Review paper

Application of habitat thresholds in conservation: Considerations, limitations, and future directions

CrossMark

Yntze van der Hoek [a,b,*], Benjamin Zuckerberg [c], Lisa L. Manne [a,b]

[a] College of Staten Island, 6S-117, 2800 Victory Blvd, Staten Island, NY 10314, USA
[b] Graduate Center of the City University of New York, 365 5th Ave, New York, NY 10016, USA
[c] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

ARTICLE INFO

ABSTRACT

Habitat thresholds are often interpreted as the minimum required area of habitat, and subsequently promoted as conservation targets in natural resource policies and planning. Unfortunately, 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. We highlight the prevalence of oversimplification/over-generalization of results from habitat threshold studies in policy documentation, the consequences of such over-generalization, and directions for habitat threshold studies that have conservation applications without risking overgeneralization. We argue that in order to steer away from misapplication of habitat thresholds in conservation, we should not focus on generalized nominal habitat values (i.e., amounts or percentages of habitat), but on the use of habitat threshold modeling for comparative exercises of area-sensitivity or the identification of environmental dangers. In addition, we should remain focused on understanding the processes and mechanisms underlying species responses to habitat change. Finally, studies could that focus on deriving nominal value threshold amounts should do so only if the thresholds are detailed, species-specific, and translated to conservation targets particular to the study area only.

Contents

* Corresponding author at: College of Staten Island, 6S-117, 2800 Victory Blvd, Staten Island, NY 10314, USA.
   E-mail address: yntzevanderhoek@gmail.com (Y. van der Hoek).

1. 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 species extinction risk increases, immediate conservation actions are required to ensure that both species and their habitats will persist. Ideally, such actions would be based on careful analyses of species- and area-specific long-term data. However, as these data are not currently available for all species and regions, we often see no choice but to rapidly implement generally applicable conservation targets (Brook et al., 2011; 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—targets such as a minimum population sizes or minimum amounts (or areas) of habitat that need to be protected to ensure species persistence (Akcakaya et al., 2011; Cardillo and Meijaard, 2012; Flather et al., 2011; Lindenmayer and Luck, 2005). Interpreting habitat thresholds, amounts or percentages of habitat at which we see dramatic changes in the state (e.g., measured through persistence probability) of a population or species, as conservation targets (e.g., interpreting a habitat threshold found at 30% forest cover across a specific landscape as evidence that we should consider 30% forest cover as a minimum forest cover required for species persistence) may be especially problematic because thresholds vary largely across species and regions (Rhodes et al., 2008; van der Hoek et al., 2013, in press). In addition, 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).

Throughout the last decades, ecologists have focused on the applicability of habitat threshold studies for conservation (Andrén, 1994; Johnson, 2013; Lindenmayer and Luck, 2005; Mönkkönen and Reunanen, 1999; 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. Similarly, earlier work (e.g., by Betts et al., 2010; Ewers and Didham, 2006; Ficetola and Denoel, 2009; Villard and Jonsson, 2009) focused on the sensitivities of threshold models and estimates and lead to a general consensus that thresholds largely depend on factors such as the statistical approach used, the scale of the study, the focal species, and the geographic location of the threshold study.

The messages of caution that Johnson (2013) and others bring forth are 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, these nuanced messages of concern and caution do not always seem to filter through to policy makers and practitioners. We propose that pointing out pitfalls and bringing forward cautionary messages alone does not sufficiently decrease misinformed application of thresholds in conservation and management. Therefore, we suggest a 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. To that purpose, we highlight the prevalence of oversimplification/over-generalization of results from habitat threshold studies in policy documentation, the consequences of such over-generalization, and directions for habitat threshold studies that have conservation applications *without* risking overgeneralization.

2. Over-generalization: dissemination and communication of threshold findings to policy makers and practitioners

Scientists and managers interested in the application of habitat thresholds for conservation have raised concerns on the dangers 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 "it will never be possible to summarize the requirements for biodiversity conservation in simple rules". Unfortunately, these cautionary points are sometimes ignored in actual policy documentation. As most of such documentation is not peer reviewed, and cannot always be found following systematic reviews, we decided to opt for a simpler search (using the keywords 'threshold habitat conservation guidelines' in the search engine Google) to at least evaluate whether there is any evidence of the use of threshold/minimum amounts of habitat as conservation target in policy or management guidelines as drafted by advisory committees, non-governmental agencies, governmental institutions, or similar organizations (and whether such use was justified and done in a proper manner). We opted to assess the first eight papers and reports we found in this manner (Table 1), and found evidence of potentially misleading generalizations in at least four of these. Although it is difficult to extrapolate from such a simple review – as we are not looking for peer-reviewed papers in a database we are basically searching the entire internet, hence our restriction to the first eight papers – we can at least conclude that potentially dangerous that overgeneralizations or misuse of thresholds happens (we cannot comment on the commonness of such actions).

We acknowledge that an assessment of 'proper use' of thresholds in conservation guidelines is a rather subjective matter, and also point out that most papers included both generalizations as well as disclaimers and species- or area-specific information, none were strictly 'misusing' or 'properly applying' the threshold concept. Nevertheless, we found the species-specific considerations of thresholds as conservation targets as presented by Wallace and Tarr (2012), McAlpine et al. (2007) and Rosenberg et al. (1999) especially good examples of how threshold studies can inform conservation without resolving in overgeneralization. We highlight the study of Wallace and Tarr (2012).

Table 1

Examples of policy/management focused reports and papers with a specific mention of threshold estimates as conservation or management targets.

Country	Title	Excerpt
Canada	Implementing Ecosystem-based Management Approaches in Canada's Forests. A Science-Policy Dialogue (McAfee and Malouin, 2008)	"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%."
Canada	How much Habitat is Enough? (Environment Canada, 2013)	"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."
Canada	Suggested Conservation Guidelines for the Identification of Significant Woodlands in Southern Ontario (Ontario Nature, 2004)	"Environment Canada recommends a minimum threshold of 30% forest cover…important to note that 30% is a minimum recommendation only. …the most critical time for land planning and conservation appears to be when the landscape has 60%–90% of its area in natural vegetation."
Australia	Planning guidelines for koala conservation and recovery: A guide to best planning practice (McAlpine et al., 2007)	"The landscapes discussed here are typical of coastal eastern Australia and these results suggest that the amount of habitat, as a percentage of the landscape, required to sustain viable koala populations may be much higher than the commonly recognized 20%–30% for mammals and birds."
Australia	Managing Natural Biodiversity in the Western Australian Wheatbelt: A conceptual framework (Wallace et al., 2003)	"Landscapes should contain a minimum of 30% to 40% habitat to minimize the risk of population extinction."
United States	Conservation thresholds for land use planners (Kennedy et al., 2003)	"…land use planners should strive to conserve at least 20% up to 50% of the total landscape for wildlife habitat, where possible."
United States	Conservation Recommendations for Priority Terrestrial Wildlife Species and Habitats in North Carolina (Wallace and Tarr, 2012)	"Longleaf forest patches that are at least 2000 acres are needed to maintain viable populations of many species associated with Longleaf Pine habitats."
United States	A land managers guide to improving habitat for scarlet tanagers and other forest-interior birds (Rosenberg et al., 1999)	"If a landscape block surrounding a 50-acre forest patch is mostly forested (say, 70%), then it may be much more likely to support tanagers than the same sized patch in a landscape block that is only 20% forested."

Wallace and Tarr (2012) present conservation guidelines that are directly derived from habitat threshold studies, but in this case the guidelines are drawn from careful analyses (including expert opinion) of an extensive literature review. Moreover, for their guidelines the authors consider each habitat type found in their area of concern separately and created specific recommendations for a list of focal species in each focal habitat. As a result, they limit extrapolating across geographic areas, habitat types or species. Their recommendations are thus highly specific. For example, they provide the recommendation that "to maximize chances of protecting the full range of priority species that use upland forests in your community, target protection of contiguous forested blocks that are more than 7500 acres in size". Moreover, they add to that a number of additional considerations that managers need to make. For example, they note that we should "protect small woodlots and canopy covers in residential areas. Although many forest bird species are restricted to large woodlots for nesting, even small (3–5 acre) woodlots may be tremendously important as migratory stopover sites". In addition, they mention that we need to "maintain large trees and provide a continuous supply of potential roost trees for bats" and recommend to "retain snags and brush piles".

Wallace and Tarr (2012) provide an example –McAlpine et al. (2007) and Rosenberg et al. (1999) provide other examples – of a way in which thresholds could be used to inform conservation that does not require generalization (across species especially). Yet, we are wary that this is exactly what happens: messages derived from scientific exploration of some abrupt change points (e.g., those reviewed by Huggett, 2005), are gradually reaching policy and management literature (e.g., "Based on the studies reviewed in this document, we suggest using a minimum critical habitat threshold of between 30% and 40%" (Rompre et al., 2010)). Despite multiple disclaimers made by authors of such management-related documentation (e.g., "The critical habitat threshold should not be considered to be the ultimate target of the forest manager. Managers should rather be cautious and try to avoid reaching this point" (Rompre et al., 2010)), oversimplified statements eventually risk being used as conservation guidelines. For example, Rompre et al. (2010)'s findings are in turn the base for the claim that 'that while there is significant species-specific variability, to provide habitat for most forest dwelling birds in the context of eastern North America generally requires more than 30% forest cover (Environment Canada, 2013; see other examples in Table 1). So, what are the consequences if we *do* assume generalized habitat thresholds to be generalizable conservation targets, i.e. minimum habitat amounts/cover required for the persistence of many species?

3. Example of consequences of oversimplification of habitat thresholds as conservation targets

Considering nominal threshold values as conservation guidelines is worrisome and potentially misleading (Lindenmayer and Luck, 2005; Wilhere, 2008). Although authors such as Lindenmayer and Luck (2005) suggest in brief how using thresholds as conservation targets could in some circumstances lead to management decisions that are counterproductive, or at least not productive, to the conservation effort ("often arbitrarily chosen "threshold levels" for measures such as total vegetation cover may in fact not stem losses of some species from landscapes"), we do not know of any literature that clearly points out the potential consequences of overgeneralization and misuse of habitat thresholds. Here, we take a simple approach to illustrate some of these consequences. First, we consider habitat thresholds as 'minimum habitat amounts or

Table 2
Persistence probabilities for 25 bird species at three different forest cover levels. Persistence probability derived from logistic regression models under two scenarios: S1, probability of birds being recorded in the same Atlas block in both First and Second Breeding Bird Atlases (i.e., probability of persistence out of four possible dynamics: absence, colonization, extinction, persistence); and S2, the probability of birds being recorded in the Second Atlas if they were at least recorded in the First Atlas (i.e., reducing the number of possibilities: a bird could either 'persist' or 'go extinct'). Persistence probabilities below 0.5 in bold.

Species	S1 30%	S1 50%	S1 70%	S2 30%	S2 50%	S2 70%
Pileated Woodpecker (*Dryocopus pileatus*)	0.57	0.62	0.67	0.83	0.85	0.87
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	**0.16**	**0.34**	0.59	**0.49**	0.79	0.94
Least Flycatcher (*Empidonax minimus*)	0.60	0.70	0.79	0.80	0.84	0.88
Common Raven (*Corvus corax*)	**0.00**	**0.01**	**0.03**	1.00	1.00	0.99
Black-capped Chickadee (*Poecile atricapilla*)	0.99	0.99	1.00	0.99	0.99	1.00
Red-breasted Nuthatch (*Sitta canadensis*)	**0.08**	**0.17**	**0.33**	**0.24**	**0.42**	0.63
Brown Creeper (*Certhia americana*)	**0.17**	**0.27**	**0.40**	**0.38**	0.51	0.64
Winter Wren (*Troglodytes troglodytes*)	**0.02**	**0.06**	**0.16**	**0.23**	**0.41**	0.63
Hermit Thrush (*Catharus guttatus*)	**0.04**	**0.16**	**0.48**	**0.27**	0.57	0.83
Veery (*Catharus fuscescens*)	0.82	0.89	0.93	0.89	0.93	0.96
Golden Crowned-Kinglet (*Regulus satrapa*)	**0.02**	**0.05**	**0.13**	**0.28**	**0.37**	**0.47**
Red-eyed Vireo (*Vireo olivaceus*)	0.97	0.98	0.99	0.99	0.99	0.99
Blue-headed Vireo (*Vireo solitarius*)	**0.04**	**0.14**	**0.40**	**0.35**	0.58	0.78
Black-and-white Warbler (*Mniotilta varia*)	**0.18**	**0.35**	0.58	0.56	0.70	0.80
Nashville Warbler (*Oreothlypis ruficapilla*)	**0.04**	**0.09**	**0.18**	**0.22**	**0.33**	**0.46**
Magnolia Warbler (*Dendroica magnolia*)	**0.03**	**0.11**	**0.32**	**0.32**	0.53	0.72
Black-throated B. Warbler (*Dendroica caerulescens*)	**0.02**	**0.08**	**0.29**	**0.16**	**0.37**	0.65
Yellow-rumped Warbler (*Dendroica coronata*)	**0.08**	**0.22**	**0.47**	0.57	0.75	0.87
Black-throated G. Warbler (*Dendroica virens*)	**0.12**	**0.31**	0.60	0.54	0.74	0.88
Blackburnian Warbler (*Dendroica fusca*)	**0.02**	**0.08**	**0.30**	**0.21**	**0.45**	0.72
Ovenbird (*Seiurus aurocapilla*)	0.59	0.85	0.96	0.80	0.94	0.99
Canada Warbler (*Wilsonia canadensis*)	**0.05**	**0.12**	**0.26**	**0.27**	**0.38**	0.51
Scarlet Tanager (*Piranga olivacea*)	0.83	0.90	0.94	0.92	0.94	0.96
Dark-eyed Junco (*Junco hyemalis (hyemalis)*)	**0.14**	**0.32**	0.58	0.64	0.80	0.90
White-throated Sparrow (*Zonotrichia albicollis*)	**0.07**	**0.17**	**0.36**	**0.07**	**0.17**	**0.36**
Number of species with persistence probability< 0.5	**18**	**18**	**14**	**13**	**8**	**3**

percentages of cover' that we should strive to protect (as directly or indirectly stated in management and policy literature (Table 1)). Now we ask, what would it mean for multiple wildlife species if habitat cover would actually be at the level of that one generic threshold we assume to exist? What would their persistence probability be?

We consider the persistence probabilities of the 25 forest-associated breeding bird species studied in Zuckerberg and Porter (2010) and van der Hoek et al. (2013). In these studies, we assessed whether bird species were recorded in the first (which included records from 1980–1985) and the second (2000–2005) New York State Breeding Bird Atlases. If a bird was recorded in a 5 × 5 km Atlas block in both Atlases, we considered the bird 'persisting' in that block (a value 1), and 'absent, going extinct, or colonizing' (a value 0) in all other atlas blocks (Gates and Donald, 2000). In addition, we considered a scenario in which we reduced our dataset to include only Atlas blocks where the bird species was recorded in the First Atlas, and assessed whether the bird persisted in those Atlas blocks (i.e., it was also recorded in the Second Atlas) or went extinct (it was not recorded in the second Atlas). We took the same approach outlined in Zuckerberg and Porter (2010) and van der Hoek et al. (2013), and created logistic regression models of the relationship between forest cover (i.e., the percentage of land cover in an Atlas block that is determined as any type of forest) and persistence (under either of the two aforementioned definitions). We subsequently consider the predicted persistence probability at three levels of forest cover. First, we often see the generalization that 'most' habitat thresholds are found near 30% habitat (Huggett, 2005; Rompre et al., 2010), so we first considered a landscape-level forest cover of 30%. Second, we consider a level of forest cover representing the average of the habitat thresholds found in New York for these same study species (Zuckerberg and Porter, 2010), ∼50% forest cover. Finally, we assessed persistence probabilities at a forest cover level that equals the average threshold value found in a study that of the neighboring state Vermont, ∼70% (van der Hoek et al., 2013).

Evidently, persistence probabilities increase, and inversely the number of species with a persistence probability lower than 0.5 decrease, as forest cover in the landscape increases (Table 2). However, it is striking to see that the estimated persistence probability is lower than 0.5 for many species, even at forest cover levels of 70%. We are aware that there are some sensitivities to the brief analysis we present here, for example one might question our definition of 'persistence', doubt the use of 'detection-only' data, or point to the fact that we include species for which 'forest cover' might not be the most determining factor of persistence. Yet, this does not diminish the point we try to demonstrate here. Populations might already be at local extinction risk at levels of habitat availability way above those at which thresholds are commonly found (e.g., the 30%–40% mentioned in Huggett, 2005 and Rompre et al. (2010)). In fact, the local persistence probability of many species would be less than 0.5, even if landscape-wide forest cover in New York was reduced to levels similar to the average of the persistence thresholds we detected for the same study species in the same region (van der Hoek et al., 2013; Zuckerberg and Porter, 2010). In other words, nominal value habitat thresholds simply cannot be interpreted as habitat

Table 3
Possible future directions, and associated questions, for threshold studies that are potentially relevant to conservation.

Direction	Potential questions
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 individuals have lower thresholds near the center of their species range versus near the boundaries? ● Are there latitudinal gradients in thresholds?
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? ● How do climate [change] and habitat thresholds interact?
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?

amounts that are required to reduce risk of population extinction, they are simply not suitable to serve as such type of conservation targets.

4. Future directions: potential of habitat threshold studies for conservation and management

Researchers could aim to study the topic of habitat thresholds by posing questions other than "how much is enough?" (Johnson, 2013; Lindenmayer and Luck, 2005; Wilhere, 2008). Such questions (Table 3) would still give us further insights in species (threshold) responses, but answering them would not yield general numeric results (e.g., 'values/amounts' of habitat at which thresholds are found). As such, they would pose smaller risks of oversimplification or misuse of nominal threshold amounts as conservation targets. For example, threshold studies could focus on comparative analyses to identify life history traits, species, or landscapes that are more vulnerable to habitat change; similar to the attempt by Pe'er et al. (2014) to derive generalities for Minimum Area Requirements (MAR). In addition, threshold estimates could continue to be used to identify and understand the processes and mechanisms determining environmental threats to populations and species, a research direction we risk ignoring in a search for 'magic numbers' (Johnson, 2013). Finally, the estimation of nominal values is not necessarily a problem, as long it is derived and interpreted strictly for the focal species – avoiding extrapolation across both species and space – using ecologically relevant predictor variables.

4.1. Identifying vulnerable species and landscapes

A primary use of threshold analyses is to identify vulnerable species or landscapes. Comparisons of habitat threshold estimates could quickly identify those species that require the largest amounts of habitat. This is a major application of threshold studies because the limited resources available for conservation efforts require species-based prioritization (Cardillo and Meijaard, 2012). Further, when we conserve habitat at the level required by sensitive species, we indirectly protect many other species (Suarez-Rubio et al., 2013). In other words, the sensitive species would serve as umbrella species. In addition, comparative threshold studies have the potential to identify traits of either species (e.g., body size) or landscapes (e.g., habitat fragmentation) associated with increased vulnerability. For example, we can ask whether a particular species is more or less vulnerable to some small change in habitat loss if it has a larger body size and/or is less mobile 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 (as measured by the survival rate of the focal organism in 'non-habitat' patches) largely influences threshold sizes. As such, it is essential to conserve and improve matrix quality to facilitate inter-patch migration and increase the availability of foraging and breeding habitat.

Pe'er et al. (2014) provide an example of the comparative exercises we propose, by using figures on Minimum Area Requirements (MAR) of various taxa (derived through literature reviews) to conduct comparative analyses. They do not necessarily restrict themselves to the results of habitat threshold studies, they use results from both Population Viability Analyses (PVAs) and empirical studies of occupancy thresholds, but do show that it is possible to obtain information on the correlations between life-history traits and MAR. For example, there are strong indications that body mass correlates with MAR, a finding that supports earlier notions of such relationships (Allen et al., 1992). However, the study by Pe'er et al. (2014) also indicates that we have to assess the value of different approaches towards assessing minimum habitat requirements, as results from PVAs were different than those from empirical occupancy studies. In this light, it is important that we assess which data best allow us to conduct comparative exercises—e.g., should we focus on percentages of habitat derived from occupancy or occurrence threshold studies, or focus on Minimum Viable Population Sizes (MVPs) and PVAs?

Box I.
An underestimated pitfall in threshold studies: space-for-time substitution.

Habitat threshold studies are often intended to assess species responses to habitat loss/fragmentation over time (Swift and Hannon, 2010). However, predictor variables in habitat threshold models can incorporate either measures of habitat taken at one point in time, or reflect habitat change over time; a difference that might lead to very different threshold interpretations. We appreciate that a lack of land-use change data requires researchers to focus on the availability of habitat across a spatial gradient instead (e.g., space-for-time substitution Pickett, 1989). However, we doubt 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 (Bonthoux et al., 2013; Fukami and Wardle, 2005; Pickett, 1989). 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, disturbance or habitat loss over time does not necessarily occur most in landscapes with low levels of habitat cover (Pardini et al., 2010), but can peak in landscapes with intermediate levels of habitat cover instead, 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 advise incorporating dynamic habitat change in threshold models, instead of habitat availability as measured across a spatial gradient at one point in time. Suarez-Rubio et al. (2013) provide an example of truly using habitat change over time a threshold study, as they approximate change in landscape composition and configuration in their study area by estimating these features at different points in time (1986, 1993, 2000, and 2009).

4.2. Identifying and understanding broad-scale environmental threats

Early studies of habitat thresholds focused on the effects of habitat loss and fragmentation on demographic processes of local and metapopulations (e.g., migration, reproductive and mortality rates; Fahrig, 2002). Through such studies we started to understand the impact of several variables (e.g., matrix quality) on the persistence/extinction probability of populations. Along this line, we see that there are still ample opportunities to utilize threshold studies to gain understanding of processes and particularities of habitat change (Box I), without requiring researchers to provide exact nominal threshold values (amounts, percentages).

Future threshold studies could also focus on interactions of climate change and habitat loss, early-warning signals in population responses, or the demographic mechanisms driving threshold dynamics. For example, habitat loss and climate change are often linked and climate change may intensify the effects of habitat loss and fragmentation (Rands et al., 2010). How habitat thresholds might change as a result of climate change impacts is a useful future question to address through threshold studies. In addition, in systems ecology we see less of a focus on the exact point of a critical transition, but more on the early warning signals (Carpenter et al., 2011; Scheffer et al., 2009, 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 as the system approaches 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. In fact, little research has been devoted to understanding the demographic mechanisms leading to threshold responses. This is surprising given that the concept of extinction threshold was originally based on demographic models (Lande, 1987). It is critical to continue where theoretical studies left off, and to keep in mind the very processes that spurred us to estimate habitat thresholds in the first place: the negative effects of habitat change on population dynamics. Identification and subsequent treatment of demographic causes for population decline probably has more conservation potential than estimating exact threshold values (Flather et al., 2011). To this purpose, researchers conducting threshold studies could include measures of abundance instead of presence–absence (Grouios and Manne, 2009), evaluate reproductive success (Vance et al., 2003), and aim for repeated sampling over longer time periods (Willis and Birks, 2006).

4.3. Threshold estimation with ecologically relevant predictor variables

Exact nominal threshold values could be appropriate as conservation targets—as long as we are always aware of the condition that we cannot extrapolate threshold amounts across study areas or species. We do propose that such exact nominal threshold values should be derived through species-specific modeling, in which we use detailed descriptors of habitat as independent variables; i.e., we define habitat in ways that are ecologically relevant to our study species (Lindenmayer and Hunter, 2010). We are aware that it is not always possible to define habitat in such a way (e.g., because we do not know the habitat needs of a species a priori, or because we do not have the data available to assess habitat availability at the scales required for threshold modeling), but argue that we should at least strive to consider more complex descriptors of habitat instead of resolving to broad non-specific classifiers (Evans et al., 2013). In other words, thresholds in habitat amounts are species-specific, and as such we should avoid the use of generic habitat variables, such as 'forest cover', as much possible. We argue that we can make habitat classification or description more detailed by using new technologies and methodologies like vegetation data derived through light detection and ranging (LiDAR) (Goetz et al., 2007), or by following up on developments in species distribution models (SDMs) for defining habitat and use in ecological modeling (Betts et al., 2014).

5. 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 oversimplification remains common in conservation and management documentation. A shift in focus, addressing research questions other than 'how much is enough?' (Table 1), is necessary in order to really stay clear of potentially harmful applications of habitat thresholds in conservation. Most importantly, we should not forget the types of questions we wanted to answer when threshold studies first emerged (Andrén, 1994; Fahrig, 2001; Mönkkönen and Reunanen, 1999): what are the actual processes and mechanisms involved in species responses to habitat change and 'why' do thresholds exist?

Acknowledgments

References

Akcakaya, H.R., Mace, G.M., Gaston, K.J., Regan, H., Punt, A., Butchart, S.H.M., Keith, D.A., Gardenfors, U., 2011. The SAFE index is not safe. Front. Ecol. Environ. 9, 485–486.
Allen, E., Harris, J., Allen, L., 1992. Persistence-time models for use in viability analyses of vanishing species. J. Theoret. Biol. 155, 33–53.
Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71, 355–366.
Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A., Lindenmayer, D.B., 2014. A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. Ecography.
Betts, M.G., Hagar, J.C., Rivers, J.W., Alexander, J.D., McGarigal, K., McComb, B.C., 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. Ecol. Appl. 20, 2116–2130.
Bonthoux, S., Barnagaud, J.-Y., Goulard, M., Balent, G., 2013. Contrasting spatial and temporal responses of bird communities to landscape changes. Oecologia 172, 563–574.
Brook, B.W., Bradshaw, C.J.A., Traill, L.W., Frankham, R., 2011. Minimum viable population size: not magic, but necessary. Trends Ecol. Evolut. 26, 619–620.
Cardillo, M., Meijaard, E., 2012. Are comparative studies of extinction risk useful for conservation? Trends Ecol. Evolut. 27, 167–171.
Carpenter, S., Cole, J., Pace, M., Batt, R., Brock, W., Cline, T., Coloso, J., Hodgson, J., Kitchell, J., Seekell, D., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. Science 332, 1079–1082.
Environment Canada, 2013. How much Habitat is Enough? third ed. Environment Canada, Toronto, Ontario.
Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., Wilkinson, D.J., Wolkenhauer, O., Benton, T.G., 2013. Do simple models lead to generality in ecology? Trends Ecol. Evolut. 28, 578–583.
Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81, 117–142.
Fahrig, L., 2001. How much habitat is enough? Biol. Conserv. 100, 65–74.
Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecol. Appl. 12, 346–353.
Ficetola, G.F., Denoel, M., 2009. Ecological thresholds: an assessment of methods to identify abrupt changes in species-habitat relationships. Ecography 32, 1075–1084.
Flather, C.H., Hayward, G.D., Beissinger, S.R., Stephens, P.A., 2011. Minimum viable populations: is there a 'magic number' for conservation practitioners? Trends Ecol. Evolut. 26, 307–316.
Fukami, T., Wardle, D.A., 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proc. R. Soc. B: Biol. Sci. 272, 2105–2115.
Gates, S., Donald, P.F., 2000. Local extinction of British Farmland Birds and the prediction of further loss. J. Appl. Ecol. 37, 806–820.
Goetz, S., Steinberg, D., Dubayah, R., Blair, B., 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. Remote Sens. Environ. 108, 254–263.
Grouios, C.P., Manne, L.L., 2009. Utility of measuring abundance versus consistent occupancy in predicting biodiversity persistence. Conserv. Biol. 23, 1260–1269.
Huggett, A.J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biol. Conserv. 124, 301–310.
Hylander, K., Ehrlen, J., 2013. The mechanisms causing extinction debts. Trends Ecol. Evolut. 28, 341–346.
Johnson, C.J., 2013. Identifying ecological thresholds for regulating human activity: Effective conservation or wishful thinking? Biol. Conserv. 168, 57–65.
Kennedy, C., Wilkison, J.B., Balch, J., 2003. Conservation Thresholds for Land use Planners. Environmental Law Institute, Washington, DC.
Lande, R., 1987. Extinction thresholds in demographic models of territorial populations. Am. Nat. 130, 624–635.
Lindenmayer, D., Fischer, J., Cunningham, R., 2005. Native vegetation cover thresholds associated with species responses. Biol. Conserv. 124, 311–316.
Lindenmayer, D., Hunter, M., 2010. Some guiding concepts for conservation biology. Conserv. Biol. 24, 1459–1468.
Lindenmayer, D.B., Luck, G., 2005. Synthesis: Thresholds in conservation and management. Biol. Conserv. 124, 351–354.
McAfee, B.J., Malouin, C., 2008. Implementing Ecosystem-Based Management Approaches in Canada's Forests. A Science-Policy Dialogue. Natural Resources Canada, Canadian Forest Service, Science and Programs Branch, Ottawa.
McAlpine, C., Rhodes, J., Peterson, A., Possingham, H., Callaghan, J., Curran, T., Mitchell, D., Lunney, D., 2007. Planning Guidelines for Koala Conservation and Recovery: A Guide to Best Planning Practice. Australian Koala Foundation and The University of Queensland, Brisbane.
Mönkkönen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: A management perspective. Oikos 84, 302–305.
Ontario Nature, 2004. Suggested Conservation Guidelines for the Identification of Significant Woodlands in Southern Ontario. Federation of Ontario Naturalists, Toronto, Ontario.
Pardini, R., Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS One 5, e13666.
Pe'er, G., Tsianou, M.A., Franz, K.W., Matsinos, Y.G., Mazaris, A.D., Storch, D., Kopsova, L., Verboom, J., Baguette, M., Stevens, V.M., 2014. Toward better application of minimum area requirements in conservation planning. Biol. Conserv. 170, 92–102.
Pickett, S.T.A., 1989. Space for time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), Long-Term Studies in Ecology: Approaches and Alternatives. Springer, New York, pp. 110–135.
Rands, M.R., Adams, W.M., Bennun, L., Butchart, S.H., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P., 2010. Biodiversity conservation: challenges beyond 2010. Science 329, 1298–1303.
Ranius, T., Fahrig, L., 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scand. J. For. Res. 21, 201–208.

Rhodes, J.R., Callaghan, J.G., McAlpine, C.A., De Jong, C., Bowen, M.E., Mitchell, D.L., Lunney, D., Possingham, H.P., 2008. Regional variation in habitat-occupancy thresholds: a warning for conservation planning. J. Appl. Ecol. 45, 549–557.

Rigueira, D.M.G., da Rocha, P.L.B., Mariano-Neto, E., 2013. Forest cover, extinction thresholds and time lags in woody plants (Myrtaceae) in the Brazilian Atlantic Forest: resources for conservation. Biodivers. Conserv. 22, 3141–3163.

Rompre, G., Boucher, Y., Belanger, L., Cote, S., Robinson, W.D., 2010. Conservation of biodiversity in forest areas management: use of critical thresholds of habitats. For. Chron. 86, 572–579.

Rosenberg, K.V., Rohrbaugh Jr., R.W., Barker, S.E., Lowe, J.D., Hames, R.S., Dhondt, A.A., 1999. A Land Managers Guide to Improving Habitat for Scarlet Tanagers and Other Forest-Interior Birds. The Cornell Lab of Ornithology, Ithaca.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., Van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. Nature 461, 53–59.

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I.A., Levin, S.A., van Nes, E.H., 2012. Anticipating critical transitions. Science 338, 344–348.

Schrott, G.R., With, K.A., King, A.W., 2005. On the importance of landscape history for assessing extinction risk. Ecol. Appl. 15, 493–506.

Suarez-Rubio, M., Wilson, S., Leimgruber, P., Lookingbill, T., 2013. Threshold responses of forest birds to landscape changes around exurban development. PLoS One 8, e67593.

Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. Trends Ecol. Evolut. 24, 271–279.

Swift, T.L., Hannon, S.J., 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biol. Rev. 85, 35–53.

Vance, M.D., Fahrig, L., Flather, C.H., 2003. Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. Ecology 84, 2643–2653.

van der Hoek, Y., Renfrew, R., Manne, L.L., 2013. Assessing regional and interspecific variation in threshold responses of forest breeding birds through broad scale analyses. PLoS One 8, e55996.

van der Hoek, Y., Wilson, A.M., Renfrew, R., Walsh, J., Rodewald, P.G., Baldy, J., Manne, L.L., 2015. 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. Divers. Distrib. in press.

Villard, M.-A., Jonsson, B.G. (Eds.), 2009. Setting Conservation Targets for Managed Forest Landscapes. Cambridge University Press, Cambridge.

Wallace, K.J., Beecham, B.C., Bone, B.H., 2003. Managing Natural Biodiversity in the Western Australian Wheatbelt: A Conceptual Framework. Department of Conservation and Land Management, Perth, Australia.

Wallace, J., Tarr, N., 2012. Conservation Recommendations for Priority Terrestrial Wildlife Species and Habitats in North Carolina. North Carolina Wildlife Resources Commission, Raleigh, North Carolina.

Wilhere, G.F., 2008. The how-much-is-enough myth. Conserv. Biol. 22, 514–517.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265.

Zuckerberg, B., Porter, W.F., 2010. Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. Biol. Conserv. 143, 952–962.