Thresholds in Songbird Occurrence in Relation to Landscape Structure

MATTHEW G. BETTS,*§ GRAHAM J. FORBES,† AND ANTONY W. DIAMOND‡

*Department of Biological Sciences, 103 Gilman Hall, Dartmouth College, NH 03755, U.S.A.
†Greater Fundy Ecosystem Research Group, 1350 Regent Street, Fredericton, New Brunswick E3C 2G6, Canada
‡Atlantic Cooperative Wildlife Ecology Research Network, University of New Brunswick, P.O. Box 45111, Fredericton, New Brunswick, Canada, E3B 6C2

Abstract: *Theory predicts the occurrence of threshold levels of habitat in landscapes, below which ecological processes change abruptly. Simulation models indicate that below critical thresholds, fragmentation of habitat influences patch occupancy by decreasing colonization rates and increasing rates of local extinction. Uncovering such putative relationships is important for understanding the demography of species and in developing sound conservation strategies. Using segmented logistic regression, we tested for thresholds in occurrence of 15 bird species as a function of the amount of suitable habitat at multiple scales (150–2000-m radii). Suitable habitat was defined quantitatively based on previously derived, spatially explicit distribution models for each species. The occurrence of 10 out of 15 species was influenced by the amount of habitat at a landscape scale (≥500-m radius). Of these species all but one were best predicted by threshold models. Six out of nine species exhibited asymptotic thresholds; the effects of habitat loss intensified at low amounts of habitat in a landscape. Landscape thresholds ranged from 8.6% habitat to 28.7% (x̄ = 18.5 ± 2.6% [95% CI]). For two species landscape thresholds coincided with sensitivity to fragmentation; both species were more likely to occur in large patches, but only when the amount of habitat in a landscape was low. This supports the fragmentation threshold hypothesis. Nevertheless, the occurrence of most species appeared to be unaffected by fragmentation, regardless of the amount of habitat present at landscape extents. The thresholds we identified may be useful to managers in establishing conservation targets. Our results indicate that findings of landscape-scale studies conducted in regions with relatively high proportions of habitat and low fragmentation may not be applicable in regions with low habitat proportions and high fragmentation.*

Keywords: forest mosaic, fragmentation, landscape thresholds, patch size, segmented logistic regression, songbirds, spatial autocorrelation

Umbrales en la Ocurrencia de Aves Canoras en Relación con la Estructura del Paisaje

Resumen: *La teoría predice la ocurrencia de niveles de hábitat umbral en los paisajes, debajo de los cuales los procesos ecológicos cambian abruptamente. Los modelos de situación indican que debajo de umbrales críticos, la fragmentación del hábitat influye en la ocupación de parches mediante la disminución de las tasas de colonización y el incremento de las tasas de extinción local. El descubrimiento de tales relaciones putativas es importante para el entendimiento de la demografía de especies y para el desarrollo de estrategias de conservación sólidas. Utilizando regresión logística segmentada, probamos los umbrales de ocurrencia de 15 especies de aves en función de la cantidad de hábitat adecuado en escalas múltiples (radios de 150–2000 m). El hábitat adecuado fue definido cuantitativamente con base en modelos espacialmente explícitos derivados previamente para cada especie. La ocurrencia de 10 de 15 especies fue influida por la cantidad de hábitat en una escala de paisaje (radio ≥ 500 m). De estas especies, todas menos una fueron mejor*

1046

predichas por los modelos de umbral. Seis de nueve especies exhibieron umbrales asintóticos; los efectos de la pérdida de hábitat se intensificaron a bajas cantidades de hábitat en un paisaje. Los umbrales de paisaje variaron entre 8.6% y 38%.7 de hábitat (x̄ = 18.5 ±2.6% [95% IC]). Para dos especies, los umbrales de paisaje coincidieron con la sensibilidad a la fragmentación; era más probable que ambas especies ocurrieran en parches grandes, pero solo cuando la cantidad de hábitat en un paisaje era baja. Esto soporta la hipótesis del umbral de fragmentación. Sin embargo, la ocurrencia de la mayoría de las especies no pareció ser afectada por la fragmentación, independientemente de la cantidad de hábitat presente a nivel de paisaje. Los umbrales que identificamos pueden ser de utilidad para que gestores establezcan objetivos de conservación. Nuestros resultados indican que los hallazgos de estudios a nivel paisaje realizados en regiones con proporciones de hábitat relativamente altas y con niveles bajos de fragmentación pueden no ser aplicables en regiones con bajas proporciones de hábitat y niveles altos de fragmentación.

Palabras Clave: autocorrelación espacial, aves canoras, fragmentación, regresión logística segmentada, tamaño del fragmento, umbrales de paisaje

Introduction

Theory predicts the occurrence of threshold levels of habitat in landscapes, below which ecological processes change abruptly (Fahrig 1998; With & King 1999). As the amount of habitat in the landscape declines, contiguous habitat is usually broken into multiple fragments (Gardner & O'Neill 1991). There also tends to be an exponential increase in the average distances between habitat fragments (With & Crist 1995). A number of theoretical models predict that below critical thresholds, habitat fragmentation influences patch occupancy by decreasing colonization rates and increasing rates of local extinction (Lande 1987; With & King 1999).

Uncovering such relationships is important for understanding the demography of species (Hanski & Ovaskainen 2000) and in developing sound conservation strategies (Pulliam & Dunning 1997). Given the rapid rate of habitat decline globally, it is essential to detect points in habitat loss where rates of population decline may accelerate or the likelihood of species occurrence drops rapidly (Balmford et al. 2003). Nevertheless, empirical tests for landscape-scale thresholds in either species demography or occurrence are still uncommon (Homan et al. 2004; Radford & Bennett 2004).

To date, efforts to detect thresholds in habitat amount have been hampered by a number of practical and theoretical concerns. First, it is essential to accurately define the distribution of habitat for species under consideration to ensure that landscape metrics are relevant to the species at hand (Fischer et al. 2004). Although this is straightforward in simulation models, it is more challenging in empirical research. Researchers have tended to rely on qualitative definitions of what likely constitutes habitat (e.g., Homan et al. 2004) or have used general land-cover classifications (e.g., "forest," Trzcinski et al. 1999; "native forest," Lindenmayer et al. 2005) that might have little bearing on the often different habitat associations of individual species. Thresholds in habitat amount appear to

be more common in agricultural landscapes and island archipelagos than in forested landscapes (Mönkkönen & Reunanen 1999). This may stem, however, partly from the difficulty in correctly identifying the amount and distribution of habitat for individual species in forest mosaics where gradients are more common than clearly identifiable patch boundaries (Wiens 1994).

Second, there is debate about the causes of threshold patterns in species occurrence in relation to landscape-scale habitat loss (Homan et al. 2004). The fragmentation threshold hypothesis states that thresholds occur as a result of increasing influence of fragmentation effects below some level of habitat amount (Andrén 1994). That is, species occurrence is influenced by a statistical interaction between landscape composition and configuration (Trzcinski et al. 1999). Nevertheless, there has been little empirical evidence to support this prediction (Fahrig 2003; Betts et al. 2006*a*). Observed thresholds could also reflect the extinction threshold hypothesis; effects of habitat loss might intensify at low habitat levels. Fragmentation per se may have little to do with observed threshold effects (Fahrig 2003). In this case a species may simply require at least some minimum habitat amount, regardless of landscape pattern (e.g., Meyer et al. 1998), and there should be no statistical interaction between landscape composition and configuration.

Third, until recently there has been a paucity of statistical approaches available to objectively identify ecological thresholds (Guénette & Villard 2005; Huggett 2005). Methods for identifying thresholds in occurrence (binomial) data appear to have lagged behind those appropriate for continuous data (e.g., Toms & Lesperance 2003). This is problematic because presence/absence data are commonly used in ecology to predict species distributions (Guisan & Thuiller 2005). Receiver-operating characteristic analysis and binomial-change point tests have been used to identify cut points (thresholds) in the independent variable that maximize prediction success (maximized specificity and sensitivity; Homan et al. 2004;

Guénette & Villard 2005). Although this is appealing from a management perspective, the identification of statistical cut points does not necessarily imply nonlinear responses to environmental gradients; model sensitivity and specificity can be maximized even if the response by a species to habitat loss is statistically significant but linear (Manel et al. 2001).

We tested for thresholds in the occurrence of 15 bird species in a primarily forested landscape as a function of the amount of suitable habitat at multiple scales. Suitable habitat was defined quantitatively with previously derived, spatially explicit distribution models for each species (Betts et al. 2006*b*). This provided the opportunity to conduct a natural experiment in which the amount of habitat in the study area could be varied independently for each species without the confounding influences introduced by varying the location or extent of the study area. We used a new approach (segmented logistic regression; Muggeo 2003) to detect thresholds in occurrence. We predicted that if the fragmentation threshold hypothesis is true, species exhibiting thresholds in occurrence should also be sensitive to habitat configuration in landscapes where habitat amount falls below a threshold level. If the extinction hypothesis is true, species exhibiting thresholds should not necessarily be sensitive to habitat configuration.

Methods

Study Area

The study was conducted in the Greater Fundy Ecosystem (GFE), New Brunswick, Canada (66.08–$64.96°$, 46.08–$45.47°$) (approximately 4000 km^2). The GFE is characterized by 89% forest cover, a maritime climate, and rolling topography (elevation 70–398 m) and is in the Acadian Forest Ecoregion (Rowe 1972; for study area details see Betts et al. 2003). Intensive forestry activities (i.e., clearcutting, conifer planting, thinning) have occurred since the early 1970s, resulting in a heterogeneous landscape mosaic, where approximately 40% of the study area is mature (>70 years), unmanaged forest (NBDNR 1993).

Bird Sampling

Our database consisted of 425 point locations sampled from 4 June to 15 July in 2000 and 2002. In 2000 birds were sampled with a systematic design ($n = 141$). Two 25-km^2 grids were established with points 250–300 m apart. All points that occurred in forest older than 60 years were sampled. The two grids were approximately 5 km apart. Grids were initially established to describe diversity of mature forest-associated songbirds in a managed and an unmanaged landscape (Fundy National Park). In the same region in 2002 we used a stratified random sampling approach ($n = 284$). Samples were located to rep-

resent the range of variation in mature forest patch size (>60 years) and habitat amount (see Betts et al. 2006*a*). Although sampling designs varied between years to address different initial study objectives, in all cases points were located ≥ 250 m apart to minimize the probability of double counting and >75 m from clearly identifiable forest edges (i.e., roads, recent clearcuts [<10 years]).

We conducted fixed-radius point counts of forest passerines (Ralph et al. 1995) at each sample point. Three 5-minute counts were conducted on separate occasions between 0530 and 1100 hours. All male birds seen or heard during this time period within a 50-m radius were recorded as present. Because mean bird counts per station tended to be low (<2) for most species and because we were interested in estimating probability of occurrence, we reduced relative abundance data to presence–absence data for use in binomial models. Presences were positively correlated with estimates of reproductive activity in our study area (Betts et al. 2005). Detectability of the species we examined may have varied as a function of local habitat characteristics (MacKenzie et al 2005). Thus, despite the fact that some of the species we examined tend to be characterized by high detectability (>90%) (Farnsworth et al. 2002), local habitat models should be regarded with some caution, particularly for species with lower detectability (e.g., Blackburnian Warbler [detectability = approximately 75% for a 10-minute count]; Farnsworth et al. 2002) (see Table 1 for scientific names of birds). Nevertheless, by statistically controlling for the effect of local habitat characteristics (see Statistical Analyses), we removed the potential bias caused by varying detectability among different habitat types on our tests for landscape thresholds.

Defining Habitat at Local and Landscape Scales

In a separate study we developed spatially explicit models for the distribution of 21 bird species based on local-scale variables derived from a geographic information system (GIS) as predictor variables (Betts et al. 2006*b*). The GIS land-cover data originated from the New Brunswick Forest Inventory (NBDNR 1993), which are based on interpreted and digitized aerial photographs taken in 1993 (1:12 500 scale, color) and updated to 2000 with satellite imagery (30-m^2 resolution; Betts et al. 2003). None of these initial models relied on landscape-scale data.

For the current study we selected a set of 15 species for which the success of spatial model prediction on independent data was the greatest (area under the receiver operating characteristic curve [AUC] ≥ 0.65; Betts et al. 2006*b*) and model calibration was adequate according to Hosmer and Lemeshow (2000) tests. We chose AUC = 0.65 as a prediction success cutoff, rather than the more frequently used AUC = 0.70, to maximize the number of species that we could examine (for species-specific AUC values see Betts et al. 2006*b*). Because early

Table 1. Threshold values ($\hat{\psi}$) of habitat amount for songbirds detected at local (150 m) and landscape (500–2000 m) spatial extents.[a]

Species	Extent (m)	$\hat{\psi}$ (%)	SE (%)	$\hat{\psi}_{adj}$ (%)[b]	AIC$\hat{\psi}$	AIC$_L$	ER ($\hat{\psi}$)[c]	AUC[d]
American Redstart,	150[e]	7.45	0.95	10.87	377	381	5.84	
Setophaga ruticilla	500	8.53	1.11	12.45	376	378	2.77	
	1000					383		
	2000[e]	20.04	2.70	29.26	375*	379	9.12	0.67
Bay-breasted Warbler,	150					336*		0.76
Dendroica castanea	500					338		
	1000	14.11	6.38	18.23	340	338	0.27	
	2000	9.53	3.90	12.31	340	338	0.32	
Blackburnian Warbler,	150	26.67	12.25	27.49	556	553*	0.24	
Dendroica fusca	500	15.18	5.08	15.65	556	555	0.42	
	1000[e]	14.75	2.89	15.21	553*	555	2.11	0.61
	2000	29.56	25.81	30.47	556	554	0.31	
Black-throated Blue Warbler,	150[e]	8.57	1.82	22.92	440	445	13.74	
Dendroica caerulescens	500	14.10	10.56	37.70	444	441	0.26	
	1000					441		
	2000[e]	8.63	0.70	23.07	435*	440	19.01	0.75
Common Yellowthroat,	150					289		
Geothlypis trichas	500	18.27	2.42	32.05	285	291	15.64	
	1000[e]	10.86	0.35	19.05	279*	290	280.06	0.78
	2000	12.43	1.17	21.81	288	289	2.04	
Golden-crowned Kinglet,	150[e]	51.51	3.82	73.90	475*	479	8.08	0.76
Regulus satrapa	500					477		
	1000					480		
	2000					480		
Magnolia Warbler,	150	32.65	9.46	40.31	447	444	0.20	
Dendroica magnolia	500[e]	24.30	2.66	30.00	443*	445	2.46	0.76
	1000[e]	38.70	3.23	47.78	445	446	2.05	
	2000	38.85	7.50	47.96	445	445	0.93	
Nashville Warbler,	150[e]	11.89	1.42	19.15	388	405	5569.16	
Vermivora ruficapilla	500	30.09	14.05	48.45	389	389	0.74	
	1000					389		
	2000[e]	20.90	1.66	33.65	386*	389	5.81	0.83
Ovenbird, *Seirus aurocappilla*	150[e]	46.53	7.83	50.58	514	518	8.67	
	500							
	1000	20.31	4.06	22.08	515	513	0.46	
	2000[e]	28.20	5.08	30.65	512*	515	3.19	0.74
Red-eyed Vireo, *Vireo olivacea*	150	13.95	7.02		470	468	0.44	
	500							
	1000					469		
	2000					467*		0.80
Ruby-crowned Kinglet,	150[e]	10.51	2.80	19.98	317*	326	84.35	0.85
Regulus calendula	500							
	1000					320		
	2000	30.41	7.01	57.81	323	320	0.34	
Swainson's Thrush,	150[e]	22.96	4.37	29.86	281*	287	17.12	
Catharus ustulatus	500							
	1000	9.62	1.77	12.51	282	282	0.90	
	2000[e]	10.15	1.66	13.20	281*	282	2.33	0.75
White-throated Sparrow,	150[e]	8.39	1.23	8.69	239*	258	14,115.09	0.92
Zonotrichia albicollis	500					241		
	1000					240		
	2000	9.86	2.68	10.21	242	241	0.41	
Yellow-bellied Flycatcher,	150	11.53	4.73	18.21	352	350	0.42	
Empidonax flaviventris	500	46.11	2.97	72.84	352	352	0.87	
	1000					352		
	2000[e]	28.73	3.01	45.39	351*	352	1.31	0.78
Yellow-rumped Warbler,	150[e]	34.25	4.46	41.77	435*	436	2.41	0.66
Dendroica coronata	500	44.82	2.56	54.66	436	436	1.03	
	1000	35.76	5.48	43.61	438	435*	0.31	
	2000	36.86	6.87	44.95	438	435*	0.32	

[a]*All landscape-extent threshold values were calculated statistically controlling for local variation and spatial autocorrelation. Best models (lowest Akaike's information criterion [AIC]) are indicated with an asterisk (*). Blank cells indicate either no threshold model converged or landscape variables were too correlated to include in the same model as local variables. In the latter case, no AIC$_L$ is reported.*
[b]*Threshold value weighted by the maximum probability of occurrence from initial spatially explicit model.*
[c]*Evidence ratio, to be interpreted as the evidence against the linear model.*
[d]*Area under the receiver operating characteristic curve.*
[e]*For this spatial extent there is greater support for a threshold model (AIC$\hat{\psi}$) in relation to the linear model (AIC$_L$).*

successional species (Common Yellowthroat, Ruby-crowned Kinglet, Nashville Warbler, and White-throated Sparrow) were characterized by very low prevalence in our initial data set (<10% of sample points), it was not possible for us to test for thresholds with data that were completely independent of those used to develop initial spatially explicit habitat models. To maximize the number of species examined, for these four species we supplemented the 2000/2002 data set with data collected in 2001 used to develop initial habitat models (Betts et al. 2006b; total $n = 743$). In 2001 data were collected with a stratified random sampling scheme that spanned a successional stage and coniferous-to-deciduous gradient (see Betts et al. 2006b). Because in model building we controlled for local variation in habitat characteristics (see Statistical Analyses) and spatially explicit habitat models

were built based on only local variables, any landscape effect detected in the current study is independent of models developed by Betts et al. (2006b).

We developed habitat-suitability maps (30-m^2 resolution) for each species by mapping the fitted values of GIS habitat models (Fig. 1). To obtain a measure of habitat amount, we summed the estimated probability of occurrence ($\hat{p}$) surrounding each sample point at four spatial extents: 150, 500, 1000, and 2000 m (after Betts et al. 2006a). The smallest habitat extent (150 m) captured variation in habitat amount at the scale of individual songbird territories. A previous comparison found negligible differences in prediction success between models based on local-scale GIS data and fine-resolution vegetation-plot data for most species (Betts et al. 2006b). The three largest of the spatial extents we selected influence forest
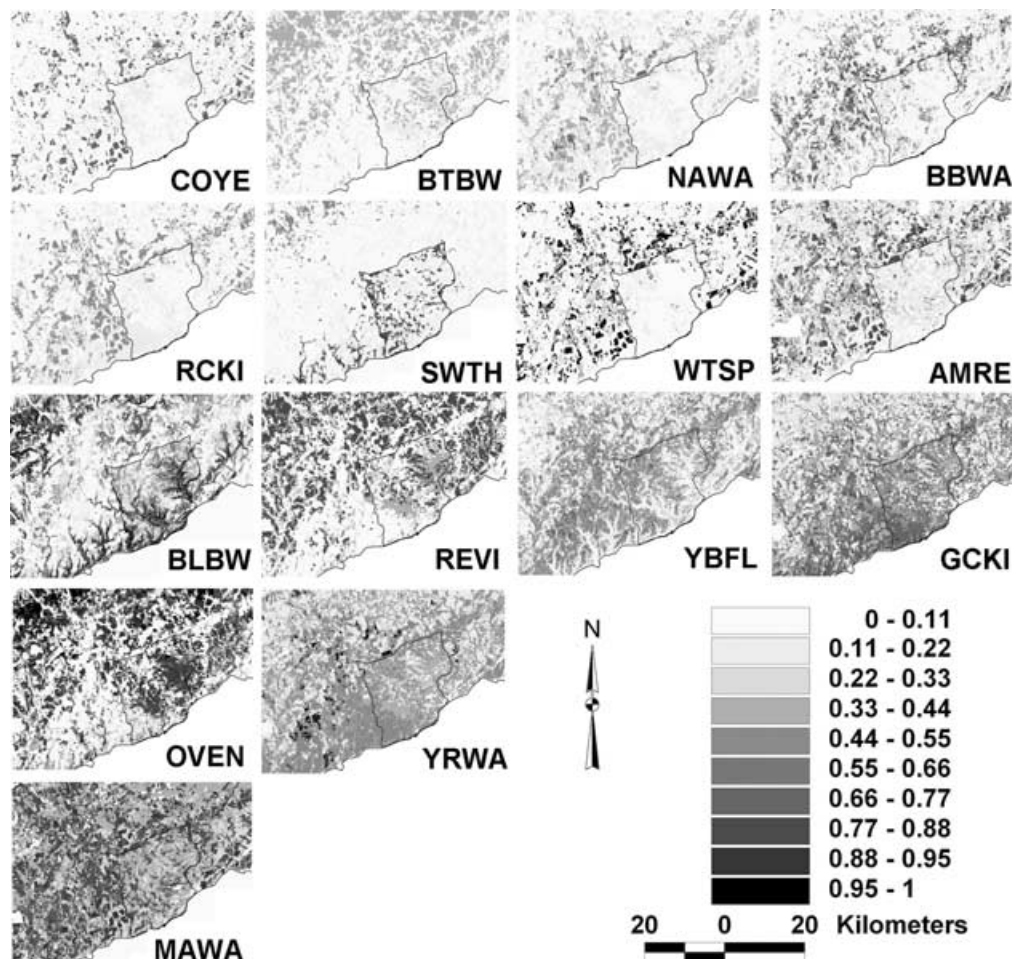

Figure 1. Quantitative habitat suitability maps (30-m^2 resolution) in the Greater Fundy Ecosystem for 15 species of songbirds that were used as the basis for testing for thresholds in species occurrence (arranged left to right in order of increasing habitat amount). Darker shading indicates higher probability of occurrence. Solid outline indicates boundaries of Fundy National Park (AMRE, American Redstart; BBWA, Bay-breasted Warbler; BLBW, Blackburnian Warbler; BTBW, Black-throated Blue Warbler; COYE, Common Yellowthroat; GCKI, Golden-crowned Kinglet; MAWA, Magnolia Warbler; NAWA, Nashville Warbler; OVEN, Ovenbird; RCKI, Ruby-crowned Kinglet; REVI, Red-eyed Vireo; SWTH, Swainson's Thrush; YBFL, Yellow-bellied Flycatcher; YRWA, Yellow-rumped Warbler; WTSP, White-throated Sparrow).

passerine habitat use (Drapeau et al. 2000) and likely include the scale relevant to migrant warblers in natal dispersal (Bowman 2003) and extraterritorial movements (Norris & Stutchbury 2001).

We used patch size as a measure of habitat configuration because it can be an important predictor of population density (Bender et al. 1998). In addition, previous work in our study area indicates that occurrence of one species (Ovenbird) is correlated with patch size even after controlling for effects of edge and landscape composition (Betts et al. 2006*a*). There is little support in the literature for other configuration variables (McGarigal & McComb 1995; Fahrig 2003). Configuration-type isolation metrics (e.g., nearest neighbor) are poor predictors of patch immigration and emigration in individual patches in relation to area-based metrics (e.g., area of habitat in a landscape-extent circle surrounding a patch; Tischendorf et al. 2003), so we did not test directly for effects of such configuration metrics. We identified patches in the forest mosaic by determining cut points in probability of species occurrence ($\hat{p}$) with receiver operating characteristic curves (see Betts et al. 2006*a*). Patch size was measured as the total area of suitable habitat separated from other patches by >30 m. Territories of our focal species are unlikely to span gaps of this size (Villard et al. 1995).

Statistical Analyses

We tested for thresholds with segmented logistic regression:

$$p = \exp[\beta_0 + \beta_{1x} + \beta_2(x - \psi)_+]/1 \\ + \exp[\beta_0 + \beta_{1x} + \beta_2(x - \psi)_+], \tag{1}$$

where p is the probability of species occurrence, x is the independent variable, ψ is the break point (threshold), and $(x - \psi)_+ = (x - \psi) \times I(x > \psi)$ being $I(A) = 1$ if A is true, β_0 is the intercept, β_1 is the slope of the left line segment (that is, for $x \geq \psi$), and β_2 is the difference-in-slopes parameter. Thus, $(\beta_1 + \beta_2)$ is the slope of the right line segment ($x > \psi$). Segmented logistic regression relies on an iterative fitting process to estimate ψ, β_0, $\beta_1 \dots \beta_i$ (Muggeo 2003). Multiple ψ and β are fitted repeatedly until estimates converge at the maximum likelihood estimate. Standard errors and confidence intervals of ψ may be obtained with linear approximation for the ratio of two random variables (Muggeo 2003). All segmented models were fitted in R 2.0.1 (R Development Core Team 2004) statistical program in the segmented package (Muggeo 2004). Segmented logistic regression requires a starting estimate for ψ. We determined this starting point from examination of both deciles plots (Homan et al. 2004) and fitted values of locally weighted nonparametric models (loess plots, smoothing parameter = 0.75). In instances where the algorithm did not converge (this sometimes

occurred when evidence for a threshold was weak), we searched systematically for a starting point in 5% increments of independent variables. We determined support for thresholds in occupancy as a function of landscape variables through the following steps. (1) We used logistic regression to test for a linear relationship between probability of occurrence and territory-extent variables (amount of habitat at 150 m; hereafter local). (2) We used segmented logistic regression to estimate thresholds at the local extent. If exploratory plots suggested the existence of two thresholds for a single independent variable, we also tested for this possibility. (3) We used Akaike's information criterion (AIC) to determine the weight of evidence for local threshold models in relation to linear models (Burnham & Anderson 2002). Low AIC values indicate higher degrees of model parsimony. The advantage of the AIC approach is that it penalizes threshold models for the addition of extra parameters (e.g., ψ and β_2) and provides information about the relative amount of support for threshold models. The relative likelihood of each model in relation to the best model can be determined based on evidence ratios (ER) derived from AIC values (Burnham & Anderson 2002). (4) In an examination of landscape thresholds, we statistically controlled for the effects of local variation by always including local variables in models (linear or threshold, according to the lowest AIC). Without including this step, detected landscape thresholds could be either a sole function of local thresholds or masked by local variation in occurrence or detectability. We repeated the procedure used in local model selection with variables at each landscape spatial extent. We did not include multiple landscape-extent variables in the same model because most of them were highly intercorrelated ($r > 0.75$).

It is often necessary to account for the potential lack of independence among sample points due to spatial autocorrelation (Legendre & Legendre 1998). We used correlograms of Moran's I (hereafter I) to test for autocorrelation in Pearson residuals of all regression model sets (Lichstein et al. 2002). If significant autocorrelation in model residuals was detected at any of the lag distances (350 m up to a maximum distance of 7000 m), we developed additional model terms to account for spatial dependency. These autocovariates were calculated as the probability of observing a species at one sample point conditional on the presence of the same species at a neighboring sample point within a distance class (Augustin et al. 1996). Thus, we considered there to be support for a landscape threshold only if a model contained autocovariates (if necessary) and a local extent variable and if landscape threshold variables had a lower AIC than models either containing only autocovariates and a local variable or autocovariates, a local variable, and a linear landscape term. This approach is conservative in that if local and landscape variables are correlated, the addition of a landscape variable is less likely to reduce AIC (Warren et al. 2005).

Discrimination of best models was measured with AUC. This was calculated with a continuous scale. Evaluation of model performance occurred over the whole range of predicted probabilities (Pearce & Ferrier 2000). We determined model calibration with the use of calibration plots. These show the relationship between average predicted probability (in fixed group size deciles) and species prevalence (Vaughan & Ormerod 2005). Problems with model calibration are evident as deviations in agreement between predicted and observed values from the 45° line. To compare the calibration of linear and threshold landscape models, we calculated the r^2 of the linear relationship between predicted and observed values with the intercept set at zero.

To test the fragmentation hypothesis, we used logistic regression to test whether the occurrence of each songbird species could be predicted by the statistical interaction between patch size (log transformed) and habitat amount. In this interaction model we chose the landscape spatial extent associated with a threshold relationship (if support for this existed). If no support for a threshold was found, we used the largest spatial extent (2000 m) because it tends to be the least correlated with patch size. As in threshold models we controlled statistically for both local variation (amount of habitat at 150 m extent) and spatial autocorrelation if it was detected. We used likelihood-ratio tests to determine statistical significance of models (Hosmer & Lemeshow 2000). Unless otherwise stated, we report 95% confidence intervals (CI) for all mean values and parameter estimates.

Results

Spatial Autocorrelation

We detected spatial autocorrelation in the residuals of global models for 5 of 15 species, indicating that the assumption of independent errors was violated. Black-throated Blue Warblers (maximum I [1750-m lag] = 0.27, $p = 0.001$) and Yellow-bellied Flycatchers (maximum I [1400-m lag] = 0.20, $p = 0.004$) exhibited the strongest autocorrelation in model residuals (Fig. 2). Other species exhibited weak spatial autocorrelation, and only at the smallest spatial extent (300 m; Common Yellowthroat: $I = 0.09$, $p = 0.04$, Golden-crowned Kinglet: $I = 0.13$, $p = 0.02$, Magnolia Warbler: $I = 0.19$, $p = 0.004$). The addition of autocovariates removed spatial dependency for all species except the Black-throated Blue Warbler. For this species slight spatial autocorrelation remained at 1400 m (Fig. 2).

Local Thresholds

Occurrence of all 15 species was positively correlated with the amount of habitat at the local extent (150 m). Confidence intervals of parameter estimates did not
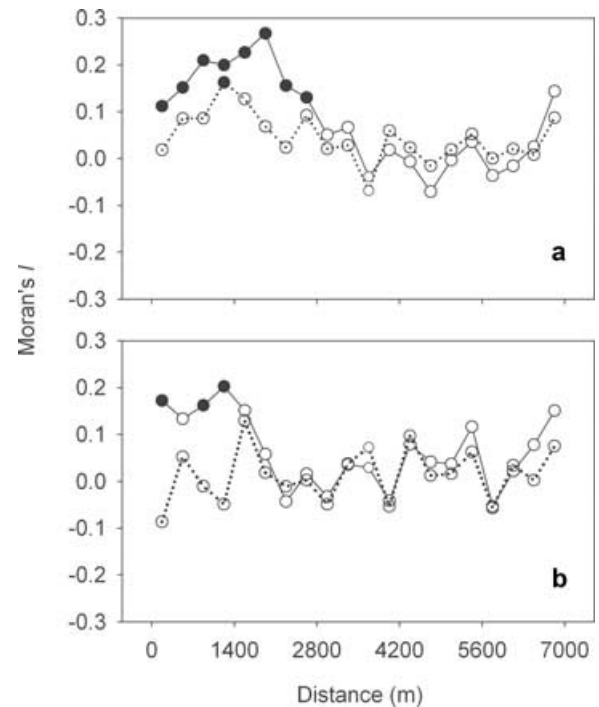

Figure 2. Degree of spatial autocorrelation in occurrence for the (a) Black-throated Blue Warbler and (b) Yellow-bellied Flycatcher with (dotted lines) and without spatial autocovariates (solid lines). Significant autocorrelation is indicated by closed circles.

bound zero for any species (see Supplementary Material), indicating that our previously derived species occurrence maps had statistical support. Nevertheless, for 9 of 15 species, we found more support for models including a threshold than for those assuming a linear relationship (Table 1). For 8 of these species, models with thresholds in amount of local habitat were at least five times more likely than linear models (ER > 5; Table 1). Local thresholds in habitat amount ranged broadly from 7.4% (American Redstart) to 51.5% (Golden-crowned Kinglet) ($\bar{x} = 22.4 \pm 11.4\%$) (Table 1).

The threshold values were partly dependent on species prevalence. With our approach the maximum amount of habitat that was possible within a certain radius was bounded by the maximum estimated probability of occurrence ($\hat{p}$) in the initial spatial model for a species. For instance, the highest probability of Black-throated Blue Warbler occurrence in the spatial model was 0.37; thus, the maximum area of suitable habitat within a 150-m radius was bounded at 2.61 ha (7.07 ha × 0.37) or 37% of the circle area. For this reason we adjusted estimated habitat threshold values ($\hat{\psi}$) by the maximum predicted probability of occurrence ($\hat{\psi}_{adj} = \hat{\psi}/\hat{p}_{max}$, where $\hat{p}_{max}$ is the maximum predicted probability of occurrence for a species). These adjusted threshold values ranged from

8.7% to 73.9% ($\bar{x} = 30.9 \pm 13.8\%$). Except for American Redstarts, all local threshold relationships exhibited an asymptotic pattern; the relationship between species occurrence and habitat amount within 150 m was initially steep, but flattened after a threshold level (see Supplementary Material).

Landscape Thresholds

Habitat amounts at landscape extents positively influenced the occurrence of 10 out of 15 species. (Table 1; Supplementary Material). Of these species the occurrence of all but the Red-eyed Vireo were best predicted by landscape threshold models (Table 1; Fig. 3). Thresholds were the strongest for the Common Yellowthroat (1000-

m radius; ER = 280.06) and Black-throated Blue Warbler (2000-m radius; ER = 19.01). Six out of nine species exhibited asymptotic thresholds; the effects of habitat loss intensified at low amounts of habitat in a landscape (Fig. 3). Three species exhibited hockey-stick type responses; amount of habitat at a given landscape extent had either a negative effect or no effect until a threshold, after which the influence was positive. Nevertheless, for two of these species, Magnolia Warbler and Swainson's Thrush, linear models were reasonable competitors for threshold models (Table 1).

Unadjusted landscape thresholds from the highest-ranked models ranged from 8.6% (Black-throated Blue Warbler) to 28.7% (Yellow-bellied Flycatcher) ($\bar{x} = 18.5 \pm 2.6\%$). Adjusted thresholds ranged from 13.2%
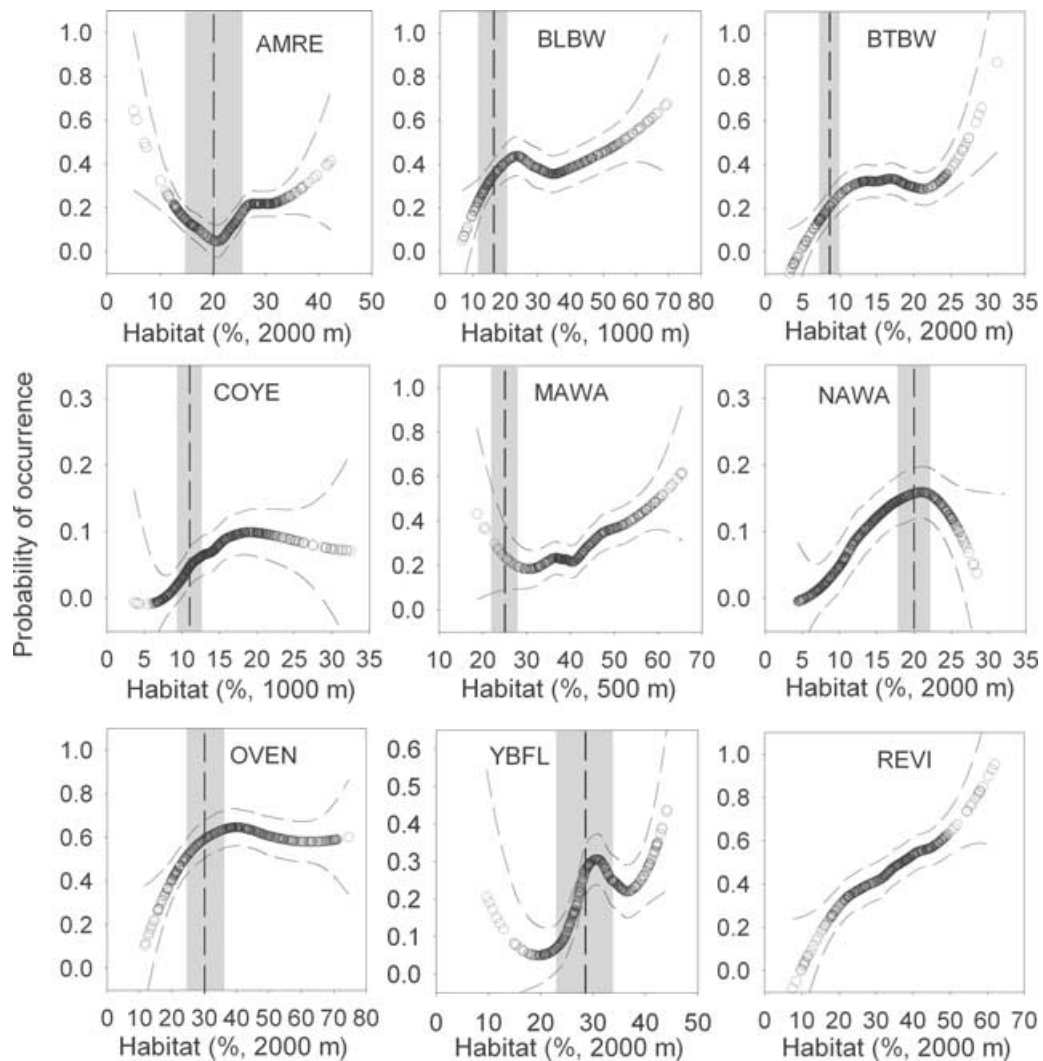

Figure 3. Effects of amount of habitat in the landscape on the occurrence of species of forest songbirds that were most influenced by landscape variables (habitat extents >150 m). Thresholds are plotted only if there was support for a nonlinear relationship (ΔAIC to linear model >1; Table 2). Dashed vertical lines and shaded zones indicate threshold values and associated 95% CI, respectively. Threshold values differ slightly from those in Table 2 because plots do not control for local variation or spatial autocorrelation. Species codes are defined in Fig. 1 legend.

to 45.4% ($\bar{x} = 26.6 \pm 6.6\%$) (Table 1). Highest-ranked models for most species exhibited adequate prediction accuracy (AUC > 0.70), except those for the American Redstart, Blackburnian Warbler, and Yellow-rumped Warbler, which all performed poorly (AUC < 0.70) (Table 1). In instances where landscape thresholds were supported, threshold models tended to be better calibrated than models with a linear effect of landscape composition (Fig. 4).

Landscape Fragmentation Hypothesis

Ovenbirds and Black-throated Blue Warblers, both of which exhibited landscape thresholds, were positively in-

fluenced by patch size at low amounts of habitat (Table 2). This supports the fragmentation threshold hypothesis. Furthermore, we found no evidence of patch-size effects for the Red-Eyed Vireo, a species with linear landscape effects. Only one species, the White-throated Sparrow, was positively influenced by patch size regardless of the amount of habitat in a landscape (logistic regression controlling for spatial autocorrelation and local habitat amount, $\chi^2 = 6.46$, $p = 0.01$). Nevertheless, the occurrence of most species appeared to be unaffected by patch size, regardless of the amount of habitat present at landscape extents. For 13 out of 15 species the interaction between patch size and habitat amount was not
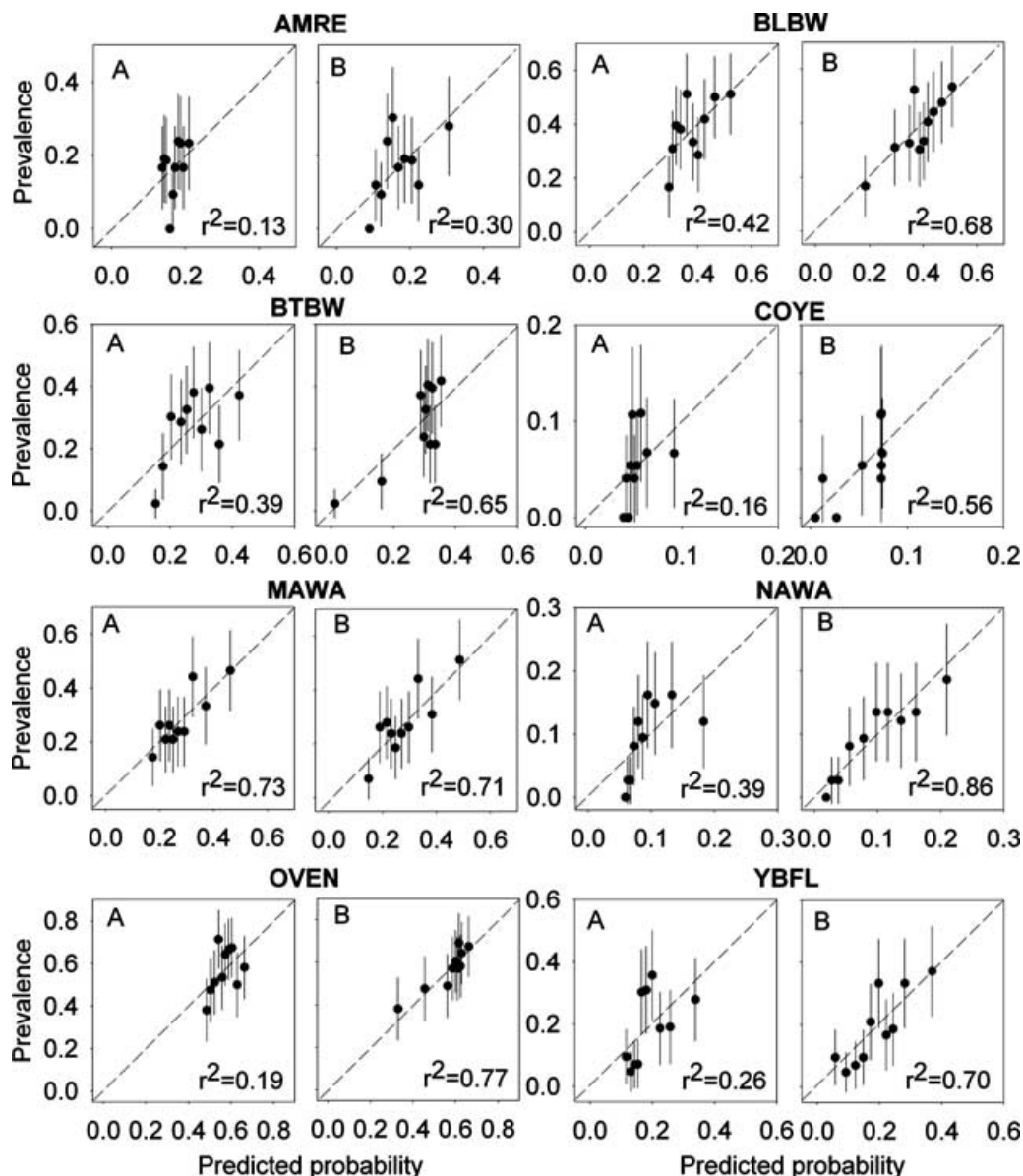

Figure 4. Relationship between predicted probability of occurrence ($\pm 95\%$ CI) and observed prevalence (calibration plots) for all songbird species exhibiting landscape thresholds: (a) nonthreshold models and (b) threshold models. The $45°$ diagonal line indicates perfect calibration. Explained variation (r^2) is for the line of best fit with the intercept set to zero. Species codes are defined in Fig. 1's legend.

Table 2. Parameter estimates used to examine the interaction between amount of habitat in the landscape and patch size (log x + 1 transformed).[a]

Species	β	SE	$-CI$	$+CI$	Z	P	Extent	Threshold[b]
American Redstart	0.020	0.046	-0.067	0.118	0.44	0.658	2000	*
Bay-breasted Warbler	0.010	0.069	-0.126	0.155	0.15	0.883	2000	
Blackburnian Warbler	-0.003	0.007	-0.017	0.010	-0.46	0.648	1000	*
Black-throated Blue Warbler[c]	-0.060	0.022	-0.106	-0.018	2.70	0.007	2000	*
Common Yellowthroat	-0.020	0.033	-0.087	0.044	-0.62	0.538	1000	*
Golden-crowned Kinglet	-0.009	0.013	-0.034	0.017	-0.68	0.495	2000	
Magnolia Warbler	0.001	0.018	-0.034	0.037	0.07	0.943	500	*
Nashville Warbler	-0.042	0.028	-0.098	0.012	-1.50	0.133	2000	*
Ovenbird[c]	-0.032	0.007	-0.046	-0.018	-4.53	<0.0001	2000	*
Ruby-crowned Kinglet	-0.013	0.043	-0.098	0.070	-0.30	0.767	2000	
Red-eyed Vireo	-0.004	0.014	-0.031	0.024	-0.27	0.787	2000	
Swainson's Thrush	-0.066	0.047	-0.165	0.018	-1.41	0.158	2000	*
White-throated Sparrow	-0.032	0.023	-0.078	0.012	-1.39	0.165	2000	
Yellow-bellied Flycatcher	-0.029	0.019	-0.068	0.010	1.46	0.145	2000	*
Yellow-rumped Warbler	0.025	0.019	-0.011	0.064	1.34	0.179	2000	

[a]*All models statistically control for local variation and spatial autocorrelation.*
[b]*An asterisk indicates detection of a threshold in species occurrence as a function of habitat amount (see Supplementary Material).*
[c]*A significant negative interaction indicates that the effects of patch size are important when the amount of habitat in a landscape is low.*

significant (Table 2). Patch size did not appear to be an important predictor even for some species that showed strong landscape thresholds (i.e., Common Yellowthroat, Nashville Warbler). These results should be interpreted with caution because in several cases confidence intervals around the parameter estimates for the interaction between patch size and habitat amount were broad.

Discussion

We detected thresholds in forest bird occurrence as a function of habitat amount at local or landscape extents for the majority of songbird species we examined (14/15). Landscape thresholds were supported for most species (9/15), even after controlling statistically for local variation in habitat and spatial autocorrelation in species occurrence. Such thresholds in occupancy as a function of habitat loss are predicted to occur in theoretical models (e.g., Fahrig 1998; With & King 1999), but to date have received conflicting empirical support (Andrén 1994; Homan et al 2004; Radford & Bennett 2004; Lindenmayer et al. 2005).

Most studies conducted on forest birds have not reported landscape thresholds (e.g., McGarigal & McComb 1995; Lichstein et al 2002), but this may be due to the paucity of adequate methods previously available for threshold detection. In some cases (e.g., Common Yellowthroat), if we had not tested for landscape thresholds, we would not have found any influence of landscape composition beyond that explained by local variation. Thus, ignoring the existence of potential thresholds could mask the influences of landscape composition on species occurrence.

Variation among studies in threshold detection could be due to problems in correctly defining the distribution of "habitat" in study landscapes. This is presumably easier in landscapes that have been highly altered by agricultural or urban development (e.g., Homan et al. 2004), where patch boundaries are less ambiguous than in forest mosaics. By defining habitat distribution quantitatively for individual species a priori, we reduced this potential problem.

The likelihood of detecting a threshold could also be influenced by the amount of habitat for a species within the study region. If large amounts of habitat exist for a species across a region, the amount of habitat surrounding most sample points may fall well above the range of putative thresholds. Using simulation models Andrén (1996) found that statistical power to detect effects of landscape-scale habitat loss and fragmentation was low in landscapes with a high proportion of suitable habitat. We did not detect an effect of the amount of habitat in the study area on the probability of finding landscape thresholds (logistic regression: $\chi^2 = 1.62$, $p = 0.20$) or asymptotic thresholds ($\chi^2 = 1.55$, $p = 0.21$). However, the relationship was in the predicted direction (see Supplementary Material).

Our results support the assertion by many researchers that threshold values should differ among species. Different species decline at different points and rates on the habitat-loss gradient (With & Crist 1995; Andrén 1996). The thresholds we detected were wide ranging (9–29%). Nashville Warblers, Ovenbirds, and Yellow-bellied Flycatchers appear to be the most sensitive to habitat loss (Table 1; Fig. 3). Variation in sensitivity to landscape structure is likely to be a function of such traits as vagility, home range size, reproductive potential, and habitat specificity (Andrén et al. 1997).

Of the two hypotheses explaining occupancy thresholds in relation to landscape structure, evidence for most species supported the extinction threshold hypothesis. Most species required some minimum amount of habitat at the landscape scale but did not appear to be sensitive to fragmentation (Fahrig 2003). Lack of evidence for fragmentation effects is congruent with predictions of simulation studies that assume that landscape-scale population persistence is determined by overall rates of births and mortality in the landscape (Fahrig 1998; Flather & Bevers 2002). Fahrig (1998) found that fragmentation may affect population persistence only under a narrow range of conditions (species with low vagility, nonephemeral habitat, high site fidelity, and high mortality in nonbreeding habitat areas). Conversely, metapopulation models (With & King 1999) tend to predict much greater fragmentation effects because colonization and extinction are assumed to be more strongly influenced by landscape pattern.

Evidence is accumulating that even some supposed forest-interior bird species move considerable distances off territory during the breeding season and may cross substantial gaps (Fraser & Stutchbury 2004). This is presumably to prospect for future territory locations (Danchin et al. 2004) or to obtain extra-pair fertilizations (Woolfenden et al. 2005). We hypothesize that as the amount of habitat in a landscape declines, these potential "resources" (extra-pair mates, alternative territories) may become too scarce to warrant continued residency or initial immigration to a landscape. Furthermore, higher mortality might result from increased movement through the matrix. Both of these mechanisms could result in landscape occupancy thresholds that are not necessarily a function of landscape pattern.

Nevertheless, it is not possible for us to reject unequivocally the fragmentation threshold hypothesis for species that were not influenced by patch size. First, our power to detect patch size effects was low for many species; Confidence intervals around interaction parameter estimates tended to be broad (Table 2). Second, unmeasured configuration variables may still be driving the landscape thresholds we observed. Few configuration variables other than patch size, however, are useful in predicting the abundance of forest birds (Bender et al. 1998; Villard et al. 1999). Third, our ability to define patches quantitatively may have been less robust for some species. Some patches may have been characterized by gradual rather than abrupt boundaries or may not have been surrounded by inhospitable matrix (Brotons et al. 2003). Matrix quality may have a strong influence on patch occupancy and population viability (Wiegand et al. 2005).

The fragmentation threshold hypothesis was supported for Black-throated Blue Warblers and Ovenbirds. Both species were more likely to occur in large patches, but only when the amount of habitat in a landscape was low. The sensitivity of these species to patch size could relate to their degree of habitat specialization. Species that

are reluctant to cross gaps in their own habitat are likely to exhibit patch-size effects, and the possibility of using multiple patches to supplement resources is reduced (Betts et al. 2006a). Previous research in a forest mosaic indicates that Ovenbirds may avoid crossing gaps during the breeding season (Robichaud et al. 2002) and are less likely to move through landscapes with low forest cover (Belislé et al. 2001).

Regardless of the mechanism, the landscape thresholds we detected for some species, by definition, indicate that the probability of species occurrence does not always decline predictably in a linear fashion with habitat loss. Thus, results of landscape-scale studies conducted in regions with relatively high habitat amounts and low fragmentation (e.g., Lichstein et al. 2002) may not be applicable in regions with low habitat amounts and high fragmentation.

The thresholds we report should not be considered thresholds in habitat, below which a population will not persist. We detected thresholds in habitat amount, below which the likelihood of species occurrence declined more rapidly. These thresholds will be useful to forest managers in the establishment of conservation targets because they may serve as pre-extinction thresholds. If landscapes can be managed to prevent habitat amounts from declining below thresholds in occurrence, it is unlikely that the entire populations will go extinct. Nevertheless, future studies should test for thresholds in demographic variables (i.e., survival, reproduction). There is also an inherent danger in managing ecosystems for minimum targets because occurrence thresholds might shift upward in poor years.

Acknowledgments

Supplementary Material

Amount of habitat for bird species examined (Appendix S1); parameter estimates and confidence limits for linear and threshold models predicting songbird occurrence as a function of habitat amount (Appendix S2); and proportion of species exhibiting habitat thresholds and

asymptotic thresholds (Appendix S3) are available in conjunction with the on-line version of this article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1523-1739.2007.00723.x.

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