



Re-approaching the small island effect

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ABSTRACT

Aim To propose a new approach to the small island effect (SIE) and a simple mathematical procedure for the estimation of its upper limit. The main feature of the SIE is that below an upper size threshold an increase of species number with increase of area in small islands is not observed.

Location Species richness patterns from different taxa and insular systems are analysed.

Methods Sixteen different data sets from 12 studies are analysed. Path analysis was used for the estimation of the upper limit of the SIE. We studied each data set in order to detect whether there was a certain island size under which the direct effects of area were eliminated. This detection was carried out through the sequential exclusion of islands from the largest to the smallest. For the cases where an SIE was detected, a log-log plot of species number against area is presented. The relationships between habitat diversity, species number and area are studied within the limits of the SIE. In previous studies only area was used for the detection of the SIE, whereas we also encompass habitat diversity, a parameter with well documented influence on species richness, especially at small scales.

Results An SIE was detected in six out of the 16 studied cases. The upper limit of the SIE varies, depending on the characteristics of the taxon and the archipelago under study. In general, the values of the upper limit of the SIE calculated according to the approach undertaken in our study differ from the values calculated in previous studies.

Main conclusions Although the classical species–area models have been used to estimate the upper limit of the SIE, we propose that the detection of this phenomenon should be undertaken independently from the species–area relationship, so that the net effects of area are calculated excluding the surrogate action of area on other variables, such as environmental heterogeneity. The SIE appears when and where area ceases to influence species richness directly. There are two distinct SIE patterns: (1) the classical SIE where both the direct and indirect effects of area are eliminated and (2) the cryptic SIE where area affects species richness indirectly. Our approach offers the opportunity of studying the different factors influencing biodiversity on small scales more accurately. The SIE cannot be considered a general pattern with fixed behaviour that can be described by the same model for different island groups and taxa. The SIE should be recognized as a genuine but idiosyncratic phenomenon.

Keywords

Habitat diversity, island biogeography, island biotas, path analysis, small island effect, species–area relationship, species richness.

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INTRODUCTION

Due to their apparent simplicity and discrete nature, scientists have long viewed islands as model systems for the investigation of questions related to biodiversity and its regulation. Notwithstanding the large literature focusing on island area and species richness, and despite the fact that the vast majority of islands are small sized, very little research has focused on the implications of small size for area effects (see Lomolino & Weiser, 2001).

Niering (1963), in his study of the higher plants on islands of the Kapingamarangi Atoll in Micronesia, presented one of the first species–area plots indicating the existence of what Lomolino & Weiser (2001) characterized as an almost cryptic phenomenon, the small island effect (SIE). The main feature of this SIE is that species number does not increase with increasing area in small islands. In short, below a certain threshold area diversity is independent of island size.

As a rule, biogeographers and ecologists have neglected the SIE. Papers discussing or commenting on this phenomenon are restricted, despite the number of studies and applications of the species–area relationship and the amount of information on small islands. To our knowledge only the following papers discuss or refer to the SIE (see Preston, 1962; Wiens, 1962; Niering, 1963; MacArthur & Wilson, 1967; Whitehead & Jones, 1969; Rusterholz & Howe, 1979; Woodroffe, 1986; Dunn & Loehle, 1988; Heatwole, 1991; Botsaris, 1996; Morrison, 1997; Brown & Lomolino, 1998; Kelt, 2000; Lomolino, 2000, 2002; Anderson & Wait, 2001; Lomolino & Perault, 2001; Lomolino & Weiser, 2001; Whittaker *et al.*, 2001; Triantis, 2002; Barrett *et al.*, 2003; Triantis *et al.*, 2003, 2005; Whittaker, 2004; Gentile & Argano, 2005).

Various authors (Wiens, 1962; Niering, 1963; MacArthur & Wilson, 1967; Losos, 1996; Lomolino & Weiser, 2001) have

suggested that within a certain range, the effects of increasing area on species richness are insignificant compared to other features of the islands and the taxa studied. In one example, MacArthur & Wilson (1967) suggested that for small, unstable islands, extinction rates could be area-independent. Environmental characteristics, intraspecific interactions, stochastic events, habitat diversity, isolation, occasional disturbances and human impact have been nominated as possible factors that contribute to the establishment of species richness on small islands (Botsaris, 1996; Losos, 1996; Whittaker, 1998; Losos & Spiller, 1999; Sadler, 1999; Lomolino, 2000; Lomolino & Weiser, 2001; Schoener *et al.*, 2001).

In this paper we present a simple mathematical procedure that permits the calculation of the range of island sizes in which the SIE can be detected. This approach, considers both area and a measure of environmental heterogeneity, i.e. ‘habitat diversity’. The results of our approach are compared to those obtained by the application of the model proposed by Lomolino & Weiser (2001). This latter model was created by adding an additional term (the breakpoint transformation) to traditional species–area models.

MATERIALS AND METHODS

In the present study we analyse 16 different data sets derived from 12 bibliographic sources. For each data set the geographical location of the archipelago, the taxon studied, the range of species richness, the range of island size and the number of habitats are presented (Table 1). Although in the work of Ricklefs & Lovette (1999) four groups were studied, namely, bats, butterflies, birds and amphibians/reptiles, the latter group was not included in our analysis, due to the different ecology of the two taxa. Additionally, in the same work, the species list for bats from two small islands (St Bartholomew and Nevis) is

Table 1 Description of the sources, geographical location, taxon, number of islands, range of species richness, range of area and the number of habitats for the data sets used in this study

Source	Geographical location	Taxon	No. of islands	Richness (range)	Area (km ² ; range)	No. of habitats
Reed (1981)	Great Britain	Land birds	73	1–79	8×10^{-3} –106.92	26
Haila <i>et al.</i> (1983)	Aland Islands, SW Finland	Land birds (1979)	44	1–56	5×10^{-3} –5.82	10
Deshaye & Morisset (1988)	Richmond Gulf, Canada	Vascular plants	31	1–222	1.7×10^{-3} –0.921	22
Nilsson <i>et al.</i> (1988)	Lake Malaren, Sweden	Woody plants	17	18–29	6×10^{-3} –0.743	19
Nilsson <i>et al.</i> (1988)	Lake Malaren, Sweden	Carabid beetles	17	4–28	6×10^{-3} –0.743	19
Nilsson <i>et al.</i> (1988)	Lake Malaren, Sweden	Land snails	17	9–23	6×10^{-3} –0.743	19
Rydin & Borgegard (1988)	Lake Hjalmar, Sweden	Vascular plants	40	5–115	5×10^{-5} – 5×10^{-2}	10
Kohn & Walsh (1994)	North Great Britain	Dicotyledonous plants	42	1–71	3.1×10^{-4} –0.996	14
Sfenthourakis (1996)	Central Aegean, Kyklades, Greece	Terrestrial isopods	43	5–38	3×10^{-2} –476.2	20
Botsaris (1996)	Central Aegean, Saronikos, Greece	Land snails	76	1–39	10^{-4} –95	6
Ricklefs & Lovette (1999)	Lesser Antilles	Birds	19	13–41	13–1510	5
Ricklefs & Lovette (1999)	Lesser Antilles	Bats	17	1–12	22–1510	5
Ricklefs & Lovette (1999)	Lesser Antilles	Butterflies	15	3–17	90–1510	5
Kotze <i>et al.</i> (2000)	Baltic Sea	Carabid beetles	24	8–26	5×10^{-3} –70	13
Davidar <i>et al.</i> (2001)	Andaman islands, S.E Asia	Forest birds	45	5–47	3×10^{-2} –1348	5
Triantis (2002)	North Aegean, Greece	Land snails	12	4–43	2×10^{-3} –208	33

'almost certainly incomplete' (Ricklefs & Lovette, 1999, p. 1147) and this probably influences the estimation of the upper limit value.

We use the term habitat diversity for the number of habitats, following Rosenzweig *et al.* (2003, p. 865), who stated that the 'number of kinds is diversity's original meaning and we believe it should be restored'. However, habitat number is not always satisfactory as an explanatory variable. Habitat types exhibit different capacities in maintaining species and, of course, they are not equally distributed among islands. In some studies (e.g. Ricklefs & Lovette, 1999; Fox & Fox, 2000) a habitat diversity index (HD) has been used, taking into account the relative area covered by each habitat. This avoids the possibility of counting rare habitats as equal to common ones. We have not followed this approach, but simply enumerated the habitat types present on each island. This in part reflects the fact that an accurate assessment of habitat area was not possible for every study, but also that measures other than habitat area (depth of litter, size of rocks, etc.) may be equally or even more significant predictors of species richness (e.g. Solem *et al.*, 1981).

We used a form of path analysis, which has been used in similar studies (e.g. Kohn & Walsh, 1994; Triantis *et al.*, 2005), to analyse the data set. Path analysis and the more general structural equation modelling are widely used in many fields (Grace & Pugsek, 1998). In general, path analysis is considered a useful tool for distinguishing the effects of multiple intercorrelated variables on response variables (Li, 1975; Sokal & Rohlf, 1995; Legendre & Legendre, 1998). It was applied in this study so that the relative direct and indirect effects of predictor or causal variables can be assessed, according to the *a priori* model shown in Fig. 1a. According to this model, island area (*A*) directly affects habitat diversity (*H*) and both of them, area and habitat diversity, directly affect species number per island (*S*), while there is an unexplained proportion (*U*) of species richness. The procedure followed is described below.

The relationship between species per island (*S*) and the explanatory variables area (*A*) and number of habitats (*H*), is given in equation 1,

$$\hat{\text{Log}}(S) = c \log(A) + d \log(H) \quad (1)$$

where $\hat{\text{Log}}(S)$ is the estimate of the dependent variable $\text{Log}(S)$ and *c* and *d* are the partial regression coefficients. From equation 1 the standardized partial regression coefficients (path coefficients) of area's (b_A) and habitats' (b_H) contribution to explaining species number can be calculated, as they are in a simple relation to the conventional partial regression coefficients:

$$b_A = c \frac{s_A}{s_S} \quad \text{and} \quad b_H = d \frac{s_H}{s_S},$$

where s_A , s_H and s_S are the standard deviations of area, number of habitats and number of species, respectively (see Li, 1975; Sokal & Rohlf, 1995, pp. 612–614). For the data sets that included islands with zero species we transformed the data using the $\log(S + 1)$ transformation. We studied

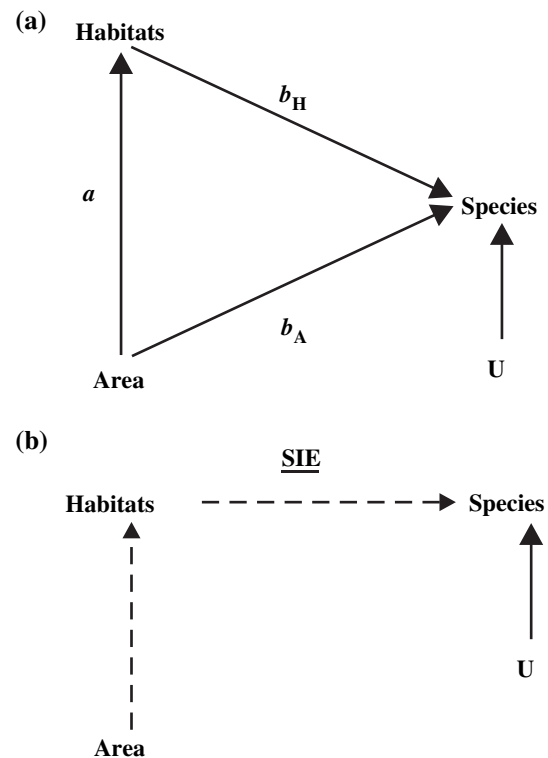


Figure 1 (a) The *a priori* path model used for the estimation of the upper limit of the SIE with species number as a function of area and number of habitats. b_A and b_H are the path coefficients for area and number of habitats, respectively. (b) The path model after the elimination of the direct effects of area.

each data set in order to detect whether there was a certain island size under which the direct effects of area were eliminated. This detection was carried out through the sequential exclusion of islands from the largest to the smallest in area and the simultaneous estimation of standardized partial regression coefficients of area (b_A). When b_A was found to be $b_A \leq 0$, the respective area was assigned as the upper limit of SIE, symbolized by *L*. We have to note here that the same results arise even if the process is reversed and we step up from the smallest to the largest island. However, as it is possible for the assumption of $b_A \leq 0$ to be met more than once when stepping up, i.e. for the first two or three islands, the sequential inclusion should be carried out until the maximum number of islands is included.

Because the successive elimination of data causes a reduction in statistical power and reduces the span of the predictor signal, we expect that the contribution of area might become statistically insignificant independent of whether b_A reaches a zero value. To overcome this problem, we considered it ecologically more appropriate to use island size as the upper limit of the SIE where area's direct contribution is apparently eliminated (i.e. when the estimated partial regression coefficient is zero) and not the size where its contribution becomes statistically insignificant. This way, our criterion is not affected

by the standard deviation of the data and subsequently by sample size, and is more conservative than the testing for a departure from zero. In the context of this model, a significant negative effect of area on species number would not be meaningful. Hence, a non-positive value of b_A would presumably indicate the elimination of the effect of area on species richness.

With the complete elimination of effects of area, the path model is transformed into a simple relationship between habitat and species number with area influencing indirectly species number through habitats (Fig. 1b). Thus, for those cases where the SIE was detected, we calculated a simple regression between species number and habitat diversity. All regressions and the estimation of parameters were carried out using an extended version of Microsoft Excel called Practical Statistics (Sincich *et al.*, 1999).

Despite the documented effect of isolation in terms of geographical distance on species richness, especially on islands (MacArthur & Wilson, 1967; Brown & Lomolino, 1998), we avoided the inclusion of a measure of geographical isolation in our method for two reasons. First, because this would add further complication to the method, not only due to the inclusion of one more parameter, but also because the effects of distance are not always significant (e.g. Sfenthourakis, 1996; Fattorini, 2002). As a result, an additional procedure for comparing competing models would be required in order to exclude statistically insignificant variables (see Grace & Pugsek, 1998). Secondly, it is not always clear which measure of geographical isolation to use, i.e. distance from the mainland, the nearest large island or just the nearest island, and usually a different measure is needed for different islands of the same island group, adding further layers of complexity to the problem (e.g. Turchi *et al.*, 1995; Sfenthourakis, 1996; Morand, 2000; Fattorini, 2002; Brose, 2003).

We compared our results to those of Lomolino & Weiser (2001), who used simple linear regression with a breakpoint transformation to estimate the upper limit of SIEs. The

breakpoint, or piecewise regression model with two pieces, used is:

$$Y = b_0 + b_1 \{ [\log_{10}(A) - T_1] \times [\log_{10}(A) \geq T_1] \}$$

where, Y denotes the species richness (S), or $\log_{10}(S)$ for semi-log and log-log versions of the model, respectively, A is the island area, T_1 the upper limit of the SIE, and $[\log_{10}(A) \geq T_1]$ a logical variable that returns the value of 0 or 1. For all data sets used in the present work, we calculated T_1 using the Small Islands Program written by M.V. Lomolino, following Lomolino & Weiser (2001).

There are two basic differences between the approaches compared herein: the statistical method used and the variables incorporated in the models. Lomolino & Weiser (2001) use the classical species–area models in order to estimate the upper limit of the SIE, whereas we use path analysis, so that the net effects of area are calculated. Lomolino & Weiser (2001) use an approach solely based on area for the detection of the presence of the SIE, whereas we also encompass habitat diversity.

RESULTS

In all the cases studied, a statistically significant relationship between number of species and area was found for the complete data set. The results for the detection of the existence of the SIE are presented in Table 2, with the L -value (upper limit of the SIE according to our approach) for each case with the respective b_A values, and the T_1 resulting from the log-log model used by Lomolino & Weiser (2001). A significant SIE was detected in six cases and we present the $\log S - \log A$ plot for each one of them (Fig. 2). The b_A values, the correlations between habitat diversity and area within the limits of the SIE, as well as between habitat diversity and species richness, are presented in Table 3. The relationship between species number and habitat diversity was statistically insignificant for the cases of carabid beetles (Nilsson *et al.*, 1988) and birds (Ricklefs & Lovette, 1999; Table 3).

Authors	b_A	L (km ²)	Islands	T_1 (km ²)	Islands
Reed (1981)	—	—	0	$< 8 \times 10^{-3}$	0
Haila <i>et al.</i> (1983)	—	—	0	0.05	2
Deshaye & Morisset (1988)	—	—	0	$< 1.7 \times 10^{-6}$	0
Nilsson <i>et al.</i> (1988) Woody plants	—	—	0	$< 6 \times 10^{-3}$	0
Nilsson <i>et al.</i> (1988) Carabid beetles	−0.05	0.043	8	0.02	4
Nilsson <i>et al.</i> (1988) Land snails	—	—	0	6×10^{-3}	1
Rydin & Borgegard (1988)	—	—	0	5×10^{-5}	1
Kohn & Walsh (1994)	−0.07	1.45×10^{-3}	8	6.3×10^{-4}	2
Sfenthourakis (1996)	−0.13	3.4	16	0.398	6
Botsaris (1996)	−0.07	0.02	33	1.26×10^{-3}	19
Ricklefs & Lovette (1999) Birds	−0.42	90	6	79.4	4
Ricklefs & Lovette (1999) Bats	—	—	0	< 5	0
Ricklefs & Lovette (1999) Butterflies	—	—	0	< 12.59	0
Kotze <i>et al.</i> (2000)	−0.10	0.571	21	$< 5 \times 10^{-4}$	0
Davidar <i>et al.</i> (2001)	—	—	0	8×10^{-3} –0.02	0
Triantis (2002)	—	—	0	0.016	2

Table 2 Results of the method proposed herein for the detection of SIE. L : the upper limit of SIE based on our method, with the number of islands included and the respective b_A values; T_1 : the upper limit of SIE according to Lomolino & Weiser (2001) with the equivalent number of islands included. —: denotes the absence of SIE

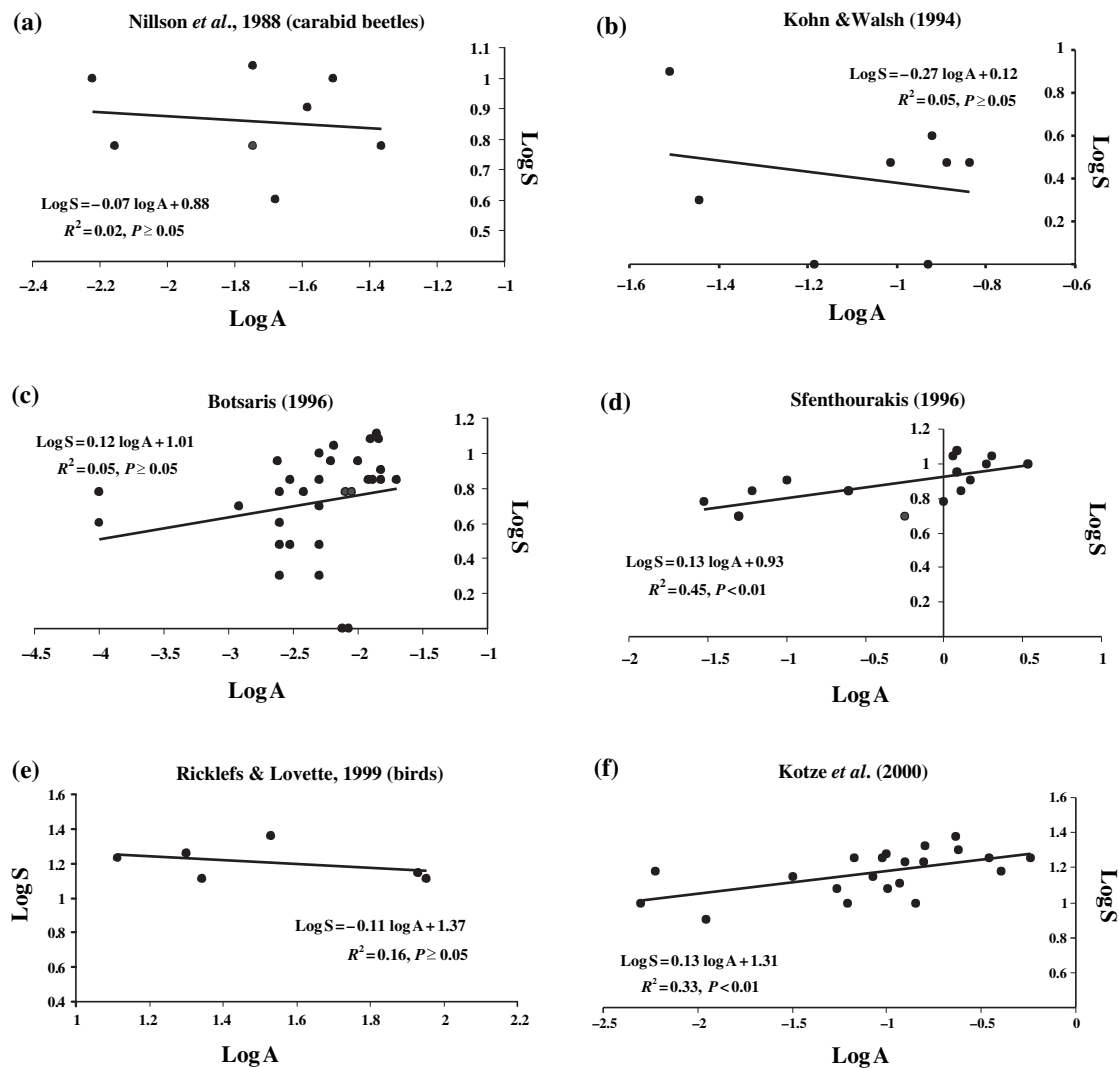


Figure 2 LogS-logA plots for the six cases where the SIE was detected. The plots show the relationship between species number and area within the calculated limits of the SIE.

Table 3 The R^2 and the statistical significance (P -value) of the simple regression between habitat and species number and between area and habitat diversity for the cases where the SIE was detected.

Authors	$R^2_{\log S - \log H}$	$R^2_{\log H - \log A}$
Nilsson <i>et al.</i> (1988) Carabid beetles	0.103 n.s.	0.066 n.s.
Kohn & Walsh (1994)	0.548*	0.046 n.s.
Sfenthourakis (1996)	0.672**	0.740**
Botsaris (1996)	0.439**	0.144*
Ricklefs & Lovette (1999) Birds	0.120 n.s.	0.165 n.s.
Kotze <i>et al.</i> (2000)	0.492**	0.731**

* $P < 0.05$; ** $P < 0.001$; n.s., not significant ($P \geq 0.05$).

In the cases of Sfenthourakis (1996) and Kotze *et al.* (2000) a significant and positive $\log S - \log A$ relationship remains, although the partial contribution of area *per se* is not significant. For these cases there is a strong correlation

between $\log H$ and $\log A$ (Table 3). In all the other cases the $\log S - \log A$ relationship is statistically insignificant.

In most of the cases studied, the sample size is large enough to allow checking for the assumptions on errors. The residuals are independent and follow a normal distribution with constant variance. Nevertheless, when using the method proposed, we needed to be careful when the sample size was small.

DISCUSSION

According to Ricklefs & Lovette (1999), area influences species richness directly in two different ways: larger islands offer larger targets for dispersing individuals (Gilpin & Diamond, 1976; Lomolino, 1990) and, in general, larger islands support larger populations (Rosenzweig, 1995). Thus, island size influences species richness by its effect on both colonization and extinction rates (Brown & Lomolino, 1998). Larger

populations have reduced extinction possibilities, as they usually tend to contain more genetic variation (e.g. Frankham *et al.*, 2002), so they can more easily respond and adapt to changes in environmental conditions. Additionally, large population size reduces vulnerability to stochastic extinction (Pimm *et al.*, 1988; Rosenzweig, 1995).

The indirect effects of area on species richness arise through its intercorrelation with other factors that affect species richness directly. The most studied and plausible of such variables is habitat diversity, which is often presumed to increase in direct relation to island area (Watson, 1964; Williams, 1964; Kohn & Walsh, 1994). If larger islands support greater habitat diversity, this increased habitat diversity might promote increased species richness (Kohn & Walsh, 1994; Ricklefs & Lovette, 1999). Moreover, island size can influence the presence of particular habitat types (e.g. Whitehead & Jones, 1969; Kohn & Walsh, 1994; Triantis *et al.*, 2005), thus it might affect the species number present on the island indirectly, particularly if a high proportion of the species involved are habitat specialists (Hart & Horwitz, 1991).

The above concepts offer, to a large extent, the theoretical basis for the *a priori* model of the path analysis used in the present work (Fig. 1a). Thus, based on this model we can estimate the magnitude of the influence of area and habitat diversity on species richness.

Despite the relatively long recognition of the SIE, the study of this phenomenon and its causes has been insufficient. Up to now, the SIE was correlated with the variation of species richness independently of island area (Brown & Lomolino, 1998). Before the work of Lomolino & Weiser (2001), the detection of SIE was solely empirical, based on the recognition of an 'anomalous' behaviour within the left part of the species–area curve. As Williamson *et al.* (2001, 2002) pointed out, the left hand side of the species–area relationship does not exhibit a steady behaviour. In some cases, the relationship flattens out and in others it becomes steep or follows the linearity of the larger islands. The first effort towards the quantification of the SIE is the work of Lomolino & Weiser (2001), who proposed a new and they claimed more general model of the species–area relationship, built on traditional models (Arrhenius, 1921; Gleason, 1922), but including the provision that richness may vary independently of island area on relatively small islands.

In the present work, we propose that the range of the SIE and its upper limit in an archipelago are signified by the elimination of the net effects of area on species richness. Our proposition is not entirely new regarding the theoretical basis of the SIE. MacArthur & Wilson in their 1967 (p. 30) monograph, discussing the 'truly anomalous' feature of species–area curve on small islands, noted that 'If the islands are so small to be unstable...the turnover rate in biota can be rapid enough so that extinction rates are not area-dependent' and according to Lomolino & Weiser (2001) species richness varies independently of area within SIE limits. The novelty of our approach is that the detection of the SIE is not based on the use of the species–area relationship and that apart from area, environmental heterogeneity is also considered.

One virtually always observes a positive correlation between species number and area, regardless of the mechanism (Connor & McCoy, 1979). The estimation of the upper limit of SIE, through the use of path analysis, offers the opportunity to detect the existence of SIE, even in cases where it is not apparent. Thus, we can distinguish two patterns of behaviour for the islands included in the SIE range with respect to the $\log S - \log A$ relationship, the classical and the cryptic. In the classical pattern, there is no relationship between area and species number when the $\log S - \log A$ is applied, such as in the cases of carabid beetles in Nilsson *et al.* (1988) (Fig. 2a), of dicotyledonous plants in Kohn & Walsh (1994) (Fig. 2b), land snails in Botsaris (1996) (Fig. 2c) and of birds in Ricklefs & Lovette (1999) (Fig. 2e). It is important to note that for these cases the relationship between area and number of habitats is either statistically insignificant or very weak (Table 3). In the cryptic pattern, despite the absence of direct area effects, there is a good correlation between logs and $\log A$, as a result of the indirect effects of area on species richness through habitats. The data sets of Sfenthourakis (1996) and Kotze *et al.* (2000) are typical of this; they show upper limits of the SIE at 3.4 km² and 0.571 km², respectively. Although no direct effects of area are observed within the limits estimated, the $\log S - \log A$ functions show a strong correlation between area and species number (Fig. 2d,f, respectively), as a result of the strong relationship between area and habitat diversity (Table 3).

In general, the calculated values of the upper limit of SIE are different from those of Lomolino & Weiser (2001), despite the fact that both methods are based on similar theoretical assumptions. Even in the cases, where the total effects of area (both direct and indirect) are eliminated, the two methods result in different estimations of SIE (see Table 2). Nevertheless, in some cases there is congruence in the absence of the SIE (see Table 2).

The two methods differ in two basic points: the method used and the variables required estimating the upper limit of SIE. Lomolino & Weiser (2001) use the classical species–area models in order to estimate the upper limit of the SIE, whereas we propose that the detection of this phenomenon should be undertaken independently from the species–area relationship, and that the net effects of area are calculated excluding the surrogate action of area on other variables such as environmental heterogeneity. Hence, the existence of the SIE should be studied separately in each case and it cannot be included in a general model. Moreover, Lomolino & Weiser (2001) use an approach exclusively based on area for the detection of the existence of the SIE, whilst we also include habitat diversity, a parameter with established influence on species richness, especially at small scales. Recently, Gentile & Argano (2005, p. 1716) concluded that the model of Lomolino & Weiser (2001) 'is not very appropriate to assess whether or not a SIE exists in a certain data set because it *a priori* assumes a SIE and imposes it on the model'.

It has been argued that confounding variation in area with variation in other environmental factors fatally weakens the search for a general understanding of diversity patterns (see Whittaker, 1998, 2000; Whittaker *et al.*, 2001). Nonetheless, the model of Lomolino & Weiser (2001), especially due to the vast

number of studies considering the relationship between area and species number, may provide some important insights for developing a more general understanding of this fundamental pattern of nature, and for conserving biological diversity.

The independence of our method from the species–area relationship and the inclusion of environmental heterogeneity allowed the detection of the SIE even where it is phenomenally absent (cryptic SIE). This is exemplified by the case of Kotze *et al.* (2000), where, according to our method, 21 islands show the SIE, whereas using Lomolino & Weiser's (2001) method no SIE was apparent. Moreover, the independence of our method from the species–area relationship allows the left hand side of the species–area relationship to exhibit variable behaviour, ranging from being flat, to following the linearity of larger islands to being steep (Fig. 2; c.f. Williamson *et al.*, 2001, 2002).

Among the upper limit values of SIE obtained, the only one that seems ecologically unrealistic is the high number for breeding birds ($L = 90 \text{ km}^2$) in the Lesser Antillean islands (Ricklefs & Lovette, 1999). This value could be considered as an indication of an erroneous approach. On the other hand, if we exclude the possibility of poor or incomplete sampling, it could be related to the high proportion of both Lesser Antillean endemic birds (36%) and of the single-island endemics (17%). It can also be attributed to the small population size of birds and their moderate habitat specialization. Ricklefs & Lovette (1999) showed that the direct effects of area on the number of bird species for all the islands studied were very low. Recently, Ricklefs & Bermingham (2004), studying birds in the Lesser Antilles, illustrated that none of the old endemic taxa lacking evidence of recent dispersal between islands is present on islands smaller than 100 km^2 . Thus, this large value for the upper limit of SIE might be due to certain characteristics of the avifauna on the Lesser Antillean islands, and this is corroborated by the fact that the use of the Lomolino & Weiser (2001) equation results in a large value too ($T_1 = 79.4 \text{ km}^2$; Table 2).

According to our model, within the limits of the SIE, species richness is established through environmental heterogeneity (expressed as habitat diversity), the indirect effects of area, and unknown or not considered factors (Fig. 1b). The contribution of habitat diversity is intense at finer scales and decreases over coarser scales, but it is present almost over the whole range of spatial scale (Shmida & Wilson, 1985). Nevertheless, in Fig. 1b we connect habitat diversity and species number with a discontinuous line, indicating that even habitat diversity might have an insignificant contribution within the range of the SIE, such as in the cases of carabid beetles in Nilsson *et al.* (1988) and birds in Ricklefs & Lovette (1999). The significance of habitat diversity is in general strongly affected by the procedure followed in the definition of habitat types, as the contribution of habitat diversity depends on how close to the natural history of the studied taxon the defined habitats are (Newmark, 1986; Looijen, 1998; Triantis *et al.*, 2003, 2005). Hence, a consideration of habitat types that does not take into account the biology of the studied taxon would result in a low contribution of habitat diversity on species richness and would increase the contribution of unknown factors. The fact that in both the works of Nilsson

et al. (1988) and Ricklefs & Lovette (1999) the same habitat types are used for all the studied taxa might lead to problems in analysis. A habitat division that is too coarse to reflect the ecological requirements of a particular group of organisms might miss the effect of habitat diversity on species richness. This can explain the fact that, apart from the elimination of area's effects, there are no statistically significant effects of habitat diversity within the SIE limits for both taxa: carabid beetles (Nilsson *et al.*, 1988) and birds (Ricklefs & Lovette, 1999). On the other hand, it is possible that for a certain taxon in an archipelago, only stochastic factors determine the species richness for a certain period of time.

As noted above, the indirect effects of area on species richness arise through its intercorrelation mainly with habitat diversity (Ricklefs & Lovette, 1999). But the effects of area on habitat diversity inside the limits of the SIE are not always established and that is why we connect area with habitat diversity by means of a discontinuous line. In the cases of Nilsson *et al.* (1988), Kohn & Walsh (1994) and Ricklefs & Lovette (1999), area exhibits no effects on habitat diversity inside the SIE and thus the classic pattern of the SIE arises with area having no effects on species richness, either direct or indirect. On the other hand, in the cryptic pattern of the SIE, area influences species richness indirectly, through its effect on habitats. In the case of Botsaris (1996), although there is an effect of area on habitats, that effect is weak and thus the relationship between species and area is statistically insignificant.

Area and habitat diversity are not the only factors influencing species richness. Thus, the unexplained variance must be related in part to parameters known to influence species richness on islands, such as geographical distance and geological history, which are not considered in the approach followed here. It is possible that the inclusion of geography and history (sea level fluctuations, for example) would explain some of the cases of the SIE. Thus, having estimated the upper limit of the SIE, it would be rewarding to investigate the possible sources of the unexplained variance. In the case of the land snails of Saronikos Gulf (Botsaris, 1996), the unexplained variance of species richness within the limits of SIE (56%) is surely related to the palaeogeography of the area and especially the sea level changes during the last glacial maximum, which led to multiple connections of islands with the nearby mainland and with one-another, structuring to a large extent the present composition of the area's malacofauna (Botsaris, 1996). On the other hand, various measures of geographical distance showed no effects on species richness, signifying the relict character of the malacofauna (Botsaris, 1996). In the case of the Lesser Antillean birds (Ricklefs & Lovette, 1999) the unexplained variance within the limits of SIE is quite high (84%), and habitat diversity has no statistically significant effects. This result, regardless of the problematic approach to habitat diversity (see above), indicates that some other factor, apart from area and habitat diversity, is important in shaping the particular biota. Ricklefs & Bermingham (2004) (see also Morand, 2000) considered the effects of distance from sources of colonists, and found geographical isolation to be significant for the recent colonist species that

predominate on small islands. Additional possible sources of unexplained variance of species richness relate to idiosyncratic characteristics (e.g. how different groups of organisms respond to habitat diversity, the number of specialist and generalist species present, and human impact) and to stochastic events (e.g. storms, hurricanes and fires), whose effects cannot be measured (see Schoener *et al.*, 2001).

The relatively restricted number of publications studying both species richness and environmental heterogeneity on islands puts a limit on our ability to detect ecological trends related to the SIE, especially regarding the ecology of the studied taxa and their dispersal ability. The application of our approach to 'habitat islands', as well as comparisons among different taxa within the same archipelago may prove worthwhile, and may provide important information for conservationists. The study of the values of the SIE's upper limit in respect to the dispersal abilities and resource requirements of different taxa in the same island group will provide significant information for the approach proposed herein.

CONCLUSIONS

The absence of area effects on species richness can be real in nature. The SIE is present where, across a range of island sizes below a particular threshold, area does not influence species richness, either directly or/and indirectly. From that point on, species richness is mainly affected by environmental diversity (Fig. 1b). Nevertheless, other factors, such as geographical isolation and geological history, should be considered as possible explanations of the unexplained variance. Using a method for the detection of the SIE that is independent of the species–area relationship allows the estimation of the net effects of area and excludes the surrogate effects of this parameter on others. After having estimated the upper limit of the phenomenon we can apply the species–area relationship in order to study its behaviour within the limits of the SIE. When the relationship between area and habitat diversity is strong, the relationship between species and area is also strong, and the SIE is cryptic. In the opposite case, the classical pattern of SIE arises.

Despite the fact that the search for governing relationships operating through time and space in a broadly consistent fashion is one of the cornerstones of biogeography (see Brown, 1995; Whittaker, 2004), the deconstruction of patterns to their basic components reveals limits to our understanding of the causes of patterns in species richness at different spatial and temporal scales (Marquet *et al.*, 2004). Variables best accounting for species richness on a local spatial or recent time scale may not be the same as those accounting for richness at regional spatial or longer time scales (Shmida & Wilson, 1985; Willis & Whittaker, 2002). Area constitutes a key macroecological descriptor. However, the net effects of area are not always that important over limited ranges of area and other key factors, such as habitat heterogeneity, should be taken into account. The insights provided by the approach proposed here offer the opportunity to isolate and quantify the different factors shaping biodiversity at fine scales of analysis.

Modern island biogeography would be strengthened by the more systematic study of environmental heterogeneity of relevance to the focal taxon. Thus, species lists from island groups have to be accompanied with substantial knowledge on the ecology of the taxon studied.

It is our belief that the SIE cannot be considered as a general pattern with a constant form that can be described by a single model for all island groups and all taxa. It is more likely that the existence of this phenomenon depends on the taxon studied and mainly on the general characteristics of the islands (e.g. geological history, habitat diversity, degree of disturbance and geographical isolation) as well as stochastic events. Thus, the SIE should be recognized as a genuine but idiosyncratic phenomenon.

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REFERENCES

- Anderson, W.B. & Wait, D.A. (2001) Subsidized island biogeography: another new twist on an old theory. *Ecology Letters*, **4**, 289–291.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.
- Barrett, K., Wait, D.A. & Anderson, W.B. (2003) Small island biogeography in the Gulf of California: lizards, the subsidized island biogeography hypothesis, and the small island effect. *Journal of Biogeography*, **30**, 1575–1581.
- Botsaris, I. (1996) The biogeography of terrestrial molluscs on the islands and islets of Saronikos Gulf. PhD Thesis (in Greek), University of Athens, Athens.
- Brose, U. (2003) Island biogeography of temporary wetland carabid beetle communities. *Journal of Biogeography*, **30**, 879–888.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Davidar, P., Yoganand, K. & Ganesh, T. (2001) Distribution of forest birds in the Andaman Islands: importance of key habitats. *Journal of Biogeography*, **28**, 663–672.

- Deshaye, J. & Morisset, P. (1988) Floristic richness, area, and habitat diversity in a hemiarctic archipelago. *Journal of Biogeography*, **15**, 747–757.
- Dunn, C.P. & Loehle, C. (1988) Species–area parameter estimation: testing the null model of lack of relationship. *Journal of Biogeography*, **15**, 721–728.
- Fattorini, S. (2002) Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). *Journal of Biogeography*, **29**, 49–68.
- Fox, B.J. & Fox, M.D. (2000) Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecology and Biogeography*, **9**, 19–37.
- Frankham, R., Ballou, J.D. & Briscoe, D. (2002) *Introduction to conservation genetics*. Cambridge University Press, New York.
- Gentile, G. & Argano, R. (2005) Island biogeography of the Mediterranean Sea: the species–area relationship for terrestrial isopods. *Journal of Biogeography*, **32**, 1715–1726.
- Gilpin, M.E. & Diamond, J.M. (1976) Calculation of immigration and extinction curves from the species–area–distance relation. *Proceedings of the National Academy of Sciences USA*, **73**, 4130–4134.
- Gleason, H.A. (1922) On the relation between species and area. *Ecology*, **3**, 158–162.
- Grace, J.B. & Pugesek, B.H. (1998) On the use of path analysis and related procedures for the investigation of ecological problems. *The American Naturalist*, **152**, 151–159.
- Haila, Y., Järvinen, S. & Kuusela, S. (1983) Colonization of islands by land birds: prevalence functions in a Finnish archipelago. *Journal of Biogeography*, **10**, 499–531.
- Hart, D.D. & Horwitz, R.J. (1991) Habitat diversity and the species–area relationship: alternative models and tests. *Habitat structure. The physical arrangement of objects in space* (ed. by S.S. Bell, E.D. McCoy and H.R. Mushinsky), pp. 47–68. Chapman and Hall, London.
- Heatwole, H. (1991) Factors affecting the number of species of plants on islands of the Great-Barrier-reef, Australia. *Journal of Biogeography*, **18**, 213–221.
- Kelt, D.A. (2000) Small mammal communities in rainforest fragments in Central Southern Chile. *Biological Conservation*, **92**, 345–358.
- Kohn, D.D. & Walsh, D.M. (1994) Plant species richness – the effect of island size and habitat diversity. *Journal of Ecology*, **82**, 367–377.
- Kotze, D.J., Niemela, J. & Nieminen, M. (2000) Colonization success of carabid beetles on Baltic islands. *Journal of Biogeography*, **27**, 807–820.
- Legendre, L. & Legendre, P. (1998) *Numerical ecology* (2nd English edn). Elsevier, New York.
- Li, C.C. (1975) *Path analysis: a primer*. Pacific Grove, CA Boxwood Press, California.
- Lomolino, M.V. (1990) The target area hypothesis: the influence of island area immigration rates of non-volant mammals. *Oikos*, **57**, 297–300.
- Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**, 17–26.
- Lomolino, M.V. (2002) "...there are areas too small, and areas too large, to show clear diversity patterns..." R.H. MacArthur (1972: 191). *Journal of Biogeography*, **29**, 555–557.
- Lomolino, M.V. & Perault, D. (2001) Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. *Global Ecology and Biogeography*, **10**, 113–132.
- Lomolino, M.V. & Weiser, M.D. (2001) Towards a more general species–area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**, 431–445.
- Looijen, R.C. (1998) *Holism and reductionism in biology and ecology. The mutual dependence of higher and lower level research programmes*. PhD Thesis, University of Groningen, Groningen, Holland.
- Losos, J.B. (1996) Ecological and evolutionary determinants of the species–area relation in Caribbean anoline lizards. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **351**, 847–854.
- Losos, J.B. & Spiller, D. (1999) Differential colonization success and asymmetrical interactions between two lizard species. *Ecology*, **80**, 252–258.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, New Jersey.
- Marquet, P.A., Fernandez, M., Navarrete, S.A. & Valdovinos, C. (2004) Diversity emerging: toward a deconstruction of biodiversity patterns. *Frontiers of Biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 191–209. Sinauer Associates, Sunderland, MA.
- Morand, S. (2000) Geographic distance and the role of island area and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups: a complementary note to Ricklefs & Lovette. *Journal of Animal Ecology*, **69**, 1117–1119.
- Morrison, L.W. (1997) The insular biogeography of small Bahamian cays. *Journal of Ecology*, **85**, 441–454.
- Newmark, W.D. (1986) Species–area relationship and its determinants for mammals in western North American national parks. *Biological Journal of the Linnean Society*, **28**, 83–98.
- Niering, W.A. (1963) Terrestrial ecology of Kapingamarangi Atoll, Caroline Islands. *Ecological Monographs*, **33**, 131–160.
- Nilsson, S.G., Bengtsson, J. & Ås, S. (1988) Habitat diversity or area *per se*? Species richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology*, **57**, 685–704.
- Pimm, S.L., Jones, H.L. & Diamond, J.M. (1988) On the risk of extinction. *The American Naturalist*, **132**, 757–785.
- Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part I. *Ecology*, **43**, 185–215.
- Reed, T. (1981) The number of breeding landbird species on British Islands. *Journal of Animal Ecology*, **50**, 613–624.

- Ricklefs, R.E. & Bermingham, E. (2004) History and the species–area relationship in Lesser Antillean birds. *The American Naturalist*, **163**, 227–239.
- Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Ecology*, **68**, 1142–1160.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, New York.
- Rosenzweig, M.L., Turner, W.R., Cox, J.G. & Ricketts, T.H. (2003) Estimating diversity in unsampled habitats of a biogeographical province. *Conservation Biology*, **17**, 864–874.
- Rusterholz, K.A. & Howe, R.W. (1979) Species–area relations of birds on small islands in a Minnesota lake. *Evolution*, **33**, 468–477.
- Rydin, H. & Borgegard, S.O. (1988) Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology*, **69**, 916–927.
- Sadler, J.P. (1999) Biodiversity on oceanic islands: a palaeoecological assessment. *Journal of Biogeography*, **26**, 75–87.
- Schoener, T.W., Spiller, D.A. & Losos, J.B. (2001) Natural restoration of the species–area relation for a lizard after a hurricane. *Science*, **294**, 1525–1528.
- Sfenthourakis, S. (1996) The species–area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. *Global Ecology and Biogeography Letters*, **5**, 149–157.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.
- Sincich, T., Levine, D.M. & Stephan, D. (1999) *Practical statistics by example using Microsoft® Excel*. Prentice Hall, New Jersey.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman & Company, New York, USA.
- Solem, A., Climo, F.M. & Roscoe, D.J. (1981) Sympatric species diversity of New Zealand land snails. *New Zealand Journal of Zoology*, **8**, 453–485.
- Triantis, K.A. (2002) Biogeography, systematics and ecology of the land snails on the archipelago of Skyros (Aegean, Greece). Master's thesis (in Greek), University of Crete, Greece.
- Triantis, K.A., Mylonas, M., Lika, K. & Vardinoyannis, K. (2003) A model for species–area–habitat relationship. *Journal of Biogeography*, **30**, 19–27.
- Triantis, K.A., Vardinoyannis, K., Weiser, M.D., Lika, K. & Mylonas, M. (2005) Species richness, environmental heterogeneity and area: a case study based on the land snails of Skyros Archipelago (Aegean Sea, Greece). *Journal of Biogeography*, **32**, 1727–1735.
- Turchi, G.M., Kennedy, P.L., Urban, D. & Hein, D. (1995) Bird species richness in relation to isolation of aspen habitats. *Wilson Bulletin*, **107**, 463–474.
- Watson, G.E. (1964) Ecology and evolution of passerine birds on the islands of the Aegean Sea. PhD thesis, Yale University, New Haven, CT, USA.
- Whitehead, D.R. & Jones, C.E. (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution*, **23**, 171–179.
- Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Whittaker, R.J. (2000) Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, **9**, 75–85.
- Whittaker, R.J. (2004) Dynamic hypotheses of richness on islands and continents. *Frontiers of biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 211–231. Sinauer Associates, Sunderland, MA.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Wiens, H.J. (1962) *Atoll environment and ecology*. Yale University Press, New Haven and London.
- Williams, C.B. (1964) *Patterns in the balance of nature and related problems in quantitative biology*. Academic Press, New York.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2001) The species–area relationship does not have an asymptote. *Journal of Biogeography*, **28**, 827–830.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2002) An asymptote is an asymptote and not found in species–area relationships. *Journal of Biogeography*, **29**, 1713.
- Willis, K.J. & Whittaker, R.J. (2002) Species diversity: scale matters. *Science*, **295**, 1245–1248.
- Woodroffe, C.D. (1986) Vascular plant species–area relationships on Nui Atoll, Tuvalu, central Pacific: a reassessment of the small island effect. *Australian Journal of Ecology*, **11**, 21–31.

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