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-
tions to other ecological patterns, such as the power functions from linear to curvilinear.

A continuum of local–regional species richness relates processes of immigration and extinction and produces a general model that explicitly incorporates the outcome of species immigration at the regional scale and extinction at the local scale, the two 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, $S_i$ 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 $S_i = 0$; (2) if $a \to \infty$ (i.e., the local area approaches the regional area), $S_i \to S_R$; (3) if the regional species pool $S_R = 0$, then $S_i = 0$; and (4) if the regional species pool is so large that $S_R \to \infty$, then $S_i$ should not reach $\infty$ but will be constrained by the size of the local area.

The theory of island biogeography posits that the number of species ($S_i$) 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 ($S_i$) 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:

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

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 $S_i$ 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).

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

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 $\delta$ varies from relatively large to small values (Fig. 1a). At the extreme, where $\delta$ 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 $\delta$ 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 ($\delta$) 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 \( \delta \) on the saturation of communities while area \( a \) is kept constant. The parameters of the model are set as \( a = 50 \) and \( \delta = 0.35 \), where \( \delta \) 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 \( \delta \) is kept constant. The parameters of the model are set as \( \delta = 0.75 \) and \( a = 50 \).
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, $E_r$, is correlated with $S_r$. In our model, $E_r$ is not affected by $S_r$. 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 Ittés 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 ($a = 1$ and 5 in Fig. 1b) the curvature is obvious. With a moderate increase in scale ($a = 50$), 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 ($I_o$) (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 ($S_R$, $I_o$) 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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**Literature Cited**


