
Predicting local–regional richness relationships using island biogeography models

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Local species richness frequently is linearly related to the richness of the regional species pool from which the local community was presumably assembled. What, if anything, does this pattern imply about the relative importance of species interactions and dispersal as determinants of local species richness? Two recent papers by Hugueny and Cornell and He et al. propose that the classical island biogeography model of MacArthur and Wilson can help answer this question, by serving as a null model of the relationship between local (island) and regional (mainland) species richness in the absence of local species interactions. The two models make very different predictions, despite being derived from apparently-similar assumptions. Here we reinterpret these two models and show that their contrasting predictions can be regarded as arising from different, implicit assumptions about how species abundances vary with species richness on the mainland. We derive a more general island biogeography model of local–regional richness relationships that explicitly incorporates mainland species abundance and subsumes the two previous models as limiting cases. The new model predicts that the local–regional richness relationship can range from nearly linear to strongly curvilinear, depending on how species abundances on the mainland vary with mainland richness, as well as on rates of immigration to and extinction from islands. Local species interactions are not necessary for producing curvilinear local–regional richness relationships. We discuss the implications of our new model for the interpretation of local–regional richness relationships.

pattern has attracted considerable interest because of the possibility of inferring from the pattern itself the underlying dynamical processes that generated it (the inverse problem, Nelson et al. 2004). Early verbal models, and heuristic interpretations of the mathematical models of Caswell (1975), suggested that linear local–regional richness relationships occur when local species interactions are too weak to limit local community membership, so that local species richness primarily reflects immigration from the regional species pool (Cornell and Lawton 1992). Other verbal models, and some mathematical theory (Case 1990, 1991), suggested that local richness should be a saturating function of regional richness when species interactions like competition are sufficiently strong to prevent further immigration once the local community is sufficiently species-rich to “fill” the local “niche space.” These models suggest that “saturation” in the mathematical sense of a local–regional richness relationship that approaches an upper asymptote arises from “saturation” in the ecological sense of high niche occupancy.

Explaining general patterns in the distribution and abundance of species is one of the most basic tests of the adequacy of ecological understanding (Brown 1995, Lawton 1999). One general pattern in ecology is the frequently-observed linear relationship between the species richness of local communities, and the richness of the regional species pools from which those local communities were presumably assembled (Ricklefs 1987, Srivastava 1999, Hillebrand and Blenckner 2002). This

However, local species interactions and dispersal, along with other processes, presumably co-determine local–regional richness relationships, and verbal models are inadequate to quantify the relative importance of these processes. Recent authors have developed mathematical null models of the local–regional richness relationship in the absence of species interactions (Caley and Schluter 1997, Hugueny and Cornell 2000, Schoolmaster Jr. 2001, Kiflawi et al. 2003, He et al. 2005). The hope is that these null models can be fit to observed data

Accepted 9 January 2006
Subject Editor: Michael Bonsall

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ISSN 0030-1299

(Kiflawi et al. 2003), or be parameterized from independent data (Hugueny and Cornell 2000), thereby removing the influence of processes other than species interactions on the local–regional richness relationship. However, there is currently no agreement on the form of the appropriate null model, with different authors deriving different models from apparently similar assumptions (e.g. compare Hugueny and Cornell 2000 with He et al. 2005). Here we show that different authors can be interpreted as having made different, implicit assumptions in the derivations of their null models. We derive a new, more general null model of local–regional richness relationships that subsumes previous models as special cases. We discuss the implications of this new model for the interpretation of local–regional richness relationships.

Island biogeography models of local–regional richness relationships

The simplest way to model the local–regional richness relationship is to treat the regional species pool as external to the local communities within the region (although in many situations a metacommunity model with an internal species pool may be more realistic; Leibold et al. 2004). The classic MacArthur–Wilson island biogeography model (MacArthur and Wilson 1963) describes how local (island) species richness depends on the rate at which new species colonize from an external regional species pool (the mainland), and the rate at which previous colonists go extinct. By assuming that different mainlands (regions) vary only in the richness of their species pools, we can examine how island richness varies with mainland richness, thereby converting the classic island biogeography model into a model of local–regional richness relationships. However, as we show below, it is impossible for mainland regions to vary in species richness while remaining identical in all other respects, in particular the total abundance of the species comprising the regions. This crucial fact has not previously been recognized. The implication is that there is no single island biogeography model of local–regional richness relationships. Different island biogeography models make different assumptions about how regions vary with respect to factors other than regional richness, and thereby make different predictions about the form of the local–regional richness relationship (Hugueny and Cornell 2000, He et al. 2005).

Three recent papers describe analytical versions of such island biogeography models (Hugueny and Cornell 2000, Kiflawi et al. 2003, He et al. 2005), while two recent papers describe simulation versions (Caley and Schluter 1997, Schoolmaster Jr. 2001). We focus on the analytical models of Hugueny and Cornell (2000);

hereafter HC) and He et al. (2005); hereafter HGCS), since the model of Kiflawi et al. (2003) is a simple extension of the HC model, and the models of Caley and Schluter (1997) and Schoolmaster Jr. (2001) are identical in their essentials to the HGCS model. To fix notation, and to make our discussion concrete, we first briefly introduce the HC and HGCS models.

HC define c_i as the probability per unit time that species i colonizes an island, e_i as the probability per unit time that species i goes extinct from an island, and S_L as island (local) species richness. HC implicitly assume a discrete time framework. In a continuous time framework, c_i and e_i respectively give the instantaneous colonization and extinction rates of species i . Below we work in a continuous time framework for the sake of consistency between the HC and HGCS models, but our conclusions are independent of this arbitrary choice. HC state that, if all species are identical (so that $c_i=c$ and $e_i=e$ for all i), if species do not interact, if all islands are identical except in that they receive colonists from different mainlands (regional species pools), and if islands are independent of one another (e.g. no island-to-island dispersal), then c and e will be independent of mainland (regional) richness S_R . If c and e are independent of S_R , the rate I at which new species immigrate to an island, and the rate E at which species go extinct from an island, are respectively given by

$$I = cS_R \left(1 - \frac{S_L}{S_R}\right) \quad (1a)$$

$$E = eS_L \quad (1b)$$

Equation (1a) says that the rate I at which new species immigrate equals the per-species colonization rate c , multiplied by regional species richness S_R , multiplied by the probability $1 - S_L/S_R$ that a colonizing species is not already present on the island. Setting Eq. (1a) equal to Eq. (1b) and solving allows us to determine the equilibrium value of S_L :

$$S_L = \frac{c}{c + e} S_R = pS_R \quad (2)$$

Equation 2 states that, at equilibrium, local (island) species richness S_L is linearly related to regional (mainland) species richness S_R , with slope p . The slope $p = c/(c+e)$ is the probability that a given species from the regional pool is present at any instant in time on an island receiving colonists from that pool, and takes on a value between 0 and 1.

HGCS incorporate into their derivation the effect of island area on colonization rate. While area (scale) is an important aspect of the local–regional relationship, in order to make the HGCS model comparable with the HC model, we will not consider island area. Assuming, like HC, that all species are identical and do not interact,

and that islands are independent of one another, HGCS state that the rate I at which new species arrive on an island is given by

$$I = I_0 \left(1 - \frac{S_L}{S_R} \right) \quad (3)$$

where I_0 is the maximum rate at which new species arrive (i.e. the rate at which new species arrive at an empty island). HGCS assume that the rate at which species go extinct from an island is given by

$$E = E_0 S_L \quad (4)$$

where E_0 is the per-species rate of extinction (denoted by e in Eq. 1b). Setting $I = E$ and solving for S_L gives

$$S_L = \frac{S_R}{1 + \delta S_R} \quad (5)$$

where $\delta = E_0/I_0$. Equation 5 states that, at equilibrium, S_L is a curvilinear (saturating) function of S_R , although the degree of deviation from linearity depends on the value of δ , and is small when δ is small. This prediction contrasts with the linear relationship predicted by the HC model.

Given the fact that both models are based on island biogeography, it is important to explore the differences and connections between them. Next we develop an alternative interpretation for the models that bridges the gap between them. Our alternative interpretation also is based on island biogeography, but goes one step further to explicitly incorporate species abundance into the theory. Our alternative interpretation of the HC and HGCS models is that they make contrasting, implicit assumptions about species abundance.

Before making explicit the contrasting, implicit assumptions of HC and HGCS, we first clarify a technical point about the derivation of HGCS. HGCS state that “ I_0 and E_0 are related to the per-species immigration and extinction rates” (HGCS, p. 362). This statement is inaccurate. E_0 is the per-species extinction rate, not related to it, and so has units 1/time. I_0 is the total (not per-species) rate at which new species arrive on an empty island, and has units of species/time. The ratio $\delta = E_0/I_0$ therefore has units (1/time)/(species/time) = 1/species, making it somewhat difficult to interpret. To obtain a more easily-interpretable version of Eq. (3) note that I_0 in Eq. (3) can be interpreted as the total rate per unit time at which species (new or otherwise) arrive on an island (empty or not). On the interpretation of I_0 as the total rate per unit time at which species arrive on an island, $1 - S_L/S_R$ gives the (unitless) probability that an arriving species represents a new species. Now note that the total rate at which species arrive will be equal to (or more generally, proportional to) the rate at which dispersing propagules of all species arrive at an island. We can thus express I_0 as the product of regional richness S_R and per-species rate of propagule production

i_0 (assumed to be the same for all species within a region). It will be clear shortly that i_0 is an inverse function of S_R in the model of HGCS. We can now rewrite Eq. (5) as

$$S_L = \frac{S_R}{1 + \frac{e}{i_0 S_R} S_R} \quad (6)$$

where we have substituted e for E_0 for consistency with the HC model.

Thinking of I_0 as the product of mainland species richness and the per-species propagule production rate has the virtue of allowing us to reinterpret HGCS and HC as making different, implicit assumptions about how species abundances on the mainland vary with S_R . HGCS assume that their I_0 is independent of S_R , but our reinterpretation of I_0 shows that for this to be the case, the per-species rate of propagule production i_0 must be inversely related to S_R (Eq. (6)). Further, i_0 can be expressed as the product of the per-capita rate of propagule production λ (assumed to be the same for all species in all regions) multiplied by species abundance n (assumed to be the same for all species within a region). Therefore, HGCS can be reinterpreted as implicitly assuming that total mainland population size $N = n S_R$ is constant, independent of S_R . Species abundance n is then inversely related to S_R : $n = N/S_R$. Reinterpreted in this way, Eq. (6) can be rewritten as

$$S_L = \frac{S_R}{1 + \frac{e}{\lambda n S_R} S_R} = \frac{S_R}{1 + \frac{e}{\lambda \frac{N}{S_R} S_R} S_R} = \frac{S_R}{1 + \frac{e}{\lambda N} S_R} \quad (7)$$

According to Eq. (7), HGCS also could be reinterpreted as assuming that per-capita propagule production rate λ is inversely related to S_R . However, it seems more biologically plausible to reinterpret HGCS as implicitly assuming that species abundance n is inversely related to S_R , so that total mainland abundance N is independent of S_R . This reinterpretation also leads naturally to a generalization of the HGCS and HC models, which we describe after first reinterpreting the HC model.

HC explicitly assume that c is independent of S_R . The constant c is equal to (or more generally, proportional to) the per-species rate of propagule production $i_0 = \lambda n$ (compare Eq. (1a) and Eq. (3)). Substituting λn for c in Eq. (2), we obtain

$$S_L = \frac{\lambda n}{\lambda n + e} \quad S_R = \frac{S_R}{1 + \frac{e}{\lambda n}} \quad (8)$$

Equation (8) shows that HC can be reinterpreted as assuming that species abundance n is independent of S_R , so that the total abundance of all species increases linearly with S_R : $N = n S_R$, where n is constant.

This assumption contrasts with the assumption of the reinterpreted HGCS model that total abundance, rather than species abundance, is independent of S_R .

The reinterpreted HC and HGCS models define the endpoints of a continuum of possible models making different assumptions about how species abundances relate to S_R . More generally, we might assume that

$$n = \frac{N_1}{S_R^x} \quad (9)$$

where n is species abundance on the mainland, N_1 is a positive constant equal to total abundance (and species abundance) when there is only one species on the mainland, and x is a constant such that $0 \leq x \leq 1$. We assume that N_1 is a constant characteristic of all mainlands, independent of S_R . When $S_R > 1$, N_1 can be thought of as the total abundance that would occur if a mainland region in question contained only one species. In this sense, N_1 is hypothetical and cannot be measured directly, since no mainland region in nature contains only one species. However, this does not prevent estimation of the value of x , which is the key parameter governing the behavior of our model (Discussion).

Total abundance N of all species still equals nS_R , by definition, but now n is defined by Eq. (9). On our reinterpretation, HC assume that $x=0$, implying that total abundance $N = N_1 S_R$, while HGCS assume $x=1$, implying that $N = N_1$. These assumptions define the limiting cases of Eq. (9). Using Eq. (9), we define the total rate I at which new species arrive on an island as

$$I = \lambda n S_R \left(1 - \frac{S_L}{S_R}\right) = \lambda \frac{N_1}{S_R^x} S_R \left(1 - \frac{S_L}{S_R}\right) \quad (10)$$

Setting Eq. (10) equal to Eq. (1b) or (4) and solving for S_L gives

$$S_L = \frac{S_R}{1 + \frac{e}{\lambda \frac{N_1}{S_R^x} S_R}} = \frac{S_R}{1 + \frac{e}{\lambda \frac{N_1}{S_R^x}}} = \frac{S_R}{1 + \frac{e S_R^x}{\lambda N_1}} \quad (11)$$

Equation (11) is a new, generalized island biogeography model of local–regional richness relationships. Figure 1 illustrates the predictions of this new model. When the per-species extinction rate e is small relative to λN_1 , the predicted local–regional richness relationship is steep and nearly linear, and depends only weakly on the relationship between species abundance and mainland richness (Fig. 1a). In this case, species on islands go extinct only rarely, and most species on the mainland will eventually reach the island and then persist for a very long time, independent of their mainland abundance (Fig. 1a). When the per-species extinction rate is of approximately the same magnitude as λN_1 , the predicted local–regional richness relationship is sensitive to the relationship between species abundance and mainland

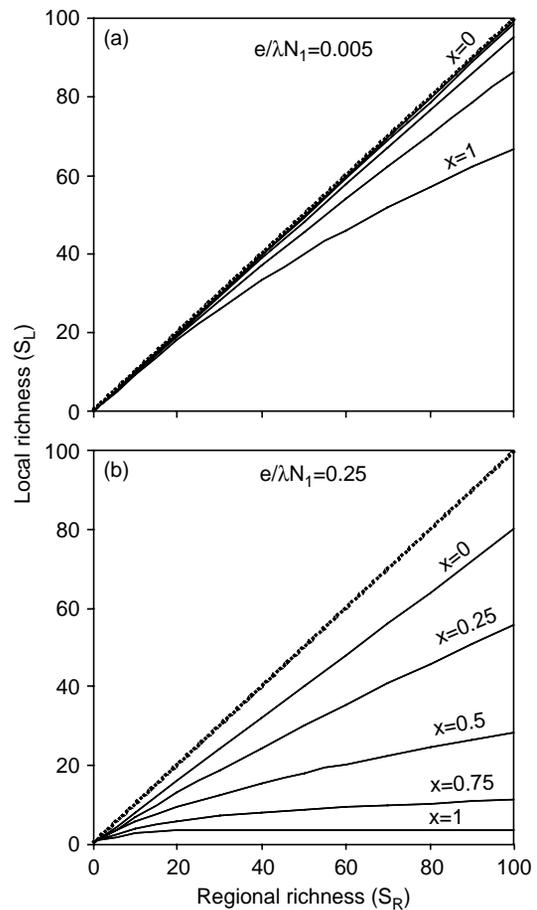


Fig. 1. Predicted local–regional richness relationships for the generalized island biogeography model (Eq. (11)). Panels (a) and (b) show predicted relationships for two different values of the composite parameter $e/\lambda N_1$ (comparable to δ in He et al. 2005; see Eq. (5) and compare Fig. 1a of He et al. 2005). In both panels, $\lambda = 0.1$ and $N_1 = 100,000$; $e = 50$ in (a) and $e = 2500$ in (b). Within each panel, solid lines show model predictions for different values of x , and dotted line shows the limit of a 1:1 relationship; dotted line is obscured in (a). Predicted S_L decreases with x for any given S_R in both (a) and (b), but close proximity of different lines in (a) prevents labeling of some lines.

richness (Fig. 1b). In this case, species on islands go extinct frequently, and will be absent most of the time unless recolonization also occurs frequently. But recolonization frequency depends on how abundant a species is on the mainland. When species abundances decline with S_R (i.e. $x > 0$), per-species rates of propagule production decline and species recolonize less frequently as S_R increases. The proportion of the regional species pool found on an island therefore declines with S_R , leading to an asymptotic curvilinear (“saturating”) local–regional richness relationship (Fig. 1b). In contrast, when species abundances are independent of mainland richness (i.e. $x=0$), recolonization frequency does not vary with S_R and the local–regional richness relationship is linear, with a slope that depends on species abundance

N_1 (Fig. 1b). Therefore, the local–regional richness relationship can vary from nearly linear to asymptotic curvilinear, even when species do not interact locally, just depending on how n varies with S_R (Fig. 1b).

Discussion

Our main conclusion is that there is no single expected relationship between local and regional richness in the absence of species interactions and other complicating or confounding factors. The expected relationship depends on how species abundances vary with regional richness, as well as on rates of extinction and immigration as highlighted by previous work (HC, HGCS). In other words, there is no single island biogeography model of local–regional richness relationships. It is impossible for mainland regions to vary only in regional richness while holding both total abundance and species abundance constant, since by definition $N = nS_R$. Since species abundances necessarily affect propagule production rates, which necessarily affect colonization rates, any island biogeography model of local–regional richness relationships can be interpreted as making some assumption about how species abundances vary with regional richness. This assumption strongly affects the predicted local–regional richness relationship.

So, what is the best null model of the local–regional richness relationship in the absence of local species interactions? If by the “best” null model we mean the null model that makes the most realistic assumption about the $n - S_R$ relationship, and so is best able to serve as a baseline against which the effects of species interactions can be judged, then probably neither the HC nor the HGCS model is best. Species abundances typically decline as regional richness increases, a phenomenon known as density compensation (Diamond 1970, MacArthur et al. 1972, Case 1975, Abele 1984, Kaspari et al. 2000, McGrady-Steed and Morin 2000). Density compensation violates the assumptions of the HC model under our reinterpretation. But it also seems unlikely that total abundance will be invariant with regional richness as assumed by HGCS under our interpretation, particularly since regions of varying richness are likely to vary in both environmental (e.g. productivity) and biological (e.g. strength of top-down effects, mean body size) factors (Diamond 1970, MacArthur et al. 1972). For instance, Kaspari et al. (2000) plot N vs species richness for ant communities at various spatial scales. Both N and S_R vary across space due to variation in productivity. Data from the two largest spatial scales (either of which might be considered the regional scale) indicate that N is approximately proportional to $S_R^{0.6}$. Using Eq. (9) and the fact that $N = nS_R$, we can express these data as $nS_R \propto S_R^{0.6}$, implying that, for ants, $n = N_1/S_R^{0.4}$. In most cases, the

true $n - S_R$ relationship probably will be intermediate between the limiting cases described by HC and HGCS.

Recent studies of the local–regional richness relationship exhibit increasing interest in quantifying the relative importance of local and regional processes in determining the form of the relationship (Caley and Schluter 1997, Kiflawi et al. 2003). Several studies use a null model as a baseline against which to judge any effects of species interactions. However, previous authors have not recognized the implicit assumptions of their null models, which may explain why different authors have chosen different null models of the local–regional richness relationship and thereby reached different conclusions. Caley and Schluter (1997) and Schoolmaster Jr. (2001) simulated local–regional richness relationships by randomly drawing samples (“local communities”) of fixed size from regional species pools of varying species richness but identical distributions of species relative abundances. These simulation models are equivalent in their essentials to our reinterpretation of the HGCS model, since in these simulation models the probability that a species is included in a sample is proportional to its relative abundance, and mean relative abundance of all species in the region is inversely related to regional richness. That is, in these simulation models $n/N = 1/S_R$, where n/N is mean relative abundance. This is essentially equivalent to our model in the limiting case where $x = 1$, since in this case $n = N/S_R$ where N is a constant (note that while we assume that n is the same for all species in a region, we could equally well have defined n as the mean abundance of all species in a region, without changing the behavior of our model). Caley and Schluter (1997) and Schoolmaster Jr. (2001) both found linear and asymptotic curvilinear local–regional richness relationships in their simulations, depending on sample size. Small sample sizes in their simulations are equivalent to high values of δ in the HGCS model, and produce an asymptotic curvilinear relationship. Like HGCS, Caley and Schluter (1997) and Schoolmaster Jr. (2001) both concluded that the form of the local–regional richness relationship cannot be used to infer the importance of local species interactions, since the relationship can take on different forms even in the absence of local species interactions. In contrast, Kiflawi et al. (2003) fit a modified version of the HC model (incorporating effects of island area and disturbance on colonization and extinction rates) to data on macro-invertebrate richness in temporary pools (“islands”). The modified HC model fit the data, leading Kiflawi et al. (2003) to conclude that the most parsimonious explanation of the data was that local species interactions were unimportant. None of these authors recognized the sensitivity of their conclusions to their implicit assumptions about the relationship between species abundances and regional richness.

Use of our generalized island biogeography model (Eq. (11)) as a null model would be an advance on previous studies, as long as the true $n - S_R$ relationship could be determined for the system under study. Unfortunately, determining the true relationship between n and S_R in most systems will be challenging because both n and S_R will depend on many species- and system-specific factors (e.g. variation among regions in environmental conditions), as well as on the often more-or-less arbitrary definitions of local and regional boundaries (Westoby 1998, Huston 1999, Srivastava 1999, Connor et al. 2000, Loreau 2000, Shurin et al. 2000, Gaston and Matter 2002, Hillebrand and Blenckner 2002, Karlson and Cornell 2002, Koleff and Gaston 2002). If the only effect of these species- and system-specific factors was to determine the relationship between n and S_R , then a model that correctly describes the phenomenological relationship between n and S_R would implicitly account for the effect of these factors on the local–regional richness relationship. However, both theory and data show that variation among regions in environmental conditions and other factors, as well as the definitions of local and regional boundaries, often will affect the local–regional richness relationship in other ways besides those mediated by effects on n and S_R (Westoby 1998, Huston 1999, Srivastava 1999, Loreau 2000, Shurin et al. 2000, Collins et al. 2002, Hillebrand and Blenckner 2002, He et al. 2005, Shurin and Srivastava 2005).

Schoolmaster Jr. (2001) found that the precise quantitative form of the local–regional richness relationship is sensitive to the shape of the regional species abundance distribution (e.g. uniform vs log-normal). We did not consider the shape of the species abundance distribution because such quantitative details would not alter our qualitative point. However, a detailed quantitative understanding of local–regional richness relationships may well require consideration of how the precise form of the species abundance distribution changes with S_R (Hubbell 2001).

Conclusions

Many different factors can and do shape the local–regional richness relationship (this study, Caswell and Cohen 1993, Westoby 1998, Huston 1999, Srivastava 1999, Fox et al. 2000, Loreau 2000, Shurin et al. 2000, Schoolmaster Jr. 2001, Shurin and Allen 2001, Hillebrand and Blenckner 2002, Karlson and Cornell 2002, Mouquet and Loreau 2003, Mouquet et al. 2003, Fukami 2004, Hillebrand 2005). Teasing out the relative contributions of these factors will be a difficult challenge, particularly because many factors do not act independently of one another and because no single factor is likely to be essential to generating the observed

relationship (Lawton 1999). However, understanding local–regional richness relationships is not an impossible task. Many seemingly intractable problems in ecology have yielded or likely will yield to a combination of improved data and increasingly sophisticated quantitative methods (e.g. the prevalence of competition, Gurevitch et al. 1992; the causes of population cycles, Turchin 2003, Kendall et al. 2005; the importance of neutral drift vs niche-based processes, Bell 2003, 2005, Chave 2004, Karst et al. 2005). We suggest that improved understanding of the processes underlying general patterns will come from cleverly combining observations, models (null and otherwise), and experiments (Shurin 2000, Shurin et al. 2000, Shurin and Allen 2001). By incorporating species abundance into island biogeography models, we hope to contribute to the development of increasingly sophisticated models of local–regional richness relationships.

Acknowledgements – We thank Shane Richards and Fangliang He for insightful discussion of the difference between the HC and HGCS models.

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