

Island Species Richness Increases with Habitat Diversity

Joaquín Hortal,^{1,*} Kostas A. Triantis,² Shai Meiri,^{1,3} Elisa Thébault,^{1,4} and Spyros Sfenthourakis⁵

1. NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot SL5 7PY, United Kingdom; 2. Biodiversity Research Group, Oxford University Centre for the Environment, South Parks Road, Oxford OX1 3QY, United Kingdom; and Azorean Biodiversity Group, Departamento de Ciências Agrárias, Centro de Investigação de Tecnologias Agrárias dos Açores, Universidade dos Açores, Terra-Chã, 9700-851 Angra do Heroísmo, Terceira, Açores, Portugal; 3. Department of Zoology, Tel Aviv University, 69978, Tel Aviv, Israel; 4. Biometris, Droevendaalsesteeg 1, Building 107, 6708 PB Wageningen, The Netherlands; 5. Section of Animal Biology, Department of Biology, University of Patras, GR-26504, Patras, Greece

Submitted December 5, 2008; Accepted May 19, 2009; Electronically published October 26, 2009

ABSTRACT: Species richness is commonly thought to increase with habitat diversity. However, a recent theoretical model aiming to unify niche and island biogeography theories predicted a hump-shaped relationship between richness and habitat diversity. Given the contradiction between model results and previous knowledge, we examine whether the relationship between species richness and habitat diversity is consistently monotonically increasing and under which circumstances, if at all, such relationships could be hump shaped. We review the empirical evidence about the shape of such relationships and show that species richness on islands usually increases with habitat diversity and that it never decreases. We also critically examine the assumptions of the theoretical model and modify them to incorporate a less restrictive definition of niche width. The modified assumptions lead to simulations that better capture real patterns, using either simple parameters or observed distributions of niche breadth. Further work is needed to incorporate ecological interactions and metacommunity dynamics if the aim is to merge niche and island biogeography theories in a realistic modeling framework.

Keywords: habitat diversity, island biogeography, niche theory, niche breadth, null models, species richness.

Introduction

A central issue in ecology is to understand how the number of species that coexist in an area relates to local conditions and to the ecological requirements of the species inhabiting it. Given that these species assemble from those species that are regionally available, solving such a question relies not only on species adaptations and between-species interactions, which are the realm of niche theory, but also on their rates of dispersal, speciation, and extinction, which are traditionally included within the island biogeography theory (Ricklefs 2008). Thus, an important challenge is to merge the two theories into a single framework. Within this con-

text, understanding the contribution of habitat diversity (and, in general, environmental heterogeneity) to species richness and species coexistence might be of central importance because it relates habitat selection (and thus the niche-driven constraints explained by niche theory) with the geographical characteristics of the studied area.

Habitat diversity is known to affect species richness independent of area per se (Williams 1964; Connor and McCoy 1979); everything else being equal, the more habitats there are in a given territory, the more species there are to be found. Habitat diversity is formally defined as the number of habitats in each territorial unit (e.g., an island; see Rosenzweig et al. 2003; Triantis et al. 2006). The related term “habitat heterogeneity” is used to refer to the environmental variability within an area, including topography, habitat type, and climate (e.g., see Tews et al. 2004; Hortal et al. 2008*b*). To date, empirical evidence shows that the number of habitats in a region is almost always positively correlated with the number of species inhabiting it (e.g., Kohn and Walsh 1994; Rosenzweig 1995; Sfenthourakis 1996; Kerr and Packer 1997; Ricklefs and Lovette 1999; Triantis et al. 2005; Jürriado et al. 2006). In fact, habitat diversity is often a better predictor of species richness than area is (e.g., Lack 1973; Kohn and Walsh 1994; Ricklefs and Lovette 1999; Triantis et al. 2003, 2008*b*, 2008*c*).

A recent theoretical model aiming to unify island biogeography and niche theories (Kadmon and Allouche 2007) casts some doubt on the generality of such positive monotonic relationships. The predictions of the model concerning relationships between species richness, area, and immigration are, in general, in accordance with the classic model by MacArthur and Wilson (1963, 1967). However, under some circumstances it predicts a hump-shaped relationship between habitat diversity and species richness. If the predictions of Kadmon and Allouche’s (2007) theoretical model are supported by data, the current received wisdom regarding the species richness–habitat diversity relationship must be reevaluated. If, how-

* Corresponding author; e-mail: j.hortal@imperial.ac.uk.

ever, they are not, the model should either be discarded or modified to provide more realistic results.

Here we first determine the empirical shape of the relationship between habitat diversity and species richness, using a number of available published data sets with information on habitat diversity. We then examine which assumptions of Kadmon and Allouche's (2007) model could lead to the prediction of a hump-shaped relationship, focusing explicitly on their definitions of niche breadth and the distribution of species abundances in the regional species pool. Finally, we examine the influence of these assumptions on model outputs via simulations that use both hypothetical and observed distributions of niche breadths.

Methods

Empirical Evaluation of the Species Richness–Habitat Diversity Relationship

We studied the shape of the relationship between richness and habitat diversity by analyzing literature data from 24 island systems (either true islands or habitat islands; table 1). These data sets were selected on the basis of the availability of habitat diversity data and the reliability of the inventories (see Triantis et al. 2003, 2008c for further details).

We used inferential statistics to assess whether each of these data sets shows a hump-shaped relationship. For each data set, we tried to fit island species richness to a quadratic model of habitat diversity (HD; i.e., $HD + HD^2$). To demonstrate the existence of a hump-shaped relationship between species richness and habitat diversity, such a model should meet at least four criteria: (1) all of its terms are significant, (2) it is more informative than a linear model between species richness and habitat diversity (which we tested using AIC_C weights), (3) the signs of the model parameters are positive for the linear terms and negative for the quadratic terms (i.e., the particular data set actually shows a hump-shaped pattern), and (4) the inflection point predicted by the fitted quadratic model is present within the range of habitat diversity values contained in the data. The latter criterion is important because if such an inflection point is outside the range of the empirical data, the observed relationship would be a monotonic increase of richness with area (see Whittaker 2009).

For each data set, we fitted models that included linear and quadratic equations of habitat diversity using ordinary least squares regression. The significance of the terms of the quadratic model was assessed using the F statistic in Statistica 6.1 (StatSoft 2003). The additional information provided by the quadratic model was assessed by the change in information according to the small sample size–corrected Akaike index (AIC_C), and it was considered to be important when its partial weighting was at least 5% greater than that

of the linear model (see Burnham and Anderson 2002; Diniz-Filho et al. 2008). We calculated AIC_C weights using SAM 3.0 (Rangel et al. 2006; latest version available at <http://www.ecoevol.ufg.br/sam/>). Although this information-theoretic approach would determine the most parsimonious model, we also provide the still widely used F and R^2 statistics as complements to the AIC approach. In addition to all of these calculations, we visually inspected the relationships to ensure that no spurious conclusion is made on the sole basis of blind statistical inference.

Theoretical Modeling of Island Richness

We modified the model proposed by Kadmon and Allouche (2007) to explore the effect of some of its assumptions on the predicted species richness–habitat diversity relationship. This model incorporates island area, immigration, habitat diversity, species richness, and reproductive rates under the framework of Hubbell's neutral theory (Hubbell 2001). Following Kadmon and Allouche (2007), the island community is modeled as a spatially implicit heterogeneous landscape consisting of A sites (where A = island area) with H habitat types. Parameters c , i , and e are the reproduction, immigration, and death rates of individuals, respectively, and J is the total community size. The overall dynamics of the island community are modeled here as a discrete-time Markov process where a single event occurs at each time step. These events are (1) births, with probability $p_b = cJ/(cJ + eJ + iA)$; (2) immigration, with probability $p_i = iA/(cJ + eJ + iA)$; and (3) deaths, with probability $p_d = 1 - p_i - p_b$. In this model, each species is able to establish and persist in only one type of (suitable) habitat, and individuals arriving at unsuitable or occupied habitats die without occupying the site. A detailed description of the model following Grimm et al.'s (2006) ODD protocol is given in the appendix.

For most combinations of values of area and rates of reproduction, immigration, and mortality, the model proposed by Kadmon and Allouche (2007) predicts a hump-shaped relationship between species richness and habitat diversity. Critically, this model assumes that each species can inhabit only one type of habitat and that each island supports a fixed number of individuals, which is determined by its area, regardless of its species richness. Therefore, if habitat diversity increases for a constant island area, the same number of individuals is divided among more habitat types and, hence, among more species. This allows for fewer individuals per species, increasing extinction rates. Thus, within the model for a given island area, richness decreases as habitat diversity increases above a certain value. Changes in mortality rates and/or reproduction rates would shift the position of the species richness peak only along the habitat diversity axis, and island area determines only the absolute

Table 1: Results of the comparison of the linear and hump-shaped relationships between species richness and habitat diversity

Taxon	Location	N_{islands}	HD model		HD + HD ² model			Inflection	Reference
			Adjusted R^2	AIC _c	Adjusted R^2	AIC _c	Signs		
All plants	Hybrides, Richmond Gulf, Canada	28	.940	262.0	.955	254.1	+, -	32.6	Deshaye and Morisset 1988
Halophytic plants	Hybrides, Richmond Gulf, Canada	28	.720	202.8	.795	193.2	+, -	18.5	Deshaye and Morisset 1988
Birds	Great Britain off-shore islands	73	.752	532.0	.790	521.1	-, +	.1	Reed 1981
Birds	Åland Islands, southwest Finland	44	.911	257.3	.914	256.9	+, +	-14.4	Haila et al. 1983
Mammals	North American mountaintops	24	.500	165.0	.496	167.0	-, +	1.3	Newmark 1986
Bryophytes	West Estonian Archipelago	32	.786	301.4	.798	301.2	+, +	-1.5	Jüriado et al. 2006
Land snails	Lake Mälaren, Sweden	17	-.032	96.5	-.005	98.0	+, -	5.1	Nilsson et al. 1988
Beetles	Lake Mälaren, Sweden	17	-.036	126.5	-.101	129.9	+, -	6.1	Nilsson et al. 1988
Plants	Lake Mälaren, Sweden	17	.045	99.9	-.024	103.4	+, +	-30.7	Nilsson et al. 1988
Birds	Lesser Antilles, Caribbean	19	.513	128.8	.490	129.1	+, +	-2.5	Ricklefs and Lovette 1999
Bats	Lesser Antilles, Caribbean	17	.268	99.0	.222	102.2	+, -	46.5	Ricklefs and Lovette 1999
Butterflies	Lesser Antilles, Caribbean	15	.534	115.5	.507	119.3	+, +	-8.1	Ricklefs and Lovette 1999
Birds	Stockholm Lakes, Sweden	29	.190	169.3	.160	172.0	+, -	8.1	Sillén and Solbreck 1977
Plants	Lake Hjälmaren, Sweden	37	.315	334.4	.370	332.7	+, -	4.7	Rydin and Borgegård 1988
Ground beetles	Baltic Sea	24	.349	139.3	.318	142.2	+, +	-130.7	Kotze et al. 2000
Birds	Andaman Islands, India	45	.668	310.1	.676	310.3	+, +	-4	Davidar et al. 2001
Land snails	Skyros, Aegean Sea	12	.833	75.1	.883	74.4	+, +	-1.3	Triantis et al. 2005
Beetles	Galápagos	13	.612	140.6	.644	142.6	-, +	2.1	Peck 2006
Insects (small orders)	Galápagos	13	.649	156.2	.657	159.0	-, +	1.5	Peck 2001
Terrestrial isopods	Astypalaia, Aegean Sea	13	.851	61.3	.935	53.7	-, +	1.2	Triantis et al. 2008a
Terrestrial isopods	Kalymnos, Aegean Sea	12	.812	59.0	.888	56.3	-, +	2.7	Triantis et al. 2008a
Plants	North Great Britain	47	.890	274.8	.890	275.3	+, +	-22.6	Kohn and Walsh 1994
Birds	Aegean Sea, Greece	30	.560	214.2	.693	205.0	-, +	3.8	Watson 1964
Arthropods	Canary Islands	7	.496	125.1	.602	135.9	-, +	1.8	Oromí et al. 2004

Note: All but two of the 24 data sets correspond to island systems; the exceptions being those that correspond to mountaintops (Newmark 1986) or lakes (Sillén and Solbreck 1977). N_{islands} = number of islands included in each data set. Several of these data sets are shown in figure 2. The significance of the terms of the ordinary least squares-fitted quadratic models of habitat diversity (HD; HD + HD²) was assessed by means of their F statistic, and adjusted R^2 values are shown for illustrative purposes; values in bold indicate significant parameters according to the F statistic. The small sample size-corrected Akaike Information Criterion (AIC_c) of the HD + HD² model is marked in bold when this model is more informative than the linear term according to the AIC_c weighting. Sign refers to the signs of the linear and quadratic parameters in the quadratic model. Inflection is the habitat diversity value corresponding to a slope of 0 predicted by the model.

richness value reached by this peak (see fig. 5 in Kadmon and Allouche 2007). It follows that the increasing importance of stochastic extinctions as the number of habitats increases is the underlying reason for the hump-shaped relationship between diversity and richness identified by the model (Kadmon and Allouche 2007, pp. 448–449).

Generalists, however, are a ubiquitous component of island communities (van Valen 1965; Sfenthourakis and Triantis 2009), so the assumption that each species can

occupy only one habitat is unrealistic (discussed below). Relaxing this assumption will diminish the importance of the area covered by each type of habitat in causing stochastic extinctions. While reducing the area of some habitats may cause some specialists to become extinct, we think that this will be more than compensated for by the addition of many generalist species through colonization and secondary adaptations or in situ diversification. We thus hypothesize that the hump-shaped species richness–

habitat diversity relationship would disappear either if the assumption that species can exploit only one habitat were modified or if the effects of metacommunity processes (Loreau and Mouquet 1999; Mouquet and Loreau 2002) were implicitly included. These modifications would diminish the number of extinctions, promoting the coexistence of more species in an island.

To allow species to exploit several habitats, we modify the model by introducing a parameter that describes niche breadth (N_b) as the number of habitats exploited by each species. The values of this parameter can be chosen either from real data on the distribution of niche widths (e.g., those in figs. 1*a* and 4) or by using a parameter (gene_{max}) to assign niche breadth to each new species after a null distribution (see appendix for details).

The different degrees of spatial clustering of individuals that arise from the metapopulation processes of different species (i.e., metacommunity processes) can be modeled by introducing a parameter that limits the number of offspring that disperse randomly, thereby allowing more offspring to remain in the habitat type where they originated. To do this, we assume that a newly produced offspring has a probability p_{move} to disperse to a random site within the island; otherwise, it disperses to an unoccupied site of the same habitat type occupied by its parent.

To explore the effects of our modifications on model outputs, we first simulated the communities of hypothetical islands of the same sizes as those in Kadmon and Allouche's (2007; see their fig. 5) model in order to allow direct comparison with their results. In these simulations, we explored the effects of the different values of several parameters, including limited variations of N_b and p_{move} . We also simulated how a community evolves in a newly formed island, using real data on the number of habitats used by different species of terrestrial isopods on the Aegean Islands, as described by Sfenthourakis (1996). We assumed that all 69 species in that study form the species pool and have equal probability of reaching the island. Here, the distribution of niche breadths among species follows the distribution of empirical data (shown in fig. 1*a*), so the variation in N_b is fixed instead of varying according to gene_{max} , and we try different values of p_{move} and i .

Results

We found evidence for a monotonic increase of species richness with increasing habitat diversity in 20 of the 24 data sets we explored (table 1). Three data sets showed no relationships, and only one met all four criteria for the hump-shaped relationship as discussed above (halophytic plants of the Hybrides Archipelago, Richmond Gulf, Canada; fig. 2*a*), although we doubt that this data set shows a true hump-shaped relationship (see "Discussion").

Among the 23 other data sets, the relationship between richness and habitat diversity ranges from nonsignificant (all three relationships from Lake Mälaren, Sweden; fig. 2*c*) to moderately or highly significant and linear (e.g., fig. 2*b*, 2*d*, 2*e*) or otherwise curved (e.g., fig. 2*f*). We found no cases of a decrease in species richness with increasing habitat diversity (table 1).

Our simulations using parameter values that are equivalent to those of Kadmon and Allouche's unmodified model yield results similar to theirs (cf. our fig. 3 to their fig. 5); no significant differences are caused by differences in the way we formulate the model or program the Markov process. As expected, allowing some species to exploit more than one habitat ($N_b > 1$) resulted in a monotonic increase in richness with increasing habitat diversity (fig. 3). The same occurs when offspring preferentially remain in their natal habitats, although under the p_{move} values we explored, richness shows saturation above a certain habitat diversity value in larger islands. This could be due to the effects of other model parameters that do not arise in smaller islands due to the strong saturation effects imposed by area limitations. No hump-shaped relationship between habitat diversity and species richness appears when p_{move} is < 1 .

The simulations based on the empirical distribution of N_b (fig. 5) further demonstrate the importance of p_{move} (and thus metapopulation structure) in model outcomes. At low immigration levels, species richness decays with the first increases in habitat diversity, reaching a steady state of a more or less constant number of species that is not affected by further increments in habitat diversity (fig. 5). This unexpected result is probably related to the higher "competitive" ability of the more generalist species; species that are able to occupy many habitat types end up displacing the rest of the species, reaching an equilibrium that is independent of the number of habitat types present on the island. The existence and species richness level of this steady state depends on the value of p_{move} ; parameter values closer to 0 allow for higher coexistence levels (fig. 5*A*). Only values assuming strong metapopulation structure (i.e., strong limitation of offspring dispersal, such as $p_{\text{move}} = 0.01$) produce positive monotonic species richness–habitat diversity relationships. In these cases, the long-term survival of most species is ensured regardless of their niche breadth, preventing the habitat generalists from taking the lead. More importantly, when immigration from the regional pool is sufficiently large (i.e., $i \geq 0.1$), the arrival of new species compensates for saturation processes, and species richness shows clear monotonic positive relationships with habitat diversity in all occasions (fig. 5*B*). It follows that, for most combinations of immigration rate and metapopulation structure, the relationship between species richness and habitat diversity will be positive and monotonic.

Discussion

Our analyses of empirical data show that the relationship between habitat diversity and species richness is, in general, positive and monotonic. Moreover, it is never negative. After visually inspecting the single data set that fulfilled all statistical criteria for a hump-shaped relationship, we seriously doubt that it truly shows a hump-shaped relationship between richness and habitat diversity (fig. 2a; see also Deshayé and Morisset 1988 and table 2 therein). Indeed, if all plant species in that system (rather than just the halophilous ones) are considered, a hump-shaped relationship is not supported, because not all of the parameters of the quadratic function are significant, and the inflection point is not located within the range of habitat diversity values found in the data set (table 1).

Could Hump-Shaped Species Richness–Habitat Diversity Relationships Have Been Overlooked?

Kadmon and Allouche (2007, p. 452) argued that the limited empirical evidence for a hump-shaped relationship between habitat diversity and richness could be the result of publication bias. Although it is true that biases are common in the data used for ecological research (Hortal et al. 2007, 2008a), the publication process per se is unlikely to be strongly biased against results that contradict mainstream ecological theory (see Palmer 1999; Meiri et al. 2004). In fact, negative results in community ecology are often viewed as novel and exciting and may therefore be more likely to be published (Purvis et al. 2003; Meiri et al. 2008). Even MacArthur and Wilson's (1967) theory was severely criticized from almost the time it was presented (see Sauer 1969; Gilbert 1980; Whittaker and Fernández-Palacios 2007, table 6.1), starting a long process of criticism and updates of the mainstream theory that continues today (e.g., Bellemain and Ricklefs 2008; Whittaker et al. 2008; Losos and Ricklefs 2009a, 2009b).

The two examples cited by Kadmon and Allouche (2007, p. 453) to support the existence of a hump-shaped species richness–habitat diversity relationship (Ralph 1985 and Currie 1991) do not provide such evidence either. Currie (1991) studied how environmental heterogeneity affects richness on a continental scale. However, environmental heterogeneity is not equivalent to habitat diversity (see above), and Currie's work does not fit the island biogeographic framework used here. Currie (1991) found that climatic variables were much stronger predictors of richness than environmental heterogeneity in all cases: the effects of environmental heterogeneity were not strong enough to enter any model. Similarly, Ralph (1985) compared bird richness with quantitative descriptors of plant community structure and not with habitat diversity. He

found a “negative correlation of *vegetation abundance* with *bird abundance*” (p. 481, emphasis ours) and not a hump-shaped relationship between richness and habitat diversity. Interestingly, Ralph (1985) did find such a negative relationship in nongrassland sites; if the whole landscape is

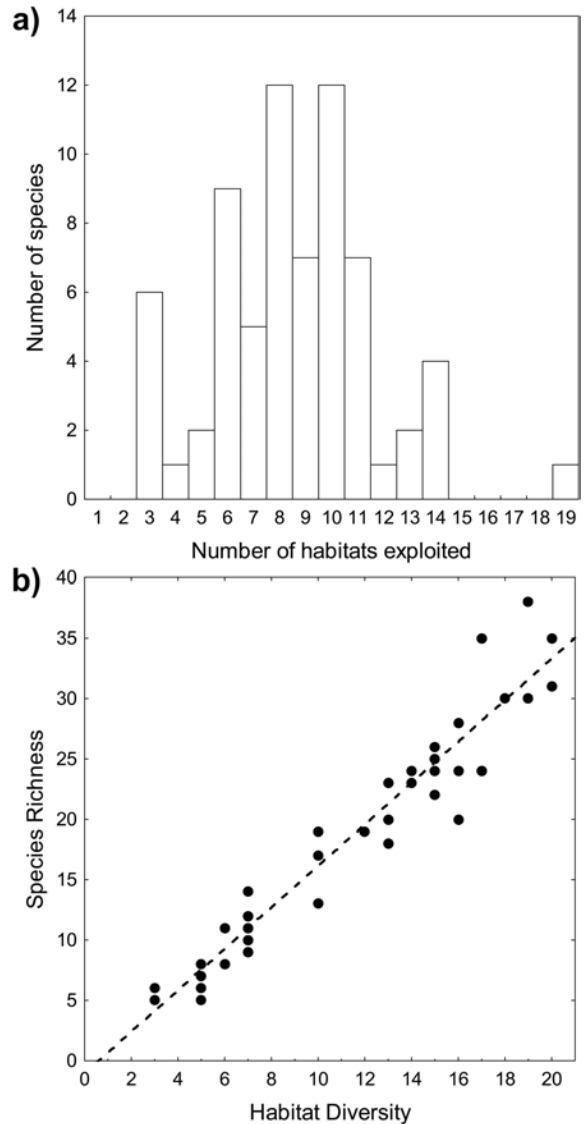


Figure 1: Relationship between habitat diversity and the diversity of terrestrial isopods inhabiting the central Aegean Islands (data from Sfenthourakis 1996). *a*, Number of habitats exploited by each of the 69 species inhabiting these islands. *b*, Relationship between species richness and habitat diversity per island; each point represents an island, and the straight line shows the general trend according to a linear regression (species richness = $-1.03 + 1.72 \times$ habitat diversity; $N = 40$, adjusted $R^2 = 0.93$, $F = 551.1$, $P < .001$). Habitat diversity and niche breadth were defined according to 29 variables pertaining to seven factors relevant to the ecology of the studied isopods (Sfenthourakis 1996).

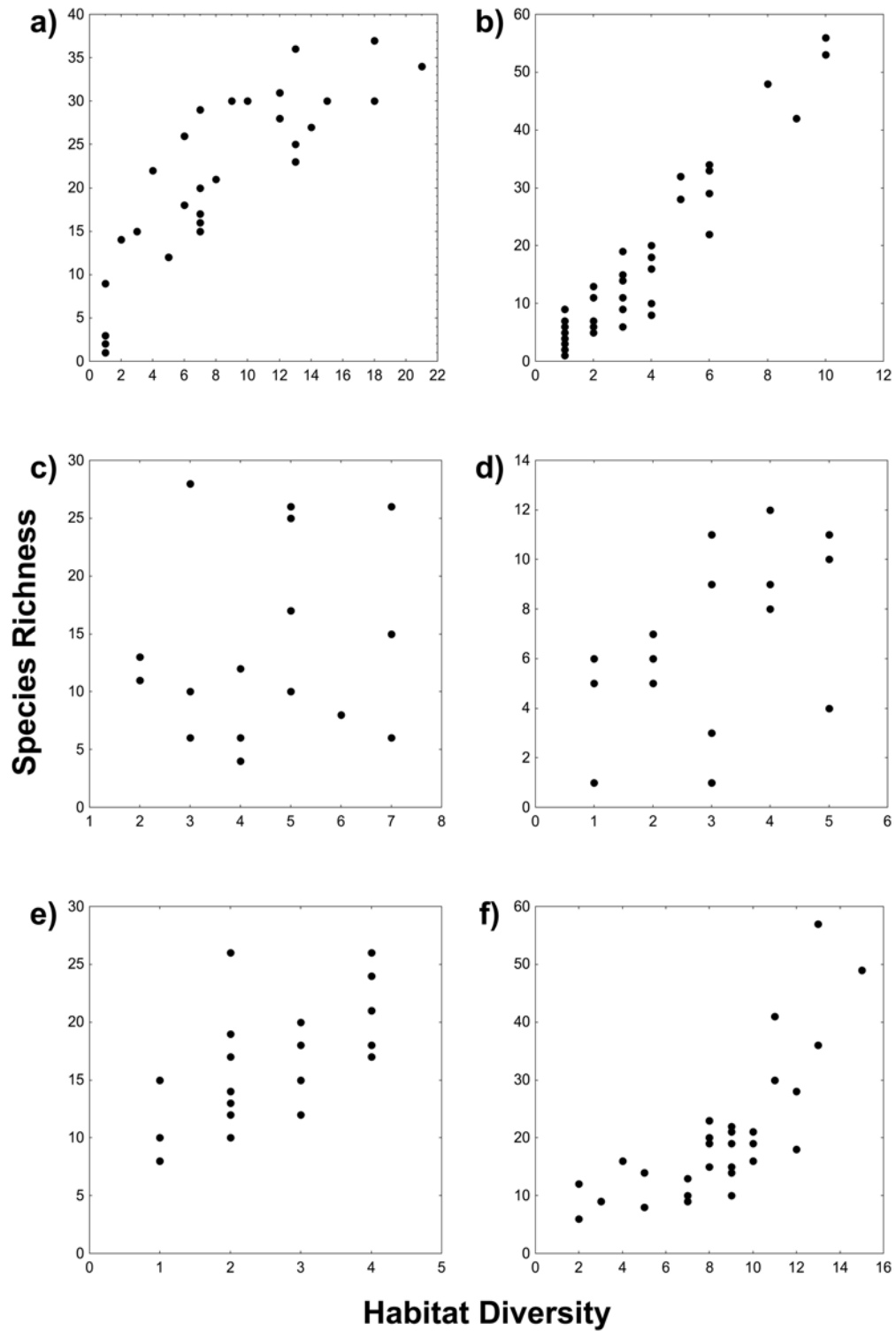


Figure 2: Examples of the observed relationship between species richness and habitat diversity (measured as number of habitat types; see text). *a*, Halophytic plants on islands of the Hybrides Archipelago, Richmond Gulf, Canada. *b*, Birds on Åland Islands, southwest Finland. *c*, Beetles on islands in Lake Mälaren, Sweden. *d*, Bats on islands of the Lesser Antilles, Caribbean. *e*, Ground beetles on islands in the Baltic Sea. *f*, Birds on islands in the Aegean Sea, Greece. See table 1 for references and model results.

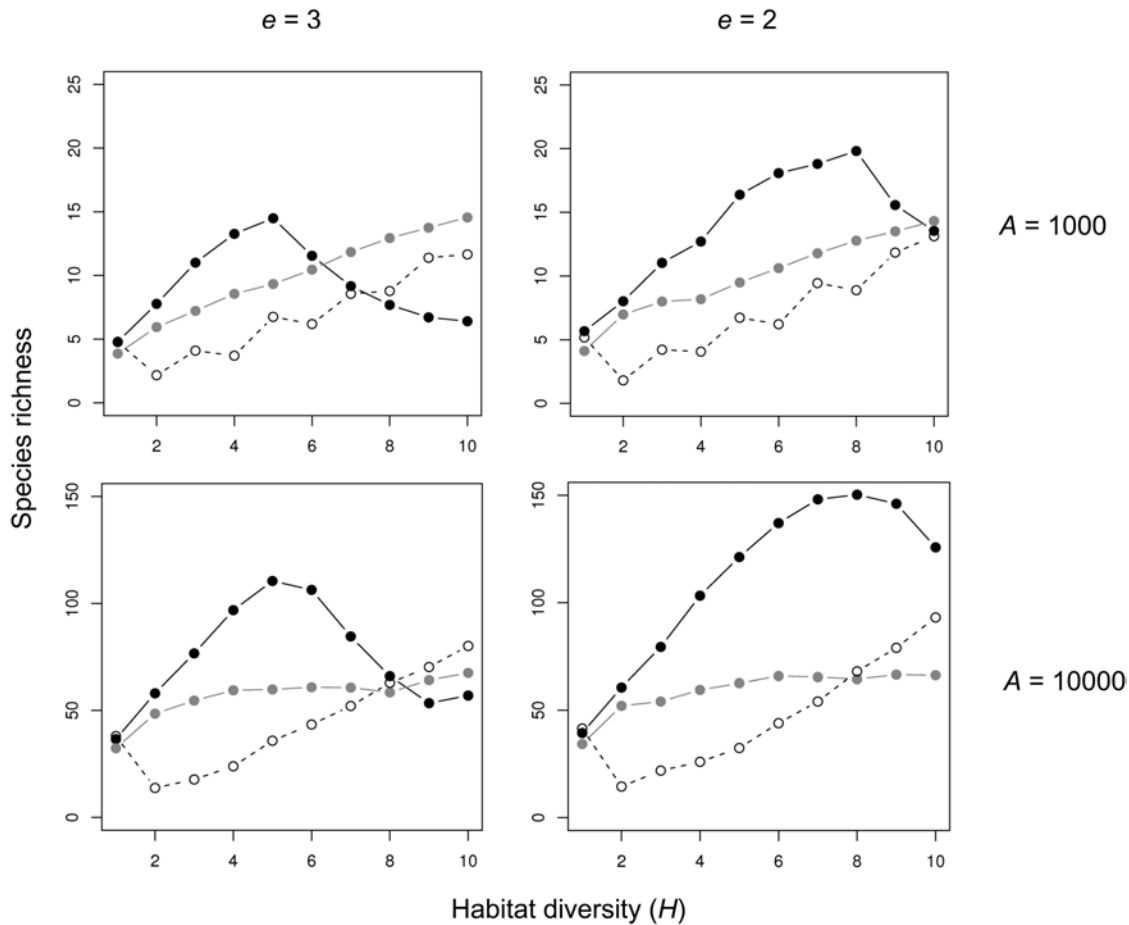


Figure 3. Results of the simulations obtained by varying the assumptions of Kadmon and Allouche’s model (2007), as discussed in the text (see appendix). Black solid curves correspond to Kadmon and Allouche’s original model, with $p_{move} = 1$ and strictly specialist species (i.e., each species can survive in only one habitat; $gene_{max} = 1$); dashed curves correspond to $p_{move} = 1$, where half of the species live in two different habitats ($gene_{max} = 0.1$); and gray solid curves correspond to $p_{move} = 0.5$ and strictly specialist species. See text for details. The graphs show the results of two different mortality rates (e) and island areas (A), as depicted in Kadmon and Allouche (2007, their fig. 5). Immigration and death rates are 0.01 and 20, respectively, in all cases. All results correspond to mean values after 50 simulations.

considered, the relationship is positive and monotonic (Ralph 1985, table 3). Crucially, obtaining an adequate description of a diversity–richness relationship requires that the habitat classification used reflects the natural history and ecological requirements of the taxon studied (Triantis et al. 2005, 2006). This was not the case in either Currie’s (1991) or Ralph’s (1985) studies. We are unaware of any documented empirical support for a hump-shaped relationship between richness and habitat diversity, nor for any negative richness–habitat diversity relationship.

Do Species Exploit Only One Type of Habitat?

Given that the species richness–habitat diversity relationship is nearly always positive and monotonic, one or more

of the assumptions of the model proposed by Kadmon and Allouche (2007) must be overly unrealistic. We believe the crucial assumption is that each species is assumed to be “able to establish and persist in only one type of habitat” so “individuals arriving in unsuitable habitats ... die without occupying the site in which they arrive” (Kadmon and Allouche 2007, p.445). This formulation of niche differentiation neglects the ecological plasticity of species. Most species, even highly specialized ones, can inhabit different habitats. For example, the Azorean habitat-specialist beetles *Trechus terceiranus* and *Trechus isabellae* colonized new habitats after the loss of those to which they were primarily adapted. While the former colonized cave entrances and small crevices after the collapse of volcanic caves (Borges and Oromí 1994), the latter colonized caves after the dis-

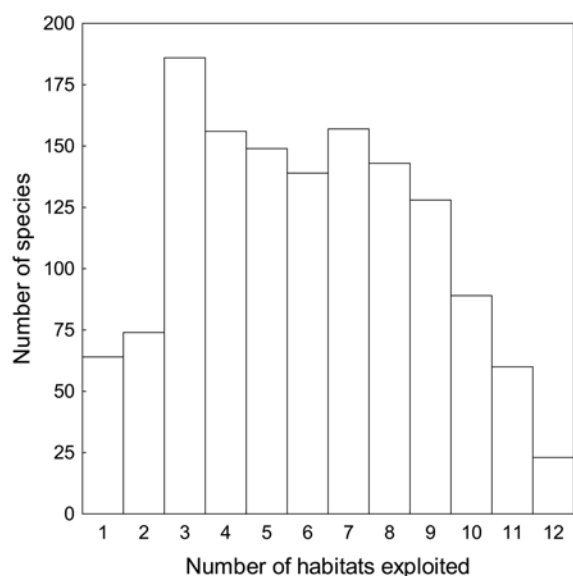


Figure 4: Number of habitats exploited by the 1,131 species of seed plants currently known for the island of Tenerife (Canary Islands; data from Hortal et al. 2007). Habitat types were extracted from a land cover map, which discriminates between structurally different habitats in terms of vegetation cover (Gobierno de Canarias, unpublished data). We assume that this classification reflects the general habitat preferences of seed plants.

appearance of the autochthonous laurel forests (Borges et al. 2007). Also, the vast majority of seed plant species in Tenerife (Canary Islands) exploit three or more habitats (fig. 4). In the case used to parameterize our modified model (Sfenthourakis 1996), no terrestrial Aegean isopod species occupies fewer than three habitats (fig. 1a). Hence, we argue that the use of multiple habitats per species is the rule, rather than the exception, and that extreme habitat specialists are rare, especially on islands.

Generalists are less prone to stochastic extinctions and are likely to be better colonizers (e.g., Kotiaho et al. 2005). Because of this, islands have relatively high proportions of generalists, even if some species become more specialized in successive phases of the taxon cycle (Wilson 1961), because of the continuous arrival of generalists from the regional pool. Thus, the appearance of new types of habitat on an island would lead to an increase in the overall number of species (fig. 1b; Davidar et al. 2001; Tews et al. 2004; Triantis et al. 2005). Some specialists will be able to exploit these new habitats, and generalists will exploit both new and old habitats (Juriado et al. 2006). The presence of riparian habitats in large Aegean islands, for example, leads to a relatively rapid increase in species richness of terrestrial isopods, regardless of the area covered by such habitats (Sfenthourakis and Triantis 2009).

It follows that the higher the number of habitats on an island, the higher the number of species that will be able to successfully colonize that island. The area covered by each habitat can be important for particular species in terms of both competitive exclusion and the minimum area required to establish viable populations. However, the overall effects of competition in limiting species richness on islands are less important, because most species will be able to exploit other available habitats if they are excluded from small, saturated ones (the main cause for the hump-shaped response of richness to habitat diversity in Kadmon and Allouche's [2007] model). Furthermore, new habitats typically appear as oceanic islands increase in size (Whittaker et al. 2008; Borges and Hortal 2009), so an increase in habitat diversity will be accompanied by a reduction in the available area per habitat in only very few occasions.

Modeling the Interplay between Niche Breadth and Metapopulation Structure

Modeling natural communities is difficult, because the interactions between multiple assumptions often result in unrealistic outputs. For example, the results of our simulations show that assuming a wide range of niche breadths and low rates of immigration from the species pool results in highly imbalanced competitive abilities. This favors generalists and saturates the island at low species richness regardless of its habitat diversity, an initially unexpected result. For similar reasons, Kadmon and Benjamini (2006) found that excessive growth rates decrease the probability that individuals of new species coming from the species pool colonize local communities after stochastic extinctions, a saturation effect common in models accounting for competitive communities (Mouquet et al. 2002).

It is unlikely that the parameter combinations leading to saturation appear in nature, for this would imply taxa with both low long-distance dispersal ability and high within-island dispersal rates. Interestingly, high immigration rates have been shown to prevent local saturation in models of metacommunity dynamics (Loreau and Mouquet 1999). Here, coexistence is enhanced by the compensation of species' competitive abilities at the regional scale and by intermediate or high levels of immigration within the landscape and from the species pool (Mouquet and Loreau 2002; Mouquet et al. 2004). This effect is corroborated by the results of our modified model (fig. 5), where high levels of immigration are accounted for by small p_{move} values and/or high immigration rates i . This allows either a strong clustering of offspring within their native habitat or a significant rate of immigration from the regional pool, enhancing coexistence at the island level. By ensuring that most individuals remain in suitable sites, these rates allow the long-term

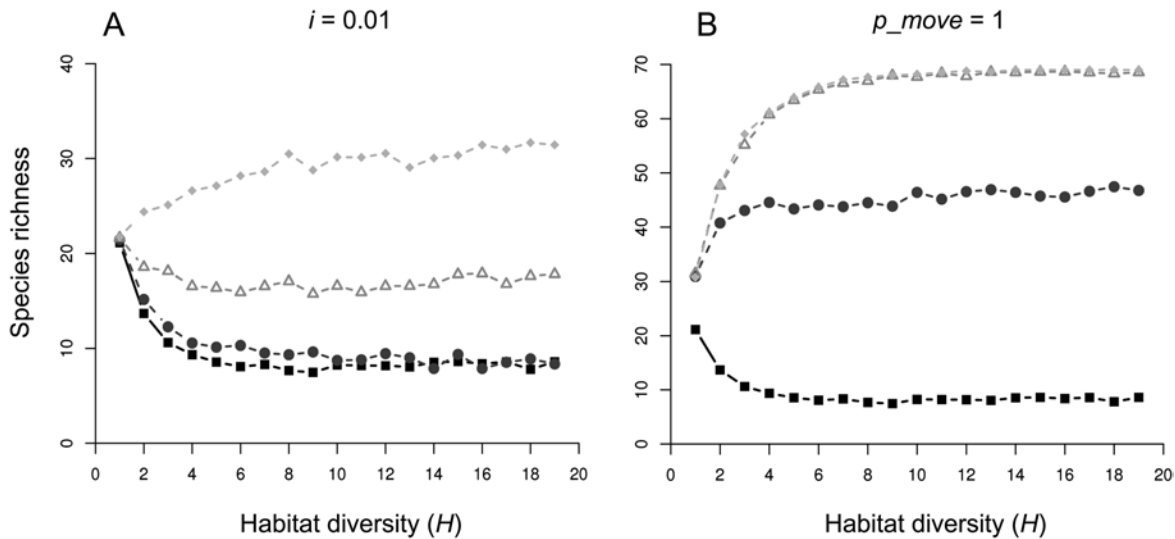


Figure 5: Results of the simulations obtained by varying some of the assumptions of Kadmon and Allouche's model (2007; appendix) according to the distribution of niche breadth in 69 species of terrestrial isopods inhabiting the central Aegean Islands (data from Sfenthourakis 1996). Niche breadth (N_b) is fixed following the distribution shown in figure 1a. *A*, Impact of dispersal rate to other types of habitat. The curve with squares shows Kadmon and Allouche's original model, modified only in the degree of niche breadth of each species ($p_{move} = 1$). The rest of the curves show increasing degrees of dispersal to habitat types that are different from that occupied by the parent: circles represent $p_{move} = 0.5$ (as in fig. 3 examples), triangles indicate $p_{move} = 0.1$, and diamonds indicate $p_{move} = 0.01$. *B*, Impact of immigration rates. The curves show increasing degrees of immigration rates: in squares for $i = 0.01$, circles for $i = 0.1$, triangles for $i = 0.5$, and diamonds for $i = 1$. Reproduction and death rates are 20 and 2, respectively, in all cases. All results correspond to mean values after 50 simulations.

survival of most species, and hence high richness is maintained by the continuous arrival of propagules.

We therefore believe that our changes significantly improve Kadmon and Allouche's (2007) model. Allowing species to exploit several habitats and limiting offspring dispersal rates are modifications grounded in expansive ecological theory, and it comes as no surprise that they result in more realistic species richness–habitat diversity relationships. A combination of both factors is nevertheless needed, with empirical distributions of niche breadth. Otherwise, habitat generalists have an advantage over specialists, an effect that is compensated for by niche pre-emption, interhabitat source-sink dynamics, and/or the strong influence of the regional pool on the diversity of local communities (Ricklefs 2007). Therefore, further improvements of this model must (1) include a description of interspecific interactions; (2) use a spatially explicit description of the metacommunity (e.g., Loeuille and Leibold 2008) that allows, for example, for the maintenance of sink populations (Rosenzweig 1995); and/or (3) use a more detailed description of the assembly of local communities from the species available in the regional pool (e.g., San-

ders et al. 2007; Starzomski et al. 2008). All these alternatives will allow higher levels of coexistence, thus producing more realistic models, albeit sacrificing the simplicity of the current one.

In conclusion, species richness increases monotonically with increased habitat diversity and never decreases. Thus, a realistic model merging island biogeography and niche theories should incorporate at least the variation in the number of habitats exploited by different species as well as a rational description of metacommunity processes.

Acknowledgments

We thank R. Kadmon, A. Phillimore, and R. Whittaker for their help and comments; A. Baselga and P. Borges for their advice; and T. Rangel and an anonymous reviewer for their constructive reviews. J.H., S.M., and E.T. were supported by the United Kingdom's Natural Environment Research Council (NERC). K.A.T. was supported by a Marie Curie Intra-European Fellowship Program and the Academic Visitors Program of the NERC Centre for Population Biology.

APPENDIX

Model Description

Purpose of the Model

In this section we describe the model we used, following the standard protocol for describing individual-based models proposed by Grimm et al. (2006). The purpose of the model is to understand how variations in island area and isolation interact with habitat heterogeneity and niche differentiation in determining patterns of species diversity. This model is a modified version of the model proposed by Kadmon and Allouche (2007), and its aim is to explore the impact of changing the allegedly unrealistic assumptions made by the original model, in particular about niche breadth and metapopulation processes on the patterns of species diversity on islands.

State Variables and Scales

The model contains two types of entities: individuals and habitats. Individuals belong to one of the S species types, which in turn are characterized by the number (Nb_k) and list of the habitat types they can occupy (niche _{k}). Individuals are further characterized by the habitat they are occupying.

The island is modeled as a spatially implicit heterogeneous landscape consisting of H different habitats. Habitats are characterized by their identity, the maximum number of individuals they can host (defined by A/H , where A is either the total number of individuals the landscape can host or the area of the island), and the number and the list of individuals present in the habitat. J is the total number of individuals present on the island.

Process Overview and Scheduling

Each time step comprises one of three events: birth of an individual, death of an individual, or immigration to the island of a suitable individual from a regional pool of species. The reproduction rate c , death rate e , and immigration rate i are the same for all individuals. The relative probabilities of these three events at each time step are defined by $p_b = cJ/(cJ + eJ + iA)$ for a birth event, $p_i = iA/(cJ + eJ + iA)$ for an immigration event, and, consequently, $p_d = 1 - p_i - p_b$ for a death event. Descriptions of these different processes are listed in table A1.

Design Concepts

Emergence. Population and community dynamics emerge from individual and species traits. Individuals' life cycles and dispersals are imposed by the rules defined in table A1.

Stochasticity. All three events (birth, death, and immigration) were interpreted as probabilities. Furthermore, all modeled processes included stochastic elements such as randomly chosen individuals for birth and death events, randomly chosen habitats for immigration and offspring dispersal, and random species types for migrants (see table A1). When they were not chosen from real data on the distribution of niche widths (see fig. 5), species niche parameters Nb_k and niche _{k} were drawn from probability distributions. A value for the number of habitats k a species can occupy, Nb_k , was then chosen randomly between 1 and $gene_{max}$, where $gene_{max}$ is the maximum number of habitats a species can potentially occupy (note that when $gene_{max} = 1$, each species can persist in only one habitat, as in Kadmon and Allouche's [2007] original model). The list of habitats a species k can occupy, niche _{k} , was determined by the random selection of Nb_k different habitats from the H habitats of the island.

Interaction. Competition for space between individuals is modeled implicitly. An individual cannot establish in a habitat that is already completely occupied by other individuals.

Observation. The species richness of the island, the total number of individuals present in the island, and the average niche width of the species present were recorded throughout the last 1,000 time steps of the simulations. For model analysis, the temporal mean of these three variables was then calculated.

Initialization

When the species pool is not defined from real data, a species pool of 122 species (similar to that in Kadmon and Allouche 2007) is created and the niche parameters Nb_k and $niche_k$ of the species are randomly generated. For each of the 122 species, a value for Nb_k is randomly chosen (between 1 and $gene_{max}$) and $niche_k$ is determined by the random selection of Nb_k different habitats from the H habitats of the island. The initial distribution of individuals in the island is randomly generated, with equal probabilities for each habitat to be colonized by an individual from a suitable species and where half of the island is initially empty.

Input

The dynamics of the model are not driven by any external environmental variation.

Submodels

Submodel Birth. Following Kadmon and Allouche (2007), we assume that birth rates are not species specific; hence, individuals of all species have the same birth rate c . A parent is thus selected randomly across all the individuals present in the island, and an offspring of the same species type as the parent (characterized by Nb_k and $niche_k$) is produced. The newly produced offspring disperses immediately to a random habitat within the island with a probability p_{move} ; otherwise, it stays in the same habitat as its parent. The offspring cannot establish and it dies immediately if the selected habitat is already fully occupied or if it arrives in an unsuitable habitat (suitable habitats are defined by its specific niche $niche_k$). We assume that p_{move} is the same for all individuals. For $p_{move} = 1$, immigration rates are similar to those in Kadmon and Allouche's (2007) model.

Submodel Death. Following Kadmon and Allouche (2007), we assume that death rates are not species specific: individuals of all species have the same death rate e . An individual is selected randomly across all the individuals present and then suppressed from the island.

Submodel Immigration. The species type of the migrant is selected randomly between 1 and S_{pool} , where S_{pool} is the species richness of the regional pool. Unless stated otherwise, the regional pool has 122 suitable species for each habitat, as chosen in Kadmon and Allouche (2007). A suitable habitat for the migrant is then chosen randomly among all the habitats the individual can occupy (defined by $niche_k$). The migrant is able to establish only if the chosen habitat is not fully occupied; otherwise, it dies immediately.

Table A1: Processes, pseudocode, and parameters

Process	Pseudocode	Parameters
Birth	Randomly choose an individual present in the island	p_{move} , $niche_k$
	Produce an offspring of this individual with probability p_{move} , dispersion of the offspring to a random habitat	
	else	
	dispersion of the offspring to the same habitat as its parent if selected habitat completely occupied or inappropriate regarding offspring niche $niche_k$	
	death of the offspring without occupying the habitat	
Death	else	
	establishment of the offspring in the habitat	
Immigration	Randomly choose an individual present in the island	S_{pool} , $niche_k$
	Death of this individual	
	Randomly select a species type for the migrant, from the regional pool of diversity S_{pool}	
	Randomly choose a suitable habitat in the island regarding the niche of this migrant $niche_k$ if selected habitat completely occupied death of the migrant without occupying the habitat	
	else	
	establishment of the migrant in the habitat	

Literature Cited

- Bellemain, E., and R. E. Ricklefs. 2008. Are islands the end of the colonization road? *Trends in Ecology & Evolution* 23:461–468.
- Borges, P. A. V., and J. Hortal. 2009. Factors driving arthropod speciation at the Azorean Archipelago. *Journal of Biogeography* 36: 178–191.
- Borges, P. A. V., and P. Oromí. 1994. The Azores. Pages 605–610 in C. Juberthie and V. Decu, eds. *Encyclopaedia biospeologica*. Tome I. Société de Biospéologie, Moulis.
- Borges, P. A. V., P. Oromí, A. R. M. Serrano, I. R. Amorim, and F. Pereira. 2007. Biodiversity patterns of cavernicolous ground-beetles and their conservation status in the Azores, with the description of a new species: *Trechus isabelae* n. sp. (Coleoptera, Carabidae, Trechinae). *Zootaxa* 1478:21–31.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference: a practical information-theoretical approach*. 2nd ed. Springer, New York.
- Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113:791–833.
- Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* 137:27–49.
- Davidar, P., K. Yoganand, and T. Ganesh. 2001. Distribution of forest birds in the Andaman Islands: importance of key habitats. *Journal of Biogeography* 28:663–672.
- Deshaye, J., and P. Morisset. 1988. Floristic richness, area, and habitat diversity in a hemiarctic archipelago. *Journal of Biogeography* 15: 747–757.
- Diniz-Filho, J. A. F., T. F. L. V. B. Rangel, and L. M. Bini. 2008. Model selection and information theory in geographical ecology. *Global Ecology and Biogeography* 17:479–488.
- Gilbert, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography* 7:209–235.
- Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, and G. Huse. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198:115–126.
- Haila, Y., O. Järvinen, and S. Kuusela. 1983. Colonization of islands by land birds: prevalence functions in a Finnish archipelago. *Journal of Biogeography* 10:499–531.
- Hortal, J., J. M. Lobo, and A. Jiménez-Valverde. 2007. Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife (Canary Islands). *Conservation Biology* 21:853–863.
- Hortal, J., A. Jiménez-Valverde, J. F. Gómez, J. M. Lobo, and A. Baselga. 2008a. Historical bias in biodiversity inventories affects the observed realized niche of the species. *Oikos* 117:847–858.
- Hortal, J., J. Rodríguez, M. Nieto, and J. M. Lobo. 2008b. Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography* 35:1202–1214.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Jüriado, I., A. Suija, and J. Liira. 2006. Biogeographical determinants of lichen species diversity on islets in the West-Estonian Archipelago. *Journal of Vegetation Science* 17:125–134.
- Kadmon, R., and O. Allouche. 2007. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *American Naturalist* 170:443–454.
- Kadmon, R., and Y. Benjamini. 2006. Effects of productivity and disturbance on species richness: a neutral model. *American Naturalist* 167:939–946.
- Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385:252–254.
- Kohn, D. D., and D. M. Walsh. 1994. Plant species richness: the effect of island size and habitat diversity. *Journal of Ecology* 82:367–377.
- Kotiaho, J. S., V. Kaitala, A. Komonen, and J. Päävinen. 2005. Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the USA* 102: 1963–1967.
- Kotze, D. J., J. Niemelä, and M. Nieminen. 2000. Colonization success of carabid beetles on Baltic islands. *Journal of Biogeography* 27: 807–819.
- Lack, D. 1973. The numbers of species of hummingbirds in the West Indies. *Evolution* 27:326–337.
- Loeulle, N., and M. Leibold. 2008. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. *American Naturalist* 171:788–799.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *American Naturalist* 154:427–440.
- Losos, J. B., and R. E. Ricklefs. 2009a. Adaptation and diversification on islands. *Nature* 457:830–836.
- . 2009b. *The theory of island biogeography revisited*. Princeton University Press, Princeton, NJ.
- MacArthur, R. H., and E. O. Wilson. 1963. *An equilibrium theory of insular zoogeography*. *Evolution* 17:373–387.
- . 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Meiri, S., T. Dayan, and D. Simberloff. 2004. Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society* 81: 579–588.
- Meiri, S., N. Cooper, and A. Purvis. 2008. The island rule: made to be broken? *Proceedings of the Royal Society B: Biological Sciences* 275:141–148.
- Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist* 159: 420–426.
- Mouquet, N., J. L. Moore, and M. Loreau. 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecology Letters* 5:56–65.
- Mouquet, N., P. Leadley, J. Méridet, and M. Loreau. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos* 104:77–90.
- 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.
- Nilsson, S. G., J. Bengtsson, and S. Ås. 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.
- Oromí, P., E. Martín, A. García, M. Báez, N. Zurita, V. Mahner, H. Lopez, et al. 2004. Phylum Arthropoda. Pages 155–300 in I. Izquierdo, J. L. Martín, N. Zurita, and M. Arechavaleta, eds. *Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres)*. 2nd ed. Consejería de Política Territorial y Medio Ambiente, Gobierno de Canarias, La Laguna, Tenerife.
- Palmer, R. A. 1999. Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. *American Naturalist* 154:220–233.
- Peck, S. B. 2001. Smaller orders of insects of the Galápagos Islands,

- Ecuador: evolution, ecology, and diversity. NRC Research Press, Ottawa, Ontario.
- . 2006. The beetles (Insecta: Coleoptera) of the Galápagos Islands, Ecuador: evolution, ecology, and diversity. NRC Research Press, Ottawa, Ontario.
- Purvis, A., C. D. L. Orme, and K. Dolphin. 2003. Why are most species small-bodied? a phylogenetic view. Pages 155–173 in T. M. Blackburn and K. J. Gaston, eds. *Macroecology: concepts and consequences*. Blackwell Science, Oxford.
- Ralph, C. J. 1985. Habitat association patterns of forest and steppe birds of northern Patagonia, Argentina. *Condor* 87:471–483.
- Rangel, T. F. L. V. B., J. A. F. Diniz-Filho, and L. M. Bini. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography* 15:321–327.
- Reed, T. 1981. The number of breeding landbird species on British Islands. *Journal of Animal Ecology* 50:613–624.
- Ricklefs, R. E. 2007. History and diversity: explorations at the intersection of ecology and evolution. *American Naturalist* 170(suppl.):S56–S70.
- . 2008. Disintegration of the ecological community. *American Naturalist* 172:741–750.
- Ricklefs, R. E., and I. J. Lovette. 1999. The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68: 1142–1160.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M. L., W. R. Turner, J. G. Cox, and T. H. Ricketts. 2003. Estimating diversity in unsampled habitats of a biogeographical province. *Conservation Biology* 17:864–874.
- Rydin, H., and S.-O. Borgegård. 1988. Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology* 69:916–927.
- Sanders, N. J., N. J. Gotelli, S. E. Wittman, J. S. Ratchford, A. M. Ellison, and E. S. Jules. 2007. Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *Journal of Biogeography* 34:1632–1641.
- Sauer, J. D. 1969. Oceanic islands and biogeographical theory: a review. *Geographical Review* 59:582–593.
- 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.
- Sfenthourakis, S., and K. A. Triantis. 2009. Habitat diversity, ecological requirements of species, and the Small Island Effect. *Diversity and Distributions* 15:131–140.
- Sillén, B., and C. Solbreck. 1977. Effects of area and habitat diversity on bird species richness in lakes. *Ornis Scandinavica* 8:185–192.
- Starzomski, B. M., R. L. Parker, and D. S. Srivastava. 2008. On the relationship between regional and local species richness: a test of saturation theory. *Ecology* 89:1921–1930.
- StatSoft. 2003. STATISTICA (data analysis software system). Ver. 6.1. StatSoft, Tulsa, OK.
- Tews J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31:79–92.
- Triantis, K. A., M. Mylonas, K. Lika, and K. Vardinoyannis. 2003. A model for the species–area–habitat relationship. *Journal of Biogeography* 30:19–27.
- Triantis, K. A., M. Mylonas, M. D. Weiser, K. Lika, and K. Vardinoyannis. 2005. Species richness, environmental heterogeneity and area: a case study based on land snails in Skyros Archipelago (Aegean Sea, Greece). *Journal of Biogeography* 32:1727–1735.
- Triantis, K. A., K. Vardinoyannis, E. P. Tsolaki, I. Botsaris, K. Lika, and M. Mylonas. 2006. Re-approaching the small island effect. *Journal of Biogeography* 33:914–923.
- Triantis, K. A., S. Sfenthourakis, and M. Mylonas. 2008a. Biodiversity patterns of terrestrial isopods from two island groups in the Aegean Sea (Greece): species–area relationship, small island effect, and nestedness. *Ecoscience* 15:169–181.
- Triantis, K. A., M. Mylonas, and R. J. Whittaker. 2008b. Evolutionary species–area curves as revealed by single-island endemics: insights for the inter-provincial species–area relationship. *Ecography* 31: 401–407.
- Triantis, K. A., D. Nogués-Bravo, J. Hortal, P. A. V. Borges, H. Aderssen, J. M. Fernández-Palacios, M. B. Araújo, and R. J. Whittaker. 2008c. Measurements of area and the (island) species–area relationship: new directions for an old pattern. *Oikos* 117:1555–1559.
- van Valen, L. 1965. Morphological variation and width of ecological niche. *American Naturalist* 99:377–389.
- Watson, G. E. 1964. *Ecology and evolution of passerine birds on the islands of the Aegean Sea*. PhD diss. Yale University, New Haven, CT.
- Whittaker, R. J. 2009. Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. *Ecology* (forthcoming).
- Whittaker, R. J., and J. M. Fernández-Palacios. 2007. *Island biogeography: ecology, evolution, and conservation*. 2nd ed. Oxford University Press, Oxford.
- Whittaker, R. J., K. A. Triantis, and R. J. Ladle. 2008. A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* 35:977–994.
- Williams, C. B. 1964. *Patterns in the balance of nature and related problems in quantitative ecology*. Academic Press, New York.
- Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95:169–193.