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Thresholds and the species–area relationship: a synthetic analysis of habitat island datasets

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ABSTRACT

Aim The application of island biogeography theory in habitat fragmentation research assumes a simple relationship between species richness and fragment area. However, previous work has suggested that in some cases thresholds can be detected, at which the form of the island species–area relationship (ISAR) changes abruptly. Piecewise regression has been advocated as a suitable statistical technique to model such thresholds. Here we first provide a comparative analysis of piecewise regression models to determine the prevalence and type of thresholds in habitat island ISARs. Second, we evaluate piecewise regression as a method for locating thresholds in the ISAR, with particular emphasis on the implications of data transformation.

Location World-wide.

Methods Seventy-six habitat island datasets were sourced from the literature. An information theoretic approach was employed to compare linear regression ISAR models with piecewise regression models. The models were applied to untransformed (species–area), semi-log (species–log area) and log–log (log species–log area) data. Three types of piecewise regression models were evaluated: continuous, discontinuous and zero slope. Model performance was compared using the Akaike information criterion. We also examined the influence on model performance of taxon, number of habitat islands, and area of smallest island.

Results Linear regression models performed best, although piecewise models were preferred in a number of cases. Cases in which no model was significant were most prevalent in untransformed space relative to the semi-log and log–log transformations. Piecewise fits were more prevalent in datasets with a larger numbers of islands.

Main conclusions Data transformation is a key part of model selection and needs to be explicitly considered, especially in terms of drawing inferences from models. Piecewise models, even if selected as the favoured model in our analyses, were often ecologically unintelligible in relation to area alone. When detected, breakpoint values ranged over five orders of magnitude, although with one exception all were under 50 ha. Our findings highlight the limitations of using individual threshold values to inform conservation practice.

Keywords

Breakpoint values, conservation biogeography, habitat islands, island biogeography, piecewise regression, scale dependency, small island effect, species–area relationship, thresholds.

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INTRODUCTION

The destruction and fragmentation of natural habitat are primary causes of terrestrial biodiversity decline (Wilcove, 1987;

Primack, 2010) and constitute a major focus of research within conservation biogeography (Ladle & Whittaker, 2011). The impacts of habitat loss and fragmentation on species diversity take time to be fully realized (Halley *et al.*, 2014),

leading to a reliance on the use of various forms of species–area relationship (SAR) to quantify and predict likely future levels of species loss from landscapes (but see also, e.g., Stork, 2010). The two principal variants of SAR are species accumulation curves (SACs), which record the cumulative sum of species as sampling area is increased, and island species–area relationships (ISARs), which record the number of species found versus area for each island or habitat patch (Box 4.2 in Whittaker & Fernández-Palacios, 2007). Both variants (and others) have been used in efforts to model and predict species losses arising from habitat fragmentation. However, as the majority of fragmentation studies use ISARs the empirical tests presented herein are exclusively concerned with ISARs.

ISARs are typically interpreted in terms of MacArthur & Wilson's (1967) equilibrium theory of island biogeography. However, debate continues as to the efficacy and applicability of island theory in the context of habitat islands (e.g. Laurance, 2008). Of particular concern is whether there may be evidence for nonlinearity, perhaps involving thresholds across which relationships change form, and how analytically such nonlinearity may best be dealt with (Lomolino & Weiser, 2001; Gentile & Argano, 2005; Ficetola & Denoël, 2009; Dengler, 2010).

The definition of nonlinearity in this context is itself problematic. In general, ISARs, whether fitted to 'habitat island' or 'true island' datasets, are rarely best fitted by linear models using untransformed data. Rather, partly for analytical convenience, linear fits have been obtained by log-transformation of data, with much debate as to whether linear fits are more satisfactorily obtained using 'species richness–log area' (hereafter semi-log) or 'log species richness–log area' (hereafter log–log) transformations. The implication of a *linear* regression fit using a semi-log transformation is of course that species richness declines *nonlinearly* with declining area. For example, Drinnan (2005) uses this logic to identify a threshold area below which the loss of species accelerates with further area loss. An alternative approach to identifying thresholds is to use piecewise regression models that fit two separate linear functions to upper and lower parts of the dis-

tribution of values of area (e.g. Gentile & Argano, 2005). However, when using log-transformed area and/or species richness data, it should be understood that any breakpoint identified is in essence identifying a change of form within an already nonlinear space (Burns *et al.*, 2009). Hence, any interrogation of threshold relationships using piecewise regression requires careful interpretation of the data transformation applied.

The use of piecewise regression to test for ecological thresholds has been advocated by several authors as it allows for rigorous identification of patch area thresholds, and evaluation of the associated error of such identifications (e.g. Toms & Lesperance, 2003; Ficetola & Denoël, 2009). Ficetola & Denoël (2009) sourced 26 papers from the literature and reviewed the methods used to detect thresholds in the relationship between habitat amount and species occurrence or richness. They found that only 35% of the studies examined used appropriate statistical techniques. A number of studies were found to have used generalized linear models whereby the breakpoint was determined visually. Ficetola & Denoël (2009) contend that visual identification of breakpoints is inadequate, arguing that only techniques such as piecewise regression have the ability to estimate both the position and probability of thresholds in habitat amount.

Previously reported threshold ISAR relationships mostly take two basic forms, which we characterize herein as shallow–steep and steep–shallow, by which we refer to the change in form of the ISAR with *increasing* area. Steep–shallow relationships are those showing an initially rapid rate of increase in richness with area, until a threshold is reached beyond which a slow rate of increase applies (Fig. 1). Steep–shallow thresholds indicate that the effect of habitat loss becomes exacerbated below the threshold level of habitat cover. This may be due, for example, to a patch extinction rate exceeding its immigration rate (Fahrig, 2001). A certain threshold area may also relate to coinciding minimum patch area requirements for multiple species or to a point at which the effects of habitat isolation are exacerbated (Andrén, 1994). Detecting steep–shallow relationships is an important

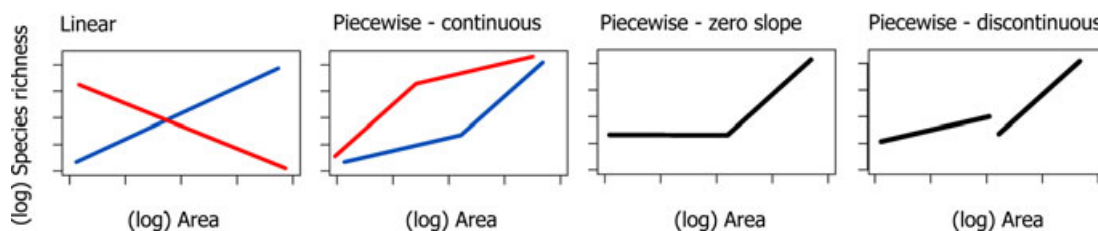


Figure 1 Schematic illustration of the alternative models used in the analysis, and their different forms. In the 'linear' plots the red line signifies a negative linear relationship and the blue line a positive linear relationship. In the continuous plots the blue lines signify a shallow–steep form (following the line from left to right) and the red line indicates a steep–shallow form of the model. The discontinuous plots do not represent the sole form of a discontinuous model; rather multiple patterns emerged through the analysis (see Fig. S1 in Appendix S2). We denote the *x*-axis as (log) Area, and the *y*-axis as (log) Species richness, but have applied the models to data that were untransformed, semi-log and log–log transformed.

task for conservation planners (Drinnan, 2005; Huggett, 2005). Shallow–steep ISARs are those that initially show a slow rate of (or no) increase in richness with increasing area, followed by a steeper phase beyond a critical threshold. Shallow–steep ISARs as so defined include those that represent the so-called small island effect (SIE: e.g. see Lomolino & Weiser, 2001), which has previously been described for some habitat island datasets (Qie *et al.*, 2011).

Piecewise regression models incorporate the inclusion of breakpoints within linear regressions, with the breakpoints representing a point at which the form of the relationship changes, either in slope or in slope and intercept (Toms & Lesperance, 2003; Gentile & Argano, 2005). Analytically, the possible forms of these relationships are in practice more numerous than the two basic forms described above and include the following set of piecewise models: continuous, zero slope, and discontinuous (Fig. 1). Continuous piecewise models incorporate a change in slope at the break-point, with the condition that the regression line being modelled is continuous. Zero slope models are a subtype of the shallow–steep continuous model whereby the slope to the left of the breakpoint is zero (i.e. there is no relationship). Zero slope models are included within the model comparison as they are recommended by Lomolino & Weiser (2001) for detection of the SIE. It is important to note, however, that this methodological approach to detecting SIEs has been the subject of dispute (e.g. Triantis *et al.*, 2006; Dengler, 2009, 2010; Tjørve & Tjørve, 2011; Triantis & Sfenthourakis, 2012). In a discontinuous piecewise model both the slope and intercept of the regression line can change at the breakpoint; that is, the regression line is not continuous. In addition to the breakpoint models, around 20 functions have been described for fitting ISARs (Triantis *et al.*, 2012). We do not attempt to determine the fit of these alternative ISAR models as our study is focused on the fit of piecewise models and their use in detecting area thresholds.

Despite existing theoretical and empirical work focusing on patch area and extinction thresholds (e.g. Drinnan, 2005; see Swift & Hannon, 2010, for a review), few previous studies have re-analysed existing datasets to explore emergent patterns (but see Ficetola & Denoël, 2009). Moreover, we are unaware of any statistical re-analysis of patch area thresholds, or for that matter any type of ecological threshold, incorporating a large number of datasets. The aim of this paper is thus twofold. First, we provide a synthetic analysis of piecewise regression models (Fig. 1), using an information theoretic approach (Burnham & Anderson, 2002) to determine the prevalence and type of thresholds in the ISARs of 76 habitat island datasets. Having done so, we examine the resulting model fits with reference to the distribution of island areas and other properties of the source datasets. Second, we evaluate piecewise regression as a method for locating thresholds in the ISAR, with particular emphasis on data transformation. We go on to provide methodological recommendations and comment on the implications of our findings for conservation biogeography.

MATERIALS AND METHODS

Data collection

Three abstracting services were searched for relevant habitat loss and fragmentation studies and datasets during May–June 2007 and May–July 2011: JSTOR (1913–2003); ISI Web of Knowledge (1980–2011); and BIOSIS Biological Abstracts (1980–2003). The search keywords were ‘habitat islands and species richness’ and ‘forest fragments and species richness’. Additionally, cross-referenced papers derived from the reference lists of sourced papers were also included.

Suitability was based on the following criteria:

1. Habitat islands were defined as discrete patches of habitat surrounded by contrasting, ‘hostile’ matrix habitat.
2. The areas and species richness of each habitat island were listed.
3. The number of habitat islands within each dataset was at least eight, as this was necessary so that all the available piecewise models could be applied (below).
4. Data from any particular study did not overlap with those from any other study accepted for analysis (data for different taxa within the same study system were allowed).

For each dataset we recorded the geographical location, the taxon studied, the habitat island type (forested or non-forested), and the range of species richness and island sizes (see Appendix S1 in Supporting Information).

Data analysis

First, we developed three versions of the datasets: untransformed (S versus A), semi-log (S versus $\log A$) and log–log ($\log S$ versus $\log A$) transformed, where S is species richness and A is area. Second, we fitted linear models to all three versions of each dataset alongside a set of piecewise models: continuous piecewise, zero slope continuous, and discontinuous piecewise regression models. As $\log(0)$ is non-defined, a $\log(x+0.1)$ was applied for the transformation of species richness in the case of the log–log transformation. All analyses were performed using R 3.0.0 (R Development Core Team, 2013).

In fitting the piecewise models, the optimal breakpoints for each continuous and discontinuous piecewise model and dataset were selected by testing 1000 evenly distributed points within the range of the data. The optimal breakpoint leading to the best-fitting model was selected from this set by a log-likelihood optimization separately for each case and model type. A benefit of this methodology is that the existence of thresholds (breakpoints) in the data is not assumed a priori; this being a criticism often levelled at such studies (see Gentile & Argano, 2005).

All models were implemented and compared as linear regressions. For each of the three versions of each dataset (i.e. untransformed, semi-log or log–log) the performance of each model was compared using Akaike’s information criterion corrected for small sample size (AIC_c; Burnham &

Anderson, 2002; code from library ‘AICcmodavg’ version 1.20; Mazerolle, 2011):

$$AIC_c = -2 \times \log\text{Lik}(\text{model}) + 2 \times k[n/(n - k - 1)],$$

where n is the number of observations and k the number of model parameters. The selection of a single best model (i.e. the statistically best-fitting descriptive model) was based on there being a difference in AIC_c value of at least two between the best and a respective weaker model (Burnham & Anderson, 2002).

In addition, because we were concerned that the initial optimization of the breakpoints could be deemed to constitute ‘hidden parameters’, we also performed a sensitivity analysis in which we ran the model selection after accounting for the initial optimization of the breakpoints and increase in model complexity by increasing the number of model parameters to $k = 4$ for the piecewise continuous model with zero slope, $k = 5$ for the piecewise continuous model, and $k = 6$ for the piecewise discontinuous model, when calculating AIC_c . As the calculation of AIC_c includes a division by $n - (k - 1)$ (with n being the number of data points and k the number of model parameters), to avoid a negative denominator the minimum number of data points was set to eight. In addition to the aforementioned linear and piecewise models, we also implemented a model with a zero slope regression line at the data mean as our simplest model (corresponding to no species–area relationship). Cases in which none of the more complex models were favoured above this ‘null model’ based on our AIC_c criterion were treated as ‘non-significant’. As an additional criterion, a standard F -test was used to check the significance of the species–area relationship for each model. Only models showing a significant species–area relationship were compared based on AIC_c . In a number of datasets no model showed a significant relationship. These cases were also labelled as ‘non-significant’. A direct comparison of models across different versions of the dataset is not possible based on AIC_c values as the model types have different dependent variables [$\log(S + 0.1)$ and S].

In a further step all analyses were re-run following the application of Cook’s distance criterion (Cook & Weisberg, 1982). This was done to remove models which were unduly influenced by a single data point. Many habitat island datasets include relatively few islands (Appendix S1) and thus outliers are a significant problem that needs to be considered. For each version of the dataset, models in which any data points had a Cook’s distance greater than one were removed from the model comparison for that version of the dataset (Cook & Weisberg, 1982). We summarize the initial results in Appendix S2 and present the results following application of Cook’s distance criterion in the main Results (below).

Plots of each dataset were checked visually to allow us to categorize linear models as either positive or negative and continuous piecewise models as either shallow–steep or steep–shallow forms (as Fig. 1). In addition, we took note of

visually peculiar relationships to inform subsequent interpretation.

The effects of the dataset characteristics

Model performance was compared between taxonomic groups, habitat type and the various dataset characteristics recorded (number of habitat islands, range of habitat island areas, and area of smallest and largest habitat island) using the Student’s t -test, ANOVA and Tukey’s honestly significant difference (HSD) post-hoc test. To determine the effect of habitat type, datasets were separated into those comprising forested habitat islands and those comprising non-forested habitat islands and model performance was compared using a test of proportions (prop.test in the basic STATS package in R). After the initial analysis the dataset selection criteria (above) were iteratively altered to progressively remove datasets with the fewest habitat islands, increasing in units of one from our pre-set minimum of eight, up to 32 habitat islands. After each iteration the analyses were re-run to determine the effect of sample size on the results (following Triantis *et al.*, 2012).

RESULTS

Over 500 articles were reviewed, from which we retrieved 76 datasets meeting the above criteria from 70 separate sources (Appendix S1). There were 53 forest habitat island datasets (70%) and 23 non-forest systems (30%); and there were 14 (18%) invertebrate, 39 (51%) vertebrate, and 23 (31%) plant datasets. The vertebrate datasets comprised 22 bird, 15 mammal and two reptile case studies.

Model performance

The application of Cook’s distance criterion resulted in the best model changing for four of the untransformed datasets, four of the semi-log transformed datasets, and six of the log–log transformed datasets (see Table S1 in Appendix S2 for overall outcome, which remains largely unchanged). Whilst this process removed a number of visually idiosyncratic, ecological unintelligible models, inspection of the plots revealed that several remained that defy ecological interpretation in terms of isolate area ($n \approx 8$; Fig. S1 in Appendix S2): these latter cases were nonetheless retained in the analysis (Table 1).

Unsurprisingly, the best model type varied depending on the data transformation undertaken prior to model fitting (Table 1). Despite the range in form of the models used, cases where no significant model was generated accounted for 51% of the untransformed datasets, 32% of the semi-log datasets, and 37% of the log–log transformations, respectively. Positive linear fits were the commonest fit and were found in respectively 18%, 32% and 32% of cases. The second best model for untransformed datasets and for the log–log datasets was the subset of piecewise continuous

Table 1 The best fit island species–area relationship (ISAR) model for 76 habitat island datasets, tallying the best fit models separately for each data transformation. The best model for each version of the dataset (i.e. untransformed, semi-log and log–log) was chosen based on Akaike’s information criterion corrected for small sample size ($\Delta AIC_c > 2$). These results were tallied following the application of Cook’s distance criterion: for results prior to this step, see Appendix S2.

| Model type | Number of datasets (percentages in parentheses) | | |
|--|---|----------|----------|
| | Untransformed | Semi-log | Log–log |
| Linear (positive relationship) | 14 (18%) | 24 (32%) | 24 (32%) |
| Linear (negative relationship) | 1 (1%) | 0 | 0 |
| Piecewise continuous (steep–shallow) | 17 (22%) | 5 (7%) | 12 (16%) |
| Piecewise continuous (shallow–steep) | 0 | 6 (8%) | 0 |
| Piecewise zero slope (i.e. flat–steep) | 1 (1%) | 11 (14%) | 5 (7%) |
| Piecewise discontinuous | 4 (5%) | 6 (8%) | 7 (9%) |
| Non-significant | 39 (51%) | 24 (32%) | 28 (37%) |

models visually classified as steep–shallow, with 22% and 16%, respectively, while the zero slope piecewise model was the second commonest best model in semi-log space, being selected for 14% of cases. The breakpoint values of piecewise models selected as the best were found to vary over five orders of magnitude (0.3–23,000 ha), although with one exception all were under 50 ha.

The sensitivity analysis in which we re-ran the model selection after increasing the number of parameters to take explicit account of the initial optimization of the breakpoints, resulted in a small number of changes to the models chosen as best (compare Table 1 with Table S2 in Appendix S2). In particular, we found greater support for linear models relative to piecewise models. However, qualitatively our results did not change, and from herein we only discuss results based on the standard AIC_c calculation.

Dataset descriptors

The proportion of cases where at least one model was significant in at least one version of the datasets was lower for invertebrate datasets (57% of cases), than for vertebrates (74%) and plants (74%) (detailed results not shown). The small sample sizes involved prohibit formal statistical testing of between-taxon differences. However, the breakdown of results by taxon shows that setting aside linear models, piecewise continuous models emerged as the best most often from vertebrate datasets, whereas discontinuous piecewise models

emerged more often for plant datasets (Table S3 in Appendix S2). There was no significant difference in the proportion of piecewise models selected as the best between forested and non-forested habitat islands ($P = 0.32$; prop.test).

Grouping the models into piecewise and non-piecewise it was found that the mean number of islands in datasets in which piecewise models performed best for at least one version of the dataset (mean \pm SD = 26 ± 12 , $n = 38$) was greater than for the remaining datasets (mean \pm SD = 19 ± 12 , $n = 38$), although this difference was non-significant ($t = 2.85$, $P = 0.1$; Student’s t -test). Datasets in which no models were significant generally had fewer islands than datasets with a significant ISAR, although the differences between the number of islands in datasets with no significant model and datasets best modelled by a linear or piecewise model were not always significant according to Tukey’s HSD post-hoc test (Fig. 2a–c). Versions of datasets in which a discontinuous model was selected as best mostly had more islands than those in which other models were selected as best. However, again these differences were not always significant according to Tukey’s HSD test (Fig. 2a–c). The size of the smallest island was smaller in versions of the datasets in which discontinuous models performed best, in comparison to those in which a linear model was best, or in which no model was significant (Fig. 2d–f). However, these differences were not always significant and, in general, the minimum island size in a dataset does not clearly discriminate between piecewise continuous (shallow–steep and steep–shallow forms) and linear models. There was no significant difference in the proportion of piecewise models selected as best based on either the area of the largest island in the dataset, or the overall range of habitat island areas in the study (results not presented). As some of the foregoing comparisons involve very few datasets, caution is necessary in interpreting these findings.

Progressively removing datasets with fewer habitat islands led in general to a larger fraction of datasets being best approximated by piecewise models and a reduction in the number of non-significant models (Fig. 3).

DISCUSSION

Data transformation

To determine the prevalence of thresholds in the ISAR of habitat islands ($n = 76$ datasets), statistical techniques incorporating a breakpoint in the linear regression were compared with simple linear regression species–area models. The models were applied to untransformed, semi-log and log–log transformed data. We found that linear regression models performed best in about half of the cases for which at least one significant model could be fitted, with proportions of the different piecewise models varying between the three different data transformations used.

Our analyses serve to highlight the danger of taking an a priori decision on data transformation without careful reflection

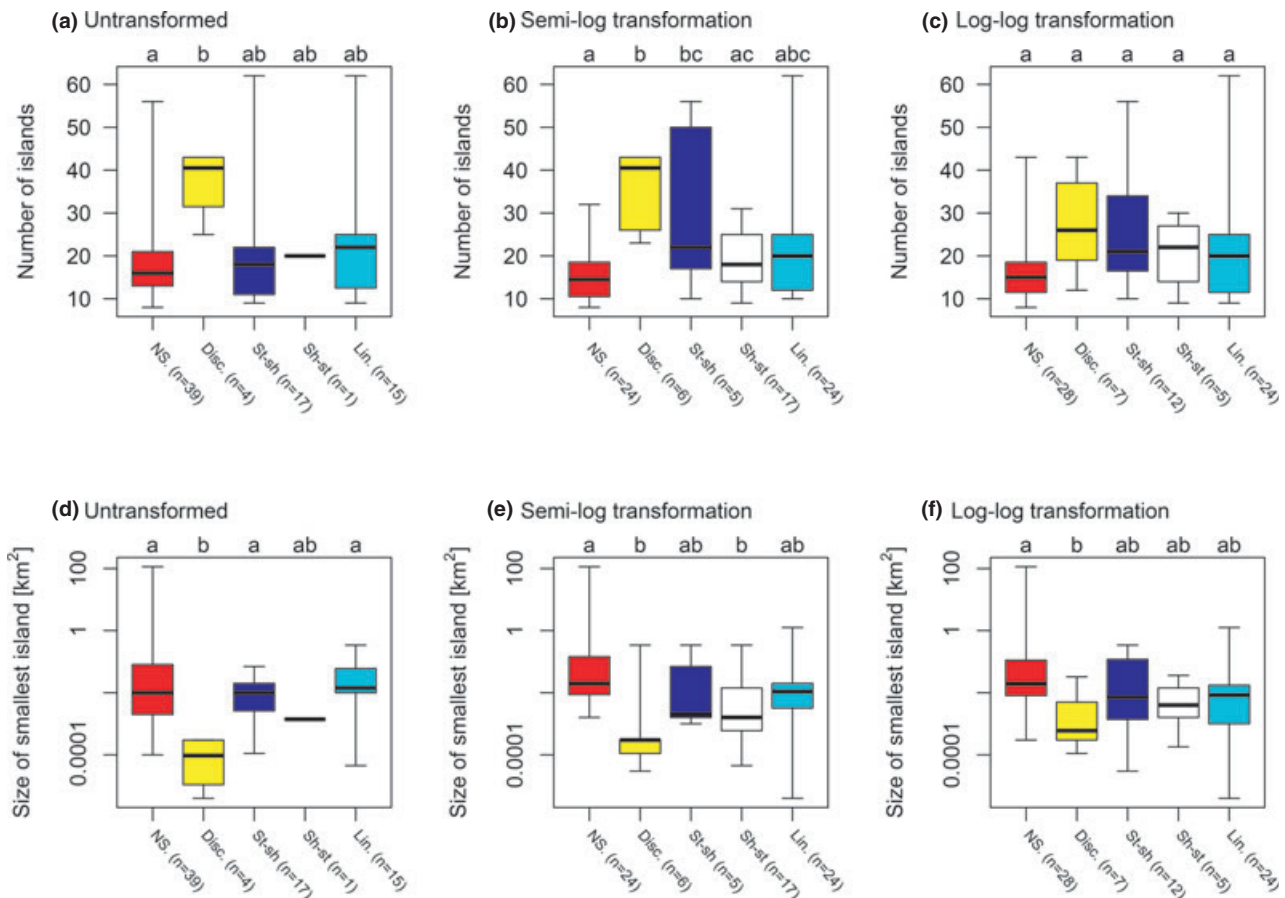


Figure 2 Box plots displaying the number of habitat islands (top row), and area of the smallest habitat island (bottom row), for each model type across the three data transformations. Significant differences between models are displayed as different lowercase letters above the box plots. Models that do not significantly differ in the dependent variable have the same lowercase letters. NS refers to datasets where no model provided a significant fit, ‘Disc’ = datasets in which a discontinuous model was selected as best, ‘st-sh’ = steep–shallow, ‘sh-st’ = shallow–steep, and ‘lin’ = a linear model. Shallow–steep refers to both shallow–steep continuous models and the zero-slope piecewise models. Note that small ‘n’ values in particular categories limit the power of the analysis to detect significance. Significance was assessed by ANOVA followed by Tukey’s HSD (honestly significant difference) post-hoc test ($P = 0.05$).

on study aims. Such a strategy may obscure significant variations in the form of the ISAR across data transformations and lead to erroneous (or incomplete) inferences surrounding the shape of the ISAR, and, ultimately, the identification of thresholds. It is important to be aware of these pitfalls and to ensure that the analytical strategy adopted is appropriate for the purpose of the particular study because it is possible for two quite different models to provide good fits to the same dataset. Figure 4 illustrates this for a dataset drawn from Watson (2003), a study of naturally fragmented montane habitat islands in Mexico. Whereas the best model in untransformed space is a piecewise continuous model of the steep–shallow form, the best in semi-log space is a zero slope piecewise model. Therefore, depending on the transformation used one could infer that there is a habitat amount threshold below which richness precipitously declines, or evidence of a traditional small island effect (*sensu* Lomolino & Weiser, 2001). With regard to the zero slope pattern found for the semi-log analysis, the data points responsible for the

initial lack of area trend each had very low (or no) species (Fig. 4). These data points almost overlay each other in the graph of the untransformed data, while the semi-log transformation in effect expands this section of space to generate the zero slope pattern.

The dataset of Kitchener *et al.* (1980) also provides a useful illustration of the change in model selection across the different versions of the dataset (Fig. 5). Visual examination of the untransformed plot suggests a threshold but the best model is actually a simple linear (positive) model. However, the best model in semi-log space is also a simple linear regression and thus, using the method of Drinnan (2005) this would be equivalent to the identification of a threshold in untransformed space. To complete the comparison, a steep–shallow piecewise continuous model was preferred in log–log space.

Hence the question arises as to what a linear (or alternatively a piecewise) relationship actually signifies when using logged variables. For instance, a linear relationship in semi-log space equates to a curvilinear relationship using the

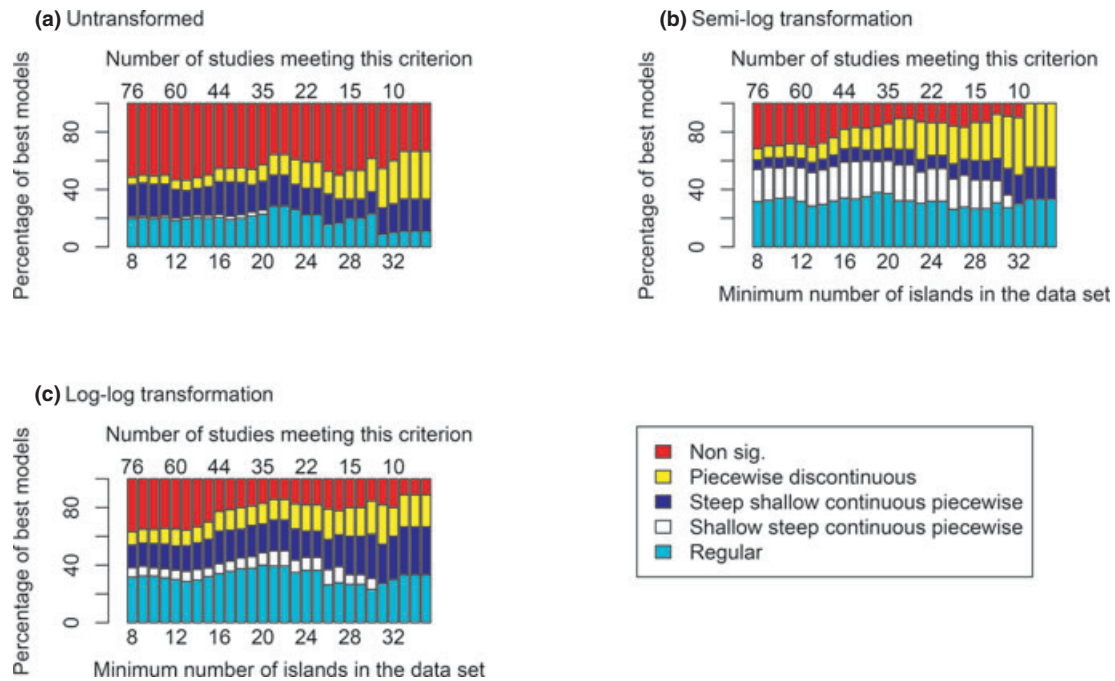


Figure 3 Percentage of models identified to be the best depending on the minimum number of habitat islands (sample size) of a dataset selected, for the three versions of each dataset (untransformed, semi-log and log–log). Note that eight represents the minimum number of habitat islands allowed by the original selection criteria for analysis. Non-sig = non-significant; regular = linear fit.

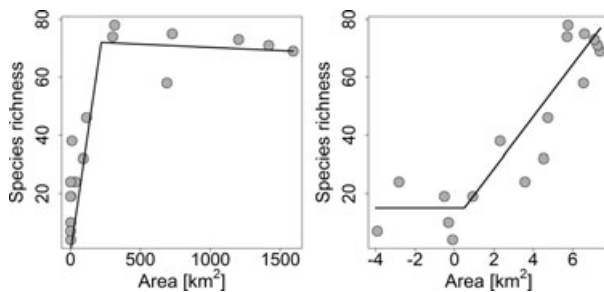


Figure 4 Variation in the best model selection across two versions of the same dataset. Left, the data plotted in untransformed space in which the best model is a continuous (steep–shallow) piecewise model. Right, the same data plot plotted in semi-log space, in which the best model is a zero slope piecewise model. Data are from Watson (2003): a study on birds in a fragmented landscape, Mexico.

untransformed data. Thus, given that 34% of datasets are best modelled by a linear model in semi-log space, an underlying curvilinear form can be described for about half of the datasets for which we are able to fit ISARs. However, our results indicate that the higher proportion of linear models that performed best in semi-log and log–log space does not correspond to an equally high proportion of piecewise models in untransformed space (Table 1). Rather, datasets in which no model provided a significant fit were in the majority in untransformed space. The likelihood of detecting thresholds and what form they take is thus to a considerable degree dependent on the data transformation applied before

analysis: an obvious point mathematically but one that is frequently given scant attention in ecological threshold analyses (but see Wilson, 2007; Burns *et al.*, 2009).

Interpreting discontinuous models

Scrutiny of plots of all ‘best’ models revealed that several of the piecewise models are difficult to interpret ecologically, particularly in the case of discontinuous piecewise models (see Fig. S1 in Appendix S2). While it is conceivable that discontinuous relationships may exist in nature (see Maron *et al.*, 2012), their detection in a few datasets most likely signifies important roles for confounding variables that were not included in our models, such as isolation or matrix effects (e.g. see Crowe, 1979; Levenson, 1981). For instance, the best model in log–log space for the Crowe (1979) dataset was a discontinuous piecewise model. Crowe (1979) tested various predictions of the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) using plants in urban habitat patches of varying age in the USA. It was found that richness in older patches (over 40 months in age) had no relationship with patch age and did exhibit a significant ISAR, whereas young patches (under 40 months) exhibited a significant species–age relationship and no ISAR. Crowe (1979) suggested that older patches could be considered at equilibrium whereas younger patches were still gaining species through colonization. This suggests that the selection herein of a discontinuous piecewise model is uninformative of the effect of area, but instead reflects a confounding variable.

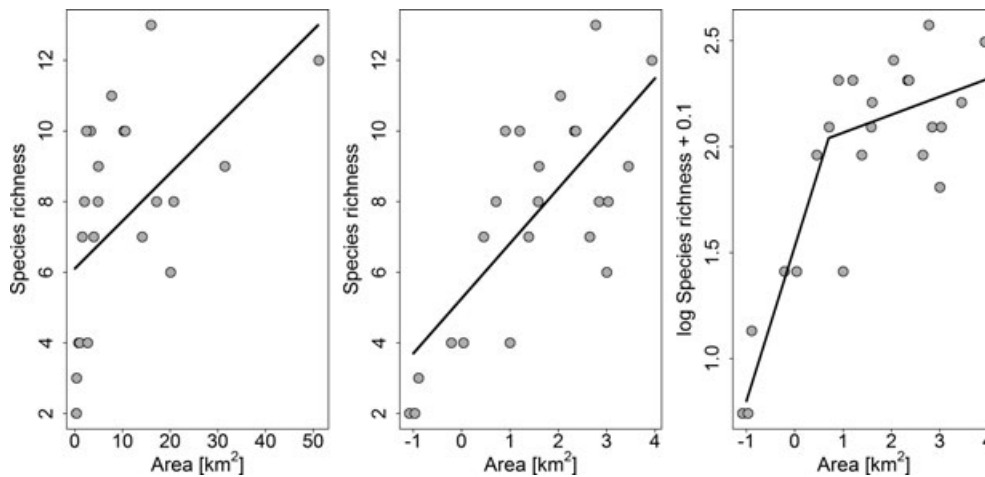


Figure 5 Variation in the best model selection across three versions of the same dataset. Left to right: untransformed, semi-log, log–log. The best model for the untransformed and semi-log transformation was simple linear (positive), and for the log–log transformation, the best was piecewise continuous (steep–shallow). Data are from Kitchener *et al.* (1980): a study on mammals in Australia.

The issue of confounding variables is not restricted to discontinuous models. For example, Watson (2003) identifies the same steep–shallow threshold and breakpoint in untransformed space that we have identified. But he states that there is a high degree of collinearity within his independent variables and thus this pattern cannot be solely attributed to area but may be a product of, for example, elevation, patch configuration, or number of microhabitats. We have not conducted formal analyses of such potentially confounding system variables because there may be many relevant factors and their availability is limited and inconsistent within the source papers (cf. Whittaker, 2010).

Ecological interpretation and the search for thresholds

Breakpoint values and dataset characteristics

Scrutiny of the piecewise models denoted in Table 1 does not suggest that there is any clear tendency to a particular patch threshold size at which rate changes occur in the ISAR. This may reflect a general lack of consistency in response to area, variations in minimum area requirements of species, or it may arise from authors of our source papers having undertaken studies specifically to analyse the effects of one or more of an array of other variables (above; Maron *et al.*, 2012). Landscape features within studies are also important in determining breakpoints. For instance, variation in isolation and of matrix permeability can determine the existence of thresholds through the mitigation or accentuation of the effects of area loss per se (e.g. With & King, 1999; Brotons *et al.*, 2003; Watson *et al.*, 2005; Watling *et al.*, 2011). Another possible explanation of variation in breakpoint values is that the main two piecewise model forms (i.e. steep–shallow and shallow–steep) may represent different parts of a triphasic sigmoidal SAR in which different parts reflect different driving processes at different scales (cf. Rosenzweig,

1995; Lomolino & Weiser, 2001; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2012). However, while sigmoid models may be plausible for particular case studies the present analysis does not provide a basis to claim generality of such a pattern. Another issue in threshold detection is that in cases where a dataset only contains a few data points there are unlikely to be many points near to the hypothetical breakpoint and there is thus potential to ‘miss’ the threshold (cf. Lomolino & Weiser, 2001; Qie *et al.*, 2011). We found some support for this proposition, as piecewise models appeared to emerge mostly in datasets with a large number of islands.

It is intriguing that piecewise continuous models emerged as best more often for the vertebrate datasets, with the steep–shallow form most common. This observation is mirrored by the fact that piecewise discontinuous models emerged as best for three (13%), five (22%), and four (17%) of the untransformed, semi-log transformed and log–log transformed plant datasets, respectively, but for none of the untransformed versions of the vertebrate datasets, and only one (3%) semi-log transformed and three (8%) log–log transformed vertebrate datasets (Table S3 in Appendix S2). There were less obvious emergent patterns for the invertebrate datasets, although it is apparent that invertebrate datasets had a higher proportion of cases in which no model provided a significant fit compared with the vertebrate and plant datasets, for the semi-log and log–log versions of the datasets. While the small sample sizes make it dangerous to speculate on these apparent differences, these results suggest specific responses of the three taxa to habitat loss that merit further investigation.

Conservation and methodological implications

Patch area thresholds have been posited as an important component of protected area network design at the landscape scale (Drinnan, 2005; Huggett, 2005). As such, we offer the

following observations with respect to future research on the topic.

Methodological implications

Piecewise regression has been advocated as an approach to identifying thresholds on the basis that it is more objective than methods such as visual inspection of breakpoints (Ficetola & Denoël, 2009). However, we have shown above that this approach requires careful consideration with regard to the choice of threshold model and data transformation (see also Connor & McCoy, 1979; Burns *et al.*, 2009; Dengler, 2009). This is clearly illustrated for the Watson (2003) dataset in which a single dataset reveals two seemingly opposing patterns depending on the transformation (Fig. 4). It could be argued that both these patterns provide partial truths about the dataset. However, we have also noted that there are confounding variables that may account for the features of the ISAR (see Watson, 2003). Thus, where possible future empirical studies of patch area thresholds should consider other potentially important variables, such as isolation, properties of the matrix and patch age.

We found a small amount of support for the zero slope model: 11 datasets (14%) were best categorized by the zero slope model in semi-log space, and five (7%) in log–log space, and therefore exhibited what has traditionally been described as an SIE (*sensu* Lomolino & Weiser, 2001; e.g. see the right hand side plot of Fig. 4). All that can be said is that the SIE pattern may be identified statistically in a low proportion of habitat island systems (see also Qie *et al.*, 2011), although it should be noted there are other methods of detecting SIE patterns (see Triantis *et al.*, 2006) that were not explored in this paper.

In terms of specific recommendations regarding data transformation in the application of piecewise models one stratagem is to fit ISARs to the untransformed data, semi-log transformed data, and log–log transformed data and consider all three results to generate a conclusion. However, in doing this it is obviously necessary to interpret a particular model in the context of the transformation used (Wilson, 2007). Our results also suggest that the choice of transformation may influence the detection of particular thresholds. For instance, if the aim of a study is to detect classical steep–shallow thresholds in a set of habitat fragments for conservation management purposes it is not advisable to rely upon piecewise regression of a semi-log transformed dataset, for the reasons outlined above and because steep–shallow thresholds were detected very infrequently in semi-log transformed data (see Table 1).

In addition to the complexity surrounding the use of data transformation we identify three further points where future studies may advance statistical methodologies in the search for patch area thresholds. First, use of the log–log transformation to model ISARs generally involves the use of $\log(x+\epsilon)$ to avoid the problem of $\log(0)$ being non-finite.

The choice of ϵ is often arbitrary and can affect the shape of the resulting relationship (Millar *et al.*, 2011), although this is not as problematic for ISAR statistics in comparison with other data. Thus, for future studies of this nature it may be preferable to avoid transformations and apply non-linear methodologies when fitting nonlinear relationships (Steinbauer *et al.*, 2012).

Second, a number of ‘best’ models were changed through our use of Cook’s distance criterion (Table S1 in Appendix S2). Despite all its advantages, the AIC_c framework was not developed to correct for problems associated with extreme values, and regression analyses, as with other statistical methods, need to be critically evaluated in this respect. The influence of data extremes is usually (if at all) checked using visual inspection of model residuals, which can be especially difficult in cases of small datasets, which are common in island biogeographical analyses. As such, we suggest the use of a more rigorous statistical test to highlight potential outliers, such as Cook’s distance.

Third, piecewise regression may occasionally lead to ecologically uninterpretable models being selected as the ‘best’ when used within a model comparison framework; this was particularly the case for discontinuous models. As such, we believe a necessary stage of the process is to use contextual data and graphical display to identify instances in which the best model may be the result of a statistical or experimental design artefact as opposed to any biological mechanism connected with isolate area.

Conservation implications

Our results do not provide the hoped for generic guidance on patch area thresholds but do highlight the importance in future research of considering the effects of data transformations and of sampling a large number of patches and a wide range of patch areas, in order to permit meaningful tests for such thresholds. Notwithstanding the methodological implications outlined above, it is perhaps noteworthy that the 17 datasets which displayed a significant piecewise continuous (steep–shallow) relationship in untransformed space (thus bypassing the data transformation quandary) contained breakpoint values which varied over five orders of magnitude of area. Thus the search for a ‘magic threshold value’ to guide land management and conservation of multiple taxa (e.g. Andrén, 1994) may be misguided (Fahrig, 2001; Betts *et al.*, 2007; Montoya *et al.*, 2010). However, it should be stressed that all these breakpoints, with the exception of the Watson (2003) system, were under 0.5 km² (50 ha), highlighting the ecological precariousness associated with very small fragments.

In sum, it is problematic to determine the prevalence of thresholds in the ISAR of habitat islands. While various piecewise models can be fitted and when grouped may be deemed statistically ‘best’ in about the same number of cases as can simple linear models, it is worth noting the following: first, that we have tried fitting four different types of

piecewise models, thus giving every chance for a piecewise model to emerge as best; second, the emergence of a piecewise model as best does not necessarily mean that the resulting model will be ecologically intelligible; and third, that initial choice of data transformation is a key determinant of the outcome of model fitting. Hence, in the search for thresholds in the ISAR, we call on authors to be explicit as to which data transformations they use at each stage of analysis, and what any particular transformation may mean in terms of inferences based on these analyses. We caution that the use of piecewise regression within a single dataset, or within a meta-analysis framework, could lead to erroneous inferences based on model performance criterion alone and, in particular, more thought needs to be given to the type of data transformation(s) employed.

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SUPPORTING INFORMATION

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

Appendix S1 Data source paper summaries and reference list.

Appendix S2 Supplementary results, including Tables S1–S3 and Fig. S1.

BIOSKETCH

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