

Regional variability in extinction thresholds for forest birds in the north-eastern United States: an examination of potential drivers using long-term breeding bird atlas datasets

Yntze van der Hoek^{1,2*}, Andrew M. Wilson³, Rosalind Renfrew⁴,
Joan Walsh⁵, Paul G. Rodewald⁶, Jennifer Baldy⁷ and Lisa L. Manne^{1,2}

¹College of Staten Island, 2800 Victory Blvd, Staten Island, NY, USA, ²The Graduate Center of the City University of New York, 365 5th Ave, New York, NY, USA,

³Gettysburg College, 300 N Washington St, Gettysburg, PA, USA, ⁴Vermont Center for Ecostudies, 20 Palmer Court, White River Junction, VT, USA, ⁵Massachusetts Audubon Society, 208 South Great Road, Lincoln, MA, USA, ⁶Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY, USA, ⁷Kalamazoo Nature Center, 7000 N Westnedge Ave, Kalamazoo Township, MI, USA

ABSTRACT

Aim Demand for quantitative conservation targets has yielded a search for generalities in habitat thresholds, particular amounts of habitat at which extinction probabilities change strongly. These thresholds are thought to vary across regions, but investigation of this variability has been limited. We tested whether thresholds (of forest separating extinction from persistence) increased as either average forest cover in landscapes decreased or the degree of fragmentation increased.

Location Massachusetts, Michigan, New York, Ohio, Pennsylvania and Vermont.

Methods We used segmented logistic regressions to estimate thresholds in the relationship between extinction probability and forest cover for 25 forest-breeding birds, comparing estimated thresholds across states. We also selected landscapes from our entire study area in which landscape-level forest cover and degree of fragmentation varied independently and compared thresholds.

Results We found that thresholds in extinction probability varied widely among species (7–90% forest cover) and within species across states [e.g. 12–90% for white-throated sparrow (*Zonotrichia albicollis*)]. Additional analyses showed no indications that thresholds correlated with the degree of fragmentation or forest cover across the landscape; we found considerable variability in thresholds across landscapes, species and even landscapes in which (average) fragmentation and forest cover were similar.

Main conclusions Extinction threshold estimates varied tremendously across species and landscapes. Thus, habitat thresholds are difficult to generalize as they depend on many factors beyond landscape fragmentation and habitat availability (e.g. landscape characteristics such as matrix quality). Our findings highlight the need to avoid oversimplification and generalization of habitat thresholds, especially as they might prove counterproductive to conservation efforts. Instead, we propose that we evaluate thresholds for individual species – preferably using species-centred habitat definitions in threshold modelling – to derive generalities for ecological and conservation applications.

Keywords

Breeding bird atlas, extinction thresholds, fragmentation, habitat loss, minimum area requirements, segmented regression.

*Correspondence: Yntze van der Hoek, College of Staten Island 6S-117, 2800 Victory Blvd., Staten Island, NY 10314, USA.
E-mail: yvan_der_hoek@gc.cuny.edu

INTRODUCTION

Natural resource managers require high-quality information about the amount of habitat needed to ensure the persistence of species on the lands they manage (Fahrig, 2001). The increasing demand for quantitative conservation targets has led to a search for broadly applicable rules to describe the relationship between habitat cover and occupancy, occurrence or persistence probabilities of species. Responses of wildlife to changes in habitat, such as loss and fragmentation, can take the form of threshold responses: there are threshold amounts of suitable habitat where there is a rapid change in the probability of persistence or extinction of the species of interest (Fahrig, 2001; Lindenmayer & Luck, 2005; Zuckerman & Porter, 2010). Estimates of such thresholds may serve as proxies for minimum habitat requirements and consequently as guidelines for resource planning and conservation (Groffman *et al.*, 2006; Rompré *et al.*, 2010; Swift & Hannon, 2010; Kato & Ahern, 2011).

Generalizations of habitat thresholds may hide the variability that exists among species, landscapes or regions (Rhodes *et al.*, 2008; Betts *et al.*, 2010; van der Hoek *et al.*, 2013). So far, studies have mainly addressed whether regional variation exists in general (e.g. Rhodes *et al.*, 2008; Betts *et al.*, 2010) or utilized theory and simulations to predict how habitat thresholds vary as a result of variation in landscape structure (e.g. degree of fragmentation, amount of forest cover and quality of matrix; Fahrig, 2002; Villard & Metzger, 2014).

Habitat thresholds may differ because different studies define different 'types' of thresholds, especially fragmentation and the extinction thresholds (Fahrig, 2001, 2002; Villard & Metzger, 2014). Here, we consider Villard & Metzger's (2014) definition: fragmentation thresholds are habitat amounts below which the effects of habitat fragmentation accelerate extinction probability independent from the effects of habitat loss per se; extinction thresholds are habitat amounts below which habitat is simply insufficiently available, leading to steep increases in extinction probability. Thus, species might show both fragmentation and extinction thresholds, which are, respectively, found in landscapes with high/low levels habitat amounts. Thresholds may also be influenced by other landscape and habitat characteristics, such as vegetation structure and composition (Betts *et al.*, 2010), the percentage habitat cover found in the wider region (Rhodes *et al.*, 2008) and the quality of the habitat or matrix (Boyle & Smith, 2010). Estimates of thresholds may also be influenced by the scale at which we assess species' responses (Holland *et al.*, 2004; Betts *et al.*, 2006, 2010) and spatial variability in demographics such as reproductive rates (Rhodes *et al.*, 2008). Finally, the estimation of the thresholds may be influenced by methodological and statistical issues in threshold detection. Variability in species detection and survey efforts (Betts *et al.*, 2010; Zuckerman & Porter, 2010; Jones *et al.*, 2011), the use of different sample sizes (van der Hoek *et al.*, 2013) and the use of various statistical

approaches (Ficetola & Denoël, 2009) may make comparisons and generalizations across studies or study sites difficult.

Here, we derived unique estimates of extinction thresholds for 25 forest generalist and obligate breeding birds. We explored how threshold estimates varied among areas and investigated whether this variability was correlated with landscape-level forest cover or fragmentation. We predicted that for most species, threshold estimates would be negatively associated with amount of forest cover and positively associated with fragmentation (Ewers & Didham, 2006; Villard & Metzger, 2014). Simulations and theoretical models show that estimates of extinction thresholds may be positively correlated with the extent of habitat fragmentation (With & King, 1999; Fahrig, 2002), whereas higher forest cover in the surrounding landscape may lower thresholds through increased rescue effects (Fig. 1). Put differently, we might find 'fragmentation thresholds' (thresholds at relatively high amounts of forest cover) in landscapes that are highly fragmented and 'extinction thresholds' (at lower amounts of forest cover) in landscapes that are little fragmented (see fig. 6 in Villard & Metzger, 2014).

Finally, forest cover may be too broad a definition of 'habitat'. However, in practice, generic and human-defined cover types are most often used as habitat proxies in conservation

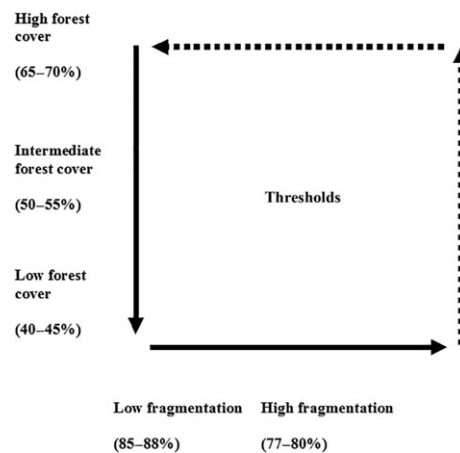


Figure 1 Predicted relationships thresholds and forest cover/fragmentation. We predicted that threshold estimates would decrease as landscapes/regions increase in forest cover or increase in fragmentation (solid arrows). Alternatively, thresholds could stay the same or even increase in landscapes with lower fragmentation or increased forest cover as a result of positive edge effects (Fahrig, 2002) or changes in species interactions (Kneitel & Chase, 2004) (dashed lines). Note: for one analysis (see Methods), we selected landscapes for each combination of forest cover and fragmentation (a landscape that was highly fragmented and had high forest cover, a landscape that was highly fragmented and had intermediate forest cover, etc.). The selected landscapes were classified based on the average forest cover (%) and aggregation (inverse of fragmentation; %) calculated across all atlas blocks within the landscape, the ranges of which are given in parentheses.

and management (e.g. in Rompré *et al.*, 2010; Environment Canada, 2013), likely because they are more easily interpreted and integrated in policy and recommendations than species-centred habitat definitions. Therefore, we elected to assess variability, generalities and applicability of thresholds in the relationship between extinction probability and availability of forest cover.

METHODS

Data: Breeding bird records

We used breeding bird atlases to estimate probability of extinction over a *c.* 25-year time period for the same 25 forest generalist and obligate species evaluated in van der Hoek *et al.* (2013) and Zuckerberg & Porter (2010). We used data from the first and the second atlases of Massachusetts (MA) (Petersen & Meserve, 2003; Kamm *et al.*, 2013), Michigan (MI) (Brewer *et al.*, 1991; Chartier *et al.*, 2011), New York (NY) (Andrle & Carroll, 1988; McGowan & Corwin, 2008), Ohio (OH) (Peterjohn & Rice, 1991; Rodewald *et al.* in prep.), Pennsylvania (PA) (Brauning, 1992; Wilson *et al.*, 2012) and Vermont (VT) (Laughlin & Kibbe, 1985; Renfrew, 2013), all states within the eastern temperate forest ecoregion with some parts of northern forest (Omernik, 1987). Specific atlas sampling and methods can be found in the above citations.

Breeding bird atlases divided their area into discrete 'blocks' (*c.* 1/6th of a 7.5 min USGS topographical quad; *c.* 5 × 5 km) and large numbers of fieldworkers surveyed birds within all or a subset of those blocks. We used data from blocks surveyed in both the first and the second atlas for each state. For Vermont, we only had access to data from 'priority blocks': randomly selected blocks that were surveyed until at least 75 species were observed at any breeding level ('confirmed', 'probable' and 'possible') (Renfrew, 2013). We standardized atlas datasets by applying the same criterion to the other atlases and excluded blocks in which fewer than 75 breeding bird species were detected. This criterion might introduce a sampling bias in our analysis, the inclusion of only high survey effort atlas blocks (that are potentially located near high densities of volunteers). For example, in Pennsylvania (Wilson *et al.*, 2012), blocks with 75+ species had significantly more effort hours (mean = 26.2 h, *n* = 3224) than those blocks with < 75 species reported (mean = 12.5 h, *n* = 1382), *z* = 17.86, *P* < 0.001. However, preliminary analyses yielded little difference between thresholds derived for this subset of atlas blocks and analyses on all atlas blocks (mean difference = 5.3%, SE = 3.6), and we found the ≥ 75 species criterion not biasing for our purposes. We excluded blocks that were not entirely within state boundaries, or consisting of more than 50% water. In total, we had data for 146 (MA), 181 (MI), 1392 (NY), 404 (OH), 673 (PA), and 175 (VT) blocks (for a total of 2971 blocks). Blocks were spaced more than 6 km apart on average, and examination of Moran's *I* correlograms (Lichstein *et al.*,

2002; Zuckerberg & Porter, 2010) did not reveal significant spatial autocorrelation (α -level = 0.01).

Non-detection of species in an atlas block does not have to indicate the absence, as detection probability is likely to be < 1 (MacKenzie *et al.*, 2002). Species likely remain undetected in occupied habitat patches when there is a small population size, difficulty of detection of individuals or limited sampling effort (Gu & Swihart, 2004). We limited the effect of heterogeneous detectability by choosing relatively common and easily detected focal species. In addition, by including only atlas blocks with 75+ species, we set a rather high standard for the effort (in hours) spent in each atlas block. Unfortunately, we were unable to benefit from recent developments addressing imperfect detection (Kéry & Schmid, 2004; Royle *et al.*, 2005) because we did not have information from repeated sampling (as in Zuckerberg & Porter, 2010). Similarly, survey hours were not available for every Atlas (hence the > 75 species criterion for inclusion instead of an hour-based criterion), making it difficult to quantify the effect of differences in effort across Atlases. Nevertheless, the effects of differences in survey effort in our analyses are likely limited because there is no evidence that effort or changes in effort (between the First and the Second Atlas) are correlated with forest cover – the predictor we are interested in assessing (Gu & Swihart, 2004; Zuckerberg & Porter, 2010). Data on survey effort (in hours) were available for both New York and Pennsylvania Atlases, and there were no significant correlations between [change in] effort and forest cover in either state (Zuckerberg & Porter, 2010). Finally, we present a study of variability in thresholds; we do not aim to provide exact estimates of extinction thresholds.

Data: Land cover and fragmentation metrics

We calculated forest cover from 1992 National Land Cover Data (NLCD) as the proportion of all deciduous, coniferous and mixed forest cover (areas where tree cover (natural or semi-natural woody vegetation > 6 m tall) accounts for 25–100% of surface cover (Vogelmann *et al.*, 2001) in each atlas block. Using 1992 data (an approximate midpoint between atlas sampling periods) instead of assessing change in forest cover over time may have introduced some bias, but was necessary due to logistic constraints. Estimates of extinction thresholds may be influenced by this choice of land cover data, but the relative differences between regions/states are likely similar in magnitude and direction.

We initially chose edge density, patch density, mean patch area and aggregation index (AI; calculated as an area-weighted mean class AI, where forest cover was weighted by its proportional area in the landscape) as fragmentation indices because their potential effect on the extinction threshold is easily interpreted, they are easily calculated [we used SDM-Tools (Vanderwal *et al.*, 2012) in R (R Core Team, 2012)], and they are commonly used throughout the literature (Hargis *et al.*, 1998; McGarigal *et al.*, 2002; Fahrig, 2003; Frohn & Hao, 2006). However, as all these metrics were significantly

correlated ($P < 0.01$) with one another, we ultimately used only one metric that is straightforward in interpretation, AI, in further analyses. We did not derive metrics that capture the 'process' of fragmentation; the fragmentation metrics mentioned here indicate how fragmented a landscape is at a given point in time.

Models and statistical analysis

State-by-state comparisons of habitat thresholds

We conducted most analyses in two ways. First, we included all data from all atlas blocks where at least 75 species were detected in both the first and the second atlas (of each state). We considered whether birds were persistent (present in both atlases), absent (not present in either), colonizing (not present in the first, but present in the second) or extinct (present in the first but not the second) (Gates & Donald, 2000) and gave extinction a value of 1 and all other dynamics value 0 (hereafter: scenario 1). This approach is consistent with other studies (Zuckerberg & Porter, 2010) but does not estimate true extinction probability because it includes occasions where a species was not present in the first atlas and can thus never 'go' extinct. Therefore, we added a second scenario in which we included only atlas blocks for which a focal bird was at least present in the first atlas (scenario 2). This approach resulted in different sample sizes (number of atlas blocks) for each species (another potential factor influencing thresholds (van der Hoek *et al.*, 2013), but it provides a better assessment of true extinction probability.

We plotted the fitted values of locally weighted nonparametric models (smoothing parameter 0.75) to visualize empirical relationships between forest cover and extinction, and to identify starting values for segmented regression models. We created threshold [segmented logistic regression (Muggeo, 2008), using the 'segmented' package (Muggeo, 2003)] and non-threshold (logistic regression) models in R (R Core Team, 2012). We used Akaike's information criterion (AIC) to compare threshold and non-threshold models per species, and per state or region, selecting the model with fewest parameters (the non-threshold model) when the difference in AIC was < 2 between the models. In addition, we deemed the threshold model insufficiently precise for further analyses when the standard error (SE) accompanying the threshold estimates was larger than the threshold estimate itself. This percentage was subjective, but a standard error larger than the estimated threshold implies that the threshold could also be found at 0% forest cover, a highly unlikely scenario. We assessed fit of each model using area under the curve (AUC).

We compared threshold and non-threshold models for all 25 species for each state under both data scenarios. However, some species, in certain states, were so rare that the number of block records was too low ($c. N < 10$) to allow modelling (see, Table S1 in Supporting Information). For that reason, we were unable to create either threshold or non-threshold

models for 12 species in Ohio and common raven (*Corvus corax*) in Massachusetts (Tables S1 and S2). In total, we were able to compare a maximum of six thresholds (one per state) per species for subsequent analysis of factors driving regional variability. This relatively low sample size, and variable numbers of blocks in each state, somewhat limited our interpretation of how landscape metrics influenced threshold estimates. Therefore, we constructed and compared additional threshold and non-threshold models based on subsets of blocks.

Threshold comparisons across nine landscapes

We wanted to test for relationships between the average percentage of forest cover or level of fragmentation (AI) in a landscape and the threshold estimate. We manually selected nine 'landscapes' of similar extent ($c. 15,000$ – $20,000$ km²); landscapes that did not overlap, consisting of (near) adjacent atlas blocks and differing from one another in average forest cover and degree of fragmentation (across the landscape). The number of atlas blocks used for analysis in each landscape differed, due to application of the ≥ 75 species criterion, but was within one order of magnitude ($c. 200$ – 300 blocks). In early analyses, $c. 200$ atlas blocks were minimally required to run segmented regression models without too many convergence failures (van der Hoek *et al.*, 2013). For these landscapes, we compared threshold and non-threshold models (under both scenarios) and considered a threshold supported when the AIC of the threshold model was at least two less than the non-threshold model AIC. Low sample sizes did not allow us to create models for several species in certain landscapes (Table S3). Too few thresholds were supported [i.e. sample size was too low, $N = 5$ maximum for Nashville warbler (*Oreothlypis ruficapilla*)] to properly use linear models to test for a relationship between forest cover and threshold value.

Threshold comparisons across landscapes in which fragmentation and forest cover vary independently

Fragmentation (or configuration) and habitat availability are frequently correlated (Didham *et al.*, 2012; Villard & Metzger, 2014) and, here, evidenced by the correlation between forest cover and aggregation (see Data: Land Cover and Fragmentation Metrics). Statistical approaches to disentangle the effects of both are often less effective and straightforward than desired (Smith *et al.*, 2009). We adopted a simple approach to address the effects of fragmentation and habitat cover independent from one another. We selected landscapes of approximately similar extent ($c. 200$ – 300 atlas blocks) that were either little or highly fragmented and had low, intermediate or high average forest cover (as calculated across the atlas blocks in the selected landscape) (Fig. 1). We consider this analysis solely as a first step in a broader investigation of the separate effects of fragmentation and forest cover in a wider landscape on habitat thresholds. For each of the six

possible combinations of habitat cover and fragmentation, we selected two landscapes, in order to also assess variability in thresholds across landscapes that were similar in habitat cover and level of fragmentation. We conducted this analysis under data inclusion scenario 1 only, to ensure that the habitat cover and fragmentation estimates calculated across each landscape applied to all species (using scenario 2 would imply using a subselection of different atlas blocks within the selected landscape for each species).

RESULTS

State-by-state comparisons of habitat thresholds

Threshold models were better models than logistic regression models (Burnham & Anderson, 2002) for 49 of 137 model comparisons; 25 species \times 4 states plus 24 species for MA and 13 species for OH) model comparisons under scenario 1 and for 29 model comparisons under scenario 2 (Table S2). AUC scores were relatively low across all supported threshold models (median 0.67; range 0.54–0.98). Support for threshold models and associated threshold estimates varied widely among species and states. The difference between the two scenarios was not a focus of our research, but we note that the threshold estimates derived under either scenario can be very different.

Under scenario 1, support for thresholds was lowest in the two states with the lowest average percentage of forest cover, MI and OH, whereas we found most support for thresholds in states with intermediate to high amounts of forest cover, NY (Fig. 2, Table S2), and we observed a similar trend for scenario 2, with support for six threshold models in PA and NY and only one in OH.

Medians of all supported thresholds per state ranged from 44% (MA) to 77% forest cover (VT) under scenario 1 and from 8% (OH) to 87% forest cover (PA) under scenario 2. The value of 8% for Ohio was the single supported threshold estimate for the state, for ovenbird (*Seiurus aurocapilla*). Threshold estimates ranged widely across species, from very low [e.g. 17% (SE = 7) for black-throated green warbler (*Setophaga virens*) in NY (scenario 1) or 8% (SE = 2) for ovenbird in OH (scenario 2)] to very high [e.g. 96% (SE = 0.3) for black-and-white warbler (*Mniotilta varia*) in PA (scenario 1) or 95% (SE = 2) for Canada warbler (*Cardellina canadensis*) in NY (scenario 2)] (Table S2). Even within a species, there were sometimes large differences across states, for example from 17% (SE = 7) in NY to 74% (SE = 21) in VT (black-throated green warbler, scenario 1) and from 8% (SE = 1.7) in OH to 82% (SE = 7) in NY (ovenbird, scenario 2). No obvious geographic trends could be detected in the species-specific threshold estimates.

The nature of the relationship between extinction probability and forest cover varied between species or within species, across states (Fig. 3 and Table S2). Whereas many relationships were negative as expected (i.e. extinction probability decreases as forest cover increases), we also often found

unimodal relationships: peaks in extinction probability at intermediate amounts of forest cover. We aim to investigate the nature of these unimodal relationships in future studies.

Threshold comparisons across nine landscapes

Support for threshold models varied widely between landscapes (between 4 and 13 species supported thresholds under scenario 1; 1–10 species under scenario 2). We found least support for thresholds in landscapes with low amounts of forest cover or high degrees of fragmentation, and some indications of positive relationships between the number of supported models and forest cover or degree of fragmentation (Fig. 4a,b). We did not test for significance of these relationships due to low sample size. Threshold estimates also varied widely across both species and landscapes and ranged from 17% to 95% forest cover (Table S3), with model AUCs ranging from 0.45 to 0.99. We found little visual support for relationships between thresholds and forest cover or aggregation, although there were a few exceptions (Fig. 4c–f). Thresholds for some species, such as black-throated green warbler, may increase with forest cover or decrease with fragmentation.

Threshold comparisons across landscapes in which fragmentation and forest cover vary independently

When we modelled extinction probability with data from selected landscapes that differed in fragmentation and forest cover, we again found considerable variability in support for thresholds and in associated threshold estimates (Table 1). We found more support for threshold models as the amount of forest in the landscape increased, with most support for thresholds in high forest cover landscapes with a low degree of fragmentation (12 and 9 species support threshold models in both replications of these ‘type’ of landscapes) and least support in landscapes with low forest cover and high levels of fragmentation (three and one species). It was difficult to make comparisons across all landscapes, as few species supported thresholds in multiple landscapes. Nevertheless, thresholds varied vastly across the landscapes: thresholds were not consistently higher in highly fragmented landscapes nor did thresholds consistently increase or decrease as the average forest cover in the landscape increased or decreased. Strikingly, thresholds differed even across landscapes that were similar in terms of fragmentation and habitat cover. For example, black-throated blue warbler (*Setophaga caerulescens*) showed support for thresholds in both of the ‘highly fragmented, high forest cover’ landscapes, but the estimated thresholds were at very different forest cover percentages (46% and 86%).

DISCUSSION

Extinction thresholds varied vastly across species and across regions. We predicted that thresholds would be higher in

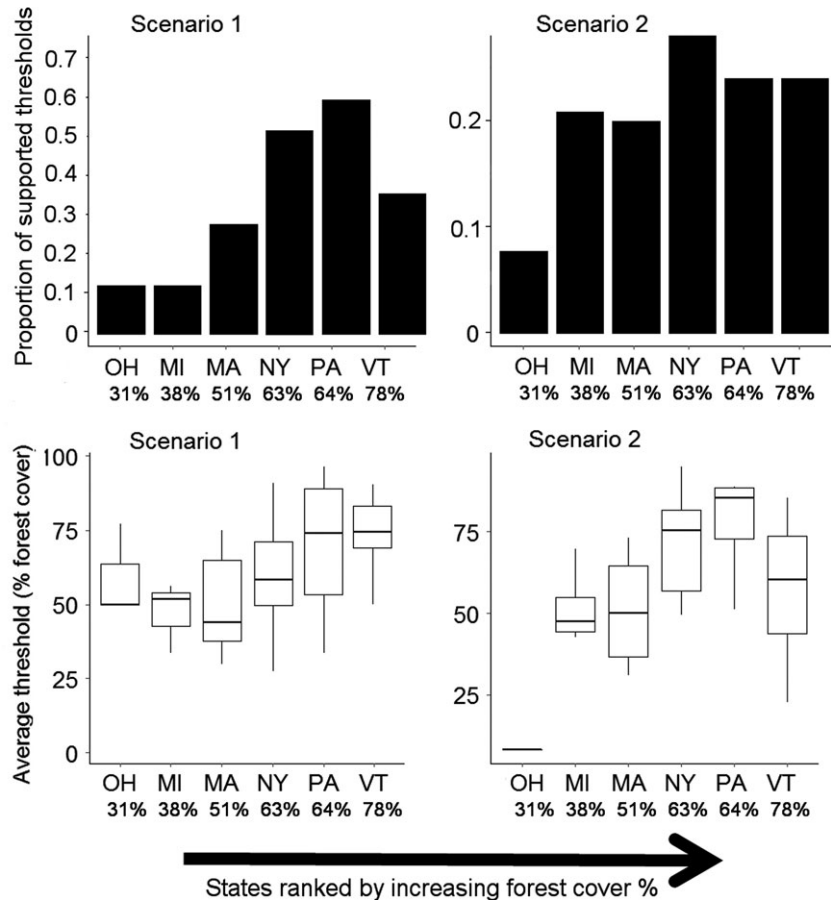


Figure 2 Proportion of selected threshold models under two scenarios. The top two panels depict the proportion of species for which threshold models were selected per state under two model scenarios. The model scenarios differed in the estimation of extinction probability, further explained in Methods. The bottom two panels show the median (horizontal line) and 25th and 75th percentiles (upper and lower ‘hinges’) of the threshold estimates for supported threshold models per state. The whiskers extend to the highest and lowest threshold estimates found per state. Percentages on horizontal axis give average forest cover per block for that state.

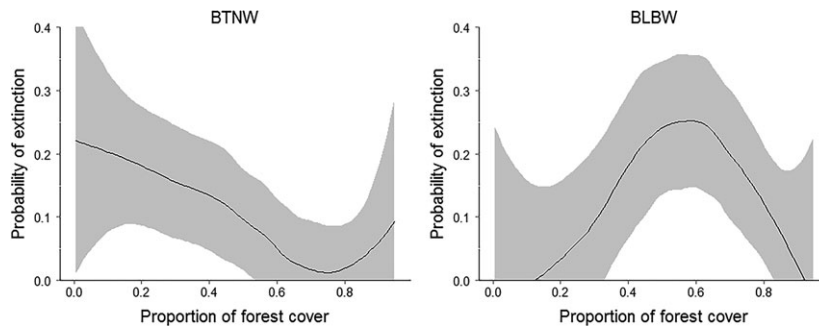


Figure 3 Loess plots of extinction dynamics for two bird species. Loess plots (+ SE) showing the relationship between proportion of forest cover in an atlas block and the probability of extinction for two species (BTNW = black-throated green warbler (*Setophaga virens*); BLBW = black burnian warbler (*Setophaga fusca*). BLBW shows a unimodal relationship between extinction probability and the proportion of forest cover.

more fragmented landscapes than in less fragmented landscapes and lower in landscapes with high average forest cover than in landscapes with low average forest cover, but cannot support this prediction. Thresholds do seem to be most common – or most easily detected using automated processes – in landscapes with intermediate to high amounts of forest cover.

We estimated thresholds following three different analyses: (1) a state-by-state comparison of thresholds, (2) a comparison of thresholds across nine different landscapes, and (3) a

comparison across landscapes in which the degree of fragmentation and the amount of forest cover varied independently. We found more support for threshold models as the average amount of forest cover in landscapes increased in all three analyses, although we did not separate the effects of fragmentation and forest cover in the first two analyses. However, as we found similar results in the third analysis, thresholds are indeed more likely to be found in landscapes with intermediate to high amounts of forest cover, in line with results from earlier empirical (Pardini *et al.*, 2010) and

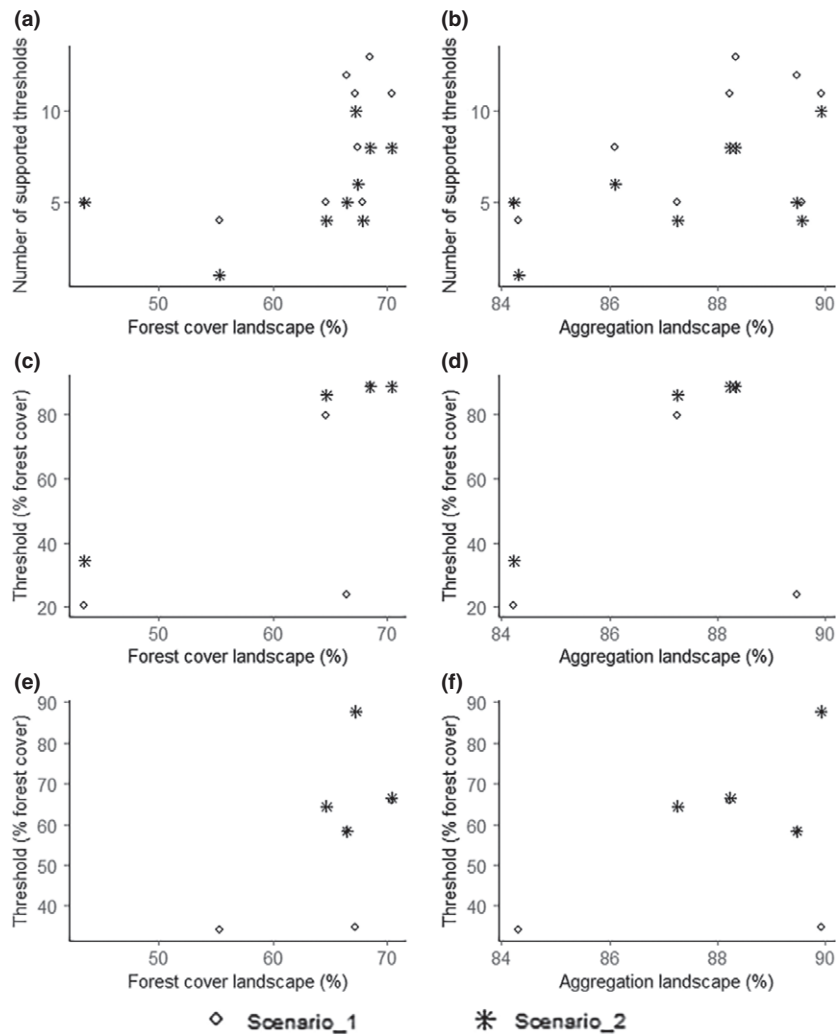


Figure 4 Number of thresholds found and estimated threshold amounts in relation to landscape characteristics. We found that the number of thresholds supported varied widely across landscapes with different amounts of forest cover (a) and degrees of fragmentation (b), under two model scenarios. The model scenarios differed in the estimation of extinction probability, further explained in Methods. Note that ‘Aggregation landscape (%)’ is inverse to degree of fragmentation (i.e. the more aggregated a landscape the lower the degree of fragmentation). Panels (c) and (d) [black-throated green warbler (*Setophaga virens*)] and (e) and (f) [blue-headed vireo (*Vireo solitarius*)] show how estimated thresholds typically varied across landscapes with different characteristics (see also Table S3).

simulation studies (Villard & Metzger, 2014). In landscapes with high amounts of forest cover, we might not detect thresholds because we merely see the more linear effects of habitat loss per se – that is, the amount of habitat in this landscape is higher than the ‘fragmentation threshold’ – and in landscapes with low forest cover, we might already be below the ‘extinction threshold’ – that is, the amount of habitat in this landscape is such that population persistence probability is declining precipitously (Villard & Metzger, 2014). In addition, we should investigate whether species interactions that lead to extinction are more common in landscapes with intermediate levels of habitat cover, and whether such species interactions might accelerate changes in extinction probability resulting in the emergence of thresholds. In extinction threshold modelling, we usually take a single-species approach (e.g. Rhodes *et al.*, 2008; Betts *et al.*,

2010; Zuckerberg & Porter, 2010), with little focus on the influence of the species interactions on extinction thresholds. We suggest that future studies take into account that marginal reductions in habitat availability (the focus of threshold studies) likely interact with other processes to influence extinction probability. Secondary extinctions induced by loss of biodiversity and shifts in trophic levels might be more probable in many cases (Komonen *et al.*, 2000; Bellingieri & Bodini, 2013).

Interestingly, thresholds for some species seem to increase slightly with more forest cover or less fragmentation (Fig. 4, Table 1), counter to our and previous predictions (Fahrig, 2002; Villard & Metzger, 2014), but may be explained by a number of factors. First, there are issues specific to the data [e.g. sample size issues (van der Hoek *et al.*, 2013) and variability in species detection and survey efforts (Betts *et al.*,

Table 1 Thresholds in landscapes with different habitat characteristics. Thresholds (in %) for 25 forest generalist and obligate species in landscapes with six different combinations of (average) degree of fragmentation (High, Low) and amount of forest cover (Low, Intermediate, and High). For each combination, we estimated thresholds in two replicate landscapes. See Table S4 for species codes

Species	Fragmentation		Low			High						
	Forest cover		Low	Intermediate	High	Low	Intermediate	High				
BAWW				80	95	53						
BCCH	31											
BHVI			34	65	66			38				
BLBW				82	61	56		44				
BRCR	15					48	27					
BTBW					86	46	69	78				
BTNW	24	21			88							
CAWA		71										
CORA												
DEJU						63						
GCKI			89		97			93				
HETH				65	65			72				
LEFL		75	69	89	68			40				
MAWA					78	84		96				
NAWA							45	74				
OVEN					56	16		43				
PIWO				66								
RBNU				28								
REVI					89							
SCTA		17	65		47							
VEER							50	54				
WIWR	71		86	68			53	28				
WTSP					58	53		54				
YBSA												
YRWA							53	81				
Number of thresholds	4	4	4	8	12	9	3	1	1	4	6	6

2010; Zuckerberg & Porter, 2010; Jones *et al.*, 2011)] and statistical approach used (Ficetola & Denoël, 2009): all factors that require further testing. For example, thresholds might vary because species responses to habitat availability may be either concave or convex, and we are thus actually comparing thresholds in forest cover above which extinction probability drops rapidly with thresholds below which the probability increases steeply (Fig. 5). Or, we might be comparing ‘peaks in extinction probability’ (in unimodal curves) with these thresholds (Fig. 3). We therefore urge researchers to address the nature of the threshold in question explicitly to avoid improper interpretation. Equally important, the data we used for modelling became increasingly left-skewed as forest cover in the landscape increased, a potential cause of a shift of a threshold to ‘the right side of the curve’ (i.e. towards higher amounts of forest cover). Transformations might reduce skewness (Fletcher *et al.*, 2005), and would consequently lead to better fitting logistic models (likely resulting in higher model AUCs). This might be useful if our main interest was to fit a logistic model, but we would consequently lose information on the focal interest of this study: at what amount of habitat is the threshold in this particular landscape? The influence of the skewness of data on the estimation of habitat thresholds seems largely overlooked in

previous studies [e.g. when segmented regression is used as in Betts *et al.* (2010) and Zuckerberg & Porter (2010)]; future studies should consider this potential cause of variability in estimated thresholds.

Second, thresholds might actually increase for some species, as some of our focal species could be considered habitat generalists, for which extinction probability is not necessarily negatively correlated with the amount of forest cover available (Table S2). In addition, such species may experience positive edge effects resulting from fragmentation (Parker *et al.*, 2005) For these species, thresholds may be lower in landscapes with less forest or in more fragmented landscapes (see Fahrig, 2003). Third, related to the aforementioned differences between generalist and specialist species, we could expect some species to do better simply because others do worse. For example, Schmiegelow *et al.* (1997) showed that the extent to which habitat specialist and habitat generalist bird species were differently affected by forest fragmentation could lead to changes in community composition. We could thus test how aspects of community turnover affect threshold estimates, especially as local extinction and turnover occur at different rates in landscapes with different degrees of fragmentation (Boulinier *et al.*, 2001). For example, our approach can be extended to a study of regional variability

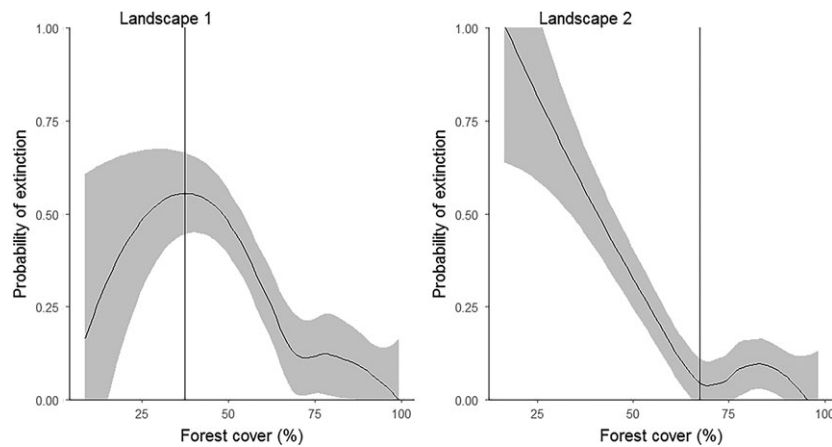


Figure 5 Estimates of extinction thresholds for veery (*Catharus fuscescens*) in two different landscapes. Thresholds were very different [37.4% (SE = 6.8) and 67.5% (SE = 7.8)] even though mean forest cover and level of fragmentation were similar in both landscapes (forest cover 68.5% and 70.4%; aggregation indices 88.3 and 88.4).

and generalities in community-level thresholds as found by Threshold Indicator Taxa Analysis (TITAN) (Baker & King, 2010).

Fourth, extinction thresholds could be affected by population-scale processes, such as higher rates of extinction at range edges in comparison with the range core (Doherty *et al.*, 2003; Holt & Keitt, 2005). This could be especially important in the region of our study, which encompasses the southern range edge of many species. For example, the white-throated sparrow showed a high threshold in Pennsylvania, where this species is at the southern edge of its range and is scarce [found in 2.9% of blocks (Bolginao, 2012)]; whereas no threshold was detected for New York state, where this species is much more widespread [37% of blocks (Peterson, 2008)].

Finally, we have addressed the separate effects of habitat configuration and availability on habitat thresholds, but have not included other important aspects of landscape structure. Regional variation in the quality of the habitat and that of the matrix (Fahrig, 2001; Betts *et al.*, 2010; Boyle & Smith, 2010) might especially drive the variability we found in habitat thresholds. Testing the effects of varying matrix quality might be difficult (Villard & Metzger, 2014), but follow-up studies in which matrix quality varies across landscapes [but habitat cover and configuration are similar across landscapes, much like the theoretical models of Fahrig (2001)] will be highly informative and might account for the differences we found between thresholds estimated for landscapes that were otherwise similar in forest cover and fragmentation (Table 1).

In order for us to be able to make predictions about real species thresholds, we might need to make models species specific. For instance, we could (1) select more specific predictor variables [such as specific types of forest (Betts *et al.*, 2010; van der Hoek *et al.*, 2013)] that better predict species extinction probability than a generic 'forest cover', (2) use a species-centred approach to define habitat (Betts

et al., 2014) or (3) include additional predictor variables that relate to other important aspects of landscape structure (e.g. matrix quality) or community composition (e.g. incorporating effects of predators/competitors).

There is not one generic threshold that can be found across species or landscapes (e.g. Rhodes *et al.*, 2008; Betts *et al.*, 2010), and we should thus be wary of oversimplification of thresholds (e.g. considering them as 'minimum habitat requirements' that can be extrapolated across regions) in conservation and management documentation (see also Lindenmayer & Luck, 2005; Wilhere, 2008; Johnson, 2013). We did not find two distinct habitat thresholds: a fragmentation threshold at high amounts of habitat and an extinction threshold at low amounts of forest cover (each of which is found in landscapes with different landscape structures). Nor were we able to test whether the range between these two thresholds differed among species according to their sensitivity to habitat configuration and habitat amount (see fig. 6 in Villard & Metzger, 2014). This does not imply that this concept is invalid, but merely that real-world situations are confounded by numerous factors. Habitat thresholds are really highly variable, difficult to generalize and more difficult to interpret in real landscapes than from theoretical concepts (Villard & Metzger, 2014).

ACKNOWLEDGEMENTS

We thank the Vermont Center for Ecostudies, the Natural Heritage Information Program, Vermont Fish and Wildlife Department, the Kalamazoo Nature Center, the New York State Department of Environmental Conservation (John Ozard), The Nature Conservancy, Massachusetts Audubon, the School of Environment and Natural Resources at Ohio State University (Matthew B. Shumar) and the Carnegie Museum of Natural History for supplying and preparing bird atlas data. Finally, this project would not have been possible

without the dedication from tens of thousands of volunteers who gathered data for each atlas.

REFERENCES

- Andrle, R.F. & Carroll, J.R. (1988) *The atlas of breeding birds in New York State*. Cornell University Press, Ithaca, NY.
- Baker, M.E. & King, R.S. (2010) A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution*, **1**, 25–37.
- Bellingeri, M. & Bodini, A. (2013) Threshold extinction in food webs. *Theoretical Ecology*, **6**, 143–152.
- Betts, M.G., Diamond, A.W., Forbes, G.J., Villard, M.-A. & Gunn, J.S. (2006) The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling*, **191**, 197–224.
- Betts, M.G., Hagar, J.C., Rivers, J.W., Alexander, J.D., McGarrigal, K. & McComb, B.C. (2010) Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications*, **20**, 2116–2130.
- Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A. & Lindenmayer, D.B. (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, **37**, 517–527.
- Bolginio, N.C. (2012) White-throated sparrow. *Second atlas of breeding birds in Pennsylvania* (ed. by A.M. Wilson, D.W. Brauning and R.S. Mulvihill), pp. 424–425. Penn State University Press, University Park, PA.
- Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H. & Pollock, K.H. (2001) Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology*, **82**, 1159–1169.
- Boyle, S.A. & Smith, A.T. (2010) Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? *Biological Conservation*, **143**, 1134–1143.
- Brauning, D.W. (1992) *Atlas of breeding birds in Pennsylvania*. University of Pittsburgh Press, Pittsburgh, PA.
- Brewer, R., McPeck, G.A. & Adams, R.J. Jr (1991) *The atlas of breeding birds of Michigan*. Michigan State University Press, East Lansing, MI.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, NY.
- Chartier, A.T., Baldy, J.J. & Brenneman, J.M. (2011) *The second Michigan breeding bird atlas, 2002–2008*. Kalamazoo Nature Center, Kalamazoo, MI.
- Didham, R.K., Kapos, V. & Ewers, R.M. (2012) Rethinking the conceptual foundations of habitat fragmentation research. *Oikos*, **121**, 161–170.
- Doherty, P.F. Jr, Boulinier, T. & Nichols, J.D. (2003) Local extinction and turnover rates at the edge and interior of species' ranges. *Annales Zoologici Fennici*, **40**, 145–153.
- Environment Canada (2013) *How much habitat is enough?* 3rd edn. Environment Canada, Toronto, ON.
- Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.
- Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65–74.
- Fahrig, L. (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications*, **12**, 346–353.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.
- Ficetola, G.F. & Denoël, M. (2009) Ecological thresholds: an assessment of methods to identify abrupt changes in species-habitat relationships. *Ecography*, **32**, 1075–1084.
- Fletcher, D., MacKenzie, D. & Villouta, E. (2005) Modelling skewed data with many zeros: a simple approach combining ordinary and logistic regression. *Environmental and Ecological Statistics*, **12**, 45–54.
- Frohn, R.C. & Hao, Y.P. (2006) Landscape metric performance in analyzing two decades of deforestation in the Amazon Basin of Rondonia, Brazil. *Remote Sensing of Environment*, **100**, 237–251.
- Gates, S. & Donald, P.F. (2000) Local extinction of British farmland birds and the prediction of further loss. *Journal of Applied Ecology*, **37**, 806–820.
- Groffman, P., Baron, J., Blett, T., Gold, A., Goodman, I., Gunderson, L., Levinson, B., Palmer, M., Paerl, H., Peterson, G., Poff, N., Rejeski, D., Reynolds, J., Turner, M., Weathers, K. & Wiens, J. (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*, **9**, 1–13.
- Gu, W. & Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, **116**, 195–203.
- Hargis, C.D., Bissonette, J.A. & David, J.L. (1998) The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology*, **13**, 167–186.
- van der Hoek, Y., Renfrew, R. & Manne, L.L. (2013) Assessing regional and interspecific variation in threshold responses of forest breeding birds through broad scale analyses. *PLoS ONE*, **8**, e55996.
- Holland, J.D., Bert, D.G. & Fahrig, L. (2004) Determining the spatial scale of species' response to habitat. *BioScience*, **54**, 227–233.
- Holt, R.D. & Keitt, T.H. (2005) Species' borders: a unifying theme in ecology. *Oikos*, **108**, 3–6.
- Jones, J.E., Kroll, A.J., Giovanni, J., Duke, S.D. & Betts, M.G. (2011) Estimating thresholds in occupancy when species detection is imperfect. *Ecology*, **92**, 2299–2309.
- Johnson, C.J. (2013) Identifying ecological thresholds for regulating human activity: Effective conservation or wishful thinking? *Biological Conservation*, **168**, 57–65.

- Kamm, M., Walsh, J., Galluzzo, J. & Petersen, W. (2013) *The Massachusetts breeding bird atlas 2*. Scott & Nix, Inc., New York, NY.
- Kato, S. & Ahern, J. (2011) The concept of threshold and its potential application to landscape planning. *Landscape and Ecological Engineering*, **7**, 275–282.
- Kéry, M. & Schmid, H. (2004) Monitoring programs need to take into account imperfect species detectability. *Basic and Applied Ecology*, **5**, 65–73.
- Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, **7**, 69–80.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000) Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, **90**, 119–126.
- Laughlin, S.B. & Kibbe, D.P. (1985) *The atlas of breeding birds of Vermont*. University of New England, Hanover and London.
- Lichstein, J.W., Simons, T.R., Shiner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, **72**, 445–463.
- Lindenmayer, D.B. & Luck, G. (2005) Synthesis: thresholds in conservation and management. *Biological Conservation*, **124**, 351–354.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) *FRAGSTATS: spatial pattern analysis program for categorical maps*. University of Massachusetts, Amherst, MA.
- McGowan, K. & Corwin, K. (2008) *The second atlas of breeding birds in New York State*. Cornell University Press, Ithaca, NY.
- Muggeo, V.M.R. (2003) Estimating regression models with unknown break-points. *Statistics in Medicine*, **22**, 3055–3071.
- Muggeo, V.M.R. (2008) *The segmented package for R version 0.2-4*. Available at: <http://cran.r-project.org> (accessed 25 April 2011).
- Omernik, J.M. (1987) Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Annals of the Association of American Geographers*, **77**, 118–125.
- Pardini, R., Bueno, A.A., Gardner, T.A., Prado, P.I. & Metzger, J.P. (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*, **5**, e13666.
- Parker, T.H., Stansberry, B.M., Becker, C.D. & Gipson, P.S. (2005) Edge and area effects on the occurrence of migrant forest songbirds. *Conservation Biology*, **19**, 1157–1167.
- Peterjohn, B.G. & Rice, D.L. (1991) *The Ohio breeding bird atlas*. The Ohio Department of Natural Resources, Columbus, OH.
- Petersen, W.R. & Meserve, W.R. (2003) *Massachusetts breeding bird atlas*. Massachusetts Audubon Society, Amherst, MA.
- Peterson, J.M.C. (2008) White-throated sparrow. *The second atlas of breeding birds in New York State* (ed. by K. McGowan and K. Corwin), pp. 570–571. Cornell University Press, Ithaca, NY.
- R Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Renfrew, R.B. (2013) *The second atlas of breeding birds of Vermont*. University Press of New England, Hanover.
- Rhodes, J.R., Callaghan, J.G., McAlpine, C.A., De Jong, C., Bowen, M.E., Mitchell, D.L., Lunney, D. & Possingham, H.P. (2008) Regional variation in habitat-occupancy thresholds: a warning for conservation planning. *Journal of Applied Ecology*, **45**, 549–557.
- Rodewald, P.G., Shumar, M.B., Boone, A.T., Slager, D.L. & McCormac, J.S. (In press) *The Second Atlas of Breeding Birds in Ohio*, The Pennsylvania State University Press, University Park, PA.
- Rompré, G., Boucher, Y., Belanger, L., Cote, S. & Robinson, W.D. (2010) Conservation of biodiversity in forest areas management: use of critical thresholds of habitats. *Forestry Chronicle*, **86**, 572–579.
- Royle, J.A., Nichols, J.D. & Kéry, M. (2005) Modelling occurrence and abundance of species when detection is imperfect. *Oikos*, **110**, 353–359.
- Schmiegelow, F.K., Machtans, C.S. & Hannon, S.J. (1997) Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology*, **78**, 1914–1932.
- Smith, A.C., Koper, N., Francis, C.M. & Fahrig, L. (2009) Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecology*, **24**, 1271–1285.
- Swift, T.L. & Hannon, S.J. (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews*, **85**, 35–53.
- Vanderwal, J., Falconi, L., Januchowski, S., Shoo, L.P. & Storlie, C. (2012) *SDMTools: species distribution modelling tools: tools for processing data associated with species distribution modelling exercises*. Available at: <http://cran.r-project.org> (accessed 20 September 2012).
- Villard, M.-A. & Metzger, J.P. (2014) Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, **51**, 309–318.
- Vogelmann, J.E., Howard, S.M., Yang, L., Larson, C.R., Wylie, B.K. & Van Driel, J.N. (2001) Completion of the 1990's National Land Cover Data Set for the conterminous United States. *Photogrammetric Engineering and Remote Sensing*, **67**, 650–662.
- Wilhere, G.F. (2008) The How-Much-Is-Enough Myth. *Conservation Biology*, **22**, 514–517.
- Wilson, A.M., Brauning, D.W. & Mulvihill, R.S. (2012) *Second atlas of breeding birds in Pennsylvania*. Penn State University Press, University Park, PA.

With, K.A. & King, A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology*, **13**, 314–326.

Zuckerberg, B. & Porter, W.F. (2010) Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. *Biological Conservation*, **143**, 952–962.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Sample size of breeding bird records used for threshold analyses.

Table S2 Overview of all threshold estimates (in % forest cover) for supported threshold models.

Table S3 Overview of all threshold estimates (in % forest cover) for supported threshold models for nine landscapes (L1–9).

Table S4 Species codes for focal species.

BIOSKETCH

Yntze van der Hoek is the primary author of this article, which is the result of his PhD research on thresholds, tipping points and habitat requirements. He previously worked in various African and South American countries, on topics ranging from community-based conservation to resource ecology. He obtained his PhD in Biology from the CUNY Graduate Center and his MSc and BSc in Forest and Nature Conservation from Wageningen University in the Netherlands. He resides in the Dominican Republic where he works on various projects.

Editor: Lluís Brotons