Variation In Habitat Thresholds: An Analysis Of Minimum Habitat Requirements Of North American Breeding Birds

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VARIATION IN HABITAT THRESHOLDS: AN ANALYSIS OF MINIMUM HABITAT REQUIREMENTS OF NORTH AMERICAN BREEDING BIRDS.

By

YNTZE VAN DER HOEK

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy,

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Abstract

VARIATION IN HABITAT THRESHOLDS: AN ANALYSIS OF MINIMUM HABITAT REQUIREMENTS OF NORTH AMERICAN BREEDING BIRDS.

By: Yntze van der Hoek

Advisor: Dr. Lisa L. Manne

Many species show dramatic changes in population extinction or persistence probability at particular habitat amounts. These ‘extinction thresholds’ could be translated to conservation targets, under the condition that we can derive generalities. I investigated the level of variation in landscape-level habitat thresholds for a suite of North American, forest-associated, breeding birds. Records from Breeding Bird Atlases and the availability of remotely-sensed land cover data allowed me to compare habitat thresholds for 25 species across the states of Massachusetts, Michigan, New York, Ohio, Pennsylvania, and Vermont. I show that variation in thresholds is considerable (Chapter II, III), as thresholds range from 7 to 90% forest cover between species, within regions, and even from 12 and 90% forest cover within species across regions (results for White-throated Sparrow (Zonotrichia albicollis)). I found no universal trend in this variation, although a few species showed a significant increase in threshold amounts with increasing forest cover in the landscape. In Chapter IV, I show that it is possible to assess vertical habitat structure with light detection and ranging (lidar) data. The availability of detailed habitat metrics, such as maximum canopy height and canopy heterogeneity, allowed me to detect detailed extinction thresholds for five species of cavity breeding birds and the Cerulean Warbler (Setophaga cerulea), a species of great conservation concern. Models also showed that some species persist at low forest cover, even though they demonstrate a peak in extinction probability at intermediate
levels of forest cover (Chapter V). These peaks in extinction probability correspond with a peak in change in amount of forest cover over time, indicating that change in habitat might be predictive of extinction probability. Estimation of species-specific thresholds, I propose, provides information that can potentially be used to set management targets (Chapter VI). I conclude that we should be wary of extrapolation of thresholds and emphasize that estimation of thresholds should be considered a tool for understanding the process of habitat loss, not a goal in itself.
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Chapter I: Introduction

By: Yntze van der Hoek

Habitat loss has likely been the largest threat to biodiversity of the 20th century (Wilson 1985, Wilcove et al. 1998, Sax and Gaines 2003) and continues to increase in magnitude during the first decades of this century (Butchart et al. 2010, Rands et al. 2010). Increasing expansion of the human population has already led to the complete alteration of well over a third of the land surface, and introduced modifications to most of the remainder (Vitousek et al. 1997). Loss of habitat can induce species extinction by destruction of all potentially suitable habitat for locally endemic species (Sax and Gaines 2003). Moreover, habitat loss can lead to declines in population sizes, either through reduction of actual habitat size or as a result of associated factors such as the fragmentation of habitat and populations (Fahrig 2003). Such declines in populations can eventually culminate in species extinction, and as such habitat loss is currently one of the most important topics of concern for conservationists.

The effects of habitat loss on species and population can be found on different levels, but are most commonly measured in terms of survival (Zitske et al. 2011) or reproductive output of species (Cardozo and Chiaraviglio 2008). For example, inbreeding might be an issue of concern under increased habitat loss, as local populations get smaller and are increasingly more isolated from other populations (Saccheri et al. 1998). In order to investigate how much habitat loss systems or species can endure without experiencing increased detrimental effects from such processes as inbreeding, researchers have for decades been trying to answer ‘how much habitat is enough for species persistence?’ (Fahrig 2001).
Metapopulation theory proved to be a useful framework in search of minimum habitat requirements, and most early studies on the relationship between species and habitat availability were based on this concept of ‘populations of populations’ (Hanski 1998). Within a metapopulation, population size is the result of local extinction and recolonization events. Loss of habitat influences such events, as it leads to a decrease in the size of those habitat patches that support local breeding populations. It also leads to increased isolation between patches, thus effectively decreasing migration between patches. The emergence of metapopulation theory, and simultaneous developments regarding population viability analysis (PVA) (Shaffer 1981), contributed to a vast body of work on patch-scale requirements for population persistence (Fahrig 2001). The critical patch size, the minimum size of a habitat patch that could ensure long-term persistence for a population, soon became the Holy Grail for ecologists.

Studies on the concept of critical patch sizes led to the discovery that minimum patch size was highly variable and dependent on species-specific life history traits, such as the reproductive rate of the organism, as well as stochastic factors such as natural disturbances (Fahrig 2001, Ockinger et al. 2010). Moreover, it became apparent that patch size alone cannot predict population persistence or extinction adequately and that the landscape surrounding patches is important as well (Desrochers et al. 2010). The amount of occupied habitat in the landscape and the quality of the non-habitat part of the landscape (the ‘matrix’) were found to be important determinants of migration rates and the survival of dispersing individuals (Fahrig 2001). As a result, researchers started to focus on landscape-level area-sensitivity and habitat requirements, leading to the discovery that many species experience non-linear responses to habitat loss and fragmentation (Radford and Bennet 2004, Betts et al. 2010, Swift and Hannon 2010, Zuckerberg and Porter 2010).
Instead of linear responses to habitat loss, many species show thresholds at particular habitat amounts. A dramatic change in population extinction or persistence probability occurs, when habitat amounts reach these thresholds. Previously, the existence of these thresholds had been proposed as a result of theoretic model studies under the concept of the extinction threshold hypothesis (Lande 1987, Andrén 1994, Fahrig 2001). Interestingly, the discovery of extinction thresholds coincided with the increasing awareness that many other phenomena in nature were non-linear as well, and the concept of thresholds and regime-shifts is now well established in ecology (Scheffer et al. 2001).

Which explanations account for the existence of habitat thresholds? There are many proposed mechanisms (Swift and Hannon 2010), but most involve the concept that populations are unlikely to persist if mortality rates surpass reproduction rates. Habitat loss can lead to overall increases in mortality rates and decrease reproductive output (Fahrig 2002), resulting in mortality rates outweighing reproductive rates (Swift and Hannon 2010). This can occur for a number of reasons. First, population sizes decline when decreasing amounts of habitat are available, leading to so-called negative ‘Allee-effects’. These Allee effects arise when the fitness of individuals is positively related to the size or density of populations. When population size gets smaller we see increased inbreeding depression (as in Saccheri et al. 1998), increased effects of demographic stochasticity on populations when populations are small, and disrupted social dynamics such as a decreased likelihood to encounter potential mates (Courchamp et al. 1999). A second cause of thresholds is that, as habitat is lost, local populations decrease in size and become less abundant, leading to decreased colonization rates. As such, local populations are less likely to be ‘rescued’ by accepting immigrating individuals from nearby source patches. In other words, the rescue effect is reduced and populations might experience increased risk of
extinction (Fahrig 2002). A third explanation—not completely separate from the aforementioned
causes—predicts that loss of habitat leads to increased probability that individuals, when
migrating between suitable habitat patches, encounter an inhospitable matrix. Reproductive rates
are low in this matrix and mortality rates are relatively high. This could lead to reduced
population sizes, which would cause a decrease in immigration rates, and thus subsequently
induce a decreased rescue effect. Finally, a fourth effect of habitat loss stems from the change of
habitat configuration that follows habitat fragmentation. This potential cause of threshold
responses, often referred to as the fragmentation threshold (Andrén 1999), concerns the
phenomenon of habitat fragmentation as a separate, but often associated, factor in the persistence
of populations. When habitat availability decreases, the spatial configuration of the [remaining]
habitat patches becomes more and more important, with fragmentation eventually exacerbating
the effects of habitat loss per se. Effects of fragmentation generally pertain to the reduction in
connectivity between patches, which effectively splits up formerly large populations into various
smaller populations that are more prone to all of the aforementioned extinction risks (With and
King 1999, Swift and Hannon 2010). In addition, populations might experience various other
negative impacts of fragmentation, such as gaps between patches becoming too substantial for
individuals to cross (other effects are reviewed in Swift and Hannon, 2010).

Although more and more studies provide evidence for the existence of extinction
thresholds in habitat amount, they are not found for every species or in every region
(Lindenmayer and Luck 2005). In addition, there are many confounding factors and sensitivities
associated with the identification and estimation of threshold (Ewers and Didham 2006, Swift
and Hannon 2010). For example, I made use of segmented regression (Muggeo 2003) throughout
this dissertation as the method to identify and estimate thresholds. Although segmented
regression is commonly used in threshold studies, it is not the only method available for identification of abrupt changes (Ficetola and Denoel 2009). A full review of the different approaches lies outside the scope of this dissertation, but it is worth mentioning that segmented regression also has its limitations in the detection of thresholds. For example, segmented regression might estimate a breakpoint at 40% forest cover for two species (A and B). Yet, for species A this breakpoint signifies the ‘threshold below which persistence probability declines rapidly’, and the threshold for species B signifies the threshold ‘above which persistence probability increases rapidly’ (Figure 1.1). The threshold, in other words, although found at the same amount or percentage of habitat cover, can pertain to two different ‘locations’. This does not have to be problematic, as long as we visualize the relationship, or look at [and report] the difference-in-slope parameter (more in Zuckerberg and Porter 2010).

There are also factors such as time lags and extinction debts (Tilman et al. 1994, Hylander and Ehrlen 2013), and negative (Zitske et al. 2011) or positive (Suarez-Rubio et al. 2013) edge effects that can influence the threshold estimates—the amount of habitat at which they are found. The most important influencing factors however, are those that are directly related to landscape-specific (e.g. matrix quality, fragmentation level) or species-specific (e.g. reproductive rate, dispersal ability) characteristics (Fahrig 2001, Rhodes et al. 2008, Blanchet et al. 2010, Ockinger et al. 2010).

Studies of habitat thresholds have developed from patch-based theoretic modeling to empirical landscape-level studies. However, despite our ability to utilize new sources of data (e.g. remote sensing), and conduct studies on multiple scales, in multiple landscapes, or for a large number of species at the same time (Betts et al. 2010, Pardini et al. 2010, Zuckerberg and Porter 2010), we have still been unable to derive generalities on the amount of habitat at which
thresholds are found. These spatial and interspecific variations in thresholds are still largely
unaddressed (but see Rhodes et al. 2008) and therefore remain important study topics, as
variation in thresholds may affect our potential to derive management policies.

I investigated the level of spatial and interspecific variation in landscape-level habitat
thresholds for a selection of North American, forest-associated, breeding birds. The increasing
availability of broad-scale citizen science (Bonney et al. 2009, Silvertown 2009) and remote
sensing data (Kerr and Ostrovsky 2003) allowed me to determine i) how common landscape-
level thresholds were, ii) at which percentage of forest cover they were most commonly found,
iii) and how they varied among species and landscapes.

Ecologists are increasingly interested in large scale, broad extent studies (Holland et al.
unprecedented broad-scale threshold analyses are now feasible by use of data from breeding bird
atlases, which are basically repeated volunteer-based bird count surveys (Dunn and Weston
2008). However, from their study, set in one particular region (the state of New York), one
would not be able to derive generalities that might lead to regionally applicable conservation
targets. Therefore, I conducted a threshold study for the state of Vermont, using identical study
species and methodologies as Zuckerberg and Porter (2010), and compared the threshold
estimates derived for New York with those for Vermont (Chapter II). Following this initial
comparison of threshold values, it quickly became apparent that both regional and interspecific
variation was large, and needed further investigation.

As a result of my initial comparisons, I explored the mechanisms underlying regional
variation (Chapter III). I was especially interested in the relationship of threshold values with
landscape-level forest cover and fragmentation. After all, if there was a clear-cut relationship between the estimated thresholds and the characteristics of the landscape, one could extrapolate results from studies set in one region to other regions. The effects of forest cover and fragmentation on the thresholds, as tested in Chapter II, seemed ambiguous, and as a result generalities were difficult to derive. A major conclusion was that thresholds should be assessed on a species-by-species basis, using more relevant models that incorporate more ecologically relevant predictor variables than ‘forest cover’, in order to properly lead to conservation targets.

Fortunately, a recent development in the field of remote sensing, the increasing availability of laser-derived light detection and ranging (lidar) data (Bradbury et al. 2005, Vierling et al. 2008), allowed me to derive aforementioned species-specific thresholds on broad scales (Chapter IV). The combination of lidar and breeding bird atlas data allowed for circumvention of the perennial trade-off between scale and detail of study. With canopy height metrics, derived from lidar analyses as predictor variables, I was able to model and estimate thresholds for bird species that are known to require specific vertical vegetation elements (e.g. snags) for breeding or foraging.

The outcome of the broad-scale comparison studies (Chapters II and III) did not deliver clear-cut rules-of-thumb for generalization of thresholds, but the lidar analysis (Chapter IV) did show the potential threshold studies can have for conservation and management purposes. However, one important issue had been overlooked in these, and most other published, studies. Although habitat loss is the main process of interest for researchers conducting threshold studies (Lindenmayer and Luck 2005), the actual predictor variable used in the majority of threshold model studies is habitat variation across a spatial gradient. In Chapter V, I point out that the relationship between species and ‘habitat change over time’ does not have to equal the
relationship between species and ‘habitat variation across space’, and emphasize that this space-
for-time substitute has peculiarities that need to be addressed in threshold studies. Moreover, I
show that extinction events might be most probable in landscapes with intermediate levels of
habitat cover and that neither forest cover nor forest cover change are adequate proxies for
habitat for all species. In addition, I make the point that extinction does not have to stem merely
from a reduction in resource or habitat availability, but that peaks in extinction probabilities at
intermediate levels of habitat cover might be the result of increased secondary extinctions as the
result of species interactions (Dunne and Williams 2009, Ferguson and Ponciano 2014). Again, it
is worth remembering that we are creating models of reality in threshold studies, but that reality
is infinitely more complex.

The difference between change over time and habitat variation across space, the potential
of lidar-based studies, and the apparent lack of generalities in threshold estimates. These are all
factors returning in Chapter VI, where I synthesize sensitivities and potential dangers of using
threshold values to set conservation targets. The idea that we have to be wary of thinking of
thresholds as ‘magic numbers’ for conservation, amounts of habitat above which there are no
effects of habitat degradation, has previously been emphasized by other authors (Lindenmayer
and Luck 2005, Tear et al. 2005, Wilhere 2008). Nevertheless, this message of caution has
largely been ignored by the policy or management oriented audience that sets actual conservation
targets (Rompre et al. 2010). As such, threshold studies could harm the very cause that started
the search for minimum habitat requirements: to counteract biodiversity loss as a result of habitat
loss. I therefore conclude Chapter VI by emphasizing the ways we should go forward in
threshold research, and indicate various ways habitat threshold studies could inform conservation
and management; this also leads to the final Chapter (VII), where I conclude this dissertation by summarizing my findings and by exploring both the potential and pitfalls of my work.
Figure 1.1. Thresholds in species persistence (adapted from Zuckerberg and Porter 2010).

Species responses to changes in habitat (forest) cover can theoretically follow different curves yet yield the same estimated threshold in forest cover (circles). For species A we might estimate a threshold in forest cover below which the probability declines steeply while for species B we have a threshold above which the probability of persistence increases rapidly.
Chapter II: Assessing regional and interspecific variation in threshold responses of forest breeding birds through broad scale analyses

By: Yntze van der Hoek, Rosalind Renfrew, Lisa L. Manne


Abstract

Identifying persistence and extinction thresholds in species-habitat relationships is a major focal point of ecological research and conservation. However, one major concern regarding the incorporation of threshold analyses in conservation is the lack of knowledge on the generality and transferability of results across species and regions. We present a multi-region, multi-species approach of modeling threshold responses, which we use to investigate whether threshold effects are similar across species and regions. We modeled local persistence and extinction dynamics of 25 forest-associated breeding birds based on detection/non-detection data, which were derived from repeated breeding bird atlases for the state of Vermont. We did not find threshold responses to be particularly well-supported, with nine species supporting extinction thresholds and five supporting persistence thresholds. This contrasts with a previous study based on breeding bird atlas data from adjacent New York State, which showed that most species support persistence and extinction threshold models (15 and 22 of 25 study species respectively). In addition, species that supported a threshold model in both states had associated average threshold estimates of 61.41% (SE=6.11, persistence) and 66.45% (SE=9.15, extinction) in New York, compared to 51.08% (SE=10.60, persistence) and 73.67% (SE=5.70, extinction) in Vermont. Across species, thresholds were found at 19.45-87.96% forest cover for persistence and 50.82-91.02% for extinction dynamics. Through an approach that allows for broad-scale comparisons of threshold responses, we show that species vary in their threshold responses with regard to habitat amount,
and that differences between even nearby regions can be pronounced. We present both ecological and methodological factors that may contribute to the different model results, but propose that regardless of the reasons behind these differences, our results merit a warning that threshold values cannot simply be transferred across regions or interpreted as clear-cut targets for ecosystem management and conservation.

**Introduction**

Motivated largely by indications of declining wildlife populations due to habitat loss and fragmentation (Andrén 1994, Simberloff 1995, Bender et al. 1998) ecologists established a vast body of work on species-habitat relationships over the last decades. From these studies, it became apparent that wildlife responses to habitat loss and fragmentation are often non-linear (Bascompte and Sole 1996, Villard et al. 1999, With and King 1999, Fahrig 2001, Flather and Bevers 2002). An increasing number of studies support the main prediction of the extinction threshold hypothesis that there are certain critical amounts of habitat required for population persistence (Lande 1987). These thresholds are often defined as a ‘range of habitat cover below which the probability of population persistence decreases dramatically’ (Hill and Caswell 1999, Fahrig 2002). Documentation of thresholds’ existence led to a rise of interest in determining critical habitat amount or minimum patch size for species or population persistence (Lande 1987, Wenny et al. 1993, Andrén 1994, McGarigal and McComb 1995, Fahrig 1997, 1998). More recently, threshold modeling extended to incorporate landscape-scale thresholds, leading to reasonable evidence for thresholds in relationships between species occurrence and habitat cover at landscape extents (Radford and Bennett 2004, Radford et al. 2005, Betts et al. 2007). In addition, first attempts in determining habitat thresholds in persistence dynamics over time,
rather than mere occurrence at a single point in time, have been fruitful and comprise a useful contribution to landscape ecology and conservation alike (Zuckerberg and Porter 2010).

Although determination of persistence and extinction thresholds are now considered major focal points of research (Lindenmayer et al. 2008, Digiovinazzo et al. 2010, Rompre et al. 2010, Kato and Ahern 2011) uncertainty and debate on numerous issues continue to persist. These issues include the mechanisms that are driving threshold responses, confounding factors (Shanahan and Possingham 2009, Swift and Hannon 2010) and the value of applying threshold modeling approaches in conservation planning and management (Mönkkönen and Reunanen 1999, Groffman et al. 2006, Juutinen et al. 2008, Muller and Butler 2010). One of the main concerns regarding the incorporation of threshold analyses in conservation is the lack of generality and transferability of results across species (Betts et al. 2006b, Blanchet et al. 2010, dos Anjos et al. 2011) and regions (Betts et al. 2007, Rhodes et al. 2008).

Spatial and interspecific variation in critical thresholds has been widely recognized (Donovan et al. 1997, Betts et al. 2006b, Betts et al. 2007, Zuckerberg and Porter 2010), but few studies have directly aimed at quantifying the mechanisms driving variation (but see Tischendorf et al. 2005, Betts et al. 2007, Schooley and Branch 2011). In order to derive conservation targets and generalizations regarding species-habitat relationships, we will need to study spatial and interspecific variation more intensely (Davies et al. 2000, Rhodes et al. 2008, Ockinger et al. 2010) and conduct studies across more species and larger geographic areas than previously pursued. In order to do so, we might be required to step away from time and budget-limited smaller scale field studies (Betts et al. 2007, Zitske et al. 2011) and instead focus on existing data sources for broad-scale analyses. Zuckerberg and Porter (2010) provide an example of a methodology through which we can assess threshold responses of breeding birds on a broad
(state-wide) scale. For their study they make use of breeding bird atlas data. These data provide a unique opportunity to model species distributions and species-habitat relationships, because of the broad scale and number of species for which analyses can be made (Trzcinski et al. 1999, Venier et al. 1999, Brotons et al. 2004, Zuckerberg and Porter 2010, Smith et al. 2011). In addition, many regions (states, countries) have repeated breeding bird atlas projects, usually spaced 20-25 years apart, thus allowing us to compare between regions and to address spatial variation in long-term persistence rather than occurrence at a single point in time (Zuckerberg and Porter 2010).

Here, we present a first multi-region comparison in a larger study that quantifies variation in thresholds found in long-term species-habitat relationships at a landscape scale. We conducted an analysis of threshold responses across a large set of breeding forest birds at the scale of an entire state (Vermont) in a similar fashion to the aforementioned study by Zuckerberg and Porter (2010). Subsequently, we compared their results to ours in what is to our knowledge the first attempt of a regional comparison of threshold responses. Here, we highlight the potential that the use of state-wide breeding bird atlases has for threshold analyses and how our approach may answer existing questions regarding the generality and transferability of models and results (Betts et al. 2007, Rhodes et al. 2008, Ficetola and Denoel 2009, Boyle and Smith 2010). In addition, we propose that our approach holds potential for further investigation of traits that may be correlated with species-specific area-sensitivity (Davies et al. 2000, Blanchet et al. 2010, Ockinger et al. 2010) and mechanisms that drive geographic variation in threshold responses (Betts et al. 2007). In this paper, we do not go into depth on the reasons behind regional variation in threshold responses, but do highlight potential ecological explanations as well as methodological biases that may lead to differences in model outcomes. Finally, we investigate
how scale influences threshold responses by comparing models that include habitat cover at
different scales. Due to the grid-based design of our data set (i.e. atlas blocks) these kinds of
comparisons across scales are straightforward, thus affording a unique opportunity to address the
influence of scale on species-habitat relationships (Holland et al. 2004, Betts et al. 2006b, Smith
et al. 2011, Thornton et al. 2011).

Methods

Bird distribution atlases present a unique opportunity to study occurrence dynamics on a broad
scale and over a relatively long term (Zuckerberg and Porter 2010). We based our analyses on a
repeated atlas project, The Atlas of Breeding Birds of Vermont, for which 1976-1981 (Laughlin
and Kibbe 1985) and 2003-2007 (Renfrew 2013) data were available. We thereafter compared
our results with a previous analysis by Zuckerberg and Porter (2010) that is based on data from
the 1980-1985 and the 2000-2005 New York State Breeding Bird Atlases. Surveys for these
atlases were conducted following a largely similar protocol, allowing analyses without large
sampling biases. We will hereby briefly summarize the sampling approach that was used for the
Vermont atlases, as fully described in Renfrew (2013), whereas further details on the New York
State Atlases can be found in McGowan and Corwin (2008) and Zuckerberg and Porter (2010).

Both Vermont Breeding Bird Atlas Projects were based on systematic sampling of
predetermined blocks by both volunteer and expert fieldworkers. These fieldworkers were
expected to determine both species occurrence and breeding bird status in each of the surveyed
blocks. Blocks measured approximately 25 km², and were based on a grid derived from U.S.
Geological Survey maps. Due to limited manpower, 179 randomly selected priority blocks were
assigned for which adequate coverage was to be achieved (Figure 2.1). The overall aim for the
Vermont Breeding Bird Atlas Projects was to determine breeding bird occurrence at three
different levels of confidence (‘possible breeding’, ‘probable breeding’, and ‘confirmed breeding’) (Laughlin and Kibbe 1985).

For our purpose, and to keep consistency with the protocol followed by Zuckerberg and Porter (2010), we considered a bird present when it was listed in an atlas under any of the aforementioned levels of confidence. In order to investigate how this decision with regards to the inclusion of data influences our results we also provide a sensitivity analysis in which we only consider a bird present in the case of ‘confirmed breeding’.

The Vermont Breeding Bird Atlas Project considered blocks to be satisfactorily surveyed when 75 or more species were observed, while at least 35 had to be confirmed as breeders. This corresponded to observations of roughly 75% of the total number of species likely to occur in an average atlas block, and nesting confirmation for half of these species (Laughlin and Kibbe 1985). Each block was surveyed by volunteers during the breeding season until, over the course of a 1-5 year period, the aforementioned predetermined coverage standard was reached (Laughlin and Kibbe 1985).

The second atlas followed a similar approach (Renfrew 2013) to the protocol outlined in the first atlas. In our analyses, we excluded data from four atlas blocks because they were not fully located within Vermont, and thus did not overlap exactly with our Vermont land cover data, or because the majority of the block consisted of water.

We assessed the change in occurrence from the first to the second atlas as persistence or extinction for each focal species. As in Zuckerberg and Porter (2010) we classified birds as persistent in an atlas block when found in both the first and second atlas, and extinct as detected in the first but not the second atlas. Focal species were 25 forest generalists or obligates, and
were the same as those studied by Zuckerberg and Porter (2010). This selection did not include rare species in order to reduce issues of low sample size and detection biases.

We determined the percentage of forest cover in each atlas block using 1992 National Land Cover Data (NLCD) (for an accuracy analysis see Stehman et al. 2003). Zuckerberg and Porter (2010) used this same data set for their analysis in New York. The date of the land cover data is midway between the two atlas projects, and we assumed that loss or gain of forest in Vermont between 1978 (onset, first atlas) and 2007 (last sampling year, second atlas) was small and thus not biasing. We based this assumption on the small change in forest cover in the Northeastern Highlands Ecoregion, which includes Vermont, between 1973 and 2000 (from 85.2% to 81.4% of the total landcover) (Drummond 2010). The HISTO command in the software program IDRISI Taiga (Eastman 2009) provided a numeric frequency histogram from which the percentage of forest cover for each atlas block could be calculated. We combined the percentages of the land cover types “mixed”, “deciduous” and “coniferous” forest to account for the total forest cover in each block.

We built threshold (segmented logistic regression (Muggeo 2003)) and non-threshold (logistic regression) models to describe the relationship between forest cover and occupancy dynamics using standard and ‘segmented’ packages (Muggeo 2008) in R (R Development Core Team 2010). Segmented regression allows one to model the probability of both persistence and extinction as:

\[ p = \frac{\exp[-\beta_0 + \beta_1 x + \beta_2 (x - \psi)_+]}{[1 + \exp[\beta_0 + \beta_1 x + \beta_2 (x - \psi)_+]}} \]

(Zuckerberg and Porter 2010). We calculated the probability \( p \) of either persistence or extinction using \( x \) as the independent variable (e.g. forest cover), \( \psi \) as the break point (threshold), and \((x - \psi)_+ = (x - \psi) \times I(x > \psi)\) being \( I(x > \psi) = 1 \) if \( x > \psi \) is true. The intercept is represented by \( \beta_0 \), the slope of the left line segment by \( \beta_1 \); \( \beta_2 \) is the difference-in-slope.
parameter. We used the fitted values of locally weighted nonparametric models (loess plots) with a smoothing parameter of 0.75 to visualize empirical relationships between forest cover (%) and occurrence and to identify initial values for segmented regression models (Figure 2.2). We explored all possible initial values between 0 and 100% forest cover in 5% steps (e.g. 35%, 40%) when model algorithms failed to converge using our initial starting point (Betts et al. 2007, Zuckerberg and Porter 2010). In total, we fitted 50 logistic models (25 species x 2 dynamics) and 50 segmented logistic regression models in this study (Figure 2.3). We took an information-theoretic approach on selecting the best models describing species-habitat amount relationships using Akaike’s Information Criterion (AIC) and delta AIC ($\Delta_i$). We selected a model as best model if the alternative model had $\Delta_i > 2$ (Burnham and Anderson 2002). Both models could be considered equivalent in their support when $\Delta_i < 2$ between threshold and non-threshold models. In this case, we selected the model with the least parameters: the non-threshold model.

Subsequently, we determined the fit of the best models to the original data by calculating the Area Under the Curve (AUC) (Burnham and Anderson 2002) using the ROCR package (Sing et al. 2005). In general, AUC values vary between 0 and 1, with 1 representing a perfect fit and 0.5 representing that the model fits no better than a random prediction would. Models with AUC values > 0.7 are usually considered acceptable, while values > 0.8 are considered excellent (Hosmer 2000, Betts et al. 2007).

Sample size might have pronounced effects on the power to detect thresholds and the percentage of forest cover at which the thresholds are estimated (Jones et al. 2011) and could thus potentially explain (part of) differences in results from the Vermont (N=175 atlas blocks) and New York (N=5074 atlas blocks) analyses. We investigated the effect of sample size by obtaining 5000 random subsets of 175 blocks from the entire New York data set and fitting a
segmented regression and logistic regression to each of these subsets. We repeated this procedure for all 25 species and both dynamics (persistence and extinction). Based on the aforementioned selection criteria (AIC, delta AIC) we obtained information on the number of times (out of 5000 simulations) threshold models were selected as the better model and the distribution and range of the associated breakpoints (measured in percentage of forest cover).

Although spatial autocorrelation is considered an important aspect of analyses such as ours (Augustin et al. 1996, Lichstein et al. 2002, Betts et al. 2006a), the atlas blocks used in our analysis were sufficiently spaced apart to exclude this as a source of error (Figure 2.1). This sample design allowed us to investigate the relationship between persistence, or extinction, and habitat amount on a larger scale. We repeated earlier outlined models of species responses, using forest cover (%) in an atlas block and all the surrounding eight atlas blocks as an independent variable. We compared AIC scores and threshold estimates of these new models with our original models and determined whether forest cover in the wider landscape or merely forest cover in the atlas block was a better predictor of species persistence or extinction.

Results

Logistic and segmented regression models converged for most species and provided us with a base for model selection (Table 2.1, Table S2.1). However, for Red-eyed Vireo (*Vireo olivaceus*) none of the models converged because it was persistent in all atlas blocks. In addition, no threshold models converged for Black-capped Chickadee (*Poecile atricapilla*) and Hermit Thrush (*Catharus guttatus*) with regards to persistence, which is likely due to this species being persistent in all but a few atlas blocks (Figure S2.1).
For extinction dynamics, we found that 9 out of 25 supported models included a threshold parameter (alternative non-threshold model $\Delta_i > 2$, Table S2.1). Six other species showed support for a threshold model (with regard to both AIC and AUC values), but we deemed the standard errors for the breakpoint estimates too large to consider these valid models to incorporate in further analyses. For persistence dynamics, threshold models were selected to describe the habitat-relationships of five species (Table S2.1). Two more species, Winter Wren (Troglodytes hiemalis) and Blue-headed Vireo (Vireo solitarius), would have supported threshold models based on mere AIC values, but visual interpretation of plotted data (Figure S2.1) did not support the existence of any thresholds and thus we did not include these species in further analyses. We interpret our results as moderate support for threshold response at landscape scale, in contrast to Zuckerberg and Porter (2010) who used a similar approach and the same set of focal species and found overall strong support for threshold models. They concluded that 15 species showed support for the inclusion of a threshold parameter in extinction responses in New York, and no less than 21 of 25 species supported threshold models for persistence.

Estimates of threshold forest amounts in extinction responses varied considerably between species, ranging from 50.82% (SE=5.03) for the Blue-headed Vireo to 91.02% (SE=5.67) for the Black-and-white Warbler (Mniotilta varia) (Table 2.1, Table S2.1). For persistence, threshold estimates varied from 19.45% (SE=3.83) for the Yellow-rumped Warbler (Setophaga coronata) to 87.96% (SE=5.83) for the Black-and-white Warbler. Discriminatory power of all selected models was high, with an average AUC of 0.73 (SE=0.02) for non-threshold models and 0.76 (SE=0.03) for threshold models. Although threshold models were in general less often selected in our analysis than in Zuckerberg and Porter’s (2010), we did find
that the selected models provided a good fit with 11 out of 14 threshold models having an AUC value > 0.7 and 8 out of 14 models having an AUC > 0.75 (Table S2.1).

Not only did the support for threshold responses in Vermont differ from that of New York, but the estimated threshold values for species also differed between the two states (Table 2.2). Four out of five species that showed support for persistence thresholds in both states had lower associated threshold estimates (threshold at lower proportion of forest cover) in Vermont as compared to New York. On average, the 5 species that supported a threshold model for persistence in both states had an associated threshold estimate of 61.41% (SE=6.11) in New York and 51.08% (SE=10.60) in Vermont. Seven species showed threshold responses in extinction in both states, with average threshold values of 66.45% (SE=9.15) in New York and 73.67% (SE=5.70) in Vermont.

Differences in the number of atlas blocks used in the Vermont and New York analyses might be one of the factors contributing to differences in threshold estimates. We obtained threshold models and associated forest cover estimates that were at times very different from the results as presented in Zuckerberg and Porter (2010) when we randomly selected 5000 subsamples of 175 atlas blocks (the sample size for Vermont) from the entire New York data and subsequently fitted threshold and non-threshold models (Figure 2.4, Figure S2.2). For most species, threshold models were selected as best models for less than half of the subsamples (<2500). More strikingly, the threshold estimates associated with supported threshold models ranged from approximately 5 to 95% forest cover for all species. When we compare the threshold estimate as derived by Zuckerberg and Porter (2010) with the distribution of threshold estimates from our simulation of subsets we see that our subsampling approach hardly gave
different results for some species (e.g. persistence for Veery) but very different ones for others (e.g. persistence for Hermit Thrush) (Figure 2.4, Figure S2.2, Table 2.2).

We included bird presence at all levels of confirmation (‘possible’, ‘probable’ and ‘confirmed’) in our analyses. However, we do note that similar analyses based on only the most conservative data (‘confirmed’) give us considerably different results. Not only did fewer species show support for threshold models for persistence (2 species) and extinction (6 species) dynamics (Table 2.3, Figure 2.5), the critical threshold estimates associated with these models also differed from our original analysis. Threshold models for persistence were supported for Blue-headed Vireo (Vireo solitarius) (threshold estimate at 94.50% forest cover (SE=2.72)) and Scarlet Tanager (82.84%, SE=6.75). Neither of these species supported a threshold model for persistence in our original analysis (including all levels of occurrence). Three species, Magnolia Warbler (Setophaga magnolia) (79.63%, SE=6.29), Yellow-rumped Warbler (Setophaga coronate) (98.20%, SE=8.12) and Blackburnian Warbler (Setophaga fusca) (46.43%, SE=15.21) supported an extinction threshold model in our conservative approach as well as our initial analysis, but with different threshold estimations. Red-breasted Nuthatch (Sitta canadensis) (60.24%, SE=9.58), Winter Wren (Troglodytes hiemalis) (97.41%, SE=16.07) and Veery (Catharus fuscens) (31.52%, SE=9.30) supported threshold models for extinction only in our more conservative (confirmed breeding only) approach.

In order to analyze the influence of forest amount in the surrounding landscape on both persistence and extinction dynamics, we created a new set of models that included the average forest cover of the focal atlas blocks plus all eight surrounding blocks as an independent variable. The average forest cover in blocks surrounding atlas blocks was not significantly correlated with the forest cover within atlas blocks (Spearman rank correlation; \( \rho =0.08, P=0.30 \)). Only 5 times
was a threshold model selected for one of the 50 models that included forest in the surrounding blocks as an extra parameter (Table 2.4; Figure 2.5). Regarding persistence, Common Raven (*Corvus corax*, 80.36%, SE=1.89), and Black-throated Green Warbler (*Setophaga virens*, 83.91%, SE=9.23-12) showed support for a threshold model that included habitat amount at this broad spatial extent. Neither species supported a threshold model for persistence in the original analysis that was based on forest cover in the atlas block alone. Brown Creeper (*Certhia americana*, 59.51%, SE=2.94), Black-throated Green Warbler, 66.31%, SE=17.71) and Blackburnian Warbler (65.56%, SE=0.84) showed support for a threshold model in extinction. Two of these species, Black-throated Green Warbler and Blackburnian Warbler, also supported a threshold response for extinction in the original analysis but at slightly different estimates (Black-throated Green Warbler 73.82%, SE=21.49; Blackburnian Warbler 69.91%, SE=5.26, Table S1).

**Discussion**

Regional and interspecific variation in species responses to habitat loss and fragmentation has previously been recognized and put forward as a warning against generalizing results of threshold studies across species and regions (Betts et al. 2006b, Betts et al. 2007, Rhodes et al. 2008, Boyle and Smith 2010, Zuckerberg and Porter 2010). We adopted a simple yet efficient approach to threshold estimation as proposed by Zuckerberg and Porter (2010) and extended it to a region (Vermont) adjacent to their original study area (New York). Even though these two regions are largely similar in landscape characteristics such as forest cover and composition, faunal species composition and climate and latitudinal aspects, we found striking differences in the results of our threshold modeling approach. We found less support for the inclusion of a threshold parameter in models of both persistence and extinction responses in Vermont.
compared to New York. In addition, there were differences between the two regions in the estimate of thresholds in forest cover below which the probability of persistence dramatically declined or extinction increased for species that did support a threshold model in both states.

Although the design of the current study did not allow us to assess the cause of regional differences in threshold responses directly, we argue that they might be related to the higher forest cover in Vermont (average atlas blocks 73.89%, SE=0.02) compared to New York (63.10%, SE=0.35) (Figure 2.6). Arguably, high forest cover in the broader surrounding landscape might indicate that forest-associated bird species are able to maintain breeding populations in atlas blocks with low forest cover, because resources (e.g. food resources) can be found in the surrounding atlas blocks with a higher forest cover (Radford et al. 2005). In general, atlas blocks with relatively high forest cover are abundant throughout the state of Vermont, whereas a considerable number of atlas blocks with low percentages of forest cover exist in New York (Figure 2.6).

Another possible explanation for the ability of bird species to apparently persist at lower amounts of forest cover in Vermont as compared to New York, might be related to the ability for bird species to disperse to and from patches within the atlas blocks with lower forest cover. For example, birds might be more likely to be detected as breeding individuals in occasional atlas blocks with low forest cover, due to the existence of source populations in high forest cover atlas blocks in the vicinity. In addition, patches of forest habitat within atlas blocks with low forest cover might be less isolated in Vermont than in New York because surrounding atlas blocks offer patches within dispersal distance (Radford et al. 2005). Finally, we might reason that forest composition and structure (forest quality) (Radford and Bennett 2004, Rhodes et al. 2008), the quality of the matrix (Ricketts 2001, Kennedy and Marra 2010) and the level of fragmentation
(Andrén 1996, Zuckerberg and Porter 2010) differ between the two study regions and contribute to differences in threshold responses in New York and Vermont. Although fragmentation might play a role in species-habitat relationships it is becoming widely accepted that habitat amount per se is a better predictor of species distributions and responses than fragmentation (Fahrig 2002, Smith et al. 2009, Smith et al. 2011). Despite this notion, we do argue that incorporating a measure of fragmentation should be part of follow-up studies in order to address whether differences in levels of fragmentation can explain part of the regional differences that appear in threshold estimates (Pardini et al. 2010).

We may have found less support for threshold models in Vermont because the forest cover in most of the surrounding landscape falls above species habitat thresholds (Betts et al. 2007). The detection of landscape-scale species-habitat relationships is likely to be lower in regions with high proportions of potential habitat (Andrén 1996). Pardini et al (2010) support this by showing that clear habitat-abundance and habitat-richness effects seem to be lacking in regions with high forest cover. Indeed, most of our study area might have forest cover above the critical values at which thresholds are usually found (10-30%; Fahrig 2001, Radford et al. 2005, Lindenmayer et al. 2008), obviating the need for a larger study including more study regions.

Species that were considered to follow threshold responses differed in the estimates of threshold values, with persistence thresholds ranging 19.45-87.96% and thresholds in extinction ranging from 50.82% to 91.02% (Table S1). This variation in species-habitat relationships has been widely recognized (e.g. Radford et al. 2005, Betts et al. 2007, Swift and Hannon 2010, Zuckerberg and Porter 2010) and been attributed to variation in area-sensitivity as a function of life-history traits such as dispersal capacity (Davies et al. 2000, Lees and Peres 2009), reproductive capacity (Andrén et al. 1997, Vance et al. 2003) and habitat specialization (Andrén
et al. 1997, Devictor et al. 2008, Pardini et al. 2010). Interestingly, in contrast to many previous studies that indicate which species were more area-sensitive than others (Betts et al. 2006b, Betts et al. 2007, Pardini et al. 2010, Zuckerberg and Porter 2010), we did not find consistency in area-sensitivity across regions. For example, when we ranked species according to their threshold estimates for persistence, we found (e.g.) Yellow-rumped Warbler on the high end of the ranking with a threshold value of 73.61% in New York but on the lower end in Vermont (19.45%). The reverse was true for Black-and-white Warbler, having a threshold estimate around 39.79% forest cover in New York but 87.96% in Vermont.

There are many plausible explanations for the results we found and the lack of consistency in threshold values across regions. As mentioned earlier, differences in levels of fragmentation, habitat amount in the wider landscape, quality of the forest and the surrounding matrix are all factors that might be correlated with variation in threshold response. Yet, some of the variation could simply come from problems in defining ‘habitat’ properly. We used a coarse variable (‘forest’) in order to facilitate comparisons with earlier work by Zuckerberg and Porter (2010), even though the breeding distribution of many of our focal birds might be better predicted by more specific variables such as ‘evergreen’, ’mixed’ or ‘deciduous’ forest or even subcomponents thereof (particular tree species, prevalence of structural components such as standing dead wood) (Betts et al. 2007, Betts et al. 2010). Indeed, variation in these more specific characteristics might be large between and within regions, and might thus result in different outcomes in threshold model studies.

Interestingly, thresholds in extinction and persistence did not always seem to occur at the same percentage of forest cover. This difference was most notable in Yellow-rumped Warbler with a threshold in persistence at 19.45% (SE=3.83) and 78.67% (SE=3.76) for extinction. Due
to an overall low number of species that supported threshold models, we are not able to explore this difference further in our current study, but we argue that differences in thresholds of extinction and persistence might be related to time-lags in regime shifts (Pardini et al. 2010). Species might seem to persist at percentages of forest cover that are lower than those where peaks in extinction probability occur because of a time-lag in the extinction process. We aim to address this interesting observation further in follow-up studies, in line with arguments that any study that addresses long-term population dynamics should address the phenomenon of time-lags (Swift and Hannon 2010).

One important factor in the comparison of thresholds in Vermont and those found in New York is the effect of sample size on our model outcome (Jones et al. 2011). The sample size (number of atlas blocks) in Vermont is low (175) compared to New York (5074). We addressed this issue of low sample size by simulating random subsets of 175 atlas blocks from the New York data set and fitting models to these subsets. Interestingly, we found support for a threshold model for less than half of all random subsets and found a wide range of threshold estimates (Figure 2.4, Figure S2.1). The latter might be due to the wide range of forest cover found in the atlas blocks in New York (Figure 2.6), with some of the random subsets containing mainly blocks with low forest cover and others mainly blocks with high forest cover. This is arguably less of a problem in Vermont, where forest cover throughout the atlas blocks seems uniformly high and where the ‘subsample’ of 175 priority atlas blocks seems a good representation of the forest cover in all atlas blocks in Vermont (Figure 2.6). However, it remains an issue that needs to be addressed. We are aware, and have shown here, that sample size may be one potential reason for the difference in outcome in support for thresholds and in associated forest cover estimates (Jones et al. 2011). Therefore, this is an additional factor that we have to take into
account when we try to extrapolate from one study or species to the next or when we try to infer conservation and management targets based on studies of threshold responses.

Bird atlas data constitutes different levels of confidence in occurrence (possible, probable, confirmed), and our model results depend on which data we include in our analyses. Considering only the most conservative level of occurrence confirmation (confirmed breeding) in our analysis may arguably improve the accuracy of estimating persistence or extinction thresholds. Basing our analysis on a conservative subset of our data (confirmed only) led to higher threshold estimates in those species that supported a threshold model, indicating that the percentage of forest required for persistence might actually be higher than previously noted here and in other studies. However, we did not extend this analysis here for three reasons. First, we wished to follow a protocol similar to the analysis by Zuckerberg and Porter (2010) in order to draw consistent and valid comparisons. Second, we found threshold models to be supported in our ‘conservative scenario’ for only 8 species-dynamic combinations (2 persistence, 6 extinction). Finally, detectability of confirmed breeding occurrences might be quite variable and might limit analyses to only those common species that are easily confirmed as breeders. Nevertheless, we suggest that any study that utilizes breeding bird atlas data should incorporate a consideration of the different results that data inclusion decisions may have. Most importantly however, we suggest that these more conservative estimates of forest requirements once more indicate that we might not be able to directly link the outcome of a threshold estimation model to the narrow conservation goals that are sometimes proposed (Rompre et al. 2010).

Smith et al. (2011) noted that forest bird occurrence varies directly with habitat amount in the surrounding landscape regardless of landscape size. We did not test for such a relationship, but did observe a lack of evidence for threshold responses when we included habitat in a larger
(~225km²) focal region in our models. The effects of habitat availability at this larger landscape extent might be diminished by a heterogeneous habitat distribution, given that forest cover in atlas blocks was not significantly correlated with forest cover in the surrounding blocks. Similar effects of declining area-sensitivity with increasing landscape scales have been recorded by Desrochers et al (2010).

What we have shown is a) an approach for comparison that can easily be repeated on an unprecedented broad scale and will eventually allow comparison across larger numbers of study areas and species than has been attempted previously, and b) a clear indication that threshold effects and/or amounts are not necessarily supported for the same species in even adjacent areas. If further studies are as promising, our methodology will provide insight into interspecific and regional variation of landscape level, long-term threshold dynamics. Ecosystem managers and conservationists would be able to derive generalities on threshold estimate predictions and gain insight into which characteristics are influencing the minimum habitat requirements for their specific region or focal species of interest. Novelties of our approach include: 1) the ability to address long-term thresholds in persistence and extinction (Zuckerberg and Porter 2010) rather than occurrence (Betts et al. 2006b, Betts et al. 2007)]; and 2) analyzing threshold responses with the use of extensive broad-scale sources of data that are already widely available. This extension of an earlier approach by Zuckerberg and Porter (2010) allows for comparisons of threshold models at scales that were previously unobtainable due to costs of field work and time consumption. In addition, we also show that 3) species vary in their threshold responses with regard to habitat amount, and that differences between regions are pronounced. This warrants the advice put forward by many ecologists that threshold values cannot simply be transferred across regions (Rhodes et al. 2008) or interpreted as clear-cut targets for ecosystem management and
conservation (Betts et al. 2010). We also warn that 4) sample size (in our study number of atlas blocks) might have large effects on the outcome of threshold studies (see also Jones et al. 2011) and that this might be one factor driving differences between threshold studies. Finally, our results indicate that 5) thresholds in long-term persistence and extinction dynamics can be found across a wide range of habitat cover or area. Generalizations such as “For most species with large home ranges (such as birds), the threshold may generally be located between 30% and 40% of the habitat...in order to protect the most sensitive species and to deal with uncertainty associated with thresholds, to maintain at least 40% of residual habitats” (Rompre et al. 2010) may oversimplify threshold analyses and may be counter-productive to conservation efforts.

We argue that while searching for thresholds in species-habitat relationships remains a valid goal for ecologists and conservationists, the differences in threshold estimates and response between species and regions are of greatest interest. Analyses that address these differences may contribute to conservation by determining which species are most at risk of being affected by habitat loss. Future research should be directed towards broad-scale comparisons in order to gain insights into consistency of species-habitat relationships, driving factors of both interspecific and regional variation, and general mechanisms underlying species-specific area-sensitivity.

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Table 2.1. Comparisons between logistic (non-threshold) and segmented (threshold) regression models for four forest breeding birds. The best models are highlighted in bold.

<table>
<thead>
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<th>Model</th>
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<td></td>
<td></td>
<td>Non-Threshold</td>
<td>116.10</td>
<td>2.89</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Extinction</td>
<td>Threshold</td>
<td>31.92</td>
<td>0</td>
<td>42.65</td>
<td>142.60</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>33.65</td>
<td>1.73</td>
<td></td>
<td></td>
<td>0.65</td>
</tr>
<tr>
<td>Blue-headed Vireo (Vireo solitarius)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>165.47</td>
<td>0</td>
<td>91.23</td>
<td>8.59</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>169.80</td>
<td>4.33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Extinction</td>
<td>Threshold</td>
<td>77.17</td>
<td>0</td>
<td>50.82</td>
<td>5.03</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>80.64</td>
<td>3.47</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-and-white Warbler (Mniotilta varia)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>75.77</td>
<td>0</td>
<td>87.96</td>
<td>5.83</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>79.52</td>
<td>3.75</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Extinction</td>
<td>Threshold</td>
<td>39.70</td>
<td>0</td>
<td>91.20</td>
<td>5.67</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>41.90</td>
<td>2.20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow-rumped Warbler (Setophaga coronata)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>151.47</td>
<td>0</td>
<td>19.45</td>
<td>3.83</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>161.00</td>
<td>9.53</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Extinction</td>
<td>Threshold</td>
<td>112.03</td>
<td>0</td>
<td>78.67</td>
<td>3.76</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>118.50</td>
<td>6.47</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. Percentage of forest cover associated with the response threshold.

2. Although the AIC and AUC values indicate support for the threshold model, visual inspection of the loess plot did not support the existence of a threshold.
Table 2.2 Comparison of estimated threshold values (% of forest cover) between New York and Vermont.

<table>
<thead>
<tr>
<th>Species</th>
<th>New York</th>
<th>Vermont</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Dynamic</td>
<td>%^2</td>
</tr>
<tr>
<td>Blue-headed Vireo (<em>Vireo solitarius</em>)</td>
<td>Extinction</td>
<td>85.62 (60)</td>
</tr>
<tr>
<td>Black-and-white Warbler (<em>Mniotilta varia</em>)</td>
<td>Persistence</td>
<td>39.79 (36)</td>
</tr>
<tr>
<td>Magnolia Warbler (<em>Setophaga magnolia</em>)</td>
<td>Extinction</td>
<td>84.41 (72)</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (<em>Setophaga coronata</em>)</td>
<td>Persistence</td>
<td>73.61 (44)</td>
</tr>
<tr>
<td>Black-throated G. Warbler (<em>Setophaga virens</em>)</td>
<td>Extinction</td>
<td>32.31 (58)</td>
</tr>
<tr>
<td>Blackburnian Warbler (<em>Setophaga fusca</em>)</td>
<td>Persistence</td>
<td>77.35 (75)</td>
</tr>
<tr>
<td>Canada Warbler (<em>Cardellina canadensis</em>)</td>
<td>Extinction</td>
<td>88.16 (45)</td>
</tr>
<tr>
<td>Dark-eyed Junco (<em>Junco hyemalis (hyemalis)</em></td>
<td>Persistence</td>
<td>59.68 (59)</td>
</tr>
<tr>
<td>Yellow-bellied Sapsucker (<em>Sphyrapicus varius</em>)</td>
<td>Extinction</td>
<td>51.91 (51)</td>
</tr>
<tr>
<td></td>
<td>Persistence</td>
<td>56.64 (38)</td>
</tr>
</tbody>
</table>

1. We derived threshold values for New York state from Zuckerberg and Porter (2010). In parentheses: The percentage of forest cover at which we found the maximum kernel density for threshold estimates of all selected (out of 5000) subsamples in our simulation approach. These subsamples consisted of 175 atlas blocks randomly taken from the original New York data.

2. Percentage of forest cover associated with the response threshold.
Table 2.3. Threshold values (% of forest cover) for species that supported a threshold model when only ‘confirmed’ breeding was considered in the analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dynamic</th>
<th>Model</th>
<th>AIC</th>
<th>%¹</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-breasted Nuthatch (<em>Sitta canadensis</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>180.6</td>
<td>60.24</td>
<td>9.58</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>192.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter Wren (<em>Troglodytes hiemalis</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>192.8</td>
<td>97.41</td>
<td>16.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>195.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Veery (<em>Catharus fuscens</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>172.9</td>
<td>31.52</td>
<td>9.30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>176.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue-headed Vireo (<em>Vireo solitarius</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>97.7</td>
<td>94.50</td>
<td>2.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>100.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magnolia Warbler (<em>Setophaga magnolia</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>168.5</td>
<td>79.63</td>
<td>6.29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>174.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow-rumped Warbler (<em>Setophaga coronata</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>161.8</td>
<td>98.20</td>
<td>8.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>168.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blackburnian Warbler (<em>Setophaga fusca</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>177.0</td>
<td>46.43</td>
<td>15.21</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>181.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scarlet Tanager (<em>Piranga olivacea</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>134.1</td>
<td>82.84</td>
<td>6.75</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>137.4</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹. Percentage of forest cover associated with the response threshold.
Table 2.4. Comparison between threshold and non-threshold models that included forest in the surrounding blocks as an extra parameter.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dynamic</th>
<th>Model</th>
<th>AIC</th>
<th>%¹</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Raven (<em>Corvus corax</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>204.2</td>
<td>80.36</td>
<td>1.89</td>
</tr>
<tr>
<td></td>
<td>Non-Threshold</td>
<td></td>
<td>208.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brown Creeper (<em>Certhia americana</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>109.1</td>
<td>59.51</td>
<td>2.94</td>
</tr>
<tr>
<td></td>
<td>Non-Threshold</td>
<td></td>
<td>113.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-throated G. Warbler (<em>Setophaga virens</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>140.9</td>
<td>83.91</td>
<td>9.23¹²</td>
</tr>
<tr>
<td></td>
<td>Non-Threshold</td>
<td></td>
<td>149.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Extinction</td>
<td>Threshold</td>
<td>29.4</td>
<td>66.31</td>
<td>17.71</td>
</tr>
<tr>
<td></td>
<td>Non-Threshold</td>
<td></td>
<td>32.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Blackburnian Warbler (<em>Setophaga fusca</em>)</td>
<td>Extinction</td>
<td>Threshold</td>
<td>46.6</td>
<td>65.56</td>
<td>8.43</td>
</tr>
<tr>
<td></td>
<td>Non-Threshold</td>
<td></td>
<td>64.5</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

¹. Percentage of forest cover associated with the response threshold.
Figure 2.1. Map of priority blocks of the First and Second Vermont Breeding Bird Atlas Projects.
Figure 2.2. Loess plots of persistence and extinction dynamics for two bird species. Loess plots showing the relationship between percentage of forest cover in an atlas block and the probability of persistence or extinction for two species (BLBW = Blackburnian Warbler (*Setophaga fusca*); VEER = Veery (*Catharus fuscescens*)). These plots were used for visual assistance in finding initial values for our segmented regression algorithms and visual checks only.
Figure 2.3. Plots of persistence data and logistic (Panel A-B) and segmented (Panel C-D) regression models. Plots showing point data (1 = persisting, 0 = not persisting) and either a fitted logistic or segmented regression model for two species (BLBW = Blackburnian Warbler (*Setophaga fusca*); VEER = Veery (*Catharus fuscescens*)). These plots were used to provide a visual check of the actual data and fitted models (in addition to the loess plots). The plots for Blackburnian Warbler are illustrative for a species with strong support for a threshold model, whereas both the data distribution and model plots of Veery are indicative of low support for a threshold model (additional figures for all species can be found in Figure S2.1). In the case of Veery, this might simply be due to it being persistent in the majority of atlas blocks.
Figure 2.4. Kernel density plots of estimated breakpoints for all subsamples (out of 5000). We superimposed an estimate of the proportion of forest cover (the threshold) associated with the maximum kernel density of our sampling results (vertical full line) and the threshold derived by Zuckerberg and Porter (2010) (vertical dotted line). Panel A shows results for models of persistence for Hermit Thrush (HETH; *Catharus guttatus*), Panel B persistence for Veery (VEER; *Catharus fuscescens*), Panel C extinction for Canada Warbler (CAWA; *Cardinellina canadensis*) and Panel D extinction of Black-capped Chickadee (BCCH; *Poecile atricapilla*). Results for the species shown were exemplary for situations where the estimated thresholds seemingly matched with (Veery, Black-capped Chickadee) or deviated from (Hermit Thrush, Canada Warbler) the proportion of forest cover associated with maximum kernel density. Similar plots for all species can be found in Figure S2.2.
Figure 2.5. Sensitivity of threshold model selection to differences in data inclusion (A) or independent variables (B). In Panel A we compare the number of species for which a threshold model was selected following a threshold analysis in which bird presence at all levels of confirmation (‘possible’ (PO), ‘probable’ (PR) and ‘confirmed’ (CO)) is included with an analysis based on ‘confirmed’ data only. We note that fewer species showed support for a threshold model for both extinction and persistence dynamics when only confirmed data were included in the analysis. In Panel B we highlight the influence of forest amount in the surrounding landscape on both persistence and extinction dynamics by comparing the number of species that support a threshold model when we used only forest cover in atlas blocks as an independent variable to an analysis in which we included forest cover in surrounding blocks as an additional variable. Fewer threshold models were selected when we included forest cover in surrounding blocks in our analyses.
Figure 2.6. Histograms of forest cover across atlas blocks in the states of Vermont and New York. The frequency of atlas blocks with a particular proportion of forest cover in each of the states. The histograms illustrate that many atlas blocks in both states have high (e.g. more than 0.6, or 60%) levels of forest cover, but also indicate that forest cover across the Vermont atlas blocks is more or less homogeneous (high cover) while atlas blocks in New York have a more variable range of forest cover (i.e. there are many blocks with low forest cover as well). The forest cover of the priority atlas blocks in Vermont seems a representative sample of the forest cover of all atlas blocks in Vermont.
Chapter III: Regional variability in extinction thresholds for forest birds in the northeastern United States: An examination of potential drivers using long-term breeding bird atlas datasets

By: Yntze van der Hoek, Andrew M. Wilson, Rosalind Renfrew, Joan Walsh, Paul G. Rodewald, Jennifer Baldy and Lisa L. Manne

Abstract

Demand for quantitative conservation targets has led to a search for generalities in extinction thresholds, the points at which extinction probabilities change strongly. Extinction thresholds are known to vary across regions, but investigation of this variability has been limited. Using long-term data from repeated breeding bird atlases in the northeastern United States and remotely sensed land cover data, we ran segmented logistic regressions to derive extinction threshold estimates for 25 forest-associated breeding birds. Thresholds in extinction probability varied widely regionally among species (7% to 90% forest cover) and within species (e.g. 12% to 90% for White-throated Sparrow (Zonotrichia albicollis)). Generally, thresholds were highest in landscapes with low fragmentation and high forest cover. We found two positive and one inverse relationship between forest cover and estimates of extinction thresholds, and three inverse and one positive relationship between extent of fragmentation and thresholds. That extinction threshold estimates increased for some species when landscape-wide forest cover increased or the extent of fragmentation decreased seems counterintuitive, but can be explained if 1) species have traits that allow them to succeed in a fragmented habitat, 2), differences in community composition lead to larger habitat requirements where habitat is more widely available or 3) the metrics (e.g. forest cover) do not adequately predict species occurrence. Future studies regarding the latter explanation are especially important, because coarse habitat metrics such as forest
cover are widely used in research literature and conservation recommendations. Our findings highlight the need to evaluate thresholds for individual species—preferably using detailed or species-centered habitat definitions in threshold modeling—to derive generalities for conservation applications.

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 precise yet broadly applicable rules to describe the relationship between native 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 is a threshold amount of suitable habitat, such that areas with less than this threshold demonstrate very low probability of hosting the species of interest (Andrén 1994, With and King 1999, Fahrig 2001, Zuckerberg and 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, Rompre et al. 2010, Swift and Hannon 2010, Kato and Ahern 2011).

Initially, the negative effect of habitat fragmentation on species’ persistence was generally considered to intensify below a threshold of 10-30% of suitable habitat (Andrén 1994). More recently, Fahrig (2001, 2002, 2003) and others have pointed out that this fragmentation threshold should be viewed as separate from the extinction threshold: the amount of habitat below which extinction probability increases rapidly (or above which extinction probability decreases rapidly (Lindenmayer and Luck 2005)). Because extinction thresholds may be found at any percentage or amount of habitat cover, generalizations 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). We are nevertheless interested in the mechanisms behind such variability. Knowledge of variability may aid the extrapolation of thresholds across studies, species and regions.

Characteristics such as vegetation structure and composition (Betts et al. 2010), the percent habitat cover, extent of fragmentation (Fahrig 2001, Fahrig 2002), or the quality of the habitat or matrix (Rhodes et al. 2008, Boyle and Smith 2010) may influence thresholds. In addition, estimates of thresholds may be influenced by the scale at which we assess species’ responses (Holland et al. 2004, Betts et al. 2006, Betts et al. 2010) and spatial variability in demographics such as reproductive rates (Rhodes et al. 2008). Methodological and statistical issues in threshold detection may also lead to variability in threshold estimates. For example, variability in species detection and survey efforts (Betts et al. 2010, Zuckerberg and Porter 2010, Jones et al. 2011), the use of different sample sizes (van der Hoek et al. 2013) or statistical approaches (Ficetola and Denoel 2009) may make comparisons and generalizations across studies or study sites difficult. We show that landscape-level thresholds estimated with similar types of data sets (breeding bird atlases) can allow comparisons across species and study areas. However, many landscape level threshold studies are based on the use of a rather generic habitat description as a predictor variable (e.g. forest cover). Many readers might argue against the use of such a broad definition of habitat, one that is based on an anthropogenic view of landscape. Indeed, we acknowledge the potential of studies that include species-centered habitat definitions (e.g. those that are derived by use of species distribution models (SDMs); Betts et al. 2014). However, generic and human-defined cover types are often used as habitat proxies in conservation and management, likely because they are more easily interpreted and integrated in policy and recommendations than species-centered habitat definitions (Betts et al. 2014). In
Canada for example, management recommendations emerged that are based on maintenance of more than 40% (Rompre et al. 2008) or 50% (Environment Canada, 2013) forest cover to ensure low risks of species extinction. Therefore, we feel that it is necessary and adequate to look for variability, generalities and applicability of thresholds in forest cover.

Increased interest in citizen science has led to availability of large data sets at unprecedented levels of scale, effort and intensity (Dickinson et al. 2010, Dickinson et al. 2012, Hampton, et al. 2013). The potential of citizen science for research is extensive, as analyses of processes at broad geographic scales and on private lands are now possible (Dickinson et al. 2010). For example, large data sets derived through citizen-science such as the North American Breeding Birds Survey (Rittenhouse et al. 2010) and breeding bird atlases (Zuckerberg and Porter 2010) provide opportunities to test how thresholds vary across landscapes and regions. In combination with remotely sensed data, these survey projects provide broad-scale, long-term data needed for landscape threshold comparisons (van der Hoek et al. 2010). With these types of data we may derive a proxy for persistence and extinction over time, rather than occurrence at one point in time.

We present a multi-region comparison of landscape-scale thresholds in long-term species-habitat relationships. We used data from six statewide breeding bird atlases and remotely-sensed land cover data from the Northeastern United States to derive unique estimates of extinction threshold for 25 forest-associated breeding birds. We explored how threshold estimates varied among the states, and selected sub-regions, and investigated whether this variability was correlated with forest cover or extent of fragmentation. We predicted that for most bird species, threshold estimates would be negatively associated with amount of forest cover (Ewers and Didham 2006) and positively associated with fragmentation (Figure 3.1).
Simulations and theoretical models show that estimates of extinction thresholds may be positively correlated with the extent of habitat fragmentation (With and King 1999, Fahrig 2002), whereas higher forest cover in the surrounding landscape may lower thresholds through increased rescue effects or other processes.

**Methods**

*Data: Breeding bird data*

We used breeding bird atlases to estimate probability of extinction over a ~25-year time period for the same 25 forest generalist and obligate species evaluated in van der Hoek et al. (2013) and Zuckerberg and Porter (2010). Data were from the first and second atlases of Massachusetts (MA) (Petersen et al. 2003, Kamm et al. 2013), Michigan (MI) (Brewer et al. 1991, Chartier et al. 2011), New York (NY) (Andrle and Carroll 1988, McGowan and Corwin 2008), Ohio (OH) (Peterjohn 1991, Rodewald et al. in prep.), Pennsylvania (PA) (Brauning 1992, Wilson et al. 2012), and Vermont (VT) (Laughlin and Kibbe 1985, Renfrew 2013); all states in the Northeastern United States, within the Eastern Temperate Forest Ecoregion with some parts Northern Forest (Omernik 1987). The vegetation in these states is predominantly deciduous forest and to a lesser extent coniferous forest. Specific atlas sampling and methods can be found in the above citations.

Breeding bird atlases divided their area (a state) into discrete ‘blocks’ (~1/6th of a 7.5 minute USGS topographic quad;~5x5km) and surveyed birds within all or a subset of those blocks. We used only data from blocks surveyed in both the first and second atlas for each state. For Vermont, we only had access to data from ‘priority blocks’. Priority blocks were randomly selected blocks that were surveyed until at least 75 species were observed at any breeding level.
confirmed, probable, and possible) (Renfrew 2013). In order to increase the comparability of state atlas data, 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. We are aware that such a criterion might introduce a bias in our analysis. For example, in Pennsylvania (Wilson et al. 2012), blocks in which 75 or more species were reported had significantly more effort hours (mean=26.2 hours, N=3,224) than those blocks with fewer than 75 species reported (mean=12.5 hours, N=1,382, z=17.86, P<0.001). However, preliminary analyses indicated little difference between thresholds derived for this ‘subset’ of atlas blocks and analyses on all atlas blocks (mean difference = 5.3%, SE=3.6). We also excluded blocks that were not entirely within state boundaries, or consisting of more than 50% water. In total, this led to the availability of presence-only 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 to assess spatial autocorrelation (Lichstein et al. 2002, Zuckerberg and Porter 2010) did not reveal significant spatial autocorrelation (α-level = 0.01).

That a species is not detected in an atlas block does not have to indicate that the species was absent, as the detection probability is likely to be less than 1 (MacKenzie et al. 2002). It is most likely that species remain undetected in habitat patches that are occupied when there is a small population size, difficulty of detection of individuals, or limited sampling effort (Gu and Swihart 2004). We aimed to limit the effect of heterogeneous detectability by choosing focal species that are relatively common, abundant and easily detected. In addition, by choosing to include only atlas blocks in which at least 75 species were detected 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 in dealing with imperfect detection (Kéry and Schmid, 2004, Royle et al.,
2007) because we did not have information from repeated sampling (similar to Zuckerberg and Porter 2010). Similarly, survey hours were not available for each Atlas (hence the > 75 species criterion instead of an hour-based criterion), making it difficult to quantify the effect of differences in effort across Atlases. Nevertheless, we argue that the effects of differences in survey effort on our analyses were likely to be 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 most important issue here (Gu and Swihart 2004, Zuckerberg and Porter 2010). For example, 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 and Porter 2010, van der Hoek et al. in prep). Finally, we point out that we are presenting a study of variability in thresholds, and that we do not aim to provide exact estimates of extinction thresholds.

Data: Land cover and fragmentation metrics

Forest cover was calculated from 1992 National Land Cover Data (NLCD) as the proportion of all types of forest cover (deciduous, coniferous and mixed) in each atlas block. We acknowledge that 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 we were logistically constrained to use the range of forest cover found across the atlas blocks as the predictor variable in our analyses. Exact estimates of extinction thresholds may be influenced by this choice of land cover data but that the relative differences between regions/states that we have calculated are likely to be similar in magnitude and direction.
We calculated fragmentation indices: edge density (ED; edge length on a per unit area basis that facilitates comparison among landscapes of varying size), patch density (PD; the numbers of patches of the corresponding patch type divided by total landscape area (m²)), mean patch area (MPA; average area of patches) and aggregation index (AI; area-weighted mean class aggregation index) for each block using SDMTools (Vanderwal 2012) in R (R Core Team 2008). We chose these metrics because their potential effect on the extinction threshold (e.g. ED captures edge effects, a potential driver of extinction) is easily interpreted and because they are commonly used throughout the literature (Hargis et al. 1998, McGarigal 2002, Fahrig 2003, Frohn and Hao 2006).

Models and statistical analysis

We conducted 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 going extinct (present in the first but not the second) (Gates and Donald 2000), and subsequently gave extinction a value of 1 and all other dynamics value 0. This approach is consistent with other studies (Zuckerberg and Porter 2010) but does not estimate true extinction probability (and thus does not estimate actual extinction thresholds) 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. This approach resulted in different sample sizes (number of atlas blocks) for each species, but did provide a better estimate of true extinction probability.
We plotted the fitted values of locally weighted nonparametric models (smoothing parameter 0.75) in order to visualize empirical relationships between forest cover and extinction. This allowed us 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, and selected a model if the AIC was > 2 lower than the alternative model (Burnham and Anderson 2002). We selected the model with the fewest parameters (the non-threshold model) when the difference was < 2 between the models. In addition, we deemed the threshold model insufficiently precise to be included in further analyses when the standard error (SE) accompanying the threshold estimates was larger than the threshold estimate itself. This cut-off was subjective, but based on the notion that a standard error larger than the threshold estimated would imply that the threshold could also be found at 0% forest cover, a scenario we deemed highly unlikely. We used Area Under the Curve (AUC) to determine the fit of each selected model to the original data.

We aimed to make threshold and non-threshold comparisons for all 25 species for each state (or sub-region) under both extinction scenarios. However, some species, in certain states, were so rare that the number of block records was too low (~N < 10) to allow modelling. 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 (Table S3.1). In total, we were able to compare a maximum of six thresholds (one per state) per species for subsequent analyses of factors driving regional variability. This relatively low sample size, and variable numbers of blocks in each state, 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.

First, we were interested in visualizing how the range of data (e.g. range of forest cover) available can influence threshold estimates. We divided the entire landscape (all six states combined) into three subsets of blocks based on forest cover: low (0-33%, N=468); intermediate (34-66%, N=1123); and high (67-100%, N=1282). We created threshold and non-threshold models for these subsets and subsequently assessed support for threshold models following the approach above. Second, we wanted to test for relationships between the average percentage of forest cover or level of fragmentation (ED, PD, MPA and AI) in a landscape and the threshold estimate. Thus, we created nine ‘landscapes’ of similar extent within the states of PA, NY, VT and MA (Figure 3.2). The number of atlas blocks used for analysis in each landscape differed, due to application of the ≥ 75 species criterion, and ranged from 200 to 288 blocks. For these landscapes we also compared threshold and non-threshold models, although low numbers of recording did not allow us to create models for several species in certain landscapes (Table S3.2). We used linear regression models to test for relationships between the average percentage of forest cover or level of fragmentation in a landscape and the threshold estimate. All these analyses were conducted under both extinction scenarios.

**Results**

In the state-based analyses, threshold models were selected as better models than logistic regression models for about 41% of all (56 out of 137; 25 species x 4 states plus 24 species for MA and 13 species for OH) model comparisons under scenario 1 and for only 23 model comparisons under scenario 2 (Table S3.1). 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 and could be even markedly different within species across 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, there seemed to be an increase in support for threshold models with more forest cover (Table S3.1). Support for thresholds was low (three species models supported threshold models) in the two states with the lowest average percentage of forest cover, MI (average forest cover in state and atlas blocks is 38% and 34% respectively) and OH (average forest cover in state/atlas blocks is 31%/44%), whereas it was relatively high in states with high forest cover. We found most (19 out of 25 species) support for threshold models in NY, a state with high forest cover (average forest cover in state/atlas blocks is 63%/62%) (Figure 3.3). We did not observe a similar trend for scenario 2. There were three threshold models supported for MI (average = 52%), only one for OH (8%), and five and four threshold models for the two states with the highest forest cover, PA (average threshold =77%; average forest cover in state/atlas is 64%/65%) and VT respectively (average threshold = 57%; average forest cover in state/atlas is 78%/74%).

Medians of all supported thresholds per state ranged from 44% (MA) to 74% (PA) under scenario 1 and from 8% (OH) to 85% (PA) under scenario 2. The value of 8% for Ohio was the single supported threshold estimate for the state, for Ovenbird (*Seiurus aurocapilla*). We did not look for a trend in these median threshold estimates because taking the median obscures the trends for individual species, and trends across states could be driven by one or few species. Threshold estimates ranged widely across species, from very low (7% (SE=5) for Brown Creeper (*Certhia americana*) in NY under scenario 1; 8% (SE=2) Ovenbird in OH under scenario 2) to
very high (96% (SE=0.3) for Black-and-white Warbler (Mniotilta varia) in PA under scenario 1; 95% (SE=2) for Canada Warbler (Cardellina canadensis) in NY under scenario 2) (Table S3.1). Even within a species there could be large differences across states, with most variability in White-throated Sparrow (Zonotrichia albicollis) (12% (SE=6) in NY to 90% (SE=5) in PA) under scenario 1 and Ovenbird (8% (SE=1.7) in OH to 82% (SE=7) in NY) under scenario 2. No obvious geographic trends could be detected in the species-specific threshold estimates.

Next, we pooled the data from all states, split the dataset into three subsets based on blocks falling into any of three categories (low, intermediate and high forest cover), and created threshold models for these subsets. We found more support for thresholds (11 out of 25 species) for the subset of intermediate forest cover blocks than for the subsets of low and high forest cover (six species for both). Threshold estimates increased with increasing forest cover (median threshold estimates 30% for low, 41% for intermediate and 82% for high forest cover subsets; Table 3.1). Not only did we see threshold models supported for different species when we made use of a different subset, which could simply indicate that thresholds are only detected if the threshold estimate falls within the range of forest cover available in the model building process, but we could even find support for different thresholds within species. For example, for Black-throated Blue Warbler (Setophaga caerulescens) the threshold estimated for the low forest cover subset was 32% (SE=3) whereas the threshold estimated for the high forest cover subset was 75% (SE=3).

Average forest cover across the atlas blocks in the nine ‘landscapes’ (Figure 3.2) ranged from 44 to 70%. Support for threshold models varied widely between landscapes (range 4-13 species under scenario 1; 1-10 species under scenario 2), but we found no relationship between the proportion of supported models and any of the landscape metrics (e.g. forest cover, patch
density) (linear models, \( P > 0.1 \)). Threshold estimates also varied widely across both species and landscapes, ranging from 17 to 95\% (Table S3.2). Model AUCs ranged from 0.45 to 0.99.

Before conducting further analyses, we ensured that we compared thresholds that were similar in nature (Figure 3.4). As pointed out by Zuckerberg and Porter (2010), curves of species responses can be either concave or convex, and yet give the same threshold estimates. In other words, we have to make sure we do not compare thresholds in forest cover above which extinction probability drops rapidly with those thresholds below which the probability increases steeply (see also Discussion). Taking this into account, and only using similar ‘locations’ in each analysis, we found little support for significant relationships between thresholds and any of the landscape metrics, although there were some exceptions (Table 3.2). Black-throated Green Warbler (Setophaga virens) was the only species for which thresholds were significantly related to more than one metric (for scenario 2). Thresholds for this species were positively correlated with forest cover in the landscape (F=88.45, \( P = 0.011 \)) and AI (F=45.11, \( P = 0.021 \)), but negatively with PD (F=42.22, \( P = 0.023 \)) and ED (F=47.10, \( P <= 0.021 \)). Sample size was very low for this species (N=4), and the significant trend was mainly driven by one threshold estimate (of 34.37\%). When this threshold estimate was removed no significant trend (\( P > 0.1 \)) was found.

We do note that there were many significant correlations between the different metrics, so they cannot necessarily be treated as independent factors. Across all atlas blocks, forest cover was negatively correlated with PD (F=8.70, \( P < 0.05 \)) and ED (F=9.64, \( P < 0.05 \)) but positively with AI (F=11.46, \( P < 0.05 \)). Note that forest cover was not correlated with MPA. In addition, we found negative relationships between AI and PD (F= 37.65, \( P < 0.001 \)) as well as between AI and ED (F=1757, \( P < 0.001 \)), and a positive relationship between PD and ED (F=42.3, \( P < 0.01 \)).
Discussion

We found large variability in extinction thresholds both across species and across regions. This variability can partially be attributed to differences in the overall habitat area or configuration available in the larger landscape (Radford and Bennett 2004, Rhodes et al. 2008). We found evidence that extinction thresholds are more often detected in landscapes with intermediate levels of forest cover than in landscapes with either high or low forest cover. In addition, we showed that there are significant relationships between threshold estimates and both the percentage of forest cover and the level of fragmentation in the landscape for at least a few species.

For four species thresholds seemingly increased with an increase in forest cover in the landscape, and decreased with increasing fragmentation (Table 3.2). We take caution in our interpretation of these results, since we have to take into account the low sample size (N=3 to N=5) used for the linear regression by which we assessed whether trends in threshold estimates exist and the multiple methodological artifacts of our study (such as the ‘location’ issue mentioned above). In addition, the possibility of these results being caused by Type I error are worth considering, as research finding in general are less likely to be true than false when sample size is small (Ioannidis, 2005). For this reason, the fact that hardly any species showed a significant decrease in threshold estimates as forest cover increased, or the extent of fragmentation decreased, across landscapes could be considered more valuable for interpretation—as these results cannot be caused by Type I error. Further, we did not separate effects of habitat per se and habitat fragmentation in our analysis nor included other important drivers of thresholds (e.g. matrix quality) (Ewers and Didham 2006) nor address the sensitivity of using presence-only data (Brotons et al. 2004). Finally, extinction thresholds could be affected
by population-scale processes, such as higher rates of extinction at range edges in comparison to the range core (Doherty et al. 2003, Holt and Keitt 2005). This could be especially important in the region of our study, which encompasses the southern range edge of many species. As an 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)). In fact, the number of confounding factors (also, variation in demographic rates driving variability (Rhodes et al. 2008)) means that we are limited in our confidence to draw generalities on regional variability in thresholds (Ewers and Didham 2006).

Despite the sensitivities associated with our analyses, there might be a possibility that thresholds for some species actually increase with increased forest cover or decreased fragmentation. Such a trend would be in contrast with previous theoretical predictions (Fahrig 2002), but may be explained by species-specific characteristics. Some species, such as Black-and-white Warbler (Parker et al. 2005), are known to experience positive edge effects resulting from fragmentation, meaning that thresholds may actually be lower in more fragmented landscapes (in this case landscapes with a lower Mean Patch Area). Additional potential reasons for increasing habitat requirements (thresholds) with increasing forest cover or decreasing fragmentation include increased interspecific competition in less fragmented habitat, which may result in net negative effects on a species that does not show any additional negative effects of fragmentation such as Brown Creeper (Villard et al. 1999), or the reduction of patch isolation in more fragmented landscapes (see Fahrig (2003) for a review of possible explanations of positive effects of habitat fragmentation). Finally, acknowledging evidence for higher rates of local
extinction and turnover in more fragmented landscapes (Boulinier et al. 2001), we could look into how aspects of community turnover affect threshold estimates. These kinds of analyses would have to follow another approach that includes community responses—instead of including a limited selection of 25 focal species. For example, we argue that our approach of coupling citizen science (e.g. breeding bird atlases or the Breeding Bird Survey) could be extended to a study of regional variability and generalities in thresholds as found by Threshold Indicator Taxa Analysis (TITAN) (Baker and King 2010).

A potential methodological driver of the variability we detected is that thresholds can be found at different ‘locations’ on a species response curve. An automated threshold detection process, such as segmented regression (Muggeo 2003), can estimate thresholds below which extinction probability increases rapidly and thresholds above which extinction probability decreases rapidly. This is similar to the notion by Zuckerberg and Porter (2010) that species can have two types of responses, indicated by concave and convex curves, but we add that this can even be the driver of variability found within species across different landscapes or regions (i.e. using different data in the modeling process). A clear illustration of this comes from the analysis in which we created nine subsets (‘landscapes’) of our data. Thresholds for Veery (Catharus fuscescens) were very different in two different landscapes (37.4% (SE=6.8) and 67.5% (SE=7.8)) even though average forest cover and level of fragmentation were nearly similar in both landscapes (forest cover 68.5% and 70.4%; aggregation indices 88.3 and 88.4) (Figure 3.4). This difference was due to variability in the location of the breakpoint along the species response curve; we can visualize that in both landscapes extinction probability increases rapidly below 65-70% but instead for one of the landscapes a breakpoint was estimated ‘on top of the curve’ (at 37.4%)—if forest cover is higher than this, the extinction probability decreases rapidly. This
characteristic of segmented regression has to be taken into account in order to make meaningful comparisons across landscapes or regions and we urge that any report on species thresholds explicitly addresses the nature of the threshold (also, multiple thresholds may exist in one species’ response (Lindenmayer and Luck 2005)).

Sample size can also have a large effect on threshold estimates (van der Hoek et al. 2013), hindering our efforts to compare the results of the state-based approach. Selecting appropriate starting values for the segmented regression is very important as well, because we found different threshold estimates using different starting values (despite efforts by Muggeo (2008) to make the algorithm less sensitive to starting values). We therefore urge those utilizing segmented regression to detect potential thresholds to check visually (e.g. by inspecting loess plots) to verify that any estimated threshold returned by the automated process truly exists in the species response curve.

Ecologists are increasingly trying to assess thresholds at landscape and regional scales, and broad-scale analyses such as ours are an important approach for assessing generalities in thresholds (despite the challenges that are inherent to broad scale analyses (e.g. accuracy, detection and simplification problems). We found that regional variability of threshold estimates was large and the direction of variability did not confirm our hypothesis that thresholds are lower in landscapes with higher forest cover or lower fragmentation. We did not find generalities in regional variability in thresholds, confirming that we should apply extreme caution when interpreting threshold estimates as potential conservation targets (Lindenmayer and Luck 2005) or when extrapolating across regions. Our approach however, does allow for many follow up studies that could explore the possibility of comparing species thresholds, as a comparative exercise that allows for identification of those species that are most vulnerable to habitat loss.
Although additional comparative studies that address community-level thresholds or thresholds in a set of species might be required to gain further insights in how and to what extent thresholds vary regionally, true generalities that can be incorporated in conservation and management have to be derived per individual species. As Evans et al. (2013) point out, simple models do not always make for more general models. In order for us to be able to make predictions about real species thresholds, we might need to make models more species-specific and relatively complex, for example by selecting more specific (such as specific types of forest (Betts et al. 2010, van der Hoek et al. 2013)) predictor variables that better predict species extinction probability than forest cover or by using a species-centered approach to defining habitat (Betts et al. 2014). We argue that our approach is adaptable to the extent that, if one uses models that accurately predict thresholds in extinction probability for one individual species (for example those based on SDMs; Betts et al. 2014), the effects of a variety of factors on thresholds can be assessed across many species and regions. We can then even think of assessing the influence of regionally varying demographic rates (Rhodes et al. 2008) on thresholds or aim to identify biogeographical patterns in threshold variability, e.g. if reduced resource availability leads to increased thresholds near the edges of a species’ range. We hope that our work will provide a new direction in threshold studies, allowing eventually for detection of generalities in species responses to habitat loss; generalities that are much in demand by ecologists and resource managers alike.

Acknowledgements

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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.
Table 3.1. Extinction thresholds for species that showed support for at least one threshold model when data were subdivided into three subsets. We subdivided all atlas data into three subsets according to the forest cover (%) in atlas blocks falling within the range 0-33% (low, N=468), 34-66% (intermediate, N=1123) or 67-100% (high, N=1282).

<table>
<thead>
<tr>
<th>Species</th>
<th>Low</th>
<th></th>
<th>Intermediate</th>
<th></th>
<th>High</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Threshold (%)</td>
<td>SE</td>
<td>Threshold (%)</td>
<td>SE</td>
<td>Threshold (%)</td>
</tr>
<tr>
<td>Pileated Woodpecker (<em>Dryocopus pileatus</em>)</td>
<td>57</td>
<td>3</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Least Flycatcher (<em>Empidonax minimus</em>)</td>
<td>33</td>
<td>6</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Common Raven (<em>Corvus corax</em>)</td>
<td>60</td>
<td>1</td>
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<tr>
<td>Black-capped Chickadee (<em>Poecile atricapilla</em>)</td>
<td>90</td>
<td>3</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Red-breasted Nuthatch (<em>Sitta canadensis</em>)</td>
<td>59</td>
<td>2</td>
<td>33</td>
<td>5E-1</td>
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<tr>
<td>Brown Creeper (<em>Certhia americana</em>)</td>
<td>33</td>
<td>2E-2</td>
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<tr>
<td>Winter Wren (<em>Troglodytes hiemalis</em>)</td>
<td>3</td>
<td>4E-14</td>
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<td>Hermit Thrush (<em>Catharus guttatus</em>)</td>
<td></td>
<td>69</td>
<td>2</td>
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<tr>
<td>Veery (<em>Catharus fuscens</em>)</td>
<td>32</td>
<td>5</td>
<td>66</td>
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<td>Golden-crowned Kinglet (<em>Regulus satrapa</em>)</td>
<td>31</td>
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<td>89</td>
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<td>Black-and-white Warbler (<em>Mniotilta varia</em>)</td>
<td>36</td>
<td>1</td>
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<tr>
<td>Black-throated Blue Warbler (<em>Setophaga caerulescens</em>)</td>
<td>32</td>
<td>3</td>
<td>75</td>
<td>3</td>
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<td></td>
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<tr>
<td>Black-throated Green Warbler (<em>Setophaga virens</em>)</td>
<td>6</td>
<td>3</td>
<td>66</td>
<td>1E-1</td>
<td></td>
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<tr>
<td>Ovenbird (<em>Seiurus aurocapilla</em>)</td>
<td></td>
<td>46</td>
<td>2</td>
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<tr>
<td>Scarlet Tanager (<em>Piranga olivacea</em>)</td>
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<td>13</td>
<td>6</td>
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<tr>
<td>Dark-eyed Junco (*Junco hyemalis (hyemalis))</td>
<td>29</td>
<td>2</td>
<td>65</td>
<td>1</td>
<td></td>
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<tr>
<td>White-throated Sparrow (<em>Zonotrichia albicollis</em>)</td>
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<td>90</td>
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<tr>
<td>Median</td>
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<td>41</td>
<td>1</td>
<td>82</td>
<td>2</td>
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<tr>
<td>Mean</td>
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<td>3</td>
<td>43</td>
<td>2</td>
<td>80</td>
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Table 3.2. Significant (alpha-levels 0.1 or 0.05) linear models between habitat metrics and threshold estimates in extinction probability.

<table>
<thead>
<tr>
<th>Species</th>
<th>Scenario</th>
<th>Metric(s)</th>
<th>Relationship</th>
<th>Significance</th>
<th>F-statistic</th>
<th>Adjusted R-square</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown Creeper (<em>Certhia americana</em>)</td>
<td>1</td>
<td>Patch Density (PD)</td>
<td>-</td>
<td>P = 0.078</td>
<td>68.4</td>
<td>0.97</td>
<td>3</td>
</tr>
<tr>
<td>Blue-headed Vireo (<em>Vireo solitarius</em></td>
<td>1</td>
<td>Mean Patch Area (MPA)</td>
<td>+</td>
<td>P = 0.034</td>
<td>28.3</td>
<td>0.90</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Patch Density (PD)</td>
<td>-</td>
<td>P = 0.048</td>
<td>19.8</td>
<td>0.86</td>
<td>4</td>
</tr>
<tr>
<td>Black-and-white Warbler (<em>Mniotilta varia</em>)</td>
<td>1</td>
<td>Mean Patch Area (MPA)</td>
<td>-</td>
<td>P = 0.030</td>
<td>438.1</td>
<td>0.99</td>
<td>3</td>
</tr>
<tr>
<td>Nashville Warbler (<em>Oreothlypis ruficapilla</em>)</td>
<td>1</td>
<td>Forest cover</td>
<td>+</td>
<td>P = 0.054</td>
<td>9.5</td>
<td>0.68</td>
<td>5</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (<em>Setophaga coronata</em>)</td>
<td>1</td>
<td>Forest cover</td>
<td>-</td>
<td>P = 0.081</td>
<td>10.9</td>
<td>0.77</td>
<td>4</td>
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<tr>
<td>Black-throated Green Warbler (<em>Setophaga virens</em>)</td>
<td>2</td>
<td>Forest Cover</td>
<td>+</td>
<td>P = 0.011</td>
<td>88.5</td>
<td>0.97</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aggregation Index (AI)</td>
<td>+</td>
<td>P = 0.021</td>
<td>45.1</td>
<td>0.94</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Patch Density (PD)</td>
<td>-</td>
<td>P = 0.023</td>
<td>42.3</td>
<td>0.93</td>
<td>4</td>
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<tr>
<td></td>
<td></td>
<td>Edge Density (ED)</td>
<td>-</td>
<td>P = 0.021</td>
<td>47.1</td>
<td>0.94</td>
<td>4</td>
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</table>
Figure 3.1. Predicted relationships thresholds and forest cover/fragmentation. Threshold estimates could increase as landscapes/regions increase in forest cover (or decrease in fragmentation), they could stay the same (consistent), or they could decrease. Thus, effects of forest cover and fragmentation are not necessarily correlated.
Figure 3.2. Selection of nine ‘landscapes’ from atlas blocks in MA, NY, PA and VT.
Figure 3.3. 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 both model scenarios. 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 3.4. Estimates of extinction thresholds for Veery (*Catharus fuscenscens*) 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).
Chapter IV: Incorporating lidar-derived structural habitat characteristics in extinction threshold studies.

By: Yntze van der Hoek, Andrew M. Wilson, Lisa L. Manne

Abstract

Ecologists are interested in finding those threshold levels of habitat amounts where extinction probability changes rapidly. Ideally, we would be able to go beyond that and model species responses to [changes in] structural habitat characteristics, such as snag abundance or canopy height metrics. With broad scale bird and light detection and ranging (lidar) data we were able to find thresholds in different canopy height metrics for five species of cavity breeding birds. In addition, we found thresholds in mean and maximum canopy heights above which the detection probability of Cerulean Warbler (*Setophaga cerulea*), a conservation priority species, increased rapidly. We show that the availability of lidar data can facilitate threshold studies across a large spatial extent, without compromising on details. These kinds of thresholds, which can be related back to specific types of forests, can potentially be used to set management targets.

Introduction

Rapid expansion of the human population over the last few decades has led to heavy disturbance, fragmentation and loss of habitat. As a consequence, ecologists and conservationists are increasingly interested in the relationship between extinction probability and the availability of habitat (Fahrig 2001); especially in the non-linear responses that species might show to habitat loss. Such responses reflect the existence of extinction thresholds: levels of habitat availability (in ha or %) where extinction or persistence probabilities change rapidly (Fahrig 2001).
The results of landscape-level studies of habitat thresholds are often difficult to interpret due to a lack of generality in thresholds across landscapes or species (Lindenmayer and Luck 2005). Moreover, we usually use broad habitat categories such as ‘forest cover’ in our studies, despite the fact that structural characteristics (e.g., canopy height and variation) might be more important in explaining species diversity, abundance and persistence (Bradbury et al. 2008). In fact, the lack of generality in habitat thresholds might partly be driven by this use of generic habitat definitions (Betts et al. 2014).

Instead of using generic measures of habitat, it might be worth including habitat definitions based on species distribution models (SDMs; Betts et al. 2014) in landscape-level studies of habitat loss and fragmentation. A species-centered approach based on SDMs allows us to create models that accurately predict thresholds in extinction probability for individual species and—because species distribution models can be created using broad-scale remote sensing data (e.g. Landsat TM satellite imagery; Betts et al. 2014)—facilitates analyses of variability and generality in species-habitat relationships across regions. However, although species-specific habitat definitions based on SDMs may prove useful as predictor variables, generic measures of habitat are likely to remain commonly used throughout conservation and management literature (Betts et al. 2014). After all, changes, thresholds or limits in the availability of human-defined cover types (e.g. forest, old growth forest) are more easily interpreted as management targets than parameters in SDMs (Betts et al. 2014).

Generic, human-defined habitat cover types in species-habitat studies might be too unspecific to allow for generalizations or proper detection of thresholds in species responses. On the other hand, habitat measures based on species-centered SMDs might be difficult to interpret by managers and policy-makers. Therefore, we suggest a third option available to us in habitat
threshold studies: use of lidar in order to derive detailed structural vegetation data for threshold modeling. For example, snag or large tree density might explain species persistence better than the amount of forest cover per se for certain species. If we can derive such detailed data at large extents, we can create species-specific threshold models across large areas; the results of which can be integrated into management and policy.

The potential of light detection and ranging (lidar) data

The main reason that extinction threshold studies have not focused on structural habitat characteristics is that such metrics have always been difficult to assess for large areas. The amount of detail provided by traditional, 2-D, remote sensing does not allow for the derivation of metrics such as canopy height, and field work to document this is labor-intensive, prohibitively so over large scales.

The emergence of 3-D remote sensing data, especially lidar, allows for assessment of vertical vegetation structure across larger scales (Vierling et al. 2008). For example, we can classify vegetation types (Bassler et al. 2011), characterize wildlife habitat (Garcia-Feced et al. 2011) or identify and map the distribution of specific habitat characteristics such as snags and large trees that certain bird species require for foraging and breeding (Falkowski et al. 2009). In extension, it is possible to utilize these lidar-derived metrics and characteristics to predict wildlife distribution, occurrence and richness (Goetz et al. 2007; Vogeler et al. 2013; Lesak et al. 2011; Bradbury et al. 2005; Clawges et al. 2008).

Incorporating lidar in threshold studies

Incorporating broad scale, but high resolution, 3D remote sensing data in threshold modeling might allow for detection of species-specific thresholds in structural habitat
characteristics (Figure 4.1). To test this idea, we created threshold models for five bird species that have known associations with snags and large (and old) trees. These species, all cavity breeders, are umbrella and keystone species, making them excellent study species from a conservation perspective (Poulin et al. 2008). In addition, we tested the possibility of deriving threshold estimates in canopy characteristics for the Cerulean Warbler (*Setophaga cerulea*), a species of great conservation concern and interest (Boves et al. 2013).

**Methods and Materials**

*Study area*

For our analyses we made use of lidar and breeding bird data from 10 counties (Erie, Crawford, Warren, McKean, Potter, Tioga, Clinton, Lycoming, Union and Snyder) located in the northern half of Pennsylvania (Figure 4.2). Lidar data for these particular counties were all derived during the same sampling period (spring 2007), limiting potential biases introduced by using lidar data from different years (Chasmer et al. 2006). The study area is dominated by broadleaved forest.

*Bird data*

We obtained records of breeding evidence (possible, probable, or confirmed) for Cerulean Warbler (*Setophaga cerulea*), Pileated Woodpecker (*Dryocopus pileatus*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Black-capped Chickadee (*Poecile atricapilla*), Brown Creeper (*Certhia americana*) and Winter Wren (*Troglodytes hiemalis*) from the repeated breeding bird Atlas of Pennsylvania (Brauning 1992, Wilson et al. 2012). These atlases were based on volunteer surveys in approximately 5x5km blocks for the periods of 1983-1989 and 2004-2009. We investigated whether change in bird survey effort between the two atlases, which was large, was correlated with forest cover or any of the other metrics we intended to analyze. We did not
find any significant relationships (Pearson correlation tests; P > 0.1 for all tests) and so deemed the atlas data suitably unbiased with regards to change in survey effort between atlas periods. For more information on Atlas protocol and accuracy, see Wilson et al. (2012).

We created a subset of Atlas blocks per species, including only those Atlas blocks where breeding was noted in the first Atlas. This ensured that a bird could only go extinct or persist. We considered extinction to have taken place in an Atlas block when the bird was detected in the first, but not the second Atlas; we considered a bird persistent in an Atlas block when detected in both Atlases. We obtained between 13 (for Cerulean Warbler) and 239 (for Black-capped Chickadee) Atlas blocks available for modeling for each species.

**Remote sensing data**

We used land cover data from National Land Cover Data (NLCD) to determine forest cover (%) (hereafter: Forest) in each Atlas block, in 1992 (a temporal mid-point between the two breeding bird Atlases, similar to van der Hoek et al. 2013). We obtained lidar data from the PAMAP program, one of the first efforts to collect lidar data for an entire state. These data were collected in spring 2007 with an airborne GPS/IMU system, flown at ~ 6500 feet (~1981m), with an average point spacing of 1.4m (43 degree field of view; rate of 40.6kHz). We obtained the raw data, as well as a high-resolution (1-m) Digital Elevation Model (DEM), from http://www.dcnr.state.pa.us/topogeo/pamap/index.aspx.

We calculated a digital crown model by subtracting the DEM from a digital surface model (DSM) based on the maximum return values (classified as forest) (see e.g. Clawges et al. 2008). We binned the canopy height values into the 5x5km breeding bird Atlas blocks, after which we calculated the mean canopy height (HMEAN), the median deviation of heights...
(HMAD), and the maximum height of canopy (HMAX) per Atlas block. These metrics are all associated with structural heterogeneity and the abundance of snags and large trees—the key features determining foraging and breeding opportunities for our study species (Hartwig et al. 2004, Poulin et al. 2008, Boves et al. 2013).

Modeling and statistical analyses

We created threshold (segmented logistic regression; Muggeo 2003) and non-threshold (logistic regression) models using the segmented (Muggeo 2008) and standard packages in R (R Core Team 2012), similar to van der Hoek et al. (2013). We compared Akaike’s Information Criterion (AIC) values of threshold and non-threshold models per species; the more complex threshold model was supported when AIC was > 2 units lower than the simpler non-threshold model (Burnham and Anderson 2002). We used Area Under the Curve (AUC) to determine the fit of each selected model to the original data.

We created only single-variable models because we wanted to illustrate clearly whether thresholds could be found for any of the variables. Multivariate models would limit interpretation of our results. We did include a separate autocovariate term in every model: the probability of detection of a species in an atlas block as a result of the detection of the same species in neighboring blocks (Zuckerberg and Porter 2010).

The number of Atlas blocks where Cerulean Warbler was detected in the first Atlas was too low (N=13) to allow modeling the extinction dynamic. Instead, we created threshold models based on detection probability of this species in each of the Atlas periods. Sample size available for these models was considerably larger (N=4397), although Cerulean Warbler was still only ‘detected’ in 13 and 15 Atlas blocks in the first and second Atlases respectively.
Although a discussion of each metric lies outside the scope of this study (but see Martinuzzi et al. 2009), we tested whether the metrics were correlated with one another by checking for Pearson correlation between any of the metrics in R (R Core Team 2012).

**Results**

There were significant ($P < 0.01$), positive, correlations between Forest and HMEAN for all of the species; and between Forest and HMAX for all species except Winter Wren. Forest was not significantly correlated with HMAD for any of the species. We found a significant negative correlation between HMAD and HMEAN for all species except Black-capped Chickadee and Cerulean Warbler; a significant correlation between HMEAN and HMAX in Cerulean Warbler only; and no significant correlations between HMAD and HMAX for any of the species.

We found support for threshold models of forest cover for Pileated Woodpecker (threshold at 99.7%; AUC=0.74)), Yellow-bellied Sapsucker (64.7%; AUC=0.97), and Cerulean Warbler (First Atlas: 36.5%; AUC=0.74; Second Atlas: 29.1%; AUCC=0.85) (Table 4.1). However, we deemed the threshold values for Pileated Woodpecker and Cerulean Warbler unlikely after visual inspection of loess plots. This is a caveat of an automated process of segmented regression (Muggeo 2003), that must be addressed in future research. We found support for HMEAN threshold models for Yellow-bellied Sapsucker (13.7m; AUC=0.83), Winter Wren (15.5m; AUC=0.74) and Cerulean Warbler (First Atlas: 15.4m; AUC=0.70. Second Atlas: 16.6m; AUC=0.75). Cerulean Warbler was the only species supporting a threshold in HMAX, at 44.4m (AUC=0.75) (based on data from the First Atlas); a threshold above which detection was more probable. No species showed support for a threshold in HMAD. Ranking models according to their AIC value showed that models based on structural habitat metrics
could potentially outperform the more commonly used (e.g. Zuckerberg and Porter 2010) Forest models (Table 4.1).

**Discussion**

From a management and conservation perspective, we might want to translate thresholds in structural vegetation variables to actual forest types, forest succession stages or forest management types. Documented thresholds in canopy heights (either maximum or mean) make sense when we consider that larger trees support a higher biomass of bark-dwelling invertebrates, a requirement for foraging for our study species (Poulin et al. 2008), but tall trees are also indicative of a specific type of forest. For example, we found a threshold for Winter Wren in mean canopy height at 15.5-m (Table 1), which matches earlier findings that a mean canopy height of 15-m or higher is most probably related to mature multistory, closed stem exclusion or old multistory forest (Falkowski et al. 2009).

Previous habitat threshold studies led to assessments of the effects of less frequently emphasized aspects of landscapes, like the quality of the matrix (Fahrig 2001), on species extinction. Studies like ours can inform conservation and resource managers in a similar manner, although we warn against the uncritical translation of thresholds to conservation targets (Lindenmayer and Luck 2005). We would also like to stress that ‘not finding thresholds’ does not mean that species do not experience negative effects of habitat loss or disturbance. For example, Black-capped Chickadee may breed in disturbed areas, but still experiences a lower proportion of successfully fledged young as a result (Fort et al. 2004).

Threshold models did not converge for all study species and models, nor were they always selected over logistic models—a result in parallel with earlier studies (Zuckerberg and
Porter 2010, van der Hoek et al. 2013)—for any, or multiple, of plausible reasons. First, our metrics, although more detailed than ‘forest cover’ might still not have been relevant for the species in question. Second, habitat amounts might not have been limiting even in the atlas block with the lowest amount of habitat available. Third, the sample size, threshold identification method or other aspects of our analyses might not have allowed us to detect species thresholds (van der Hoek et al. 2013). Fourth, the species might actually not exhibit threshold responses, simply because resources or habitat availability are not the main factor determining their extinction probability. This supports the idea that threshold responses may be common, but are not universal (Lindenmayer and Luck 2005).

Black-capped Chickadees and Brown Creepers might not have shown thresholds because they have relatively low habitat requirements, requirements that are exceeded in our entire study area (e.g. earlier threshold studies show an extinction threshold for Black-capped Chickadees at ~24% forest cover in New York (Zuckerberg and Porter 2010)). Species such as Cerulean Warbler (with support for thresholds of detection) are known to select specific microhabitat features (Boves et al. 2013), whereas the Black-capped Chickadee (no support for thresholds), a considerably more abundant and widely distributed species, can maintain high breeding densities even in disturbed habitats (Fort et al. 2004).

We largely ignored the flaws of segmented regression in obtaining accurate threshold estimates. A closer examination of loess plots engenders doubt on the usefulness and reliability of some of the thresholds we estimated. For example, for Yellow-bellied Sapsucker we found a threshold in maximum canopy height at 51.0-m, a height that coincides with the height of the tallest trees found in Pennsylvania. If the threshold is accurate, we would infer that Yellow-bellied Sapsucker, at least in this part of Pennsylvania, experiences a decrease in extinction
probability when maximum canopy height falls ‘below’ a height of 51.0-m (Figure 4.3a). We think it unlikely that this is a correct interpretation of our results, based on available knowledge of the species (Hartwig et al. 2004), and conclude that we estimated a breakpoint that does not translate to a real threshold. In contrast, an example of a true threshold would be the threshold in mean canopy height found for Winter Wren (Figure 4.3b, Table 4.1), if mean canopy height falls below 15.5-m extinction probability increases rapidly. This is, to our knowledge, the first time such a threshold for Winter Wren has been described.

We are aware that some readers might find it limiting that we did not detect thresholds in each species response, but we see our study as an important first step in assessing species habitat requirements through a combination of threshold modeling and lidar vegetation assessments. For example, Cerulean Warbler is a rapidly declining species and is considered a priority species for research, conservation and management. We note that there are possible thresholds in the mean and maximum canopy height above which Cerulean Warbler detection probability increases rapidly. Cerulean Warbler prefers large trees, or forests with a high canopy, as was previously mentioned by several authors (e.g. Boves et al. 2013). Ideally, this study will lead to follow-up studies with a specific narrow focus on habitat thresholds, information that can guide informed management measures for this species.

We applaud developments to use more species-specific and ecologically relevant definitions of habitat in studies of species-habitat relationships. Recent developments in the use of SDMs to measure habitat from a species-centered perspective seem to hold large potential for further studies (Betts et al. 2014), and we are certain we will soon see incorporation of SMDs in extinction threshold studies. We present a parallel effort in the search for generalities in species responses to habitat loss and fragmentation; an effort which can moreover lead to more specific,
yet interpretable, management targets. Although thresholds in structural habitat variables have previously been shown to exist (Poulin et al. 2008), we have now shown that they can be assessed at broad scales using lidar-data. Our study is merely a first step in bringing lidar data into threshold studies, a development we consider key to our desire to obtain ecologically relevant threshold information at large spatial extents. There has always been a trade-off between the coverage of large areas and detailed (vertical and horizontal) resolution, but we conclude that we can now utilize lidar to achieve both simultaneously.

Acknowledgements

We would like to thank Carnegie Museum of Natural History, Daniel W. Brauning, Robert S. Mulvihill and the thousands of volunteers who gathered, prepared and supplied bird Atlas data. We thank the PAMAP and PASDA programs for making lidar data freely available for research purposes. This research was supported by the Graduate Center of the City University of New York.
Table 4.1. Overview of threshold models. Threshold models in bold were selected (AIC > 2 lower) over logistic models (not shown), all other models were within 2 AIC (2 lower, 2 higher) units from the more parsimonious logistic model. We show the fit of the model (AUC) as well as the associated threshold (in% or m) and how the model ranked (based on AIC) out of 4 alternative threshold models per species. Models left blank (-) did not converge.

<table>
<thead>
<tr>
<th>Species</th>
<th>Metric</th>
<th>Delta AIC</th>
<th>AUC</th>
<th>Threshold</th>
<th>Rank</th>
</tr>
</thead>
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<tr>
<td>Pileated Woodpecker (<em>Dryocopus pileatus</em>)</td>
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<td>0</td>
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<td>99.7%</td>
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</tr>
<tr>
<td></td>
<td>HMAD</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>HMEAN</td>
<td>3.6</td>
<td>0.73</td>
<td>22.9 m</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>HMAX</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Yellow-bellied Sapsucker (<em>Sphyrapicus varius</em>)</td>
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<td>0</td>
<td>0.97</td>
<td>64.7%</td>
<td>1</td>
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<tr>
<td></td>
<td>HMAD</td>
<td>25.1</td>
<td>0.78</td>
<td>6.0 m</td>
<td>4</td>
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<tr>
<td></td>
<td>HMEAN</td>
<td>17.9</td>
<td>0.83</td>
<td>13.7 m</td>
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<td></td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>HMAD</td>
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<td>0.77</td>
<td>8.9 m</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>HMEAN</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>HMAX</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>0.77</td>
<td>65.6%</td>
<td>2</td>
</tr>
<tr>
<td></td>
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<td>0</td>
<td>0.78</td>
<td>8.0 m</td>
<td>1</td>
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<tr>
<td></td>
<td>HMEAN</td>
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<td>0.74</td>
<td>15.0 m</td>
<td>4</td>
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<td></td>
<td>HMAX</td>
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<td>0.76</td>
<td>33.3 m</td>
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<tr>
<td>Winter Wren (<em>Troglodytes hiemalis</em>)</td>
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<td>HMAD</td>
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<td>8.1 m</td>
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<td>0.74</td>
<td>15.5 m</td>
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<tr>
<td></td>
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<td>5.6</td>
<td>0.73</td>
<td>44.5 m</td>
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</tr>
<tr>
<td>Cerulean Warbler (<em>Setophaga cerulea</em>), First Atlas</td>
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<td>0</td>
<td>0.74</td>
<td>36.5%</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>HMAD</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>HMEAN</td>
<td>2.6</td>
<td>0.70</td>
<td>15.4 m</td>
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</tr>
<tr>
<td></td>
<td>HMAX</td>
<td>2.5</td>
<td>0.75</td>
<td>44.4 m</td>
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</table>
Cerulean Warbler (*Setophaga cerulea*), Second Atlas\(^2\)  

<table>
<thead>
<tr>
<th></th>
<th>Forest</th>
<th>0</th>
<th>0.85</th>
<th>29.1 %(^1)</th>
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<td>-</td>
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</tr>
<tr>
<td>HMEAN</td>
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<tr>
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<td>18.1</td>
<td>0.75</td>
<td>51.6 m</td>
<td>3</td>
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</tbody>
</table>

\(^1\)This threshold was not supported by visual evidence (loess plot).

\(^2\)Due to sample size limitations we were not able assess thresholds in extinction dynamics, but created separate models—based on detection data—for each Breeding Bird Atlas.
Figure 4.1. Overview of how two streams of research, one of extinction thresholds and one of inclusion of lidar in ecology, may merge and allow for broad-scale and yet detailed threshold studies.
Figure 4.2. The study area consisting of 10 counties in northern Pennsylvania, USA.
Figure 4.3. Typical response curves with extinction thresholds. Plots of locally weighted nonparametric models (loess) show thresholds in HMAX and HMEAN for (a) Yellow-bellied Sapsucker (*Sphyrapicus varius*) and (b) Winter Wren (*Troglodytes hiemalis*) respectively. The threshold in HMAX at 51.0-m for Yellow-bellied Sapsucker seems unlikely to be accurate (as this would mean that extinction probability peaks in areas with the highest trees in the entire study area), but the threshold in HMEAN for Winter Wren seems to be a true threshold: when HMEAN becomes lower than 15.5-m extinction probability increases rapidly.
Chapter V: Examination of extinction thresholds reveals that extinction probability peaks at intermediate levels of forest cover for certain forest breeding birds.

By: Yntze van der Hoek and Lisa L. Manne

Abstract

We add to a growing body of work on species responses to habitat loss, by presenting the observation of ‘hump-shaped’ relationships in loess plots of the relationship between extinction probability and forest cover (a habitat proxy). We tested if these hump-shaped curves could be the result of peaks in change in forest cover over time (CHANGE) in landscapes with intermediate to high forest cover. In addition, we tested whether CHANGE might be a more valid predictor of extinction probability than the often used predictor forest cover availability (FOREST) by creating logistic regression models with CHANGE or FOREST as predictor variables for 25 forest-associated breeding birds. Hump-shapes indicated high probabilities of extinction at intermediate levels of forest cover and CHANGE peaked in landscapes with intermediate levels of forest cover. CHANGE was the only significant predictor of extinction probability for four species, whereas FOREST was the only significant predictor for eight species. For two species, Black-and-white Warbler (Mniotilta varia) and Blackburnian Warbler (Setophaga fusca), both FOREST and CHANGE were significant predictors of extinction probability. Hump-shaped loess curves indicated that extinction events often peak at intermediate to high levels of forest cover, possibly as the result of peaks in change in forest cover in landscapes with intermediate levels of cover. Our results suggest that both forest cover and forest cover change can predict extinction probability for some species, but that neither is an adequate predictor for every species. This, we argue, is an important consideration in the discussion on the
conservation applications of species-habitat studies, and an indication that more detailed and species-specific approaches are required in threshold modeling.

**Introduction**

The effects of habitat loss, one of the largest current threats to biodiversity (Wilcove et al. 1998, Sax and Gaines 2003), on the extinction risk of species is one of today’s most studied and challenging topics in ecology (Sutherland et al. 2009). Studies of critical patch sizes (Fahrig 2001, Wilhere 2008), the effects of increased fragmentation on connectivity (Bailey et al. 2010, Schooley and Branch 2011) and especially studies of thresholds in species responses to habitat loss (Swift and Hannon 2010) have become commonplace in the last decade (Fahrig 2001, Rhodes et al. 2008, Betts et al. 2010, Swift and Hannon 2010, Zuckerberg and Porter 2010).

Many authors of publications on threshold studies, or other assessments of species responses to habitat loss and fragmentation, indicate their interest in species responses to habitat change over time (Denoël and Ficetola 2007, Betts et al. 2010, Montoya et al. 2010, Zuckerberg and Porter 2010). However, ‘change’ in habitat over time is rarely used as a predictor variable in landscape-scale threshold studies (but see Suarez-Rubio et al. 2013). We understand that the lack of long-term habitat data at the landscape scale restricts many researchers to the use of a gradient of habitat across the landscape as a substitute. But, we are also aware that habitat loss as a process often coincides with a drop in habitat quality, which may subsequently induce a decline in population growth rates and the size of the remaining populations (Hylander and Ehrlén 2013). Furthermore, those working on habitat thresholds should also keep in mind that habitat loss and disturbance might be highest in landscapes with intermediate habitat cover (Pardini et al. 2010), that thresholds might depend on the historical rates of change in addition to the amount of habitat currently available across the landscape (Schrott et al. 2005), and that threshold models
based on data collected at one point in time will not incorporate extinction debts (Hylander and Ehrlen 2013) and time lags (Rigueira et al. 2013).

For a larger project on the minimum habitat requirements of North American breeding birds we created threshold models (Muggeo 2003) to assess generalities in extinction thresholds (van der Hoek et al. 2013). During this project, we observed the existence of hump-shaped curves when we visualized the relationship between forest cover and extinction probability, with extinction probability peaking at intermediate to high levels of forest cover. Here, we explored the prevalence of such hump-shapes in the relationship of 25 forest associated breeding birds with forest cover. Next, we hypothesized that these peaks in extinction probability are correlated with habitat change over time, and investigated if change in forest cover over time correlated with availability of forest cover across a spatial gradient or if change in forest cover over time peaked in landscapes with intermediate to high forest cover—this would correspond with the notion that forest fragmentation (by development) in the Northeastern United States peaks in landscapes with around 85-90% forest cover (Riiters et al. 2012). Second, we investigated how models based on habitat change rather than availability performed by creating logistic regression models with either change or availability as the predictor variable.

We are aware that some readers might find ‘forest cover’ an inadequate proxy for habitat whether it captures a temporal change or not. We agree that a more detailed predictor variable would be ideal (e.g. the amount of early-seral broadleaved forest (Betts et al. 2010) or the amount of (standing) dead wood (Bütler et al. 2004, Poulin et al. 2008)), and suggest that future studies use ecologically relevant habitat proxies as predictor variables. However, we also recognize that the predictor variable ‘forest cover’ has been widely used in past threshold studies (Trzcinski et al. 1999, Fahrig 2001, Angelstam et al. 2003, Pardini et al. 2010, Zuckerberg and
Porter 2010), and is more widely available. Forest cover is therefore the most common variable used in policy and management related documentation (Wallace et al. 2003, Rompre et al. 2010, Environment Canada 2013), which is why we found it worthwhile to assess the specifics of this metric.

**Methods**

*Data: Breeding bird data*

We utilized the following data sources: Michigan Breeding Bird Atlas I (Brewer et al. 1991) and II (Chartier et al. 2011), the First (Andrle and Carroll 1988) and Second (McGowan and Corwin 2008) New York Breeding Bird Atlas, the First (Brauning 1992) and Second (Wilson et al. 2012) Atlas of Breeding Birds in Pennsylvania, Massachusetts Breeding Bird Atlas I (Petersen et al. 2003) and II (Kamm et al. 2013) and the First (Laughlin and Kibbe 1985) and Second (Renfrew 2013) Atlas of Breeding Birds of Vermont. These studies of breeding bird status distribution occurred during two separate time periods spaced approximately 20-25 years part. For all atlas projects volunteers and experts assessed breeding bird status at three levels of confidence (‘possible’, ‘probable’, and ‘confirmed’ breeding) in predetermined atlas blocks measuring approximately 5x5km. The location of atlas blocks was based on a grid of blocks overlaying the study area (the particular state). Sampling protocols are the same for each state; see each atlas for more detail.

The focal breeding bird species in our analyses were the same 25 forest generalists or obligates considered in van der Hoek et al. (2013) and Zuckerberg and Porter (2010). We considered birds to persist in an atlas block when found in both atlas periods, whereas extinction meant that birds were recorded only in the first atlas. We did not use every atlas block for our
analyses, as we excluded data from blocks with fewer than 75 breeding bird species recorded. We did this in order to achieve a coarse minimum level of adequately sampled blocks across states and to provide consistency across atlas projects (for Vermont, we only had access to data from ‘priority blocks’, which were randomly selected blocks that were surveyed until a minimum of 75 species were observed at any breeding level (confirmed, probable, and possible)(Renfrew 2013)). We are aware that the exclusion of blocks with fewer than 75 species detected may have effects on our models, but argue that these effects do not confound our conclusions because we are not presenting exact threshold estimates in this study but instead are focused on the general nature of species responses. In addition to the restriction to blocks with more than 75 species, we excluded blocks that were not fully located within the confines of the state in which an atlas was conducted, and blocks that consisted of a majority of water from our analyses. As a result, we obtained bird detection data for 181 atlas blocks (MI), 1392 blocks (NY), 673 blocks (PA), 146 blocks (MA) and 175 blocks (VT). Significant spatial autocorrelation would be important to take into account in our analyses (Araujo et al. 2002, Zuckerberg and Porter 2010); we used Moran’s I correlograms, created in R (R Core Team 2012) using the spdep package (Bivand et al. 2013), to test for spatial autocorrelation (Lichstein et al. 2002). We did not find significant spatial autocorrelation at any lag distance up to 500 km (P > 0.01), and because the atlas blocks were considerably spaced apart (>6 km on average between blocks) (Figure 5.1), we did not continue any further analyses of spatial autocorrelation nor did we include autocovariate terms in our analyses.

_Data: Land cover metrics_

We used the percentage of all forest cover (deciduous, coniferous and mixed) in each atlas block as derived from the 1992 National Land Cover Data (NLCD) as a predictor variable (for an
accuracy analysis see (Stehman et al. 2003)). We used the forest cover (proportion) per atlas block at this (1992) point in time as a predictor in our models. Forest cover was calculated by constructing numeric frequency histograms of land cover classes in the program ArcMap 10.1 (ESRI 2012).

**Models and statistical analysis**

We performed our analyses under two different data inclusion scenarios: 1) we included all atlas blocks regardless of the status of the breeding record of the focal bird, and 2) we included only atlas blocks where the focal bird was present in the first atlas.

For either scenario, we deemed a bird persistent when there was a form of breeding evidence in both atlases, absent when not recorded in either atlas, colonizing when recorded only in the second atlas and gone extinct when present in the first but not the second atlas. Under Scenario 1, blocks with extinction subsequently received a 1 and all other (colonization, absence, persistence) dynamics a 0. This scenario really explores the probability that an extinction event takes place given all possible dynamics rather than actual probability of extinction but. We included this scenario because it is consistent with earlier use in literature (Zuckerberg and Porter 2010), warranting analyses of the sensitivities of this modeling approach. In contrast, the second scenario explores the actual probability of extinction because we considered only sampling units where a bird was at least present in the first atlas. For extinction dynamics, blocks where the birds went extinct took a value of 1 and a 0 where the bird persisted (and vice versa).

Next, we visualized the relationship between forest cover and extinction probability using fitted values of locally weighted nonparametric models (loess plots with smoothing parameter 0,75) (Muggeo 2003, Ficetola and Denoel 2009, Zuckerberg and Porter 2010) using R (R Core
We created a total of 250 (25 x 5 x 2) of these loess plots; one for each species, each state and both scenarios and visually assessed the prevalence of hump-shaped curves (peaks at intermediate forest cover) in these loess plots.

Finally, we approximated forest cover change over the period between two atlas periods by calculating the difference between the proportions of forest cover in 1972 and 2000 per atlas block. We standardized this difference by dividing it by the total proportion of forest cover in 1972. We calculated proportions of forest cover in 1972 and 2000 by extracting USGS Land Cover Trend data from atlas blocks in all five focal states. Since USGS Land Cover Trend data are only accurately available for a limited number of sample blocks we obtained data for 157 atlas blocks in total. For this subset of atlas blocks, we visualized the relationship between forest cover change (CHANGE) and forest cover (FOREST) with a loess plot (smoothing parameter 0.75) and determined whether there was a significant relationship between the two variables using a linear model. Thereafter, we created logistic regression models (for both scenarios) that included either FOREST or CHANGE as predictor variables and determined whether either predictor variable was significant.

Results
We analyzed 250 loess plots for extinction dynamics (25 species x 5 states x 2 scenarios). Under scenario 1, we noticed that many curves for loess models (53) had a hump-shaped nature (as Blackburnian Warbler (Setophaga fusca) in Figure 5.2).

Some, but not all, loess plots for extinction dynamics with a hump-shape under scenario 1 had a hump-shape under scenario 2. At first sight, many loess plots seemed of a humped-shaped nature under this scenario, but a visual inspection of the data showed that the hump-shape in
extinction probability at intermediate levels of forest cover could be biased by having more samples (atlas blocks) in this region and hardly any at lower amounts of forest cover (Figure 5.3). Therefore, assessing the exact number of loess models that depicted a hump-shape became a subjective exercise we did not pursue. Nevertheless, hump-shaped curves remained evident for at least some species under scenario 2. This was particularly clear for Nashville Warbler (Oreothlypis ruficapilla) in Michigan and for Pileated Woodpecker (Dryocopus pileatus) in all five states (Figure 5.3).

We found no significant relationship between forest cover change (CHANGE) and forest cover per se (FOREST) (Wald tests; $F=0.009; P=0.92$). Instead, forest cover change seemed to peak at intermediate levels of forest cover when visualized through loess plots (Figure 5.4). We do note the large standard error in this loess approximation.

For scenario 1, FOREST was a significant predictor for Veery (Catharus fuscescens)($F = 5.36; P < 0.05$), Black-throated Green Warbler (Setophaga virens)($F = 2.82, P < 0.1$) and Hermit Thrush (Catharus guttatus)($F = 2.87, P < 0.1$) and CHANGE was a significant predictor for Magnolia Warbler (Setophaga magnolia)($F = 2.77; P < 0.05$), Red-breasted Nuthatch (Sitta canadensis)($F = 2.87, P < 0.1$) and Golden-crowned Kinglet (Regulus satrapa)($F = 2.99, P < 0.1$)(Table 1). FOREST was a significant predictor for extinction probability of seven species under scenario 2, including again Black-throated Green Warbler ($F = 18.5, P < 0.01$). CHANGE was again a significant predictor for Magnolia Warbler ($F = 11.44, P < 0.01$), as well as Blackburnian Warbler (Setophaga fusca)($F = 3.02, P< 0.1$) and Black-and-white Warbler (Mniotilta varia)($F = 4.51, P < 0.05$). Interestingly, both CHANGE and FOREST were thus significant predictors of the extinction probability of latter two species. Some of the species for which CHANGE was a significant predictor also showed a hump-shaped relationship between
forest cover and extinction probability. This was most noticeable for Golden-crowned Kinglet and Magnolia Warbler (Figure 5.5).

**Discussion**

Hump-shaped loess curves indicate that extinction events often peak at intermediate to high levels of forest cover (roughly 30-80%), rather than at low amounts of forest cover. Under scenario 1, these peaks in extinction events may be explained by higher numbers of samples (atlas blocks) with intermediate to high levels of forest cover or because the species could never go extinct because they were absent to start with (Figure 5.6). Therefore, we analyzed the species responses under an additional scenario in which we reduced the data to those atlas blocks where the focal bird was present in the first atlas (i.e. it could now either persist or go extinct). Surprisingly, we found that some, albeit not many, species’ extinction responses were still represented by a hump-shaped loess curve under scenario 2, for example Nashville Warbler and Pileated Woodpecker (Figure 5.3). These species showed persistence at low percentages or amounts of forest cover despite a peak in extinction probability at intermediate habitat amounts. This supports the notion that landscapes at intermediate levels of native vegetation cover hold the most potential for biodiversity management and conservation efforts (Pardini et al. 2010).

*Habitat change, not habitat availability, as a predictor of extinction probability*

We showed that high probabilities of extinction at intermediate levels of habitat could be the result of peaks in change in forest cover. We found no correlation between *change of forest cover* and the *proportion of forest cover at one point in time*, but a peak in *change of forest cover* in atlas blocks (and thus landscapes) with intermediate levels of forest cover. Moreover, we found change in forest cover to be a significant predictor of extinction probability for some
species, which indicates that change in forest cover might be a better predictor of extinction probability than forest cover per se, at least for these particular species.

We have not addressed why forest cover change might be most pronounced in landscapes with intermediate to high levels of forest cover, but argue that it might be related to distribution of land ownership (Riitters et al. 2012) and the clustering of protected areas (newly protected areas cluster around existing protected areas) (McDonald et al. 2007). Landscapes with a high forest density may be protected from conversion, whereas areas with low forest density have already been converted and experience little in terms of land cover change. In fact, Riiters et al. (2012) found that forest fragmentation by development (e.g. conversion of land cover to urban area, infrastructure) in the Northeastern United States increased with forest cover density in the landscape, with peaks around 85-90% forest cover.

*Other explanations for peaks in extinction probability at intermediate levels of habitat cover*

Many readers would likely support the suggestion that forest cover [change] is too generic and broad a habitat proxy. Indeed, we found that both FOREST and CHANGE were significant predictors of extinction probability for only few species (Table 5.1), reflecting that neither are adequate habitat proxies for the majority of species. For example, occurrence of Nashville Warbler is not only correlated with forest cover, but also with marsh (Chartier et al. 2011) and shrubland (Schlossberg and King 2008). The presence of these types of land cover in blocks with low forest cover may thus explain persistence in particular atlas blocks with low forest cover. Similarly, there are indications that occurrence of Pileated Woodpecker, the only species where the majority of extinction events were consistently found at mid-to-high levels of forest cover across all five states, correlates with the presence of specific habitat characteristics (snags,
specific tree species) rather than forest cover per se (Hartwig et al. 2004). The presence of such structural habitat variables could allow for persistence even in blocks with generally low amounts of cover (Blewett and Marzluff 2005). Therefore, we suggest that future studies, for example those with a threshold modeling approach, take into account habitat measures or metrics that are more ecologically relevant to the focal species. For example, measures of detailed vertical habitat characteristics such as canopy height (Goetz et al. 2007) or habitat definitions based on species distribution models (SDMs; Betts et al. 2014) might be more adequate for landscape-level studies of habitat loss and fragmentation. However, we do argue that studies like ours, that make use of generic habitat measures such as forest cover, are necessary if only due to the persistence of such broad habitat proxies in conservation and management. Forest cover might be less of a true representation of species habitat than it is an anthropogenic concept, but exactly for that reason it is easily interpreted and integrated into policy and management (Environment Canada 2013, Betts et al. 2014). One might place doubts on the validity of this use of generic and broad habitat definitions, but the fact that such definitions are used does imply that we need to analyze their applicability.

Finally, another possible explanation for the hump-shaped curves could be that species interactions that lead to extinction are more common in landscapes with intermediate levels of habitat cover. In extinction threshold modeling we usually take a single-species approach (Radford and Bennett 2004, Radford et al. 2005, Rhodes et al. 2008, Betts et al. 2010, Swift and Hannon 2010, Zuckerberg and Porter 2010). More recently, there has been a growing interest in understanding community-level thresholds (Baker and King 2010, Suarez-Rubio et al. 2013), but even here there is little focus on the influence of the species interactions on extinction thresholds. An extensive investigation of the effects of species interactions lies outside the scope of this
study, but we suggest that future studies take into account that marginal reductions in habitat availability (the focus of threshold studies) are not necessarily the only determinant of extinction probability. Instead, secondary extinctions induced by loss of biodiversity and shifts in trophic levels might be more probable in many cases (Komonen et al. 2000, Bellingeri and Bodini 2013, Roslin et al. 2013). As such extinction may be most pronounced in landscapes with intermediate to high levels of forest cover because it is in these landscapes that we see the first, and likely largest, reduction in biodiversity and number of trophic levels occurs (Roslin et al. 2013).

Concluding remarks

Habitat availability across a spatial gradient and change in habitat over time are two separate factors to consider in species-habitat modeling. Careful examination of either factor in our studies on the effect of habitat change on biodiversity is required, as these two factors do not necessarily induce the same species’ response (Bonthoux et al. 2013, Fukami et al. 2013, Pickett 1989). We emphasize that both forest cover and change in forest cover are unlikely to be perfect proxies for habitat. This is something to consider when we deduct conservation targets from studies on species responses to habitat loss (Lindenmayer et al. 2005, Johnson 2013) and supports the idea that a species-centered approach might be a worthwhile future direction (Betts et al. 2014). In addition, extinction might peak in landscapes with intermediate levels of habitat availability; thus indicating that conservation and management actions might be most efficient when targeted towards countering habitat change in such landscapes.

Acknowledgements

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Bureau of Wildlife (John Ozard), the Nature Conservancy (Kimberly Peters), Massachusetts Audubon (Joan Walsh) and the Carnegie Museum of Natural History (Andrew Wilson) for supplying and preparing bird atlas data, and the thousands of volunteers who gathered data. In addition, we would like to thank Timothy H. Keitt and two anonymous reviewers for many helpful suggestions.
Table 5.1. An overview of all significant CHANGE and FOREST models.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>Scenario 1</th>
<th>Scenario 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Least Flycatcher (<em>Empidonax minimus</em>)</td>
<td>FOREST</td>
<td>0.39</td>
<td>9.83 ***</td>
</tr>
<tr>
<td>Red-breasted Nuthatch (<em>Sitta canadensis</em>)</td>
<td>CHANGE</td>
<td>2.87 *</td>
<td>0.11</td>
</tr>
<tr>
<td>Hermit Thrush (<em>Catharus guttatus</em>)</td>
<td>FOREST</td>
<td>2.87 *</td>
<td>0.81</td>
</tr>
<tr>
<td>Veery (<em>Catharus fuscens</em>)</td>
<td>FOREST</td>
<td>5.36 **</td>
<td>2.09</td>
</tr>
<tr>
<td>Golden-crowned Kinglet (<em>Regulus satrapa</em>)</td>
<td>CHANGE</td>
<td>2.99 *</td>
<td>1.15</td>
</tr>
<tr>
<td>Black-and-white Warbler (<em>Mniotilta varia</em>)</td>
<td>FOREST</td>
<td>1.20 14.35 ***</td>
<td>1.15 4.51 **</td>
</tr>
<tr>
<td>Magnolia Warbler (<em>Setophaga magnolia</em>)</td>
<td>CHANGE</td>
<td>2.77 *</td>
<td>11.44 ***</td>
</tr>
<tr>
<td>Black-throated B. Warbler (<em>Setophaga caerulescens</em>)</td>
<td>FOREST</td>
<td>0.07 4.60 **</td>
<td></td>
</tr>
<tr>
<td>Black-throated G. Warbler (<em>Setophaga virens</em>)</td>
<td>FOREST</td>
<td>2.82 *</td>
<td>18.5 ***</td>
</tr>
<tr>
<td>Blackburnian Warbler (<em>Setophaga fusca</em>)</td>
<td>FOREST</td>
<td>0.41 26.25 ***</td>
<td></td>
</tr>
<tr>
<td>Ovenbird (<em>Seiurus aurocapilla</em>)</td>
<td>FOREST</td>
<td>1.01 6.56 **</td>
<td></td>
</tr>
<tr>
<td>Canada Warbler (<em>Cardellina canadensis</em>)</td>
<td>FOREST</td>
<td>1.89 3.64 *</td>
<td></td>
</tr>
<tr>
<td>White-throated Sparrow (<em>Zonotrichia albicollis</em>)</td>
<td>FOREST</td>
<td>0.25 7.7 ***</td>
<td></td>
</tr>
</tbody>
</table>

F-statistic derived from logistic regression.

Level of significance: *P < 0.01, **P < 0.05, ***P < 0.01
Figure 5.1. Maps of atlas blocks. All the atlas blocks in our five study states (MA, MI, NY, PA, VT) (top left) and the remaining blocks after we performed the exclusion criteria of only retaining blocks where \( \geq 75 \) species were recorded in both atlas sampling periods (bottom right).
Figure 5.2. **Loess plots of extinction dynamics for two bird species.** Loess plots showing the relationship between percentage of forest cover in an atlas block and the probability of extinction for two species (BTNW = Black-throated G. Warbler (*Setophaga virens*); BLBW=Blackburnian Warbler (*Setophaga fusca*). BLBW shows a clear hump-shaped relationship between extinction probability and the proportion of forest cover. Loess plots are based on a data-inclusion scenario where all data were included (absence, colonization, extinction, persistence) (scenario 1).
Figure 5.3. **Loess plots of extinction dynamics for three different bird species.** Loess plots for three species, Blackburnian Warbler (*Setophaga fusca*; BLBW), Nashville Warbler (*Oreothlypis ruficapilla*; NAWA) and Pileated Woodpecker (*Dryocopus pileatus*; PIWO) for a scenario where blocks where birds were not present (absence, colonization) in the first atlas were excluded from the analysis (scenario 2). Black dots represent atlas blocks (samples). Blackburnian Warbler shows a hump-shaped curve that seems driven by the low number of samples at lower levels of forest cover. In contrast, Nashville Warbler and Pileated Woodpecker seem to demonstrate actual peaks in extinction probability at intermediate to high levels of forest cover.
Figure 5.4. Relationship proportion of forest cover and proportion of change in forest cover. Loess plot of the relationship between the proportion of forest cover in atlas blocks in 1992 (x-axis) and the proportional change in forest cover between 1972 and 2000 (y-axis).
Figure 5.5. Loess plots for the species for which ‘change in forest cover’ was a significant predictor. Loess plots with smoothing parameter 0.75 show the relationship between extinction probability and forest cover (%). Hump-shaped curves are especially apparent for GCKI (Golden-crowned Kinglet (*Regulus satrapa*)) and MAWA (Magnolia Warbler (*Setophaga magnolia*)), and less obvious for RBNU (Red-breasted Nuthatch (*Sitta canadensis*)), BAWW (Black-and-white Warbler (*Mniotilta varia*)) and BLBW (Blackburnian Warbler (*Setophaga fusca*)).
Figure 5.6. Distribution of atlas blocks with different dynamics along a forest cover gradient. A) a kernel density plot of atlas blocks with absence, colonization and extinction or persistence for the Blackburnian Warbler (*Setophaga fusca*) in Vermont; B) a common pattern of kernel density plots: the majority of blocks with absences are found left of the peak of our typical hump-shaped curve, while extinction and colonization mainly occur in blocks with intermediate forest cover and persistence in blocks with a high forest cover.
Chapter VI: Extending the debate on the applicability of habitat thresholds for conservation: new directions for threshold studies.

By: Yntze van der Hoek, Benjamin Zuckerberg and Lisa L. Manne

Abstract

Habitat thresholds are increasingly promoted as conservation targets in natural resource policies and planning. However, several recent reviews and messages of caution on the application of habitat thresholds in conservation have largely fallen on deaf ears; leading to a dangerous oversimplification and generalization of the concept. Therefore, we urge scientists to increase their emphasis and communication of model sensitivities and variability in quantifying threshold estimates, but most importantly we advocate a broad shift in the use of conservation thresholds away from obtaining single nominal values with little specificity. Instead of focusing on single estimates, thresholds should be viewed as a comparative exercise in analyzing area-sensitivity or identifying environmental dangers. In addition, we should return to a focus on the understanding of the processes and mechanisms underlying species responses to habitat change. Finally, we argue that studies could focus on deriving nominal value threshold amounts, but only if the thresholds are detailed and species-specific. Such detailed threshold studies could benefit from developments in remote sensing technologies (e.g. LiDAR) and modeling approaches (e.g. species distribution modeling (SDM)).

On the applicability of habitat thresholds for conservation

‘Magic bullets’ (Huggett 2005) and ‘magic numbers’ (Flather et al. 2011, Lindenmayer et al. 2005) in ecology have an undeniable draw to conservationists and ecosystem managers. As global and regional extinction risk increases, we have no choice but to rapidly implement
justifiable and generally applicable conservation targets (Flather et al. 2011). Social factors and economic trade-offs add to the pressure to obtain such targets in a rapidly changing world (Wilhere 2008). However, there are issues concerning the search for general conservation targets (Akçakaya et al. 2011, Cardillo and Meijaard 2012, Flather et al. 2011, Lindenmayer and Luck 2005). For example, habitat thresholds vary largely across species and regions (van der Hoek et al. 2013), and conservation practitioners might not be aware of the many sensitivities (Swift and Hannon 2010), confounding factors (Ewers and Didham 2006) and potential pit-falls that plague threshold studies (Lindenmayer and Luck 2005, Suding and Hobbs 2009, Wilhere 2008).

Recent reviews have focused on the applicability of habitat threshold studies for conservation (Johnson 2013, Lindenmayer and Luck 2005, Swift and Hannon 2010). Johnson (2013) argues, like Lindenmayer and Luck (2005) before him, that there are limitations to applying ecological thresholds to conservation efforts. This message of caution is timely and well-justified because overgeneralization and simplification of habitat thresholds in management documentation is still commonplace (e.g., Environment Canada 2013, Kennedy et al. 2003, McAfee and Malouin 2008, Rompre et al. 2010, Wallace et al. 2003); a development that can potentially prove counterproductive to our ultimate goals of reducing, halting or reversing extinction risk. However, nuanced messages of concern and caution do not always filter through to policy makers and practitioners. Therefore, we should focus on conditions under which habitat threshold studies do hold strong potential for conservation and management, to more effectively steer managers away from the pitfalls of the ‘magic number’ approach. Herein, we briefly highlight the prevalence of oversimplification/over-generalization in policy documentation before summarizing new directions for habitat threshold studies that more strongly apply to conservation.
Dissemination and communication of threshold findings to policy makers and practitioners

Many authors of threshold papers emphasize that their results should not be interpreted as exact conservation targets and yet threshold values have slowly gained foothold as ‘magic numbers’. Authors of primary research papers often highlight the assumptions, confounding factors and sensitivities related to their threshold models, but these messages seem to be largely ignored in policy and management literature.

Some authors of peer-reviewed articles and policy papers express concerns of overgeneralization. For example, Ranius and Fahrig (2006) state that ‘within a forest region there are thousands of species with different habitat requirements’ and that as such ‘it will never be possible to summarize the requirements for biodiversity conservation in simple rules’. Unfortunately, we do not see such caution in actual policy documentation (Table 6.1). Generalization seems the norm, as the notion that threshold values depend on many factors is largely lost in management recommendations. Some recommendations related to forest management in British Columbia, Canada, profess that ‘less than 30% deviation [from the range of natural variation] is low risk and greater than 70% deviation is high risk. These figures were chosen because some research has shown habitat thresholds around 30% and 70%.’ (McAfee and Malouin 2008). Interestingly, for this statement the authors of the report refer to a review by Dykstra (2004), who herself noted that ‘the literature on thresholds in habitat amount is currently inadequate to provide general, quantitative, scientific basis for forest management in B.C.’.

Why are single habitat threshold values so easily incorporated as conservation targets into management and policy documentation, despite all the caveats? We argue that this is partly due to the way primary research is presented. For example, when authors mention that the majority of estimated thresholds fell between 10-30% habitat (Homan et al. 2004), then this might as well
be the main message managers take from their article. That there were also a number of thresholds that did not fall between 10-30% is easily forgotten. In addition, we agree with Johnson (2013) that economic and societal pressures drive a need for generalized conservation targets. In other words, when presented a range of habitat thresholds (e.g., 10-70%), it is clear that an agency focused on sustainable development will find the middle ground that is both scientifically credible and economically viable. Researchers should make management suggestions more specific, target their research on the local responses of species to habitat loss, and focus on identifying the actual processes that lead to biodiversity loss (Lindenmayer and Luck 2005, Wilhere 2008, Johnson 2013). Eventually managers have to balance the realism of resource scarcity, competing societal needs, and deliver results quickly and for a minimal cost; habitat thresholds represent the perfect, and misapplied, management linchpin (Wilhere 2008).

**Oversimplified messages might be counterproductive for conservation efforts**

We acknowledge that it might be impossible to derive species, habitat, or landscape-specific thresholds for every single case. However, a narrow focus on generalized threshold values in policy and management literature may lead to some potentially detrimental situations for conservation.

First, there is the danger that threshold values are misused; one could justify clearing or cutting the amount of habitat in excess of threshold values (Huggett 2005). This would be a harmful interpretation of thresholds, because we know that there is no single nominal value that will apply to all species in all landscapes (Swift and Hannon 2010). Furthermore, a threshold is merely the point where loss of individuals or species increases dramatically as a response of habitat loss; populations and species might experience negative effects above the threshold (Lindenmayer and Luck 2005). Third, determining thresholds in habitat availability is something
slightly different than assessing the effects of habitat loss. Habitat loss or conversion is usually associated with a loss of habitat quality and structure. Therefore, the amount of habitat we should actually preserve will need to depend on the quality of the remaining habitat, the quality of the matrix, the type and duration of the conversion, and other case-specific variables (Lindenmayer and Luck 2005).

Frequently, when researchers estimate thresholds for 5-10 species, the thresholds vary widely across the species. For example, five out of six species may have a threshold near 30% forest cover, but one species has a threshold of 88%. Such variation is often not captured (and thus not translated to policy) in concluding statements. In discussion sections, it is common to read statements such as ‘thresholds are mainly found near 30%’. Although this statement might be true, we should not focus on ‘average’ or most common thresholds, but rather on the highest ones, if we want to properly set conservation targets for all species. After all, species might be lost and populations in decline at habitat amounts way above average thresholds. Similarly, the broad range of habitat at which we find species-specific thresholds may diminish the applicability of results from community level threshold studies. We see a growing interest in assessing thresholds for communities of species, for example by use of the fairly novel threshold indicator analysis (TITAN) (Baker and King 2010, Suarez-Rubio et al. 2013). Such analyses group together species with different responses to environmental changes, obscuring the traits that may make some species more or less likely to demonstrate threshold responses. For example, habitat specialists might decrease in population size as a result of habitat loss but some generalists might actually do better (Rigueira et al. 2013). A full discussion of TITAN and its potential and pitfalls (Cuffney and Qian 2013) lies outside the scope of this paper. Nevertheless,
We emphasize that the conservation applications of TITAN studies would be worth considering in future studies and papers.

We acknowledge that we are not the first authors to warn against the overgeneralization of thresholds. In fact, Johnson (2013) reiterated the idea of adopting tiered risk-sensitive regulatory limits in policy and management (Bestelmeyer 2006, Environment Canada 2013). This system, where we define different limits in conservation risk, should incorporate uncertainty, stochasticity and be overall more conservative than using single value critical thresholds as conservation targets. For example, it would include the recognition of a cautionary limit, the level of habitat change at which we first recognize that there is change in response variable (e.g. population abundance). We applaud this effort towards a more conservative incorporation of thresholds in regulatory documentation, but argue that this approach does nothing to diminish the effects of species and landscape specific variation in thresholds. If single value thresholds vary largely between studies, species or landscapes, then so will the proposed cautionary, target and critical limits.

Potential of habitat threshold studies for conservation and management

Despite the caveats we do think that studies of habitat thresholds are potentially powerful when used appropriately. Specifically, we think that habitat thresholds studies might contribute to conservation when used 1) as a comparative exercise to identify life history characteristics, species, or landscapes that are relatively sensitive to habitat change; 2) to identify and understand threatening processes to populations and species; or 3) when habitat thresholds are derived specifically for species of interest, with ecologically relevant predictor variables (Table 6.2). We outline these possible, conservation-relevant, future directions for threshold studies below.
Threshold studies as a comparative exercise

Thresholds could be used to identify vulnerable species or landscapes. When comparing thresholds across species we might find those species that consistently require the highest amounts of habitat. This may be a major application of threshold studies, because—as Cardillo and Meijaard (2012) rightly point out—the limited resources available for conservation efforts require species-based prioritization. When we retain habitat at the level required by the most sensitive species, we indirectly protect many other species (Suarez-Rubio et al. 2013). Such sensitive species could be the indicator or umbrella species many conservationists are looking for (Lindenmayer and Luck 2005, Ranius and Fahrig 2006). In addition, comparative threshold studies might allow us to identify particular traits of either species (e.g. body size) or landscapes (e.g. amount of deciduous trees in a forested landscape) which would subsequently allow us to make predictions of the vulnerability to habitat changes for other species and landscapes. Is a particular species more or less likely to become threatened as a result of some small change in habitat loss if we know that it has a larger body size and less mobility than other species (Cardillo and Meijaard 2012)? Similarly, we could identify landscape characteristics that determine where thresholds are found. For example, Fahrig (2001) found that the quality of the matrix largely influences thresholds. As such, it would be useful to conserve and improve matrix quality in order to facilitate inter-patch migration and increase the availability of foraging and breeding habitat.

With the increased availability of species presence and abundance data at broad scales and remote sensing techniques we are now increasingly able to perform comparative research at a broad, landscape, extent. For example, we could gain from the increased prevalence of citizen-science derived breeding bird atlases (Dunn and Weston 2008), and use such bird atlas data to
assess regional and interspecific variation in habitat thresholds (van der Hoek et al. 2013). As a result, we can now start empirical studies on such questions as: Are there generalities in thresholds, or do thresholds correlate with landscape-specific variables (such as the quality of the matrix (Fahrig 2001))? Moreover, we can start to consider thresholds from a biogeographic perspective (Do species have lower thresholds near the center of their species range versus near the boundaries? Are there latitudinal gradients in thresholds?), or link the habitat threshold studies to closely related topics such as the effects of range contraction through climate change.

Habitat loss may be one of the most detrimental factors contributing to the loss of biodiversity, but the effects of climate change cannot be neglected (Butchart et al. 2010, Rands et al. 2010). We would like to emphasize that habitat loss and climate change are interlinked and that climate change may intensify the effects of habitat loss and fragmentation (Rands et al. 2010). Perhaps the most evident interaction of climate change and habitat loss can be found when looking at climate change induced species range shifts (MacLean et al. 2008, Visser et al. 2009, Both et al. 2010). Species at the edge of their range may have the opportunity to shift their range as a response to climate change, but only when the newly occupied landscape allows establishment and persistence. In contrast, range expansion will be inhibited when habitat availability, or the degree of habitat connectivity, is too low to support metapopulation persistence (Opdam and Wascher 2004). How thresholds themselves would change as a result of climate change effects, is a future question to address through threshold studies.

Threshold studies to identify and understand threatening processes

Other areas of ecology, such as systems ecology, have also focused on threshold dynamics and the idea of ‘tipping points’. Much of this research, whose case studies range from community
shifts in lakes (Carpenter et al. 2008) to paleoclimatic transitions (Dakos et al. 2008), identifies when small changes in environmental conditions trigger extreme system responses that are not easily reversed and lead to an abrupt shift towards a contrasting state. These events are referred to as critical transitions and are analogous to thresholds. Notably, however, many of these studies focus less on the exact point of a critical transition, but more on the early warning signals (Scheffer et al. 2009, Carpenter et al. 2011, Scheffer et al. 2012) preceding a threshold response. As an example, one of these early warning signals is the phenomenon of ‘critical slowing down’ where the recovery time of a system from a disturbance increases closer to the transition point (Scheffer et al. 2012). There is little information as to what would constitute early warning signals for populations inhabiting landscapes nearing habitat thresholds; however, a greater emphasis on altered demographic and population-level warning signals would deemphasize the search for the magic number.

Unfortunately, over the last decade, little research has been devoted to the understanding of the demographic processes leading to threshold responses. This is surprising given that the concept of extinction threshold was originally based on demographic models of territorial species (Lande 1987). We argue that it is critical to continue where theoretical studies (e.g. Fahrig 2002) left off, and to keep in mind the very processes that made us interested in estimating habitat thresholds in the first place: the negative effects of habitat change on population dynamics. Identification and subsequent treatment of causes for population decline probably has more conservation potential than aiming to find general threshold values (Flather et al. 2011). For example, since thresholds are found when mortality balances reproduction it may be useful to incorporate measures of reproduction and long-term persistence. To this purpose, researchers
conducting threshold studies could include measures of abundance instead of presence-absence, look at reproductive success and aim for longer, or repeated, sampling periods.

That there is no substitute for understanding the causes of species extinction (Lindenmayer and Luck 2005), also means that we need to know to which factors species actually respond. Currently, the most commonly used predictor variable in extinction threshold studies is habitat amount (in % or ha) (e.g. Zuckerberg and Porter 2010) but occasionally researchers aim to find thresholds in more specific habitat variables such deadwood values (Angelstam et al. 2003), or density of large trees (Poulin et al. 2008). In addition, predictor variables can concern either measures of habitat taken at one point in time, or actually reflect habitat change over time; a difference that could lead to potentially very different threshold interpretations. We argue that modeling species responses using a gradient of habitat characteristics across an area does not always make a perfect substitute for modeling species responses over time. Many authors claim in their articles that they are interested in species responses to habitat change (e.g. loss of forest cover) over time. Long-term species occurrence data are indeed used in some studies in order to approach a measure of persistence/extinction over time as response variables (Zuckerberg and Porter 2010), but ‘change’ in habitat over time is hardly ever used as a predictor variable. We understand that the lack of long-term habitat data at the landscape scale restricts many researchers to the use of a gradient of habitat across the landscape as a space for time substitute. However, we raise doubts on the assumption that a spatial gradient of habitat values is always a good proxy for habitat loss over time because habitat loss as a process often coincides with a reduction in habitat quality. Subsequently, a decline in habitat quality can induce a decline in population growth rates and the size of the remaining populations (Hylander and Ehrlen 2013). Furthermore, landscapes with low habitat
cover might not necessarily experience the highest amount of disturbance or habitat loss (Pardini et al. 2010) and thresholds might depend on the historical rates of change in addition to the amount of habitat currently available across the landscape (Schrott et al. 2005). Finally, threshold models based on data collected at one point in time will not incorporate extinction debts (Hylander and Ehrlen 2013) and time lags (Rigueira et al. 2013); these are additional factors to be considered when assessing species responses. For these reasons, when possible, we would advise incorporating habitat change over time in models (as done by Suarez-Rubio et al. (2013)).

Specific threshold modeling with ecologically relevant predictor variables

We posit that exact nominal threshold values could be appropriate as conservation targets when resulting from a more refined focus on estimating habitat. To derive such specific thresholds, however, we would need to redouble our efforts to capture habitat (Lindenmayer and Hunter 2010), and include detailed environmental variables that are ecologically relevant to our study species. Sometimes, we need to consider more complex descriptors of habitat (Evans et al. 2013). In other words, thresholds in habitat amounts seem to be species-specific, and yet we still use mainly generic habitat variables, such as ‘forest cover’, in our modeling approaches; variables that are not necessarily predictive of the presence of our study species.

A first step in threshold modeling with more detailed predictor variables could be to focus only on those specific vegetation types associated with a species’ presence or breeding habitat. For example, instead of considering all forest cover equal we could focus on coniferous or deciduous forest, two variables easily obtained from traditional remote sensing data such as the National Land Cover Data (NLCD) (Fry et al. 2011, Wickham et al. 2013). Even more informative, we could look at thresholds in the availability of a specific type of forest at a
specific successional stage, such as the done by Betts et al. (2010) for early-seral broadleaved forest. They were able to make use of the gradient nearest neighbor method (Ohmann and Gregory 2002). This method allows for integration of vegetation measurements from different sources: regional grids of field plots, mapped environmental data, and Landsat Thematic Mapper (TM) Imagery. For areas where all these data sources are available, it is possible to predict vegetation structure and composition at a relatively high (30-m pixel) resolution and rather large spatial extent (landscape scale). However, there are more approaches for defining habitat in threshold studies to explore, based on the use of light detection and ranging (lidar)(Goetz et al. 2007) or species distribution models (SDMs; Betts et al. 2014).

Studies such as the one by Betts et al. (2010) seem more informative for conservation than studies that make use of broad land cover types as predictor variables. After all, early-seral broadleaved forest cover is arguably a better proxy for a species’ habitat than ‘forest cover’. Unfortunately, the data used by Betts et al. (2010)—grids of field plots and other detailed data—are not always available for predictive modeling at broad spatial extents. Usually, we see a trade-off between the scale and the detail at which threshold studies can be performed. For example, persistence of some bird species might be better explained by the density of snags than the amount of forest cover (Poulin et al. 2008) and thresholds in more specific habitat proxies such as deadwood and snags have been the topics of previous studies (Bütler et al. 2004, Guénette and Villard 2005). However, surveying habitat characteristics such as snag abundance and canopy height through field work is costly and time-intensive, and can therefore only be done across relatively small spatial extents. Of course, traditional, passive, remote sensing techniques might allow us to obtain land cover characteristics across large extents, but they do not provide
information on vertical habitat features like canopy height or snag density. So, how could we overcome this trade-off between scale and detail?

Light detection and ranging (lidar), an active laser-based remote sensing technique, seems to have the potential to avoid the perennial scale-detail trade-off. Not only does lidar allow us to obtain detailed information on vertical habitat features, it allows us to analyze entire stands of forest, or even landscapes, in a relatively fast and affordable manner (Martinuzzi et al. 2009, Bassler et al. 2011, Tattoni et al. 2012). Modeling species responses with these kinds of data allows us to estimate thresholds in canopy height metrics. Such thresholds would be more accurate and translatable to conservation targets than thresholds in forest cover, and these conservation targets could moreover be achieved by a certain type of forest management (Martinuzzi et al. 2009, Vogeler et al. 2013). For example, in a preliminary study, we found that a bird species with a known preference for snags, Brown Creeper (Certhia americana), had a threshold in a canopy heterogeneity metric; a threshold above which extinction probability decreased rapidly. That extinction probability of this species decreases when canopy heterogeneity increases, coincides with the previously detected positive relationship between canopy heterogeneity and snag density (Martinuzzi et al. 2009). Thus, it is plausible that thresholds in lidar-derived characteristics can yield the species-specific conservation targets we so desire. We would have to consider this approach species-by species and region-by-region, but we could start with those species commonly considered umbrella or indicator species. After all, from the dissemination of detailed information on their threshold responses we could potentially extrapolate conservation targets to other species with lower habitat requirements (Poulin et al. 2008, Roberge et al. 2008).
Finally, we point to recent developments in the use of species distribution models (SDMs) to assess species responses to habitat loss and fragmentation (Betts et al. 2014). Keeping a species-centered approach, SDMs allow for definitions of habitat that are relevant to the focal species instead of definitions that are human-defined (i.e. forest cover). Betts et al. (2014) show that this species-centered approach allows for better predictions of species responses to habitat loss than approaches based on the use of generic measures of landscape structure. They did not search for thresholds in the availability of SDM defined habitat, but we argue that this new approach certainly has the potential to be utilized in threshold studies. Interestingly, Betts et al. (2014) point out that SDMs are, in potential at least, better predictors of species habitat than fine definitions of habitat type (e.g. using ‘black oak conifer forest’ instead of ‘oak forest’ or ‘forest’) as the latter is still based on an anthropogenic view of habitat. We welcome these new developments and agree with the authors that increased use of species-centered approaches will eventually allow for searches of greater generality in species responses to habitat change (Betts et al. 2014).

**Concluding remarks**

To summarize, we are wary of the use of threshold values as clear-cut conservation targets without a stronger evaluation of threshold value limitations and generalizability across multiple species and regions. Johnson (2013), Lindenmayer and Luck (2005) and Wilhere (2008) have also cautioned against the uncritical application of thresholds as conservation targets, but yet oversimplification remains common in conservation and management documentation. Therefore, we argue that it might be more effective to aim for a shift in focus; to ways in which thresholds do inform conservation. We are aware that we have not been fully comprehensive with regards to all the possible new directions and questions. For example, we have not addressed the issue of
community-level thresholds, for which new developments (e.g. TITAN (Baker and King 2010)) have emerged in the last few years. Nevertheless, it is apparent that with a new direction in threshold studies, and the availability of new datasets (e.g. citizen-science derived databases) and technologies (e.g. lidar), there is still ample potential for threshold studies to inform conservation. And, even if some of these conservation applications are indirect, threshold studies remain worthwhile research efforts. After all, threshold studies will always be an academic contribution to the knowledge of extinction dynamics under increased global habitat loss (Cardillo and Meijaard 2012). This, in itself, is a perfectly valid scientific exercise.

**Acknowledgements**

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Table 6.1. Examples of policy papers with a specific mention of threshold estimates as conservation targets.

<table>
<thead>
<tr>
<th>Country</th>
<th>Title</th>
<th>Statement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canada</td>
<td>Implementing Ecosystem-based Management Approaches in Canada’s Forests: A Science-Policy Dialogue (McAfee and Malouin 2008)</td>
<td>“A less than 30% deviation [from the range of natural variation] is low risk and a greater than 70% deviation is high risk. These figures (30% and 70%) were chosen because some research has shown that habitat supply thresholds around 30% and 70%”</td>
</tr>
<tr>
<td>Canada</td>
<td>How much Habitat is Enough? (Environment Canada 2013)</td>
<td>“50% forest cover or more at the watershed scale equates to a low risk approach that is likely to support most of the potential species”</td>
</tr>
<tr>
<td>Australia</td>
<td>Managing Natural Biodiversity in the Western Australian Wheatbelt: A conceptual framework (Wallace et al. 2003)</td>
<td>“Landscapes should contain a minimum of 30 to 40 percent habitat to minimize the risk of population extinction”</td>
</tr>
<tr>
<td>United States</td>
<td>Conservation thresholds for land use planners (Kennedy et al. 2003)</td>
<td>“…land use planners should strive to conserve at least 20 percent up to 50 percent of the total landscape for wildlife habitat, where possible.”</td>
</tr>
</tbody>
</table>
Table 6.2. Possible future directions, and associated questions, for threshold studies that are potentially relevant to conservation.

<table>
<thead>
<tr>
<th>Direction</th>
<th>Potential questions</th>
</tr>
</thead>
</table>
| **Threshold studies as a comparative exercise**             | • Are there generalities or trends in species- or landscape-specific variation in thresholds?  
|                                                             | • Can we use threshold studies to identify vulnerable species or landscapes?              
|                                                             | • Do species have lower thresholds near the center of their species range versus near the boundaries?  
|                                                             | • Are there latitudinal gradients in thresholds?                                       
|                                                             | • How do climate [change] and habitat thresholds interact?                             |
| **Threshold studies to identify and understand threatening processes** | • What would constitute early warning signals for populations inhabiting landscapes nearing habitat thresholds?  
|                                                             | • What are the demographic processes leading to threshold responses?                  
|                                                             | • Do species actually show threshold responses to habitat change over time?           |
| **Specific threshold modeling with ecologically relevant predictor variables** | • Are there thresholds in more detailed, and ecologically relevant, habitat variables (such as vertical habitat structure)?  
|                                                             | • Can we utilize new technologies, such as lidar, to detect such thresholds at broad scales?  |
Chapter VII: Discussion

Habitat loss is currently recognized as one of the most threatening processes for the persistence of species and biodiversity (Wilson 1985, Sax and Gaines 2003). Studies that assess the processes and impacts of habitat loss are therefore considered crucial for conservation efforts (Brooks et al. 2006). We currently recognize that ecosystem, community, and even population responses to habitat loss are best studied on a landscape-scale, and as such there is a call for more broad-scale studies of the effects of habitat loss—studies that can inform conservation and management (Rands et al. 2010).

In this dissertation, I took a broad-scale approach to explore the habitat requirements of North American breeding bird species. Various authors recognize that species-habitat relationships are often non-linear, and this observation culminated in the proposition of the extinction threshold hypothesis which states that there are specific amounts of habitat where there is a dramatic change in the probability of species extinction or persistence (Lande 1987, Andrén 1999, Fahrig 2001, Betts et al. 2010, Swift and Hannon 2010). Ideally, the detection of such thresholds could inform conservation, as threshold amounts of habitat could become the conservation targets desired by managers and policy makers (Lindenmayer and Luck 2005). However, it may be difficult to generalize as there is large regional and interspecific variation in thresholds (Rhodes et al. 2008, Betts et al. 2010, Zuckerberg and Porter 2010). In addition, thresholds are difficult to interpret because there are considerable accuracy (Shanahan and Possingham 2009), methodology (Ficetola and Denoel 2009) and scale and spatial extent issues (Holland et al. 2004, Betts et al. 2006, Desrochers et al. 2010) to take into account when modeling species responses.
I am interested in the sensitivities, generalities and variation of species-habitat relationships, and as such my first aim was to investigate whether landscape-level thresholds, derived for a suite of forest associated birds, vary regionally. Zuckerberg and Porter (2010) previously assessed thresholds in the relationships between extinction probability and forest cover across New York State for 25 bird species. In Chapter II, I present a comparison between the threshold estimates they derived for New York, and habitat thresholds I estimated for the state of Vermont. Not only did I find that threshold responses were not ubiquitous—less than half of the species showed more support for a threshold than a linear response—I also found considerable variation in threshold estimates across species and the between the two states.

After establishing that regional variation in thresholds is considerable, I focused on the causes of variation. After all, if we were able to assess the causes of variation, then we might be able to extrapolate results or derive generalities useful for management. To this purpose, I extended my comparative approach by estimating habitat thresholds for Michigan, Ohio, Pennsylvania, and Massachusetts (Chapter III). Subsequently, I compared the species-specific threshold amounts between all these states (as well as Vermont and New York), and between carefully selected ‘sub-regions’. Again, the results of my analyses confirmed that regional variation in thresholds is large and that estimates vary widely between species. Moreover, I found that threshold estimates vary widely within species across the various states or sub-regions. There was no universal trend in this variation that applied to all species, but a few species showed a significant increase in threshold amounts with increasing forest cover in the landscape. At first, these results seem to be in contrast with theoretical predictions that habitat requirements (threshold amounts) increase as landscapes get more and more fragmented (Fahrig 2002). However, as I explain in Chapter III, some species experience positive effects of
fragmentation or habitat loss because of species-specific traits or trade-offs in community composition. For example, some species may experience positive edge effects as a result of increased fragmentation (Parker et al. 2005). Alternatively, species may gain benefits from a reduction in patch isolation under certain conditions (Fahrig 2003). Whatever the cause of variation we can already conclude that not all species respond similarly to habitat loss. But, the next question is, did I actually analyze species responses to habitat change?

In Chapter IV, I present a new species-centered approach to habitat threshold studies. The availability of light detection and ranging (lidar) data allows us to measure detailed habitat aspects at landscape scales; aspects such as snag abundance or canopy height in which we can subsequently detect thresholds. This is an important development in threshold modeling, because habitat is species-specific and should be addressed as such, for example through a new species-centered direction in landscape ecology that is based on species distribution models (SDMs) (Betts et al. 2014). In fact, I myself questioned whether forest cover or forest cover change are adequate predictor variables (Chapter V), and concluded that a species-centered approach does indeed have more future potential in threshold studies. However, generic habitat measures are likely to remain commonly used throughout conservation and management literature, as they seem more easily interpreted by managers and policy-makers than thresholds in—for example—SDM based habitat measures. Whether this is justified or not is part of the debate (Betts et al. 2014), but either way it does imply that we need to analyze the validity and generality of thresholds in broad measures of habitat cover—which is in large the theme of this dissertation.

In line with most work on landscape-level thresholds (e.g. Betts et al. 2010, Zuckerberg and Porter 2010), I utilized a space-for-time substitution in order to assess thresholds in habitat availability across a spatial gradient, instead of habitat change over time. Some of the species-
habitat relationships explored in Chapters II and III exhibited a ‘hump shape’ when visualized through loess plots. When I investigated this phenomenon further (Chapter V), I found that some species persisted at low amounts of forest cover, even though they demonstrated a peak in extinction probability at intermediate levels of forest cover. These peaks in probability of extinction at intermediate levels of forest cover correspond with a peak in change in forest cover over time. As a result, I argue that change in forest cover over time might be a better predictor of extinction probability for at least some bird species. In addition, my findings support the suggestion that those landscapes with intermediate levels of native vegetation cover hold the most potential for immediate management and conservation efforts (Pardini et al. 2010). Finally, the hump-shaped curves in Chapter V also raise questions regarding 1) the role of interspecific interactions in determining extinction risk and 2) the value of using generic measures of habitat, like either forest cover or forest cover change, in predicting extinction or persistence probability.

Many authors have discussed the applicability of habitat threshold studies for conservation and management, occasionally pointing to the dangers of oversimplification of the threshold concept (Guénette and Villard 2005, Huggett 2005, Lindenmayer and Luck 2005, Groffman et al. 2006, Alados et al. 2010, Swift and Hannon 2010). In line with their work, I conclude my dissertation by addressing points of concern when applying threshold values and by providing suggestions for future research (Chapter VI). Variation in estimates and lack of generalities are issues of concern when taking single, nominal value, threshold amounts derived for one species, or one region, and applying them as conservation targets in other situations. I argue that scientists could play a larger role in diminishing the potentially harmful oversimplification of threshold studies by emphasizing the sensitivities of models and the variability of thresholds. More importantly, they could shift the focus of threshold studies to
more species-specific, detailed, and ecologically relevant thresholds or extend comparative work on the relative sensitivity of species and landscapes to habitat change.

Finally, determining the level and consistency of interspecific variation in thresholds would be an additional point to start future studies—a point I did not elaborate on in Chapter VI. I also did not specifically analyze interspecific variation across my study species, although I recognize that it would be interesting to see which traits make species more susceptible to extinction (i.e. which species have consistently higher threshold estimates than other species) (Blanchet et al. 2010, Ockinger et al. 2010). At first glance, it did not seem that my study species showed any specific pattern, as there was a lot of variation even within species across regions. For example, White-throated Sparrow (*Zonotrichia albicollis*) was on the high end of the spectrum of thresholds in Pennsylvania (~90% forest cover), but had a relatively low threshold estimate in Vermont (~12%). This lack of consistency might make it difficult to continue analyses of interspecific variation, but there is an additional—and perhaps more important—issue that we have to take into account. Since many of my study species are closely related, they represent only two orders (Passeriformes, Piciformes) and 13 families, it is important to correct for phylogenetic relatedness—an additional analysis which in itself can be a source of error (Revell 2010). Therefore, I suggest an extension of my research to more species, from a larger pool of families. If then, after the appropriate corrections, we consistently see outliers—species that have very high or low threshold estimates—then we would be able to select these species and derive more detailed thresholds for them. Such species could eventually be considered umbrella or indicator species, and the dissemination of detailed information on their persistence and extinction dynamics could greatly benefit the conservation of other species with lower habitat requirements (Poulin et al. 2008, Roberge et al. 2008).
In conclusion, evidence for habitat thresholds is abundant, but not ubiquitous, and threshold amounts vary too much between species and regions to allow for generalization towards single nominal conservation targets. This does not imply that threshold studies cannot inform conservation and management, but rather that we need to carefully consider the sensitivities of thresholds. Also, to reiterate slightly from Chapter VI, we still have little empirical proof of the suggested causes of habitat thresholds. I argue that more research on the mechanisms that cause thresholds could greatly benefit the integration of thresholds in conservation and management. After all, as Lindenmayer and Luck (2005) point out, when making ecological studies applicable to conservation, it is a ‘focus on causes, not symptoms, which enhances efficacy and efficiency’.
Appendix: Supporting Tables and Figures

Table S2.1. Comparisons between logistic (non-threshold) and segmented (threshold) regression models for 24 study species. Red-eyed Vireo (*Vireo olivaceus*) was also included in the analysis but excluded from this table because none of the models converged. This species thus did not support a logistic or a threshold relationship with forest cover. In fact, it was present in all surveyed atlas blocks. We compared the AIC for all models using delta AIC ($\Delta_i$), and selected a model when $\Delta_i > 2$ compared to the other model. We selected the model with the least number of parameters (non-threshold) when the difference between two models was $\Delta_i \leq 2$. In addition, we present the estimated threshold in the percentage of forest cover (%) and the associated standard error (SE) for the threshold models. For the selected models, we also present the Area Under the Curve statistic (AUC). The best model is highlighted in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dynamic</th>
<th>Model</th>
<th>AIC</th>
<th>$\Delta_i$</th>
<th>%</th>
<th>SE</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pileated Woodpecker (<em>Dryocopus pileatus</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>213.30</td>
<td>0.00</td>
<td>18.92</td>
<td>107.2</td>
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<tr>
<td></td>
<td></td>
<td>Non-Threshold</td>
<td>215.20</td>
<td>1.90</td>
<td>0.48</td>
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<tr>
<td></td>
<td>Extinction</td>
<td>Threshold</td>
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<td>37.51</td>
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<td>Yellow-bellied Sapsucker (<em>Sphyrapicus varius</em>)</td>
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<td>Threshold</td>
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<td>2.89</td>
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<td>31.92</td>
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<td>42.65</td>
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<td></td>
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<td>1.73</td>
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<td>Least Flycatcher (<em>Empidonax minimus</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
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<td></td>
<td>Extinction</td>
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<td>20.17</td>
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<td>0.00</td>
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<td>0.62</td>
<td></td>
</tr>
<tr>
<td>Common Raven (<em>Corvus corax</em>)</td>
<td>Persistence</td>
<td>Threshold</td>
<td>213.67</td>
<td>0.00</td>
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<td></td>
<td>Non-Threshold</td>
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Table S3.1. Overview of all threshold estimates (in % forest cover) for supported threshold models. Threshold estimates are only shown for supported models (AIC at least 2 lower than logistic regression model).

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<td>Average forest cover (state)</td>
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<td>White-throated Sparrow (<em>Zonotrichia albicollis</em>)</td>
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*Low sample size (N<10); no models were created.
Table S3.2. Overview of all threshold estimates (in % forest cover) for supported threshold models for the nine artificially created ‘landscapes’ (L1-9). Threshold estimates are only shown for supported models (AIC at least 2 lower than logistic regression model).

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*Low sample size (N<10); no models were created.*
Figure S2.1, Panel A
Figure S2.1, Panel B

Figure S2.2, Panel A
Figure S2.2, Panel B

Figure S2.2. Kernel density plots of estimated breakpoints (proportion of forest cover) for all subsamples (out of 5000) that supported a threshold model. Superimposed on these plots we see an estimation of the proportion of forest cover (the threshold) associated with the maximum kernel density of our sampling results (vertical full line) and the original threshold derived by Zuckerberg and Porter (2010) (vertical dotted line). Panel A contains results for thresholds in persistence, Panel B for thresholds in extinction. Explanation species codes: PIWO=Pileated Woodpecker (*Dryocopus pileatus*), YBSA=Yellow-bellied Sapsucker (*Sphyrapicus varius*), LEFL=Least Flycatcher (*Empidonax minimus*), CORA=Common Raven (*Corvus corax*), BCCH=Black-capped Chickadee (*Poecile atricapilla*), RBNU=Red-breasted Nuthatch (*Sitta canadensis*), BRCR=Brown Creeper (*Certhia americana*), WIWR=Winter Wren (*Troglodytes hiemalis*), HETH=Hermit Thrush (*Catharus guttatus*), VEER=Veery (*Catharus fuscens*), GCKI=Golden-crowned Kinglet (*Regulus satrapa*), REVI=Red-eyed Vireo (*Vireo olivaceus*), BHVI=Blue-headed Vireo (*Vireo solitarius*), BAWW=Black-and-white Warbler (*Mniotilta varia*), NAWA=Nashville Warbler (*Oreothlypis ruficapilla*), MAWA=Magnolia Warbler (*Setophaga magnolia*), BTBW=Black-throated B. Warbler (*Setophaga caerulescens*), YRWA=Yellow-rumped Warbler (*Setophaga coronata*), BTNW=Black-throated G. Warbler (*Setophaga virens*), BLBW=Blackburnian Warbler (*Setophaga fusca*), OVEN=Ovenbird
(Seiurus aurocapilla), CAWA=Canada Warbler (Cardellina canadensis), SCTA=Scarlet Tanager (Piranga olivacea), Dark-eyed Junco (Junco hyemalis (hyemalis)), WTSP=White-throated Sparrow (Zonotrichia albicollis).
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Peterjohn, B. G. and Rice, D.L. 1991. The Ohio breeding bird atlas. Ohio Department of Natural Resources, Columbus, OH.


Yntze van der Hoek was born in de Tynje, Opsterland, the Netherlands, on August 25th, 1984 to Bieuwkje van der Hoek-van der Meer and Klaas van der Hoek. At a young age he moved to the vicinity of Zwolle, the Netherlands, where he attended the Carolus Clusius College (VWO).

After a year in Ghana, where he volunteered as a primary and secondary school teacher, he returned to the Netherlands to obtain his Bachelor of Science in Forest and Nature Conservation, with a major in ecology, at the Wageningen University and Research Centre, Wageningen.

Having discovered the excitement travel can bring, and yearning for more experiences abroad, Yntze took another year to travel after completion of his Bachelor degree. This time around, he focused on his passions of wildlife, conservation biology, and ecology and decided to volunteer in an animal rehabilitation center in the Ecuadorian rainforest. During his prolonged stay in South America he traveled to several countries, and added Spanish to his vocabulary, before returning to Wageningen to pursue a Master of Science degree.

As part of this Master degree, Yntze found himself an internship position in Kenya at the Loita Foundation. Here, he explored the prospects and challenges of community-based nature conservation whilst collaborating closely with local Maasai communities as well as Dr. I.M.A. Heitkonig (Wageningen) and Dr. J.G. Grootenhuis (Nairobi). In addition, he conducted thesis research at the Lopé National Park in Gabon on the impacts of prescribed savanna burning on the diet and behavior of African forest buffalo (*Syncerus caffer nanus*). This thesis research was advised on by Dr. P. van Hooft (Wageningen) and Dr. K.J. Jeffery (Libreville). Yntze obtained his Master degree and decided, now a natural course of action, to explore more of the world and take a job as tour guide at the Dutch travel agency Djoser.

Yntze worked as a tour guide in Argentina, Bolivia, Brazil, Chile, Cuba, Paraguay, Peru and Venezuela for nearly a year before moving to New York City in 2010 to start a PhD in Biology at the Graduate Center of the City University of New York. While at CUNY, he received advisement from Dr. L.L. Manne on his exploration of species-habitat relationships of forest breeding birds and taught undergraduate courses at the College of Staten Island.