BIODIVERSITY RESEARCH

Robust methods for detecting a small island effect

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ABSTRACT

Aim The small island effect (SIE), i.e. the hypothesis that species richness below a certain threshold area varies independently of island size, has become a widely accepted part of the theory of island biogeography. However, there are doubts whether the findings of SIEs were based on appropriate methods. The aim of this study was thus to provide a statistically sound methodology for the detection of SIEs and to show this by re-analysing data in which an SIE has recently been claimed (Sfenthourakis & Triantis, 2009, *Diversity and Distributions*, **15**, 131–140).

Location Ninety islands of the Aegean Sea (Greece).

Methods First, I reviewed publications on SIEs and evaluated their methodology. Then, I fitted different species–area models to the published data of area (A) and species richness (S) of terrestrial isopods (Oniscidea), with log A as predictor and both S (logarithm function) and log S (power function) as response variables: (i) linear; (ii) quadratic; (iii) cubic; (iv) breakpoint with zero slope to the left (SIE model); (v) breakpoint with zero slope to the right; (vi) two-slope model. I used non-linear regression with $R^2_{adj.}$, AIC_c and BIC as goodness-of-fit measures.

Results Many different methods have been applied for detecting SIEs, all of them with serious shortcomings. Contrary to the claim of the original study, no SIE occurs in this particular dataset as the two-slope variants performed better than the SIE variants for both the logarithm and power functions.

Main conclusions For the unambiguous detection of SIEs, one needs to (i) include islands with no species; (ii) compare all relevant models; and (iii) account for different model complexities. As none of the reviewed SIE studies met all these criteria, their findings are dubious and SIEs may be less common than reported. Thus, conservation-related predictions based on the assumption of SIEs may be unreliable.

Keywords

Aegean islands, island biogeography, model complexity, non-linear regression, Oniscidea, species–area relationship.

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INTRODUCTION

The term *small island effect* (SIE) describes situations when species richness (S) on (true or habitat) islands below a certain threshold area (breakpoint) varies independently of island size (A) (Lomolino, 2000; Triantis *et al.*, 2006). While it appears that the term SIE was first applied by Woodroffe (1986), the idea itself dates back to Niering (1963), MacArthur & Wilson (1967) and Whitehead & Jones (1969). Following the *Millennium Guest Editorial* by Lomolino (2000) in the *Journal of Biogeography*, SIE analyses became more common, most of them supporting a widespread occurrence of SIEs (see the Review section). Meanwhile, the SIE found its way into textbooks (Lomolino *et al.*, 2006; Whittaker & Fernández-Palacios, 2007), and Whittaker & Fernández-Palacios (2007, p. 96) conclude that the SIE 'is comparatively common in island datasets'.

While the SIE is becoming more and more part of the theoretical framework of island biogeography and biodiversity research, there are still serious doubts whether it exists at all

(Williamson *et al.*, 2001; Burns *et al.*, 2009; Dengler, 2009). These concerns are prompted by the inadequate ways in which authors of SIE studies have substantiated their claim for its existence (see Dengler, 2009): partly, they did it only graphically, partly they used regression analyses but did not account for the higher model complexity of models with a breakpoint. In the first part of this contribution, I provide a comprehensive review of methods applied for SIE detection and evaluate their appropriateness from a statistical point of view.

A recent publication claiming to have found an SIE is Sfenthourakis & Triantis (2009) in this journal. As this article also provides the original data, I take this opportunity to re-analyse these with more appropriate statistical methods for addressing the question of SIEs. Supported by the empirical findings, I then discuss what might be the appropriate criteria for the existence of an SIE, whether they are met in this particular case and whether they are likely to be met at all. My considerations are embedded in the wider context of multimodel inference in studies on species–area relationships (SARs), of which small islands with a potential SIE are only one special case. As both SIE studies (e.g. Sfenthourakis & Triantis, 2009) and species–area analyses in general (e.g. Veech, 2000; Fahrig, 2003; Desmet & Cowling, 2004) are widely used to draw conclusions for conservation, I finally will address the consequences of my findings in the conservation context.

APPROACHES TO DETERMINE SMALL ISLAND EFFECTS

A query in the *Web of Science* (accessed on 2009-10-09) revealed 18 studies in international journals that used the term SIE either in the title or in the topic, most of them being quite recent (Woodroffe, 1986; Heatwole, 1991; Morrison, 1997; Kelt, 2000; Lomolino & Weiser, 2001; Barrett *et al.*, 2003; Triantis *et al.*, 2003, 2006, 2008; Russell *et al.*, 2004; Gentile & Argano, 2005; Panitsa *et al.*, 2006; Ackerman *et al.*, 2007; Hannus & von Numers, 2008; Kotze, 2008; Morrison & Spiller, 2008; Burns *et al.*, 2009; Sfenthourakis & Triantis, 2009). Of these, Triantis *et al.* (2003) and Kotze (2008) are reviews or conceptual studies without data analyses of their own, while Russell *et al.* (2004) uses the term in the abstract but does not actually deal with this topic. Table 1 provides an overview of the methods used and their major shortcomings for the remaining 15 studies and for two further relevant articles mentioned in the review of Triantis *et al.* (2006), i.e. Niering (1963) and Lomolino (2000).

A wide array of different methods has been applied for the detection of SIEs (Table 1). Individual studies often used more than one method, and different methods applied to the same dataset typically yielded inconsistent results on the existence and extent of an SIE. Most importantly, the authors of all of the SIE studies I reviewed reached conclusions based on methods that are not sufficient for accurate detection. My points of criticism are briefly mentioned in the column 'Methodological shortcomings' of Table 1, and – where necessary – further explained later.

The most frequent problem in SIE studies is that in comparing models with different numbers of fitted parameters, authors did not account for different model complexity (Table 1). The SIE models reviewed have one to three additional parameters compared to the respective model without SIE (Table 1). In such cases, it is inadmissible to use the uncorrected R^2 value as a criterion for selecting the best model (Loehle, 1990; Quinn & Keough, 2002; McGill, 2003; Johnson & Omland, 2004). Instead, other criteria are to be used that penalize for the extra parameters, e.g. $R^2_{adj.}$, Akaike information criterion (AIC), AIC for small n (AIC_c), or Bayesian information criterion (BIC) (Quinn & Keough, 2002; Johnson & Omland, 2004). Recent statistical literature sees the information criteria, AIC/AIC_c and BIC, as the best solutions for the selection among multiple possible models (Mac Nally, 2000; Burnham & Anderson, 2002; Johnson & Omland, 2004; Link & Barker, 2006). Quinn & Keough (2002) and Link & Barker (2006) favour BIC because AIC tends to favour complex models and thus is not sufficiently parsimonious, while Kuha (2004) suggests that AIC and BIC be used jointly. By contrast, Burnham & Anderson (2002) see AIC/AIC_c as the superior approach for theoretical considerations and based on extensive simulations. Preferences of BIC over AIC appear to be at least partly based on the erroneous application of AIC instead of AIC_c when the ratio of observations to estimated parameters (n/K) was below 40 (Burnham & Anderson, 2002). Only Morrison & Spiller (2008) and Burns *et al.* (2009) used AIC/AIC_c as criterion in SIE studies. However, the first authors incorrectly assumed only one extra parameter for their SIE model instead of two (T and z_2, see Table 1), and the second authors used AIC despite of n/K ratios of only 5.4 and 16.2.

Lomolino & Weiser (2001) found SIEs to be much more frequent and stronger for logarithmic than for power models (see also Hannus & von Numers, 2008; Morrison & Spiller, 2008). This means that probably in many cases the normal power function would have been the best model, and the SIE variant of the logarithm function was only preferred over the normal logarithm function because it is more similar to the power function (i.e. in semi-log representation, the slope of the power function is increasing with area). Even if the 'true' relationship is not a power function, a logarithmic model cannot possibly retain its linearity in semilog space towards the smallest areas because it then necessarily would predict negative species richness values (Dengler, 2009), which are impossible. Thus, if a logarithm function is applied and sufficiently small islands are included, necessarily a 'SIE' will be detected. However, this is not a real pattern but a mathematical artefact because of an inappropriate model.

A further, widely neglected problem occurs when islands with no species are excluded from the analysis. Researchers may be prompted to do so for two reasons. First, they may consider unoccupied islands uninteresting. Secondly, they may omit such islands as these cause 'trouble' when fitting a power law in its linearized form because log (0) is undefined. From a statistical perspective, islands with no species must not be excluded in SAR studies (Williams, 1996; Dengler, 2009)

Table 1 Overview of methods for the detection of small island effects (SIEs) applied in the reviewed literature. In the column 'articles', all reviewed studies using a certain method are listed together with the number of SIEs they have found among the given number of datasets. For the sake of clarity, some minor variants of the presented methods that only occur in single articles have been omitted. In the mathematical representation of the models, S stands for species richness, A for area, H for habitat diversity, while c_i, z_i and T are fitted parameters.

No.	Method	Criterion for SIE	Methodological shortcomings	Articles
1	Visual inspection	Apparent lack of slope at the left-hand end of the curve	No statistical method	Niering (1963): 1 SIE out of 1; Woodroffe (1986): 0 SIEs out of 2; Heatwole (1991): 0 SIEs out of 1; Kelt (2000): 1 SIE out of 1; Lomolino (2000): 7 SIEs; Panitsa et al. (2006): 0 SIEs out of 2
2	Comparison of $S = c + b_1 \log A$ vs. $S = c + (\log A > T)\, z\, (\log A - T)$	Higher R^2 of the SIE model	(i) No penalization for one additional parameter; (ii) artefacts of logarithm function for S near zero	Lomolino & Weiser (2001): 91 SIEs out of 102; Triantis et al. (2006): 9 SIEs out of 16; Hannus & von Numers (2008): 1 SIE out of 2; Triantis et al. (2008): 2 SIEs out of 2; Sfenthourakis & Triantis (2009): 1 SIE out of 1
3	Comparison of $\log S = c + b_1 \log A$ vs. $\log S = c + (\log A > T)\, z\, (\log A - T)$	Higher R^2 of the SIE model	No penalization for one additional parameter	Lomolino & Weiser (2001): 76 SIEs out of 102; Barrett et al. (2003): 1 SIE out of 1; Gentile & Argano (2005): 4 SIEs out of 6; Hannus & von Numers (2008): 0 SIEs out of 2; Triantis et al. (2008): 2 SIEs out of 2
4	Comparison of $\log S = c + z \log A$ vs. $\log S = (\log A \leq T)\, (c_1 + z_1 \log A) + (\log A > T)\, (c_2 + z_2 \log A)$	Higher R^2 of the SIE model	(i) No penalization for three additional parameters; (ii) discontinuous function	Gentile & Argano (2005): 6 SIEs out of 6; Sfenthourakis & Triantis (2009): 0 SIEs out of 1; Triantis et al. (2008): 2 SIEs out of 2
5	Comparison of an unspecified 'linear' model vs. an unspecified 'curvilinear' model	Higher R^2 of the SIE model	No penalization for additional parameter(s)	Morrison (1997): 1 SIE out of 2
6	'Path analysis': de facto comparison of $\log S = z_1 \log A + z_2 \log H$ vs. $\log S = (\log A \leq T)\, z_3 \log H + (\log A > T)\, (z_1 \log A + z_2 \log H)$	Existence of a subgroup of smaller islands for which, in a multiple regression with log A and log H as predictors, the effect of log A is ≤ 0	(i) No penalization for two additional parameters; (ii) high correlation between H and A causes imprecise parameter estimates; (iii) 'forcing' the regression through the origin; (iv) problematic habitat definition; (v) deviating concept of SIE ('cryptic SIE')	Triantis et al. (2006): 6 SIEs out of 16; Hannus & von Numers (2008): 0 SIEs out of 2; Triantis et al. (2008): 2 SIEs out of 2; Sfenthourakis & Triantis (2009): 1 SIE out of 1
7	Non-significant slope	Existence of a subgroup of smaller islands for which the linearized power-law relationship becomes insignificant ($P > 0.1$)	Any relationship becomes insignificant when the number of replicates and/or the range of the predictor variable is reduced sufficiently	Ackerman et al. (2007) 1 SIE out of 1
8	'Null model approach'	Significantly higher mean differences between observed values and those predicted by a null model for smaller islands	(i) Appropriateness of selected null model questionable; (ii) individual-based null model not applicable in many cases; (iii) deviating concept of SIE	Burns et al. (2009) 0 SIEs out of 2
9	Comparison of $\log S = c + z \log A$ vs. $\log S = c + (\log A \leq T)\, z_1 \log A + (A > T)\, [z_1 T + z_2\, (\log A - T)]$	Lower AIC/AIC_c of the SIE model	(i) Erroneous AIC/AIC_c calculation (see text); (ii) deviating concept of SIE ('SIE sensu lato')	Morrison & Spiller (2008): 1 SIE out of 1; Burns et al. (2009): 2 SIEs out of 2

AIC, Akaike information criterion.

because towards the far-left, the shape of the species–area curve is mostly determined by the successively increasing fraction of islands without any species. The exclusion of islands with no species that fall within the pre-set size range of a study thus likely leads to the erroneous detection of an SIE. Estimating the extent of this problem is difficult as the method sections of articles are usually not explicit about this aspect of sampling. For example, Morrison (1997) surveyed 133 islands occupied by plants and 49 unvegetated islands, but only the first appear in his analyses of the SARs (his Figures 3 and 4). Such biased sampling has likely occurred in many cases where there are islands with one species but no islands with no species in the dataset. This applies to 41 of 102 datasets analysed by Lomolino & Weiser (2001) and many datasets in other studies (Lomolino, 2000; Barrett *et al.*, 2003; Triantis *et al.*, 2006; Burns *et al.*, 2009).

Burns *et al.* (2009) recently proposed that the logarithmic transformation of the axes (used to allow the application of linearized versions of the logarithm or power function) might cause the detection of an SIE where there is none. They tried to demonstrate this claim with a simulated example of a linear relationship of the form $S = A$ with 'an even scatter about the best fit line'. While for areas larger than 2 units, their islands actually had a mean richness of $S(i) = i$, the mean values for the two smallest island sizes were $S(1) = 2$ and $S(2) = 2.5$. Consequently, Burns *et al.* (2009) found a flatter slope for these, but this does not support their claim of a mathematical artefact.

Finally, the different methods for SIE detection are based on four deviating concepts of SIEs (Table 1). The classic concept, defining an SIE (SIE *sensu stricto*) as a situation where species richness varies independently of area below a certain threshold (MacArthur & Wilson, 1967; Lomolino, 2000; Triantis *et al.*, 2006), forms the basis of methods 1, 2, 3 and 7. By contrast, methods 4 and 9 test whether the SAR slope for small islands is different (flatter) but not necessarily zero (SIE *sensu lato*). Method 6 tries to test only the direct effect of area ('cryptic SIE'; for further discussion, see 'The Cryptic SIE Remains Cryptic' below). Yet another hypothesis is tested with method 8 (Burns *et al.*, 2009) that compares the SAR observed with one predicted under certain null model assumptions. The authors would accept an SIE when the species richness pattern was less predictable for smaller sized islands than for larger sized islands. The problem with this approach is that we are far from a consensus about the most appropriate null model and each different null model would yield different results. Moreover, the null model preferred by Burns *et al.* (2009) is based on abundance information (i.e. number of individuals), which is not available in most SIE studies and which cannot be obtained at all for certain organisms, such as clonal plants. While it may be useful to apply the deviating SIE concepts (i.e. SIE *sensu lato*, cryptic SIE, null model approach) under certain circumstances, one should be aware that this means testing hypotheses that do not directly relate to the SIE *sensu stricto*.

RE-ANALYSIS OF THE DATA OF SFENTHOURAKIS & TRIANTIS (2009)

Methods

The data taken from Sfenthourakis & Triantis (2009, their Table 1) consist of species richness counts of terrestrial isopods (Oniscidea; ranging from 1–34 species) for 90 Aegean islands, sized 0.0023–8261 km^2. I conducted regression analyses for a wide range of different variants of the power function (fitted in log S-space) and logarithm function (fitted in S-space) (for details, see Dengler, 2009). I used power and logarithm functions as the 'basic' functions because the majority of SIE publications did the same. These two functions usually fit SARs well (see Dengler, 2009, and references cited therein), and they allow the easy creation of variants that incorporate the SIE and similar effects. The selection of variants of these two basic functions aimed to reflect the basic idea of the SIE, i.e. that area becomes irrelevant or less relevant for areas of a certain size. This change in relevance of area can be modelled as a sharp change at a certain point (log $A = T$) (see equation 4–6) or as a gradual transition (equation 2 and 3). When there is a single breakpoint T, there are three possibilities: zero slope of the SAR below T (i.e. classical SIE; equation 4), zero slope of the SAR above T (equation 5) or different slopes of the SAR below and above T (equation 6). Accordingly, in the case of the power model, I fitted the following curve shapes to a log–log representation of the area–richness data: linear (equation 1), quadratic (equation 2), cubic (equation 3), linear with zero slope below the breakpoint ('left-horizontal'; equation 4), linear with zero slope above the breakpoint ('right-horizontal'; equation 5) and linear with two different slopes ('two-slope'; equation 6).

$$\log S = c + z_1 \log A \tag{1}$$

$$\log S = c + z_1 \log A + z_2 (\log A)^2 \tag{2}$$

$$\log S = c + z_1 \log A + z_2 (\log A)^2 + z_3 (\log A)^3 \tag{3}$$

$$\log S = c + (\log A > T) z_1 (\log A - T) \tag{4}$$

$$\log S = c + (\log A \leq T) z_1 \log A + (\log A > T) z_1 T \tag{5}$$

$$\log S = c + (\log A \leq T) z_1 \log A \\ + (\log A > T)[z_1 \log T + z_2 (\log A - T)] \tag{6}$$

In these equations, S stands for species richness, A for standardized area, while c (intercept), z_i (slopes) and T (breakpoint) are fitted parameters. The logical expressions in round brackets return 1 if they are true and 0 if they are false.

For the equivalent variants of the logarithm function, the same curve types were fitted to a semilog representation of the data, i.e. with S instead of log S as the dependent variable (i.e. equations 1–6 with log S replaced by S). In addition, the normal variant of the power function was fitted in S-space (see Dengler, 2009), while in several trials to fit the normal variant

of the logarithm function analogously in log S-space, iterations did not converge.

The regression analyses were carried out with the non-linear regression module of STATISTICA 8.0 (Statsoft, Inc., 2008). I used the default settings of the program (loss function = (OBS-PRED)^2; estimation method = quasi-Newton; convergence criterion = 0.0001; step-width for all parameters = 0.5; starting values for all parameters = 0.1), unless the iterative process did not converge. In these cases, I altered the starting values until the programme found a minimum. For each model, I calculated the predicted values of S for all islands. These were used to determine R^2 and $R^2_{adj.}$ (Quinn & Keough, 2002) as well as AIC_c and BIC (least squares case; see Burnham & Anderson, 2002) of each of the models and both in S- and log S-space. For the model selection, I finally calculated the difference in AIC_c ($\Delta AIC_{c,i}$) and Akaike weights (w_i) for each model i within the set of competing models (Burnham & Anderson, 2002), as well as the corresponding values for BIC (ΔBIC_i, $\Pr\{g_i\}$). Akaike weights are the normalized likelihood values across all compared models so that they sum up to 1 (Johnson & Omland, 2004). They can be interpreted as 'the probability that model i is the best model for the observed data, given the candidate set of models' (Johnson & Omland, 2004).

Results

In S-space, the four-parameter model 'two-slope logarithm function' yielded the highest explained variance (R^2) and remained to be the best among the 13 compared models when accounting for different model complexities by means of $R^2_{adj.}$, AIC_c or BIC (Table 2, see Fig. 1). Similarly, in log S-space, the four-parameter model 'two-slope power function' performed best according to all four criteria (Table 2). Both models estimated the slopes of the SARs to be less steep for the smaller islands than for the larger islands (Table 2), but still significantly different from zero ($P = 0.002$ for the two-slope logarithm function in S-space and $P = 0.004$ for the two-slope power function in log S-space).

In S-space, the cubic power function performed only slightly worse than the best model and still better than the third-ranked model, the left-horizontal logarithm function (i.e. the classic SIE model) (Table 2). According to Akaike weights (w_i), the chance that the SIE model was the best among the tested models was only 8.6% and the evidence ratio of the two-slope model over the classical SIE model was 5.1. When only the SIE model and the normal logarithmic model were compared, the SIE model was indeed much better with $\Delta AIC_c = 68.46$ (see Table 2 and Fig. 1). However, the normal power functions, irrespective for which space they were fitted, were also much better than the logarithm function with ΔAIC_c of 45.44 and 36.97 (see Table 2 and Fig. 1).

In log S-space (Table 2), the cubic power function was ranked second according to R^2, $R^2_{adj.}$ and AIC_c, while for BIC, the normal power (fitted for log S) was second-best. In the direct comparison of normal and left-horizontal power functions, the latter model (SIE model) was marginally better according to $R^2_{adj.}$ but worse according to AIC_c and BIC. Interestingly, not only the left-horizontal model but also the right-horizontal model (i.e. no increase in species richness above a certain island size) achieved a higher R^2 than the normal power function.

Among those models that assume a breakpoint, the position of the breakpoint along the x-axis varied widely (Table 2). While the power SIE model had the breakpoint at $x = -1.758$ (i.e. 0.017 km^2), the logarithmic SIE model had its breakpoint at $x = -0.057$ (i.e. 0.877 km^2), thus involving four or 43 islands. The breakpoints for the two-slope models also had different positions, namely 0.600 km^2 (39 islands) for the power version and 2.239 km^2 for the logarithmic version (54 islands). The right-horizontal models did not bring any improvement for the logarithmic version and involved only a single island (Crete) in the horizontal part of the curve for the power version.

Discussion

Considering the overall shape of the species–area curve, the logarithm function provided a much worse fit than the power function (see Table 2 and Fig. 1). This finding is in line with many other studies that report the prevalence of power functions over logarithm functions for SAR at any spatial scale (see reviews/meta-analyses by Connor & McCoy, 1979; Rosenzweig, 1995; Dengler, 2009). When the 'true' relationship is a power function, the SIE version of the logarithm function will necessarily be superior to the normal logarithm function, as it approximates the concave upward shape of a power function in semilog representation. The fact that quadratic and cubic variants of the logarithm and power functions performed moderately well should not be overinterpreted, because these variants – while convenient to simulate gradual transitions of slopes – cannot be used for a general description of a SAR as they necessarily predict decreasing species richness for some spatial scales. This, however, is theoretically impossible for a statistical population (see Dengler, 2009; Tjørve, 2009).

Sfenthourakis & Triantis (2009) claimed that they found an SIE up to 1 km^2 (i.e. 45 islands) in the dataset with the method of Lomolino & Weiser (2001) for the logarithm ('semilog') function (No. 2 in Table 1) and up to 4.558 km^2 (i.e. 58 islands) with the method of Triantis et al. (2006, i.e. no. 6 in Table 1). By contrast, they did not detect any SIE with the method of Gentile & Argano (2005; i.e. no. 5 in Table 1). The first value (1 km^2) is very close to the result determined in this study (0.877 km^2), and the difference is probably only because of the fact that the method of Lomolino & Weiser (2001) determines the breakpoint by successively increasing T with an increment of 0.1 and then recalculating R^2 until a maximum is achieved. By contrast, I used non-linear regression that achieves the optimal solution in an iterative process that allows T to take any value.

Whilst this agrees with Sfenthourakis & Triantis (2009) in rating the left-horizontal logarithm function (SIE model) as

Table 2 Results of the non-linear regression analyses of species–area data of isopods on 90 Aegean islands. The best models according to the different criteria are marked in bold. Note that c refers to species richness for models fitted for S and to $\log_{10}$ of species richness in the case of models fitted for $\log S$. T is $\log_{10}$ of the area in km^2 of the breakpoint. Note that the number of estimated parameters (k) used for the calculation of the information criteria, is $p + 1$ (i.e. the model parameters + the variance of the residuals; see Burnham & Anderson, 2002). The abbreviation n.a. (not applicable) denotes values that were not defined (i.e. logarithms of negative values).

Function	Logarithm	Logarithm, quadratic	Logarithm, cubic	Logarithm, left-horizontal	Logarithm, right-horizontal	Logarithm, two-slope	Power	Power	Power, quadratic	Power, cubic	Power, left-horizontal	Power, right-horizontal	Power, two-slope
S-space	S	S	S	S	S	S	S	$\log S$	$\log S$	$\log S$	$\log S$	$\log S$	$\log S$
No. of fitted parameters p	2	3	4	3	3	3	2	2	3	4	3	3	4
Parameter estimates													
c	8.721	6.431	6.333	4.047	8.721	5.605	7.203	0.800	0.770	0.757	0.389	0.801	0.705
z_1	5.015	4.077	4.313	7.826	5.015	1.409	0.202	0.223	0.211	0.243	0.230	0.226	0.129
z_2		1.185	1.271			8.485			0.015	0.027			0.268
z_3			−0.064							−0.009			
T				−0.057	>3.920	0.350					−1.758	3.229	−0.225
Model performance in S-space													
R^2	0.8106	0.9112	0.9124	0.9136	0.8106	**0.9188**	0.8857	0.8744	0.7172	0.9186	0.8700	0.9111	0.7968
$R^2_{adj.}$	0.8085	0.9092	0.9093	0.9116	0.8063	**0.9159**	0.8844	0.8730	0.7107	0.9158	0.8670	0.9091	0.7897
Δ_i (AIC$_c$)	71.73	5.73	6.80	3.27	73.91	**0.00**	26.29	34.76	110.00	0.16	40.04	5.86	82.49
Δ_i (BIC)	67.15	3.46	6.80	1.01	71.65	**0.00**	21.72	30.18	107.74	0.16	37.78	3.59	82.49
w_i (AIC$_c$)	0.0000	0.0252	0.0148	0.0861	0.0000	**0.4420**	0.0000	0.0000	0.0000	0.4082	0.0000	0.0236	0.0000
Pr$\{g_i\}$ (BIC)	0.0000	0.0609	0.0115	0.2080	0.0000	**0.3444**	0.0000	0.0000	0.0000	0.3181	0.0000	0.0571	0.0000
Model performance in log S-space													
R^2	n.a.	0.7878	0.7782	0.7914	n.a.	0.8025	0.7610	0.7896	0.7980	0.8082	0.7944	0.7915	**0.8102**
$R^2_{adj.}$	n.a.	0.7829	0.7704	0.7866	n.a.	0.7956	0.7583	0.7872	0.7934	0.8015	0.7897	0.7867	**0.8036**
Δ_i (AIC$_c$)	n.a.	7.81	14.04	6.27	n.a.	3.58	16.33	4.85	3.37	0.94	4.96	6.22	**0.00**
Δ_i (BIC)	n.a.	5.55	14.04	4.01	n.a.	3.58	11.76	0.27	1.10	0.94	2.70	3.96	**0.00**
w_i (AIC$_c$)	n.a.	0.0089	0.0004	0.0193	n.a.	0.0741	0.0001	0.0392	0.0822	0.2766	0.0371	0.0197	**0.4424**
Pr$\{g_i\}$ (BIC)	n.a.	0.0162	0.0002	0.0352	n.a.	0.0436	0.0007	0.2271	0.1500	0.1628	0.0677	0.0360	**0.2605**

AIC, Akaike information criterion; BIC, Bayesian information criterion.
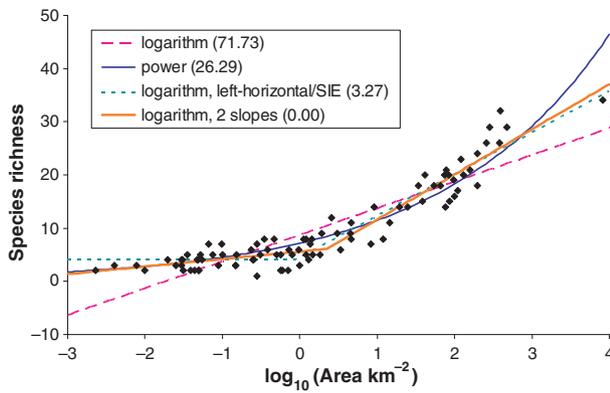
Figure 1 Species–area data of isopods on 90 Aegean islands and four different models fitted to these data in S-space with non-linear regression. The Δ_i (AICc) values are given in brackets (the lowest value denotes the 'best' model).

more suitable than the normal logarithm function, the support for the SIE function vanished when taking a wider range of possible functions into account. In particular, the functions with two different slopes got much higher support than either of the corresponding SIE functions in the respective S-spaces. Their slopes in the left part were significantly different from zero – thus rejecting the existence of an SIE *sensu stricto* in this dataset.

By contrast, an SIE *sensu lato*, i.e. a flatter slope of the SAR for small islands, was confirmed in both S-spaces. However, the thresholds for the SIEs *sensu lato* (0.017 and 0.877 km^2) strongly deviated from the thresholds determined by Sfenthourakis & Triantis (2009) with their methods. While it would be worthwhile to find plausible explanations for the decreased SAR slope of small islands, this is beyond the scope of this article, and I am not in the possession of the relevant information to test competing hypotheses that could lead to such an SAR. The underlying reasons could be those brought forward for a general SIE (see MacArthur & Wilson, 1967; Triantis *et al.*, 2006) but as well be completely idiosyncratic (e.g. systematic differences in the environmental conditions of the small vs. the large islands by chance).

In their second approach, Sfenthourakis & Triantis (2009) determined the SIE with what they call 'path analysis' (Triantis *et al.*, 2006). Here, an SIE is stated, when below a certain threshold, the direct effect of area on S (i.e. its partial regression coefficient) becomes zero or negative after eliminating the effect of habitat diversity. Apart from also not accounting for the higher complexity in the SIE model (see Table 1), this approach has two drawbacks. First, it defines the SIE differently from Lomolino (2000), who simply speak of an SIE, when species richness below a threshold is 'independent of island area' as it only takes the direct effects of area into consideration but excludes (or tries to exclude) the effects of area mitigated through higher habitat diversity on larger islands. By contrast, the classical definition of Lomolino (2000), on which the method of Lomolino & Weiser (2001) is based, includes both the direct and indirect effects of area.

Consequently, both methods yielded different results. Second, Sfenthourakis & Triantis (2009) used the simple number of habitat types, roughly grouped into 16 categories, mostly according to vegetation structure and land use (e.g. salt marshes or olive groves), as their measure of habitat diversity. These habitat definitions are idiosyncratic, generally not transferable among island datasets and constructed from an anthropogenic view. Moreover, this approach does not account for the proportional areas of the habitats on the islands. Nor does it reflect the varying degrees of similarity between the habitat types (e.g. are groves of olives and fruit-bearing trees more similar to each other than either of these two habitat types to salt marshes?). Thus, it is questionable as to the meaning of an SIE and of its upper limit L if habitats are defined and used in such a way.

DOES THE SMALL ISLAND EFFECT EXIST AT ALL?

In this article, I demonstrated that in one particular dataset (Sfenthourakis & Triantis, 2009) no SIE in the sense of Lomolino (2000) and Lomolino & Weiser (2001) occurs, contrary to the authors' conclusions. While it was not my intention to re-analyse the data of all studies that reported an SIE (see Review section), a closer look at the most comprehensive meta-analysis on this topic so far (Lomolino & Weiser, 2001) may help to elucidate the question raised in the section heading. These authors reported the existence of SIEs for a large proportion of 102 island datasets, based on often marginal increases in the uncorrected R^2-values of the SIE models compared to the non-SIE models. On average, the authors found an increase in R^2 by only 0.075 for the logarithmic models and 0.028 for power models. These low values suggest that in many cases, the authors' conclusion might not withstand a re-analysis based on information criteria, particularly as their datasets typically consist of much fewer islands (mean sample size: 26.8) than that of the Aegean isopods. Further, as demonstrated in the Review section, all previous SIE studies included at least one methodological drawback that biases the outcomes of SIE studies towards the detection of SIEs.

THE CRYPTIC SMALL ISLAND EFFECT REMAINS CRYPTIC

Is then the other approach to detect an SIE proposed by Triantis *et al.* (2006) and applied as one alternative by Sfenthourakis & Triantis (2009) more promising? As the authors admit, this approach uses a deviating definition of SIE from Lomolino (2000; see Discussion section above), and thus they speak of a 'cryptic SIE'. Their aim was to 'extract' from the overall SAR the one part that is caused by area directly ('area *per se*') but to omit those parts that are caused indirectly via increased habitat diversity and then to test whether the remaining 'pure' SAR shows a left-horizontal shape. It has frequently been acknowledged that the existence of SARs is a result of two main factors, namely area *per se* (i.e. larger areas usually are inhabited by more individuals and these by chance

tend to comprise more different species) and habitat diversity (i.e. larger areas usually encompass a larger variety of different habitat conditions because of the typical distance decay in ecological similarity, thus allowing species of different niches to co-exist) (e.g. Nilsson *et al.*, 1988; Ricklefs & Lovette, 1999; Gaston & Blackburn, 2000; Triantis *et al.*, 2003; Whittaker & Fernández-Palacios, 2007). To disentangle these two processes by including a measure of habitat diversity into the SAR models (Nilsson *et al.*, 1988; Ricklefs & Lovette, 1999; Triantis *et al.*, 2003) seems hardly plausible since there are infinite possibilities of how to quantify habitat diversity – and each will result in different outcomes. Accordingly, if the intention is to test for a 'cryptic SIE', apart from solving the other methodological shortcomings of the method of Triantis *et al.* (2006) (see Table 1), one should apply a uniform habitat definition for all island datasets to be compared. To find such a general, globally applicable and, at the same time, ecologically meaningful measure of habitat diversity will certainly not be an easy task.

I propose another approach for incorporating habitat diversity into SIE/SAR analyses. Since the correct methods of fitting SARs are very different from those of interpreting the root causes of aspects of any given SAR, these tasks should be separate and sequential. Finding the best model for an SAR may then be followed by, for example, examining how slopes (*z*-values) vary with spatial scale and elucidating the underlying causes of this variation (Turner & Tjørve, 2005; Dengler, 2009). Likewise, the deviations of empirical data from fitted curves (i.e. the residuals) can be explained by differences in present and historic environmental conditions. Here, habitat diversity comes into play as the residuals of the overall SAR can be regressed against the residuals of the habitat diversity–area relationship. The variance explained by the latter predictor in comparison to other environmental parameters will characterize the relative importance of habitat diversity in a specific case. That way, it is also possible to test which of the many possible measures of habitat diversity results in the highest explained variance and thus is most meaningful in a specific case.

HOW TO DETECT A SMALL ISLAND EFFECT?

Based on the arguments presented, four criteria seem indispensable for the unambiguous demonstration of SIEs:
1 If islands with no species fall within the geographical and range-size limits of the study, they must be included in the analyses.
2 The comparison should include a wide range of different models (at least one variant without an SIE, one with an SIE *sensu stricto* and one with an SIE *sensu lato*).
3 The model selection needs to be carried out in the same *S*-space for all models.
4 The applied goodness-of-fit measure should adequately account for varying model complexity (i.e. AIC_c or BIC).

The logarithm function ('semilog model'), despite its wide application in SIE studies (see Table 1), is generally inappro-

priate for richness data close to zero, which usually occur when small islands are analysed (see Review section). Instead, I suggest using variants of the power function, such as normal power function (no SIE), left-horizontal power function (SIE *sensu stricto*) and two-slope power function (SIE *sensu lato*). Actually, the inclusion of the last model is a way to implement the proposal in Dengler (2009) to test for the scale-dependence of *z*. On the one hand, it does not assume a breakpoint at all nor a certain position of it; on the other hand, it also allows not only for SIEs *sensu lato* but also for decreasing slopes with increasing area as they are to be expected for very large islands (see Preston, 1962; Dengler, 2009). Such a continuous two-slope model (four parameters) has previously been applied in SIE studies by Morrison & Spiller (2008) and Burns *et al.* (2009), while Gentile & Argano (2005) proposed a discontinuous two-slope model (No. 4 in Table 1), which appears basically inappropriate for modelling macroscopic processes in nature and is even more complex (five parameters).

This case study deviates from all previous SIE studies in applying non-linear regression (see Quinn & Keough, 2002) for fitting the models. This approach proved to be particularly powerful as it allows the modelling and comparison of practically any type of functional relationship directly (see previous applications to SARs by Dengler & Boch, 2008; Dengler, 2009). Further, it enables the direct modelling of power laws and their variants, i.e. with *S* instead of log *S* as response variable (Quinn & Keough, 2002, p. 150). This approach can be superior to the linearized version because (i) the goodness-of-fit can directly be compared with other functions fitted in *S*-space; (ii) areas with $S = 0$ can be included easily without applying a 'log $(S + 1)$'-transformation (e.g. Barrett *et al.*, 2003; Triantis *et al.*, 2006), which has been criticized much (e.g. Wilson, 2007). Moreover, unlike the 'manual' approach of Lomolino & Weiser (2001) to find the optimal breakpoint by applying two separate linear regressions repeatedly, the non-linear regression modules of statistical packages (such as STATISTICA; StatSoft, Inc., 2008) do this automatically and by varying all parameters with infinitesimal step-width when approaching the optimum.

One further problem potentially involved in the analysis of island SARs but not addressed here (or in any other SAR study known to me) is spatial autocorrelation. In other fields of macroecology, spatial autocorrelation has recently received increasing attention, as it could lead to biased estimates of goodness-of-fit measures and parameters (Dormann *et al.*, 2007; Kühn, 2007). Future studies should thus test the relevance of spatial autocorrelation for island SARs and how best to correct for it within the framework of non-linear regression modelling.

Finally, I wish to highlight the difference between unequivocally finding an SIE (*sensu stricto* or *sensu lato*) in a particular dataset and promoting SIEs as a general biogeographical phenomenon with a common cause. Unlike nested-plot SARs, species richness data of islands are also influenced by many other environmental (e.g. altitude, distance to mainland) and

historic factors (e.g. island age), which usually cause a much higher scatter of the data points around the regression line (see MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007; Dengler, 2009). Thus, if for certain small areas, species richness apparently is not dependent or less dependent on area, this may well be caused by unequal distribution of other island characteristics between size classes (e.g. the combination of smaller temperate islands with larger arctic islands). Such a flattening of the SAR 'by chance' could happen in all size classes, not only for small islands. Only if it should occur more frequently for the smallest sized islands, would there be a justification to assume a causal relationship between small size of islands and flatness of the corresponding SAR segment.

CONCLUSIONS AND OUTLOOK

As all previous studies that claimed SIEs violated at least one of the methodological pre-requisites presented in this article, it is presently an open question how frequent SIEs are or whether they occur at all. However, the impression raised in recent literature that SIEs are ubiquitous (Lomolino & Weiser, 2001; Whittaker & Fernández-Palacios, 2007) is probably not true, given the arguments provided here.

Thus, it would be highly desirable in the future to analyse a comprehensive number of island datasets with the methods proposed in this article. Instead of solely focussing on SIEs *sensu stricto*, I suggest that neither a constant slope across all spatial scales nor a zero slope towards the left-hand end should be assumed *a priori*, but it should be tested whether and where the slope changes (see Dengler, 2009). If in a meta-analysis, other SARs also frequently exhibit shallower, yet non-zero slopes towards smaller island sizes (as in the example, re-analysed here), one may consider calling this phenomenon an SIE *sensu lato* – as contrasted to the SIE *sensu stricto* of Lomolino (2000) – and to seek for common underlying reasons.

The results of this study suggest that it might be pre-mature to apply those ideas in conservation that other authors developed under the assumption of SIEs being widespread. Sfenthourakis & Triantis (2009), for example, concluded that the focus of nature conservation should be on the protection of islands 'near the SIE threshold'. They justified this with the finding that their SIE threshold coincided with the point below which the proportion of habitat specialists (which are particularly susceptible to environmental change) rapidly decreased. However, this coincidence does not hold for the thresholds of the SIEs *sensu lato* determined in this article, which removes any support for the priority setting proposed by Sfenthourakis & Triantis (2009). Further, if SIEs are not as widespread as others propose, then it may be dangerous to assume further reductions in already small habitat fragments will not further reduce species richness. Finally, from a more general perspective, the present study suggests that one should be very cautious in applying SARs for the prediction of effects of habitat loss, hotspot determination or optimal reserve planning (e.g. Veech, 2000; Lomolino, 2001; Fahrig, 2003; Desmet & Cowling, 2004;

Ulrich & Buszko, 2004; Whittaker & Fernández-Palacios, 2007; Guilhaumon et al., 2008). In such analyses, typically only one or at best few, mostly simple SAR models have been included and often the same methodological shortcomings were involved as demonstrated here for SIEs. Thus, predictions and suggestions of such studies may be unreliable. For example, Guilhaumon *et al.* (2008) demonstrated that a model selection procedure similar to the one applied here (i.e. comparison of many different models; AIC as goodness-of-fit measure) led to a selection of diversity hotspots dramatically different from those previously determined with 'traditional' approaches.

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