GEOGRAPHIC ANALYSIS OF SPECIES RICHNESS AND COMMUNITY ATTRIBUTES OF FOREST BIRDS FROM SURVEY DATA IN THE MID-ATLANTIC INTEGRATED ASSESSMENT REGION

EMMANUELLE CAM[1], JOHN R. SAUER[2], JAMES D. NICHOLS[2], JAMES E. HINES[2] and CURTIS H. FLATHER[3]

[1]North Carolina State University Department of Forestry, Raleigh, NC USA; U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA; [2]U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA; [3]U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado 80526 USA

Abstract. Species richness of local communities is a state variable commonly used in community ecology and conservation biology. Investigation of spatial and temporal variations in richness and identification of factors associated with these variations form a basis for specifying management plans, evaluating these plans, and for testing hypotheses of theoretical interest. However, estimation of species richness is not trivial: species can be missed by investigators during sampling sessions. Sampling artifacts can lead to erroneous conclusions on spatial and temporal variation in species richness. Here we use data from the North American Breeding Bird Survey to estimate parameters describing the state of bird communities in the Mid-Atlantic Assessment (MAIA) region: species richness, extinction probability, turnover and relative species richness. We use a recently developed approach to estimation of species richness and related parameters that does not require the assumption that all the species are detected during sampling efforts. The information presented here is intended to visualize the state of bird communities in the MAIA region. We provide information on 1975 and 1990. We also quantified the changes between these years. We summarized and mapped the community attributes at a scale of management interest (watershed units).

1. Introduction

Development of human populations affects ecological systems in a wide variety of ways. This led Karr (1987) to advocate use of integrated biological, chemical and physical monitoring for assessment of human impacts on these systems. In this integrative approach, as in conservation biology or community ecology in general, estimation of species richness of local communities (or of groups defined taxonomically or ecologically) is a basic step. Investigation of variation in species richness over space and time, and identification of factors associated with these variations (including anthropogenic factors) are major research aims in those fields.

One of the main difficulties encountered when focusing on animal communities is that exhaustive lists of the species present in the study area are seldom obtained during sampling sessions (Connor and Simberloff 1978, Burnham and Overton 1979, Preston 1979, Gilbert and Lee 1980, Herwitz et al. 1996, Nichols

Environmental Monitoring and Assessment **63:** 81–94, 2000.
© 2000 *Kluwer Academic Publishers. Printed in the Netherlands.*

and Conroy 1996, Nichols et al. 1998ab, Boulinier et al. 1998a). Species richness can be estimated using the observed number of species present in the sample on condition that all the species present in the area of interest are detected. This condition is probably not met in many cases: species can be missed by investigators, and this often holds for plants as well (Gilbert and Lee 1980, Hervitz et al. 1996).

Incomplete detection of species is likely to affect estimation of quantities other than species richness *per-se*, but computed from richness measured in two points in time or space, such as extinction probability or extinction rate (Diamond and May 1977, Hervitz et al. 1996, Nichols et al. 1998b). Indeed, a species recorded as present in the past in a given area would be considered as "extinct" if it is not recorded in some later year, but this might only be linked to failure to detect the species in question during the later sampling session. Similarly, failure to detect a species present in one location while it was recorded elsewhere can lead to erroneous conclusions concerning the similarity of the species composition of the two sites (Nichols et al. 1998b). The bias in estimates of species richness linked to failure to correct observed numbers for species detection probability might be mitigated in studies focusing on biogeographical issues or fundamental community ecology using data collected repeatedly over long periods of time. In these cases one can take advantage of the cumulative field effort over time to obtain a more accurate estimate of richness, under the assumption that temporal variations in species richness can be neglected. However, the objectives in conservation biology sometimes preclude use of this kind of data. Assessment of the contemporary state of ecological systems requires resorting to data collected within short periods of time. Investigation of temporal changes in species richness requires estimation of the richness corresponding to two specific points in time.

Now, our ability to measure species richness is crucial for biomonitoring, and for understanding the functioning of ecological systems. Elaboration of management plans and assessment of their efficiency depend on our ability to assess the state of animal communities, and to test relevant hypotheses. Temporal and spatial variation in local species richness form the basis of assessment of management plans, and of studies investigating the influence of anthropic disturbance on ecological communities. The difficulty in enumerating all the species in a community has long been recognized (e.g., Preston 1979), and this led to development of estimation methods that explicitly incorporate species detection probability (Otis et al. 1978, Burnham and Overton 1978, 1979). This kind of approach has recently received a growing attention (Nichols and Conroy 1996, Nichols et al. 1998ab, Boulinier et al. 1998ab) and software is now available that permits use of appropriate statistical inference procedures (Hines et al. 1999).

Here we present applications of this approach to estimation of species richness and derived parameters such as extinction probability and turnover (Boulinier et al. 1998b, Nichols et al. 1998a), or relative species richness (Cam et al. in press). We focus on bird communities in the mid-Atlantic region. Our source of data is the North American Breeding Bird Survey (BBS; Robbins et al. 1986). This work has

been carried out as part of the Mid-Atlantic Integrated Assessment (MAIA) project (Jones et al. 1997). We illustrate the use of the capture-recapture approach and provide maps of community attributes for various groups of species in the MAIA region. The methods are broadly applicable to survey information from a variety of taxa, and should be of direct use in additional studies in other regions.

2. Methods

2.1 SAMPLING DESIGN AND ESTIMATION OF SPECIES RICHNESS

Several approaches can be used to sample an area to estimate species richness (Nichols and Conroy 1996). The approach we used here is based on quadrat sampling: the total area of interest is subdivided into several small sampling units (quadrats). Investigators select a subset of quadrats at random and enumerate the species present in each of these quadrats (Nichols and Conroy 1996). This results in a "detection history" for each species (Boulinier et al. 1998a, Nichols et al. 1998ab): a row of zeros and ones indicating the quadrats where the species was not recorded or recorded, respectively.

Several estimators can be used for estimating species richness from such a sampling design (reviewed by Bunge and Fitzpatrick 1993). The approach we chose is based on estimators developed for capture-recapture data from closed animal populations (e.g., see Otis et al. 1978, Burnham and Overton 1979, White et al. 1982, Pollock and Otto 1983, Pollock et al. 1990, Rexstad and Burnham 1991, Nichols and Conroy 1996, Boulinier et al. 1998a, Nichols et al. 1998ab). This approach requires sampling the community of interest repeatedly within a short period of time (Boulinier et al. 1998a, Nichols et al. 1998a). This aims at meeting the underlying assumption of "closure" of the community (Pollock and Otto 1983, Pollock et al. 1990): extinction and colonization probabilities are supposed to be negligible within that period of time (Boulinier et al. 1998a). Estimates based on these capture-recapture models can be computed using the software program CAPTURE (Rexstad and Burnham 1991), or COMDYN (Hines et al. 1999); we used the latter.

The richness estimates are computed using models differing in their assumptions about sources of variation in detection probability (e.g., heterogeneity among species, influence of time, observer; reviewed by Boulinier et al. 1998a). Following the suggestion of Boulinier et al. (1998a), we used model M(h), which permits variation in detection probabilities among species in the community (Otis et al. 1978, White et al. 1982). We used the jackknife estimator for this model proposed by Burnham and Overton (1978, 1979). The data required for estimation with this estimator are observed frequencies, f_h, which correspond to the number of species observed on exactly $h = 1, 2, 3, 4,..., K$ sampling units (Boulinier et al. 1998a, Nichols et al. 1998a).

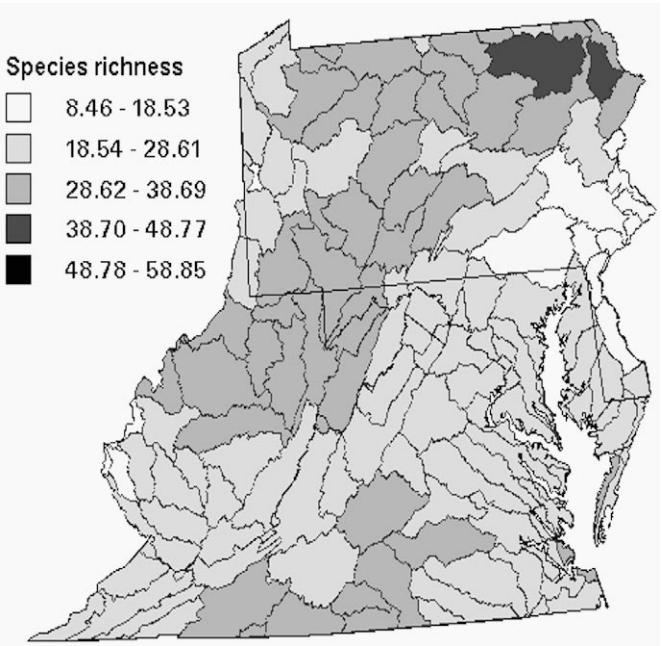

Figure 1. *Estimated species richness in forest birds, 1990.*

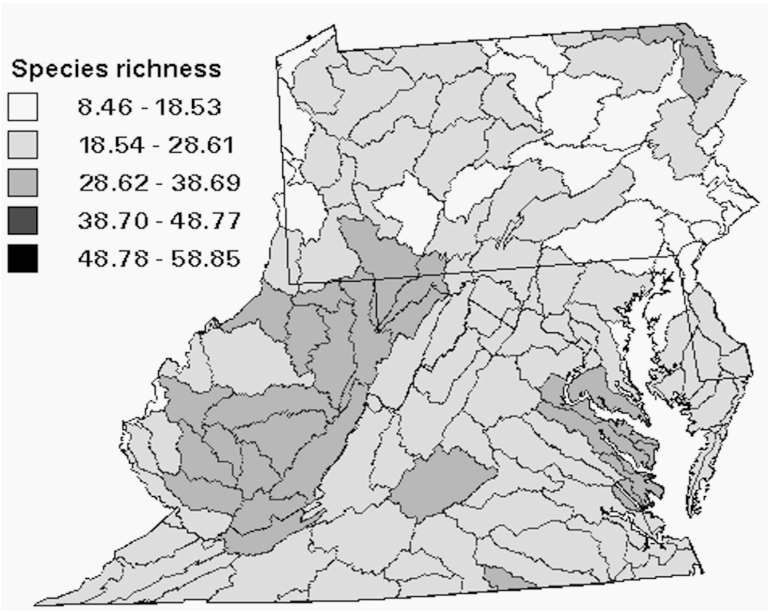

Figure 2. *Estimated species richness in forest birds, 1975.*

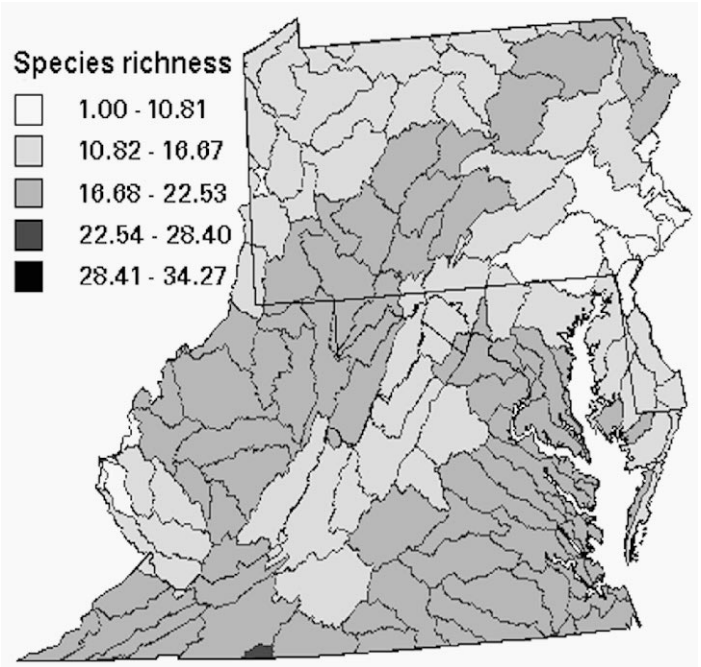

Figure 3. *Estimated species richness in area-sensitive birds, 1990.*

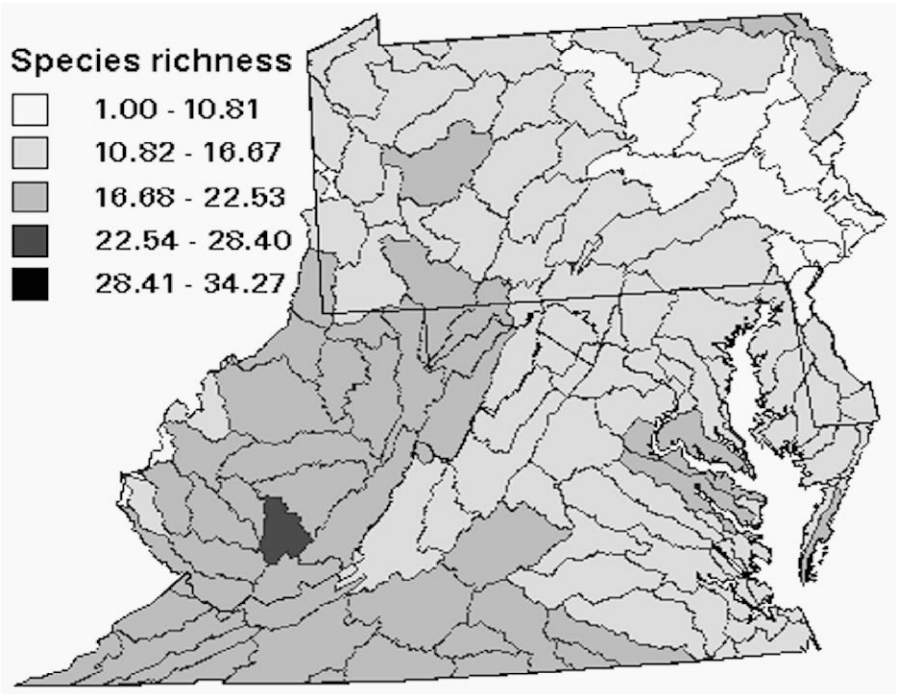

Figure 4. *Estimated species richness in area-sensitive birds, 1975.*

2.2 AVIAN DATA

We used data from the BBS (Robbins et al. 1986) to compute metrics describing the state of avian communities in the MAIA region. This survey started in 1966 and continues at present. The data are collected once a year in the spring, on more than 4,000 permanent survey routes located along secondary roads in North America. The sampling design is standardized: the routes are 39.4 km long, with 50 stops spaced at 0.8 km intervals. The observer drives along the route, and records all the species seen or heard during a 3-minute observation period at each stop.

2.3 MAPPING OF COMMUNITY ATTRIBUTES

Most of the community attributes presented here were mapped at a scale of management interest: the watershed. We used the coverage developed by Jones et al. (1997) for the MAIA region and watershed boundaries. We estimated watershed means by first using inverse distancing (Isaaks and Srivastava 1989) to interpolate mean abundance for a systematically located grid of points. Then values from points falling in each watershed were averaged. The basic data correspond to one value per route: we used these data to specify the data range and 5 classes of equal width which were used in maps. In case the same attribute is represented for 2 years (e.g., 1975 and 1990), we used the values from 1990 to specify these classes.

3. Species Richness

We estimated species richness from BBS data for two groups of birds of management interest: forest-breeding species, and area-sensitive species as defined in Robbins et al. (1989, see also Boulinier et al. 1998b for lists of species). Distinct regional and temporal patterns exist (Figures 1–4).

4. Community Dynamics

Estimation of quantities describing temporal change in local species richness requires sampling the community of interest at two temporal scales (Nichols et al. 1998a), following Pollock's robust design (Pollock 1982). This approach requires specification of *primary* and *secondary* sampling periods (Nichols et al. 1998a). Change is estimated between primary periods (i.e., years i and j, 1975 and 1990), and secondary sampling is conducted within primary periods (i.e., the stops sampled in each year within a BBS route). Local extinction probability corresponds to the probability that a species present in the community at time i is present in the community at time j, with $j > i$. This parameter (1) is computed using R_i, the num-

ber of species observed in primary session *i*, and by estimating the number of species belonging to R_i that are still present in primary session *j* (denoted as $M_j^{R_i}$). Local turnover (2) is the probability that a species in the community at time *j* was not present at time *i*. This parameter is computed using R_j, the number of species observed in primary session *j*, and by estimating the number of species belonging to R_j that were present in primary session *i* (denoted as $M_i^{R_j}$). Local extinction probability and turnover are estimated as:

$$1-\hat{\phi}_{ij}=1-\frac{\hat{M}_j^{R_i}}{R_i} \quad (1); \qquad 1-\hat{\phi}_{ji}=1-\frac{\hat{M}_i^{R_j}}{R_j} \quad (2),$$

where ϕ_{ij} denotes the complement of extinction probability and ϕ_{ji} the complement of turnover. Note that our estimates are based only on 2 points in time (Figures 5–8), but that Boulinier et al. (1998b) used the average year-to-year extinction probability and turnover to address the influence of forest habitat fragmentation on community stability.

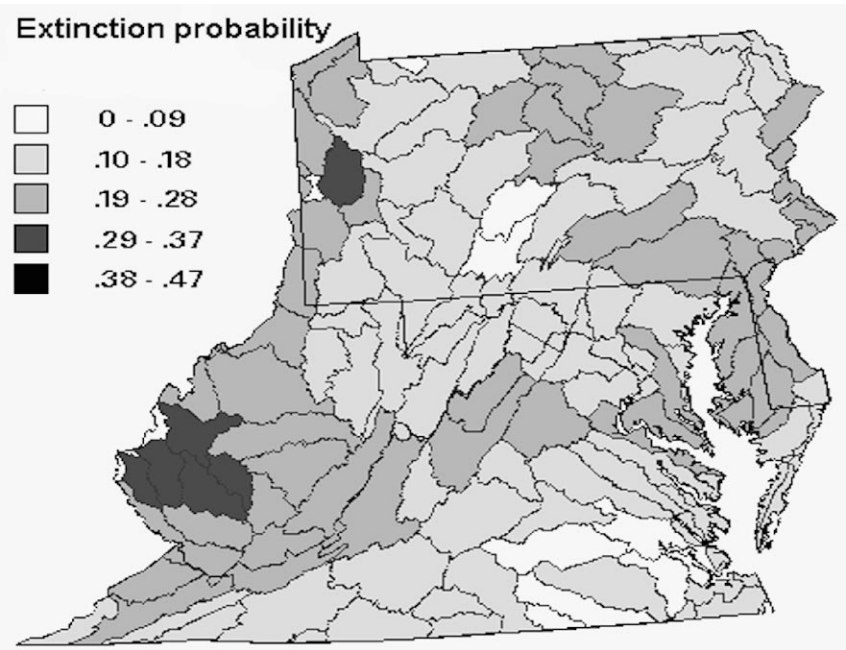

Figure 5. *Estimated local extinction probability between 1975 and 1990 in forest birds.*

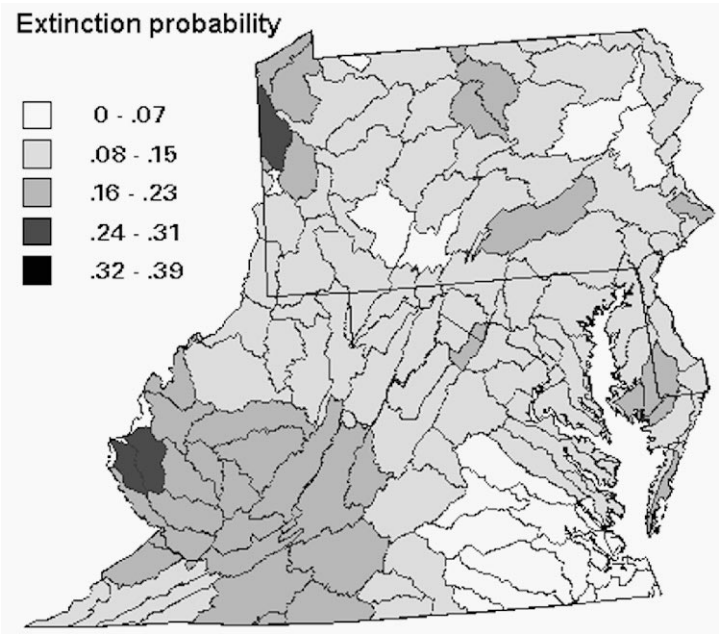

Figure 6. *Estimated local extinction probability between 1975 and 1990 in area-sensitive birds.*

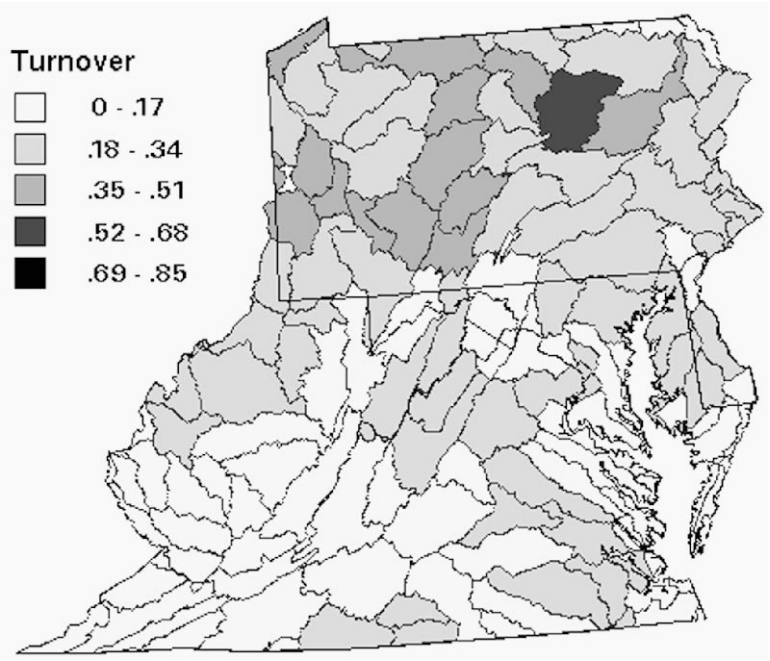

Figure 7. *Estimated local turnover between 1975 and 1990 in forest birds.*

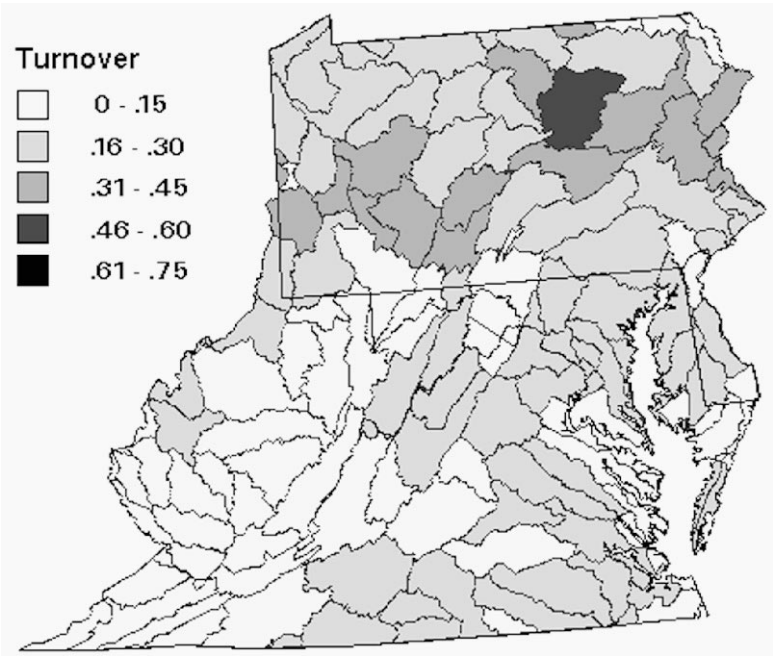

Figure 8. *Estimated local turnover between 1975 and 1990 in area-sensitive birds.*

5. Relative Species Richness

The degree of completeness of a local community relative to a "potential" community, or a species pool (i.e., relative species richness; Cam et al. in press) is also of particular interest for ecological assessment. This can be assessed using capture-recapture models. This requires definition of a reference species list, and estimation of the number of species in that list present at a site in a given year (Cam et al. in press). Here we developed a reference list (or species pool) from regional data: we accomplished this by listing all the species detected within the intersection between a circular scene radius 80 km centered on the route of interest, the state, and the physiographic stratum (Bystrak 1981) to which the route belonged, for all years of the BBS.

Let R denote the number of species in the pool. Relative species richness is computed as the ratio between the estimated number of species in that pool that are present on the route of interest in year j, (denoted as M_j^R), and the number of species in the pool (Cam et al. in press).

$$\hat{\phi}_j = \frac{\hat{M}_j^R}{R} \qquad (3)$$

In order to insure statistical independence of the two terms in equation (3), we did not include species detected only on the specific route of interest in the year of

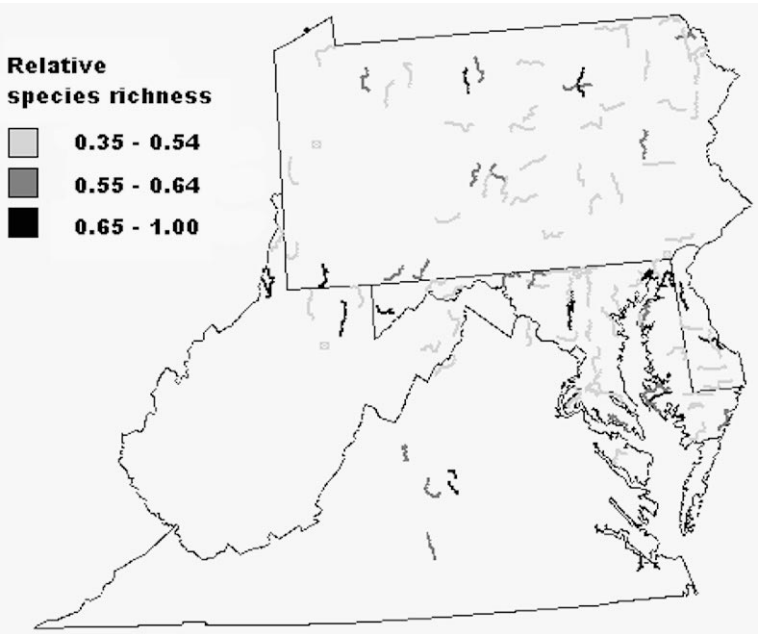

Figure 9. *Estimated relative species richness, 1992.*

interest. This parameter is sensitive to the number of BBS routes used to specify the species pool (Cam et al. in press). Consequently, we only retained data from routes that have a minimum of 5 routes in the area used to specify the pool, to avoid problems linked to small sample size. Exclusion of data from areas with a lower density of routes precluded use of the previous approach to mapping. As data were too sparse to allow interpolation, we present a route level map (Figure 9).

6. Conclusion

Variation in species richness over time or space provides a basis for studying human impacts on ecological communities, or assessing management plans. Many studies in community ecology investigate the relationship between spatial variation in environmental characteristics and in species richness, or the relationship between their temporal variation. When species detection probabilities are lower than 1, temporal or spatial variances in observed species richness are likely to be biased (Nichols et al. 1998b): they reflect not only true variances in species richness, but also sampling variances linked to detection probabilities lower than 1. In situations where not all the species are detected during sampling sessions, we recommend use of approaches to estimation of species richness that permit correction of count data for species detection probabilities (Nichols and Conroy 1996).

Here we have presented some extensions of the probabilistic approach to estimation of species richness from presence-absence data to estimation of parameters describing changes in local richness over time (see Nichols et al. 1998a for additional information). This estimation procedure has been successfully used by Boulinier et al. (1998b) for investigating the relationship between forest habitat fragmentation and temporal variability in forest bird communities. Spatial variation in species richness, and in community composition, can also be addressed using this kind of statistical inference procedure (Nichols et al. 1998b).

We have also presented an extension to estimation of relative species richness, that is, the richness of the target community relative to that of a reference community ("completeness"; Cam et al. in press). This metric has been used to address the question of the influence of urbanization on bird communities in the MAIA region (Cam et al. in press). This metric allows flexibility in the specification of the "reference community". The species pool can correspond to the list of species found in an undisturbed location (i.e., predisturbance or "original" community). In this case this relative state can be viewed as a measure of ecological integrity (Karr 1987, 1991). Integrity is a key-concept developed to respond to the urgent need to evaluate human impacts on ecological systems; it is an operational assessment tool relevant to conservation (Karr 1987, 1990, 1991). The pool can also correspond to an historical list of species. In the latter case, relative richness permits assessment of temporal change in the state of the community of interest (Cam et al. in press). In addition, this parameter permits comparisons of several communities in different locations.

This metric is not only relevant to conservation, but also to recent theoretical and empirical studies that investigated the influence of regional factors on local richness (Ricklefs 1987, Cornell and Lawton 1992, Cornell 1993, Ricklefs and Schluter 1993, Angermeier and Wiston 1998, Karlson and Cornell 1998). Local richness might depend on both local and regional environmental factors (Ricklefs and Schluter 1993). Differences in local richness in two locations might also reflect differences in the size of the species pools available at each location. Thus, it might be desirable to compare relative species richness rather than richness *per-se* (Cam et al. in press). Furthermore, a relationship between local richness and richness at a larger spatial scale could have important consequences in terms of specification of management goals. Indeed, a dependency of local richness on richness at a larger scale would imply that an integrative approach to management at various spatial scales is necessary. This would indicate that the state of local communities cannot be understood without investigating factors influencing species richness at a larger scale.

Distinct regional and temporal patterns exist in species richness, extinction probability, turnover, and integrity of forest birds in the MAIA region. The various metrics indicate spatio-temporal variation in the number of species of forest-breeding birds in the MAIA region. The most striking temporal trends correspond to a decrease in species richness in southwestern watersheds, while richness

increased in extreme northeastern units. The state of forest bird communities has not changed in the upper portion of the Chesapeake Bay between 1975 and 1990 (a very urbanized area; Jones et al. 1997): species richness remained low. The same trend is observed in area-sensitive species. However, caution must be exercised when interpreting the maps: the values are estimated with a certain level of precision (which has not been displayed here). In addition, change in colors at the watershed level might reflect a very slight change in species richness between 1975 and 1990 (i.e., the two values for a given watershed might both be very close to the cut points).

The methods and analyses presented here were directed toward forest-breeding birds, and constitute a component of an assessment of the conditions of the forests in the MAIA region (Stolte 1998). They also provide a useful addition to projects in progress for assessing bird community integrity in the MAIA region. Brooks et al. (1998) and O'Connell et al. (1998) have been monitoring birds at a variety of sites throughout MAIA, and have proposed measures of bird community integrity based on relative species composition of birds in generalist and specialist guilds. Regional-scale patterns documented from BBS data will assist in interpretation of patterns documented from the extensive study of O'Connell et al. (1998). Jones et al. (1998) have analyzed patterns of bird species diversity relative to landscape indicators in the MAIA (e.g., Jones et al. 1997). Distinct regional and temporal patterns exist in species richness, extinction probability, turnover, and relative species richness in forest birds in the MAIA region. Our future work will examine environmental correlates of these spatial patterns in the context of watersheds (Jones et al. 1997).

Acknowledgments

Emmanuelle Cam was supported by a Cooperative Agreement between the United States Department of Agriculture's Forest Service and North Carolina State University's Department of Forestry. We are grateful to Ian Thomas, Jane Fallon and Greg Gough for their help with GIS, and to an anonymous referee for his/her comments on an earlier version of this manuscript.

References

Angermeier, P.L. and Winston, M.R.: 1998, 'Local vs. Regional Influences on Local Diversity in Stream Fish Communities of Virginia', *Ecology* **79**, 911–927.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. and Pollock, K.H.: 1998a, 'Estimating Species Richness: the Importance of Heterogeneity in Species Detectability', *Ecology* **79**, 1018–1028.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. and Pollock, K.H.: 1998b, 'Higher Temporal Variability of Forest Breeding Bird Communities in Fragmented Landscapes', *Proceedings of the National Academy of Sciences, USA* **95**, 7497–7501.

Brooks, R.P., O'Connell, T.J. Wardrop, D.H. and Jackson, L.E.: 1998, 'Towards a Regional Index of Biological Integrity: the Examples of Forested Riparian Ecosystems', *Environmental Monitoring and Assessment* **51**(1–2), 131–143.

Bunge, J. and Fitzpatrick, M.: 1993, 'Estimating the Number of Species: A Review', *Journal of the American Statistical Association* **88**, 364–373.

Burnham, K.P. and Overton, W.S.: 1978, 'Estimation of the Size of a Closed Population When Capture Probabilities Vary Among Animals', *Biometrika* **65**, 625–633.

Burnham, K.P. and Overton, W.S.: 1979, 'Robust Estimation of Population Size When Capture Probabilities Vary Among Animals', *Ecology* **60**, 927–936.

Bystrak, D.: 1981, 'The North American Breeding Bird Survey', in: *Estimating Numbers of Terrestrial Birds, Studies in Avian Biology 6*, C. J. Ralph and M. J. Scott (eds.), Cooper Ornithological Society, Lawrence, KS, 34–41pp.

Cam, E., Nichols, J.D., Hines, J.E., Sauer, J.R. and Flather, C.H.: in press, *Estimation of Relative Species Richness for Assessing the Degree of Completeness of Ecological Communities: Avian Communities and Urbanization in the Mid-Atlantic States.*

Connor, E.F. and Simberloff, D.S.: 1978, 'Species Number and Compositional Similarity of the Galapagos Flora and Fauna,' *Ecological Monographs* **48**, 219–248.

Cornell, H.V. and Lawton, J.H.: 1992, 'Species Interactions, Local and Regional Processes and Limits to the Richness of Ecological Communities: a Theoretical Perspective', *Journal of Animal Ecology* **61**, 1–12.

Cornell, H.V.: 1993, 'Unsaturated Patterns in Species Assemblages: the Role of Regional Processes in Setting Local Species Richness', in: *Species Diversity in Ecological Communities. Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D. (eds.), University of Chicago Press, Chicago.

Cresswell, J.E. and Vidal-Martinez, V.M.: 1995, 'The Investigation of Saturation in the Richness of Communities: Some Comments on Methodology', *Oikos* **72**, 301–304.

Diamond, J.M. and May, R.M.: 1977, 'Species Turnover Rates on Islands: Dependence on Census Interval', *Science* **197**, 266–270.

Gilbert F.S. and Lee, S.B.: 1980, 'Two Perils of Plant Population Dynamics', *Oecologia* **46**, 283–284.

Herwitz, S. R., Wunderlin, R.P. and Hansen, B.P.: 1996, 'Species Turnover on a Protected Subtropical Barrier Island: a Long-Term Study', *Journal of Biogeography* **23**, 705–715.

Hines, J.E., Boulinier, T., Nichols, J.R., Sauer, J.D. and Pollock, K.H.: 1999, 'COMDYN: Software to Study the Dynamics of Animal Communities Using a Capture-Recapture Approach', *Bird Study* in press.

Isaaks, E. H. and Srivastava, R. M.: 1989, *An Introduction to Applied Geostatistics*, Oxford University Press, New York. 561pp.

Jones, K.B., Riitters, K.H., Wickham, J.D., Tankersley, R.D., 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*, United States Environmental Protection Agency, Office of Research and Development, Washington DC.

Jones, K.B., Riitters, K.H., Wickham, J.D., Neale, A.C. and O'Neill, R.V.: 1998, 'Patterns of Breeding Bird Diversity and Landscapes in the United States Mid-Atlantic Region', in: *Abstracts, MAIA Working Conference*, Sheraton Inner Harbor Hotel, Baltimore, MD, November 30 – December 2, 1998, pp. 19.

Karlson, R.H. and Cornell, H.V.: 1998, 'Scale-Dependent Variation in Local vs. Regional Effects on Coral Species Richness', *Ecological Monographs* **68**, 259–274.

Karr, J.R.: 1987, 'Biological Monitoring and Environmental Assessment: a Conceptual Framework', *Environmental Management* **11**, 249–256.

Karr, J.R.: 1990, 'Biological Integrity and the Goal of Environmental Legislation: Lessons for Conservation Biology', *Conservation Biology* **4**, 244–250.

Karr, J.R.: 1991, Biological Integrity: a Long-Neglected Aspect of Water Resource Management. *Ecological Applications* **1**, 66–84.

Nichols, J.D. and Conroy, M.J.: 1996, 'Estimation of Species Richness', in: *Measuring and Monitoring Biological Diversity. Standard Methods for Mammals,* Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R. and Foster, M. (eds.), . Smithsonian Institution Press, Washington, DC., pp. 226–234.

Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. and Sauer, J.R.: 1998a, 'Estimating Rates of Local Extinction, Colonization and Turnover in Animal Communities', *Ecological Applications* **8**, 1213–1225.

Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. and Sauer, J.R.: 1998b, 'Inference Methods for Spatial Variation in Species Richness and Community Composition When Not All Species are Detected', *Conservation Biology* **12**, 1390–1398.

O'Connell, T.J., Jackson, L.E. and Brooks, R.P.: 1998, 'The Bird Community Index: A Tool for Assessing Biotic Integrity in the Mid-Altantic Highlands', in: *Abstracts, MAIA Working Conference*, Sheraton Inner Harbor Hotel, Baltimore, MD, November 30 – December 2, 1998, pp. 4.

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R.: 1978, 'Statistical Inference from Capture Data on Closed Animal Populations', *Wildlife Monographs* **62**.

Pollock, K.H. 1982. 'A Capture-Recapture Sampling Design Robust for Unequal Catchability', *Journal of Wildlife Management* **46**, 252–257.

Pollock, K.H., Nichols, J.D., Brownie, C. and Hines, J.E.: 1983, 'Statistical Inference for Capture-Recapture Experiments', *Wildlife Monographs* **62**.

Preston, F.W.: 1979, 'The Invisible Birds', *Ecology* **60**, 451–454.

Pollock, K.H. and Otto, M.C.: 1990, 'Robust Estimation of Population Size in Closed Animal Populations from Capture-Recapture Experiments', *Biometrics* **39**, 1035–1049.

Preston, F.W.: 1979, 'The Invisible Birds', *Ecology* **60**, 451–454.

Rexstad, E. and Burnham, K.P.: 1991, *User's Guide for Interactive Program CAPTURE. Abundance Estimation of Closed Animal Populations,* Colorado State University, Fort Collins, Colorado, USA.

Ricklefs, R.E.: 1987, 'Community Diversity: Relative Roles of Local and Regional Processes', *Science* **235**, 167–171.

Ricklefs, R.E. and Schluter, D.: 1993, 'Species Diversity: Regional and Historical Influences', in: *Species Diversity in Ecological Communities. Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D. (eds), University of Chicago Press, Chicago.

Robbins, C.S., Dawson, D.K. and Dowell, B.A.: 1989, 'Habitat Area Requirements of Breeding Forest Birds of the Middle Atlantic States', *Wildlife Monographs* **103**.

Stolte, K.W., Smith, W.H. and Stallings, C.: 1998, 'Analysis of Forest Health in the MAIA Region', Page 35 in *Abstracts, MAIA Working Conference*, Sheration Inner Harbor Hotel, Baltimore, MD, November 30 – December 2, 1998, pp. 35

White, G.C., Anderson, D.R., Burnham, K.P and Otis, D.L.: 1982, *Capture-Recapture Removal Methods for Sampling Closed Populations,* Los Alamos National Laboratory Publication LA-8787-NERP.