



A model for the species–area–habitat relationship

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Abstract

Aim To propose a model (the choros model) for species diversity, which embodies number of species, area and habitat diversity and mathematically unifies area *per se* and habitat hypotheses.

Location Species richness patterns from a broad scale of insular biotas, both from island and mainland ecosystems are analysed.

Methods Twenty-two different data sets from seventeen studies were examined in this work. The r^2 values and the Akaike's Information Criterion (AIC) were used in order to compare the quality of fit of the choros model with the Arrhenius species–area model. The classic method of log-log transformation was applied.

Results In twenty of the twenty-two cases studied, the proposed model gave a better fit than the classic species–area model. The values of z parameter derived from choros model are generally lower than those derived from the classic species–area equation.

Main conclusions The choros model can express the effects of area and habitat diversity on species richness, unifying area *per se* and the habitat hypothesis, which as many authors have noticed are not mutually exclusive but mutually supplementary. The use of habitat diversity depends on the specific determination of the 'habitat' term, which has to be defined based on the natural history of the taxon studied. Although the values of the z parameter are reduced, they maintain their biological significance as described by many authors in the last decades. The proposed model can also be considered as a stepping-stone in our understanding of the small island effect.

Keywords

Species–area, choros model, habitat diversity, area *per se*, habitat hypothesis, species richness, insular biotas, islands, small island effect.

INTRODUCTION

The species–area relationship is not only one of ecology's few laws (Schoener, 1976) but it is also one of the longest known, probably the second ever observed and described after the latitudinal diversity gradient (Hawkins, 2001). Descriptions of this relationship appeared during the nineteenth century. Williams (1964) credited Watson (1859) with the earliest 'discovery' of the pattern, while Dony (1963) and Bramson *et al.* (1998) place the discovery earlier (1835) by Watson again. Rosenzweig (1995) cites de Candolle as the first author bringing forward this pattern. However, there is no doubt that the first plot relating species

with area, was made by Watson in 1859 (Dony, 1963; Rosenzweig, 1995).

Scientists have identified, throughout the years, two major mechanisms of species addition, the increase of area and the increase of habitats. These mechanisms are theoretically supported by area *per se* (Preston, 1960, 1962a, b; MacArthur & Wilson, 1963, 1967) and the habitat hypothesis (Williams, 1964), respectively. The question of whether area *per se* or habitat diversity is more important in influencing species richness has been the subject of a continuous debate (Williams, 1964; MacArthur & Wilson, 1967; Power, 1972; Abbott, 1974; Simberloff, 1976; Maly & Doolittle, 1977; Connor & McCoy, 1979; Gilbert, 1980; Kitchener *et al.*, 1980a, b, 1982; Williamson, 1981, 1988; Buckley, 1982, 1985; Tonn & Magnuson, 1982; Boecklen & Gotelli, 1984; Rafe *et al.*, 1985; Boecklen, 1986; Gibson, 1986; Rydin & Borgegard, 1988; Kohn & Walsh, 1994; Sfenthourakis,

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1994, 1996; Botsaris, 1996; Ricklefs & Lovette, 1999; Fox & Fox, 2000; Davidar *et al.*, 2001; Tjørve, 2002).

Despite this continuous debate, many authors have implied that the area *per se* and the habitat hypothesis are not mutually exclusive but mutually supplementary. Harner & Harper (1976) studied hectare plots in Pinyon–Juniper ecosystems, woodlands in Northern Utah and northern Mexico, and showed that apart from area, habitat is also important for species richness and concluded that both area and habitat are significant. Additionally, they note ‘area and heterogeneity are tightly interconnected in nature’, which means that either can serve as an alternate for the other. Boström & Nilsson (1983) attempted to hold habitat levels constant while varying area. Their results revealed no species–area curve, implying that habitat alone yields species–area curves. Gibson (1986) found that a direct effect of area was detectable only in patches smaller than 0.1 ha, while in larger islands or reserves, the distinction of area and habitat diversity effect becomes increasingly difficult. Rafe *et al.* (1985) found that area and habitat diversity are strongly correlated and both influence species richness. Newmark (1986), although in his study no correlation between habitat types and species richness was revealed, noted that the interconnection between area and habitat diversity could not be rejected. Rosenzweig (1995) after using data from Haila (1983) and Haila *et al.* (1983), found a significant linear relation between species and habitats. He stated, ‘... at this scale area means nothing. It must work through habitats or extinction rates’. In his conclusions, he supported the idea that the change in habitat diversity causes, to a large extent, the species area curves on islands’. Kohn & Walsh (1994) concluded that both habitat diversity and island size contribute to species number on islands. Ricklefs & Lovette (1999) found that area and habitat diversity are interconnected and that both constitute the main contributors of the species richness of four Lesser Antillean faunal groups.

Although scientists have long noted the importance of habitat diversity in determining species richness, except area, till today two obstacles have prevented the use of habitat diversity widely. The first one is the difficulty of defining habitat types for each taxonomic group, so that comparisons could be made in a global level. By comparison, area is more tractable, less ambiguous, and less arbitrary and of course more easily measured than habitat diversity. The second obstacle is the absence of a simple and easily usable mathematical model connecting species richness and habitat diversity, the application of which will not demand complicated procedures and calculations. In this direction at least three models have been proposed (Buckley, 1982; Rafe *et al.*, 1985; Tjørve, 2002). The first two models have been generally neglected by biogeographers and ecologists mainly because of their assumptions to be used and their degree of complicatedness.

The aim of this work is to propose a simple and easily usable mathematical model, that unifies the two dominant explanatory mechanisms of species richness, the area *per se* hypothesis and the habitat hypothesis.

We thus introduce the term choros (K), an ancient Greek word that describes the dimensional space. Choros is introduced to approach the actual ability of a region to maintain a particular number of species of a certain taxon. Substantially this term combines the total effect of a region’s area and habitat diversity to the determination of the region’s species richness. Choros (K) arises as the result of the multiplication of the area of the region with the number of the different habitat types present on the region ($K = H^*A$), where H is the number of habitats on the region and A is the total area of the region.

The species richness of the region is then expressed as a power function of the choros (K),

$$S = cK^z \quad (1)$$

Equation 1 is analogous to the one proposed by Arrhenius (1921),

$$S = cA^z \quad (2)$$

with the substitution of area (A) with choros (K).

In this paper we present a comparison between the classic species–area relation (Eqn 2) and the choros model (Eqn 1).

MATERIALS AND METHODS

Twenty-two different data sets derived from seventeen sources (Table 1) were analysed in this study:

Kitchener *et al.* (1980) studied the lizard species in twenty-three reserves in the Western Australian wheatbelt. The habitat variable they used was the vegetation associations. They referred only to the number of associations in each reserve and not the total number of them in the studied area.

Kitchener *et al.* (1980) studied the non-volant mammals in twenty-three reserves in the Western Australian wheatbelt. The habitat variable they used is based on the classification of vegetation, which comprises a matrix of canopy density classes against plant life forms, divided into a series of height classes.

Reed (1981) studied the land bird species breeding on British islands and adduces a list of seventy-three islands. The habitat types he used were based on Fuller (1974).

Kitchener *et al.* (1982) studied the avian fauna in twenty-two reserves in the western Australia wheatbelt. They used the same habitat variable as in Kitchener *et al.* (1980) for non-volant mammals.

Haila (1983) and Haila *et al.* (1983) studied the land birds breeding on forty-four islands in the Vargaskar Archipelago of the Aland Islands (South-west Finland). They visited the islands in three different years (1976, 1979 and 1980). In the years 1976 and 1979 they surveyed all the forty-four islands, when in 1980 they surveyed thirty-five. The ten habitat types used were based on the vegetation types.

Newmark (1986) studied the non-volant mammalian species in twenty-four western North American national parks. In his analysis he used twenty-five different vegetative cover types.

Deshaye & Morisset (1988) studied the vascular plants on thirty-four islands of a hemiarctic archipelago located in

Table 1 Authors, geographical position, taxon studied, number of islands or 'habitat' islands and reserves, and the number of habitats as defined by the authors in each work

Authors	Geographical situation of the study area	Taxon	No of islands	No of habitats
Kitchener <i>et al.</i> (1980)	Western Australia	Lizards	23	–
Kitchener <i>et al.</i> (1980)	Western Australia	Non-volant mammals	23	569
Reed (1981)	Great Britain	Land birds	73	26
Kitchener <i>et al.</i> (1982)	Western Australia	Birds	22	549
Haila (1983)	Aland Islands,	Land birds (1976)	44	10
Haila <i>et al.</i> (1983)	South west Finland	Land birds (1979)		
		Land birds (1980)	35	
Newmark (1986)	North America	Non-volant mammals	24	25
Nilsson <i>et al.</i> (1988)	Lake Malaren, Sweden	Woody plants	17	19
		Carabid beetles		
		Land snails		
Deshaye & Morisset (1988)	Richmond Gulf, Canada	Vascular plants	34	22
Rydin & Borgegard (1988)	Lake Hjalmaren, Sweden	Vascular plants	40	10
Kohn & Walsh (1994)	North Great Britain	Dicotyledonous plants	45	14
Sfenthourakis (1994, 1996)	Central Aegean, Greece	Terrestrial isopods	42	20
Botsaris (1996)	Central Aegean, Greece	Land snails	77	6
Ricklefs & Lovette (1999)	Lesser Antilles	Birds	19	5
		Bats		
		Butterflies		
		Reptiles & Amphibians		
Kotze <i>et al.</i> (2000)	Baltic Sea	Carabid beetles	24	13
Davidar <i>et al.</i> (2001)	Andaman islands, South east Asia	Forest birds	45	5

Richmond Gulf, Canada. The twenty-two types of habitats used, were defined based on five abiotic variables.

Nilsson *et al.* (1988) studied the woody plants, carabid beetles and land snails on seventeen islands in Lake Malaren, Sweden. In total they referred nineteen habitat types. The determination of habitat types was based on the classification of the vegetation through the use of similarity indices.

Rydin & Borgegard (1988) studied the vascular plants on forty islands in Lake Hjalmaren, Sweden. They used in total ten different habitat types.

Kohn & Walsh (1994) gave the number of dicotyledonous plant species from forty-five small islands off Shetland Mainland in Great Britain. They defined fourteen different habitats according to physical characteristics of the islands of presumed importance to plants.

Sfenthourakis (1994, 1996) studied the biogeography of land isopods on forty-two islands of central Aegean. He described twenty different habitat types, based on detailed observations of both biotope structure and habitat preferences of isopod species.

Botsaris (1996) studied the malacofauna of the Saronikos Archipelago in western central Aegean and gave a species list for seventy-seven islands and islets. He reported six different habitat types. The discrimination of the habitat types was based on the CORINE and NATURA projects.

Ricklefs & Lovette (1999) studied birds, bats, butterflies, reptiles and amphibians on nineteen islands in the Lesser Antilles. Habitat diversity was quantified based on the total areas of five vegetation types on each island.

Kotze *et al.* (2000) studied the carabid beetles on twenty-four islands in the south-western archipelago of Finland in the Baltic Sea. In total they used thirteen different habitat types based on the vegetation of the islands.

Davidar *et al.* (2001) studied forest birds on forty-five islands in the Andaman Islands off the coast of South-east Asia. They used five different habitat types, which correspond to the various forest types, present on the islands.

Because the two models are both power functions, taking the logarithm of both sides of equations 1 and 2, we obtain the following linear equations in $\text{Log}(S)$ and $\text{Log}(A)$ or $\text{Log}(K)$, respectively,

$$\text{Log}(S) = \text{Log}(c) + z\text{Log}(K) \quad (3)$$

and

$$\text{Log}(S) = \text{Log}(c) + z\text{Log}(A) \quad (4)$$

We use the conventional logarithmic transformations to estimate the equation parameters for purposes of comparison, as linear regression is the classic method used (Rose-nzweig, 1995). All regressions and the estimation of parameters were made with Practical Statistics (Sincich *et al.*, 1999). We also performed a Student's test in order to study the statistical difference between the slopes of equations 3 and 4 (Zar, 1984).

For the comparison of the two models, we use as a measure of the goodness-of-fit, the r^2 values. As the two models have the same number of parameters, the r^2 s are comparable, without any modification (Kvalseth, 1985;

Loehle, 1990). Note that the choros model (Eqn 1) has the same number of parameters as the classic species–area relation (Eqn 2). Thus higher explanatory power is not expected from our model, as in other proposed models with more than two parameters, e.g. $S = cA^z e^{-kA}$ (Plotkin *et al.*, 2000) and $S = S_{\max} / [1 + \text{Hillslope}^{\text{Log}(A_s/A)}]$, Lomolino (2000).

As an additional, and more general, measure of goodness-of-fit, we use the Akaike's Information Criterion (AIC) (Sakamoto *et al.*, 1986). In many statistical papers it is concluded that AIC is one of the most appropriate model selection criteria (Sakamoto *et al.*, 1986; Wada & Kashiwagi, 1990; Ludden *et al.*, 1994; Burnham & Anderson, 1998; Li *et al.*, 2002) and it has been used in many ecological papers (Anderson *et al.*, 1994; Quang & Becker, 1996; Stenseth *et al.*, 1999; Frescino *et al.*, 2001; Van Buskirk *et al.*, 2002).

The AIC is defined as:

$$\text{AIC} = -2 \ln(L_m) + 2p$$

where L_m is the maximum likelihood of the model, p is the number of free parameters of the model.

Comparing two models, the one with the lowest value of AIC is considered to be better. The selection of the 'best model' is based on the difference of AIC values for the compared models and not on their actual values; the bigger the difference the more appropriate the 'best model' is. Sakamoto *et al.* (1986) suggested that an absolute difference greater than one or two could be considered statistically significant. We calculated the difference of the AIC value for

equation 4 minus the AIC value for equation 3 ($\Delta\text{AIC} = \text{AIC}_{(\log S - \log A)} - \text{AIC}_{(\log S - \log K)}$). A positive difference indicates that the choros model gives a better fit to the data.

In all the studied cases we avoid to omit the islands with none of the species present on them, although Williams (1996) proposes the opposite, because our aim is not to study the meaning of the species–area relation for each island group but the comparison of the classical model of species–area relation with the choros model. It is obvious that when a specific island group is studied the zero values include important biogeographical information.

RESULTS

Table 2 shows, for each data set analysed, the r^2 and the P -values of the regressions, for the two equations 3 and 4. In twenty of twenty-two studied cases, except the case of carabid beetles and snails in the work of Nilsson *et al.* (1988), the r^2 value of the choros model is higher than that of the classic species–area model. The use of AIC revealed that in twenty of twenty-two cases, the values of AIC for the choros model were lower than the values of the classic species–area model ($\Delta\text{AIC} > 0$, Table 2). The two cases where the values of AIC were lower for the species–area model are the ones concerning carabid beetles and snails (Nilsson *et al.*, 1998).

Table 2 The r^2 -values for the logarithmic form of the two models. The difference of the AIC values (ΔAIC) of the two models [$\Delta\text{AIC} = \text{AIC}(\log S - \log A) - \text{AIC}(\log S - \log K)$]

Authors	r^2 (logS–logA)	r^2 (logS–logK)	ΔAIC
Kitchener <i>et al.</i> (1980)	0.487*	0.576*	4.41
Kitchener <i>et al.</i> (1980)	0.622*	0.672*	3.27
Reed (1981)	0.671*	0.713*	9.97
Kitchener <i>et al.</i> (1982)	0.738*	0.761*	1.97
Haila (1983) 1976	0.889*	0.905*	6.83
Haila (1983) 1979	0.849*	0.878*	9.56
Haila (1983) 1980	0.880*	0.900*	6.35
Newmark (1986)	0.683*	0.695*	0.9
Deshaye & Morisset, 1988)	0.819*	0.861*	9.67
Rydin & Borgegard (1988)	0.720*	0.784*	9.61
Kohn <i>et al.</i> (1994)	0.735*	0.817*	15.47
Sfenthourakis (1994, 1996)	0.895*	0.907*	5.08
Botsaris (1996)	0.534*	0.571*	6.42
Nilsson <i>et al.</i> , 1988) (Snails)	0.365***	0.360***	–0.15
Nilsson <i>et al.</i> (1988) (Beetles)	0.555***	0.507***	–1.75
Nilsson <i>et al.</i> (1988) (Plants)	0.581*	0.598*	0.69
Ricklefs & Lovette (1999) (Birds)	0.547*	0.625*	3.61
Ricklefs & Lovette (1999) (Bats)	0.404**	0.408**	0.10
Ricklefs & Lovette (1999) (Butterflies)	0.498***	0.584*	2.81
Ricklefs & Lovette (1999) (Reptiles and amphibians)	0.249 ^{n.s.}	0.293 ^{n.s.}	1.14
Kotze <i>et al.</i> (2000)	0.469*	0.514*	2.16
Davidar <i>et al.</i> (2001)	0.689*	0.699*	1.49

* $P < 0.001$, ** $P < 0.01$, *** $P < 0.05$, n.s. = not significant. With bold the higher r^2 value for each data set is denoted.

The results for the goodness of fit from r^2 and AIC are in absolute symphony not only for the best model in each case but also for the statistical significance of the improvement that the better model offers.

z-parameter

In almost all the studied data sets, the estimates of z parameter for the choros model were lower than those for the classic model. Significant statistical difference between the slopes of the logarithmic form of the two models (Equations 3 and 4) was found in the cases of Sfenthourakis (1994, 1996), Kohn & Walsh (1994), Deshayé & Morisset (1988) and in the three different data sets of Haila (1983). In all the other cases no significant statistical difference was found (Table 3).

DISCUSSION

The power of our model

As we have shown (Table 3) in the majority of the cases studied, the model proposed in this paper has a better fit to the data than the classic species–area model. This means that the species richness in each case study is better explained by choros (K) rather than area alone.

The only two exceptions were the cases of carabid beetles and snails in the work of Nilsson *et al.* (1998). Nilsson *et al.* (1988), correctly state that the number of plant species cannot be *a priori* considered as a measure of habitat diversity for many organisms. But that is also valid in their study, because the habitat types they define with a mathe-

matical formula based on the vegetation sampling squares of their work cannot *a priori* be considered as the true habitats especially for carabid beetles and snails. But even if we accept that this definition can approach some of the habitats for these two taxa, it cannot describe all the types of habitats, for carabid beetles and snails. The only taxon that this procedure could be appropriate for is vascular plants. Probably this is the reason for the absence of any relation between area and habitats and between species of land snails and carabid beetles and habitats. This may also explain the lower fit of our model for snails and beetles and the higher fit for vascular plants.

Newmark (1986) noted that one of the reasons complicating the assessment of the relative importance of area *per se* and habitat diversity in explaining species–area relationships is the inadequacy of the existing definitions of the term ‘habitat’. Since then almost nothing has been added to our knowledge of what habitat really represents. As Nilsson *et al.* (1988) say, ‘it seemed hard to decide a priori what should be viewed as a habitat for a carabid beetle or a land snail’, and Kohn & Walsh (1994, p. 368) add ‘habitats are difficult to define’.

According to Looijen (1995, 1998), definitions of habitat in the ecological literature refer to at least four different concepts. For example, Ricklefs (1979) defines habitat as the vegetative cover of an environment when according to Whittaker *et al.* (1973) ‘habitat is an m -dimensional space in which species exist’. The latter definition, with small changes, seems to be the most accepted in the last decades (Krebs, 1988, 1994; Looijen, 1995, 1998), but it is too broad for comparisons to be attainable (Newmark, 1986), resulting to the fuzziness on its applications. Another important problem

Table 3 The values of the z -parameter for the logarithmic forms of the Arrhenius model ($S-A$) and the choros model ($S-K$). The results of the Student’s test for the significance of the differences between the slopes of the two equations

Authors	z ($S-A$)	z ($S-K$)	
Kitchener <i>et al.</i> (1980)	0.24	0.19	n.s.
Kitchener <i>et al.</i> (1980)	0.29	0.23	n.s.
Reed (1981)	0.34	0.30	n.s.
Kitchener <i>et al.</i> (1982)	0.18	0.14	n.s.
Haila (1983) 1976	0.47	0.34	s*
Haila (1983) 1979	0.51	0.37	s*
Haila (1983) 1980	0.55	0.41	s*
Newmark (1986)	0.12	0.10	n.s.
Deshayé & Morisset (1988)	0.74	0.51	s**
Nilsson <i>et al.</i> (1988) (Snails)	0.15	0.13	n.s.
Nilsson <i>et al.</i> (1988) (Beetles)	0.37	0.32	n.s.
Nilsson <i>et al.</i> (1988) (Plants)	0.10	0.09	n.s.
Rydin & Borgegard (1988)	0.36	0.30	n.s.
Kohn <i>et al.</i> (1994)	0.48	0.37	s***
Sfenthourakis (1994)	0.20	0.17	s***
Botsaris (1996)	0.19	0.17	n.s.
Ricklefs & Lovette (1999) (Birds)	0.21	0.17	n.s.
Ricklefs & Lovette (1999) (Bats)	0.35	0.27	n.s.
Ricklefs & Lovette (1999) (Butterflies)	0.26	0.22	n.s.
Ricklefs & Lovette (1999) (Reptiles and amphibians)	0.14	0.16	n.s.
Kotze <i>et al.</i> (2000)	0.13	0.11	n.s.
Davidar <i>et al.</i> (2001)	0.18	0.16	n.s.

n.s. = not significant ($P > 0.05$), s: significant, * = $P < 0.001$, ** $P < 0.01$, *** $P < 0.05$.

with the definition of habitat is that the term biotope is being used interchangeably with habitat, the latter more in English and the former more in other European languages (Looijen, 1995, 1998). Clearly, these problems can be resolved only by having unambiguous and mutually exclusive definitions of terms.

It is obvious that the main disadvantage of the proposed model lies on the fuzziness, which covers the specific and clear determination of the ecological term 'habitat'. Habitat has to be defined based on the close study of the natural history of the studied taxon, in a way, which will allow comparisons among different studies.

It can be argued that the choros model's improvement in fit coming from the inclusion of habitats in a model, is not significant enough in order to be necessary. The answer comes from Rosenzweig (1995) who states that because both area and habitats are so tightly interconnected in nature, either can act as surrogate variable for the other, improving the fit to a curvilinear relationship and so hiding the effect of the other. He also comments that in the case of multiple linear regressions there is a statistical trap, whereby only one of the variables actually works and the second only seems to work, and that is because of their tight interconnection.

The importance of our model is not just the better fitness compared with the Arrhenius species–area relation, but relies on the fact that for the first time a mathematical model which is trying to explain species richness and embodies habitats is simple and effective.

The need for a species–area–habitat model

We believe that the species richness does not depend solely either on area or habitats but on both of them. In many studies it has been implied or established that area and habitat diversity are interconnected (Power, 1972; Kitchener *et al.*, 1980a, b; Reed, 1981; Rafe *et al.*, 1985; Newmark, 1986; Kohn & Walsh, 1994; Williamson, 1998; Ricklefs & Lovette, 1999) and thus habitat hypothesis and area *per se* hypothesis may not be mutually exclusive (Newmark, 1986; Kohn & Walsh, 1994; Rosenzweig, 1995; Ricklefs & Lovette, 1999).

In at least three different works, there has been not only a quantitative approach of the effects of island area and habitat diversity on islands' species richness but also of the degree of their interconnection. Kohn & Walsh (1994) used path analysis with correlated causes (Sokal & Rohlf, 1981) in order to access quantitatively the direct and indirect effects of habitats and island size on species richness. They managed to calculate the direct effects of area and habitat diversity on species richness, respectively, but also the indirect effects of area through habitats. An analogous approach was contacted by Fox & Fox (2000) who studied mammals in south east Australia. Similarly, Ricklefs & Lovette (1999) distinguish four components of the variation of species richness on islands, island area, habitat, the interconnection between area and habitat while the last component is related to remaining or unexplained variation. They present the relative magnitude of each of these components for the four studied animal groups (Fig. 4 in their paper).

Kohn & Walsh (1994) concluded that both of these variables contribute to the total species number; proposing that area *per se* and habitat hypothesis are not mutually exclusive, as also Newmark (1986), Rosenzweig (1995), Ricklefs & Lovette (1999) and Fox & Fox (2000) did, but mutually supplementary and that a model for species richness on islands should include both area and habitats.

This mutual supplementation is pronounced through the choros factor (K), which has the ability to express the total value of the effects of area habitat diversity and their inter-correlation on species richness.

z-parameter

In their famous monograph MacArthur & Wilson (1967), proposed that the value of z reflects to the isolation of island group and habitat heterogeneity and depends on the studying taxon. Rosenzweig (1995) and after him Brown & Lomolino (1998) established three different categories of species–area curves: Between biogeographical provinces, within biogeographical provinces and of islands or isolated habitat patches. The typical value of z is 0.5–1, 0.1–0.2 and 0.2–0.5, respectively. Despite the reduction of the z -values, in all the cases examined in this work (even in those achieving significant statistical differences), the z -values remained within the limits proposed for each category. The only exception is the case of Deshayes & Morisset (1988), where the very high value of z was reduced to a more 'acceptable' size for the small islands studied.

Small islands

As MacArthur & Wilson (1967) and many others have observed (Wiens, 1962; Niering, 1963; Whitehead & Jones, 1969; Woodroffe, 1986; Dunn & Loehle, 1988; Botsaris, 1996; Lomolino, 2000; Lomolino & Weiser, 2001), species richness may be uncorrelated with island area for relatively small islands. This phenomenon is known as the small island effect. The main feature of small island effect is that an increase of species number along with the increase of area in small islands is not observed. On small islands, habitat characteristics, occasional disturbances, isolation and intraspecific interactions are likely to determine how many species have the ability to maintain populations (Botsaris, 1996; Losos, 1996; Whittaker, 1998; Lomolino 2000, 2001).

Our model in many cases can predict the behaviour of species richness on small islands at least better than the Arrhenius equation can. Suggestively, we present two cases from Reed (1981) and Botsaris (1996). Coquet and Hibre islets in Reed (1981) have the same size (0.065 km²), and are situated almost equidistantly from the mainland (1.3 and 1.9 km, respectively). Coquet has eight species and seven habitats while Hibre has ten species and twelve habitats. The classic equation predicts the same number of species for these two islands, almost 8.5 species, while choros model predicts eight and nine species, respectively. In Botsaris (1996), the islets Hydrousa and Markelos have equal total

area, 0.0025 km², their distance from mainland is 1.2 and 0.6 km, respectively. On Hydrousa four land snail species and one habitat type have been reported. On Markelos six species and two habitat types were present. The Arrhenius equation predicts 5.5 species for the two islets, when the proposed model predicts five species for Hydrousa and six for Markelos.

The examples above indicate that in the case of small islands where habitat diversity is the main determinant of species richness observed, the choros model has the ability to approach and describe the small island effect. Of course there are many cases of small islands where stochastic events settle the number of species present, which cannot be approached through a generalized model.

CONCLUSIONS

The variation of species richness is better described by the choros model than by the classic species–area relation.

The choros model considers the interrelation between area and habitats and expresses the combined effects of these. The proposed model offers higher explanatory power for the generating mechanisms of species richness compared with area *per se* or the habitat hypothesis.

The discrimination between habitat and biotope is needed in future studies. Habitat has to be defined based on the natural history of the taxon studied, in a way, which will allow comparisons among different studies. When habitat types will be defined based on the biology of the species studied, we expect that the choros model will exhibit high correlation between species richness and the ‘choros’ of the region.

The proposed model can be considered a stepping-stone for the understanding of the small island effect as habitat diversity has been identified as one of the main determinants of species richness on small islands.

ACKNOWLEDGMENTS

We are grateful to our colleagues, Dr P. Lymberakis, Dr G. Koumoundouros, Dr S. Giokas, Dr A. Trichas, N. Poulakakis, A. Parmakelis, D. Sfakianakis, Professor R.A.D. Cameron, and two anonymous referees for their critical comments on the manuscript.

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