Do empirical thresholds truly reflect species tolerance to habitat alteration?

Jean-Sébastien Guénette and Marc-André Villard

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The search for thresholds in natural phenomena is not new. Nonetheless, the detection of thresholds in species response to habitat alteration has recently received a lot of attention from conservation biologists and ecosystem managers. Ecological phenomena such as species occurrence and processes exhibiting a step function or threshold in their response to the alteration of habitat structure have obvious implications for conservation. Furthermore, researchers should try to identify a specific cut-off value or at least, a narrow range of values along an alteration gradient for application purposes. Owing to the paucity of objective statistical methods, or to the failure of researchers to apply them in ecology, specific threshold values or ranges are rarely identified. In this paper, we examine issues related to the detection of threshold responses to habitat alteration, specifically 1) the selection of meaningful parameters of biological response and indicators of habitat alteration, and 2) statistical considerations associated with the identification and interpretation of nonlinear responses (focusing on breakpoint regression and ROC analysis). We use theoretical data sets with predefined thresholds to validate threshold values determined by these methods. We also distinguish and interpret different types of thresholds that can be observed empirically. Then, we examine the robustness of threshold values to differences in sample size and in the extent of the habitat alteration gradient sampled and finally, we explore issues concerning data partitioning to control for confounding effects of other factors (e.g., stand composition, geographical variation). The issues discussed here will have direct implications in future research assessing threshold responses to habitat alteration.

J.-S. Guénette and M.-A. Villard (correspondence: villarm@umoncton.ca), Chaire de recherche du Canada en conservation des paysages and Département de biologie, Univ. de Moncton, Moncton, Nouveau-Brunswick, Canada E1A 3E9.

Identifying critical thresholds in species response to habitat alteration is a promising approach to address ecological questions and to provide answers that are meaningful from a management perspective. This approach is not a new one as it is very similar to dose-response curves used in health sciences (e.g., Greiner et al. 2000, O'Meara and Sevin 2001). In ecology, threshold responses have been sought in studies inspired from island biogeography to identify the minimum area of habitat fragments ensuring the presence of species (e.g., Robbins et al. 1989). The threshold concept recently gained momentum in the study of habitat fragmentation effects, where several authors have sought thresholds in habitat loss beyond which these effects become significant (Andrén 1994, Hill and Caswell 1999, Flather and Bevers 2002). Several authors have also examined nonlinear responses of certain species to gradients in habitat alteration or surrogates thereof, either empirically (Jansson and Angelstam 1999, Villard et al. 1999) or

through simulation modelling (With and King 1999, Fahrig 2001). These approaches have obvious appeal for conservation planning because one can use them to identify threshold values or ranges in habitat alteration beyond which a given biological response changes suddenly. Documenting such thresholds for a wide range of species could then provide specific numerical targets for habitat management over spatial scales relevant to the organisms under study. For example, a target could be identified using species regionally most sensitive to alterations of their habitat (Jansson and Angelstam 1999, Mönkkönen and Reunanen 1999, With and King 1999, Fahrig 2001).

First, it is important to sort through the quickly expanding terminology surrounding the concept of a threshold. Thresholds in species responses are generally examined for nonlinear (or step) functions represented by a logistic curve (Fig. 1). A threshold corresponds to a range of values over which a certain property changes at a fast rate (Fig. 1a). One can also focus on specific values corresponding to the lower or higher portions of a threshold (Fig. 1b–e), or on the inflexion point. Fahrig (2001) defines an ecological threshold as the quantity of habitat at which effects of habitat configuration (fragmentation sensu strictu) are added to those of habitat loss and affect the persistence of populations. This type of threshold is also referred to as a "fragmentation threshold". Muradian (2001) proposed a more inclusive concept of ecological threshold, i.e. the critical values of an independent variable around which the system flips from one stable state to another. Extinction thresholds represent the amount or proportion of habitat in the landscape at which population persistence is ensured (With and King 1999, Fahrig 2002, Ovaskainen et al. 2002). Unfortunately, the concept of critical threshold is too often used loosely to refer either to ecological thres-

holds or to extinction thresholds. Moreover, the expression "critical threshold" is itself pleonastic; a threshold is, by definition, a critical point where a given property changes from one state to another.

In this paper, we will use the terms "occurrence threshold" or "persistence threshold" to refer to a value along a gradient in habitat alteration above which the occurrence or persistence of a species, respectively, become unlikely. Similarly, we will use a variety of other terms to refer to thresholds in other parameters of biological response (e.g. abundance, reproductive activity, etc.).

Several studies examining species/habitat relationships have identified threshold values. For example, Bütler et al. (2004a, b) found thresholds in the occurrence of the three-toed woodpecker *Picoides tridactylus* along a gradient in the density and basal area of dying trees and snags. Hansen et al. (1995) reported abundance thresholds in bird species corresponding to small changes in tree density. At the landscape scale, Jansson and Angelstam (1999) reported an occurrence threshold for the long-tailed tit *Aegithalos caudatus* corresponding to the distance among patches of suitable habitat. Reunanen et al. (2002) found an occurrence threshold in the presence of the Siberian flying squirrel *Pteromys volans* along a gradient in the area of habitat fragments.

If ecological thresholds are to become powerful tools in conservation planning and resource management, researchers must further explore their variability among species, geographical locations, landscape types, etc. Furthermore, numerous statistical issues should be explored 1) to objectively identify thresholds and 2) to understand the sensitivity of such "objective thresholds" to sample size, extent of habitat alteration gradient sampled, etc. Even when focal species or processes exhibit a "step function" (threshold) in their response to habitat alteration, researchers should still identify a specific cut-off value or, at least, a narrow range of values for applications to conservation. Moreover, the fact that thresholds vary among species and study areas can also complicate their application (Mönkkönen and Reunanen 1999, Fahrig 2001, Muradian 2001). To address this issue, Mönkkönen and Reunanen (1999) suggested using the persistence thresholds of the most sensitive species in a given region. In this case, the habitat requirements of those "umbrella-species" should ideally encapsulate those of less sensitive species found in the same guild (Bonn and Schröder 2001, Fleishman et al. 2001, Carignan and Villard 2002, Roberge and Angelstam 2004).

This paper addresses ecological and statistical issues associated with the analysis of nonlinear responses to habitat alteration. More specifically, we will 1) examine issues related to the selection of parameters of biological response and indicators of habitat alteration and 2) review statistical approaches and considerations when examining the shape of species' responses to identify specific threshold values or threshold ranges.
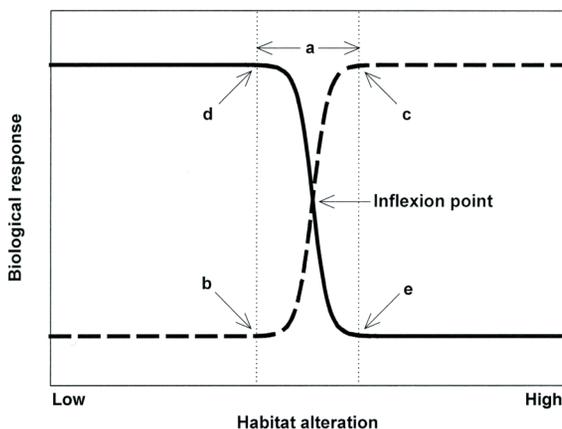

Fig. 1. Hypothetical logistic curves showing the response of species tolerant (solid line) or sensitive (dashed line) to habitat alteration, as well as critical parameters related to threshold ranges. The threshold range corresponds to "a". One may also be interested in the inflexion point, or in the level at which the curves start increasing or level off (b and c or d and e).

Selection of appropriate variables

Most empirical studies investigating threshold responses to harvesting intensity have focused on single species deemed particularly sensitive to the alteration of their habitat (Jansson and Angelstam 1999, Reunanen et al. 2002, Bütler et al. 2004a, b). Thus, the validity of recommendations based on such single-species studies depends on the quality of the focal species as umbrellas for other, ecologically similar species. However, the mere presence of these putative umbrella species at a site may be a relatively coarse estimate of their actual demographic status such as their probability of persistence. Various options exist to address this concern. First, one may use a fitness parameter (e.g., index of reproductive activity – Vickery et al. 1992, Gunn et al. 2000) as a response variable. For example, we compared threshold values obtained for the probability of presence and the probability of reproductive activity of the blue-headed vireo *Vireo solitarius* (Guénette and Villard unpubl.). As expected, the threshold values were higher for reproductive activity than for the mere presence of the species. Angelstam (2004) found the same pattern in the black grouse *Tetrao tetrix*. Consistent occupancy of a site by a species can also be used to obtain a more sensitive indicator of habitat quality than presence/absence during a single year or season. For example, one could search for a threshold response to habitat alteration using several levels of site occupancy: absent, present 1 yr, present 2 yr, etc. Ordinal logistic regression allows fitting models to this type of response variable (Hosmer and Lemeshow 2000).

Alternatively, one might argue that thresholds should be defined based on variations in species richness or total abundance of indicator taxa or guilds along a gradient in habitat alteration. This more "comprehensive" approach may be problematic, however, given the fact that response to habitat alteration tends to be species-specific (Villard et al. 1999, Hagan and Meehan 2002, Lichstein et al. 2002). We prefer the approach proposed by Mönkkönen and Reunanen (1999), which is to focus on threshold values exhibited by species most sensitive to habitat alteration.

Researchers aiming to provide recommendations concerning the effects of forestry on biodiversity must choose among a variety of indices or measurements of habitat alterations associated with silvicultural treatments. At the stand level, one can use variables such as canopy closure, density or basal area of snags or larger trees, etc. The problem with some of these variables, such as canopy closure, is that they may classify old-growth stands with canopy gaps as being more altered than second-growth stands or older plantations. Furthermore, using a single variable rarely succeeds in capturing the complex changes to stand structure/composition brought about by some forms of intensive silviculture. An alternative is to derive multivariate axes using appropriate statistical techniques (e.g., principal components analysis). This approach facilitates extraction of a linear combination of variables reflecting "harvesting intensity" (Guénette and Villard unpubl.). However, this is not always the case, because the linear combinations obtained may be dominated by variables reflecting both harvesting intensity and stand composition, for example.

Determination of cut-off value

Owing to their multivariate nature, ecological relationships are rarely characterized by sharp thresholds. Hence, an objective method must be used to determine threshold values when species exhibit significant, yet relatively gradual, nonlinear responses. When using a binary response variable (e.g., presence/absence), logistic regression is the most widely used modelling method. Manel et al. (1999b) compared model performance among three methods: logistic regression, multiple discriminant analysis, and artificial neural networks. Based on a series of performance criteria, they found that logistic regression outperformed the two other methods. However, the disadvantage of this method is that it does not directly provide a cut-off value to discriminate between predicted presence and absence. Several authors have simply used the x value corresponding to a predicted probability of 0.5 (e.g., Bisson and Stutchbury 2000, Madden et al. 2000), thus assuming that when $p < 0.5$, the event is unlikely to occur whereas it is likely to occur if $p > 0.5$. In some cases, the cut-off value was subjectively adjusted (0.25 instead of 0.5) to account for the proportion of false negatives (Reunanen et al. 2002). Not only are these criteria subjective, they also fail to account for the effect of species occurrence (or prevalence) on the shape of the logistic curve (Manel et al. 1999a, 2001). Indeed, in the case of rare species, the predicted probability of presence may never reach 0.5. Thus, the model predicts that the species is always absent, irrespective of habitat quality.

Thresholds in a species' binary response can also be identified based on relation optimisation. For example, Collingham et al. (2000) used Cohen's kappa, the proportion of correctly-predicted presences and absences after accounting for chance. This is considered to be one of the most appropriate methods for assessing prediction error for presence/absence data because it makes full use of both presence and absence scores, it measures agreement rather than association, and it varies between 0 and 1 (Fielding and Bell 1997). However, this measure may be sensitive to the sample size and to the distribution of values among classes (Forbes 1995). Another method, commonly used in medicine (see Zweig and Campbell 1993), has recently been applied in ecology: ROC analysis (Manel et al. 2001). ROC (receiver-operating characteristic) analysis makes it possible to determine a cut-off value based on a graph of all sensitivity and specificity pairs resulting from continuously varying the decision threshold over the entire range of data (DeLeo 1993). Sensitivity is the proportion of true positives correctly predicted, and specificity is

the proportion of true negatives correctly predicted (Manel et al. 2001). The area under the corresponding curve (AUC) represents an accurate measure of model performance, with 1.0 representing a perfect model (i.e. perfect discrimination of presence and absence) and 0.5 indicating no significant difference between the two events.

DeLeo (1993) suggested criteria for choosing a cut-off value from a ROC plot: 1) the point where optimum sensitivity is obtained; 2) the point where optimum specificity is obtained; 3) the point at which sensitivity and specificity are equal; and 4) the point where the sum of sensitivity and specificity is maximized. Maximum sensitivity or specificity could always be ensured by declaring all events positive or negative, respectively. Therefore, to choose our cut-off value, we used the point where sensitivity and specificity are maximised, because that point provides the best discrimination between predicted presence and absence.

To illustrate ROC analysis, we used a data set collected in deciduous forests of New Brunswick over a period of three years (n = 197 stations). We visited sampling stations three times each year during the peak of the breeding season of most forest birds. In this paper, we examine the relationship between the probability of presence of the ovenbird *Seiurus aurocapillus* and a gradient in harvesting intensity. This gradient is the second axis of a principal components analysis conducted on 15 local vegetation variables. This principal component explained 19% of the observed variance and was correlated with density and basal area of larger trees (> 20-cm dbh), canopy closure, and snag density, hence we interpreted it as a gradient in harvesting intensity (Guénette and Villard unpubl.).

Logistic regression shows that the probability of ovenbird presence in deciduous stands is negatively related to harvesting intensity (Table 1, Fig. 2, Guénette and Villard unpubl.). According to the area under the ROC curve, the performance of the model is high (AUC = 0.80; p < 0.001; Swets 1988). Sensitivity and specificity were maximized when y = 0.89. If we compare the threshold value obtained by this method with an arbitrary cut-off value of 0.5, the former seems more ecologically relevant: below this threshold, the ovenbird was present in almost all stations. The noise apparent above the threshold might reflect the influence of other factors such as landscape structure or the fact that some individuals occupy marginal habitat such as selection cuts (Bourque and Villard 2001).
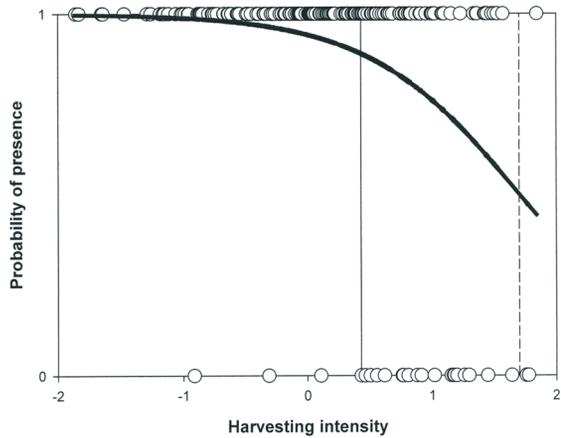

Fig. 2. Probability of presence of the ovenbird as a function of a PCA axis representing a gradient in harvesting intensity (n = 197). The dashed line indicates the threshold corresponding to a cut-off value of 0.5, whereas the solid line represents the value determined by using ROC analysis.

When using continuous dependent variables, there can be more than two stable states. However, it is conceivable that above a certain point, there is a discontinuity in the relationship between the predictor and the response variable. For example, the abundance of a species may increase more quickly when habitat quality reaches a certain threshold. In that case, we can use breakpoint regression (also known as piecewise regression), a nonlinear regression procedure that determines two relationships and a breakpoint that describes the highest proportion of the variance (Dodds et al. 2002). Breakpoint regression could be viewed as an analog to ROC analysis applicable to continuous variables such as species richness or abundance. This technique, like ROC analysis, is increasingly used in ecological research (see Losos and Schluter 2000, Dodds et al. 2002). Lomolino and Weiser (2001) used it to relate species richness to island area. They ran 101 regressions for each data set, incrementing the trial breakpoint by 0.1 at each iteration through the range of 0.0–10.0 (log-transformation of island area [m²]). They subsequently selected the value yielding the highest r² as the optimal breakpoint. They concluded that breakpoint regression can be used to test for the significance, and to explore patterns of variation in nonlinear relationships.

Table 1. Parameters of a logistic regression model predicting the presence/absence of the ovenbird in deciduous stands (n = 197) as a function of harvesting intensity.

Parameter	B	SE	Wald	DI	p
Harvesting intensity	−1.636	0.387	17.912	1	< 0.001

Types of empirical thresholds

Theoretically, three types of thresholds could be expected for a binary response variable. Thresholds are often represented schematically as a perfect relationship, i.e. no false positives or false negatives (Fig. 3a). Hereafter, we will refer to these thresholds as "Type I". Such a perfect relationship implies that the species in question only responds to the variable considered. However, owing to their multivariate nature, ecological relationships rarely if ever exhibit type I thresholds. On the other hand, when it is possible to control other significant variables, some quasi-perfect relationships of this type can be obtained (Guénette and
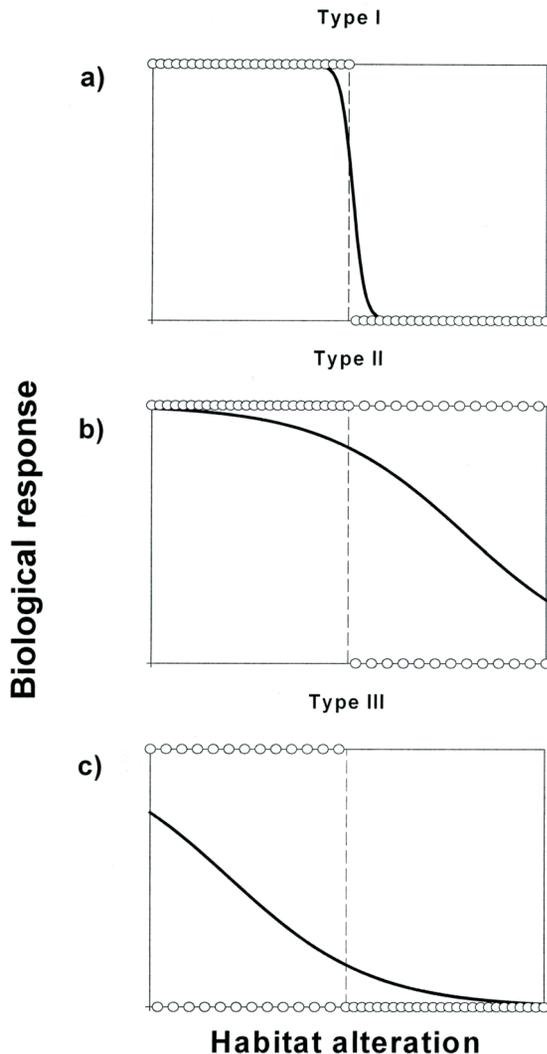

Fig. 3. Three types of thresholds that can be obtained as a function of habitat alteration, or inversely, habitat quality: a) type I, when the discrimination between predicted presence and absence is perfect, b) type II, where the species is always present below the threshold, and c) type III, where the species is always absent above the threshold.

Villard unpubl.). In general, however, we observe two other types of empirical thresholds. A threshold of type II (Fig. 3b) can be defined as the point along a gradient in habitat alteration below which the species is always present. Statistically, the sensitivity is equal to one. Above thresholds of this type, the species is only present in some stands. This implies that other variables come into play. For example, individuals observed in some marginal stands located above the threshold can be transients that do not actually reproduce in those stands. In conservation terms, this threshold is the least risky because species are relatively frequent along the entire gradient, even above the threshold. Therefore, a management plan based on type II thresholds should increase the probability of persistence of the species in some areas, while maintaining at least marginal habitat in portions of the land base falling above the threshold.

Empirical threshold type III (Fig. 3c) provides the clearest signal with respect to conservation. A species showing this type of threshold is only present in some stations below the threshold and consistently absent above this threshold. This pattern may reflect the fact that the species' presence is influenced by either one or many other variables or that the species does not saturate the suitable habitat. This type of threshold is thus very insightful for conservation. However, thresholds of type III should be applied conservatively by ecosystem managers, for example by adding a safety margin to the observed threshold value.

Validation of ROC-derived thresholds

To validate ROC analysis as a threshold detection method, we built a data set (n = 401 stations) with a pre-defined type III threshold (60.00) above which no stations were occupied by a hypothetical species. Below this threshold, species presence was randomly determined. We used the method previously described to build the logistic regression model. The area under the ROC curve was 0.84, indicating that the model has a high performance (see below). Using logistic regression parameters and the cut-off value obtained from ROC analysis, we calculated the threshold. The ROC procedure provided a cut-off value of 0.22, and an associated threshold of 60.09 (Fig. 4). This suggests that ROC analysis provides very accurate threshold values. The absence of noise in this data set only increased the area under the ROC curve. Swets (1988) pointed out that, to be considered useful, a model should have an area under the curve of at least 0.7. Thus, we recommend that thresholds only be provided to ecosystem managers when models reach such a performance.
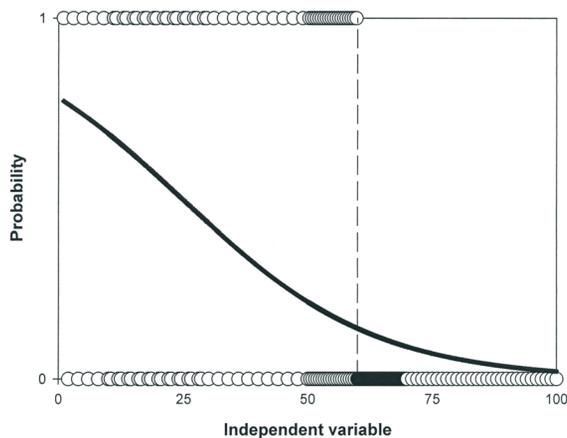
Fig. 4. Detection of extinction threshold for a hypothetical species. The threshold was predefined at 60.00 units, and ROC analysis detected a threshold at 60.09 units (dashed line). Above this threshold, the species is always absent (threshold type III – Fig. 3).

Sample size effect on threshold detection

Although we have found methods that enabled us to objectively identify threshold values in a species' response to the environment, we wanted to examine the robustness of these threshold values to differences in 1) sample size and 2) the extent of an ecological gradient that is sampled in a survey. To address the effect of sample size, we randomly removed data points (5–95% of the actual data points, 5% increments) from the observed relationship previously described for the ovenbird (Fig. 2) and recalculated the threshold value using ROC analysis after each iteration (50 times). We then plotted 1) the area under the ROC curve corresponding to each new model obtained and 2) the corresponding threshold values against sample size. Linear regression was used to assess sample size effect.

Sample size had a significant effect on model performance ($R^2 = 0.247$, $p < 0.001$; Fig. 5a) and on the threshold values found ($R^2 = 0.360$, $p < 0.001$; Fig. 5b). However, these relationships hinged on some influential points falling below a sample size of 145 and 100 respectively. When removing these points, the relationships became nonsignificant. These results are consistent with those of Cumming (2000). He concluded that model reliability increased with sample size. In our case, threshold values remained constant above a certain sample size (n = 100, 51% of the actual data points).

We also hypothesized that the portion(s) of an ecological gradient that are actually sampled influence the threshold values obtained. For example, a data set representing only the extreme values of a gradient might yield a strong threshold when in fact the logistic curve based on a more representative (i.e. continuous) gradient should be more
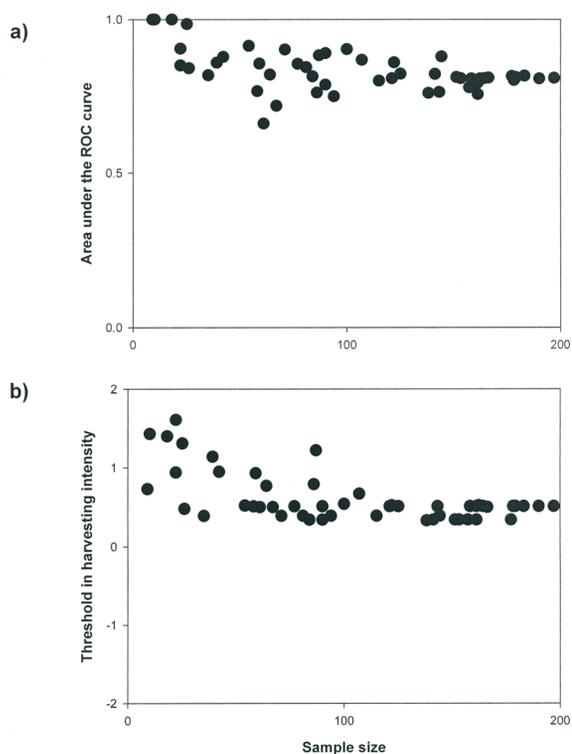

Fig. 5. Variation in a) the area under the ROC curve and in b) thresholds found in probability of presence of the ovenbird as a function of sample size. We randomly removed 5–95% from the original data set at each iteration

shallow, and the relationship possibly nonsignificant. To simulate this scenario, we randomly removed 5–95% of the data points (5% increments), starting from the center of the gradient. The area under the ROC curve increased nearly significantly with sample size ($R^2 = 0.074$, $p = 0.057$; Fig. 6a). The corresponding threshold values were also influenced by the removal of data points ($R^2 = 0.135$, $p = 0.009$; Fig. 6b). However, this is probably due to the high number of outliers appearing below a sample size of 100. Thus, as suggested by Hirzel and Guisan (2002), increasing sample size also increases sampling efficiency. However, the latter simulation also points out that relatively continuous gradients should be obtained when studying nonlinear relationships, because sampling the extremes of a gradient could artificially inflate the predictive power of models and yield misleading threshold values.

Data partitioning

Osborne and Suárez-Seoane (2002) recommended geographical partitioning of data sets when sampling is conducted over a large area. Spatial data partitioning improves distribution models because it better accounts for regional heterogeneity in predictor variables. On the other hand,
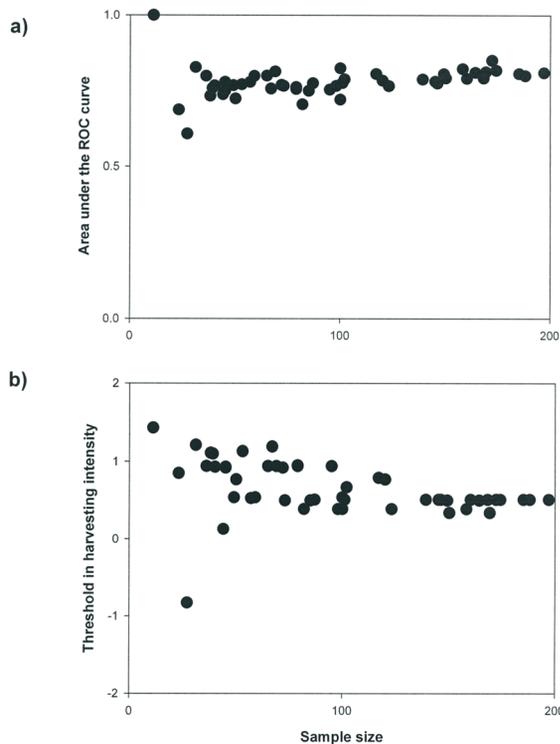
Fig. 6. Variation in a) the area under the ROC curve and in b) thresholds in the probability of presence of the ovenbird as a function of sample size. We randomly removed 5–95% from the actual data set at each iteration, starting from the center of the gradient.

Lichstein et al. (2002) suggested to control for local level effects before investigating landscape level relationships. Most studies assessing the relative influence of these two spatial scales concluded that species distribution is mainly influenced by variables characterizing local stand composition and structure (Drapeau et al. 2000), suggesting that landscape effects can only play a significant role when local conditions are favourable to species (Hagan and Meehan 2002, Lichstein et al. 2002). Therefore, it is wise to control for local-scale habitat relationships before investigating threshold responses to landscape-scale habitat alteration. One way to address this issue is to exclude stations with locally unsuitable habitat from analyses. Measuring vegetation structure and composition can be time-consuming, but the assumption that all habitat patches are equally suitable in terms of microhabitat can confound the interpretation of the actual relevance of landscape effects (Hagan and Meehan 2002).

Even at a relatively fine scale, it can be a good idea to partition data in terms of habitat type because most ecological studies are conducted in heterogeneous landscapes. For example, it is common practice to pool all sampling stations into a single data set, regardless of local habitat types sampled. Let us say a researcher samples forest birds

in coniferous, mixed, and deciduous stands, a given species would not be expected to react the same way to harvesting intensity in these three different stand types. Indeed, the probability of presence of the ovenbird in relation to harvesting intensity varied according to local stand type. The ovenbird was much more frequent in mixed and deciduous stands than in coniferous stands. Using the overall data set, the area under the ROC curve was 0.69 (relatively weak discrimination; lots of noise on either side of the threshold). For the three subsets, AUC = 0.69 for coniferous forests (n = 119), 0.93 for mixed woods (n = 103) and 0.80 for deciduous stands (n = 197). These results suggest that in mixed stands, harvesting intensity discriminates almost perfectly the presence/absence of this species.

In the two situations described above, it is necessary to determine this partitioning in an objective manner. The first option is to apply a stepwise logistic regression and to partition the data set according to the most influential variable. However, we can also use classification or regression trees to determine thresholds in species-habitat relationships. These methods are seldom used in ecology (but see De'ath and Fabricius 2000) but widely used to test predicted medical outcomes (e.g. Tafeit et al. 2000, Guzick et al. 2001). Those trees are constructed by repeatedly splitting the data set according to a simple rule based on a single explanatory variable. At each split, the data set is partitioned into two mutually exclusive groups, each of which is as homogeneous as possible (De'ath and Fabricius 2000). For each split, the χ^2 test is used to determine the optimal cut-off value. Selker et al. (1995) compared the performance of logistic regression and classification trees to predict binary outcomes. Based on the area under the ROC curve, they concluded that logistic regression had a slightly higher predictive performance.

Conclusions

As ecological researchers and ecosystem managers are increasingly seeing thresholds in species response to habitat alteration as potentially useful tools for conservation planning, we suggest to use, whenever possible, dependent variables reflecting the relative fitness of individuals rather than mere presence/absence or abundance. Otherwise, management recommendations may underestimate the requirements of certain species and, therefore, fail to provide the resources required for population persistence. Attention should also be paid to the type of empirical threshold obtained. For example, type III thresholds (Fig. 3c) may be the most critical with respect to conservation planning.

To objectively define thresholds in species response, we recommend the use of methods taking into account the frequency of occurrence of target species when determining a cut-off value (e.g., ROC analysis, classification trees). Moreover, researchers conducting studies in relatively large and ecologically diverse areas should consider partitioning

their data a posteriori to control some factors. This procedure ensures that thresholds obtained are not confounded by complex interactions among variables relevant to different spatial scales. Finally, if the objective is to determine thresholds for a guild or a community, we recommend the use of thresholds obtained for the most sensitive species rather than those obtained from species richness or total abundance of these species groups.

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