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Thresholds in the long-term responses of breeding birds to forest cover and fragmentation

Benjamin Zuckerberg *, William F. Porter

Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA

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ABSTRACT

Mitigating the effects of habitat loss requires estimating the minimum amount of habitat necessary for the persistence of wildlife populations in a changing landscape. Assessing minimum habitat amounts, however, relies on identifying ecological thresholds in species' responses to landscape change. Using two repeated state-wide atlases, our objective was to investigate the responses of 25 forest birds to a range of forest cover and fragmentation. Repeat atlases allow for the analysis of four population dynamics including: (1) colonization, (2) persistence, (3) extinction, and (4) absence. Our objective was to test the hypothesis that forest birds demonstrated thresholds in these four basic dynamics to varying amounts of forest cover and fragmentation.

We found thresholds to be a common, though not pervasive, characteristic of how forest birds respond to forest cover and pattern. We found that the probability of persistence was positively correlated with forest cover and 22 species demonstrated threshold responses. In addition, 15 of 25 birds demonstrated discrete thresholds in extinction dynamics. The existence of a colonization threshold has received significantly less attention in ecology. We also found that 17 out of 25 species demonstrated thresholds in their colonization response to a greater amount of forest cover. The effects of forest fragmentation, independent of forest amount, were less clear. We found support for incorporating the effects of fragmentation, but this fragmentation effect was found both below and above threshold points. We conclude that incorporating ecological thresholds in environmental planning should be species-specific and focus on populations on the verge of rapid ecological change.

1. Introduction

There has been growing interest in the study and identification of ecological thresholds in the responses of wildlife populations to a changing and potentially hostile landscape (Huggett, 2005; Luck, 2005; Groffman et al., 2006; Andersen et al., 2009). The study of ecological thresholds, however, has posed practical and scientific challenges in ecology. The practical challenges of finding empirical evidence for thresholds include a reliance on occurrence data collected for a few species over a few years, studies of a limited geographic context, and the use of a variety of analytical tools for identifying thresholds (Lindenmayer and Luck, 2005; Ficetola and Denoël, 2009). These challenges have led to a scientific deficiency in our understanding of thresholds in the broad-scaled responses of wildlife populations to environmental change and the role of thresholds in environmental management.

There are two competing hypotheses predicting how species respond, in terms of population extinction and persistence, to declining amounts of habitat. The *proportional area hypothesis* predicts that species have a relatively linear response to habitat loss (i.e., the probability of extinction is proportional to habitat amount) (Fahrig, 2003). A competing hypothesis suggests that there is a discrete threshold (i.e., breakpoint) along a continuum of habitat amount where the likelihood of a population going extinct increases dramatically. This *extinction threshold hypothesis* predicts a dramatic change in the state of a population which occurs over a relatively short range of change in habitat cover (Lande, 1987; Andrén, 1994). Extinction thresholds have been identified in a number of simulation studies where a minor change in habitat amount results in a dramatic decrease in the likelihood of a population persisting (Bascompte and Sole, 1996; Hill and Caswell, 1999; With and King, 1999; Fahrig, 2001; Flather and Bevers, 2002). As an example, Fahrig (1997) suggested that metapopulation survival would be maintained as long as habitat composition remained above 20%. Other simulation studies, however, have found that threshold values will vary across landscapes and species of varying life history characteristics, resulting in threshold values ranging from 5% to 90% habitat loss (Bascompte and Sole, 1996;

* Corresponding author. Current address: Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, United States. Tel.: +1 607 254 2174; fax: +1 607 254 2104.

E-mail addresses: bz73@cornell.edu (B. Zuckerberg), wfporter@esf.edu (W.F. Porter).

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With and King, 1999, 2001). Regardless of where a discrete threshold exists along a continuum of habitat cover, these theoretical findings suggest that species might exhibit non-linear responses to habitat amount.

Theoretical studies on thresholds have spurred recent efforts searching for empirical evidence of extinction thresholds in bird populations. In Australia, Radford et al. (2005) found that the species richness of woodland-dependent birds in 24 landscapes (measuring 100 km^2) demonstrated clear threshold responses to habitat cover and declined sharply in landscapes with less than 10% habitat cover. Betts et al. (2007) tested for thresholds in the occurrence of 15 forest breeding birds with habitat amount assessed at multiple scales (150–2000 m radii). They found evidence for landscape thresholds ranging from 8.6% to 28.7% habitat cover. The existence of thresholds in wildlife populations has not always been supported. In a study of bird and reptile assemblages in a plantation landscape, Lindenmayer et al. (2005) found little evidence for thresholds in bird or reptile richness in landscapes ranging from 1000 to 2000 m radii. This variation in results has led some to question the usefulness of thresholds in applied ecology and environmental management (Lindenmayer and Franklin, 2002; Lindenmayer and Luck, 2005).

A basic assumption in the interpretation and management of ecological thresholds is that these changes are reversible. In some cases, however, the return path to the original state may be different (e.g., a hysteretic response) (Groffman et al., 2006). That is, species will colonize landscapes following a different threshold relationship than that which they demonstrated when the population went extinct. The prospect of a *colonization threshold* has received little theoretical and empirical attention, but it is critical to have studies examining patterns of colonization and extinction for environmental management and restoration to be successful. The rate of colonization can possibly be affected by species' sensitivities to patterns of fragmentation, demographic limitations, and the rate of land use change (Schrott et al., 2005a,b; With et al., 2006).

At very low levels of habitat, habitat patches may be fewer and increasingly isolated (Fahrig, 2003). In these landscapes, the *fragmentation threshold* hypothesis predicts that the effects of habitat fragmentation *per se* (i.e., independent of habitat amount) are exacerbated at low levels of habitat amount (i.e., below the extinction threshold) (Fahrig, 1998; Flather and Bevers, 2002). In his review on the effects of habitat fragmentation on birds and mammals, Andrén (1994) found that the negative effects of patch size and isolation may not occur until the landscape consists of 10–30% of the original habitat. In general, however, most empirical studies have found that habitat amount, as opposed to habitat configuration, has a greater effect on species abundance and occurrence (McGarigal and McComb, 1995; Meyer et al., 1998; Trzcinski et al., 1999; Villard et al., 1999; Cushman and McGarigal, 2003). Little consensus exists, however, on the relative importance of habitat fragmentation on thresholds in wildlife populations.

Using New York State's two Breeding Bird Atlases (1980–1985 and 2000–2005), our goal was to test the predictions of the extinction and fragmentation threshold hypotheses in the long-term responses of 25 forest breeding birds to a range of forest cover and fragmentation. First, we tested the prediction that most species would exhibit thresholds in probabilities of extinction, colonization, persistence, and absence in response to a wide range of forest cover. Second, we tested the prediction that thresholds for these different dynamics will not be coincident. Third, we tested the predictions of the fragmentation threshold hypothesis which predicts that the aggregation of forest habitat, independent of forest cover, will be an important driver of population dynamics below the threshold point.

2. Methods

2.1. New York State Breeding Bird Atlas

The New York State Breeding Bird Atlas (hereafter BBA) is a comprehensive, statewide survey with the objective of documenting the distribution of breeding birds in New York. The BBA was conducted in two time periods: the first atlas project (hereafter atlas 1980) was conducted from 1980 to 1985 (Andrle and Carroll, 1988) while the second atlas (hereafter atlas 2000) was conducted from 2000 to 2005 following the same protocol of the first BBA (McGowan and Corwin, 2008). Sampling was conducted in each year of the atlas and both surveys used a grid of 5335 blocks (although two blocks were eliminated in the second atlas) each measuring 5 × 5 km that covered the entirety of New York State (128,402 km^2). This represents one of the largest and finest resolution atlas data sets in the world (Gibbons et al., 2007).

Full details of the sampling methodology can be found in McGowan and Corwin (2008), but in brief, the BBA implemented a set of protocols to achieve consistent coverage within each atlas block. The state was stratified into 10 regions and one or two regional coordinators in each area were responsible for recruiting volunteers in each atlas and overseeing coverage and data quality of the blocks in their region. Atlas observers were assigned to survey one or more blocks and were expected to spend at least 8 h in the block, visiting each habitat represented, and recording a suggested target of 76 species. This standard was derived from pilot studies, species detection curves, and past atlas projects (Smith, 1982). Effort was recorded for each atlas survey and reported as the number of person-hours spent surveying per block (the sum of the number of hours spent in each block × the number of people surveying each block) (McGowan and Zuckerberg, 2008). Although there have been a number of recent advances for quantifying heterogeneous detection probabilities among species when dealing with imperfect, large-scale survey data (Kéry and Schmid, 2004; MacKenzie, 2006; Royle et al., 2007), we were not able to take advantage of these methods because information on how many times a block was sampled (i.e., repeated sampling) was not available. In this study, however, we are making the assumption that large differences in survey effort expended are indicative of differences in coverage and should be accounted for in analysis. The cumulative databases, including only the highest breeding code for each species reported in each block, resulted in 361,595 records for atlas 1980 and 383,051 records for atlas 2000.

Species demonstrated four basic changes in distribution between the two atlas surveys including colonization, persistence, extinction, and absence (Gates and Donald, 2000). These four separate dynamics were the focus of this analysis. We classified colonizations as blocks where a species was not detected in the first atlas but was detected in the second atlas; persistence as found in both atlases; extinction as detected in the first but not the second atlas; and absence as not recorded in either atlas.

We identified 25 species that are forest generalists or ob ligates (O'Connell et al., 1998, 2000; DeGraaf and Yamasaki, 2001). Forest generalist species occur primarily in forested areas, but use these forests relatively indiscriminately and exhibit no obvious trends toward requiring forest interior versus forest edge habitat. Forest obligates tend to select contiguous forest patches, make preferential use of interior forest conditions within a core area of a forest patch, and generally demonstrate an avoidance of forest edge. We did not include species that actively use forest edges or early successional habitats for breeding purposes. To look for thresholds over a range of potential responses, we selected forest birds that offered a wide variation in distributions throughout New York State but did not include rare species (i.e., species occupying an average occurence of <20%). Species ranged in their average occupancy across both atlas periods from 20% (Golden-Crowned Kinglet [*Regulus satrapa*]) to 97% (Black-capped Chickadee [*Poecile atricapillus*]), and New York State was well within breeding range for all species included in this study.

2.2. Forest cover data and pattern analysis

Forest habitat was identified using the 1992 National Land Cover Data (NLCD). All land cover analyses focused on Forest Upland Areas that are characterized by tree cover (natural or semi-natural woody vegetation, generally greater than 6 m tall) and tree canopy accounts for 25–100% of the cover (Anderson et al., 1976). This classification included deciduous, mixed, and coniferous forest types. The 1992 NLCD has a resolution of 30 m and the user's accuracy for forest land was one the highest for any cover type in Federal Region 2 (0.84) (Stehman et al., 2003). It was not logistically possible to assess land cover change between the two time periods given the state-wide scale of this analysis and the resolution of the atlas data. The range of forest cover throughout the study area, however, offers a common space-for-time substitution by which to assess species' response to forest cover and pattern.

We eliminated atlas blocks with greater than 50% water cover. These 259 atlas blocks tended to be located along the coastlines. In the remaining survey blocks, we analyzed forest cover and configuration within each 25 km^2 atlas block using FRAGSTATS version 3.2 (McGarigal et al., 2002) and FRAGSTATSBATCH tool (Mitchell, 2005). Forest cover was calculated as the percentage of each atlas block classified as forest (PLAND). To measure forest fragmentation, we chose the clumpiness index (CLUMPY) because it has several properties that make it less susceptible to correlations with the amount of forest (McGarigal et al., 2002). When the clumpiness index reaches 0 then the forest is maximally disaggregated (i.e., fragmented) and reaches 1 when forest is maximally clumped. Consequently, we chose to use the clumpiness index as a metric for describing forest fragmentation *per se*, avoiding the use of an interaction term (Betts et al., 2006a, 2007) or calculating the residuals of a configuration variable regressed on forest amount (Koper et al., 2007).

2.3. Statistical analyses

First, we identified the starting threshold point by inspecting the fitted values of locally weighted nonparametric models (loess plots, smoothing parameter = 0.75) for each species and for each dynamic separately (i.e., colonization, persistence, extinction, and absence). The use of the loess plots was strictly for visualization purposes and for estimating a starting threshold point for segmented logistic regression (Muggeo, 2003; Betts et al., 2007; Ficetola and Denoël, 2009). Next, we used segmented logistic regression for modeling the relationship between the probability of colonization, persistence, extinction, or absence and forest cover separately as:

$$p = \exp\left[\beta_0 + \beta_1\chi + \beta_2(\chi - \psi)_+\right] / \left[1 + \exp\left[\beta_0 + \beta_1\chi + \beta_2(\chi - \psi)_+\right]\right]$$

where p is the probability, χ is the independent variable (e.g., forest cover), ψ is the break point (threshold), and $(\chi - \psi)_+ = (\chi - \psi) \times I(\chi > \psi)$ being $I(A) = 1$ if A is true, β_0 is the intercept, β_1 is the slope of the left line segment (i.e., for $\chi \leqslant \psi$), and β_2 is the difference-in-slope parameter. Consequently, $(\beta_1 + \beta_2)$ is the slope of the right line segment ($\chi > \psi$). We used the difference-in-slope parameter (β_2) to detect whether the form of the response curve is concave or convex (Fig. 1). For all dynamics, the difference-in-slope parameter would be negative for a convex curve and positive for a concave curve (Fig. 1). All these parameters are estimated by segmented logistic regression using an iterative fitting process (Muggeo, 2003). Given an initial starting threshold value as determined by inspecting the loess plots, multiple ψ and β are fitted until estimates converge at the maximum likelihood estimate (Muggeo, 2003). Standard errors and confidence intervals of ψ may be obtained with linear approximation for the ratio of two random variables (Muggeo, 2003).

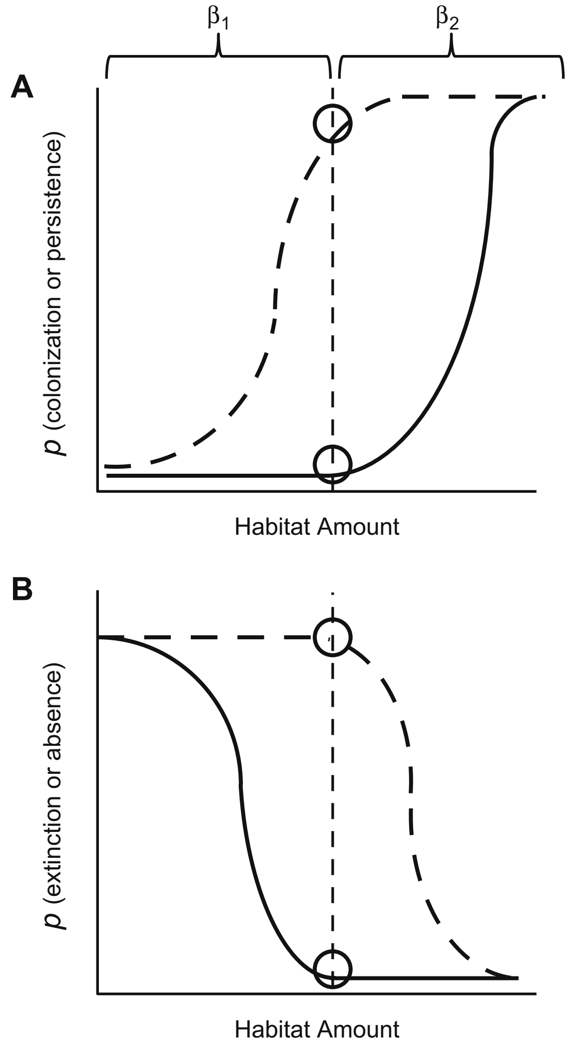

Fig. 1. Theoretical responses a species can exhibit to varying amounts of habitat. The circles represent thresholds that can be found along different response trajectories. Populations will generally have a positive relationship between the probability of colonization or persistence (A) and habitat amount, but can exhibit two different types of responses resulting in convex (dashed line) or concave (solid line) curves. Conversely, the probability of extinction or absence (B) will have a negative relationship to habitat amount, but can also exhibit convex (dashed line) or concave (solid line) responses. Note that the threshold estimates could be the same for each curve despite representing unique relationships (i.e., an asymptotic versus exponential relationship). The difference-in-slope above (β_2) and below (β_1) the threshold point can be used to estimate the shape of the curve.

If the algorithm did not converge using a starting threshold point, we searched systematically for a starting point in 5% increments of forest cover (Betts et al., 2007). We used an information-theoretic approach for model selection and assessing the strength of evidence in support of a threshold response (Burnham and Anderson, 2002; Anderson, 2008). First, for each species and dynamic, we used logistic regression to test for a non-threshold relationship between the probability of change (e.g., colonization events) and forest composition (PLAND). Second, we used segmented logistic regression to estimate a threshold in relation to forest cover using an initial threshold point from the loess plots. Third, we determined the weight of evidence for threshold models in relation to non-threshold models by calculating the Akaike's information criterion (AIC), model probabilities *Prob*(H|data), and the evidence ratio that the threshold model is the stronger model (Burnham and Anderson, 2002; Anderson, 2008). Fourth, we used the difference-in-slope parameter to report whether the response curve was concave (positive β_2) or convex (negative β_2). The AIC approach in model selection penalized threshold models for the addition of extra parameters (e.g., ψ and β_2) and provided Bayesian posterior probabilities for threshold and non-threshold models. We applied this procedure to all 25 species and for each dynamic, resulting in a total of 100 model comparisons. Effort for each block and each atlas period was log transformed and the difference in effort was calculated (ΔEffort). These three effort covariates (effort in atlas 1980, effort in atlas 2000, and ΔEffort) were included in all models as additional covariates. All segmented models were fitted using the "segmented" package (Muggeo, 2008) and implemented in R Development Core Team (2008).

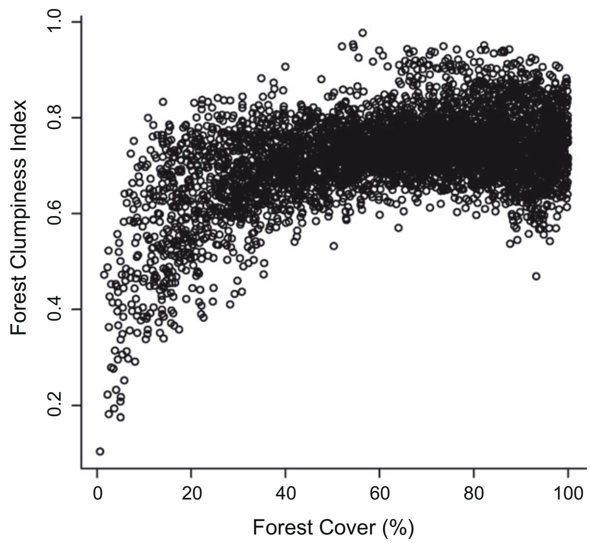

Fig. 2. A scatterplot of clumpiness index values across the range of forest cover in New York State.

To test the hypothesis that thresholds should be the result of fragmentation effects at low habitat amounts, we ran a second model selection process based on the inclusion of the clumpiness index variable at low and high levels of habitat amount. For each threshold model, we added the clumpiness variable as an additional predictor variable specified below and above the estimated threshold point independently. This second round of model selection compared three models: (1) the estimated threshold model,

Table 1
Model comparisons for four forest breeding birds and each dynamic. Threshold estimates varied for different population dynamics and species. We report the model, AIC values, model probabilities (Prob(H|Data)), threshold values ($\hat{\psi}$) of forest amount and the associated standard error (SE), the Area Under the Curve statistic (AUC), goodness-of-fit test (GOF), the evidence ratio interpreted as the evidence in support of the threshold model (ER), and the untransformed beta estimate associated with the change in effort. The best model is highlighted.

Species	Dynamic	Model[a]	AIC	Prob	$\hat{\psi}$ (%)	SE	AUC[b]	GOF	ER	Δ Effort
Veery	Colonization	**Threshold (−)**	**934.58**	**1.00**	**37.31**	**2.49**	**0.76**	**0.15**	**100**	**−0.22**
(*Catharus fuscescens*)		Nonthreshold	1035.29	0.00				0.51		
	Persistence	**Threshold (−)**	**5277.27**	**1.00**	**43.65**	**1.61**	**0.66**	**0.34**	**100**	**−0.39**
		Nonthreshold	5524.98	0.00				0.00		
	Extinction	**Threshold (+)**	**3064.20**	**1.00**	**47.01**	**2.32**	**0.67**	**0.43**	**100**	**0.43**
		Nonthreshold	3206.55	0.00				0.00		
	Absence	**Threshold (+)**	**2111.16**	**1.00**	**36.79**	**2.00**	**0.77**	**0.20**	**100**	**−0.35**
		Nonthreshold	2298.99	0.00				0.00		
Red-eyed Vireo	Colonization	**Threshold (−)**	**125.73**	**0.70**	**31.06**	**10.91**	**0.89**	**0.10**	**2.33**	**4.42**
(*Vireo olivaceus*)		Nonthreshold	127.40	0.30				0.83		
	Persistence	**Threshold (−)**	**2028.73**	**1.00**	**19.11**	**3.02**	**0.72**	**0.59**	**100**	**−0.14**
		Nonthreshold	2046.21	0.00				0.00		
	Extinction	**Threshold (+)**	**808.96**	**1.00**	**31.74**	**6.64**	**0.71**	**0.86**	**100**	**−1.39**
		Nonthreshold	818.60	0.00				0.30		
	Absence	**Threshold (+)**	**241.67**	**1.00**	**34.88**	**8.26**	**0.95**	**0.70**	**100**	**−3.83**
		Nonthreshold	251.18	0.00				0.60		
Yellow-rumped Warbler	Colonization	**Threshold (−)**	**3110.96**	**1.00**	**58.05**	**3.61**	**0.75**	**0.55**	**100**	**−0.28**
(*Dendroica coronata*)		Nonthreshold	3140.07	0.00				0.00		
	Persistence	**Threshold (+)**	**4477.00**	**0.99**	**73.61**	**4.70**	**0.83**	**0.55**	**99.00**	**0.36**
		Nonthreshold	4485.80	0.01				0.01		
	Extinction	**Threshold (+)**	**1500.44**	**0.55**	**78.40**	**8.04**	**0.76**	**0.43**	**1.22**	**−1.96**
		Nonthreshold	1500.79	0.45				0.29		
	Absence	**Nonthreshold**	**4675.80**	**0.67**			**0.83**	**0.52**	**0.49**	**−0.01**
		Threshold (+)	4677.21	0.33	62.78	13.58		0.03		
Ovenbird	Colonization	**Threshold (−)**	**1062.82**	**1.00**	**51.08**	**4.49**	**0.82**	**0.33**	**100**	**2.31**
(*Seiurus aurocapilla*)		Nonthreshold	1096.38	0.00				0.00		
	Persistence	**Threshold (−)**	**4233.70**	**1.00**	**66.22**	**2.37**	**0.82**	**0.21**	**100**	**0.55**
		Nonthreshold	4326.86	0.00				0.00		
	Extinction	**Threshold (+)**	**1697.82**	**1.00**	**82.32**	**2.90**	**0.81**	**0.64**	**100**	**−0.11**
		Nonthreshold	1738.79	0.00				0.00		
	Absence	**Threshold (+)**	**1774.45**	**1.00**	**75.28**	**4.53**	**0.91**	**0.553**	**100**	**−2.86**
		Nonthreshold	1800.37	0.00				0.002		

[a] Threshold models are given a positive sign if the difference-in-slope parameter is positive (concave response curve) or a negative sign if the difference-in-slope parameter is negative (convex response curve).
[b] AUC values greater than 0.75 indicate excellent discriminatory power.

(2) the threshold model with the clumpiness index added as a predictor variable below the threshold point, and (3) the threshold model with the clumpiness index added as predictor variable above the threshold point.

Spatial autocorrelation can be an important component for analyzing distributional shifts in species' occurrences (Araujo et al., 2002). We used correlograms of Moran's I to test for autocorrelation in the Pearson residuals of the original logistic regression models (Lichstein et al., 2002; Betts et al., 2006b). If we detected significant autocorrelation in model residuals at any of the lag distances (5 km up to a maximum distance of 500 km), we incorporated a separate autocovariate term. These autocovariates were calculated as the probability of observing a species within an atlas block conditional on the presence of the same species within a neighboring atlas block within an eight-cell neighborhood (Augustin et al., 1996). Correlograms and autocovariates were developed using the spdep package (Bivand, 2006) and implemented in R Development Core Team (2008).

We calculated the AUC (Area Under the Curve) statistic for the best model as identified by the AIC model selection process (non-threshold or threshold model). AUC is the preferred metric for model discrimination because it is threshold independent (Fielding and Bell, 1997). In addition, we calculated the unweighted sum of squares test for global goodness-of-fit (GOF) for every model (Hosmer et al., 1997). Calibration plots were also used as a graphical goodness-of-fit plot (Pearce and Ferrier, 2000; Vaughan and Ormerod, 2005). AUC and calibration statistics were calculated using the PresenceAbsence package (Freeman and Moisen, 2008) and implemented in R Development Core Team (2008).

3. Results

3.1. Variation in forest cover

In 4777 atlas blocks, forest cover ranged from 0.63% to 100% ($\bar{x}$ = 63.10% SE = 0.35). This range of forest cover was not randomly distributed throughout the state. Areas of high forest cover were located in the Adirondack and Catskill Mountains. Western New York, the Hudson River Valley, and the New York City metropolitan area were characterized by low forest cover. Clumpiness index values ranged from 0.10 (disaggregated) to 0.98 (aggregated) ($\bar{x}$ = 0.72 SE = 0.001). Overall, clumpiness was significantly correlated with forest cover (OLS regression: β = 0.17 (SE 0.01), $p < 0.001$), however, this correlation was noticeably non-linear and clumpiness index values declined sharply and with low forest cover (Fig. 2). In general, we found that higher clumpiness values consistently reflect landscapes with a higher aggregation of forest patches and less edge (Cushman et al., 2008).

3.2. Variation in effort

Total survey hours expended per block were not normally distributed in either atlas and were transformed using a log transformation for all analyses. The average number of hours expended per block were similar in both atlas periods (atlas 1980: $\bar{x}$ = 27.66 h/block; atlas 2000: $\bar{x}$ = 29.32 h/block), but generally demonstrated an overall increase in effort of 1.5 h/block in the second atlas (McGowan and Zuckerberg, 2008). Across all the species included in this analysis, we found that the amount of effort expended in

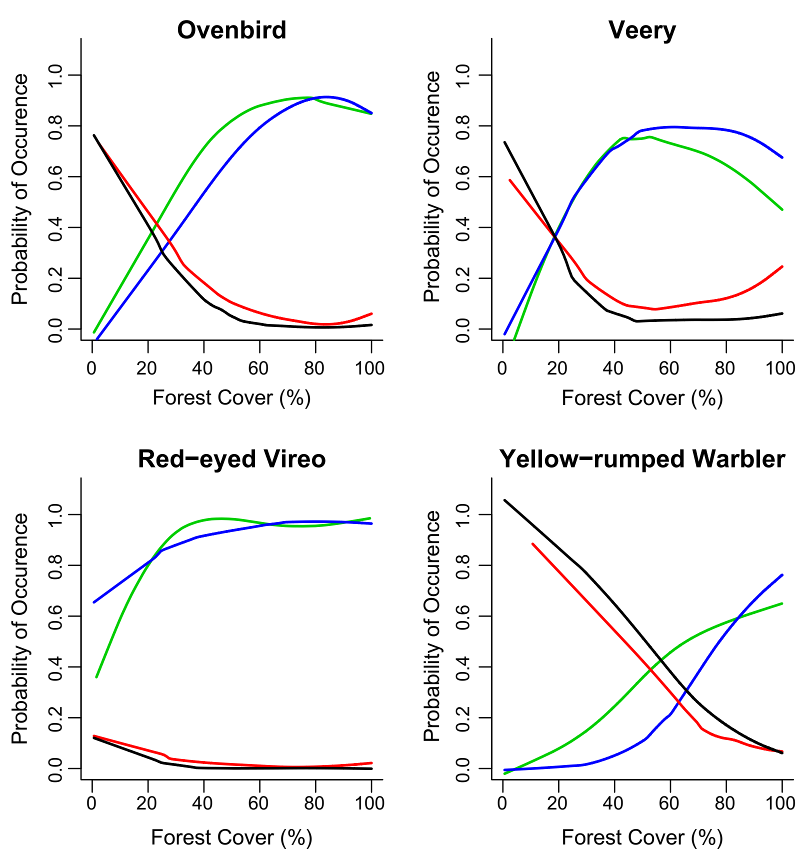

Fig. 3. Examples of threshold responses of four forest breeding birds to a range of forest cover within atlas blocks in New York State. Changes in probability relates to separate dynamics including colonization (green lines), persistence (blue lines), extinction (red lines), and absence (black lines). Probability estimates were derived from loess regression (span = 0.75) that was used for purposes of visualization. These plots provided a visual starting point for threshold estimates for use in segmented regression models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

blocks where species were detected was slightly higher than those blocks where species were not detected for atlas 1980 (β = +1.07 h SE = 1.01, $p < 0.001$) and atlas 2000 (β = +1.03 h SE = 1.00, $p < 0.001$). The effect of changes in effort between the two atlases varied widely for specific species and their dynamics (Table 1; Supplementary material). Of importance in this study, however, is whether changes in expended survey effort were correlated with the variation in forest cover throughout the study area. We found no evidence that changes in effort were significantly associated with forest cover ($R = 0.005$, $p = 0.72$).

3.3. Evidence of thresholds

We found that the loess plots were useful for visualizing thresholds in species responses to a variation of forest cover (Fig. 3). These starting threshold points were then used in the segmented regression models. Once a starting point was provided, the segmented regression routine was successful for developing locally parametric logistic regression models (i.e., threshold models) for comparison with global logistic models (i.e., non-threshold models) (Fig. 4). Given the large number of sample points for every species, the global logistic regression model generally produced linear predicted values when compared to the threshold models (Fig. 4).

Of the 100 models tested in this analysis, we found that 65 models showed evidence of thresholds (Supplementary material). Regarding extinction dynamics, 15 out of 25 species (60%) displayed strong support (Prob(H|Data) >0.70) for models containing a threshold parameter compared to non-threshold models. Of those 15 species demonstrating extinction thresholds, 11 species had an evidence ratio greater than 10 (i.e., the threshold model was 10 times more likely than the non-threshold model). Extinction threshold estimates ranged from 24.37% (Black-capped Chickadee) to 88.16% (Canada Warbler [*Wilsonia canadensis*]) forest cover with an average threshold estimate of 58.02% (SE = 6.00) forest cover (Fig. 5). In all these species, extinction patterns were concave and the threshold points represented a dramatic increase in the probability of extinction at low levels of forest cover (Fig. 1). An effective discriminatory model (i.e., the model accurately divides the locations into detections and nondetections) will have an AUC value close to 1.0 while a poor model (i.e., a model that is no better than random assignment) will have an AUC near to 0.5 (Freeman and Moisen, 2008). For extinction threshold models, we found that the discriminatory powers of the extinction threshold models were generally low. AUC values ranged from 0.61 (Pileated Woodpecker [*Dryocopus pileatus*]) to 0.81 (Ovenbird [*Seiurus aurocapilla*]), but all species averaged an AUC of 0.68 (SE = 0.01). As evidence to the poor discriminatory power of the extinction models, we found only two species, the Ovenbird ($\hat{\psi}$ = 82.32 SE = 2.90) and Black-capped Chickadee ($\hat{\psi}$ = 24.37 SE = 4.36), to have an extinction threshold model with an AUC value greater than 0.75, suggesting excellent discriminatory power.

The probability of persistence was positively correlated with increasing levels of forest cover (Table 1; Fig. 3). Of the 25 forest breeding birds included in this analysis, 22 (88%) showed greater support for persistence models that included a threshold parameter (Supplementary material). Of those 22 species, 20 had an evidence ratio in support of the threshold model greater than 10. We found persistence thresholds ranged from 19.11% to 95.83% with an average threshold estimate of 60.97% (SE = 4.46) forest cover (Fig. 5). Only four species, the Winter Wren (*Troglodytes troglodytes*) ($\hat{\psi}$ = 95.83% SE 1.78), Yellow-rumped Warbler (*Dendroica coronata*) ($\hat{\psi}$ = 73.61% SE 5.46), Blue-headed Vireo ($\hat{\psi}$ = 61.80% SE 5.18), and Black-throated Blue Warbler (*Dendroica caerulescens*) ($\hat{\psi}$ = 69.30% SE 5.46), demonstrated responses where the probability of persistence dramatically increased above the threshold. The majority of forest birds (18) demonstrated a concave response where the threshold estimate represented the beginning of an asymptotic pattern in the probability of persistence with higher levels of forest cover. AUC values ranged from 0.65 (Least Flycatcher [*Empidonax minimus*]) to 0.87 (Black-throated Blue war-

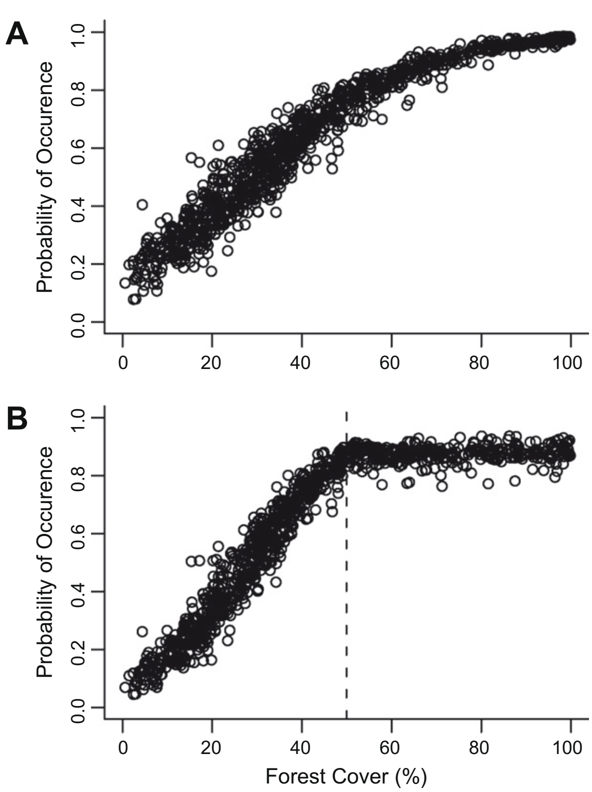

Fig. 4. Predicted probabilities for the relationship between colonization and forest cover for the Ovenbird as an example of the global logistic model (non-threshold model) (A) and the local threshold model (B). In this case, a threshold value of 51.08% (SE 4.49) forest cover (dashed lined) was estimated using the segmented regression and used in model selection.

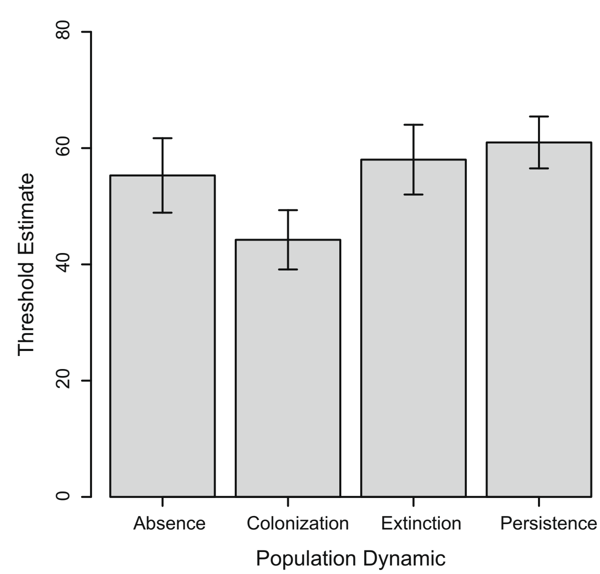

Fig. 5. Barplots of the mean and standard error of threshold estimates for four different population dynamics including absence, colonization, extinction and persistence. Threshold estimates were lower for colonizing events, while thresholds associated with extinctions and persistence generally occurred with over 50% forest cover.

bler) and species had an average AUC of 0.78 (SE = 0.01). We found that the threshold persistence models for 15 species had an AUC value greater than 0.75.

Like persistence dynamics, the probability for colonization was positively correlated with higher levels of forest cover (Table 1; Fig. 3). For 17 of 25 species (68%), we found greater support (Prob(H|Data) >0.70) for colonization models which included a threshold parameter compared to those models assuming no threshold relationship (Supplementary material). Of those 17 species, 14 had evidence ratios greater than 10. Colonization thresholds ranged from 14.15% to 91.22% forest cover, but the average threshold estimate for all species was a relatively low 44.23% (SE = 5.10) forest cover (Fig. 5). Only one species, Winter Wren ($\hat{\psi}$ = 91.22% SE 1.22) demonstrated a concave response where the probability of colonization increased dramatically above the threshold point. The remaining species exhibited thresholds that represented the beginning of an asymptotic pattern in the probability of colonization at higher levels of forest cover. AUC values ranged from 0.66 (Pileated Woodpecker [*Dryocopus pileatus*]) to 0.94 (Black-capped Chickadee) and all models averaged an AUC of 0.76 (SE = 0.02). We found that the threshold colonization models for 10 species had an AUC value greater than 0.75.

The response patterns associated with extinctions were similar to patterns of absence (Table 1; Fig. 1). Fourteen of 25 species (56%), demonstrated strong support ((Prob(H|Data) >0.70) for absence models containing a threshold parameter compared to non-threshold models (Supplementary material). Of those 14 species demonstrating evidences for thresholds, we found 12 species had an evidence ratio greater than 10 in support of a threshold model. Threshold estimates for absences ranged from 17.30% to 85.88% with an average threshold estimate of 55.30% (SE = 6.41) forest cover (Fig. 5). Only three species exhibited convex response curves in absences including Black-throated Blue warbler ($\hat{\psi}$ = 65.02% SE 4.60), White-throated Sparrow (*Zonotrichia albicollis*) ($\hat{\psi}$ = 69.81% SE 4.28), and Winter Wren ($\hat{\psi}$ = 71.75% SE 2.43). For these three species, the probability of prolonged absence reached an asymptote at low levels of forest cover. The other 11 species demonstrated concave response patterns in which the threshold estimates represented a point of rapid increase in the probability of absence. For absence threshold models, we found AUC values ranged from 0.68 (Pileated Woodpecker) to 0.97 (Black-capped Chickadee) and a relatively high average AUC of 0.82 (SE = 0.02). We found that 12 out of 14 species had an AUC value greater than 0.75.

Table 2
Evaluation of thresholds models including the clumpiness index value. We present only fragmentation models with considerable support (competing models had a ΔAIC > 4) for the inclusion of the clumpiness variable. Model selection favored the incorporation of the clumpiness metric in 39 out of the 68 threshold models, but was just as likely to be added above the threshold point as below it. The sign of the parameter estimate ($\hat{\beta}$) reflects whether the population dynamic was positively or negatively correlated with increasing forest aggregation. We report the dynamic, original threshold values ($\hat{\psi}$) of forest cover, the position of the clumpiness variable above or below the threshold estimate, the parameter estimate associated with the clumpiness variable ($\hat{\beta}$), and standard errors (SE).

Species name	Dynamic[a]	$\hat{\psi}$ (%)	Position[b]	$\hat{\beta}$	SE
Pileated Woodpecker	Colonization (−)	24.27	Below	5.05	1.30
	Absence (+)	24.40	Below	−4.40	0.96
Yellow-bellied Sapsucker	Persistence (−)	56.64	Below	5.07	1.00
Least Flycatcher	Persistence (−)	80.00	Below	1.56	0.50
Black-capped Chickadee	Persistence (−)	20.17	Below	−4.43	1.54
	Absence (+)	17.30	Below	8.24	3.13
Winter Wren	Colonization (+)	91.22	Below	4.57	0.79
	Absence (−)	71.75	Above	−6.67	0.81
Hermit Thrush	Persistence (−)	40.42	Above	5.63	0.61
Veery	Colonization (−)	37.31	Above	−4.17	1.49
	Persistence (−)	43.65	Above	−5.64	0.63
	Extinction (+)	47.01	Above	7.30	0.84
	Absence (+)	36.79	Above	5.64	1.23
Golden Crowned-Kinglet	Persistence (−)	80.79	Below	6.56	1.28
Red-eyed Vireo	Colonization (−)	31.06	Below	−5.74	2.72
	Absence (+)	34.88	Below	4.25	1.94
Blue-headed Vireo	Colonization (−)	47.16	Above	6.50	1.00
	Persistence (+)	61.80	Above	5.65	0.64
	Extinction (+)	85.62	Below	−6.10	1.33
Black-and-white Warbler	Extinction (+)	39.90	Above	1.92	0.74
Nashville Warbler	Persistence (−)	82.29	Above	4.27	0.85
	Absence (+)	82.14	Above	−4.06	0.86
Magnolia Warbler	Persistence (−)	60.11	Above	4.81	0.62
Black-throated B. Warbler	Persistence (+)	69.30	Above	4.83	0.68
	Absence (−)	65.02	Above	−6.59	0.79
Yellow-rumped Warbler	Colonization (−)	58.05	Below	3.99	1.00
	Persistence (+)	73.61	Above	4.34	0.79
Black-throated G. Warbler	Persistence (−)	50.64	Above	6.47	0.63
Blackburnian Warbler	Persistence (−)	77.35	Below	10.92	1.19
Ovenbird	Persistence (−)	66.22	Below	2.82	0.63
	Extinction (+)	82.32	Above	10.88	2.51
Canada Warbler	Colonization (−)	76.79	Below	4.81	1.10
	Absence (+)	43.15	Above	−3.37	0.55
Scarlet Tanager	Colonization (−)	30.12	Below	3.51	1.22
	Persistence (−)	70.00	Above	−6.90	0.80
	Extinction (+)	88.16	Above	6.92	1.17
	Absence (+)	43.15	Below	−4.23	0.82
Dark-eyed Junco	Persistence (−)	30.94	Above	3.90	0.61
White-throated Sparrow	Absence (−)	69.81	Above	−3.89	0.73

[a] Threshold models are given a positive sign if the difference-in-slope parameter is positive (concave response curve) or a negative sign if the difference-in-slope parameter is negative (convex response curve).
[b] Position refers to the whether the model selection process chose the model with the clumpiness variable specified.

The goodness-of-fit tests generally supported the model selection process (Table 1; Supplementary material). Models that had less support had significant ($p < 0.05$) goodness-of-fit tests, suggesting poor fit (Hosmer et al., 1997). The calibration plots provided a graphical representation of the goodness-of-fit statistic. When the data supported including a threshold parameter in a logistic regression model, threshold models tended to be better calibrated than the non-threshold models. Specifically, non-threshold models tended perform poorly when predicting the tails of probability distribution.

3.4. The Influences of fragmentation

We developed models adding the clumpiness metric as a measure of fragmentation below and above (i.e., position) the thresholds points for all models that supported the addition of a threshold parameter (Table 2). For five of the 15 species demonstrating thresholds in their probabilities of extinction, we found strong support (ΔAIC > 4) for the inclusion of the clumpiness metric in the threshold model (Table 2). Of these five species, fragmentation was important above the threshold estimate and demonstrated a positive relationship between the probability of extinction and clumpiness where probabilities of extinction were higher in less fragmented landscapes. Consequently, we found greater support for fragmentation being important above the threshold point than below it ($\chi^2 = 8.6$, $p = 0.04$).

Of the 18 species with threshold colonization models, eight had strong support for the inclusion of the clumpiness variable to the threshold model (Table 2). We found that the parameter estimates for the clumpiness metric were positive for six of these species, suggesting that the probability of colonization was higher in landscapes in which forest patches were less fragmented (Table 2). We found no obvious trend towards fragmentation having a greater influence on the probability of colonization below the threshold point for most of these species ($\chi^2 = 0.63$, $p = 0.43$) (Table 2). Two species, Veery (*Catharus fuscescens*) and Red-eyed vireo (*Vireo olivaceus*), were more likely to colonize more fragmented landscapes.

Of the 22 species demonstrating thresholds in their probabilities of persistence, we found that 16 species exhibited strong support for the inclusion of the clumpiness variable in the threshold model. Similar to colonization dynamics, 13 of these species were more likely to remain in landscapes that were less fragmented. We found no evidence of fragmentation being more important below the threshold points of persistence ($\chi^2 = 0.25$, $p = 0.62$). The four species that were more likely to persist in fragmented landscapes included Veery, Red-eyed vireo, and Black-capped Chickadee (Table 2).

Concerning absences, 11 out of the 13 species demonstrating thresholds in absence patterns supported the inclusion of the clumpiness variable (Table 2). In addition, like extinction dynamics, eight out of these 12 species had a higher probability of being absent from areas of high forest fragmentation. As with the other dynamics we did not find any evidence for the influence of fragmentation to be more apparent below the threshold ($\chi^2 = 0.24$, $p = 0.62$).

4. Discussion

The presence and implications of thresholds is long recognized as critical to ecology and natural resource management (Andrén, 1994; Fahrig, 2003; Guénette and Villard, 2005; Huggett, 2005; Lindenmayer and Luck, 2005; Groffman et al., 2006; Lindenmayer et al., 2008; Andersen et al., 2009). In this study, we adapted an objective and repeatable analytical approach for identifying and exploring ecological thresholds in long-term population dynamics. As expected for forest breeding birds, we found that probabilities of colonization and persistence were higher in landscapes with higher amounts of forest while probabilities of extinction and absence were higher in landscapes with less forest (Fig. 3). More importantly, however, we found support for our predictions that thresholds were a common, though not pervasive, characteristic of how forest birds respond to patterns of forest cover. The shape of the relationship leading to these thresholds varied in two distinct forms, concave or convex, and had important implications in the interpretation of the threshold point. This ability to study thresholds in population responses allowed for a comparison of extinction and colonization dynamics that, while often presumed to be the same, appeared to be quite different (Fig. 5).

4.1. Thresholds in avian population dynamics

We found evidence of thresholds in 68% of model comparisons and documented a threshold relationship in at least one dynamic (i.e., extinction, colonization, persistence, or absence) for every species. In patterns of persistence and extinction, we found varying support for the predictions of the *extinction threshold hypothesis*. Most studies addressing extinction thresholds focus on population persistence as measured by species occurrence data collected over a few years. Consequently, our findings regarding thresholds in persistence dynamics represent the most logical comparison to past estimates of extinction thresholds. We found that the probability of persistence was positively correlated with forest cover, and 22 species demonstrated thresholds (Supplementary material). Most of these species demonstrated a convex response curve where the threshold represented a point below which the probability of persistence declined dramatically at low levels of forest cover. As an example, we found that the persistence of Ovenbirds dropped quickly in landscapes with less than 66.22% (SE 2.37) forest cover (Table 1). For all 22 species, the average threshold value for persistence was 60.97% (SE 4.46%) forest cover (Fig. 5). This estimate is high compared to past studies, but many of these previous threshold estimates are based on landscape simulations or from a limited number of empirical studies conducted over shorter time periods and using smaller landscapes (e.g., 2000 m radii, Betts et al., 2007). Our findings suggest that at broader spatial (25 km^2) and temporal (20 years) scales, thresholds in the long-term persistence of forest breeding bird populations may exist at higher levels of forest cover than previously suggested. The prevalence of thresholds in persistence dynamics, however, supports the general prediction of the extinction threshold hypothesis that species will exhibit non-linear responses in population persistence in response to declining habitat cover.

The use of occurrence data alone may not adequately describe extinction dynamics. In terms of extinction dynamics, 15 of 25 forest breeding birds demonstrated discrete thresholds in their response to the amount of forest cover within atlas blocks. For most of these species, the pattern consisted of a concave response curve where the threshold represented a rapid increase in the probability of extinction at low levels of forest cover (Fig. 3). As an example, the Veery demonstrated a non-linear increase in its probability of extinction in landscapes with less than 47.01% forest cover (SE 2.32) (Table 1). For all species, the similarity in the range of forest cover associated with extinction and persistence thresholds suggests that these two dynamics may represent similar responses to changing forest cover (Fig. 5). This assumption does not hold for all species, however. For example, Blackburnian Warblers (Dendroica fusca) demonstrated a clear threshold in persistence dynamics, but we found no support for a threshold in their extinction probabilities (Supplementary material). Thus, persistence and extinction thresholds may not be coincident between species' dynamics.

In contrast to extinction dynamics, the process by which species colonize landscapes with varying amounts of habitat cover has received little attention. For the forest birds included in this analysis, thresholds were a common feature of colonization. For most of these species, colonization responses consisted of a convex curve where the threshold represented a point above which the probability of colonization began to level off at higher levels of forest cover, suggesting a saturation point (Fig. 3). This slowing in the rate of colonization happened at relatively low levels of forest cover compared to other dynamics ($\bar{x}$ = 44.22% SE = 5.10) (Fig. 5). Like persistence dynamics, the probability of colonization was positively correlated with greater amounts of forest cover, but thresholds for persistence were found at higher levels of forest cover (Fig. 5). This suggests that birds may be colonizing landscapes with lower amounts of forest, but greater amounts of forest cover are needed to maintain populations over the long term.

Although thresholds associated with different population dynamics occurred along different points of the forest cover continuum, the trajectories of colonization and extinction paralleled patterns of persistence and absence, respectively (Fig. 3). This suggests that species were more likely to colonize atlas blocks that were similar to those in which they were retained, and were more likely to go extinct in blocks that were similar to those in which they were absent. Gates and Donald (2000) used atlas data in conjunction with environmental data to investigate the relationship between local extinctions and habitat suitability for six declining species in Britain. They found that areas where each species became extinct were more similar in land-use type, climate and topography to areas where a species was never present than those where it was retained. Although we did not explicitly test this hypothesis, the patterns of responses tend to support this correspondence of large-scale population dynamics having similar relationships to habitat amount.

4.2. Fragmentation effects above and below the threshold

Although we found evidence of thresholds in the responses of bird populations to forest cover, the effects of habitat configuration and the implications of the *fragmentation threshold hypothesis* were less clear. Many questions remain regarding the effects of habitat configuration, independent of habitat amount, on wildlife populations (Fahrig, 2002; McGarigal and Cushman, 2002; Fahrig, 2003), and most studies have found that habitat amount is relatively more important than habitat configuration on patterns of species' occurrences (see review by Fahrig (2003)). We found that model selection favored the incorporation of the clumpiness metric in 39 out of the 68 threshold models (Table 2). In addition, we found that although species responses were influenced by forest fragmentation (as measured by the clumpiness metric) this effect was found below and above threshold points (Table 2). Higher fragmentation could lead to populations occupying insufficiently sized forest patches leading to increased exposure to unsuitable habitats (Rodewald, 2003) and increased edge effects (i.e., brood parasitism and nest predation) (Donovan et al., 1995; Robinson et al., 1995; Donovan and Flather, 2002). We found that, with some exceptions, rates of colonization and persistence were more likely in less fragmented landscapes while extinction and absence were more likely in landscapes of high fragmentation. In addition, several species demonstrated counterintuitive responses where probabilities of colonization or persistence were lower in landscapes of more aggregated forest cover (Table 2). Other studies have found similar positive effects of fragmentation on population occurrence. In these cases, fragmentation could provide refugia for prey species, competitive release, and could lead to population stability

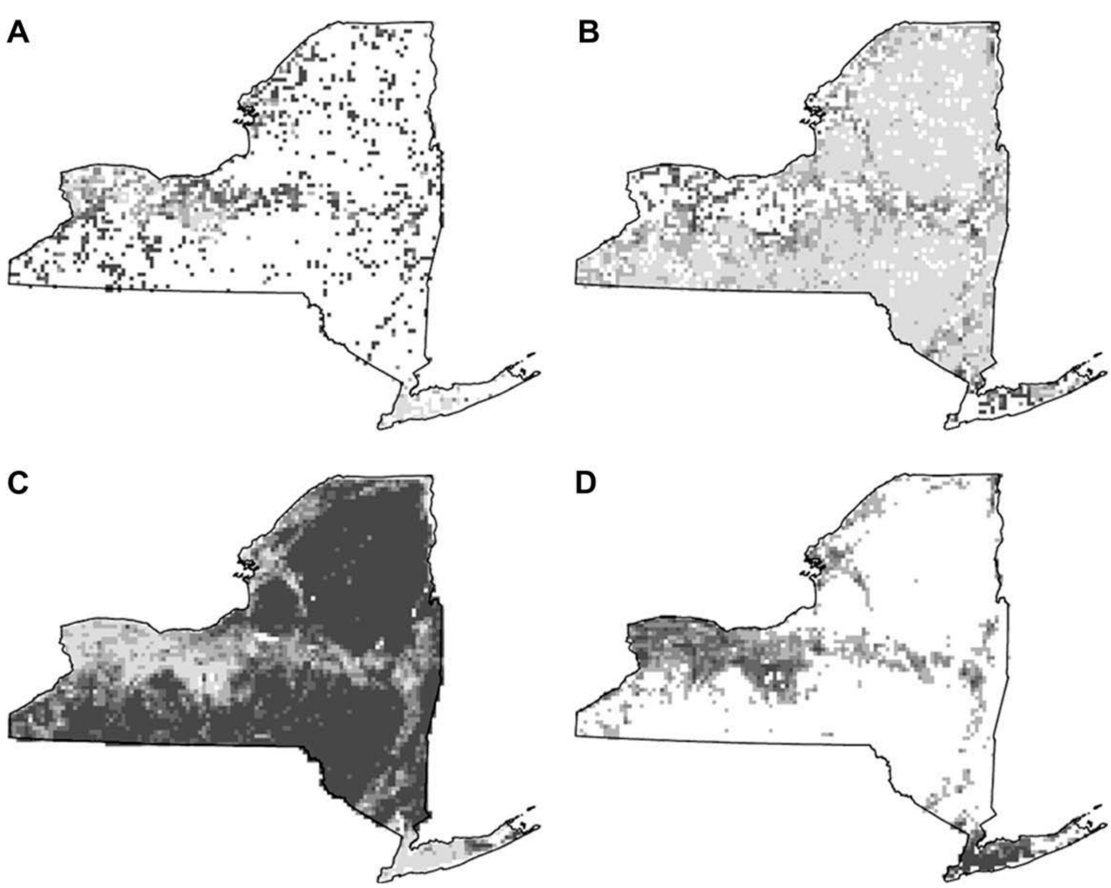

Fig. 6. Predicted probabilities in Breeding Bird Atlas blocks based on threshold models for the Ovenbird (*Seiurus aurocapilla*) in New York State. Dark areas represent high probabilities and light areas represent low probabilities for four different dynamics including colonizations (A), extinction (B), persistence (C), and absence (D). Thresholds in species responses can be used to more accurately predict the likelihood of population dynamics for purposes of environmental planning and assessment.

when local disturbances are asynchronous (Fahrig, 2003). Given these results, it would be misleading to only be concerned with habitat configuration at low levels of habitat amount.

5. Conservation implications and conclusions

Although all the species in this study are considered forest breeding birds, we found a wide range of threshold values for extinction, colonization, persistence, and absence dynamics. Other studies on threshold dynamics have found a similar variability in threshold estimates and species' responses to habitat availability (Jansson and Angelstam, 1999; Homan et al., 2004; Radford and Bennett, 2004; Betts et al., 2007; Denoël and Ficetola, 2007). Lindenmayer and Luck (2005) suggest that this variation in findings could be due to factors such as the assemblage or species being studied, the range of cover over with which a threshold is hypothesized to occur, or the timing, duration, and intensity of landscape change. In our study, the variability in threshold estimates could be due to the problems associated with identifying "habitat" using a generalized land cover type (i.e., forest). As an example, extinction models, which generally lacked predictive power, may be better modeled using unaccounted for environmental variables (e.g., road density, population density, and acid precipitation data). Our finding that habitat amount was successful in modeling colonizations and retentions, however, suggests that the use of generalized land cover for characterizing habitat may be useful in modeling certain dynamics and not others, even for the same species. In addition, life history characteristics including mortality rates in non-breeding habitats, gap-crossing behavior, rates of juvenile dispersal, and matrix effects all might influence population response to changing habitat cover.

In environmental management, thresholds can be viewed as rapid shifts in species-habitat relationships (Huggett, 2005; Groffman et al., 2006; Denoël and Ficetola, 2007; McIntyre et al., 2000). For wildlife populations inhabiting landscapes affected by human-induced habitat loss, the study of thresholds is an exercise in preventative management that relies on identifying landscapes of rapid ecological change before they occur (Fig. 6). The study of colonization dynamics will be critical as a number of regions throughout the northeastern United States are recovering from centuries of widespread agriculture and timber harvesting (Zipper et al., 1990; Yahner, 2000; Confer and Pascoe, 2003). In both these land use scenarios, forecasting changes in broad-scale population dynamics requires the identification of which species are more likely to demonstrate thresholds in response to shifting patterns of habitat availability.

Thresholds based on short-term occurrence may better serve as "pre-extinction thresholds" (Betts et al., 2007) relating to a spatial pattern of occurrence as opposed to true extinction or colonization dynamics (Radford et al., 2005; Betts et al., 2007). The ability to detect thresholds in persistence dynamics that represent long-term population persistence is of significant conservation value. Our findings emphasize that, whenever possible, the focus of threshold analysis should ultimately be on identifying thresholds in the persistence of populations over multiple generations (Lindenmayer and Luck, 2005). In addition, we found forest aggregation effects to be important on both sides of the threshold. Consequently, scientists and land managers should not assume that the effects of habitat configuration are restricted to low levels of habitat amounts, and should attempt to assess species responses over as wide a range of habitat cover as possible.

Using thresholds for population modeling, monitoring and management would be a major advance in our ability to forecast rapid ecological changes (Groffman et al., 2006). The use of long-term data, such as repeat atlases, allows for the identification of thresholds in multiple species and population dynamics. Given the wide range of threshold values for many of the species and dynamics included in this study, it is problematic to offer generic recommendations on how to best conserve forest bird communities. As such, the search for a single value representing an "extinction threshold" may be a misguided quest (With and King, 1999; Fahrig, 2001). Incorporating threshold dynamics in regional conservation planning should strive to be species-specific and focus on identifying sensitive species and populations occupying landscapes that are on the verge of rapid ecological change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.01.004.

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