

FOREST FRAGMENTATION AND BIRD COMMUNITY DYNAMICS: INFERENCE AT REGIONAL SCALES

THIERRY BOULINIER,^{1,2,3,6} JAMES D. NICHOLS,³ JAMES E. HINES,³ JOHN R. SAUER,³ CURTIS H. FLATHER,⁴ AND
KENNETH H. POLLOCK⁵

¹Laboratoire d'Ecologie, C. N. R. S.—UMR 7625, Université Pierre et Marie Curie, 75252 Paris, France

²North Carolina Cooperative Fish and Wildlife Research Unit, North Carolina State University,
Raleigh, North Carolina 27695 USA

³U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA

⁴U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado 80526 USA

⁵Institute of Statistics, North Carolina State University, Box 8203, Raleigh, North Carolina 27695-8203 USA

Abstract. With increasing fragmentation of natural areas and a dramatic reduction of forest cover in several parts of the world, quantifying the impact of such changes on species richness and community dynamics has been a subject of much concern. Here, we tested whether in more fragmented landscapes there was a lower number of area-sensitive species and higher local extinction and turnover rates, which could explain higher temporal variability in species richness. To investigate such potential landscape effects at a regional scale, we merged two independent, large-scale monitoring efforts: the North American Breeding Bird Survey (BBS) and the Land Use and Land Cover Classification data from the U.S. Geological Survey.

We used methods that accounted for heterogeneity in the probability of detecting species to estimate species richness and temporal changes in the bird communities for BBS routes in three mid-Atlantic U.S. states. Forest breeding bird species were grouped prior to the analyses into area-sensitive and non-area-sensitive species according to previous studies. We tested predictions relating measures of forest structure at one point in time (1974) to species richness at that time and to parameters of forest bird community change over the following 22-yr-period (1975–1996). We used the mean size of forest patches to characterize landscape structure, as high correlations among landscape variables did not allow us to disentangle the relative roles of habitat fragmentation per se and habitat loss.

As predicted, together with lower species richness for area-sensitive species on routes surrounded by landscapes with lower mean forest-patch size, we found higher mean year-to-year rates of local extinction. Moreover, the mean year-to-year rates of local turnover (proportion of locally new species) for area-sensitive species were also higher in landscapes with lower mean forest-patch size. These associations were not observed for the non-area-sensitive species group.

These results suggest that landscape structure may influence forest bird communities at regional scales through its effects on the total number of species but also on the temporal rates of change in community composition. Evidence for higher rates of local extinction and turnover in more fragmented landscapes suggests that bird communities function as metapopulations at a regional scale, and points out the importance of colonizations and recolonizations from surrounding landscapes to local community dynamics. Further, our results illustrate that the methods used to estimate the community parameters can be a powerful statistical tool in addressing questions relative to the dynamics of communities.

Key words: biodiversity; capture–recapture; community dynamics; detectability; forest bird communities; habitat fragmentation; landscape ecology; local extinction rate; species richness; turnover rate.

INTRODUCTION

Dramatic reduction and fragmentation of forest cover in several parts of the world have prompted many to ask what the impacts of such changes are on animal abundance, species richness, and community dynamics

(e.g., Askins et al. 1990, Faaborg et al. 1995, Freemark et al. 1995, McGarigal and McComb 1995, Flather and Sauer 1996). Because of the importance of understanding the relationship between habitat fragmentation and community dynamics for ecological theory (MacArthur and Wilson 1967, Gilpin and Hanski 1991, Opdam 1991, Rosenzweig 1995), and for the management and conservation of biodiversity (Fahrig and Merriam 1994), there is a general interest in empirical studies on this subject. This general interest in associations between habitat loss and fragmentation and forest bird

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⁶ Present address: Laboratoire d'Ecologie, C.N.R.S.—UMR 7625, Université Pierre et Marie Curie, 7 Quai St. Bernard, 75252 Paris, France. E-mail: tboulini@snv.jussieu.fr

communities has led to the publication of several studies that have identified the roles of specific factors tied to the process of fragmentation (e.g., Martin 1988, Patton 1994). For example, in North America, forest fragmentation has been shown to have an array of effects on neotropical migratory birds through habitat loss, small forest-patch size, reduced proximity of patches, more edge, and negative interactions with species from surrounding nonforest patches (Whitcomb et al. 1977, 1981, Faaborg et al. 1995, Freemark et al. 1995, Robinson et al. 1995).

Landscapes with reduced forest cover are usually associated with higher forest fragmentation, i.e., higher disruption in the continuity of forest habitat (e.g., Robinson et al. 1995). It is useful to maintain a conceptual distinction between habitat loss and habitat fragmentation (Hanski 1999), but when they occur together, which is often, it may nevertheless be interesting to test predictions relating fragmentation in a broad sense (including habitat loss, increased amount of edge, and higher isolation among patches) to community dynamic parameters. This is what we did in this work. Although some studies have examined fragmentation at broad spatial scales (e.g., Robinson et al. 1995; for reviews see Opdam 1991, Andr  n 1994), effects of fragmentation on birds are nevertheless frequently considered at the scale of the forest patch (e.g., Blake and Karr 1987, Robbins et al. 1989, Askins et al. 1990, Hinsley et al. 1995). Much of the ecological theory that is brought to bear on the issue of fragmentation concerns the characteristics of specific habitat patches and the animal populations and communities that inhabit them at one point in time. Conversely, little is known on the dynamics of communities within landscapes. Thus, our interest in the present work was not on single habitat patches but on groups of habitat patches within a landscape, and on the potential effect of fragmentation on temporal changes of communities at that level. In a previous paper, we reported lower species richness and higher temporal variability in species richness over a 22-yr period for forest bird communities in more fragmented landscapes (Boulinier et al. 1998b). In the present work, we tested whether these patterns could be explained by a difference among landscapes in rates of change in community composition. Specifically, we investigated predictions relating rates of change in community composition (local extinction and turnover rates) to landscape structure.

Specific predictions can be derived from related theoretical work involving local extinction and colonization processes among habitat patches. For example, ideas from the theory of island biogeography (MacArthur and Wilson 1963, 1967) have been applied frequently to discussions of fragmentation (Wilcove et al. 1986). Likewise, if we consider communities at a landscape scale as collections of metapopulations, then some predictions can be deduced from consideration of the persistence of each species in the landscape (Hanski and Simberloff 1997). Further, local factors,

such as predation and brood parasitism on forest-interior bird species, have been reported to be higher in more fragmented landscapes (Robinson et al. 1995), and thus are suspected to alter the probability of local extinction of such species.

One important methodological problem faced when comparing changes in animal communities with landscape structure is that the probability of detecting a species is likely to vary among species and areas (Boulinier et al. 1998a). If this is the case, and if total counts of species observed are used (as has been done in most published studies, e.g., Freemark and Collins 1992, Greenberg et al. 1997, Wilson et al. 1997) then analyses may yield misleading results. For example, the number of species observed in an area is determined jointly by the number of species actually present and by their respective probabilities of being detected by the observer. In most surveys involving the sampling of an extensive number of locations, species detection probabilities are very likely <1 . For instance it has been shown that the probability of detection of species on routes of the North American Breeding Bird Survey (BBS) varies among species and among states (Boulinier et al. 1998a). One way of estimating the number of species present in an area is to use a capture–recapture approach that relies on the pattern of detection–nondetection of species in a series of temporal or spatial replicates (Burnham and Overton 1979, Bunge and Fitzpatrick 1993, Colwell and Coddington 1994, Nichols and Conroy 1996, see Boulinier et al. 1998a, b for an application with BBS data). It was proposed recently to apply the same approach to estimate parameters of community dynamics (Nichols et al. 1998a, b). In this paper we use this approach to test hypotheses relating forest bird–community dynamics to landscape structure in the eastern U.S.

In order to do so, we merged two independent, broad-scale monitoring efforts: BBS and digital Land Use and Land Cover data from the U.S. Geological Survey (U.S. Department of the Interior 1987). By linking these data spatially, we were able to couple information on forest bird communities with land-use and habitat patterns immediately surrounding each BBS survey route. We tested predictions relating measures of forest fragmentation at one point in time (1974) to parameters reflecting forest bird community change over the following 22-yr period (1975–1996). In order to facilitate the interpretation of our results in light of more classical studies dealing with associations between species richness and fragmentation, we first report a test of the relation between landscape fragmentation and species richness.

HYPOTHESES AND PREDICTIONS

The ecological literature contains competing hypotheses about effects of habitat fragmentation on species composition (e.g., see Villard et al. 1995). Based on the work of Preston (1960), Haila et al. (1993: p. 717) predicted that “species accrual in assemblages of

single fragments over years follows the pattern of random sampling." This prediction contrasts with North American studies suggesting that forest fragmentation leads to nonrandom reductions in species richness caused by losses of area-sensitive species (Whitcomb et al. 1981, Blake and Karr 1987, Robbins et al. 1989). The effect of fragmentation is notably expected to be different depending on whether the forest-breeding bird species considered are interior or edge specialists (Faaborg et al. 1995). We thus classified forest-breeding bird species of the mid-Atlantic region of North America into two groups, area-sensitive and non-area-sensitive, based on the work of Whitcomb et al. (1981) and Robbins et al. (1989). We predicted that relationships between mean forest-patch size and bird-community variables would hold for the area-sensitive group of bird species but not necessarily for the non-area-sensitive group.

One of the fundamental relationships of biogeography is the species–area relationship: the tendency for number of species within a taxonomic group to increase with increasing area (Preston 1960, 1962, MacArthur and Wilson 1963, 1967, Connor and McCoy 1979). We thus predicted that, for area-sensitive species, species richness would increase with increasing forest-patch size.

The two main parameters considered in this study (the rate of species local extinction and the rate of species local turnover) reflect year-to-year changes in community composition. Hypotheses and predictions about these quantities may depend on whether the studied communities are at equilibrium (*sensu* MacArthur and Wilson 1963, 1967) over the period considered, and must include consideration of the regional species pool. Such considerations are rarely made in studies that deal with species richness at one point in time, but their importance is clear if one is interested in the actual dynamics of local communities (Ricklefs and Schluter 1993). For example, let K denote the number of species in the regional pool within a geographic area of interest, N the number of species in a local community (e.g., a community sampled by a BBS route), ϕ the probability that a species present in the community in one year is present in the next year (i.e., does not go locally extinct), and γ the probability that a species not present in the community in one year (a member of $[K - N]$) is present the next (i.e., colonizes during the year). For a community in a state of dynamic equilibrium, the expected number of local extinctions will equal the expected number of local colonists:

$$E[N(1 - \phi)] = E[\gamma(K - N)]. \quad (1)$$

Eq. 1 can be used to deduce predictions about community dynamics for the equilibrium situation.

If Eq. 1 does not hold, then species richness for the community is increasing or decreasing over time, and predictions about parameters reflecting community change may depend on the direction of the overall change in species richness and on details about the rate

parameters, ϕ and γ . We can draw some inferences about whether the community is in equilibrium by examining the estimated rates of change in species richness between years, $\lambda_i = N_{i+1}/N_i$, and by testing for potential linear trends in the logarithm of species richness over the study period.

For area-sensitive species, local extinction probabilities are predicted to be higher for landscapes with smaller forest patches. This prediction follows from the tendencies for single-species population sizes to be smaller on smaller islands or patches (MacArthur and Wilson 1963, 1967) and for smaller populations to have higher extinction probabilities (e.g., MacArthur and Wilson 1963, 1967, Bailey 1964, Boyce 1992). Other potential effects of fragmentation, such as reduced connectivity among patches and greater exposure to biotic factors related to the amount of habitat edge, should also lead to increased extinction probabilities in more fragmented landscapes. As this prediction does not seem to depend on whether the studied communities are at equilibrium, it should hold regardless of changes in species richness.

Exact predictions about the relationship between fragmentation and the number of local colonizing species in both equilibrium and nonequilibrium situations will depend on the relative saturation of the community (the magnitude of $K - N$), as well as on details of the rate parameters. We computed a turnover statistic reflecting the proportion of species that are new at a particular time, in the sense that they were not present the previous sampling period (Nichols et al. 1998a). In the equilibrium situation, this turnover parameter should behave similarly to the extinction probability and should be larger for area-sensitive species in landscapes with lower forest-patch size (MacArthur and Wilson 1967, Simberloff 1972). In nonequilibrium situations, a general prediction depends on the direction of change in each landscape, and is therefore not possible. However, if the overall changes in species richness are similar among the compared landscapes, we would expect turnover to be higher in more fragmented ones (T. Boulinier, J. D. Nichols, and J. E. Hines, *unpublished simulation results*).

Predictions about the relationship between rates of temporal changes in species composition and landscape metrics would have been easier if we had had information on landscape structure at several points in time and could have described potential landscape changes. Unfortunately, we had landscape metrics only for the beginning of the period over which we estimated community-dynamic parameters. It can nevertheless be reasonably assumed that information on landscape structure at one point in time provides a strong basis for conservative predictions relating landscape structure to bird communities over a subsequent period of time. For instance, highly fragmented landscapes are likely to have remained fragmented over the study period (see *Discussion*).

MATERIALS AND METHODS

Geographic information on forest bird communities

The BBS provides information on the presence of bird species at a regional scale. The survey consists of >4000 roadside routes located on secondary roads throughout the United States and southern Canada. Each route is 39.4 km long and is surveyed once each year in June. A competent observer conducts 50 three-minute point counts at 0.8-km intervals on the roadside, recording all birds heard or seen. Data were summarized for each route in lists of species detected on groups of 10 consecutive point counts. Five summary lists of species were thus available per route. We focused our attention on those bird species that are associated with forest habitat according to the classification of Peterjohn and Sauer (1993). We further partitioned forest birds into two subcategories, area-sensitive and non-area-sensitive species, based on the findings of Robbins et al. (1989; see also Appendix).

Estimating parameters of bird-community dynamics

The different groups of sampling stations within each survey route were taken as sampling replicates of the bird communities associated with each route. For each survey route, species richness of the two groups of forest birds (area-sensitive and non-area-sensitive species) was estimated for each year using the jackknife estimator (Burnham and Overton 1979). The use of this capture-recapture approach is based on the recognition that some species are likely missed in sampling efforts. It takes into account potential heterogeneity in detectability among species and among survey routes. The application of this approach to BBS data is explained and justified by Boulinier et al. (1998a). The estimates of species richness were computed using software COMDYN (Hines et al. 1999); software CAPTURE (Rexstad and Burnham 1991) could have also been used.

Using the robust design approach (Pollock 1982), Nichols et al. (1998a) recently proposed a series of estimators to study the dynamics of communities. Among these, we used the estimator of the rate of change in species richness (which estimates the ratio of total number of species for two points in time), and two estimators which deal with changes in community composition between two points in time: the rate of local extinction and the rate of local turnover (proportion of locally new species). The rate of local extinction between time t and time $t + 1$ is one minus the survival rate of local species, which is the ratio of the number of species estimated to be present at time $t + 1$ among those detected at time t , over the number of species detected at time t . Similarly, the rate of local turnover is computed as the proportion of species at time $t + 1$ that are locally new since time t (see Nichols et al. [1998a] for a detailed description of the estimators). Estimates and associated variances were computed using COMDYN, which was developed specif-

ically for the study of the dynamics of animal communities (Hines et al. 1999), and which is available interactively on the Internet.

Linking forest structure with parameters of bird communities

Land Use and Land Cover Classification data from the U.S. Geological Survey (U.S. Department of the Interior 1987) were used to quantify landscape structure within a circular area of radius 19.7 km centered on each BBS route (area = 1200 km²). A radius of half the length of a BBS route was chosen to guarantee that each landscape scene would contain the whole route (the center of each circular area was placed on the midpoint of each route). High-altitude photographs, usually at scales smaller than 1:60 000, were used to digitize and transfer land-use and land-cover data to 1:250 000 base maps in grid format (U.S. Department of the Interior 1987). These landscape data were in raster format with each grid cell 200 m on a side. Several variables were measured and computed to characterize the landscape associated with each survey route (e.g., Flather and Sauer 1996). For the purpose of this paper, we focused on the three main variables describing forest cover and fragmentation: (1) the proportion of forested area, (2) the mean size of forest patches, and (3) the number of forest patches. These three variables are clearly not independent, but correspond to different aspects of the potential effects of forest fragmentation. As these variables were computed for each landscape scene, they incorporate both areas immediately surrounding the survey route and areas more distant to the route. We carried out our analyses on all survey routes for three northeastern U.S. states: Maryland, New York, and Pennsylvania, where several important studies of the effect of woodlot size on bird communities have been performed (e.g., Whitcomb et al. 1981, Robbins et al. 1989).

The natural logarithm ($x + 0.5$) of the mean forest-patch size and the arcsine of the square root of the proportion of forested area were used in the analyses in order to conform better to the assumption of normality of the residuals. For the year-to-year rate of change in the number of species, we computed the mean of the logarithm of point estimates (i.e., the geometric mean). The proportion of routes for which there was a significant linear trend in the logarithm of species richness was also investigated for the three states. For the year-to-year rate of local extinction, the mean of the estimates was computed over the study period for each route (considering only routes with ≥ 15 point estimates). The same was done to obtain the mean of the year-to-year turnover rates (proportion of new species).

Analyses were conducted using SAS (SAS Institute 1985), with variables describing community dynamics treated as dependent variables, the landscape metrics as independent continuous variables, and the state as a factor. Each analysis was conducted independently for the

TABLE 1. Summary of the forest-landscape characteristics (mean $\pm$ 1 SE) of the Breeding Bird Survey routes in Maryland, New York, and Pennsylvania in 1974.

Characteristic	Maryland	New York	Pennsylvania
Number of routes surveyed in 1975	47	90	77
Mean number of forest patches	168.1 ($\pm$ 11.7)	116.5 ($\pm$ 9.24)	90.5 ($\pm$ 8.93)
Mean forest-patch size (ha)	152.7 ($\pm$ 54.6)	717.6 ($\pm$ 199.5)	1348.0 ($\pm$ 531.3)
Mean proportion of forested area	0.35 ($\pm$ 0.03)	0.53 ($\pm$ 0.02)	0.58 ($\pm$ 0.03)
Mean probability of detection†			
Area-sensitive species	0.85 ($\pm$ 0.02)	0.89 ($\pm$ 0.01)	0.84 ($\pm$ 0.02)
Non-area-sensitive species	0.88 ($\pm$ 0.02)	0.89 ($\pm$ 0.01)	0.91 ($\pm$ 0.01)

† Mean ($\pm$ 1 SE) estimated probability of detection of forest species on the BBS survey routes in 1975 is reported.

three community parameters and pairwise interactions among the independent variables were tested. Within a multivariate analysis of variance framework, analyses of covariance were first conducted independently for area-sensitive and non-area-sensitive species. An analysis of covariance was further carried out on the within-route difference between the community dynamics parameter of area-sensitive and non-area-sensitive species. This was done in order to test for a difference in the slope of the relation between the community dynamics parameters and the landscape metrics.

RESULTS

General characteristics of the bird communities and forest fragmentation

Species richness was estimated for a total of 214 survey routes in 1975 (47, 90, and 77 for Maryland, New York, and Pennsylvania, respectively), and mean year-to-year extinction and turnover rates were computed over the 1975–1996 period for 122 of these routes (41, 46, and 35, for Maryland, New York, Pennsylvania, respectively). The characteristics of the landscape associated with each survey route differed among the three states considered (see Table 1). Survey routes in Pennsylvania were more forested than in Maryland and New York. In particular, the mean size of forest patches was larger in Pennsylvania than in the two other states. On average, the landscapes associated with the survey routes in Maryland were very fragmented with little forest cover, while New York landscapes were moderately fragmented. The overall mean estimated

probability of detection of species on each route in 1975 was >0.8 for the three states (Table 1).

The three variables describing landscape forest structure were highly correlated (Table 2). When the number of forest patches was high, both the proportion of forested area and mean forest-patch size were low (Table 2). Over all states, proportion of forested area explained 88% of the variance in mean forest-patch size. This covariation implied that it would have been difficult to disentangle the relative effects of the degree of forest cover from other forest-patch characteristics. All three measures provided qualitatively similar results when used in the bird-community analyses. Here, we present only the results when mean forest-patch size was used as a measure of forest fragmentation in its broad sense.

Species richness and forest fragmentation

There was evidence that species richness in 1975 was positively associated with habitat fragmentation for both area-sensitive and non-area-sensitive species, but also that the relationship between species richness and habitat fragmentation varied among the three states (Fig. 1, Table 3). As predicted, the total number of area-sensitive species was positively associated with the mean size of forest patches in the area surrounding each survey route in Maryland and New York (Fig. 1A and C; $r = 0.47$, $P > 0.0009$ and $r = 0.46$, $P > 0.0001$, respectively). The relationship was nonsignificant for Pennsylvania (Fig. 1E and F; $r = 0.18$, $P = 0.127$). For the non-area-sensitive species, a positive association between species richness and mean size of forest

TABLE 2. Correlation coefficients for the relationships among the three variables describing forest fragmentation around the survey route for the three states.

Statistic	Proportion of forested area			Number of forest patches		
	Maryland	New York	Pennsylvania	Maryland	New York	Pennsylvania
Proportion of forested area (arcsine square-root[x])	...	...	...	-0.5302	-0.7652	-0.7189
Mean forest-patch size (log[$x + 0.5$])	0.9092	0.9509	0.9144	-0.7970	-0.8552	-0.8328

Notes: In 1974, Maryland, $n = 47$; New York, $n = 90$; Pennsylvania, $n = 77$. $P < 0.0001$ for all data.

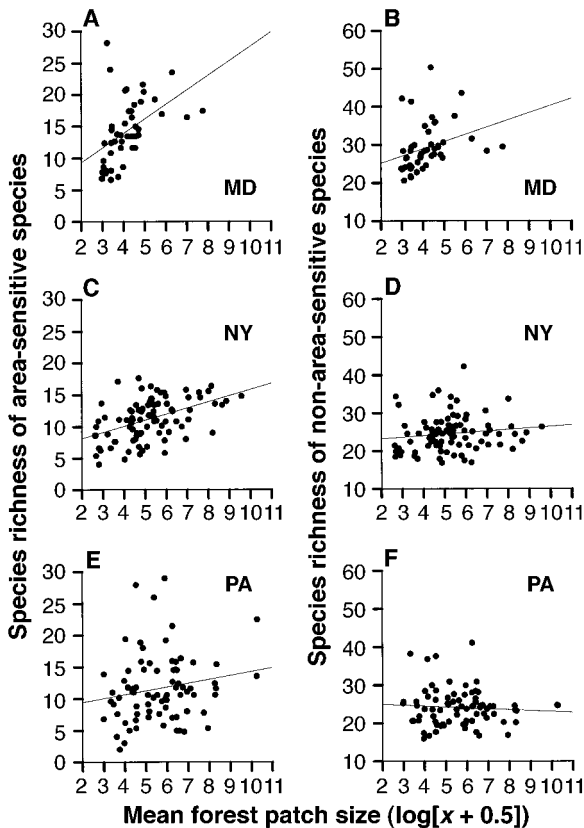


FIG. 1. Relation between species richness in 1975 and transformed mean forest-patch size in 1974 for area-sensitive and non-area-sensitive bird species for Maryland (MD; panels A and B), New York (NY; panels C and D), and Pennsylvania (PA; panels E and F).

patches was only observed in Maryland (Fig. 1A and B compared to Fig. 1C–F). The analysis of covariance of the difference in number of area-sensitive and non-area-sensitive species further showed a marginally significant difference between the two groups of species in the slope of the relationship between species richness and habitat fragmentation (Table 3).

One may note that most survey routes in Maryland were situated in landscapes with a smaller mean size of forest patches (with a transformed value of <5 ; see Fig. 1A and B), which was not the case for the New York and Pennsylvania survey routes (Fig. 1C–F). The total number of area-sensitive species on each route showed the strongest positive association with mean forest-patch size in the states where the landscapes showed the greatest degree of fragmentation.

Changes in species richness and community equilibrium

Most of the breeding bird survey (BBS) routes did not show a significant linear trend in logarithm of species richness over the 22-yr period, but there was a slight excess of positive trends for area-sensitive species: for area-sensitive species, 5, 5, and 17 routes showed significant positive trends among the 46, 63, and 50 routes of Maryland, New York, and Pennsylvania, respectively, compared to 3, 1, and 0 routes which showed significant negative trends (routes with ≥ 15 estimates of species richness). Rates of change in species richness showed the same patterns. Thus, overall, there was no evidence of large change in total number of area-sensitive and non-area-sensitive species within each of the routes over the study period, and most routes could be assumed to

TABLE 3. Results of analyses of covariance relating species richness in 1975 to mean forest-patch size and state.

Source	df	Type III ss	F	P
A) ANCOVA with species richness of area-sensitive species as the dependent variable (model $r^2 = 0.180$, $P < 0.0001$)				
State	2	24.795	0.69	0.5045
Mean patch size ($\log[x + 0.5]$)	1	488.055	27.03	0.0001
Mean patch size ($\log[x + 0.5]$) $\times$ state	2	109.689	3.04	0.0501
Error	208	3756.137		
B) ANCOVA with species richness of non-area-sensitive species as the dependent variable (model $r^2 = 0.172$, $P < 0.0001$)				
State	2	40.502	0.79	0.4553
Mean patch size ($\log[x + 0.5]$)	1	141.771	5.53	0.0196
Mean patch size ($\log[x + 0.5]$) $\times$ state	2	179.925	3.51	0.0317
Error	208	5332.693		
C) ANCOVA with the difference in species number between the two groups as the dependent variable (model $r^2 = 0.060$, $P < 0.0243$)				
State	2	2.946	0.05	0.9506
Mean patch size	1	103.739	3.57	0.0602
Error	208	6042.128		

Notes: Analyses of covariance were first conducted independently for area-sensitive and non-area-sensitive species (A and B). An analysis of variance was also conducted on the difference in number of area-sensitive species and non-area-sensitive species within each route (C). This latter multivariate analysis-of-variance approach provided a test for a potential difference between the slopes relating species richness and habitat fragmentation for the two groups of species. Pairwise interactions were included.

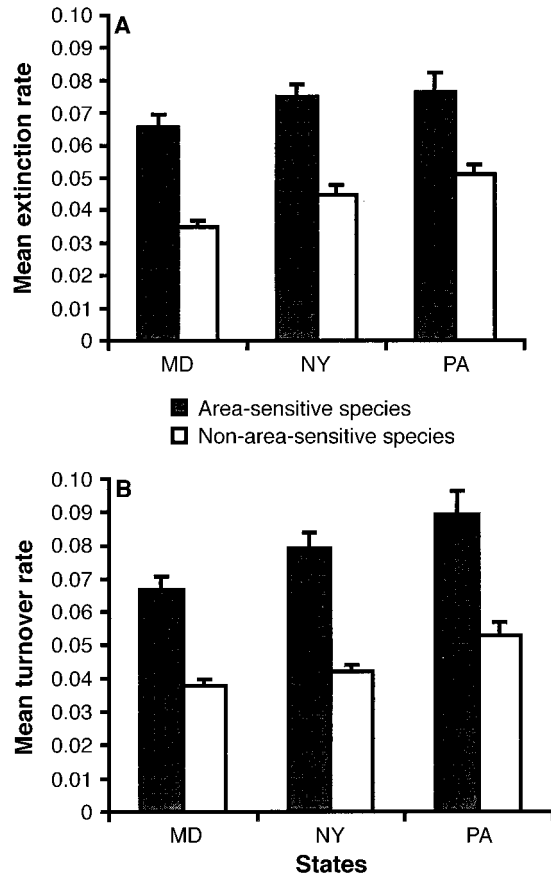


FIG. 2. (A) Mean year-to-year local extinction rate and (B) local turnover rate for area-sensitive and non-area-sensitive species in the three states. Error bars show one standard error of the mean.

be in equilibrium or show a slight increase in species numbers over the period considered.

Changes in community composition and forest fragmentation

We report here the results concerning the two parameters reflecting change in community composition over the 1975–1996 study period. Annual estimates of local extinction rate were small and varied mostly between 0.0 and 0.3. For area-sensitive species, the mean rates of local extinction were 0.065, 0.075, and 0.076, respectively, for Maryland, New York, and Pennsylvania (Fig. 2A). The corresponding values for non-area-sensitive were lower: 0.035, 0.045, and 0.051, respectively, for Maryland, New York, and Pennsylvania (Fig. 2A, paired t tests: $n = 41$, $t = 7.52$ for Maryland; $n = 46$, $t = 6.15$ for New York; $n = 35$, $t = 4.46$ for Pennsylvania; $P < 0.0001$ for all tests). As predicted, there was a negative relation between the mean year-to-year local extinction rate and the mean forest-patch size for all three states for area-sensitive species, but not for non-area-sensitive ones (Fig. 3; Table 4). The analyses of covariance showed that this relation did not

vary among the states ($P > 0.30$ for the pairwise interactions), and that the mean average rate of extinction differed among the states for the two groups of species (Table 4, models A and B). Moreover, the analysis of covariance of the difference in mean extinction rates of area-sensitive and non-area-sensitive species confirmed that the slope of the relationship between extinction rate and habitat fragmentation was different between the two groups (Table 4, model C; Fig. 3).

The annual estimates of turnover rates on each BBS route also varied mostly between 0.0 and 0.3. For area-sensitive species, the mean rates of local turnover were 0.067, 0.079, and 0.089 respectively for Maryland, New York, and Pennsylvania. The corresponding values for non-area-sensitive were lower: 0.038, 0.042, and 0.053, respectively for Maryland, New York, and Pennsylvania (Fig. 2B, paired t tests: $n = 41$, $t = 6.36$ for Maryland; $n = 46$, $t = 7.09$ for New York; $n = 35$, $t = 5.37$ for Pennsylvania; $P < 0.0001$ for all tests). As predicted, mean year-to-year local turnover rates on BBS routes were correlated negatively with mean forest-patch size for area-sensitive species but not for non-area-sensitive ones (Fig. 4; Table 5). There was also no evidence that this relation varied among states ($P > 0.30$ for the pairwise interactions), but the difference

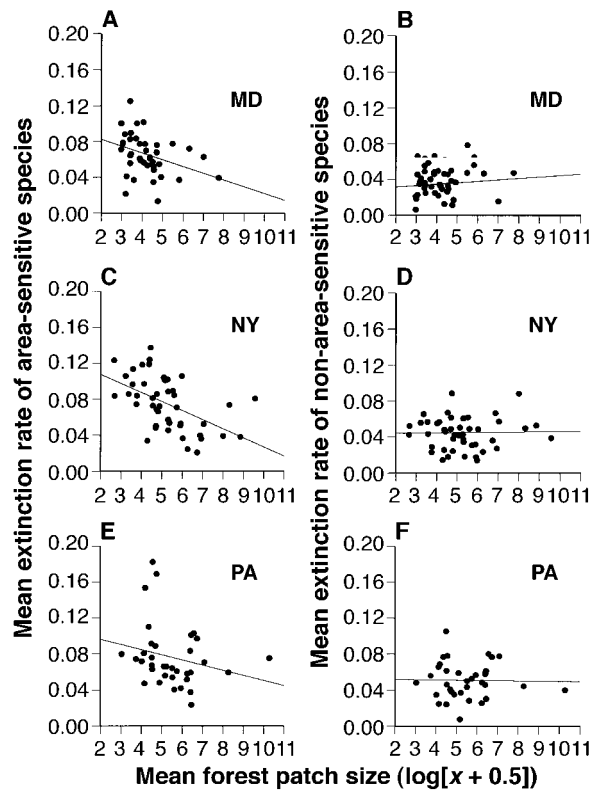


FIG. 3. Relation between mean local extinction rate between 1975 and 1996 and mean forest-patch size for area-sensitive and non-area-sensitive bird species for Maryland (MD; panels A and B), New York (NY; panels C and D), and Pennsylvania (PA; panels E and F).

TABLE 4. Results of analyses of covariance relating mean annual local extinction rate to mean forest-patch size and state.

Source	Estimate	df	Type III ss	F	P
A) ANCOVA with mean annual local extinction rate of area-sensitive species as the dependent variable (model $r^2 = 0.165$, $P < 0.0001$)					
State	...	2	0.00887	6.03	0.0032
Mean patch size ($\log[x + 0.5]$)	-0.0082	1	0.01446	19.66	0.0001
Error		118	0.08678		
B) ANCOVA with mean annual local extinction rate of non-area-sensitive species as the dependent variable (model $r^2 = 0.124$, $P < 0.0014$)					
State	...	2	0.00206	6.66	0.0018
Mean patch size ($\log[x + 0.5]$)	0.0004	1	0.00003	0.10	0.7567
Error		118	0.03655		
C) ANCOVA with the difference in mean annual local extinction rate between the two groups as the dependent variable (model $r^2 = 0.142$, $P < 0.0004$)					
State		2	0.00131	0.78	0.4625
Mean patch size		1	0.01581	18.76	0.0001
Error		118	0.09944		

Notes: Analyses of covariance were first conducted independently for area-sensitive and non-area-sensitive species (A and B). An analysis of variance was also conducted on the difference in mean annual local extinction rate of area-sensitive species and non-area-sensitive species within each route (C). This multivariate analysis-of-variance approach provided a test for a potential difference between the slopes relating mean annual local extinction rate and habitat fragmentation for the two groups of species. Pairwise interactions were not significant ($P > 0.30$).

between the mean average rate of turnover of area-sensitive and non-area-sensitive species differed among states (Table 5; Fig. 2B).

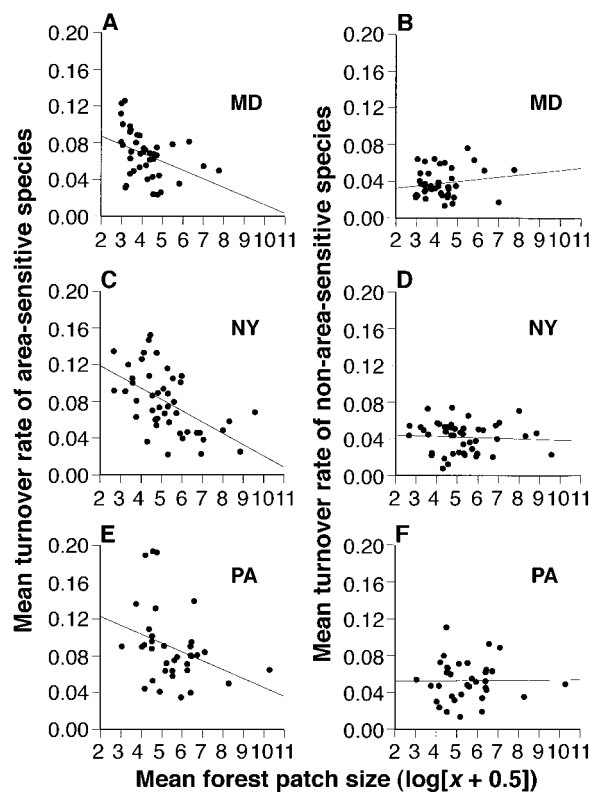


FIG. 4. Relationship (between 1975 and 1996) of mean local turnover and mean forest-patch size for area-sensitive and non-area-sensitive bird species for Maryland (panels A and B), New York (panels C and D), and Pennsylvania (panels E and F).

DISCUSSION

For the group of forest-breeding bird species considered to be area-sensitive at the scale of the forest patch (Robbins et al. 1989), we found lower species richness, and higher mean extinction and turnover rates over a 22-yr period, in landscapes with smaller mean forest-patch size. The same associations were not found for species considered to be non-area-sensitive. These results raise important issues related to the respective roles of local and regional effects on the dynamics of species richness in landscapes (Ricklefs 1987, Cornell 1993). They further provide a mechanistic explanation for the underlying processes behind the pattern of higher temporal variability in species richness in more fragmented landscapes that we first documented using this data set (Boulinier et al. 1998b). In particular, they show that the dynamics of local species richness and composition over the study period were potentially affected by local landscape attributes as well as by contributions from the regional species pool.

These findings are in agreement with our predictions made under a dynamic equilibrium model where characteristics of the landscapes and forest patches affect extinction and colonization processes (MacArthur and Wilson 1963, 1967, Gilpin and Hanski 1991, Hanski 1999). Among the characteristics of landscape structure that may affect local extinction and colonization, the overall amount of favorable habitat may be the main factor, but distance between habitat patches, increased amount of edge, and negative biotic effects associated

TABLE 5. Results of analyses of covariance relating mean annual local turnover rate to mean forest-patch size and state.

Source	Estimate	df	Type III ss	F	P
A) ANCOVA with mean annual local turnover rate of area-sensitive species as the dependent variable (model $r^2 = 0.243$, $P < 0.0001$)					
State	...	2	0.02266	12.33	0.0001
Mean forest-patch size ($\log[x + 0.5]$)	-0.0108	1	0.02507	27.28	0.0001
Error		118	0.10842		
B) ANCOVA with mean annual local turnover rate of non-area-sensitive species as the dependent variable (model $r^2 = 0.109$, $P < 0.0034$)					
State	...	2	0.00400	6.27	0.0026
Mean forest-patch size ($\log[x + 0.5]$)	0.0002	1	0.00001	0.04	0.8393
Error		118	0.03762		
C) ANCOVA with the difference in mean annual local turnover rate between the two groups as the dependent variable (model $r^2 = 0.190$, $P < 0.0001$)					
State		2	0.00974	4.85	0.0095
Mean forest-patch size		1	0.02623	26.11	0.0001
Error		118	0.11856		

Notes: Analyses of covariance were first conducted independently for area-sensitive and non-area-sensitive species (A and B). An analysis of variance was also conducted on the difference in mean annual local turnover rate of area-sensitive species and non-area-sensitive species within each route (C). This multivariate analysis of variance approach allowed us to test for a potential difference between the slopes relating mean annual local turnover rate and habitat fragmentation for the two groups of species. Pairwise interactions were not significant ($P > 0.30$).

with fragmentation may also play prominent roles (Faaborg et al. 1995, Robinson et al. 1995).

Any large-scale study involving measures of landscape patterns to infer ecological processes has the drawback of not being experimental, and therefore of allowing only weak inference at the specific scale considered (Wiens 1989, Wiens et al. 1993). Our study benefited from the sampling design of the Breeding Bird Survey, but the bird communities sampled corresponded to those situated along the survey routes, rather than to the actual communities associated with the entire landscape considered when characterizing each particular survey route. The lack of an experimental design (we did not allocate degrees of fragmentation randomly to the survey routes) prevents strong inference on the causal nature of the associations. The fact that we dealt with the existing pattern of forest fragmentation associated with the BBS survey routes also prevented us from contrasting landscapes with strong differences in specific components of fragmentation. For example, a powerful test of the independent effect of forest cover and fragmentation per se on bird community dynamics would require comparing landscapes with independent variations in different components of landscape structure (see Andr  n 1996 and Trzcinski et al. 1999 on related issues).

Most of the BBS routes did not show evidence of any linear trend in the logarithm of species richness over the 22-yr period studied, although there was some evidence of an excess of significant positive trends relative to negative trends in Pennsylvania. It could be interesting to determine whether a specific group of species was responsible for increases in local colonization events in this state and whether these trends were associated with landscape changes. However, we lack information on local landscape changes that might en-

able this type of analysis. Data at the state level suggest that such changes may have been limited in all three states (in thousands of hectares, forest cover in Maryland was respectively 1199, 1074, and 1094 in 1967, 1976, and 1986; in New York it was 6948, 7489, and 7544 in 1968, 1980, and 1993; and in Pennsylvania, it was 6909, 6809, and 6849 in 1965, 1978, and 1989; T. Frieswyk, U.S.D.A. Forest Service, *personal communication*), although changes at more local scales may have been important.

Whatever the determinants of local community composition, the temporal dynamics of local species richness observed involved local turnover in species composition and implies a strong dependence of local species richness on the richness of the surrounding landscapes (Brown and Kodric-Brown 1977). If the surrounding landscapes have comparable levels of fragmentation then this could lead to species extinction at larger scales due to stochastic effects (chance synchrony in the loss of potential recolonists among a group of adjacent landscapes). Such a mechanism could lead to time-delayed extinction that would not be due to a competition-colonization trade-off among species (Tilman et al. 1994), but to stochastic dynamics of communities in fragmented habitat at different scales. If local communities are dependent on large and more or less distant forest patches for colonization, as suggested for midwestern U.S. landscapes (Robinson et al. 1995), then this could be investigated in further analyses involving larger scales. In any case, our approach permits the estimation of parameters of change within landscapes and thus could enable the testing of predictions related to such processes. In particular, resulting parameter estimates of community-level vital rates could be used in models investigating links be-

tween spatial processes at different scales and community stability (e.g., Kareiva and Wennergren 1995).

Methodologically, our approach accounted for potential heterogeneity in detection probabilities among species and among landscapes associated with each survey route. This was especially important (1) because it has been shown that strong heterogeneity in the probability of detecting North American bird species exists (Boulinier et al. 1998a), and (2) because of the large spatial and temporal scales involved. For instance, when comparing the number of species estimated to be present on a survey route 22 yr apart, it is clearly important to be able to take into account potential differences in the probability of species detection to prevent any potential bias. It can be noted that sampling variability, acknowledged by the estimation procedures we used, may be partly responsible for the relatively low value of the determination coefficients of the relationships tested. The low value of the determination coefficients underlines that mean forest-patch size only explained a fraction of the variation of the estimated community parameters.

In conclusion, our tests of predictions regarding associations between landscape attributes and rates of change in forest bird communities showed that the local dynamics of extinction and turnover were indeed positively associated with the level of forest fragmentation. This provides empirical insight into the processes responsible for the relationship between community stability and habitat fragmentation (Boulinier et al. 1998b), and has implications for the use of dynamic equilibrium approaches for landscape management and conservation. The data available did not allow us to actually tease apart the potential separate effects of the different components of habitat fragmentation, but clearly showed that different levels of fragmentation in the eastern United States are associated with different patterns of change in composition of forest bird communities within landscapes. This study is the first application of estimators that describe community dynamics while taking into account the potential heterogeneity in detection probabilities among species and among sampling locations. It clearly shows their potential broad application in landscape ecology, and in studies of biodiversity dynamics.

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APPENDIX

Lists of area-sensitive and non-area-sensitive species are available in ESA's Electronic Data Archive: *Ecological Archives* E082-013.