

THE LOCAL–REGIONAL RELATIONSHIP: IMMIGRATION, EXTINCTION, AND SCALE

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Abstract. While local processes (e.g., competition, predation, and disturbance) presumably cause species exclusion and thus limit diversity in individual communities, regional processes (e.g., historical events, immigration, and speciation) are assumed to provide a source of species to colonize and thus enrich local communities. Ecologists have attempted to distinguish between these two sets of processes using graphical evidence for local assemblage saturation. However, such efforts have been controversial and are antithetical to the fact that local diversity bears an imprint of both. We examine the local–regional species richness relationship from the perspective of the theory of island biogeography and develop a model that can produce the full range of observed local–regional richness relationships from linear to curvilinear. Importantly, unlike previous models, we do not require species interactions to produce the curvilinear pattern. Curvilinear relationships arise if per-species stochastic extinction rates are substantially higher than colonization rates, while linear relationships result if colonization rates are higher than extinction rates. Because we also show that merely changing the sampling scale can make local–regional relationships appear either saturated or unsaturated, an inference of ecological processes, derived solely from local–regional relationships, is unwarranted.

Key words: biodiversity; equilibrium; extinction; immigration; island biogeography; local processes; regional processes; spatial scale; species richness.

INTRODUCTION

One of the important advances in ecology over the past two decades has been the widespread recognition that local species assemblages are common products of both local and regional scale processes (Strong 1979, Terborgh and Faaborg 1980, Ricklefs 1987, 2004, Cornell and Lawton 1992, Cornell and Karlson 1997, Gaston and Blackburn 2000, Shurin and Srivastava 2005). Local processes include those factors, such as competition, predation, parasitism, and disturbance, which govern the membership of species in an assemblage. In contrast, regional processes include those factors, such as long-distance immigration, speciation, and historical events, which provide a source of species to colonize and enrich local assemblages. Local scales are thus defined by the spatial extent of community interactions, whereas regional scales are defined by the geographical distribution of potential colonists for the target community (Srivastava 1999). The relative influence of local and regional processes on species richness varies among assemblages, but no community is likely

to be structured by processes operating solely at local or regional scales (see also Loreau 2000).

Much of the evidence that local community structure is influenced both by local and regional processes has been drawn from interpretations of the local–regional species richness relationship (see reviews of Ricklefs 1987, Cornell and Lawton 1992, Cornell and Karlson 1997, Srivastava 1999). The local–regional species richness relationship is an empirical relationship between the number of species at the local scale and the number in the region within which each local assemblage occurs, and from which it is presumed to draw its members. While other views and cautions have been expressed (e.g., Huston 1999, Lawton 1999, Srivastava 1999, Gaston 2000, Loreau 2000, Hillebrand and Blenckner 2002, Ricklefs 2004, Shurin and Srivastava 2005), it has been widely hypothesized that if the structure of a local assemblage is dominated by strong species interactions, its richness will tend to be “saturated” with respect to the regional species pool, i.e., an increase in regional richness will have little effect on the local assemblage. In this case, local richness approaches an asymptote with respect to regional richness, resulting in a curvilinear relationship between local and regional richness (Cornell and Lawton 1992).

Alternatively, if the structure of a local assemblage is dominated by regional processes it is defined as “un-

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saturated.” In this case, increases in the regional species pool will proportionally increase local species richness, creating a linear relationship between local and regional richness. The robustness of the graphical test for saturation relies on the premise that patterns (linear vs. curvilinear local–regional richness functions) map uniquely to processes (saturation due to species interactions vs. unsaturated). This premise has been called into question recently through the demonstration of “pseudo-unsaturated” communities: strongly interactive communities that nonetheless show linear local–regional richness relationships due to statistical and methodological artefacts (Caley and Schluter 1997, Huston 1999, Hillebrand and Blenckner 2002, Fukami 2004, Shurin and Srivastava 2005) or the effects of predators (Shurin and Allen 2001), disturbance (Caswell and Cohen 1993, Mouquet et al. 2003) and assembly time (Mouquet 2003). The opposite error of pseudosaturation, or noninteractive communities with curvilinear local–regional richness relationships, has only been shown in the case of inappropriate local or regional scales (Caley and Schluter 1997, Srivastava 1999, Shurin et al. 2000). We use a new noninteractive model based on island biogeography theory to (1) examine whether stochastic processes of extinction and colonization can create real curvilinear relationships between local and regional richness and (2) demonstrate why the sampling scale influences local–regional relationships.

While the theory of island biogeography (MacArthur and Wilson 1967) has played a fundamental role in ecology and biogeography and has frequently been invoked to interpret the local–regional relationship (Terborgh and Faaborg 1980, Ricklefs 1987, Rosenzweig and Ziv 1999, Mora et al. 2003), its potential role in generating a mechanistic understanding of saturated and unsaturated assemblages has surprisingly not been explored. The central concept of MacArthur and Wilson’s theory is that the number of species in an insular habitat “is determined by a dynamic balance between immigration of new species and the local extinction of species already present” (Strong 1979). Therefore, the theory inevitably predicts that local species richness is the outcome of species immigration at the regional scale and extinction at the local scale, the two processes that an explanation of the local–regional relationship must incorporate. From island biogeography theory, we derive a general model that explicitly incorporates the processes of immigration and extinction and produces a continuum of local–regional species richness relationships from linear to curvilinear.

AN ISLAND BIOGEOGRAPHIC MODEL OF LOCAL-REGIONAL RELATIONSHIPS

A variety of models have previously been employed to describe or explain the local–regional relationship. A number of these models relate local–regional relationships to other ecological patterns, such as the power

species–area function (Holt 1993, Rosenzweig and Ziv 1999, Srivastava 1999, Shurin and Srivastava 2005), statistical sampling of the lognormal species–abundance distribution (Caley and Schluter 1997), and an additive partitioning of the components of species diversity (Lande 1996, Loreau 2000). Such models are useful in expanding and refining the saturation question, but do not automatically explain patterns in terms of mechanisms. Mechanistic models, summarized in Table 1, include assembly models (Morton and Law 1997, Fukami 2004) and various expansions of metapopulation models (Caswell and Cohen 1993, Loreau and Mouquet 1999, Huguency and Cornell 2000, Shurin and Allen 2001, Mouquet and Loreau 2002). These models have been concerned primarily with the role of species interactions in affecting the relationship between local and regional richness, and the effect of immigration from a species pool in disrupting local competitive exclusion. These models do not explore the effects of stochastic immigration and extinction processes in the absence of species interactions, the subject of the model we now describe.

Let us denote a to be the area of a local assemblage that is embedded in an indefinitely large region, S_L to be the number of species in the local assemblage, and S_R to be the number of species in the regional species pool. Irrespective of the mathematical form, a reasonable local–regional model must then intuitively meet the following four conditions: (1) if the local assemblage $a = 0$, then the number of species present $S_L = 0$; (2) if $a \rightarrow \infty$ (i.e., the local area approaches the regional area), $S_L \rightarrow S_R$; (3) if the regional species pool $S_R = 0$, then $S_L = 0$; and (4) if the regional species pool is so large that $S_R \rightarrow \infty$, then S_L should not reach ∞ but will be constrained by the size of the local area.

The theory of island biogeography posits that the number of species (S_L) on an island (or in an area) is ultimately determined by the equilibrium between the processes of immigration and extinction (MacArthur and Wilson 1967). There are two basic formulae in the theory. The first one is that immigration rate (I) is a function of the size of an island (a), the number of species already present (S_L) and the size of the regional species pool (S_R). The second is that extinction rate (E) is a function of the size of the island and the number of species already present. A simple immigration model that captures the features of the theory and has been widely used in the literature (Gilpin and Diamond 1976, Minshall et al. 1985) takes the following form:

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

where I_0 is the maximum immigration rate and v is a parameter that describes the effect of area on immigration rate I . The linearity between I and S_L stems from the assumption that species are equivalent in dis-

TABLE 1. Summary of selected mechanistic models that examine the effects of regional richness on local richness. The species pool is either independent of the local community (external) or represents dispersal between local-scale patches embedded within a metacommunity (internal).

Study	Species pool type	Interaction type	Key results
Caswell and Cohen (1993)	external	competitive hierarchy, or no competition	Slope of the linear local–regional relationship depends on relative strengths of competition and disturbance.
Morton and Law (1997)	external	two trophic levels, interaction strengths determined by body size	Curvilinear local–regional relationships are due to noninvasible community end states.
Loreau and Mouquet (1999)	external	competitive hierarchy mediated by differences between species in demographic traits	Immigration rescues species from competitive exclusion, increasing local richness.
Shurin and Allen (2001)	internal	competitive hierarchy among prey species, plus keystone predation	Shared predators increase the likelihood of linear local–regional relationships in competitive communities.
Mouquet and Loreau (2002)	internal	competitive hierarchy mediated by differences between species in demographic traits	Local richness can be limited by competition but still vary with immigration intensity.
Mouquet et al. (2003)	external	competitive hierarchy differs between resources	Interactive communities can have linear local–regional relationships at intermediate assembly times.
Fukami (2004)	combination of internal and external	two trophic levels, interaction strengths determined by body size	Assembly history affects beta diversity and scale dependence of local–regional relationships.

persal and colonization abilities (Strong 1979); this is why Hubbell (2001) considers the theory of island biogeography as a neutral theory.

Extinction increases with the number of species already present in the local assemblage but decreases with island area (MacArthur and Wilson 1967, Simberloff 1974). The extinction rate is commonly modeled as follows (Gilpin and Diamond 1976, Minshall et al. 1985):

$$E = E_0 a^{-x} S_L \quad (2)$$

where E_0 and x are constants. Again the linearity between E and S_L stems from the assumption of species equivalence (Strong 1979). It is worth mentioning that I_0 and E_0 are related to the per species immigration and extinction rates, i.e., the respective slopes of I and E curves of Eqs. 1 and 2.

Armed with Eqs. 1 and 2, we can easily derive the relationship between local species richness (S_L) and regional species richness (S_R) at equilibrium ($I = E$):

$$S_L = \frac{a^z S_R}{a^z + \delta S_R} \quad (3)$$

where $\delta = E_0/I_0$, $z = v + x$. It is easy to verify that the model in Eq. 3 meets all four of the conditions mentioned earlier: (1) $S_L = 0$ if $a = 0$, (2) $S_L = S_R$ if $a \rightarrow \infty$, (3) $S_L = 0$ if $S_R = 0$, and (4) $S_L = (1/\delta)a^z = (I_0/E_0)a^z$ if $S_R \rightarrow \infty$. This is the famous power model of species–area relationships, suggesting that when the number of species in the region is indefinitely large, S_L will not approach ∞ , but rather is constrained by the size of the local area.

If the area of a local assemblage is fixed, the local–regional species richness relationship will change in appearance from being curvilinear to linear as δ varies from relatively large to small values (Fig. 1a). At the extreme, where δ is very small (i.e., I_0 is extremely large relative to E_0 ; immigration is the dominant process), Eq. 3 becomes

$$S_L = S_R \quad (4)$$

Of course, we would not expect real ecological communities to show equality between local and regional richness, because we would never expect local extinction to be zero; this is simply the limiting case. The more important conclusion from Eq. 4 is that when the immigration rate dominates the extinction rate, the relationship between local and regional richness will be approximately proportional. In contrast to the proportional sampling model, when δ in Eq. 3 is very large (i.e., E_0 is large relative to I_0 ; local extinction is the dominant process), the dependence of local species richness on regional richness will be very weak resulting in the curvilinear local–regional relationship (Fig. 1a). It is clear from Eq. 3 and Fig. 1a that what really matters is the ratio of extinction and immigration, not either of them alone.

It is evident from Eq. 3 that local species richness (S_L) does not only depend on regional species richness (S_R), but also on the area of local assemblage (a), and the relative ratio (δ) of the extinction and immigration rates. More importantly, this model can produce the entire spectrum of possible local–regional relationships from curvilinear to linear. This is manifest both in the

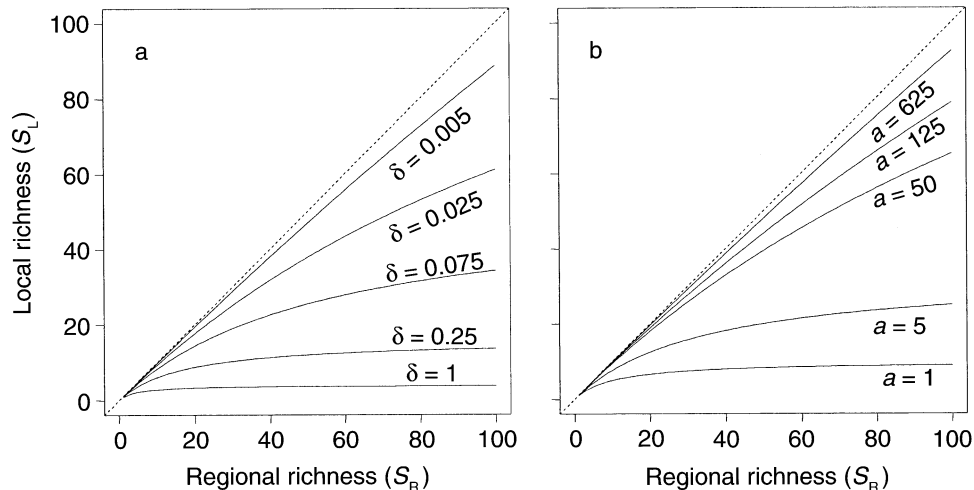


FIG. 1. (a) Local-regional relationships predicted from Eq. 3, showing the influence of the extinction/immigration ratio δ on the saturation of communities while area a is kept constant. The parameters of the model are set as $a = 50$ and $z = 0.35$, where z is a parameter scaling the effect of area. The range of regional richness (S_R) varies from 0 to 100. The dashed line is the 1:1 identity. (b) Local-regional relationships predicted from Eq. 3, showing the influence of local area a on the saturation of communities while δ is kept constant. The parameters of the model are set as $z = 0.75$ and $\delta = 0.1$.

algebra of Eq. 3 and the results shown in Fig. 1. The crucial point is that per capita extinction rates in Eq. 3 are independent of S_L so that the curvilinear local-regional species richness relationships depicted in Fig. 1 cannot be interpreted to arise from competitive community saturation.

In addition to the effects of immigration and extinction on the local-regional relationship, it is obvious from Eq. 3 that this relationship also depends on the area at which the local assemblage is sampled. Given that δ is fixed, a small area (i.e., small a) will result in a curvilinear local-regional relationship, while a large area will have a linear pattern (Fig. 1b).

DISCUSSION

Although it has been widely recognized that local and regional processes can both be important in contributing to local species richness (Strong 1979, Ricklefs 1987, Cornell and Lawton 1992, Loreau 2000), the two perspectives are still often considered independently and the primary use of plots of the relationship between local and regional species richness is to discriminate between saturated and unsaturated local assemblages. The island biogeographic model of local-regional species richness relationships we propose implies that there is a continuum of local-regional richness relationships even in the absence of species interactions. Eq. 3 shows that, given local assemblages sampled at a fixed scale, the curvature of the local-regional relationship is determined by the relative difference between the rates of local extinction and regional immigration. If extinction is a dominant process, the relationship will appear curvilinear, while a linear pattern will result if immigration dominates. This finding suggests that linear and curvilinear local-regional

species richness relationships represent different balances of the same processes.

The curvature in local-regional relationships in our model is influenced by the ratio of per species extinction risk (E_0) to immigration likelihood (I_0). This should not be confused with the ratio of the number of extinctions to the number of immigrants, which of course is always one at equilibrium. Therefore, local-regional relationships, whether primarily affected by species interactions or neutral processes (this model), should be better understood by the ratio of extinction to immigration probabilities than by examining one process (e.g., immigration) in isolation. This differs from the conventional description of the local-regional relationship in which local interactions are emphasized to cause saturation (see Table 1) but otherwise the key role of extinction is ignored. Extinctions in a truly saturated community (defined as one primarily limited by species interactions) will come from two sources, background stochastic rates of extinction as well as extinctions caused by community interactions (e.g., Caswell and Cohen 1993). Extinctions in a non-interactive, unsaturated community are caused only by stochastic processes. All else being equal, the average species in a saturated community therefore has a higher risk of extinction than its counterpart in an unsaturated community. Saturated communities will therefore tend to have high ratios of extinction to immigration rates, and unsaturated communities will have low ratios. Other authors have also urged that local-regional relationships be understood by considering relative rates of stochastic extinctions, interaction-caused extinctions, and immigrations (Caswell and Cohen 1993, Mouquet and Loreau 2002; B. Hugué and H. Cornell, *personal communication*).

The island biogeographic model that we have presented is very different from previous mechanistic models of local–regional relationships (Table 1). The majority of these models are concerned with interactive communities, that is, they consider situations where the extinction likelihood of an average species, E_0 is correlated with S_L . In our model, E_0 is not affected by S_L . If species interactions are removed from these interactive models, however, all predict linear local–regional relationships. By contrast, our model generates the full spectrum of linear and curvilinear relationships without invoking species interactions.

The theory of island biogeography relies on a dynamic equilibrium between immigration and extinction that leads to relative constancy in local richness over ecological time scales. However, this steady state does not preclude the possibility of changes in local richness over longer, evolutionary time scales, as would be expected in an unsaturated community through increases in the species pool via speciation or immigration (see also Rosenzweig 1995:248). Ricklefs and Bermingham (2004) have recently shown that the slopes of species–area curves differ with lineage age, but are otherwise consistent with island biogeography theory in the short term. The theory of island biogeography also assumes an external species pool, that is, a species pool which is independent of the local communities it supplies with propagules. This assumption is a good approximation for many but not all ecological communities, and is complemented by other models based on assumptions of an internal species pool, represented by propagule dispersal between local community patches (Table 1). The implications of our model for local–regional relationship with internal dispersal remain to be seen.

In addition to the effect of immigration and extinction, the shape of the local–regional relationship is also subject to change in the local sampling scale (Cornell and Karlson 1996, Caley and Schluter 1997, Huston 1999, Loreau 2000, Bartha and Itz s 2001). The model in Eq. 3 explicitly incorporates the scale effect and predicts that small scales lead to a curvilinear pattern and large scales to a linear one, irrespective of other local and regional processes (Fig. 1b). In a similar vein to the findings of previous researchers (Caley and Schluter 1997, Hillebrand and Blenckner 2002, Fukami 2004, Shurin and Srivastava 2005), the effect of local scale on the local–regional relationship as described in Eq. 3 is nonlinear. When scales are small (e.g., $a = 1$ and 5 in Fig. 1b) the curvature is obvious. With a moderate increase in scale (e.g., $a = 50$), the linear relationship quickly starts to emerge. It is interesting to observe in Fig. 1b that the two lines at $a = 125$ and 625 differ much less than the two at $a = 1$ and 5, even though in both cases the scale difference is fivefold. The pattern shown in Fig. 1b is nearly identical to Fig. 4 of Caley and Schluter (1997), although our result is based on a mechanistic model whereas Caley and Schluter's (1997) results arise purely from statistical

patterns. Moreover, Eq. 3 provides a general method that allows us to consider simultaneously the effects of the local scale and ecological processes (immigration/extinction), thus enhancing our ability to distinguish the effects of these two components.

It is noteworthy that, besides the effect of local scale, regional scale also influences the shape of the local–regional relationship (Angermeier and Winston 1998, Karlson and Cornell 1998, Srivastava 1999, Shurin et al. 2000, Hillebrand and Blenckner 2002). While the change in the local scale may reflect the change in the intensity of local interactions such as competition, the change in the regional scale has been observed to alter the importance of environmental variables (e.g., climate), the size of the regional species pool (S_R), and species dispersal abilities (I_0) (Karlson and Cornell 1998, Shurin et al. 2000). Although our model does not explicitly incorporate regional area, it does include the last two of these variables (S_R , I_0) known to be affected by regional scale, thus creating options for future incorporation of regional scale effects.

The important conclusion of our model is that strong interspecific interactions are not required to create real curvilinear local–regional relationships. This finding is the flipside of previous results showing that communities with strong interactions can lead to linear local–regional relationships (Huston 1999, Shurin and Allen 2001, Hillebrand and Blenckner 2002, Mouquet 2003, Fukami 2004, Shurin and Srivastava 2005). Together these results suggest that patterns in local–regional plots cannot reliably indicate the strength of interactions or the presence or absence of competitive exclusion. Therefore, inferences about community saturation based solely on an examination of local–regional species richness relationships are unwarranted and can be misleading. More direct evidence of species exclusion would be necessary to infer community saturation. In order for the local–regional relationship to be useful for inferring ecological processes, it is necessary to also explicitly account for sampling scales.

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