Integrating the Effects of Area, Isolation, and Habitat Heterogeneity on Species Diversity: A Unification of Island Biogeography and Niche Theory

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ABSTRACT: We present an analytical model that unifies two of the most influential theories in community ecology, namely, island biogeography and niche theory. Our model captures the main elements of both theories by incorporating the combined effects of area, isolation, stochastic colonization and extinction processes, habitat heterogeneity, and niche partitioning in a unified, demographically based framework. While classical niche theory predicts a positive relationship between species richness and habitat heterogeneity, our unified model demonstrates that area limitation and dispersal limitation (the main elements of island biogeography) may create unimodal and even negative relationships between species richness and habitat heterogeneity. We attribute this finding to the fact that increasing heterogeneity increases the potential number of species that may exist in a given area (as predicted by niche theory) but simultaneously reduces the amount of suitable area available for each species and, thus, increases the likelihood of stochastic extinction. Area limitation, dispersal limitation, and low reproduction rates intensify the latter effect by increasing the likelihood of stochastic extinction. These analytical results demonstrate that the integration of island biogeography and niche theory provides new insights about the mechanisms that regulate the diversity of ecological communities and generates unexpected predictions that could not be attained from any single theory.

Keywords: colonization-extinction processes, community dynamics, demography, neutral theory of biodiversity, species-area relationship, species diversity.

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Two of the most influential theories in community ecology are the theory of island biogeography (MacArthur and Wilson 1963, 1967) and niche theory (Hutchinson 1957). Both theories attempt to explain the distribution and organization of species in ecological communities, but they differ in their consideration of the factors controlling the number of species in a community. Island biogeography theory emphasizes the role of area and geographical isolation as the basic determinants of species diversity through their effects on colonization and extinction rates (MacArthur and Wilson 1967; Brown and Kodric-Brown 1977; He et al. 2005). In contrast, niche theory emphasizes the role of habitat heterogeneity and niche partitioning as the main factors structuring ecological communities (Hutchinson 1957; MacArthur 1972; Petren 2001; Silvertown 2004). Surprisingly, although both theories have occupied a central role in community ecology for several decades (Higgs 1981; Austin 1985; Brown and Lomolino 2000; Pulliam 2000; Chase and Leibold 2003), attempts to integrate the basic elements of the two theories are extremely rare, and we are still lacking a general model that incorporates the key elements of both theories.

In this article, we attempt to fill this gap by developing a unified model that incorporates the basic elements of island biogeography and niche theory. Our main objective is to provide an initial assessment of whether and how variations in area and isolation interact with habitat heterogeneity and niche differentiation in determining patterns of species diversity. More generally, we are interested in testing whether combining the basic elements of island biogeography and niche theory in a unified model generates novel predictions that could not be derived from any single theory.

Our unified model is conceptually similar to the classical model of island biogeography (MacArthur and Wilson 1967), but it differs from the original model in two important aspects. First, instead of formulating the model in

terms of colonization and extinction processes, we employ an individual-based modeling approach in which the processes of colonization and extinction (and the resulting dynamics of species richness) are derived from fundamental processes of reproduction, mortality, and immigration. Such a demographic approach facilitates a more detailed analysis (and, thus, a better understanding) of the mechanisms regulating the number of species in a community. Second, while MacArthur and Wilson's (1967) model and its recent successors (De Blasio 1998; Bell 2000; Lomolino 2000; Hubbell 2001; Wootton 2005) ignore the potential effects of niche differentiation, we assume that individuals of different species differ from each other in their habitat requirements and explicitly incorporate habitat specialization into the model.

The article is organized in four parts. The first section provides a brief review of the main elements of each theory. In the second section, we present the unified model. In the third section, we analyze the model and derive general predictions concerning the interactive effects of area, isolation, and habitat heterogeneity on species diversity. In the fourth section, we discuss the implications of the analytical results for our understanding of the mechanisms controlling the diversity of ecological communities.

Main Elements of Island Biogeography and Niche Theory

One possible reason for the lack of a theory integrating the principles of island biogeography and niche theory is the fact that each theory relies on a conceptually different view of community structure. Niche theory represents an "equilibrial" view of ecological communities, in the sense that species composition is assumed to be constant over time (Chave et al. 2002). Such compositional equilibrium ("coexistence") requires some form of niche partitioning, that is, functional differences among species in the manner by which they affect, and are affected by, the environment (MacArthur and Levins 1967; Tilman 1982). Niche partitioning increases the strength of intraspecific competition relative to that of interspecific competition and, thus, facilitates coexistence and maintenance of species diversity (Chesson 2000; Amarasekare 2003).

In contrast to niche theory, island biogeography theory represents a "nonequilibrial" view of ecological communities in the sense that species composition is constantly changing over time (Chave et al. 2002). According to this view, species diversity in a local community reflects a dynamic balance between colonization (arrival of new species) and extinction of species already present in the community. Island biogeography theory ignores functional differences among species and, in recent formulations (De

Blasio 1998; Bell 2000; Hubbell 2001; He et al. 2005), explicitly considers all species to be ecologically equivalent.

In addition to these conceptual differences, the two theories focus on different factors as the main determinants of species diversity. Niche theory emphasizes the role of environmental heterogeneity as the main factor structuring ecological communities (MacArthur 1972; Whittaker et al. 1973; Rosenzweig 1995). In spite of a continuous confusion over the niche concept (Leibold 1995), and independently of whether the term niche is used to describe attributes of the environment (Grinnell 1917; Hutchinson 1957) or the role of the species in the environment (Elton 1927), it is widely accepted that heterogeneous environments provide more niches than relatively uniform environments and may therefore support more diverse communities.

Island biogeography theory emphasizes the roles of area and geographical isolation as the main determinants of species diversity. Based on the assumption that colonization rates are determined by the degree of geographical isolation and extinction rates are determined by the size (area) of the island, the theory predicts that species richness should be positively correlated with island size and negatively correlated with the degree of isolation (MacArthur and Wilson 1963, 1967). Later developments of the theory recognized that isolation may also influence extinction rates because islands close to the mainland are characterized by higher immigration rates than remote islands, which reduces the likelihood of stochastic extinctions (the rescue effect; Brown and Kodric-Brown 1977). It has further been suggested that the area of an island may influence the rate of colonization because large areas receive more colonizers than small areas (the passive sampling hypothesis; Connor and McCoy 1979). These extensions of the original theory still consider area and isolation as the primary determinants of species richness.

While the original theory of island biogeography focused on true islands, later developments have been applied to a wide spectrum of islandlike habitats (e.g., Harris 1984; Patterson and Atmar 1986; Fox and Fox 2000; Cook et al. 2002). Recently, Hubbell (2001) extended the original theory into a general theory of biodiversity and demonstrated that the extended theory may explain some of the most fundamental patterns of species diversity. His "local community model" is conceptually similar to the original model proposed by MacArthur and Wilson (1967), and its parameters (J, the size of the local community, and m, the probability that a new recruit would be an immigrant) reflect the roles of area and isolation, respectively. Thus, in spite of significant developments (see also Loreau and Mouquet 1999; Bell 2000; Lomolino 2000; He et al. 2005; Wootton 2005), current formulations of island biogeography theory still rely on area and isolation as the fundamental determinants of local species richness and ignore

the potential consequences of habitat heterogeneity and niche partitioning.

The model presented here differs from all previous models in that it integrates the effects of area and isolation (the main elements of island biogeography) with those of habitat heterogeneity and niche differentiation (the main elements of niche theory) within a unified demographic framework. This modeling approach allows us to test for possible interactions between the main elements of the two theories and to link the observed interactions to their underlying demographic mechanisms.

The Unified Model

Our model describes the dynamics of a local (island) community that receives immigrants from a regional species pool on the mainland. As in previous studies of island biogeography, species composition of the modeled community is constantly changing over time as a consequence of stochastic extinction and immigration events. All species in the community are trophically similar, and the only possible interaction among species is competition for space.

The Regional Species Pool

Following Hubbell (2001), we assume that the regional species pool is evolved by neutral processes of speciation, extinction, and random drift (Hubbell 2001). In contrast to Hubbell (2001), however, we assume that these processes take place in a heterogeneous world that contains a large number of habitats, each supporting a different (nonoverlapping) set of species. The distribution of species abundances in each habitat in the regional species pool is given by a log series, $\Omega(x) = \theta(1 - x)^{\theta-1}/x$, where θ is the biodiversity number (Ewens 1972; Hubbell 2001; Vallade and Houchmandzadeh 2003; Alonso and McKane 2004). All habitats are assumed to be equivalent in terms of their biodiversity number, and the actual distribution of species abundances for a given θ is generated using Ewens's sampling formula (Ewens 1972; Hubbell 2001).

Several previous models of mainland-island systems have assumed, implicitly (e.g., MacArthur and Wilson 1967) or explicitly (e.g., Bell 2000), a uniform distribution of species abundances on the mainland. We therefore analyzed also models assuming uniform distribution of species abundances in the regional species pool. These analyses made our results directly comparable to a wider spectrum of previous models and enabled us to evaluate the robustness of our results to different assumptions concerning the distribution of species abundance in the source communities. A uniform distribution of species abundances can also be interpreted as a representation of an extremely diverse community.

The Local (Island) Community

The island is modeled as a spatially implicit heterogeneous landscape consisting of A sites, where each site can be occupied by one individual at most. Each site is conceptualized as having a unit area, so that A also indicates the total area of the island. Habitat heterogeneity is introduced by assigning each site to one of H different types of habitats. These habitats represent a sample of the habitats available on the mainland. In order to ensure that all species are ecologically equivalent (i.e., no species has an advantage on other species), we assume that each habitat has exactly the same area. Thus, each habitat is represented by A/H sites, which sets an upper limit to the size of the habitat community. Niche differentiation is introduced by the assumption that each species is able to establish and persist in only one type of habitat. Individuals arriving in unsuitable habitats (either locally produced offspring from other habitats or immigrants from the regional species pool) are unable to establish, and they die without occupying the site in which they arrive.

The community is neutral in the sense that individuals of all species have the same birth, death, and immigration rates in their suitable habitats. Each individual dies at rate e and gives birth to one offspring at rate c. A newly produced offspring is immediately dispersed into a random site within the island. Immigration of suitable individuals from the regional species pool to each site on the island occurs at a rate i, which reflects the degree of geographic isolation because all individuals are assumed to have the same dispersal ability. The individuals compete for space because dispersed offspring and immigrants can establish only in suitable vacant sites. The overall dynamics of the island community is modeled as a continuous-time Markov process where within a short enough time interval only a single event (reproduction, mortality, or immigration) may occur. Note that in contrast to Hubbell's model, where the size of the community is unrealistically assumed to be constant, in our model the size of the community is determined by the same demographic processes that determine the abundance of individual species. The main objective of our analysis is to evaluate the combined effects of area (A, the total number of sites on the island), isolation (as expressed by i, the immigration rate), and habitat heterogeneity (H, number of habitats on the island), on the steady state number of species in the local community.

Calculation of Species Richness

In the appendix in the online edition of the *American Naturalist*, we provide a detailed description of the procedure by which we determine the steady state number of

species in the local community. Here we only briefly present the main steps of the derivation method.

The expected number of species in a given (single) habitat is calculated in three steps. First, we calculate the steady state distribution of the size of the habitat community $p(J)$, where $J = 0, 1, \ldots, A/H$, using an adaptation of the method described by McKane et al. (2000, 2004). This method was originally developed as an analytic solution for the distribution of species abundances in Hubbell's neutral model, but it can also be applied to calculate the size distribution of a community if all species in the community have the same demographic rate. Such an adaptation requires a definition of the transition rates of community size from J to $J + 1$ and from J to $J - 1$ individuals. In our model, an increase in community size can be caused by local reproduction or immigration, while a decrease is caused by mortality. The transition rates can therefore be derived from the demographic parameters as

$$b_J = \frac{c}{A} J \left(\frac{A}{H} - J \right) + i \left(\frac{A}{H} - J \right),$$
$$d_J = eJ, \tag{1}$$

where J is the size of the habitat community; b_J and d_J are the rates of transitions from J to $J + 1$ and from J to $J - 1$ individuals, respectively; c, e, and i are the rates of reproduction, mortality, and immigration, respectively; A is the total number of sites; and H is the number of habitats on the island. This formulation assumes that all habitats have the same area (A/H) and that the species pool of each habitat has a different, nonoverlapping set of species with the same abundance distribution.

In the second step, we calculate the distribution of species abundances under each possible community size J, using the analytical solution of Hubbell's local community model (McKane et al. 2004). For a given distribution of habitat-specific abundances in the regional species pool, this procedure requires only two parameters: J, the size of the habitat community, and m, the probability that an individual that dies in the community will be replaced by an immigrant from the regional species pool (Hubbell 2001; McKane et al. 2004). In our model, the parameter m is derived from the demographic parameters as

$$m = \frac{i}{i + c[(J - 1)/A]}. \tag{2}$$

While our model does not assume any coupling between reproduction and mortality, values of species richness obtained from this analytical procedure show an almost perfect fit to those generated by model simulations (fig. A1 in the online edition of the *American Naturalist*). Our

analytical derivation also applies for a broader definition of neutrality, where species differ from each other in their per capita demographic rates but the overall fitness is kept constant by introducing a trade-off between reproduction and mortality (fig. A1, *bottom*).

In the third step, we integrate the abundance distribution of each species at each community size according to the steady state distribution of community size. This integration gives the probability for each species of being present in the habitat community. By summing these probabilities, we obtain the expected number of species in a given habitat. Since all habitats are assumed to be equivalent and there is no overlap in species composition between habitats, species richness of the local community is determined by multiplying the expected number of species in a single habitat by the number of habitats on the island.

Model Analysis

Figure 1 shows the combined effects of area, habitat heterogeneity, immigration rate, and reproductive rate on species richness, assuming a species pool with uniform distribution of species abundances. This version of the model can be considered a demographic representation of MacArthur and Wilson's (1967) assumption that all species are identical in their colonization probabilities. As predicted by MacArthur and Wilson's model, species richness always increases with area and decreases with geographical isolation (decreasing immigration rate in our model). At very large areas, the species-area curve may approach its asymptotic level, which is equal to the number of potential species in the regional species pool. Increasing immigration rate flattens the species-area curve and shifts the point at which the species-area curve approaches its asymptotic level into smaller areas (fig. 1). These results imply that communities inhabiting small islands are more sensitive to isolation than communities inhabiting large areas and that the relative importance of immigration in maintaining species diversity increases with decreasing island size. Similarly, an increase in the immigration rate reduces the sensitivity of species richness to changes in island size. All these patterns and interactions are consistent with the predictions of MacArthur and Wilson's (1967) model.

While the general effects of area, isolation, and their interaction are consistent with those predicted by island biogeography theory (MacArthur and Wilson 1967; Hubbell 2001), our model provides further predictions that cannot be obtained from existing models. One nonintuitive prediction concerns the role of habitat heterogeneity as a determinant of species richness. In contrast to niche theory, which predicts a positive correlation between species richness and habitat heterogeneity, our model shows that an increase in habitat heterogeneity may have positive,
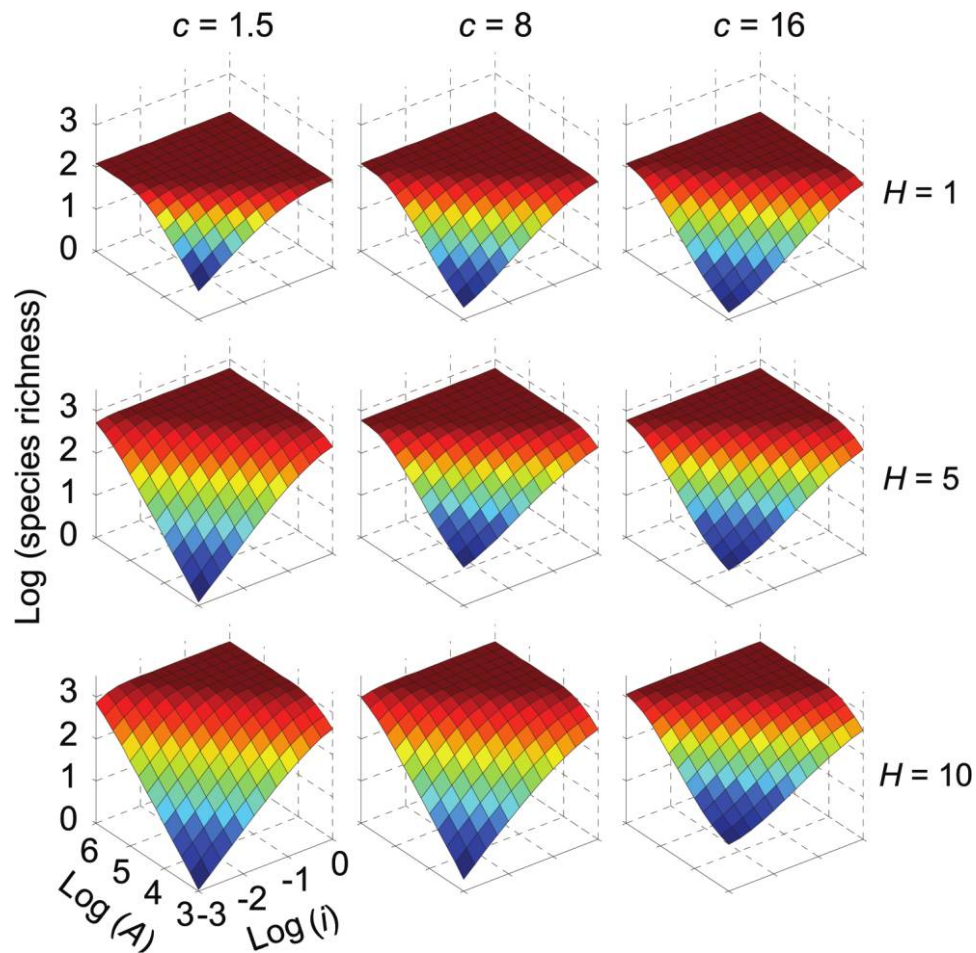
Figure 1: Effects of area (*A*) and immigration (*i*) on species richness under different levels of reproduction (*c*) and habitat heterogeneity (*H*). Results shown are for a model assuming regional species pool with a uniform distribution of 122 species in each habitat. Note the log scale of all variables.

negative, or nonmonotonic effects on species richness (figs. 1, 2). When both the area and the immigration rate are relatively low (e.g., *A* = 1,000 and *i* = 0.001 in figs. 1, 2), increasing habitat heterogeneity has a negative effect on species richness at relatively low reproductive rates, a unimodal effect at intermediate reproductive rates, and a positive effect at very high reproductive rates (figs. 1, 2). Increasing reproductive rate shifts the level of heterogeneity that maximizes species richness from relatively low to higher values of habitat heterogeneity (fig. 2). Some parameter combinations show even more complex relationships between habitat heterogeneity and species richness, such as local maximum followed by a local minimum and then a further increase in species richness (not shown). Only when both the area of the island and the immigration rates are very high does habitat heterogeneity show a consistent positive effect on species richness, as predicted by niche theory.

Another interesting prediction of our model concerns the response of species richness to variation in the reproductive rate and its interaction with island size, isolation, and heterogeneity. When both the area of the island and the immigration rate are very large, species richness attains its asymptotic level and is therefore not influenced by changes in the reproductive rate (figs. 1, 2). At lower levels of area and/or immigration rate, the predicted relationship between species richness and the reproductive rate is unimodal, and the level of reproductive rate that maximizes species richness increases with increasing habitat heterogeneity (figs. 1, 2). In the extreme case of a uniform environment (*H* = 1), species richness decreases with increasing reproductive rate over most levels of area and
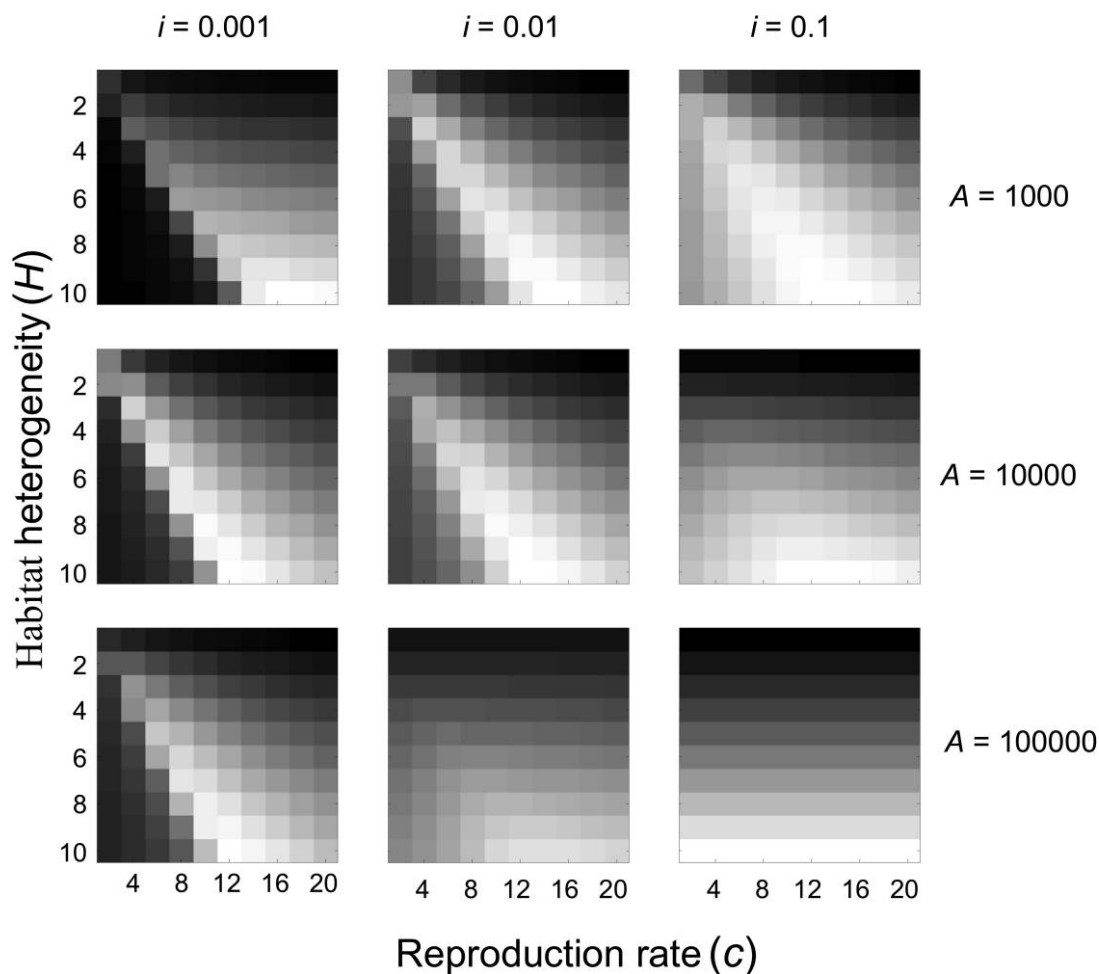
Figure 2: Effects of reproduction rate (*c*) and habitat heterogeneity (*H*) on species richness under different levels of immigration (*i*) and area (*A*). The scaling of species richness (expressed in levels of gray) is standardized according to the minimum and maximum values in each plot, to better visualize the response of species richness to variation in reproductive rate and habitat heterogeneity. Results shown are for a model assuming regional species pool with a uniform distribution of 122 species in each habitat.

immigration rate (fig. 2). These results indicate that factors affecting reproductive rates, such as resource availability and productivity, may have contrasting effects on species richness, depending on the area, isolation, and heterogeneity of the relevant landscape.

Assuming a log-series distribution of species abundances in the regional species pool (as in Hubbell's [2001] model) does not change any of the qualitative predictions of our model (figs. 3, 4). The effects of area and immigration rate on species richness are always positive, but the two factors interact with each other such that immigration has a stronger effect on species richness in relatively small areas and area has a stronger effect on species richness under relatively low immigration rates (fig. 3). As a result, increasing immigration rate flattens the species-area curve (fig. 3). The patterns obtained for the effects of

habitat heterogeneity and reproductive rate, as well as the manner by which the two factors interact with each other and with area and immigration rate, are also qualitatively similar to those obtained for a uniform distribution of species abundances (cf. figs. 2, 4). While the qualitative effects of all factors are similar in the two versions of the model, the absolute levels of species richness obtained for a uniform distribution of species abundances are always higher than those obtained for a log-series distribution, and consequently, species richness attains its asymptotic levels at lower values of area and immigration rate (cf. figs. 1, 3).

A further analysis of the model indicated that increasing mortality always reduces the steady state number of species in the community. This qualitative pattern was independent of area, habitat heterogeneity, reproduction, or im-
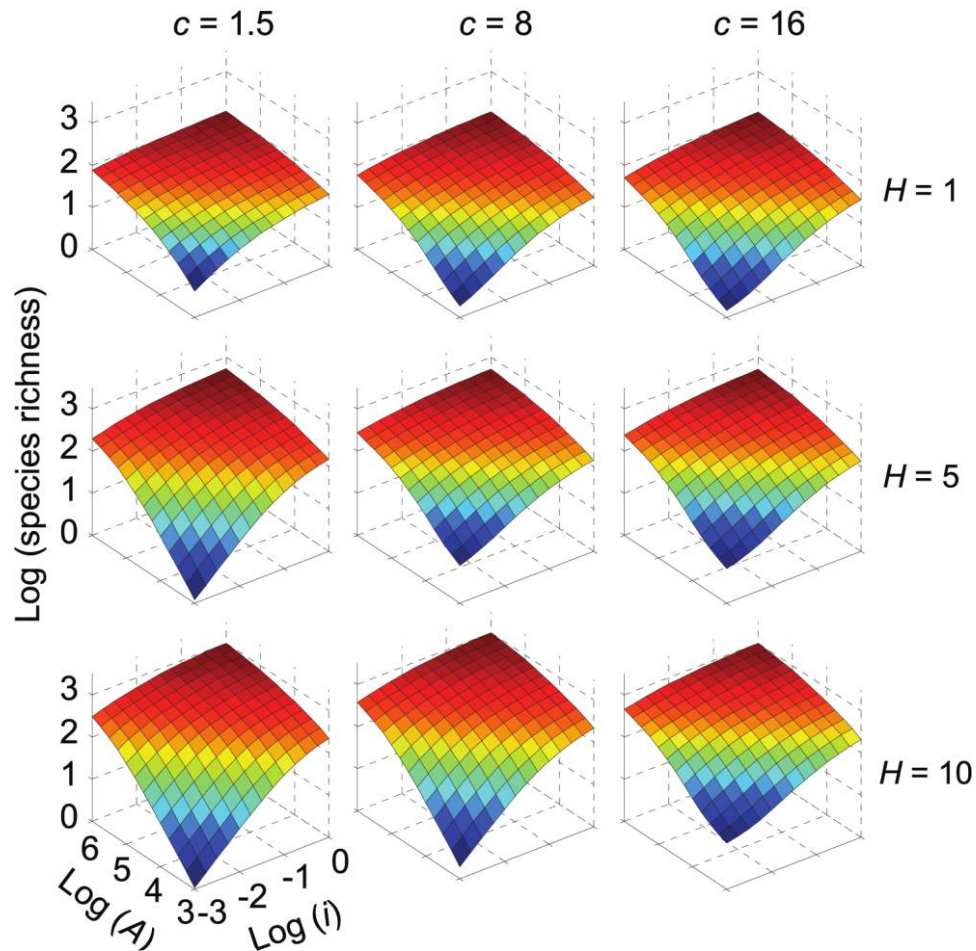
Figure 3: Effects of area (*A*) and immigration (*i*) on species richness under different levels of reproduction rate (*c*) and habitat heterogeneity (*H*). Results shown are for a model assuming regional species pool with a log-series distribution of 122 species in each habitat, generated by the Ewens sampling formula using community size of 1,000,000 individuals and a biodiversity number of 10. Note the log scale of all variables.

migration rates. In those cases where the levels of area and immigration produced hump-shaped relationships between habitat heterogeneity and species richness, increasing mortality shifted the peak of the response to lower levels of heterogeneity (fig. 5).

Discussion

The model presented in this study integrates the effects of area, isolation, demographic stochasticity, habitat heterogeneity, and niche partitioning in a unified framework that is based on fundamental demographic processes and is tractable for analytical analysis. By doing so, the model captures the main elements of island biogeography theory and niche theory and allows testing for possible interactions between the basic elements of the two theories.

The qualitative patterns obtained for the effects of area

and immigration on species richness (figs. 1, 3) are consistent with those predicted by island biogeography theory (MacArthur and Wilson 1967). The observed interactions between the effects of area and immigration are also fully consistent with the predictions of island biogeography theory. Thus, incorporating habitat heterogeneity and niche partitioning in our demographic formulation of island biogeography theory does not change the qualitative predictions of MacArthur and Wilson's (1967) model or any of its successors (Bell 2000; Hubbell 2001; He et al. 2005).

In contrast, the patterns obtained for the effect of habitat heterogeneity on species richness are more complicated than those predicted by existing theories. While niche theory predicts a monotonic positive effect of habitat heterogeneity on species richness, our model demonstrates that habitat heterogeneity may have monotonic positive, monotonic negative, or nonmonotonic effects on species
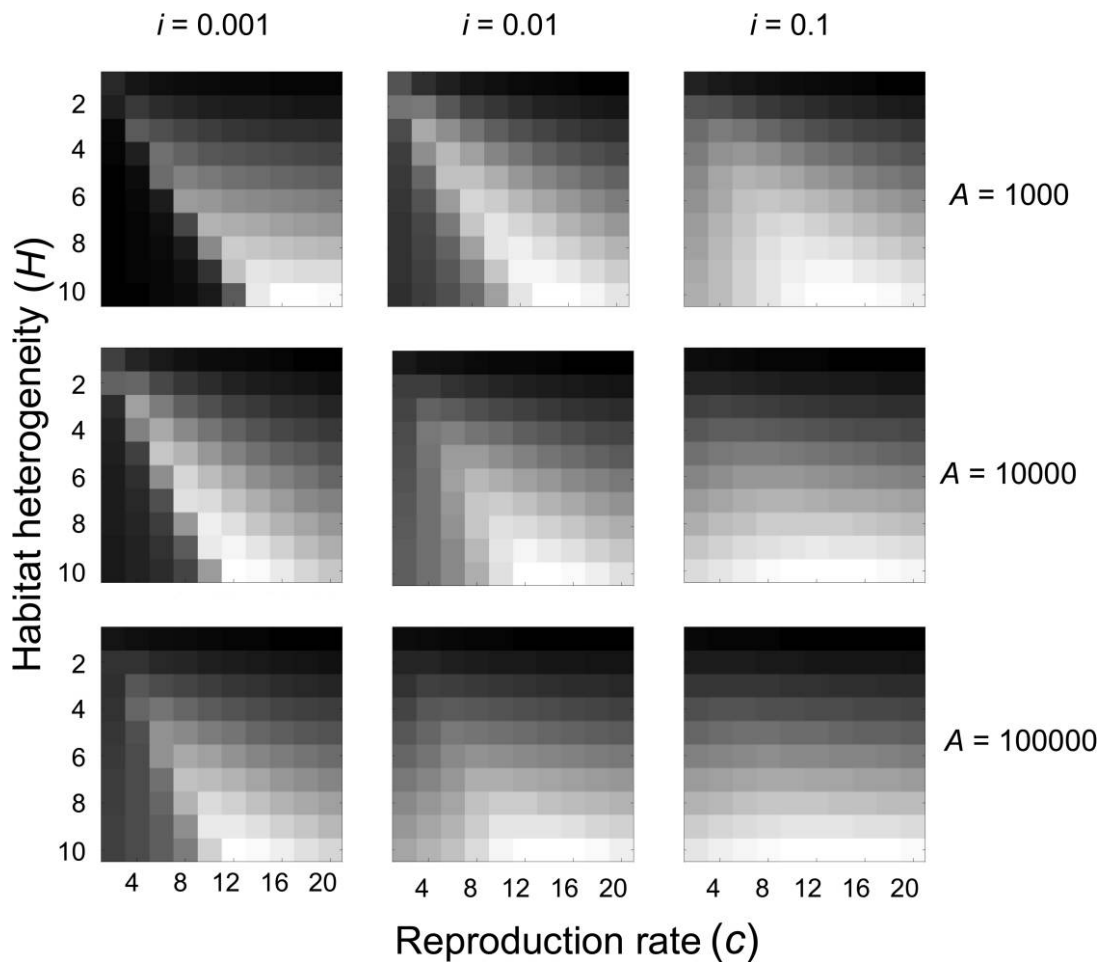
Figure 4: Effects of reproduction rate (*c*) and habitat heterogeneity (*H*) on species richness under different levels of immigration (*i*) and area (*A*). The scaling of species richness (expressed in levels of gray) is standardized according to the minimum and maximum values in each plot, to better visualize the response of species richness to variation in reproductive rate and habitat heterogeneity. Results shown are for a model assuming regional species pool with lognormal distribution of 122 species in each habitat, generated by the Ewens sampling formula using community size of 1,000,000 individuals and a biodiversity number of 10.

richness (figs. 2, 4). This finding indicates that the mechanisms by which habitat heterogeneity affects the diversity of ecological communities are more complex than has usually been assumed, based on niche theory.

We attribute the contrasting effects of habitat heterogeneity on species richness to the fact that an increase in habitat heterogeneity has two opposite effects on species richness. On the one hand, increasing heterogeneity increases the potential number of species that may exist in a given area by providing suitable conditions to a larger number of species. On the other hand, an increase in habitat heterogeneity reduces the amount of suitable area available for each species and, thus, increases the likelihood of stochastic extinction. These contrasting mechanisms may result in unimodal relationship between species rich-

ness and habitat heterogeneity. Increasing reproduction rate reduces the likelihood of stochastic extinction and, therefore, shifts the threshold at which the positive effect of heterogeneity turns into a negative one to higher levels of heterogeneity (figs. 2, 4). Only when both the island size and the immigration rates are very high, the likelihood of stochastic extinction is reduced to such levels that the net effect of habitat heterogeneity on species richness becomes positive independent of the reproductive rate (figs. 2, 4). These results indicate that the effect of habitat heterogeneity on species richness of islands or islandlike habitats cannot be fully understood without taking into consideration the effects of area, dispersal, and reproduction rates.
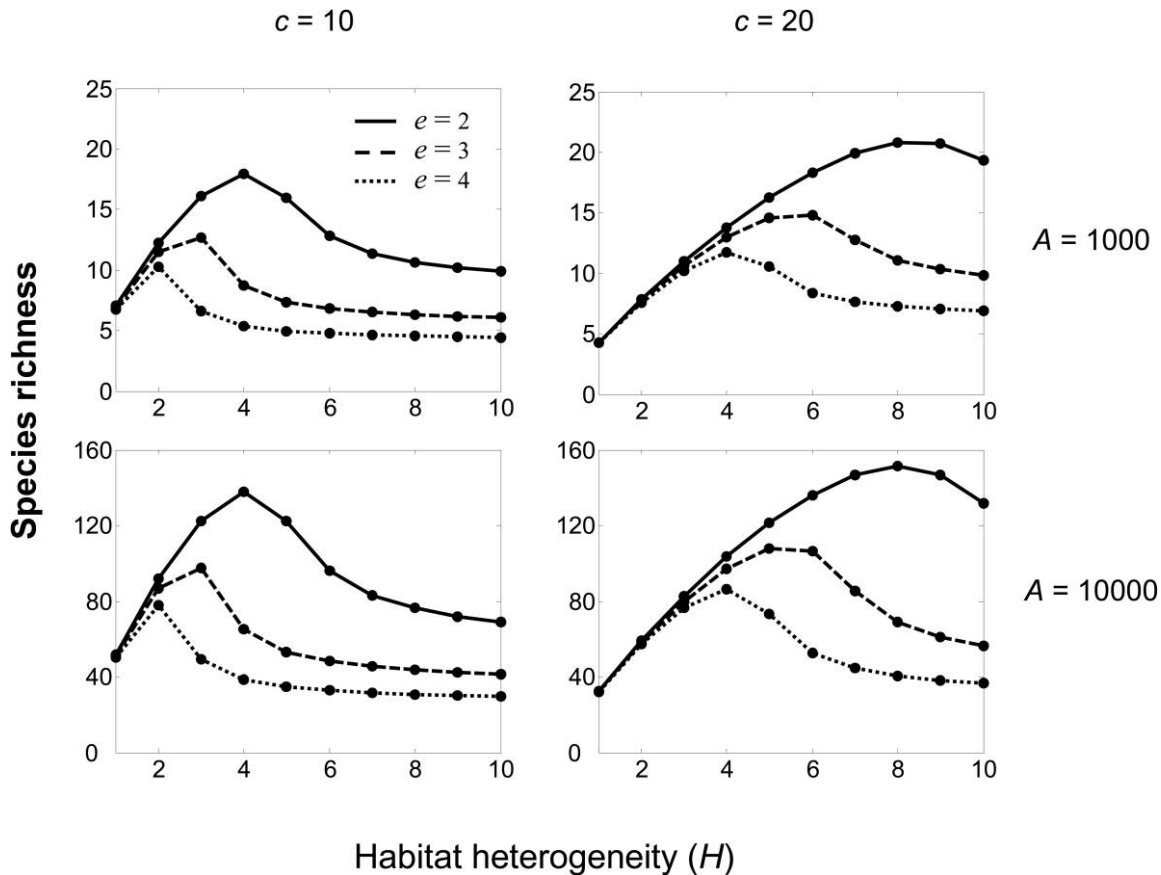
The negative component of the effect of habitat het-

Figure 5: Effect of mortality rate (e) and habitat heterogeneity (H) on species richness under different levels of reproduction (c) and area (A). Results shown are for a model assuming regional species pool with a uniform distribution of 122 species in each habitat.

erogeneity on species richness reflects the combined effects of two distinct mechanisms. The first mechanism is the increase in the likelihood of stochastic extinction caused by reducing the absolute area available for each species. The second mechanism is the increase in the likelihood of stochastic extinction caused by a greater loss of propagules from suitable to unsuitable habitats. Both mechanisms have been discussed with respect to habitat fragmentation (e.g., Andren 1994; Bevers and Flather 1999; Flather and Bevers 2002; Sole et al. 2004). However, while most previous studies have focused on the consequences of fragmentation in the framework of a uniform habitat, our model extends these ideas into a multihabitat framework and shows that the same mechanisms may cause a decrease in species richness with increasing habitat heterogeneity. Although the definition of habitat heterogeneity in our model is very simple (the number of habitats in the relevant system), this conclusion is expected to be general and to apply for any factor that increases the spec-

trum of environmental conditions within an area of a fixed size.

Our analytical results further demonstrate that an increase in the reproductive success may lead to a decrease in species richness (figs. 2, 4). This counterintuitive result supports previous findings based on numerical simulations (Kadmon and Benjamini 2006) and can be attributed to the fact that higher reproduction in the local community reduces the ratio of immigrants to locally produced individuals in the pool of potential colonizers. Since only new immigrants have the potential to increase local species richness, the result is a decrease in the steady state number of species. This mechanism was termed the "dilution effect" (Kadmon and Benjamini 2006) because the increase in the number of locally produced individuals dilutes the concentration of new immigrants in the pool of potential colonizers and therefore decreases the likelihood that new species will be added to the community following stochastic extinctions. The dilution effect is more common

at relatively high reproductive rates (figs. 2, 4) because such conditions are associated with more intense competition for vacant sites. It should be noted, however, that the dilution effect is not expected to occur if immigrants are characterized by stronger competitive ability than locally produced individuals (as is often the case with invading species).

Thus, increasing reproduction affects the number of species in a local community by two contrasting mechanisms: it increases species richness by decreasing the likelihood of stochastic extinction but decreases species richness by the dilution effect. The first mechanism dominates at relatively low levels of reproduction (when competition for vacant sites is not very strong), and the second mechanism dominates at relatively high levels of reproduction (which facilitate intense competition between local offspring and new immigrants). As a result of these contrasting effects, species richness shows a hump-shaped response to variation in the reproductive rate (figs. 2, 4). An increase in habitat heterogeneity counterbalances the dilution effect and, consequently, shifts the peak of the response to higher reproductive rates (figs. 2, 4).

Our finding that variation in reproduction has contrasting effects on species richness provides a possible explanation for the commonly observed hump-shaped relationship between species richness and productivity (Grime 1973; Rosenzweig and Abramsky 1993; Kassen et al. 2000). The fact that reproduction may have positive, negative, or unimodal effects on species richness is also consistent with empirically observed relationships between species richness and productivity (Waide et al. 1999; Mittelbach et al. 2001). According to our model, such variation in productivity-diversity patterns may reflect underlying variation in the degree of habitat heterogeneity.

Another expression for the interaction between the effects of area, habitat heterogeneity, and reproduction rate is the dependence of the slope of the species-area curve on the levels of habitat heterogeneity and reproduction. At a relatively low reproductive rate, increasing heterogeneity increases the slope of the species-area curve by facilitating species richness of relatively large areas and decreasing species richness of relatively small areas (figs. 1, 3). Increasing reproductive rate has a small effect on species richness when it is already at, or close to, its asymptotic level (figs. 1, 3), while its effect on species richness of small areas depends on the level of habitat heterogeneity; it increases the number of species when habitat heterogeneity is high and reduces the number of species in a uniform environment (figs. 2, 4). As a result of this interaction, habitat heterogeneity may facilitate or flatten the slope of the species-area curve, depending on the re-

productive rates of the species in the community (figs. 1, 3).

Our results are highly relevant for the current debate over the relative importance of niche-based versus neutral theories of species diversity (Whitfield 2002; Chase 2005; Hubbell 2005; Gravel et al. 2006). While several recent studies have integrated elements of both types of theories in a unified model (Mouquet and Loreau 2002, 2003; Tilman 2004; Bell 2005; Schwilk and Ackerly 2005; Gravel et al. 2006), all of these studies focus on the relative importance of niche-based versus dispersal processes and ignore the potential consequences of stochasticity caused by increasing habitat diversity. As shown in this study, ignoring this source of stochasticity may lead to misleading conclusions about the manner in which habitat heterogeneity and niche partitioning affect the number of species in a community. Furthermore, our results demonstrate that the degree to which species richness is limited by dispersal from the regional species pool strongly depends on the area of the island (figs. 1, 3). This finding indicates that area is a crucial determinant of the relative importance of regional versus local effects on species diversity, a conclusion consistent with previous results based on a colonization-extinction model (He et al. 2005). Variation in area also affects the sensitivity of species richness to variation in habitat heterogeneity and may even turn the effect of habitat heterogeneity from positive to negative (figs. 2, 4). These results demonstrate that any theory attempting to reconcile the debate over "neutrality versus the niche" (Whitfield 2002) should take into account the potential effects of area limitation.

It should be emphasized that the mechanisms causing the reduction in species richness with increasing habitat heterogeneity in our model are not limited to neutral communities. As a result, negative, unimodal, or even more complex effects of habitat heterogeneity on species richness are obtained also when some of our restrictive assumptions are relaxed (e.g., species are allowed to partially overlap in their among-habitat distributions). Yet, empirical evidence for nonpositive relationships between habitat heterogeneity and species richness is rather limited (Tews et al. 2004). One reason for this might be that actual demographic rates in natural communities are usually at the levels where the relationship between species richness and habitat heterogeneity is positive. Another possible explanation is the well-known bias toward the publication of positive results and the ignoring of results that contrast with mainstream paradigms. A typical example is Currie's (1991) analysis of large-scale patterns of diversity in North America. Although this article is often cited as evidence for the positive effect of habitat diversity (expressed by tree species diversity) on animal species richness, only one of the four groups of animals examined in this study (am-

phibians) showed a clear positive relationship with tree species diversity (fig. 4 in the original article). Two other groups (birds and mammals) showed patterns more consistent with a hump-shaped response, but these groups were argued to be "not functionally related to tree richness in any simple fashion" (Currie 1991, p. 31). At a smaller scale, Ralph (1985, p. 481) found a clear evidence for hump-shaped response of birds to vegetation diversity in northern Patagonia, but since the observed pattern contradicted his prediction, he considered it "paradoxical" and claimed that "the explanation of this paradoxical situation lies in the specific habitat relationships of each of the bird species to each plant species." Our results suggest that such hump-shaped patterns may reflect general principles rather than individualistic responses.

Conclusions

The model presented in this study combines the main elements of island biogeography and niche theory but nevertheless retains the concept of neutrality in the sense that all species and all habitats are ecologically equivalent and no species has an advantage on other species in the community. Thus, our model should be best interpreted as a neutral (null) model for the combined effects of area, isolation, and habitat heterogeneity on species richness. As such, it provides a starting point for more complex models that will incorporate the effects of area, isolation, and habitat heterogeneity on species richness, as well as a reference line for a better interpretation of empirical data.

However, the contribution of our model is beyond being a neutral "reference" for more complex models or empirically documented patterns. By integrating the main elements of island biogeography and niche theory, the model provides novel predictions that could not be obtained from any single theory. Examples for such predictions are the possible negative and unimodal effects of habitat heterogeneity on species richness, the interaction between the effects of habitat heterogeneity and the rates of reproduction and immigration in determining species richness, and the scale-dependent relationship between heterogeneity and species richness. These theoretical findings provide new insights into the mechanisms that regulate the diversity of ecological communities and call for a critical reevaluation of the numerous published data on the relationships between area, habitat heterogeneity, and species diversity.

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