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Fragmentation Effects on Forest Birds: Relative Influence of Woodland Cover and Configuration on Landscape Occupancy

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Abstract: *Habitat fragmentation has been shown to influence the abundance, movements, and persistence of many species. We asked the following questions: (1) Do species respond mainly to habitat loss or to the changes in habitat configuration resulting from this loss? (2) Do species exhibit sharp thresholds in their response to forest cover or configuration? We compared the relative influence of forest cover and configuration on 15 bird species in 33 landscapes (6.25 km²) in eastern Ontario, Canada. Forest cover in these landscapes varied between 3.4% and 66.8%. The metrics we used to quantify forest configuration were correlated to forest cover, so we regressed these configuration metrics against cover and used the residuals in logistic regression models. Of the 15 forest bird species included in the analyses, the presence of only 3 (Downy Woodpecker [*Picoides pubescens*], Brown Creeper [*Certhia americana*], and White-breasted Nuthatch [*Sitta carolinensis*]) was not significantly related to either cover or configuration of woodland. Forest cover and configuration each were significant predictors of the presence of 6 species in landscapes occupied in both years, and 3 species responded both to cover and configuration. Models based on single years showed variability in the landscape characteristics that were significant predictors of the presence of each species. These results indicate that (1) landscape structure was an important predictor of bird distribution, (2) both forest cover and configuration were important predictors of species presence, and (3) responses were species-specific. Effects of forest cover and configuration on species presence generally were not characterized by sharp thresholds, preventing the application of simple management rules. Although forest cover is an important feature of landscape structure, our results indicate that woodland configuration is a far from negligible component that should also be incorporated in conservation strategies.*

Efectos de la Fragmentación Sobre Aves de Bosque: Importancia Relativa de la Cobertura y Configuración Forestal

Resumen: *Se ha mostrado que la fragmentación del hábitat influye sobre la abundancia, los movimientos y la persistencia de muchas especies. En el presente trabajo hicimos las siguientes preguntas: (1) ¿responden las especies principalmente a la pérdida de hábitat o a los cambios en la configuración del hábitat resultantes de esta pérdida? (2) ¿presentan las especies umbrales de respuesta a la cobertura forestal y su configuración? Comparamos la influencia relativa de la cobertura forestal y su configuración sobre 15 especies de aves en 33 localidades (6.25 km²) en el oriente de Ontario, Canadá. La cobertura forestal en esas localidades fluctuó entre 3.4% y 66.8%. Las medidas utilizadas en la cuantificación de la configuración forestal fueron correlacionadas con la cobertura; así, se hizo la regresión de las medidas de configuración contra cobertura y los residuos se utilizaron en modelos de regresión logística. De las 15 especies de aves de bosque analizadas, la presencia de solo 3 (*Picoides pubescens*, *Certhia americana* y *Sitta carolinensis*) no estuvo relacionada significativamente con la cobertura ni la configuración del bosque. La cobertura y configuración forestal fueron predictores significativos de la presencia de 6 especies en localidades ocupadas en ambos años. Tres es-*

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pecies respondieron tanto a la cobertura como a la configuración. Los modelos basados en un año mostraron variación en las características del paisaje que fueron predictores significativos de la presencia de cada especie. Estos resultados indican que (1) la estructura del paisaje fue un predictor importante de la distribución de las aves; (2) tanto la cobertura como la configuración forestal fueron predictores importantes de la presencia de especies; y (3) las respuestas fueron específicas. Los efectos de la cobertura y la configuración forestal sobre la presencia de especies generalmente se caracterizaron por no presentar umbrales definidos, lo cual no permite la aplicación de reglas simples de manejo. Aunque la cobertura forestal es una característica importante de la estructura del paisaje, nuestros resultados indican que la configuración del bosque es un componente que, lejos de ser insignificante, debe ser incorporado a las estrategias de conservación.

Introduction

Habitat fragmentation is a process through which a focal habitat type is partially or completely removed, thereby altering its original configuration. Habitat loss, changes in configuration, and a *simultaneous* combination of these phenomena can potentially reduce population persistence in a landscape. Venier and Fahrig (1996) have shown positive correlations between habitat cover and local abundance and distribution of a hypothetical species in simulated landscapes. They suggest that as habitat cover decreases so does the success of dispersers, which in turn results in the more restricted distribution and decreased local abundances they observed. Habitat configuration or its alteration has been shown to influence the presence or abundance (Askins & Philbrick 1987; Verboom et al. 1991; Villard et al. 1995), movements (Wegner & Merriam 1979; Wiens & Milne 1989; Machtans et al. 1996; Sutcliffe & Thomas 1996), and persistence (Hanski et al. 1994, 1995) of species.

Fahrig (1997) investigated the relative influence of habitat cover and configuration using a spatially explicit simulation model. She found that total habitat cover in a landscape had a much greater effect than its spatial configuration, especially when cover exceeded 20%. She concluded that the current emphasis on habitat spatial pattern may be "misplaced" in the face of the more pressing problem of habitat loss. McGarigal and McComb (1995) compared the relative influence of (late-seral) forest cover and configuration on the abundance of bird species in a sample of landscapes. They found that more species were affected by cover than by configuration metrics. The late-seral stands they studied, however, were embedded in a matrix of 0- to 40-year-old conifer plantations. Studies documenting significant effects of isolation on bird species distribution, abundance, dispersal, or persistence in fragmented forests have generally been conducted in agricultural or suburban landscapes (e.g., Askins & Philbrick 1987; Robbins et al. 1989; Verboom et al. 1991; Lens & Dhondt 1994; Villard et al. 1995). The conifer plantations separating late-seral stands in McGarigal and McComb's (1995) landscapes may be substantially more permeable to bird movements

than agricultural and suburban areas. Therefore, it is important to test the generality of these findings.

Although some species can adjust the scale of their movements to the particular spatial arrangement of their habitat (Wegner & Merriam 1990), most species would be expected to show thresholds in their response to landscape structure. At the individual level, there might be species-specific thresholds in habitat dispersion beyond which individuals cannot maintain a positive energetic balance. On a population level, habitat may be so fragmented that recolonizations following local extinctions are too slow to ensure regional persistence (Hanski et al. 1995). Thresholds in habitat occupancy are predicted by analytical models of population response to landscape change (Lande 1987; Pulliam & Dunning 1997). The existence of thresholds in habitat cover and configuration consistent among large numbers of species would have important implications for conservation.

We examined the relative influence of forest cover and configuration on the presence and abundance of bird species nesting in forest fragments embedded in a matrix of cultivated fields. Because changes in habitat cover and configuration occur simultaneously, the proportion of habitat and its configuration in the landscape tend to covary (Gustafson & Parker 1992; Andrén 1994). To measure the relative influence of habitat cover and configuration, we statistically removed the effect of cover when relating species presence-absence to configuration metrics. We addressed the following questions: (1) can we accurately predict species presence solely from forest cover in a landscape, its particular configuration, or both? (2) is there evidence for sharp thresholds in the effects of forest cover or configuration on the presence of individual species?

Fahrig (1997) uses the term *fragmentation* to refer strictly to the separation of formerly continuous habitat into several pieces (fragments) representing the same overall amount of habitat. In this narrow sense, fragmentation describes a situation in which a habitat fragment is fractured and the resulting pieces drift apart. We use fragmentation in the broader sense (Wiens 1989, 1994) to refer to both habitat loss and changes in habitat configuration because these phenomena occur simultaneously

in real-world landscapes. The particular spatial arrangement of habitat at a given point in time is called "configuration."

Methods

Study Area

We conducted our study in agricultural landscapes near Ottawa, Ontario (45°25'N, 75°45'W; Fig. 1). Aerial photographs indicate that woodland has been fragmented in the study area at least since the mid 1930s. All forest fragments were characterized by mature deciduous stands dominated by sugar maple (*Acer saccharum*) and

red maple (*A. rubrum*), along with white and red ash (*Fraxinus americanus* and *F. pensylvanicum*). Conifers were never dominant and were represented mainly by eastern white cedars (*Thuja occidentalis*), which were concentrated along the edges of some of the fragments. Except for two large fragments (132 and 3300 ha, respectively) in the Kinburn region, there were no sizeable water bodies within or adjacent to the 121 forest fragments included in our study. Finally, one or a few buildings were present along the edge of 21 (17%) of the fragments.

Study Design

We selected three 10 × 10 km squares centered around clusters of forest fragments surveyed by Villard et al. (1992). We chose the boundaries of these squares to minimize variability in the structure and floristic composition of forest stands, both within and among each of the three squares. Within each square, we surveyed all closed-canopy forest fragments that were at least 5 ha in size and a few additional fragments of <5 ha.

We divided each of the 10 × 10 km squares into 16 squares of 2.5 × 2.5 km. Of these 48 squares, 33 included at least three bird census points and were selected for further analyses (Fig. 1). In one case (Kinburn region), a 2.5 × 2.5 km square had to be offset slightly to include three census points. This scale is large enough to encompass the breeding dispersal of most species of forest-dwelling passerines (Villard 1991), and a previous study (Villard et al. 1995) has shown that isolation of local populations of Neotropical migrant species from the nearest occupied fragment over a scale of hundreds of meters was sufficient to significantly reduce fragment occupancy in three of the four species examined.

Bird Surveys

We surveyed each forest fragment three times during the breeding season (last week of May to first week of July) in 1989 between sunrise and 1130. In 1990 all census points were visited twice, and 26% of these points were visited three times to confirm the presence of any of the four target species selected for another study (Villard et al. 1995) that had been detected only during the first visit. The lower sampling effort in 1990 could have caused a reduction in the fraction of occupied landscapes relative to 1989. Of the 15 species included in the analyses, the fraction of occupied landscapes differed significantly in only two species between the 2 years (*G* tests, *p* < 0.05). The Pileated Woodpecker and Chestnut-sided Warbler had significantly lower frequencies of occurrence in 1990 (see Table 1 for scientific names). We considered this sampling effect when examining results for these two species.

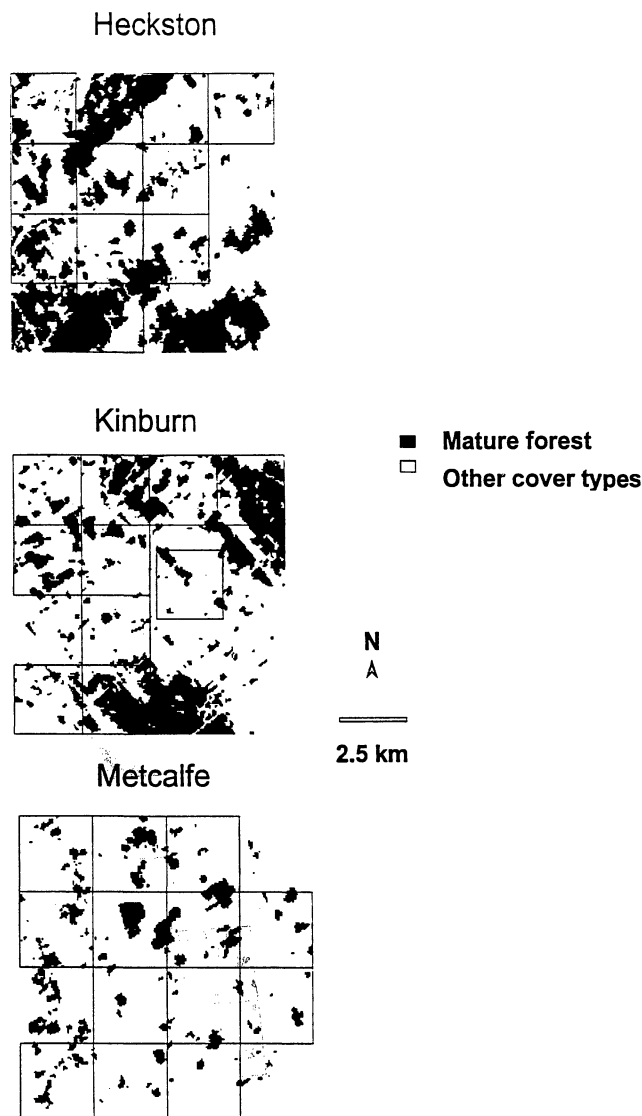


Figure 1. The three study regions and 33 landscapes. Nonforest mainly represents cropfields with scattered farm buildings and villages.

Table 1. "Best" logistic regression models for predicting the presence of each of 15 forest bird species in 33 landscapes in 1989, 1990, or both years.

Species	Year	n/33 ^b	Independent variable ^a			
			COVER	TE ^c	NF ^c	MNN ^c
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	1989	0.24	1.35**			
	1990	0.21				
	1989-1990	0.12				
Downy Woodpecker (<i>Picoides pubescens</i>)	1989	0.88				
	1990	0.79				
	1989-1990	0.70				
Hairy Woodpecker (<i>Picoides villosus</i>)	1989	0.61 [†]				
	1990	0.42				
	1989-1990	0.24	1.02*	-1.62 ⁺		
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	1989	0.45	2.44***			
	1990	0.18		0.70 ⁺		-2.50*
	1989-1990	0.12				
Least Flycatcher (<i>Empidonax minimus</i>)	1989	0.54				
	1990	0.73		-2.47**		
	1989-1990	0.52		-1.55*		
Brown Creeper (<i>Certhi americana</i>)	1989	0.31				
	1990	0.18				
	1989-1990	0.12				
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	1989	0.82				
	1990	0.76				
	1989-1990	0.67				
Wood Thrush (<i>Hylocichla mustelina</i>)	1989	0.91			1.85 ⁺	
	1990	0.94				
	1989-1990	0.88				
Veery (<i>Catharus fuscescens</i>)	1989	0.91			3.77**	
	1990	0.91		-8.34***		
	1989-1990	0.85		-3.33**	2.28*	
Black-and-white Warbler (<i>Mniotilta varia</i>)	1989 ^d	0.88	15.58***			
	1990	0.94	8.40*			
	1989-1990 ^d	0.88	15.58***			
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	1989	0.70				
	1990	0.33	2.42***			-2.39*
	1989-1990	0.27	1.86***			
Black-throated Green Warbler (<i>Dendroica virens</i>)	1989	0.33				
	1990	0.18				
	1989-1990	0.12	0.76 ⁺			
Ovenbird (<i>Seiurus aurocapillus</i>)	1989	0.94			3.59*	
	1990	0.91	5.00*			
	1989-1990	0.88	7.17*		2.39*	
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	1989	0.58	1.87**	1.64 ⁺		
	1990	0.61	3.64***	2.89*		
	1989-1990	0.48	2.01**	2.53**		
Scarlet Tanager (<i>Piranga olivacea</i>)	1989	0.82	2.94***			-3.46**
	1990	0.82				
	1989-1990	0.70			1.32 ⁺	-1.69**

^aRegression coefficients are indicated below each variable included in the model (intercepts omitted). Results of likelihood-ratio test: [†]p < 0.10, *p < 0.05, **p < 0.01, ***p < 0.001. For variable codes, see Table 3.

^bFraction of the 33 landscapes occupied by each species.

^cWe used the residuals of the relationship of each configuration variable with forest cover to statistically remove the effect of the latter.

^dIdentical models: the landscapes occupied were the same in both cases.

To census birds, observers walked through smaller fragments, following their long axis, or walked in a straight line in different portions of large fragments (>150 ha). During subsequent visits, we searched additional portions of fragments when one of the target species had not been detected on previous visit(s). These target species were the Wood Thrush, Black-and-white Warbler,

Ovenbird, and Scarlet Tanager. In all species, most of the individuals detected were singing males. The few exceptions (silent individuals seen) were also scored as presences for the corresponding species.

The duration of censuses was not standardized per unit area of forest. On each separate visit to a fragment or census point (in large fragments), surveys ended

when any one of these events first occurred: (1) the observer had walked across the fragment along its long axis, (2) at least one individual of all four target species had been detected, or (3) searches through new portions of a fragment (during second or third visits) failed to provide detections of target species. In practice, observers spent comparable survey time in small and large fragments because they were less likely to encounter all four target species in small fragments and therefore spent more time per unit area in small than in larger fragments. Our analyses thus should be conservative with regard to fragmentation effects because, on average, species present in landscapes with low values of forest cover or where forest is highly dispersed were slightly more likely to be detected. On the other hand, our data set might be biased against rare species associated with highly forested landscapes.

Data Set

Bird presence-absence and landscape pattern were determined for each 2.5×2.5 km square. Each square (hereafter referred to as *landscape*) was the sampling unit used in statistical analyses. To determine whether the values of the response variables were statistically independent among the 33 landscapes, we tested for spatial autocorrelation (see below).

For each landscape, we measured the number of forest fragments (NF) and median forest fragment area (MEDFA) on 1:15 000 aerial photographs. Forest fragment size included the area extending outside the landscape boundary. Forest fragments <5 ha were not included in these measures. We used FRAGSTATS (McGarigal & Marks 1995) to calculate percent forest cover (COVER), total length of edge between forest and nonforest (TE) not including the forest-landscape boundary intersection, and mean nearest-neighbor distance (MNN). The COVER, TE, and MNN were measured from LANDSAT-TM images (resolution 30 m) on which we had performed a supervised classification of forest and nonforest cover types. We conducted several iterations of the supervised classification until its precision was high, as judged from aerial photographs and ground-truthing.

After we excluded all bird species that could not be detected efficiently with our survey method (e.g., raptors and Ruby-throated Hummingbird [*Archilochus colubris*]), our data set comprised 49 species. Of these, we included in subsequent analyses only those species requiring forest habitats for nesting and foraging because all our landscape metrics strictly characterize woodland, not the matrix. To support our decisions, we referred to a survey conducted in Gatineau Park, an extensive forest tract located within 65 km of all sites (Villard 1991). With the exception of two species (Red-winged Blackbird [*Agelaius phoeniceus*] and Brown-headed Cowbird [*Molothrus ater*]), none of the species we excluded

from the analyses was detected in Gatineau Park. There, Red-winged Blackbirds used old beaver ponds for nesting, whereas Brown-headed Cowbirds could fly to distant agricultural areas to forage, based on the potential range of their daily movements (Thompson 1994). We also excluded species occasionally nesting in isolated trees (e.g., Northern Flicker [*Colaptes auratus*]) and species regularly using elements of the landscape matrix for foraging (e.g., Blue Jay [*Cyanocitta cristata*]). Finally, we excluded from further analyses species that were present in <5 (15%) or in all of the 33 landscapes (in any of the 2 years). The final data set comprised 15 species (Table 1).

Statistical Analyses

To compare the predictive power of forest cover and configuration, we used logistic regressions. We excluded median fragment area from these analyses because its distribution was too skewed to allow transformations. We controlled statistically for the correlation between forest cover and the various configuration indices by fitting a linear model for mean nearest-neighbor distance among fragments and quadratic models for total length of edge and number of fragments (Table 2) and then using the residuals as values for the independent variables. We used the likelihood ratio test to determine the statistical significance of the addition of each variable to logistic regression models. To make sure that model results were not unduly influenced by unusual observations, we examined the Hosmer-Lemeshow statistic, Pearson chi-square, and deviance to assess the goodness of fit of each model. We rejected models that failed to meet the goodness-of-fit criteria proposed by Hosmer and Lemeshow (1989). All computations were performed with SYSTAT 7.0 (SYSTAT 1997).

One of our configuration variables, the number of forest fragments present in the landscape, may be biased by sampling effort. As indicated above, observers spent comparable survey time in small and large fragments, so landscapes containing more fragments were more intensively surveyed. We will take this into account when examining the results.

Table 2. Relationship between forest cover and configuration variables for 33 landscapes near Ottawa, Canada.*

Variable	Model		Intercept	r ²	p > F
	COVER	COVER ²			
TE	1.35	-0.41	0.41	0.74	0.0001
NF	0.35	-0.37	0.38	0.26	0.0108
MNN	-0.54		0.05	0.29	0.0013

*Values of configuration variables were standardized to a mean of zero and unit variance; second-order terms were entered in the models when significant ($\alpha = 0.05$). For variable codes, see Table 3.

The fact that most of our landscapes are spatially clustered (Fig. 1) raises the possibility of a lack of statistical independence in our response variables due to spatial autocorrelation. We tested for spatial autocorrelation in the presence-absence data of the 15 bird species included in the logistic regression analysis. A significant positive spatial autocorrelation would indicate that the closer two landscapes are, the more likely they are to have similar bird assemblages. We computed a Mantel test statistic (Mantel 1967) between a geographical distance matrix and an ecological distance matrix calculated using the Jaccard similarity index (Legendre & Legendre 1984). Ecological distance values were obtained by subtracting similarity values from 1. The Jaccard index calculates the similarity of species assemblages in pairs of landscapes based on the number of species present in both landscapes, divided by the total number of species present. Species absent in both landscapes are thus excluded from the calculations. This is preferable because species may be absent for several different reasons (Legendre & Legendre 1984). We computed a Mantel test using the RT program (Manly 1996). Probability values were calculated based on 4999 random permutations of one of the two matrices.

Results

Forest cover ranged from 3.4% to 66.8%. Variance in configuration metrics was also high (Table 3). All three configuration variables were correlated to forest cover (Table 2), and in two cases (total length of edge, number of fragments) the relationship with cover was quadratic. In the case of mean nearest-neighbor distance among fragments, the relationship was linear with a negative slope. The amount of edge increased with forest cover until the latter reached approximately 40% and then decreased slightly as cover increased further (Fig. 2). Thus, it was important to use residual values of configuration variables after fitting cover.

Mantel tests indicated that our 33 landscapes could be considered independent statistical objects. There was no significant spatial autocorrelation in the composition

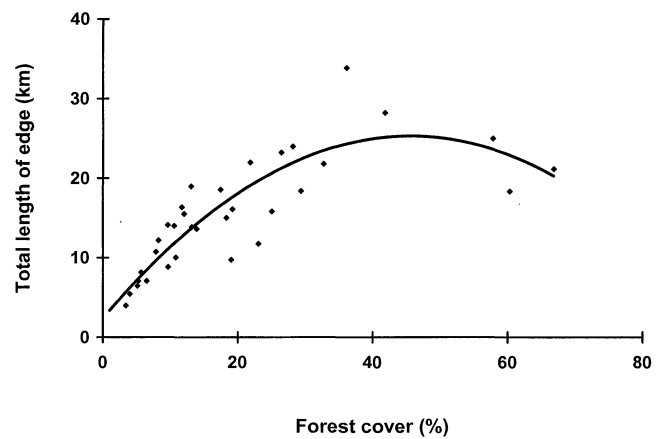


Figure 2. Relationship between forest cover and total length of edge in the 33 landscapes included in the study. See Table 2 for regression parameters.

of the assemblage of 15 species included in the logistic regressions, whether we considered landscapes occupied at least 1 year ($F = 0.00$, $p = 0.99$) or landscapes occupied both years ($F = 1.14$, $p = 0.35$).

Logistic regressions on the presence-absence data of each of the 15 target species (Table 1) indicate that (1) landscape structure (here, forest cover and configuration) was a significant predictor of continuous landscape occupancy over 2 years for nine species; (2) the presence of only three species (Downy Woodpecker, Brown Creeper, and White-breasted Nuthatch) was not significantly related to landscape structure in either year (Table 1); (3) forest cover and configuration were equally good predictors of species presence, whether 1-year or 2-year models were considered; and (4) the effects of forest cover or configuration were not very consistent between years in single-year models. This may reflect important year-to-year changes in landscape occupancy ($n/33$ in Table 1), as exemplified by the Pileated Woodpecker and Chestnut-sided Warbler. Models predicting consistent presence over 2 years should be more robust to stochastic changes in distribution and thus more likely to identify variables relevant to the probability of persistence of individual species.

As expected, species presence was positively related to forest cover and negatively related to mean nearest-neighbor distance among fragments. The effect of the number of fragments was positive, when significant, whereas the direction of the effect of total length of edge varied among species. Total length of edge was a significant predictor of the presence of four species in the 2-year models. Its effect was positive for only one of these species (White-throated Sparrow), indicating that, for a given percentage of forest cover, the probability of presence of this species increased with the dispersion of the forest. In contrast, the other three species seemed to

Table 3. Summary statistics of landscape structure metrics in 33 landscapes near Ottawa, Canada.

Variable*	Mean	SD	Minimum	Maximum
COVER (%)	20.45	16.47	3.40	66.84
TE (km)	15.42	6.96	3.95	33.85
NF	4.79	1.29	2	8
MNN (m)	208.24	127.24	66.59	629.20
MEDFA (ha)	81.34	297.56	7.50	1727.20

*COVER, forest cover in the landscape; TE, total length of edge in the landscape; NF, number of forest fragments; MNN, mean nearest neighbor distance; MEDFA, median fragment area.

benefit from a more compact distribution of forest cover. The significant positive effect of number of fragments on Veery presence (Table 1; Fig. 3) seemed to contradict this interpretation. This relationship might actually reflect the slightly greater sampling effort in landscapes with more dispersed forest.

We examined the shape of logistic regression curves for each significant predictor separately (Figs. 3 & 4). Slopes were rather shallow in all cases, except perhaps for the relationships between forest cover and presence of Black-and-white Warbler and Ovenbird (Fig. 4). Thus, our focal species generally did not exhibit sharp thresholds in their responses to landscape structure.

Discussion

Relative Influence of Forest Cover and Configuration

Our results indicate that the presence of many species can be significantly predicted by landscape structure, irrespective of microhabitat features. Indeed, only 3 of

the 15 species considered did not respond significantly to either forest cover or configuration in any of the models. Forest cover and configuration were equally good predictors of the presence of the woodland bird species included in this study. For landscapes occupied during the 2 years of the study, forest cover and configuration each significantly predicted the presence of 6 of the 15 species considered. The Ovenbird, however, could be omitted from the list of species responding significantly to configuration to account for the possible influence of sampling effort on our variable “number of fragments.”

The statistical approach we used was intentionally conservative with regard to configuration effects. Using the residuals of configuration variables after fitting forest cover may give precedence to the influence of cover if little variability is left in the residuals. For example, the residuals of mean nearest-neighbor distance among fragments (MNN) significantly predicted the presence of only 1 of the 15 species in 2-year models. If forest cover decreases in a given landscape over time, the lower probability of presence of a hypothetical species could reflect the reduced amount of habitat available. It could

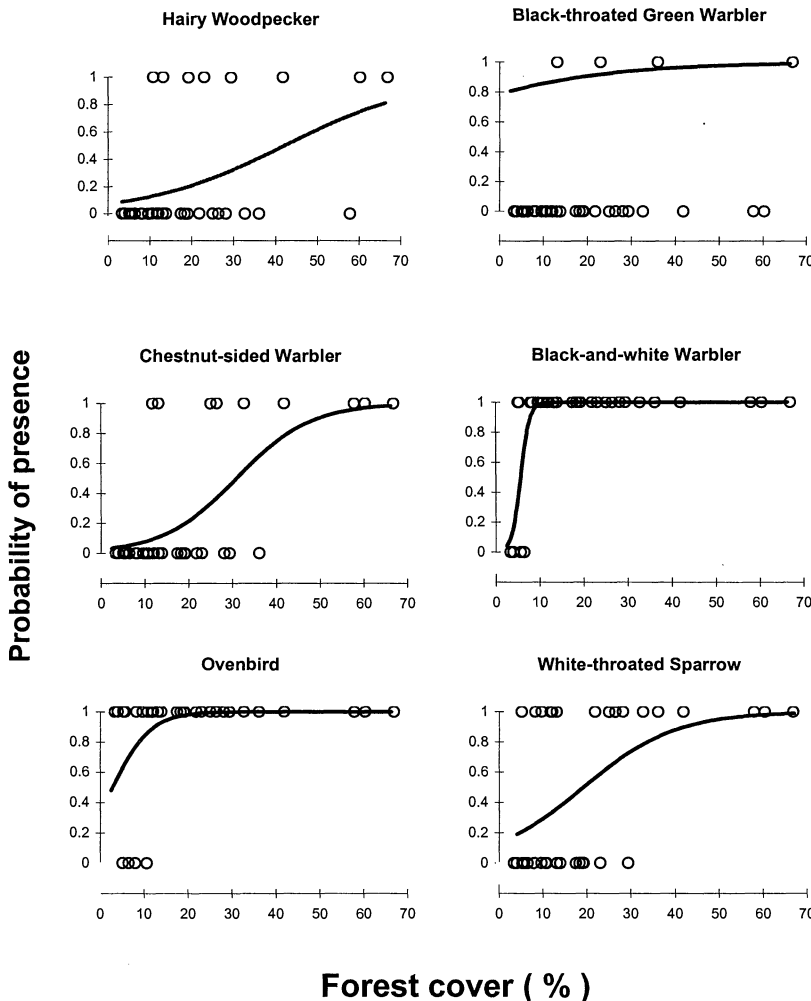


Figure 3. Logistic regressions showing significant relationships between forest configuration metrics and probability of continuous presence of forest bird species in 1989 and 1990. Many of the final logistic regression models included two independent variables (Table 3). Values on the x-axes differ slightly from actual values after we corrected for the effect of forest cover on configuration variables (see methods).

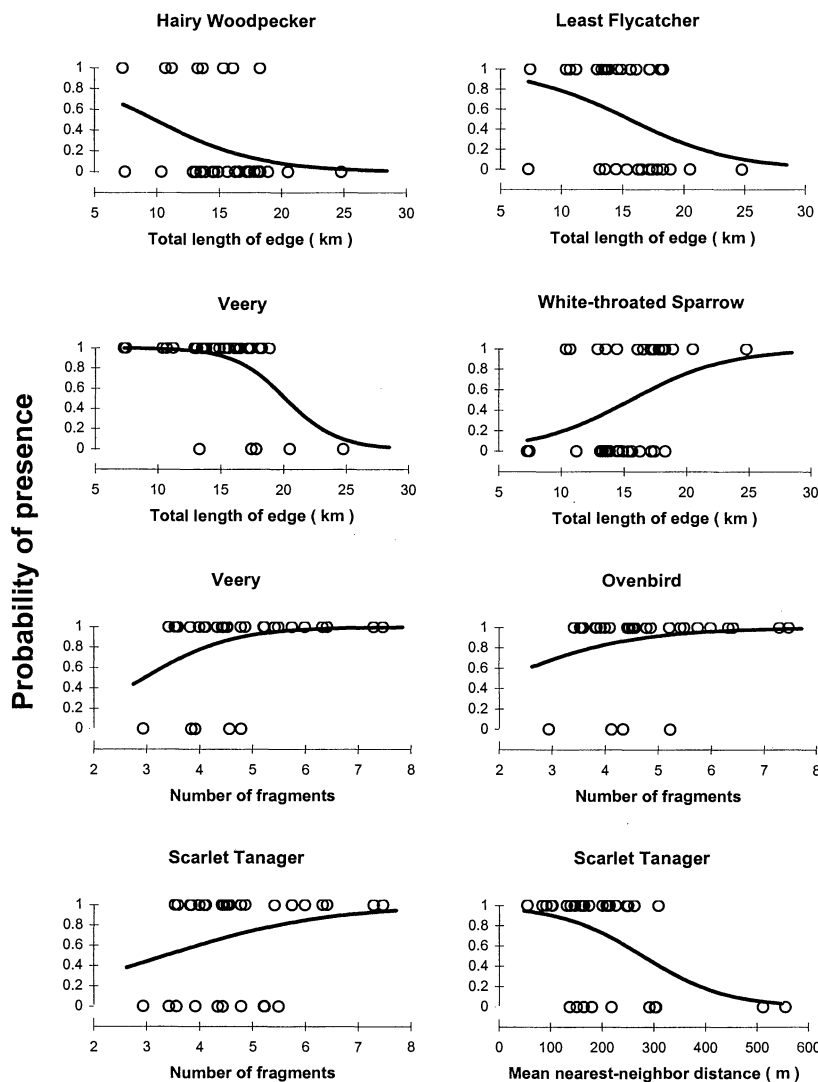


Figure 4. Logistic regressions showing significant relationships between forest cover in the landscape and probability of continuous presence of forest bird species in 1989 and 1990. Many of the final logistic regression models included two independent variables (Table 3).

also result from a lower connectivity among the remaining forest fragments. Thus, the observed effect of forest cover on bird species presence might include a configuration effect. Indeed, when we fit actual mean nearest-neighbor distance (not residuals) first in 2-year models, this variable was a significant predictor for 5 of the 15 species rather than only 1. The fact that our approach was conservative with regard to configuration effects makes even more compelling our finding that cover effects were not clearly dominant. It is possible that our survey method was biased against uncommon bird species associated with highly forested landscapes. The fact that rare species were excluded from the analysis, however, should reduce this potential problem.

Some of the effects of forest configuration that we found were consistent with previous studies, but others were somewhat unexpected. Villard et al. (1995) used a patch-centered approach to investigate significant predictors of presence of four species in forest fragments of the Metcalfe region (Fig. 1). They found a significant

positive influence of proximity to the nearest fragment occupied the previous year on the presence of Black-and-white Warblers, Ovenbirds, and Scarlet Tanagers, whereas this variable was not significant for the Wood Thrush. In Maryland and adjacent states, Robbins et al. (1989) also reported negative effects of isolation from surrounding woodland (within 2 km) on the abundance of the same three species. Here, we used a landscape-level approach and found consistent results for two of the four species: no effect of mean-nearest neighbor distance on Wood Thrushes, a significant effect on Scarlet Tanagers, but no effects on Black-and-white Warblers or Ovenbirds. This suggests that results obtained from a patch-centered approach may not translate directly to the landscape scale. These apparent inconsistencies may reflect, to some degree, the limits of our statistical approach.

Many forest bird species from the regional avifauna were rare or absent from the 33 landscapes included in this study (Villard 1991). Although the rarity of some of these species undoubtedly reflects the unavailability or

insufficient amount of suitable habitat (e.g., Golden-crowned Kinglet [*Regulus satrapa*]; Pine Warbler [*Dendroica pinus*]), others (e.g., Black-throated Blue Warbler [*Dendroica caerulescens*]) may be sensitive to forest fragmentation by agriculture. A fragmentation experiment (e.g., Schmiegelow et al. 1997) would be required to test the sensitivity of these species.

Landscape-Scale Studies

There is a lot of variation in what is considered a landscape scale, even when the same taxon is under investigation. In studies on forest birds, for example, landscape scales may vary from 3 km² (McGarigal & McComb 1995) to 625 km² (Edenius & Elmberg 1996). In our study we used 6.25 km². Although some degree of arbitrariness cannot be avoided when selecting a landscape scale, this scale should be large enough to encompass demographic units that are relatively independent, at least over short temporal scales. The absence of spatial autocorrelation in the species assemblages considered here indicates that our landscapes were statistically independent with respect to their species composition.

In future studies, it would be interesting to vary the scale of landscape units to examine changes in species response to landscape structure according to the spatial resolution. Spatially extensive data sets (e.g., breeding bird atlas data) would be required to perform this type of analysis. Atlas data may also allow the use of response variables that are more ecologically meaningful than presence or abundance, such as probable or confirmed breeding. The degree of standardization of sampling effort in atlas data sets may be insufficient for this purpose, however. A standardized method for collecting reproductive success data over landscape or even regional scales (e.g., Gunn et al., in press) would be extremely useful in achieving this goal.

Conservation Implications

Our study was prompted largely by the suggestion that, as habitat is lost, the particular configuration of the remaining habitat cannot mitigate the overall effects of habitat loss per se (Fahrig 1997). In model simulations, Fahrig (1997) found that beyond 20% habitat cover, species persistence was virtually ensured, irrespective of habitat configuration. In a review of fragmentation effects on birds and mammals, Andr en (1994) also noted that habitat configuration had little or no effect on species richness or abundance beyond a 20–30% threshold in habitat cover. In contrast, our findings indicate that, within the range of forest cover we considered (3–67%), configuration was a far from negligible component of landscape structure for predicting the presence of forest birds. These results are conservative with regard to configuration effects because (1) the range in forest cover in

our landscapes extended far beyond 20–30% and (2) forest cover may have included a significant but “hidden” portion of configuration effects, as explained above.

Significant effects of forest configuration on species presence can be interpreted in a variety of ways depending on the life history of the species considered. Poor dispersers would be expected to be sensitive to habitat configuration or to the spatial pattern of habitat loss, as shown by Dytham (1995). For a given percentage of forest cover, its particular configuration may determine the relative ease with which natal dispersers move across the landscape (Machtans et al. 1996) and with which nest predators (Wilcove 1985; Andr en & Angelstam 1988) and brood parasites (Brittingham & Temple 1983; but see Hahn & Hatfield 1995) penetrate into fragments. Forest configuration may also be important to species with large area requirements. In landscapes with intermediate or high degrees of forest fragmentation, the presence of these species may depend on the particular configuration of fragments. This might explain why the Pileated Woodpecker was more sensitive to landscape structure than were the Downy Woodpecker, Brown Creeper, and White-breasted Nuthatch, the only species that did not respond significantly to forest cover or configuration in any of the three models. For resident species, this hypothesis might be especially relevant during the winter months, when access to resources is especially critical.

Our study does not provide simple rules of thumb for designing landscape-level conservation strategies for the forest avifauna. In fact, we found little evidence for sharp thresholds in the landscape characteristics to which the various bird species responded significantly. Obviously, some variability in vegetation structure and composition exists among the 33 landscapes, and it may contribute to the shallowness of the slopes in univariate models. In spite of this, our logistic models indicate biologically meaningful landscape effects. Models that were strongly influenced by unusual observations were systematically rejected. Nonetheless, our results do stress the species specificity of fragmentation effects and the need to take this into consideration when designing conservation strategies.

We support Fahrig’s (1997) conclusion that ecologists should devote more attention to the problem of habitat loss, in addition to configuration effects. In many landscapes, changes to habitat configuration aiming to increase connectivity would do little to compensate for the effects of excessive habitat loss. The general emphasis on habitat configuration as opposed to habitat cover may reflect a search for short-term solutions to habitat fragmentation. The interest of conservation biologists in movement corridors (e.g., Saunders & Hobbs 1993) is a good example of this tendency. Conservation strategies proposing to maintain or reestablish connectedness are also easier to sell to government agencies or resource-based industries than are strategies specifying minimum

thresholds in habitat area to be protected or restored. Results from this study stress the importance of considering habitat cover and configuration simultaneously if we are to develop sound conservation strategies for forest bird species. This will be a major challenge requiring difficult decisions, given the relative specificity of species' responses to forest cover and configuration.

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