guilds were positively associated with forest edge, yet negatively associated with forest fragmentation (Table IV). That these generalist guilds are positively 'associated with forest edge is not surprising. That they are negatively associated with forest fragmentation is counter intuitive. This result may have to do with collinearity between these two variables; when two correlated variables are included in a multi-. ple regression analysis one can often get illogical signs. In this ease, forest edge (which had the expected sign) explained the majority of the variability and forest fragmentation explained only a small amount.

A plot of generalist and specialist richness on the threedimensional, landscape indicator space (see Figure 2) supports the results of the multiple regression analysis, generalist richness was greatest on relatively disturbed areas, and lowest on relatively undisturbed areas, whereas specialist richness showed the opposite pattern. Similarly, specialists showed a tighter pattern across the three-dimensional indicator space than did generalists.

4. Discussion

An important goal of regional-scale, environmnental monitoring programs is to evaluate status and trends of ecological resources at regional scales with the aim of targeting those areas that are in need of improvement or further investigation (Messer et al. 1991). Important aspects of implementing this type of program are identification, testing, and implementation of ecological indicators. Assessing the ability of indicators to track conditions in ecological resources is critical to this process (Hunsaker et al. 1990). Lack of comprehensive monitoring data has prevented an assessment of the sensitivity of indicators to ecological conditions at a regional scale. However, a new set of land cover databases being developed by the Multi-Resolution Land Characteristics Consortium (MRLC), coupled with the de-'velopment of landscape pattern indicators (O'Neill et al. 1997), offers an unprecedented opportunity to assess habitat conditions nationwide over the next 5 to 10 years.

The results of this study show that landscape indicators derived from the MRLC land cover data offer potential for regional and national scale habitat assessments. Although variable, our results show that breeding bird richness is sensitive to landscape condition. Flather et al. (1992) showed a strong association

Table V

Results of backward regression analysis relating species richness of individual demographic guilds (dependent variable) to landscape indicators (independent variables). Landscape indicators included in the model were significant at p <.05. The sign in parentheses indicate the direction of association.

Guild	Variable	Variation Explained	Total Variation Explained
Generalists			
omnivore	Ripa(+)	3.0%	
	fe (+)	27.0%	30.0%
Nest Predator / Brood Parasite	fe(+)	20.0%	
	ffrg (-)	3.0%	
	rd (-)	5.0%	
	alc (-)	3.0%	31.0%
Exotic	fe(+)	40.0%	
	ffrg (-)	3.0%	
	rd (-)	3.0%	46.0%
Resident	fe(+)	30.0%	
	ffrg (-)	6.0%	
	alc (-)	3.0%	39.0%
Temperate Migrant	fe(+)	11.0%	
	fsc3 (-)	2.0%	
	rd (-)	5.0%	
	f09 (+)	2.0%	20.0%
Shrub Nester	flc (-)	3.0%	
	alc (-)	8.0%	
	ripf (+)	10.0%	21.0%
Forest Generalist	ffrg (-)	2.0%	
	flc (-)	2.0%	
	alc (-)	6.0%	
	ripf (+)	7.0%	18.0%
Specialists			
Bark-prober	ffrg (-)	8.0%	
	flc (-)	3.0%	
	alc (-)	5.0%	
	ripf (+)	6.0%	22.0%
Ground Gleaner	fe(-)	23.0%	
	fsc3 (+)	3.0%	
	f09 (-)	2.0%	28.0%

Upper Canopy Forager	rd (-)	4.0%	
	f09 (+)	3.0%	
	alc (-)	1.0%	
	ripf (+)	21.0%	29.0%
Lower Canopy Forager	rd (+)	3.0%	
	flc (+)	31.0%	34.0%
Singlebrooded	flc (+)	43.0%	
	ripf (-)	2.0%	45.0%
Forest Ground Nester	fsc3 (+)	30.0%	
	f09 (+)	4.0%	
	ripf (-)	3.0%	37.0%
Open Ground Nester	flc (+)	6.0%	
	alc (+)	11.0%	17.0%
Canopy Nester	rd (-)	4.0%	
	alc (-)	17.0%	
	ripf (+)	3.0%	25.0%
Interior Forest Obligate	fsc3 (+)	5.0%	
	ffrg (-)	46.0%	
	flc (+)	1.0%	53.0%

between breeding bird abundance and landscape pattern over a broad area of the eastern US. However, this study only determined the direction of the association (e.g., negative or positive) and did not ascertain the relative importance of each landscape variable. At the national scale, breeding bird diversity is strongly associated with climate variables, including minimum and maximum temperature and precipitation, but landscape variables appear to be important determinants of bird species richness at regional scales (O'Connor et al. 1996).

A weaker association between landscape variables and generalists than that observed for specialists may reflect the fact that breeding bird samples are taken along roads which tend to have a certain amount of edge associated with them. Roadside edges are likely to go undetected by the Landsat satellite, the sensor used to generate the digital land cover map used in this study. Additionally, generalists tend to be more plastic in their use of habiits (O'Connell et al. 1998b) and would, therefore, show a lower fidelity for any specific habitat.

In our study, forest edge was by far the most important determinant of species richness in the composite generalist and specialii guilds, forest edge was negatively associated with richness in the specialist guild and positively associated with the generalist guild. In the mid-Atlantic, nearly all forest edge is created by either agriculture or human development (urban and residential). Therefore, forest edge is an indicator of human disturbance and landscape modification. Flather et

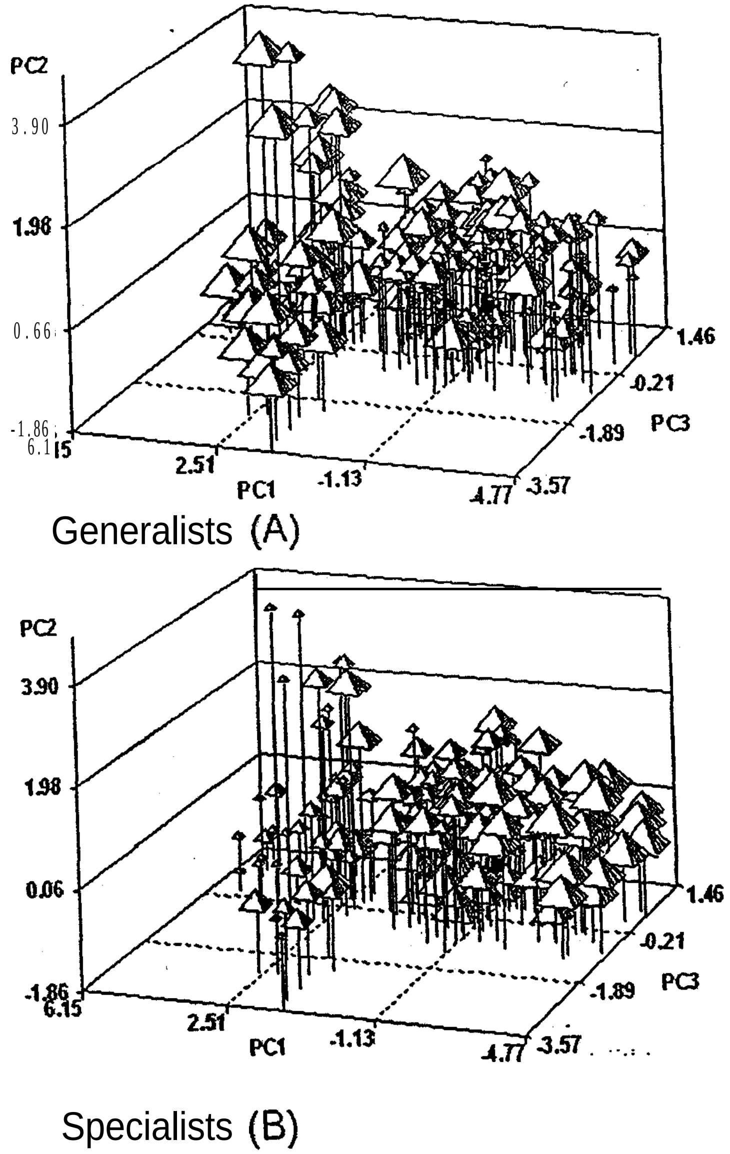

Figure 2. Ranks of guild species richness plotted on a three-dimensional landscape indicator graph generated from a principal components analysis (see Table III for interpretation). Breeding bird ranks for (A) generalists and (B) specialists the split into five classes and they arc depicted as different sized pyramids (5 sizes); the larger pyramid the higher the rank of species richness.

al. (1992) found approximately 80% of the permanent residents in eastern US forests to be positively associated with contagion, which is inversely related to fragmentation and edge. These findings also fit our general understanding of specialist and generalist species; specialists generally require huger blocks of natural habitats (e.g., forests) with smaller amounts of edge and generalists tend to thrive in, more mixed environmental settings (O'Connell et al. 1998b). We were unable to assess the impact of urban sprawl on breeding bids because most of the survey routes were in rural areas along secondary roads. As a result, our data were very skewed toward non-urban areas (Figure 3).

Correlations of landscape variables with breeding bird richness might be improved by comparing landscape pattern against a more integrated index of breeding bird condition. O'Connell et al. (1998ab) have developed a Bird Community Index that integrates the responses of functional, structural, and compositional guilds. We intend to incorporate this index into the next phase of our study.

Similar to the study of Flather et al. (1992), we found considerable variability in the response of individual guilds to landscape variables. Exotic and resident species richness had the strongest association to landscape indicators of the generalist guilds; both were positively associated with forest edge. Exotic species tend to thrive in disturbed environments and resident species tend to adjust well to ur-

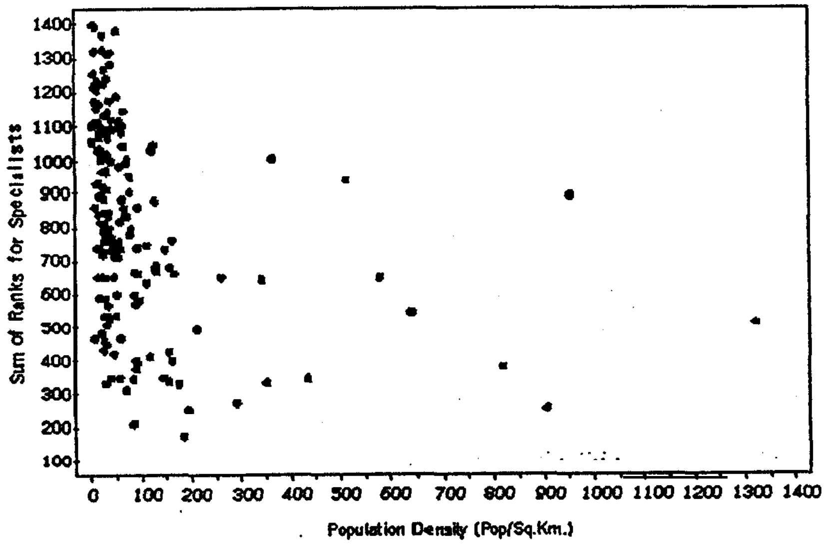

Figure 3. A comparison of 1990 population density and demographic specialist ranks on the 181 samples sites in the mid-Atlantic region.

ban and agricultural environments. Of the specialists, interior forest obligates and single-brooded guilds had the strongest association with landscape condition. Forest fragmentation explained the greatest proportion of the variability in interior forest obligates; this finding is consistent with many other studies of forest bids (Whitcomb et al. 1981, Kattan et al. 1994, Wilson et al. 1994). Because they breed only once a year, single-brood species may require higher quality habitat in order to be successful. Relatively low correlation between landscape indicators and other guilds may reflect our inability to measure other important aspects of habitat, including the quality of ground and canopy cover. Therefore, it may be necessary to collect additional habitat data in order to evaluate habitat quality relative to the entire suite of bird guilds.

Several factors may account for the unexplained variability in breeding bird richness models. First, habitat conditions along breeding bird survey routes may be important determinants of which birds are seen and heard At the time of this study, the spatial distribution and configuration of breeding bird routes was unknown. However, a digital coverage of the routes in the mid-Atlantic region is now available and we intend to add a near-road habitat assessment to our study. Second, as mentioned above, we may not be able to detect all of the important aspects of habitat that influence bird species richness. For example, our data were insufficient to assess the quality of the forest canopy relative to canopy specialists. At present, only ground surveys can provide these data. Third, O'Connell et al. (1998ab) developed their bird guild rankings from sites in the mid-Atlantic Highlands portion of the region. Bird guilds outside of the Highlands area, including the Piedmont and Coastal ecoregions, may have different levels of expected richness and bird community structure. We propose to explore these differences in the next phase of our study. Fourth, we did not evaluate observer bias and this, in part, may have accounted for additional variability in the bii data. Fifth, an unknown amount of variability may result from competitive interactions among birds, including neotropical migrants whose numbers can fluctuate tremendously as a result of environmental conditions outside the region. Finally, year to year variability in climate may have a profound influence on bird populations (O'Connor et al. 1996). Despite some of these uncertainties, landscape pattern appears to play an important role in determining the number and types of breeding bids in a given area.

The results of this study have significant implications for a national habitat assessment. It soon will be possible to generate the landscape indicators used in this study at a scale of 30 meters across the entire coterminous US. The National Breeding Bird Survey collects data on breeding birds on approximately 3,700 routes across the US. Because these data are available nationally, it should be possible to quantify the relationships between breeding bird richness and landscape pattern in each region of the US. Once regional models are constructed, it should be possible to evaluate some aspects of breeding bird habitat across the United States.

Acknowledgments

We thank Tim O'Connell and Robert Brooks of Pennsylvania State University for help in compiling and analyzing demographic species guilds, and Curt Flather of the U.S. Forest Service for providing center point locations for the BBS routes. We are grateful to Sam Droege and John Sauer of the National Breeding Bird Survey for providing bird data used in this study. Lastly, we thank Tom DeMoss and Steve Paulsen of the EPA for their support in making this study possible. This project was supported by the EPA's Environmental Monitoring and Assessment Program and the National Exposure Research Laboratory.

The research described in this article has been funded in part by the EPA. The work has not been reviewed by the EPA, and no official endorsement should be inferred.

References

Blackstock, T.H., Stevens, J.P., Howe, EA. and Stevens, D.P.: 1995, 'Changes in the extent and fragmentation of heathland and other semi-natural habii between 1920–22 and 1987–88 in the Llyn Peninsula, Wales, UK', *Biol. Conserv.* 72, 33–44.

Croonquist, M.J. and Brooks, R.P.: 1991, 'Use of avian and mammalian guilds as indicators of cumulative impacts in riparian-wetland areas', *Environ. Man.* 15, 701-714.

Cutler, A.: 1991, 'Nested faunas and extinction in fragmented habitats', *Conserv. Biol.* 5,496505.

Danielson, B.J.: 1992, 'Habitat selection, interspecific interactions and la&cape composition', *Evol. Ecol.* 6, 399–411.

ESRI: 1996, *Introduction to ArcView GIS*, Environmental Systems Research Institute, Redlands, California.

Flather, C.H., Brady, S.J. and Inkley, D.B.: 1992, 'Regional habitat appraisals of wildlife communities: a landscape-level evaluation of a resource planning model using avian distribution data', *Landscape Ecol.* 137-147.

Hansen, AJ. and Urban, D.L.: 1992, 'Avian response to la&cape pattern: the role of species' life histories', *Landscape Ed.* 7, 163–180.

Holling, C.S.: 1992, 'Cross-scale morphology, geometry, and dynamics of ecosystems', *Ecol. Mongr.* 62, 447–502.

Houghton, R.A.: 1994, 'The worldwide extent of land-use change', *BioScience* 44, 305–313.

Hunsaker, C.T., Graham, R.L., Suter, G.W., O'Neill, RV., Barnthouse, L.W. and Gardner, R.H.: 1990, 'Assessing ecological risk on a regional scale', *Environ. Man.* 14, 325–332.

Jones, K.B., Riitters, K.H., Wickham, J.D., Tankersley, Jr., RD., O'Neill, R.V., Chaloud, D.J., Smith, E.R. and Neale, A.C.: 1997, *An ecological assessment of the United States Mid-Atlantic region: a landscape atlas.* EPA 600-R97-130, US Environ. Prot. Agency, Washington, DC, USA.

Kattan, G. H., Alvarez-Lopez, H. and Giraldo, M.: 1994, 'Forest fragmentation and bird extinctions: San Antonio eighty years later', *Conserv. Biol.* 8, 138–46.

Knick, S.T. and Rotenberry, J.T.: 1995, 'Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds', *Conserv. Bid.* 9, 1059–1071.

Koopowitz, H., Thornhill, A. D. and Andersen, M.: 1994, 'A general stochastic model for the prediction of biodiversity losses based on habitat conversion', *Conserv. Biol.* 8, 425–38.

Lacy, RC. and Lindenmayer, D.B.: 1995, 'A simulation study of the impacts of population subdivision brushtail possum Trichosurus caninus Ogilby (Phalangeridae: Marsupii), in south-eastern Australia. II. Loss of genetic variation within and between sub-populations', *Biol Conserv.* **73**, 131–143.

Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., McMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J. and Riser, P.G: 1991, 'The sustainable biosphere initiative: an ecological research agenda', Ecology **72**, 371–412.

MacMahon, J.A.: 1976, 'Species and guild similarity of North American desert mammal faunas: a functional analysis of communities', in: *Evolution of desert biota*, Goodall, D.W. (ed.), Univ. Texas Press, Austin, Texas USA, p. 133-148.

McCollin, D.: 1993, 'Avian distribution patterns in a fragmented wooded landscape (North Humberside, U.K): role of befsveen-patch and within-patch structure', *Global Ecol. Biogw. Letters* **3**, 48–62.

McIntyre, N.E.: 1995, 'Effects of forest patch size on avian diversity,' *Landscape Ecol.* **10**, 85–99.

Messer, J.J., Linthurst, RA. and Overton, W.S.: 1991, 'An EPA program for monitoring ecological status and trends,' *Environ. Man.* **17**, 67–78.

Noss, R.F. and Cooperrider, A.Y.: 1994, *Saving nature's legacy: protecting and restoring biodiversity.* Island Press, Washington, DC.

Noss, RF., LaRoe, E.T. and Scott, J.M.: 1995, *Endangered ecosystems of the United States: a preliminary assessment of* loss and *degradation.* U.S. National Biol Serv. Rpt 28, Washington, DC.

O'Connell, T.J., Jackson, L.E. and Brooks, R.P.: 1998a, *The bird community index: a tool for assessing biotic integrity in the mid-Atlantic Highlands.* Penn State Cooperative Wetlands Center Report No. 98-4, University Park, PAUSA

O'Connell, T.J., Jackson, L.E. and Brooks, Rl?: 1998b, 'Abii community index of biotic integrity for the mid-Atlantic Highlands', *Environ. Mon.* Assess. **51**, 145–156.

O'Connor, R.J., Jones, M.T., White, D., Hunsaker, C.T., Loveland, T., Jones, B. and Peston, E.: 1996, 'Spatial partitioning of environmental correlates avian biodiversity in the conterminous United States,' *Biodiv. Letters* **3**, 97–1 10.

O'Connor, l&J., Jones, M.T., White, D., Hunsaker, C., Loveland, T., Jones, B. and Preston, E: 1996, 'Spatial partitioning of environmental correlates of avian biodiversity in the conterminous United States,' *Biodiversity Letters* **3**, 97–110.

Ojii D.S., Galvin, K.A. and Turner, II, B.L.: 1994, 'The global impact of land-use change', *BioScience* **44**, 300–304.

O'Neill, R V., Krummel, J. R., Gardner, R H., Sugihara, G, Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S., Dale, V.H. and Graham, RL.: 1988, 'Indices of landscape pattern', *Landscape Ecol.* **1**, 153–62.

O'Neill, R.V., Hunsaker, C.T., Jones, K.B., Riitters, K.H., Wickham, J.D., Schwarz, P., Goodman, LA, Jackson, B. and Baillargeon, W.S.: 1997, 'Monitor& environmental quality at the landscape scale', *BioScience* **47**, 5 13-520.

Peterjohn, B.G: 1994, 'The North American Breeding Bii Survey', *J. American Birding Assoc.* **26**, 387-398.

Pulliam, H.R., Dunning, Jr., J.B. and Liu, L.: 1992, 'Population dynamics in complex landscapes: a case study', *Ecol. Appl.* **2**, 165–177.

Riitters, K.H., O'Neill, R.V. and Jones, K.B.: 1997. 'Assessing habitat suitability at multiple scales: a landscape-level approach', *Biol. Conserv.* **81**, 191–202

SAS: 1990, *SAS/SAT User's Guide, Version 6, Fourth Edition, Vol. 2, SAS Institute Inc., Cary, North Carolina, USA.*

Saunders, D.A., Hobbs, RJ. and Margules, C.R.: 1991, 'Biological consequences of ecosystem fragmentation: *a review*', *Conserv. Biol.* **5, 18–32.**

Schlesinger, W.H., Reynolds, J.F., Cunningham, GL., Huenneke, L.F.,Jarrell, W.M., Vi R.A. and Whitford, W.G: 1990, 'Biological feedbacks in global desertification', Science **247, 1043–1048.**

Scott, J.M., Davis, F., Csuti, B., Noss, R, Butterfield, B., Groves, G, Anderson, H., Caicco, S., D'Erchia, F., Edward, Jr., T.C., Ullii J. and Wright, R.G: 1993, 'GAP Analysis: a geographic approach to protection of biological diversity', *Wildl. Monogr.* **123, 1–41.**

Short, J. and Turner, B.: 1994, 'A test of the vegetation mosaic hypothesis: a hypothesis to explain the decline and extinction of Australian mammals', *Conserv. Biol.* **8, 439–49.**

Short, H.L. and Hestbeck, J.B.: 1995, 'National biotic resource inventories and GAP analysis', *Bioscience 45, 535-539.*

Szaro, R: 1986, 'Guild management: an evaluation of avian guilds as a predictive tool', *Environ Man.* **10, 681–688.**

Turner, M. G: 1989, 'Landscape ecology: the effect of pattern on process', *Annu. Rev Ecol. Syst.* **20,** 171-97.

Turner, S. J., O'Neill, R.V., Conley, W., Conley, M.R. and Humphries, H.C.: 1991, 'Pattern and Scale: statistics for landscape ecology', p. 17–49, in M. G Turner and R H. Gardner (eds.) *Quantitative Methods in Landscape Ecology.* Springer-Verlag, New York.

United Nations Environmental Programme (UNEP): 1992, *World Atlas of Desertification.* Edward Arnold, London.

Van Home, B. and Wiens, J.A.: 1991, 'Forest bii habitat suitability models and the development of general habitat models' U.S. Fii and Wildl. Serv., *Fish Wildl. Res.* **8, 3** lpp.

Verboom, J., Schotman, A., Opdam, P. and Metz, J.A.J.: 1991, 'European nuthatch metapopulations in a fragmented agricultural landscape', *Oikos* **61, 149–56.**

Vogelmann, J.E., Sohl, T. and Howard, SM.: 1998, 'Regional characterization of land cover using multiple sources of data', *Photogr. Engin. Remote Sens.* **64, 45–57.**

Whitcomb, RF., Robbii, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and Bystrak, D.: 1981, 'Effects of forest fragmentation on avifauna of the eastern deciduous forest', pp. 125–205, in R.L. Burgess and D.M. Sharpe (eds.), *Forest island dynamics in man-dominated landscapes.* Springer-Verlag, New York.

Wilson, M.F., de Santo, T.L., Sabag, C. and Armesto, JJ.: 1994, 'Avian communities of fragmented south-temperate rainforests *in* Chile', *Conserv. Biol.* **8, 508–520.**

Woodley, S.J., Kay, J. and Francis, G: 1993, *Ecological integrity and the management of ecosystems. St Lucie Press,* Ottawa, *Canada.*