RELATIONSHIPS AMONG NORTH AMERICAN SONGBIRD TRENDS, HABITAT FRAGMENTATION, AND LANDSCAPE OCCUPANCY

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Abstract. Fragmentation of breeding habitat has been hypothesized as a cause of population declines in forest-nesting migratory birds. Negative correlations between the degree of fragmentation and bird density or fecundity at local or regional scales support the fragmentation hypothesis. Yet, in spite of reduced fecundity and densities in fragmented systems, many forest-nesting passerine species have increased in numbers over time. We hypothesized that range-wide population change in species for which habitat fragmentation negatively affects reproductive success should depend on the proportion of the population that actually occupies fragmented landscapes. We predicted that fragmentation-sensitive species (e.g., species that occur in reduced densities in fragmented landscapes) should increase globally in numbers at a greater rate than species that readily occupy fragmented landscapes, because fragmentation-sensitive distributions place a large proportion of the global population in contiguous landscapes that are superior for breeding. We used Breeding Bird Survey (BBS) data and associated landscape metrics to test this prediction for 10 species of forest-nesting passerines in the United States that experience reproductive dysfunction associated with habitat fragmentation: Ovenbird (*Seiurus aurocapillus*), Red-eyed Vireo (*Vireo olivaceus*), Wood Thrush (*Hylocichla mustelina*), Northern Cardinal (*Cardinalis cardinalis*), Worm-eating Warbler (*Helmitheros vermivorus*), Kentucky Warbler (*Oporornis formosus*), Indigo Bunting (*Passerina cyanea*), Scarlet Tanager (*Piranga olivacea*), Acadian Flycatcher (*Empidonax virescens*), and Hooded Warbler (*Wilsonia citrina*).

Our approach was to: (1) quantify landscape features associated with BBS routes across the eastern United States, (2) classify landscapes around BBS routes as ''fragmented'' or ''contiguous,'' (3) estimate the proportion of detected individuals that occurred in fragmented landscapes on a species-by-species basis, and then (4) associate 10-yr trends for each species with the proportion of breeding individuals occupying fragmented landscapes. Regression analysis indicated a significant, negative relationship between the proportion of the breeding population occupying fragmented landscapes and the population trend from 1970 to 1980. Although this result links habitat fragmentation to population change and provides support for the fragmentation hypothesis, other factors (e.g., land use change, weather, varying life history traits, varying winter survivorship, habitat amount thresholds) could generate similar results. More work is needed to partition the relative influence of these factors on regional bird population dynamics if conservationists are to understand more clearly the effects of fragmentation on the distribution and abundance of species across their ranges.

Key words: area sensitivity; Breeding Bird Survey; forest passerines; habitat fragmentation; habitat selection; landscape occupancy; macroecology; neotropical migratory birds; population trends.

Introduction

Several species of migratory birds have undergone population declines in recent decades (Robbins et al. 1989, Peterjohn et al. 1997). For example, Wood Thrushes (*Hylocichla mustelina*), which breed in east-ern North American forests and winter in the Neotropics, have declined, on average, 1.7% per year since 1966 throughout their range (Peterjohn and Sauer 1994). However, long-term population trends estimated for migratory birds vary among species. Red-eyed Vireos (*Vireo olivaceus*), which often co-occur with Wood Thrushes, have increased by an average of 1.4% per year since 1966 (Peterjohn and Sauer 1994). A central challenge for ecologists and conservation biologists is to identify the mechanisms that cause such population change (James and McCulloch 1995, Sauer et al. 1996).

Migratory bird populations may be limited by (1)

events on the North American breeding grounds, which may reduce reproductive success and survival (Robbins 1979); or (2) events during migration or on tropical wintering areas, which may reduce survivorship (Robbins et al. 1989, Sherry and Holmes 1996) and may influence future breeding success (Marra et al. 1998). Identification of causal mechanisms of population change in migratory songbirds, however, has been elusive because population trends vary across a species' range (James et al. 1992) and because dispersal dynamics within and among habitats are poorly understood (e.g., Nolan 1978, Greenwood and Harvey 1982).

Fragmentation of North American breeding habitat, defined in this paper as the reduction and isolation of breeding habitat, has been hypothesized as a cause of population declines in migratory species (e.g., Brittingham and Temple 1983, Wilcove 1985, Böhning-Gaese et al. 1993; see reviews in Askins et al. 1990, Faaborg et al. 1995). Initially, fragmentation studies focused on local patterns of species distribution and abundance in relation to patch area and isolation (Haila 2002). More recently, studies have focused on fitness measures such as nesting success (the probability that a nest will fledge young) or fecundity (the number of offspring per adult per year) in relation to patch size or other indices of fragmentation (e.g., Brittingham and Temple 1983, Donovan et al. 1995, 1997, Robinson et al. 1995, Trine 1998, Porneluzi and Faaborg 1999). Species showing a positive association between patch size and bird density or patch size and fecundity generally have been thought to be "sensitive" to habitat fragmentation and have received much attention from conservation biologists.

However, low density or fecundity in fragmented habitats does not necessarily lead to population declines at either the local (subpopulation) or the landscape scale (the system of interacting subpopulations, sensu Pulliam 1988). Local "sink" populations on fragments can be rescued from extinction by immigration from other "source" populations (e.g., Brawn and Robinson 1996, Dias et al. 1996), and the overall dynamics of the source–sink system may not be impacted by poor reproductive success in fragments if breeding individuals generally avoid small patches or if the landscape is dominated by larger patches that are used for breeding (Donovan and Lamberson 2001). For example, Ovenbird (*Seiurus aurocapillus*) populations in fragmented landscapes are characteristically low in density, have a male-biased sex ratio, and experience low fecundity (reviewed in Van Horn and Donovan 1994), yet Ovenbird populations have been stable or increasing across their range since 1966 (Peterjohn and Sauer 1994). Ovenbird populations may be increasing range-wide despite the "negative" effects of fragmentation because most females breed in contiguous landscapes where fecundity is higher. Thus, there is a potential interaction among habitat fragmentation, land-

scape occupancy patterns, and population growth in bird species.

We hypothesized that range-wide population change in species whose reproductive success is negatively affected by habitat fragmentation should depend on the proportion of the population that actually nests in fragmented landscapes. We predicted that species with a large proportion of their global population in contiguous landscapes should have population growth rates greater than those of species that occur readily in fragmented systems. We tested this prediction for 10 species of forest-nesting passerines in the United States that experience reproductive dysfunction associated with habitat fragmentation (Robinson et al. 1995). These species were the Ovenbird, Red-eyed Vireo, Wood Thrush, Northern Cardinal (*Cardinalis cardinalis*), Worm-eating Warbler (*Helmitheros vermivorus*), Kentucky Warbler (*Oporornis formosus*), Indigo Bunting (*Passerina cyanea*), Scarlet Tanager (*Piranga olivacea*), Acadian Flycatcher (*Empidonax virescens*), and Hooded Warbler (*Wilsonia citrina*).

Our approach was to: (1) quantify landscape features associated with Breeding Bird Survey (BBS) routes across the eastern United States, (2) classify the landscapes around BBS routes as "fragmented" or "contiguous," (3) estimate the proportion of detected individuals that occurred in fragmented landscapes on a species-by-species basis, and (4) examine the relationship between 10-yr trends for each species and the proportion of the population occupying fragmented landscapes.

METHODS

Breeding Bird Survey

The BBS is a large-scale, roadside survey of birds breeding in the United States and southern Canada. Routes occur along secondary roads that are randomly located in order to sample habitats that are representative of the entire survey region. The primary objective of the BBS has been the estimation of population change for songbirds (Robbins et al. 1986). Initiated in 1966, >4000 routes are now surveyed annually by experienced observers during the peak of the breeding season. Each route is 39.4 km long and consists of 50 survey stops located at 0.8-km intervals. A 3-min point count is conducted at each stop, during which the observer records all birds heard or seen within 0.4 km of the stop. We evaluated 1606 BBS routes, all located in the eastern and central United States (Fig. 1).

Landscape features of Breeding Bird Survey routes

Digital land use and land cover data from the U.S. Geological Survey (USGS) were used to quantify landscape structure within a circular scene of radius 19.7 km centered on each BBS route (~1200 km²). This radius guaranteed that each landscape scene would wholly contain the route. The USGS data were derived
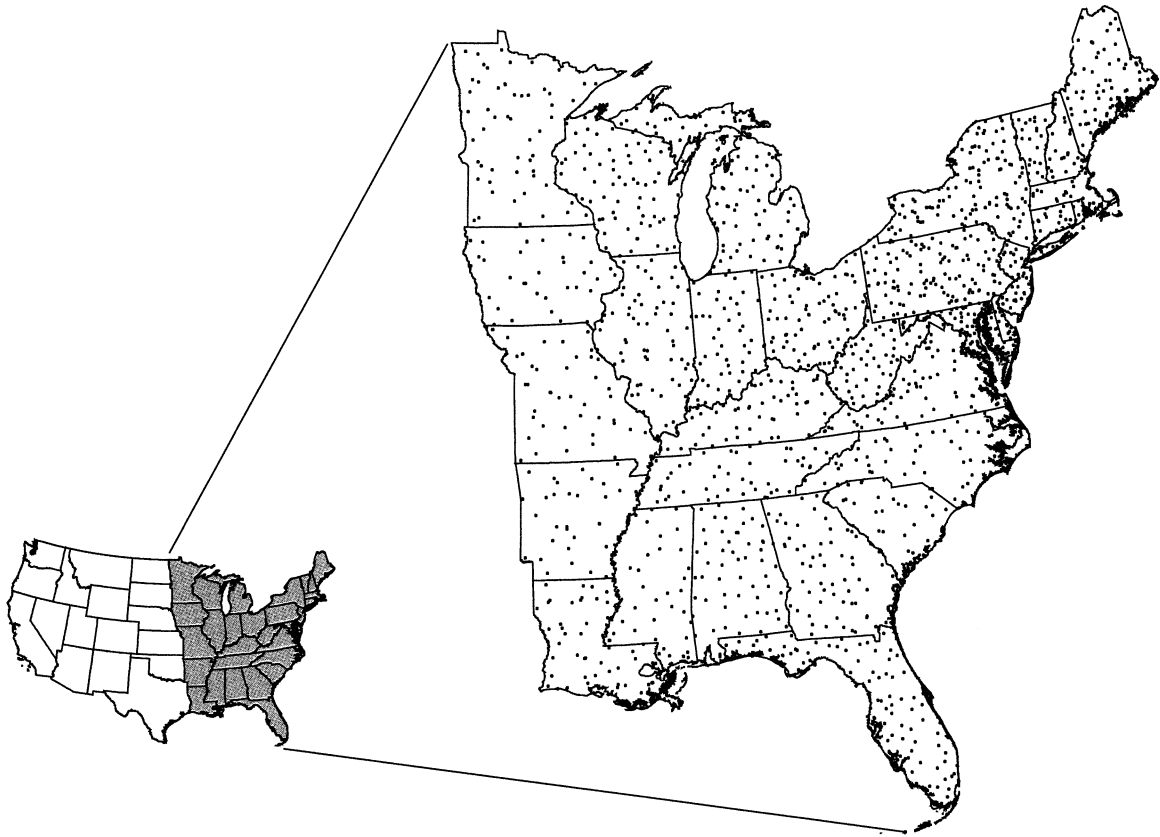
Fɪɢ. 1.   Map of Breeding Bird Survey (BBS) route locations across the eastern United States.

from high-altitude aerial photographs, usually at scales smaller than 1:60 000, which were digitized and transferred to 1:250 000 base maps (USDI, Geological Survey 1987). The high-altitude photographs were taken between 1969 and 1985. Most images were taken in the mid-1970s (mean 1975, 1 sᴅ = 3.25 yr), with 50% of the images being taken between 1973 and 1977. Raster format data (4-ha grid) provided information on nine broad land types including: urban or built-up land, agricultural land, rangeland, forest land, water, wetland, barren land, tundra, and perennial snow or ice, based on criteria specified in Anderson et al. (1976).

We used FRAGSTATS (McGarigal and Marks 1995) and DISPLAY (see the Supplement) to estimate landscape structure metrics for each BBS route (see Flather and Sauer 1996). These metrics generally described the amount and arrangement of forest habitats within each landscape surrounding BBS routes (Table 1). Many of these measures have been shown to be associated with the distribution and abundance of birds (Whitcomb et al. 1981, Ambuel and Temple 1983, Lynch and Whigham 1984, Freemark and Merriam 1986, Blake and Karr 1987, van Dorp and Opdam 1987, Lescourret and Genard 1994, Robinson et al. 1995, Donovan et al. 1995).

Clustering landscapes

We used Ward's minimum variance method (SAS Institute 1989) to cluster the BBS landscapes into discrete ''fragmented'' and ''contiguous'' landscape classes. We included the 11 forest landscape metrics listed in Table 1 in the initial clustering routine, and did not discriminate between metrics that described ''habitat amount'' and metrics that described ''habitat arrangement.'' Although there is currently much debate about which metrics have a greater effect on bird distribution (e.g., Fahrig 1997, 1998, Hill and Caswell 1999, Trzcinski et al. 1999, Villard et al. 1999), we elected to use both amount and arrangement metrics to describe forest fragmentation in our study region. We recognize that these metrics are highly intercorrelated, making it difficult to interpret which variables are most important in discriminating among fragmented and contiguous landscapes. However, our intent was to develop an effective classifier, rather than to interpret the relative contribution of habitat amount vs. arrangement.

The Ward's method of clustering uses a least-squares method to compute similarity of landscape structure among BBS routes and to produce cluster groups (in our case, two) of approximately equal size. With the

TABLE 1. Landscape metrics associated with each Breeding Bird Survey (BBS) route.

Variable	Description	Unit
Area	mean patch area of forest patches	ha
Edge	length of edge between forest and other land cover types	km
No-pat	number of forest patches	
Fd-grid	grid fractal dimensions for forest land (see Milne 1991); measure dispersion of forest patches throughout the landscape scene	
Fd-pa	perimeter–area fractal dimension for forest land (see Krummel et al. 1987); measures convolution of forest patch boundaries	
Wt-area	weighted mean patch area of forest patches (see Turner et al. 1996)	ha
Tc-area	total core area for forest land, measured as area of forest land ≥200 m from an edge (to minimize potential impacts from nest parasitism and nest predation)	ha
Mn-core	mean core area of forest patches	ha
Sd-core	standard deviation of core area among forest patches	ha
Mn-dist	mean nearest neighbor distance among forest patches based on shortest edge-to-edge distance	m
Sd-dist	standard deviation of nearest neighbor distance among forest patches based on shortest edge-to-edge distance	m

use of any clustering algorithm, there is no guarantee that the resulting classification will sort the observations into the user's a priori expectation (in our case, fragmented and contiguous landscapes). However, we chose a limited set of landscape attributes that are commonly associated with measuring fragmentation to increase the likelihood that the resulting classification would partition our landscapes into sets that could be interpreted as fragmented and contiguous systems. We then used stepwise discriminant function analysis (Proc Stepdisc; SAS Institute 1989) to determine which minimum set of attributes contributed to the differentiation of landscape cluster groups (the level to add or remove a variable was set to 0.1), and then used only those significant variables to re-cluster the landscapes. We used discriminant function cross-validation procedures

(Proc Candisc; SAS Institute 1989) to estimate misclassification rates for the new cluster solution.

Landscape occupancy patterns of selected forest passerines

We analyzed landscape-level occupancy for 10 species of forest-nesting passerines that experience reproductive dysfunction associated with habitat fragmentation. Importantly, the fecundity of each of these species has been studied across a wide gradient of fragmentation, and additionally appears to be negatively impacted by fragmentation in several geographically distant locations (Table 2). We examined BBS data from 1970 to 1980 to determine the proportion of detected individuals that occurred on fragmented and contiguous routes. We assumed that routes where a species

TABLE 2. BBS birds of interest and literature sources indicating reduced fecundity as a function of fragmentation.

Species	Habitat fragmentation literature
Ovenbird	Gibbs and Faaborg (1990), Porneluzi et al. (1993), Villard et al. (1993), Wenny et al. (1993), Van Horn and Donovan (1994), Donovan et al. (1995), Linder and Bollinger (1995), Robinson et al. (1995), Van Horn et al. (1995), Burke and Nol (1998).
Red-eyed Vireo	Yahner (1993), Donovan et al. (1995), Robinson et al. (1995), Brawn and Robinson (1996).
Wood Thrush	Hoover and Brittingham (1993), Donovan et al. (1995), Robinson et al. (1995), Brawn and Robinson (1996), Trine (1998), Weinberg and Roth (1998).
Worm-eating Warbler	Robinson (1992), Wenny et al. (1993), Robinson et al. (1995), Hanners and Patton (1998).
Northern Cardinal	Conner et al. (1986), Robinson et al. (1995), Halkin and Linville (1999).
Kentucky Warbler	Gibbs and Faaborg (1990), Jesse (1991), Wenny et al. (1993), Robinson et al. (1995).
Indigo Bunting	Robinson et al. (1995), Suarez et al. (1997), Dearborn et al. (1998), Payne and Payne (1998).
Scarlet Tanager	Robinson et al. (1995), Roberts and Norment (1999).
Acadian Flycatcher	Walkinshaw (1961), Robinson et al. (1995).
Hooded Warbler	Odgen and Stutchbury (1994), Robinson et al. (1995); R. Dettmers (*personal communication*).

of interest had never been detected since 1966 represented unsuitable habitat, and eliminated those routes from our analysis.

The mean number of individuals observed for each species on each route was determined first by identifying the date of the satellite imagery associated with the route, and then by searching for the first three years of BBS abundance data closest to the imagery date within a 9-yr window centered on the imagery date. This procedure was chosen for two reasons. First, we expected the reliability of annual bird counts on a BBS route to be low, given that each route is run on a single morning in any given survey year. An average over three years would help to control for annual variation in bird counts that could be attributable to daily variation in bird activity. Second, not all BBS routes are surveyed each year, and routes that were run during unfavorable conditions (e.g., bad weather) were eliminated from the data set. A 9-yr window was selected to maximize the number of routes used in the analysis without including bird counts that were temporally distant from the year of the landscape photography. If three survey years were located within the 9-yr window, we computed the mean count of individuals for the route. Routes in which three data points could not be located were eliminated from our analysis.

We summed the mean count of individuals for each bird species across all suitable routes, as well as for fragmented and contiguous routes separately. We estimated the proportion of total individuals occupying fragmented landscapes by dividing the total mean count on fragmented landscapes by the total mean count across all landscapes. In this manner, we used the distribution of individuals in fragmented landscapes to index the degree to which species are sensitive to fragmentation.

In calculating this index, we assumed that the BBS data are an accurate reflection of how individuals are distributed geographically. It is known, however, that the proportion of individuals detected can vary by observer, species, and geographic location (i.e., among states), the latter being potentially a function of differences in landscape structure and species composition (Sauer et al. 1994, Boulinier et al. 1998, Nichols et al. 2000). Although it would be desirable to account for variable detection rates in our analysis of the BBS, the survey methodology does not currently permit us to account for this bias analytically at the individual species level. Consequently, we assumed that any biases would not appreciably affect the relative ranking of species along our fragmentation–sensitivity axis.

Associations between landscape occupancy patterns and population trends

We used the BBS survey data to examine population trends for each of the 10 forest-nesting species of interest. Because landscape data were derived primarily from the mid-1970s, we evaluated trends from 1970 to 1980. This relatively short period also minimizes the probability that major landscape changes occurred during the period considered.

We used the route-regression approach based on estimating equations to estimate the population trend (percentage change per year) for each species (Geissler and Sauer 1990, Sauer et al. 1999). Trends were estimated as a weighted average of trends on individual routes, and were based on routes within the United States only. This geographic restriction on the bird trend analysis was necessary because we had landscape data only for routes that occurred in the United States. Observer effects were incorporated in the model to prevent bias associated with increases in observer quality over time (Sauer et al. 1994), as were effects of missing counts, which also tend to bias trend estimates. The trend analyses assume that fluctuations in indices of abundance are representative of the population as a whole.

We used linear regression to associate abundance trend estimates with the proportion of the total individuals occupying fragmented habitats across species. Influence statistics were used to determine if any of the 10 species had a disproportionately large effect on the regression estimates (Neter et al. 1990). Influence statistics examined included DFFITS (which measures the difference between fitted value of Y_i for the ith case when all n cases are used in fitting the regression function and the predicted value of Y_i for the ith case obtained when the ith case is omitted in fitting the regression function) and DFBETAS (which measures the influence of the ith case on each regression coefficient).

We predicted that abundance trends should be negatively associated with the proportion of a species' population occupying fragmented landscapes. That is, we predicted that species with low proportions of occurrence in fragmented landscapes would have higher rates of increase during the 1970s than species with high proportions of occurrence in fragmented landscapes.

RESULTS

Landscape features of Breeding Bird Survey routes

Of the 1606 BBS routes analyzed (Fig. 1), 29 were eliminated from analyses because of missing or incomplete landscape data. Among the remaining 1577 routes, the percentage of forest habitats in the landscapes surrounding BBS routes ranged from 0.1% to 97.8.5%. The median amount of forest habitat was 47.6%. Consequently, landscapes in the eastern United States represented a broad gradient of forest amount. The 10 bird species selected for this study have different geographic ranges; therefore, the sample size of fragmented and contiguous landscapes associated with each species varied (Table 3).

TABLE 3. Number of ''contiguous'' and ''fragmented'' BBS routes, nest height, and migratory status of the 10 species analyzed.

Species	No. contiguous routes	No. fragmented routes	Nest height	Migratory status†
Acadian Flycatcher	266	309	midstory/canopy	NTMB
Hooded Warbler	241	158	ground/shrub	NTMB
Indigo Bunting	455	539	ground/shrub	NTMB
Kentucky Warbler	215	248	ground/shrub	NTMB
Northern Cardinal	402	538	ground/shrub	resident
Ovenbird	458	558	ground/shrub	NTMB
Red-eyed Vireo	458	536	midstory/canopy	NTMB
Scarlet Tanager	380	424	midstory/canopy	NTMB
Wood Thrush	458	558	midstory/canopy	NTMB

† NTMB, neotropical migratory bird.

Clustering landscapes

Eleven variables were used to cluster landscapes into two initial landscape types. Of these, five variables were significant in differentiating landscape clusters: total length of forest edge, number of forest patches, fractal dimension based on perimeter/area relations of forest patches, weighted mean patch size of forest patches, and total core area of forest. Canonical discriminant analysis revealed that the two groups differed significantly in these variables (Hotelling-Lawley Trace, $F = 957.17$, df $= 5$, 1573, $P = 0.0001$).

We defined those landscapes with a smaller area of core forest, smaller weighted mean forest patch size, higher numbers of forest patches, and lower dispersion of forest habitats throughout the landscape (as reflected in Fd-grid) as members of the fragmented set (Table 4). Total length of the forest edge was actually lower in what we called fragmented landscapes. This occurred because edge measures reach their maximum values in landscapes with a moderate amount of habitat (Hargis et al. 1998), and such landscapes were classified in our analysis as contiguous landscapes.

Our final classification resulted in 812 fragmented and 765 contiguous BBS landscapes. Discriminant function analysis was used to estimate misclassification rates from this cluster solution. Because simple resubstitution estimates of error are known to be biased, we used cross-validation procedures to estimate misclassification rates (Snapinn and Knoke 1989). Of the 765 landscapes classified as contiguous by the cluster routine, 752 (98.3%) were correctly reclassified into the contiguous cluster (Fig. 2a). Of the 812 landscapes classified as fragmented by the cluster routine, 712 (87.7%) were correctly reclassified into the fragmented cluster (Fig. 2b). The 113 misclassified routes (7.1% of the total) had characteristics intermediate between the fragmented and contiguous landscape types (Fig. 2c,d).

Associations between landscape occupancy and population trends

The proportion of observed individuals occupying fragmented landscapes ranged from 0.167 (Worm-eating Warbler) to 0.578 (Northern Cardinal); see Table 3 for the number of landscapes classified as fragmented and contiguous for each species. During the 1970–1980 period, Scarlet Tanagers showed the greatest rate of increase among the 10 forest nesting species (+3.11% per year across all routes) and Northern Cardinals showed the lowest rate of increase (−1.65% per year).

Regression analysis indicated that there was a significant, negative relationship between the proportion of breeding individuals occupying fragmented landscapes and the population trend from 1970 to 1980 (Fig. 3; MS $= 8.08$, $F = 6.75$, df $= 1$, 8, $P = 0.032$, $R^2 = 0.46$). Linear models explained a greater proportion of the variation among species trends than did nonlinear models. None of the 10 species had undue influence on the regression coefficients or fitted values (DFFITS and DFBETA coefficients $< |1|$ for all species, with the exception of the Northern Cardinal, whose DFFITS was −1.3, which does not indicate a degree of influence

TABLE 4. Results of stepwise discriminant analysis of BBS landscapes clustered in ''fragmented'' and ''contiguous'' landscapes based on five significant metrics.

Variable	R^2	F	P	Fragmented	Contiguous
Tc-area (ha)	0.7287	4231.0	0.0001	13269.5	65607.7
No-pat	0.0798	136.5	0.0001	127.3	47.4
Edge (km)	0.1315	238.2	0.0001	990.8293	1258.7885
Wt-area (ha)	0.0062	9.8	0.0001	1383.9	16950.3
Fd-grid	0.0024	3.8	0.0001	1.5	1.9

Note: Average metrics for ''fragmented'' and ''contiguous'' landscapes are shown for each metric.
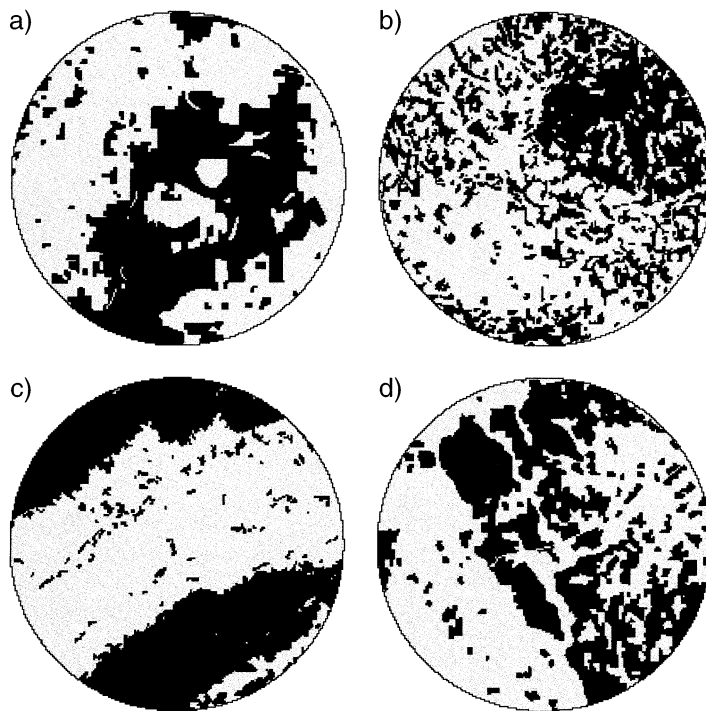
Fig. 2. Examples of landscapes surrounding BBS routes that were (a) classified as contiguous (route 904 in Louisiana), (b) classified as fragmented (route 26 in Alabama), (c) incorrectly classified as fragmented (route 65 in Pennsylvania), and (d) incorrectly classified as contiguous (route 6 in Arkansas). All landscapes shown have approximately 40% forest habitat (black).

that requires remedial action (Neter et al. 1990). However, when the Northern Cardinal was excluded from the regression analysis, the relationship was not significant at the $\alpha = 0.05$ level ($F = 1.85$, $P = 0.21$).

DISCUSSION

Past studies throughout eastern and central North America have confirmed that fragmentation is a general threat to the 10 species included in the present analysis (Table 2). However, the link between habitat fragmentation and regional population change requires a consideration of species occupancy patterns at the landscape scale. We hypothesized that, given that fragmentation negatively influences fecundity, broad-scale population trends would depend on the type of landscapes occupied during the breeding season. Our key result, that population trends were negatively related to the proportional occupancy of fragmented landscapes, provides additional support for the hypothesis that fragmentation of breeding habitat throughout the breeding range of forest species could spur global population declines.

It is important to note that, of the 10 species investigated, only two (Wood Thrush and Northern Cardinal) showed range-wide population declines over the period of this study, although the Wood Thrush trend was not significantly different from zero. The fact that regional population declines were uncommon cautions against uncritical generalizations of local studies to broader geographic areas. Although the literature has demonstrated the negative impacts of fragmentation on oc-

currence, abundance, and reproductive output (see reviews in Askins et al. 1990 and Faaborg et al. 1995) at local scales, our results suggest that extrapolating these patterns to infer range-wide dynamics may be misleading. Accumulating evidence suggests that the patterns in species occurrence and population dynamics are affected by mechanisms that operate at different spatial and temporal scales (Wiens et al. 1993, Donovan
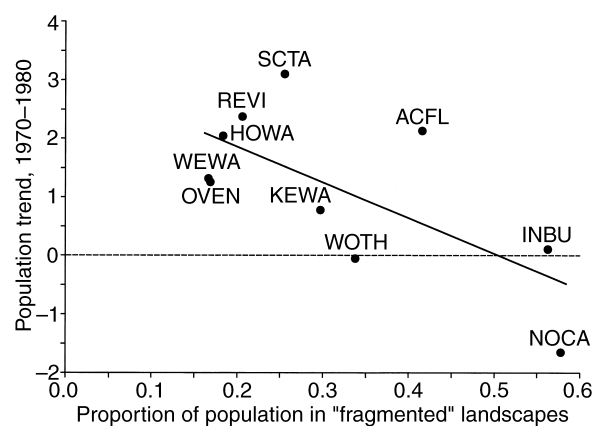

Fig. 3. Regression of trend and proportion of birds occupying fragmented landscapes for 10 forest-nesting passerines in the eastern and central United States (ACFL, Acadian Flycatcher; HOWA, Hooded Warbler; INBU, Indigo Bunting; KEWA, Kentucky Warbler; NOCA, Northern Cardinal; OVEN, Ovenbird; REVI, Red-eyed Vireo; SCTA, Scarlet Tanager; WEWA, Worm-eating Warbler; WOTH, Wood Thrush).

et al. 1997, Drapeau et al. 2000). If the mechanisms responsible for local population dynamics (e.g., birth–death processes) are different than the mechanisms operating at range-wide scales (source–sink processes), then it should not be surprising that apparently contradictory conclusions regarding the impacts of fragmentation on avian populations can be reached.

We examined landscape occupancy across a large portion of a species' range because several investigators have hypothesized that many forest-nesting passerines have a source–sink population structure (Donovan et al. 1995, Robinson et al. 1995, Dias et al. 1996). Hence, evaluation of trends at a local scale can be confounded by dispersal (Pulliam 1988, Bevers and Flather 1999). Although the BBS can be used to estimate trends on individual routes, temporal shifts in abundance can result from differences in birth, death, immigration, or emigration from the site. Because fragmentation is thought to impact birth rates and survivorship, dispersal among different localities can confound any negative impacts that habitat fragmentation may have on local population trends (Brawn and Robinson 1996).

Although "scaling up" from local to range-wide scales may be misleading, are the patterns that we documented consistent when "scaling down" from global to regional scales? Preliminary analysis of occupancy patterns and trends for each physiographic region suggests that the regression pattern in Fig. 3 does not hold when species are analyzed separately at the physiographic scale (C. H. Flather and T. M. Donovan, *unpublished data*). Seven of the 10 species analyzed show no relationship between physiographic trend and the proportion of individuals in fragmented landscape. Interestingly, Acadian Flycatchers, Ovenbirds, and Wood Thrushes appeared to increase in regions that were highly fragmented. Regional trend analysis, however, may also be confounded if dispersal among regions is frequent. Clearly, more information is needed to elucidate the frequency and scale of dispersal among populations to refine our predictions and tests.

We did not examine trends for other forest-nesting species because there is insufficient data, to date, to suggest that fragmentation could be negatively affecting trends, and we wanted to restrict our analysis to those species that have clearly been shown to be negatively affected by habitat loss and fragmentation. However, our analysis of only 10 species warrants discussion of several caveats. First, with a limited sample there is an increased likelihood that one or a few data points may control the pattern observed. If these points are unusual for reasons other than the mechanism hypothesized, then inferences may be erroneous (Neter et al. 1990). Although we found that no single species had an inordinate influence on the predicted trend or the slope parameter (although elimination of the Northern Cardinal did result in an estimated slope that was

not significantly different than zero), "area-sensitive" and "edge" species appear to drive the regression pattern. In the present study, these species were the Worm-eating Warbler and Ovenbird (two species that are widely recognized as forest-interior, area-sensitive species) and the Indigo Bunting and Northern Cardinal (two species that nest in edge, second-growth, or urbanized habitat). The "Grinnelian niche" (sensu James et al. 1984) of the Worm-eating Warbler and Ovenbird may occur more readily in contiguous landscapes, leading to reduced densities in fragmented areas. In contrast, the "Grinnelian niche" of the Northern Cardinal and Indigo Bunting may occur more readily in fragmented landscapes than in contiguous landscapes, placing a large number of breeding individuals in fragmented landscapes. Because the best breeding habitat for these species would be edge or second-growth habitat within more contiguously forested landscapes (Robinson et al. 1995), the range-wide growth rates could be explained by the hypothesized mechanism if landscape context, as characterized by degree of fragmentation, affects reproduction (e.g., through elevated nest predation and cowbird parasitism in more fragmented landscapes; Robinson et al. 1995).

Second, our set of species was too small to control for potential confounding covariates related to basic differences in species ecology. For example, although the species analyzed are related by their similar response to fragmentation, they differ in several basic life history attributes (Table 3). Nine out of the 10 species are neotropical migrants and open-cup nesting species, but there is much less similarity in nest location. Six species are ground- and low-nesting species, whereas four nest in the midstory and canopy. These differences in life history can confound tests of our fragmentation hypothesis (see Sauer et al. 1996) in a number of ways. For example, nest height may be a confounding life history factor (Martin 1995), although visual inspection of our regression results (Fig. 3) suggests that the pattern would hold if ground-low-nesting species and midstory-canopy-nesting species were analyzed separately. Migratory status is another potentially confounding life history attribute. The Northern Cardinal was the only permanent resident in our analysis, and therefore is influenced by harsh environmental conditions during the winter months. The trend observed for the Northern Cardinal could be driven by severe winters during the late 1970s (Robbins et al. 1989) rather than by the distribution of individuals in fragmented habitats. A superior analysis would control for some of these potentially confounding covariates, but this was not possible, given the small number of species examined.

Potential confounding covariates are not restricted to life history characteristics, but also include factors such as land use change. Land use shift or natural successional changes during the 1970s that increased or

decreased habitat availability might produce a similar regression pattern in Fig. 3. For example, if edge or second-growth habitat declined sharply during the 1970s, declines in species such as Northern Cardinals and Indigo Buntings would result in a population decline if habitat amount were to limit population growth. That is, population declines would be a function of habitat amount, not habitat quality (as we have assumed). Controlling for the potential effects of land use change requires information on landscape change over time, but classified imagery for multiple time periods over the geographic extent of our study was not available.

Another limitation of our study concerns the use of bird counts along BBS routes to reflect the abundance of various species within a landscape. This approach assumes that habitats along roadside routes, and their associated birds species, are representative of the larger landscape. Few studies have addressed this issue directly. Bart et al. (1995) and Keller and Scallan (1999) found that forest habitats in Ohio and Maryland occurred with a lower frequency along roadside routes than in off-road areas. However, they also found that the magnitude of habitat change that occurred along roads from 1963 to 1988 was similar to that observed in off-road areas and regionally. Consequently, it appears that habitat-driven bird population trends that are derived from roadside counts may be representative of the change occurring over a much broader area. The generality of this claim, however, awaits further study in other geographic areas.

A final caveat is related to the scale of our landscape analysis and whether the spatial extent of our landscapes is expected to influence bird occurrence along BBS routes. Our choice of spatial extent (a circular scene of radius 19.7 km centered on each BBS route, ~1200 km²) was determined by the linear dimension of each route and our desire to ensure that all bird survey stops along a route would occur within our landscape boundary. Does this scale have any ecological relevance to the species being studied? Answering this question requires some estimate of dispersal. We used mean body mass values from Dunning (1993) in conjunction with allometric relationships estimated by Sutherland et al. (2000) to derive estimates of maximum natal dispersal distances. The mean maximum natal dispersal distance across all 10 species was 20.5 km (range 13.5–33.0 km). Thus, although our spatial scale was determined by the design attributes of the BBS, it appears that this scale also has relevance to the ecology of the species being investigated here.

With these caveats in mind, our regression results suggest areas of future analysis and research consideration. The first, and potentially foremost from a conservation standpoint, is to generate better information on the frequency and scale of dispersal among bird populations. This information is needed so that cause and effect can be more firmly established as populations change in numbers. Second, sorting out the relative importance of changes in habitat amount and habitat arrangement in explaining observed population dynamics is not trivial. Alteration of habitat arrangement rarely occurs in the absence of habitat loss, making it difficult to tease apart their joint influence on population dynamics. Although the relative effects of habitat amount and arrangement on population parameters such as birth, death, and dispersal rates are sorely needed, there is growing theoretical and empirical evidence that habitat amount is the dominating influence on changes in population persistence and species abundance (Andrén 1994, Fahrig 1997, Trzcinski et al. 1999), although the evidence is hardly unanimous (see Hill and Caswell 1999, Villard et al. 1999).

Finally, there is a need to focus on mechanisms of habitat selection in birds and the scales at which habitat selection is occurring (Johnson 1980). In other words, what mechanisms drive the occurrence patterns observed for different species across different landscape types? Identifying the relative influence of local-scale habitat features (such as proximity to edge, stem density, etc.) vs. landscape-scale habitat features (such as patch size, patch position in the landscape) is an area of research that is ripe for investigation.

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SUPPLEMENT

DISPLAY software for estimating metrics of landscape structure is available in ESA's Electronic Data Archive: *Ecological Archives* A012-003-S1.