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Ecological thresholds: an assessment of methods to identify abrupt changes in species–habitat relationships

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Habitat thresholds are usually defined as "points of abrupt change" in the species–habitat relationships. Habitat thresholds can be a key tool for understanding species requirements, and provide an objective definition of conservation targets, by identifying when habitat loss leads to a rapid loss of species, and the minimum amount of habitat necessary for species persistence. However, a large variety of statistical methods have been used to analyse them. In this context, we reviewed these methods and, using simulated data sets, we tested the main models to compare their performance on the identification of thresholds. We show that researchers use very different analytical tools, corresponding to different operational definitions of habitat thresholds, which can considerably affect their detection. Piecewise regression and generalized additive models allow both the distinction between linear and nonlinear dynamics, and the correct identification of break point position. In contrast, other methods such as logistic regression fail because they may incorrectly detect thresholds in gradual patterns, or they may over or underestimate the threshold position. In conservation or habitat modelling, it is important to focus efforts efficiently and the inappropriate choice of statistical methods may have detrimental consequences.

Ecological thresholds are usually defined as "points or zones of abrupt change in ecological relationships" (Huggett 2005, Groffman et al. 2006). In recent years, determining whether ecological thresholds actually exist, and quantitatively estimating their value, has been considered a major challenge facing ecologists (Pulliam and Dunning 1997). Their existence and importance have been strongly debated, because of their relevance for understanding ecosystem dynamics and their potential implications for ecosystem management (Huggett 2005, Lindenmayer and Luck 2005, Groffman et al. 2006). The threshold concept has applications in multiple fields of ecology, including the analysis of shifts in ecosystem state, the determination of critical loads, and the evaluation of the effects of extrinsic factors (Groffman et al. 2006). Threshold analysis can allow quantitative assessment of species requirements, help to evaluate whether environmental changes will have critical consequences on ecosystem dynamics, and can identify conservation targets (Groffman et al. 2006, Denoël and Ficetola 2007).

Thresholds for species–habitat relationships have been proposed on the basis of empirical and theoretical studies showing that the relationship between habitat loss, patch size and isolation is nonlinear. During the process of habitat fragmentation, isolation increases abruptly when habitat loss reaches a critical threshold (Andrén 1994, With and Crist 1995, Keitt et al. 1997). When habitat cover falls below this threshold, the extinction of species that are negatively affected by isolation can happen abruptly (With and King 1999, Fahrig 2001, 2002). The identification of habitat thresholds, if they are actually present, can provide information on the minimum amount of habitat necessary for species persistence, and allow an objective definition of conservation targets. On the one hand, increasing habitat availability generally increases the probability of persistence for a given species. On the other hand, when availability rises above a threshold value, further increases in habitat availability will not significantly improve species persistence (Fahrig 2001, 2002). Therefore, ecological thresholds can help to determine the optimal allocation of resources for ecosystem management.

Even if thresholds are generally defined as zones of "abrupt change", there is no clear consensus on the statistical tools suitable for their identification (Olden 2007), and there is a wide discrepancy between the various methods that have been used to analyse them. This lack of an established methodology is a major obstacle to the objectivity and the promulgation of studies on ecological thresholds (Lindenmayer and Luck 2005, Betts et al. 2007).

Here we show that researchers use very different operational definitions of habitat thresholds, which can considerably affect threshold detection. In some cases, researchers try to identify sharp changes and break points in the relationships (Fig. 1a), which correspond to the above definition of a threshold as an ''abrupt change''. However, in cases where the threshold concept is applied in the absence of abrupt change, the operational definition of threshold may not be straightforward (Fig. 1b). In the latter case, researchers consider as a ''threshold value'' simply the value above which the probability of presence rises above a given figure [e.g. 50% (Bergman et al. 2004, Butler et al. 2004)]. These differences are probably related to the variety of statistical procedures used, with notable effects on the identification and position of the thresholds. To illustrate the large differences between approaches, we first reviewed the existing literature on the topic and compared the methods used to evaluate the presence and location of thresholds. Then, we analysed simulated datasets to show how these different approaches can produce very different results. We focused particularly on thresholds in the relationship between species distribution and habitat availability, and we aimed to find the most valuable methods for a straightforward understanding of species ecology and the application of efficient conservation measures. In a broader context, our results may be of interest for other fields of ecology where threshold patterns have been proposed, from the cellular to the ecosystem level (Bernays et al. 2003, Groffman et al. 2006).

Abrupt vs gradual change: an analysis of the literature

Our analysis included 26 papers that used statistical methods to evaluate thresholds in the relationships between habitat features and species occurrence or richness (Table 1). We found these papers by performing searches in the ISI Web of Science, and by inspecting papers cited by the retrieved papers. We observed three main groups of methods used to analyse thresholds.

A) The majority of papers (46%) used only generalized linear models (GLMs) or modifications of GLMs (such as linear mixed models). As the names themselves suggest, these methods are not designed to detect nonlinearity in relationships, or sharp transitions. Logistic regression (i.e. GLM assuming binomial error distribution, which is linear on the logit scale) was the most popular technique. The authors often considered as a ''threshold'' the value for a given environmental variable above which the probability of species presence rises above a given value (e.g. 0.5). Alternatively, some authors used receiver operating characteristic curves (ROC). They assessed the performance of models for many possible threshold values, and selected as ''threshold'' the value for the environmental variable maximizing the specificity and sensitivity of the model (Guénette and Villard 2005, Liu et al. 2005).

B) A second group (27% of papers) used nonlinear models, such as generalized additive models (GAMs), and nonlinear transformations of GLMs (Table 1). These methods are able to test whether relationships are nonlinear, but are not able to explicitly test whether an abrupt transition is present, and where it is located. Most authors that used these methods visually inspected the plots to evaluate the position of the threshold (for example, the position of the inflection point).

C) Finally, 35% of papers used techniques explicitly designed to detect the presence of discontinuities and abrupt changes. The methods used to detect abrupt transitions varied, and included piecewise/broken stick regression (Table 1). All these methods explicitly test 1) whether there is nonlinearity in the relationship and 2) whether an abrupt transition (= the threshold) can explain this nonlinearity.

Several papers used more than one approach, and the authors compared the relative performance of GLMs, GAMs and methods estimating discontinuities (Radford et al. 2005, Schmidt and Roland 2006).

Differences among methods used to identify thresholds: an analysis using simulations

To demonstrate the difference between the three analytical methods, we constructed eight series of artificial datasets with known properties, corresponding to the following

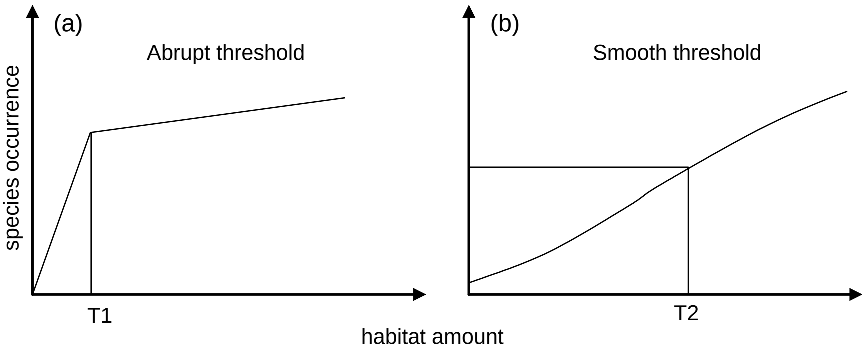

Figure 1. Two different approaches to the individuation of ecological thresholds. (a) ''Abrupt threshold'': the threshold is located where there is a sharp change in the relationship between species occurrence and habitat availability; redrawn from Homan et al. (2004). (b) ''Smooth threshold'': the threshold is located when species occurrence falls below a given value, also in absence of abrupt changes; redrawn from Guenette and Villard (2005).

Table 1. Papers on ecological thresholds reviewed. Only papers performing statistical analyses to evaluate the presence of thresholds are included. O: species occurrence; R: species richness.

Paper	Taxon	Species richness or occurrence?	Linear methods	Nonlinear methods	Methods estimating discontinuities	Methods used
Bergman et al. 2004	butterflies	O	X			Logistic regression
Betts et al. 2006	birds	O	X			Binomial generalized linear mixed models
Betts et al. 2007	birds	O			X	Piecewise regression
Butler et al. 2004	birds	O	X			Logistic regression
Denoël and Ficetola 2007	amphibians	O			X	Piecewise regression and strucchange
Dodd et al. 2006	mammals	O			X	Piecewise regression
Drinnan 2005	birds, amphibians, fungi, plants	R		X		Linear regression on log-transformed data
Ecke et al. 2006	mammals	O	X	X		Classification trees, logistic regression and exponential regression
Guénette and Villard 2005	birds	O	X			Logistic regression and ROC plot
Homan et al. 2004	amphibians	O	X		X	Piecewise regression and binomial changepoint test
Jansson and Angelstam 1999	birds	O	X			Logistic regression
King et al. 2007	birds	O	X			Logistic regression
Lindenmayer et al. 2005	birds, reptiles	R			X	Piecewise regression
Maron 2007	birds	O	X			Logistic regression
Potvin et al. 2005	mammals	O		X		Generalized additive logistic regression
Radford et al. 2005	birds	R	X	X	X	Linear, nonlinear and piecewise regression
Radford and Bennett 2004	birds	O	X			Logistic regression
Riley et al. 2005	amphibians	R			X	Piecewise regression
Rhodes et al. 2008	mammals	O	X		X	Piecewise regression
Rodriguez and Andren 1999	mammals	O	X			Logistic regression
Sarre et al. 1995	reptiles	O	X			Logistic regression
Schmidt and Roland 2006	butterflies	R		X	X	Polynomial and piecewise regression
Schultz and Crone 2005	butterflies	O		X		Incidence function analysis
Silva et al. 2005	mammals	R	X	X		Linear regression, smoothing and polynomial regression
Suorsa et al. 2005	birds	O	X			Logistic regression
van der Ree et al. 2004	mammals	O	X			Logistic regression

scenarios: Six scenarios assumed an abrupt change in the species–habitat relationship when habitat cover decreased below 30, 50 or 70%, and a maximum probability of presence of 0.6 or 0.9 (thereafter called: Abrupt0.3_0.6; Abrupt0.3_0.9; Abrupt0.5_0.6; Abrupt0.5_0.9; Abrupt0.7_0.6; Abrupt0.7_0.9: Table 2, Fig. 2). These six scenarios therefore corresponded to abrupt thresholds, with different species occurrence, positions, and sharpness of transitions. Following Toms and Lesperance (2003), we defined abrupt change as a slope break. We calculated the change as the ratio between the pre-threshold and post-threshold slopes. Two additional scenarios assumed a steady decrease in species frequency with habitat loss, with the probability of presence decreasing from 1 to 0 (Fig. 3a: thereafter called "steady_1") and with suitability decreasing from 0.7 to 0 (Fig. 3b: thereafter "steady_0.7"). These two scenarios therefore corresponded to situations without a threshold, with different slopes of the species-habitat relationship.

For each scenario, we randomly generated 150 data from a binomial distribution, with habitat cover ranging from 0 to 100%. Habitat cover was uniformly distributed; therefore we had 15 data points per decile class of habitat. This figure corresponds to the number of landscapes investigated in a typical large scale study (Homan et al. 2004). Each dataset was generated 20 times (see Dormann et al. 2007 for a similar approach). The parameters of the binomial distribution for the different levels of habitat cover are depicted by the lines in Fig. 2 and the dashed lines in Fig. 3. Figure 3e–h depicts one realization for each of four scenarios as examples. The simulated data sets were then analysed individually using three techniques: logistic regression, GAMs and binomial piecewise regression. Almost 90% of papers used at least one of these three methods (or minor modifications of them) (Table 1).

Logistic regression allows the evaluation of linear relationships between continuous independent variables and binomial response variables (such as presence/absence) (Menard 1995). We therefore used logistic regression to test whether there is a significant relationship between habitat cover and landscape occupancy. Subsequently, we identified the thresholds for landscape cover for which: 1) the probability of occupancy rises above 50% (thereafter, P50%). Because the logistic curve is symmetric, and it has an upper and a lower limit $(0 \leq y \leq 1)$, the P50% thresholds corresponds also to the inflection point of the curve, which has been also used in identifying thresholds (Butler et al. 2004); 2) the ROC threshold maximising sensitivity and specificity (Guénette and Villard 2005).

Table 2. Parameters of the six scenarios assuming an abrupt change. See also Fig. 2. Change b: change in slope determined by the threshold (i.e. the ratio between pre- and post-threshold slopes); [a]: maximum probability of presence.

	Threshold position	P max[a]	Change b
Abrupt0.3_0.6	0.3	0.6	11.7
Abrupt0.5_0.6	0.5	0.6	5
Abrupt0.7_0.6	0.7	0.6	2.1
Aprupt0.3_0.9	0.3	0.9	18.7
Abrupt0.5_0.9	0.5	0.9	8
Abrupt0.7_0.9	0.7	0.9	3.4

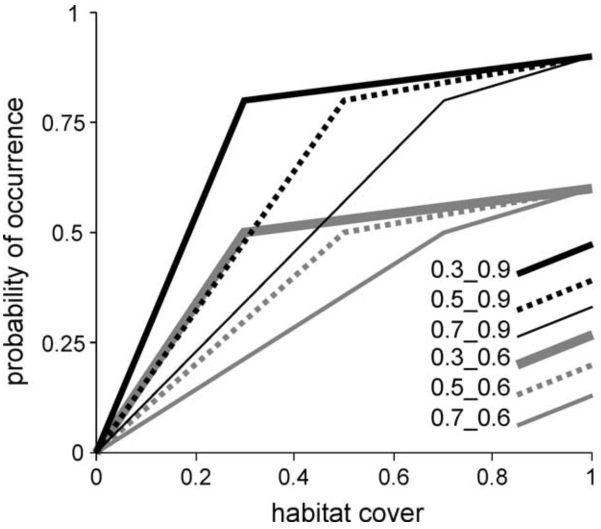

Figure 2. Probability of occurrence in the six scenarios with abrupt change that were used to build the simulated data. For each scenario, the first value represents the position of the threshold and the second value the maximum probability of occurrence.

GAMs are a semi-parametric extension of GLMs, but the response curves are data driven, and are therefore particularly suited for evaluating curvilinear relationships. In GAMs, increasing values for the effective degrees of freedom (edf) means increased complexity and non-linearity of the response curve (Wood 2006). We therefore identified a clearly nonlinear response if $\text{edf} \geq 2$. Following the most frequently applied approach with GAMs (Potvin et al. 2005), threshold position was visually estimated in GAMs with $\text{edf} \geq 2$, on the basis of the plots of fitted values (Fig. 3g–h). To improve the reliability of the estimate, the threshold position was evaluated by several independent observers. We printed the probability plots obtained from the GAMs obtained from the simulated data sets (e.g. broken lines in Fig. 3e–f). For each realization, the threshold position was estimated by 10 different researchers and students working in conservation ecology who were unaware of its true position. We then averaged the 10 estimates. The estimates were quite similar across observers (average standard error: 6% of the mean) confirming that threshold position can be reliably evaluated using this approach. The largest standard errors, representing the largest incertitude among observers, were associated with the datasets with less abrupt thresholds (Abrupt0.7_0.6 and Abrupt0.7_0.9).

Finally, piecewise regression [segmented regression (Muggeo 2003, 2004)] is a technique that allows the inclusion of break points in linear regression, and the simultaneous evaluation of the location and the standard error of the threshold. We therefore used piecewise regression to evaluate whether the addition of a break point significantly increased the fit of a GLM $(p < 0.05)$. We assumed a binomial error distribution in both GAMs and piecewise regression. The significance of all models was calculated using likelihood-ratio tests. All models were fitted in R <www.r-project.org>. Means are ± standard errors.

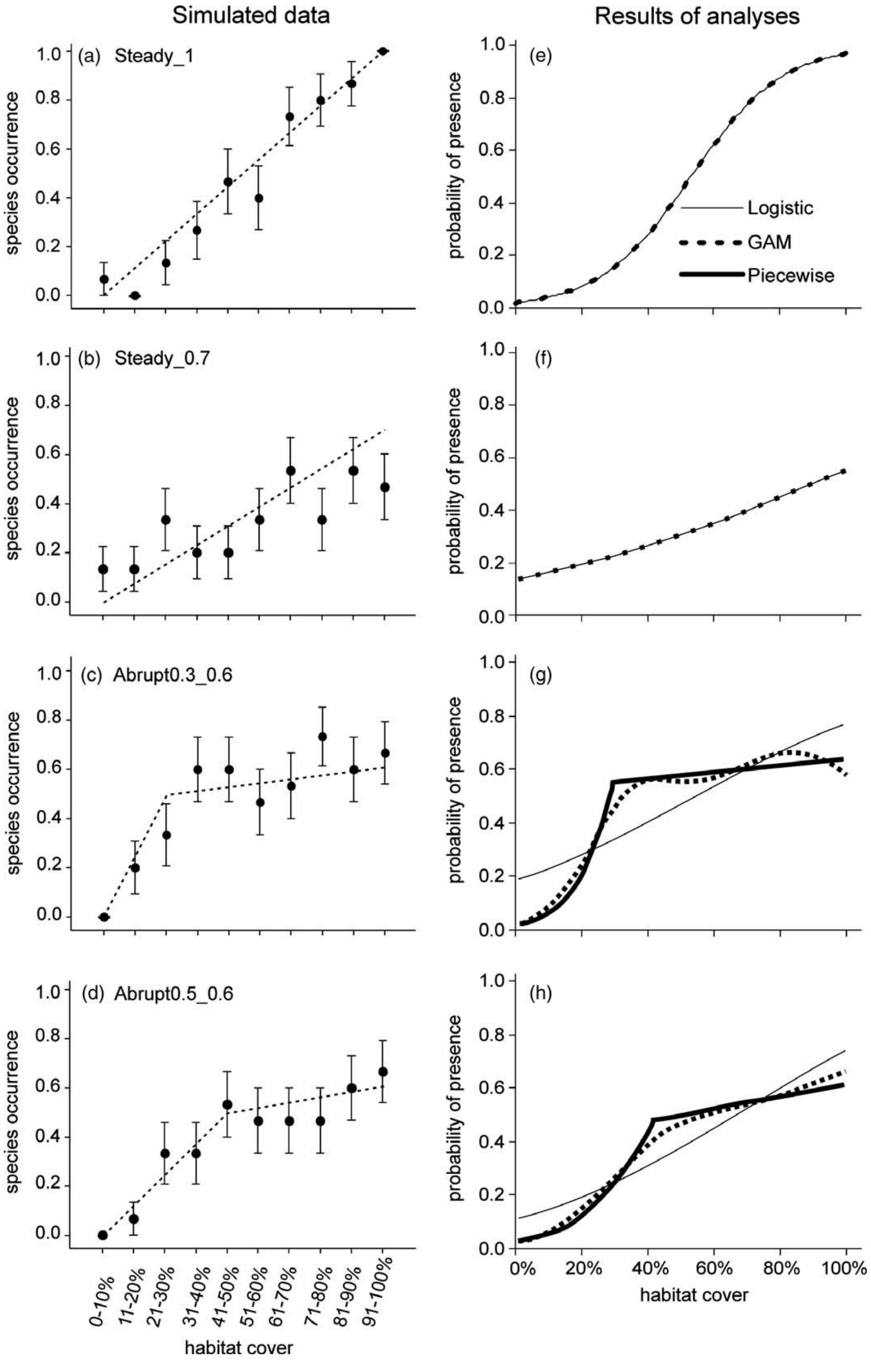

Figure 3. Test of the scenarios using simulations. The figure represents the analysis of one realization for four scenarios; the approach was analogous for the other four scenarios. Left panels (a–d): species occupancy in one realization of 150 simulated landscape assuming (a–b) a continuous increase of probability of occurrence at increasing values of habitat availability; (c–d) an abrupt threshold in the species–habitat relationship (Abrupt0.3_0.7 and Abrupt0.5_0.7). The probability of occurrence is drawn by the broken lines. Error bars represent standard errors. Right panels (e–h): probability of species presence obtained analysing the realizations in the left panels, using logistic regression (continuous line), generalized additive model (bold broken line) and piecewise regression (bold continuous line). In (e–f), logistic regression and GAM converged to the same result, while piecewise regression did not converge. For each scenario name, the first value represents the position of the threshold and the second value the maximum probability of occurrence.

Results of simulations: steady decline datasets

For the steady decline, logistic regression fitted significant models to 100% of simulated datasets. It was therefore always possible to estimate a "threshold" for these simulated data. Two examples of the fitted models are shown in Fig. 3e–f. Using the P50% method, the mean estimated threshold position was 0.5 ± 0.01 for steady_1 and 0.74 ± 0.02 for steady_0.7; using the ROC threshold method, the mean estimated position was 0.48 ± 0.02 for steady_1 and 0.68 ± 0.07 for steady_0.7 (Table 3). In other words, if the P50% or the ROC threshold method are employed, logistic regression can always identify a threshold, even if it was not present in the distribution model used to perform simulations (Fig. 3a–b). The fit of logistic regressions was good (mean Nagelkerke's $R^2 = 0.42$ and 0.24 for steady_1 and steady_0.7, respectively; Table 3).

Piecewise regression failed to converge to any threshold in 95% of cases when analysing steady_1, and in 75% of cases when analysing steady_0.7 (Table 2). That is, in most cases piecewise regression correctly identified that, in the simulated data, the decline is linear and there is no threshold. The proportion of false positives identified by piecewise regression (i.e. the proportion of cases in which piecewise regression incorrectly detected a threshold) was not significantly different between steady_1 and steady_0.7 (likelihood ratio test, $\chi^2_1 = 3.38$, $p = 0.07$) indicating that the performance remains similar when analysing two datasets with different properties.

When analysing the steady decline datasets, GAMs did not detect non-linearity in 65–70% of cases, and converged to a linear model (Table 2, Fig. 2e–f). That is, in the majority of cases, GAMs correctly identified the lack of threshold in these datasets. The proportion of false positives identified by GAMs was not significantly different between steady_1 and steady_0.7 (likelihood ratio test, $\chi^2_1 = 0.11$, $p = 0.74$) indicating that the performance remains similar when analysing two datasets with different proprieties. In the cases in which GAM identified a non-linearity, the mean position of the threshold was 0.39 for steady_1 and 0.44 for steady_2.

Results of simulations: abrupt decline dataset

Logistic regression fitted a significant model to 90 to 100% of simulated datasets assuming abrupt change (Table 3). For several scenarios, the position of the threshold estimated by the P50% and the ROC was very different from the true position of the threshold, which was outside the interval of variation of simulations (Table 3, Fig. 4a).

It should also be noted that the probability of species presence predicted by logistic regression was close to a linear pattern for some of the datasets that assumed the most abrupt change (if plotted using untransformed axes; e.g. Fig. 3g–h). For these datasets, predicted probability of presence was more linear than the pattern obtained from the steady decline datasets (compare Fig. 3e and Fig. 3g). This occurred because the average regression coefficients were smaller when analysing the datasets with more abrupt declines (Table 3) (linear regression, $F_{1,5} = 6.5$, $p = 0.05$). Moreover, regression coefficients were larger in datasets with high maximum probability of presence ($F_{1,5} = 67.5$, $p < 0.001$). In other words, if threshold presence was estimated by the visual inspection of predicted probabilities and/or of the derivative plot (Butler et al. 2004), logistic regression would have detected a clearer threshold pattern in the datasets with less abrupt thresholds and with highest maximum probability of presence.

When analysing the abrupt decline datasets, piecewise regression converged to a threshold in 30–95% of cases (average: 70%). The proportion of simulations fitted by significant piecewise regression was different among the six scenarios ($\chi^2_5 = 26.7$, $p < 0.001$). Piecewise regression detected thresholds more often when the change in slope was large (Spearman's correlation: $r_S = 0.88$, $N = 6$, $p = 0.02$; Table 3). In most cases, the mean estimated threshold position corresponded closely to its actual position (Table 3, Fig. 4a).

GAMs identified a nonlinear relationship in 40–100% of cases (average: 69%). The proportion of simulations fitted by nonlinear GAMs was different among the six scenarios ($\chi^2_5 = 26.1$, $p < 0.001$). GAMs detected thresholds more often when the change in slope was large ($r_S = 0.88$, $N = 6$, $p = 0.02$; Table 3). In many cases, the mean estimated threshold position corresponded closely to its actual position; the interval of variation of simulations always included the actual threshold position (Table 3, Fig. 4a).

To compare the accuracy of the four methods in identifying threshold position, we calculated the error of the estimates, i.e. the absolute value of the difference between estimated and actual threshold position. We then used analysis of variance followed by Tukey's post-hoc tests to compare performance in the six scenarios, across the four methods. The error was significantly different among methods ($F_{3,375} = 5.6$, $p < 0.001$). Moreover, there were significant differences among the six scenarios ($F_{5,375} = 14.9$, $p < 0.001$), with lower errors associated to Abrupt0.3_0.6, Abrupt0.3_0.9 and Abrupt0.5_0.9 than to the other scenarios (Fig. 4a). This probably occurred because the change in slope was greater in these scenarios (Table 2). P50% and ROC were the methods with the largest errors; for many scenarios they completely failed in detecting the true position of the threshold (Fig. 4a). P50% and ROC had similar levels of errors (Tukey's post hoc, $p = 0.99$), and they had significantly higher errors than GAM and piecewise regression ($p < 0.03$ in all pairwise comparisons). GAM and piecewise regression were the methods with the best overall performance (Fig. 4); the mean error was not significantly different between them ($p = 0.68$). Moreover, there was a significant interaction between method and scenario ($F_{15,375} = 8.2$, $p < 0.001$), indicating that some methods performed better in one particular scenario. For example, ROC did not perform well for Abrupt0.5_0.6, while it demonstrated better performance for Abrupt0.3_0.6 (Fig. 4a).

Discussion

Although a promising and attractive concept, ecological thresholds have often been approached using techniques that are not able to discriminate between steady and abrupt

Table 3. Results of the statistical analyses of the simulated datasets using logistic regression, generalized additive models and piecewise regression. Estimates of threshold position are averaged across the 20 simulations. In GAM, the estimation of location of the threshold was done by several researchers who were unaware of the true position of the threshold.

True position of threshold	Datasets with abrupt change						Datasets without abrupt change	
	0.3_0.6	0.5_0.6	0.7_0.6	0.3_0.9	0.5_0.9	0.7_0.9	Steady_1	Steady_0.7
	0.3	0.5	0.7	0.3	0.5	0.7	–	–
Analysis using logistic regression (= smooth threshold method)								
% datasets fitted by a significant model	90%	100%	95%	100%	100%	100%	100%	100%
Threshold at which probability of occupancy >50%	0.59	0.69	0.77	0.23	0.36	0.45	0.50	0.74
Maximum accuracy ROC threshold	0.35	0.74	0.50	0.28	0.37	0.45	0.48	0.68
Regression coefficient	2.0	2.5	3.2	4.0	5.0	5.3	5.3	3.5
R^2_N	0.11	0.14	0.20	0.26	0.39	0.42	0.42	0.24
Analysis using generalized additive models								
% datasets fitted by nonlinear GAM	75%	75%	50%	100%	75%	40%	30%	35%
Location of threshold	0.37	0.45	0.53	0.43	0.55	0.59	0.39	0.44
R^2_N(a)	0.17	0.17	0.23	0.37	0.41	0.38	b	c
Analysis using piecewise regression (= abrupt threshold method)								
% datasets fitted by significant piecewise regression	80%	80%	55%	95%	80%	30%	5%	25%
Location of threshold	0.30	0.43	0.61	0.34	0.47	0.57	d	e
R^2_N	0.18	0.23	0.24	0.38	0.44	0.45	d	e

R^2_N: Nagelkerke's R^2.

[a] Calculated only for models with edf ≥2 (see text).

[b] In 70% of cases, the results of GAM were nearly identical to logistic regression.

[c] In 65% of cases, the results of GAM were nearly identical to logistic regression.

[d] In 95% of cases, the model did not converge.

[e] In 75% of cases, the model did not converge.

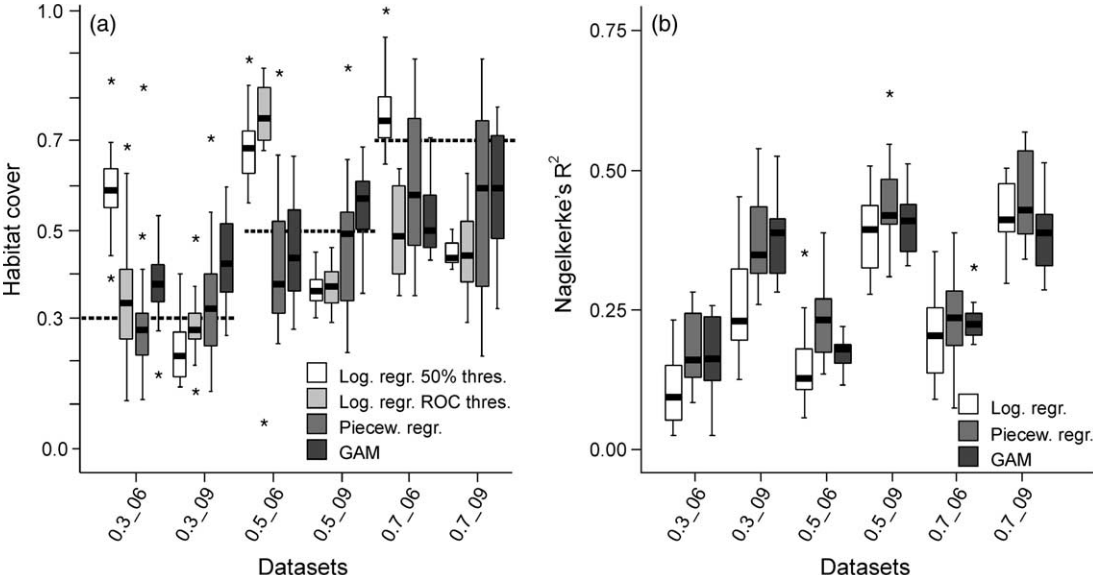

Figure 4. Boxplots comparing different modelling approaches (logistic regression, piecewise regression and generalized additive models) in the analysis of datasets with an abrupt decline (comparison across 20 realisations of the same parameter set). Asterisks represent outliers. (a) Estimated threshold position for the six abrupt change scenarios; the dashed lines represent the true threshold positions. (b) Variation explained by different modelling approaches. For each scenario, the first value represents the position of the threshold and the second value the maximum probability of occurrence.

transitions. Logistic regression gave significant curves for the datasets with and without an abrupt threshold. Moreover, logistic regression can fail at correctly detecting the position of a threshold. Although in some situations the maximum accuracy ROC threshold can be close to the actual position of the threshold (Fig. 4a), the identification of this statistical cut-off point does not automatically imply a nonlinear response. The sensitivity and specificity of all logistic models can be maximised, even if the species response to habitat loss is significant but linear (Manel et al. 2001, Betts et al. 2007). For this reason, ROC thresholds can be detected in all binomial models, independent of the presence of break points in the relationships, and logistic regression is not an appropriate tool to detect the presence of thresholds. Indeed, ROC did not reliably detect threshold position in the majority of scenarios (Fig. 4a). Logistic regression fails in the detection of abrupt thresholds, because it simply allows identification of the point at which it becomes more likely that the species will be present than absent. This is not the same concept as an ''abrupt change'' in the habitat occupancy relationship, which is better described by techniques that are able to discriminate between linear and nonlinear patterns.

Methods such as GAMs are more appropriate than GLMs, because they have a better fit and assume a curvilinear pattern (Table 3, Fig. 3, Fig. 4). Also, the results can be visually similar to those obtained by theoretical and simulation studies (With and King 1999, Fahrig 2001). However, these methods have the drawback of not providing an estimate of the position of the break point, which must therefore be judged subjectively. Averaging the estimates of multiple observers might decrease the subjectivity of this approach, and provides quite reliable results (Fig. 4). Techniques able to evaluate the existence of ''abrupt thresholds'', such as piecewise regression, have the advantage of being able to estimate the position and probability of these thresholds accurately, particularly when the change in slope is large (Fig. 4). They are therefore the most suitable approach for an objective study of abrupt changes. Although piecewise regression was the only one of these techniques used consistently in the literature (Table 1), recent statistical advances have made other methods available, such as Bayesian change-point analysis (Beckage et al. 2007) and the detection of structural changes (Zeileis et al. 2003, Denoël and Ficetola 2007), which have been seldom used to date. The use of simulations and comparative studies is encouraged to evaluate the power of these different methods, and to find the conditions under which the application of a given approach is most appropriate.

Our analysis focused on the most frequent applications of the threshold concept to the analysis of species-habitat relationship. Nevertheless, real world situations can be more complex than the theoretical scenarios depicted here. The threshold position for a given species may be context dependent, for example where species' movements are influenced by habitat quality (Olden 2007). In these cases, the actual position of the threshold can change in different landscapes (Rhodes et al. 2008), making its identification difficult and hindering the transfer of management recommendations to different geographical areas (McAlpine et al. 2008, Ficetola et al. 2009). Moreover, natural patterns can have a variety of shapes, and smooth transitions or diffuse thresholds can occur (Maggio et al. 2002, Toms and Lesperance 2003). Furthermore, in principle more than one threshold can exist, corresponding to multiple transition points. Although appealing, these concepts have been only rarely explored and applied to species–habitat relationships. Ecology and conservation can greatly benefit from varying threshold concepts, but their application requires the explicit definition of ecological hypotheses corresponding to different patterns, and the identification of the statistical tools most suitable to detect them.

Conclusion: insights for ecology and conservation

The presence or absence of thresholds and their detection can be of key importance in understanding ecological processes [e.g. fragmentation, shifts in ecosystem state, critical loads (Andrén 1994, With and Crist 1995, Keitt et al. 1997, Sankaran et al. 2005, Groffman et al. 2006)] and for conservation ecology (Lindenmayer and Luck 2005). However, the variety of approaches used to define and identify ecological thresholds is a major obstacle to these applications. Here we highlight several topics, where using appropriate tools to analyse habitat thresholds can provide important insights for ecological theory and for conservation practice.

First, the role of isolation in the fragmentation process is still widely debated (Fahrig 2003). If species are negatively affected by isolation, models predict that they would exhibit an extinction threshold when habitat cover falls below the threshold value (Fahrig 2001, 2002). In other words, thresholds in the relationship between species distribution and habitat cover suggest a detrimental effect of isolation during fragmentation. However, studies on thresholds can help answer this question only if appropriate statistical methods that are able to detect abrupt change are used, since inappropriate methods (such as logistic regression) are not able to distinguish systems with and without thresholds.

Secondly, the identification of interspecific differences in threshold location would suggest varying susceptibility to loss of habitat and connectivity. Consequently it may be possible to rank species according to their sensitivity to these processes, and thus to identify key indicators or conservation priorities. However, such an approach requires the use of suitable methods to identify threshold values. Piecewise regression has been shown to be the most suitable method for this objective as it provides a straightforward estimation of break points.

Third, the large differences among analytical methods hamper comparisons between studies and meta-analyses. We would like to promote the widespread use of methods allowing 1) to test whether a threshold exists and 2) to reliably assess the location of the threshold. This would help in finding general patterns, and would also allow us to answer general questions. For example, is the threshold response greater in some taxa, habitats, or in species sharing life history traits?

Finally, as conservation efforts depend on quantitative data on habitat requirements, a simplistic approach in computing such values could have detrimental consequences, leading to species becoming extirpated and funding inadequately allocated. Procedures explicitly designed to detect ecological thresholds should be used in future studies, thereby helping ecologists and managers to identify areas suitable for target species, and thus to make appropriate decisions to sustain species diversity and maintain valuable habitats.

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