Chapter 17: New Perspectives on Local and Regional Diversity: Beyond Saturation

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<A> Introduction

A persistent question in ecology concerns the relative roles of macroscopic processes such as immigration or speciation versus small-scale biotic and abiotic factors as agents of community structure (Ricklefs and Schluter 1993). This issue lies at the heart of several major conceptual debates and many important applied problems. Small-scale and whole-system experimental studies have elucidated the importance of biotic interactions and abiotic constraints for governing the structure and function of ecological communities (Carpenter et al. 1995; Brown et al. 2001). However, broad-scale geographic comparisons have traditionally emphasized the importance of the geologic, migratory and evolutionary history of biotas for patterns in diversity (Brown 1995; Maurer 1999). This contrast has led to the suggestion that while species interactions may be important within local communities, they offer little mechanistic insight into biogeographic patterns. Instead, larger scale regional processes are often considered dominant in generating differences among communities (Ricklefs 1987; Maurer 1999). The local and regional schools of thought diverge both in scale and the processes they

consider most important for influencing community structure. Conceptual and empirical synthesis of the two approaches remains one of the most important challenges in modern ecology.

The study of patterns such as local and regional species richness has been central to testing metacommunity ideas, particularly those associated with neutral theory (e.g., see Chase et al., Chapter 14). Here, we provide a detailed exploration of one of these patterns (the correlation between local and regional species richness) as it relates to two issues concerning metacommunities. First we illustrate the need to study both mechanisms and patterns in metacommunities. Second we show the critical importance of the choice of spatial scale for our perception of patterns and processes in metacommunities, and provide guidance on alternatives to choosing specific scales.

One popular approach to estimating the strengths of local and regional processes is to examine the shape of the relationship between local and regional species richness. The technique is based on the hypothesis that strong local interactions place limits on local diversity. In this case, richness within local communities approaches an upper asymptote with increasing regional richness. Saturated patterns are consistent with models where local interactions predominate over dispersal in limiting local diversity. Alternatively, if local richness is unconstrained by local interactions but instead depends on the supply of colonists from the region (the "patch dynamics perspective"; see Holyoak et al., Chapter 1 and Chase et al., Chapter 14), then local and regional richness should be positively correlated over their entire range. The approach was first introduced by Terborgh and Faaborg (1980) and has since been applied to data from a broad array of taxa and locations (see reviews in Cornell and Lawton 1992; Srivastava 1999; Hillebrand and Blenckner 2002). This method is attractive in that it offers a simple statistical test

of a hypothesis (saturation vs. linearity), and that it uses data that are widely available for many types of communities and organisms. However, a number of problems with inferring processes from patterns of local-regional diversity have been pointed out (Srivastava 1999; Fox et al. 2000; Loreau 2000; Shurin and Allen 2001; Hillebrand and Blenckner 2002). These issues generally relate either to the processes underlying patterns of local and regional diversity, or to the appropriate geographic definitions of local and regional scales. Thus, saturated or linear patterns of diversity may not inform us as to the relative importance of local and regional processes.

In this synthesis, we review theoretical foundations for understanding local and regional species diversity and the relationship between the two. We consider two broad categories of issues relating to the control of local and regional diversity: the different types of processes that might reasonably be classified as "local" or "regional," and the appropriate definitions of the two spatial scales. Different types of biotic and abiotic local interactions might have qualitatively different effects on diversity and species coexistence. Regional processes might include dispersal in a metapopulation or biogeographic sense, speciation, source-sink effects or broad-scale climatic or ecosystem processes. Here we review ecological theories that incorporate processes at local and regional scales and assess their predictions regarding the maintenance of local and regional diversity.

The second issue relates to the appropriate definitions of the local and regional spatial scales. A number of studies have pointed out that neither the local or the regional scale can be consistently defined by spatial boundaries that are directly tied to the underlying mechanisms (Westoby 1998; Srivastava 1999; Loreau 2000). We argue that studies should explicitly incorporate spatial scale as a continuous variable rather than drawing arbitrary distinctions (Kolasa and Romanuk, Chapter 9, use hierarchy theory to arrive at a similar conclusion).

Different definitions of local and regional scales can produce qualitatively different patterns of diversity. Saturation of diversity implies convergence of species-area relations from different regions at small (i.e., local) spatial scales (Westoby 1998). Thus, the slope of the local-regional relationship should increase with the ratio of the local to regional areas if communities are saturated, but not if they are unsaturated. We show using data from a survey of local-regional studies that the slope of the relationship between local and regional richness does indeed increase as the local area becomes larger relative to the regional scale. Thus, although most studies have found linear or unsaturated patterns, the overall pattern of local and regional richness across taxa is consistent with a saturated model of diversity. However, because a diversity of mechanisms can produce either saturated or unsaturated patterns, the distinction between the two is unhelpful for estimating the roles of the two types of processes. Finally, we discuss evidence for the importance of local and regional processes from experimental and observational studies in a number of natural systems. We identify several gaps in our understanding of diversity at multiple spatial scales and propose a number of questions that demand further attention.

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<A> Theory--a continuum of processes

Here we review several theories of local and regional diversity that have been developed to explicitly incorporate mechanistic local interactions and dispersal among patches within a region (summarized in Table 17.1; Levins and Culver 1971; Hubbell 2001; Shurin and Allen 2001). Models based on species-area relations have been applied to questions of local and regional diversity (Westoby 1998; Srivastava 1999; Loreau 2000); however, these are entirely pattern based and do not make predictions regarding the roles of different processes, and will not be considered further here.

The simplest models of the factors that influence local and regional diversity come from island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Levins 1969). If local habitats have no intrinsic limits to their diversity and interspecific interactions do not affect species' distributions, then local diversity should be a constant proportion of the regional species pool (i.e., local richness is a linear function of regional richness). If each species in the region exists in its own metapopulation unaffected by the presence of other organisms, then every species occupies a proportion of the habitat (P_i) equal to $1-e_i/c_i$, where e_i and c_i are the species-specific extinction and colonization rates, respectively. In this case, local diversity is the sum of the proportional occupancies across all species in the regional pool. That is, mean local diversity for the region (D) is given by $\sum_{k} P_i$, where k is the number of species in the regional pool.

Increasing the size of the regional pool (k) leads to linear increases in the mean number of species found within patches (D) because each species' occupancy is independent of all others. This prediction is the basis for the conclusion that linear, positive relationships between local and regional diversity are indicative of non-interactive local communities (Hugueny and Cornell 2000).

A counterpoint to island biogeography theory is illustrated by models of competition in metapopulations with hard upper limits to local diversity and global dispersal (Levins and Culver 1971; Hastings 1980; Tilman 1994; Yu and Wilson 2001). Such models are most often motivated by communities of sessile species competing for space where each patch can be occupied by only a single individual. Competition in such a system can be pre-emptive (i.e., by priority rules) or by dominance (i.e., competitive hierarchies). In this case, species interact by excluding colonists from local sites, not by affecting neighboring individuals, and local diversity within sites has a maximum of one. As outlined in Mouquet et al., Chapter 10, the requirement for

regional coexistence of multiple species with dominance competition is a tradeoff between dispersal ability and competitive rank (Levins and Culver 1971), while regional coexistence is impossible with pre-emptive competition (Yu and Wilson 2001). Mean local diversity in the region is again the sum of the proportional occupancies among members of the regional pool. However, since we assume absolute local competitive exclusion, the models predict saturated or curvilinear relationships between local and regional diversity at sufficiently high levels of regional richness or dispersal rates (Figure 17.1). Linear relationships may occur at low levels of regional richness and slow dispersal, provided there is a very strong tradeoff between colonization rate and competitive ability (Shurin and Allen 2001). However, the conditions for proportional sampling of the regional pool become increasingly stringent as more species are added to the region. The contrast between metapopulation models with and without local competition illustrates the two hypothesized relationships between local and regional richness, with strong local exclusion leading to saturating patterns and non-interactive communities giving rise to linear functions. In metapopulation models of competition, saturation occurs at high rates of dispersal, while proportional sampling may be observed when dominant competitors are poor colonizers (Figure 17.1, Table 17.1).

A third possibility is that species compete locally within patches and dispersal is constrained to occur within a neighborhood of patches as in neutral biogeographic models (Hubbell 2001). Such a system allows for the possibility of non-equilibrial regional coexistence in the case of pre-emptive competition (Hubbell 2001; Yu and Wilson 2001). Neutral theories also predict saturation of local diversity if a single-occupancy site or patch is considered to be the local scale. However, because of localized dispersal, species are more likely to interact via propagules with nearby species than with those farther away. Thus, the local scale may instead

be defined as the neighborhood of patches in close enough proximity to actually exchange propagules due to localized dispersal (Mouquet et al., Chapter 10). If we expand our definition of the local scale to the neighborhood of patches, then we may expect linear relationships between local and regional diversity. This occurs because in richer "regions," there are more species available to colonize local patches. Thus, whether we expect linear or saturated local–regional patterns in neutral biogeographic models depends on the spatial extent of the local and regional scales (see further discussion of scale issues below).

None of the above models explicitly consider local population dynamics but instead treat patches simply as occupied or unoccupied. This is equivalent to assuming that migrants found local populations but make no significant contribution the size of extant populations, and that local interactions take place on a much faster time scale than dispersal. Another potential role of dispersal in communities is that immigrants may have significant impacts on local population dynamics (Pulliam 1988; Loreau and Mouquet 1999; Amarasekare and Nisbet 2001). If the number of propagules is large relative to local population sizes, then dispersal can sustain populations that would otherwise undergo extinction based on their local birth and death rates (a source-sink system). In such a community, the relationship between local and regional richness again depends on the rates of dispersal of members of the regional pool. If colonization rates are much greater than local extinction, but low enough that sink populations are rarely maintained by immigration, then local exclusion should lead to saturation of local diversity. In this case, dispersal rates are high on the continuum considered by patch dynamic models, but still low relative to local demographic rates (Figure 17.1). As dispersal rates increase (as in the right half of Figure 17.1), local populations become increasingly influenced by immigration and more species are maintained locally. When many species exist as sink populations in some parts of

their range, increasing regional diversity may lead to greater numbers of local populations and higher local diversity (Figure 17.1, low exclusion scenario). In this case, local diversity is "super-saturated", or greater than local conditions would allow in the absence of immigration. Alternatively, if sink populations exert large influence on other species in local communities, then increasing habitat connectivity may lead to exclusion of populations that would otherwise persist (Figure 17.1, high exclusion scenario; Amarasekare and Nisbet 2001). Thus, if source-sink dynamics play a significant role in the determining the number of species maintained in a community, then we may expect to see saturation of local diversity at *low* dispersal rates, and either linear or saturated local–regional patterns with *high* dispersal. This prediction contrasts with that of patch-dynamic models where a colonization–extinction balance is considered most important.

All of the above models assume that local interactions serve primarily to place limits on local diversity. However, a wide variety of species interactions can give rise to facilitation and promote colonization by species that would otherwise be excluded. For instance, habitat modification may mitigate physical stress for plants and marine invertebrates (Bertness et al. 1999). Processing chains can also increase resource availability and quality for detritivores (Heard 1994). Indirect interactions mediated via shared competitors or predators can also give rise to facilitation. Shurin and Allen (2001) showed in a metacommunity model that keystone predators that facilitate local coexistence among competitors can promote both local and regional diversity in many situations. The model modifies metapopulation models of competition by incorporating a predator that allows for local coexistence of a dominant and subordinate competitor where the dominant species would otherwise exclude the weaker. If predators facilitate as many or more species than they exclude, then the conditions for linear local–regional

richness patterns become much less restrictive than in metapopulation models of competition alone. If keystone predation or other forms of interspecific facilitation play important roles in shaping community structure, then we may expect to find positive relationships between local and regional diversity in the presence of strong local interactions. Thus, mechanisms of local interactions have the potential to affect both local and regional species richness and the shape of the relationship between the two.

Finally, current theoretical foundations for understanding local and regional diversity do not include variation in the local environment among patches. However, empirical evidence and theoretical results indicate that spatial heterogeneity may play an important role in generating both local and regional diversity. For instance, Levine and Rees (2002) found that a colonization–competition tradeoff was inadequate to explain relative abundance patterns with respect to seed size and competitive abilities in annual plant communities. Instead, a model that incorporated environmental heterogeneity among patches matched observed patterns where small-seeded species that are good dispersers but poor competitors are most abundant. The model invoked spatial heterogeneity that generated differences in species' competitive abilities among patch types. Condit et al. (2002) showed that observed patterns in beta diversity of trees in Panama and the Amazon were inconsistent with a neutral model of colonization and pre-emptive competition. Instead, differentiation among sites appeared to correspond to spatial scales of variation in the physical environment. Finally, Chase and Leibold (2002) found that diversity showed hump-shaped relationships with productivity at the local scale and monotonic patterns at the regional scale (see also Loreau et al., Chapter 18). This pattern suggests that increasing productivity promotes regional diversity and increases local diversity at low levels while having the opposite effects in very eutrophic systems. Theories to explain the effects of productivity on

diversity have focused largely on the local scale (reviewed in Srivastava and Lawton 1998). The reasons for enhanced diversity in highly productive regions are unknown. However, these examples suggest that spatial heterogeneity in local conditions should be considered when attempting to explain local and regional diversity.

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<A> Why we should consider continuous space

The concept of species saturation is typically formulated in terms of local and regional scales. Species interactions are assumed to take place at the local scale and in ecological time. Regional scales contain the species pool from which local sites draw potential colonists. Operationally defining either of these scales involves substantial subjectivity, and neither scale can be easily tied to underlying mechanisms in any particular community. Below we present four arguments for treating space as a continuous variable to avoid the problems of arbitrarily assigning discrete definitions of what is considered "local" or "regional".

First, the shapes of patterns of local and regional richness are very sensitive to the definition of local scale. In simulations of community assembly in a multiple-patch (metacommunity) landscape, the relationship between local and regional richness depends on whether the patch or a neighborhood of patches is considered as "local" (T. Fukami, unpubl. results). If the size of the local scale exceeds the scale of local interactions, we expect "local" richness estimates to be increasingly influenced by beta diversity, the turnover in species between local patches, and thus for local–regional richness plots to appear more linear (Huston 1999; Loreau 2000). Empirical results support this supposition. In a meta-analysis of 63 local-regional richness plots, Hillebrand and Blenckner (2002) found that studies were more likely to find linear patterns when the local area occupied a greater proportion of the region. Although

similar analysis of a single large dataset showed no effect of local scale on the curvilinearity of local–regional richness plots (Caley and Schluter 1997), the smallest local scale (2500 km^2) of this study was probably still too large to reflect the scale of interspecific interactions (Westoby 1998). Because different species likely experience local interactions at distinct spatial scales, defining local scales will always be difficult.

Second, the relationship between local and regional richness is also sensitive to the scale at which regions are defined. This can be easily demonstrated by sampling species–area curves for multiple region sizes. Unsaturated communities will appear to have curvilinear local–regional richness plots when the largest regions have higher regional richness, and when the between-region species–area curve has a higher exponent than the within-region species–area curves (Srivastava 1999). Both of these conditions generally hold in ecological systems (Rosenzweig 1995) so such "pseudosaturation" is to be expected. For example, in a global comparison of lake zooplankton richness (Shurin et al. 2000), local richness initially appeared to saturate with regional richness. However, after standardizing the size of regions by using the residuals of the species–area relations, local richness was clearly proportional to regional richness. Thus, different definitions of the regional scale can produce qualitatively different patterns of local and regional diversity.

The third reason to treat scale explicitly is to incorporate processes operating at scales other than local and regional. At least two other scales may be important in determining diversity. For many organisms, especially sessile species, individuals only interact with other organisms over very small spatial scales. However, if an individual is considered as the local community (as in many patch-dynamic models), then local diversity cannot be greater than one. In this case, localities or clusters of patches that exchange propagules may better represent the

local scale, while groups of localities separated over larger scales correspond to metacommunities (Mouquet et al., Chapter 10). Groups of metacommunities with distinct geologic or evolutionary histories represent different regions. Thus, there may be two additional scales at which important processes take place, one smaller (the individual or patch) and one larger (the metacommunity) than the local scale. Because patches and metacommunities present all the same problems of definition as local and regional, a continuous treatment of scale may be preferable to a discrete one.

Fourth, processes leading to species saturation are also likely to be scale-dependent. For instance, invasion resistance, which is closely linked to saturation of local communities, can depend on spatial scale. Invasion success depends not only on characteristics of the local community, but also on traits of invading species (Kolar and Lodge 2002). Since these traits are phylogenetically constrained, we expect species from different regions to exhibit different suites of traits. We illustrate this point with two scenarios, one with a potential invader originating within the same biogeographic region as the target community, and one with an invading species originating outside the region. The potential invader originating within a region is more likely to share a common phylogeny with species native to the target community, and thus have traits similar to those already found within the community. If we assume that trait similarity leads to competitive exclusion (the competitive exclusion principle; MacArthur 1972), the potential invader from within the region will have lower invasion success than the species originating outside the region. This leads to the expectation that invasion success will be inversely related to the distance between the target community and the invader's point of origin. There is remarkably little empirical data that can be used to assess this scale-dependence of invasion success. Experiments with pond zooplankton show that local communities resist invasion by most species

found within 10 km (Shurin 2000), suggesting saturation at landscape scales. However, zooplankton communities are frequently invaded by exotic species, indicating that they are unsaturated on a global scale (Ricciardi and MacIssac 2000). Many of the most dramatic invasions with the greatest impacts on local communities involve species belonging to novel functional groups from the perspective of the invaded site. Snakes in Guam, zebra mussels in North America, and annual grasses in California may all be examples. These cases illustrate that the apparent saturation of a community depends greatly on the size of the area over which potential invaders are drawn. Many communities are "unsaturated" or invasible with respect to a global species pool.

Comparative and experimental studies of the relationship between diversity and invasibility also suggest that saturation of diversity is scale dependent. Many small-scale experiments have found a negative relationship between local native diversity and invasion success (Tilman 1997; Stachowicz et al. 1999; Levine 2000; Shurin 2000; Kennedy et al. 2002). By contrast, observational surveys over broad spatial scales often find positive correlations between the numbers of native and introduced species (Stohlgren et al. 1999; Levine 2000; Sax 2002; Shea and Chesson 2002). Sax et al. (2002) found that island chains have experienced many more invasions than extinctions, indicating that diversity at the scale of archipelagos is increasing and apparently not saturated. One explanation for this apparent contradiction may be that experimental studies manipulate local diversity (at scales of < 1 to a few m^2) whereas observational studies deal with diversity at broader regional scales (10 m^2 - 100s of km^2). The prediction that diversity confers invasion resistance (Elton 1958) is based on the idea of greater or more complete resource use in more diverse communities, clearly a local scale phenomenon. However, it is unclear how regional diversity should affect invasibility. If high regional diversity

is driven by greater environmental heterogeneity, then more diverse regions may have more available niche space and therefore be more invasible. Alternatively, if more diverse regions have longer evolutionary histories but similar ecological capacities to support species (Stephens and Weins 2003), then more diverse regions may be closer to saturation and less invasible. The relationship between invasibility and regional diversity remains an open question for empirical and theoretical study. However, the contrast between observational and experimental studies of invasions suggests that species saturation via ecological constraints is only expected to occur at relatively small local scales.

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<A> How space could be treated continuously

Because of the problems of drawing boundaries for discrete scales such as local and regional, introducing space as a continuous variable into models and empirical studies is an important next step. We now describe several ways in which scale can be incorporated into analysis of patterns as a continuous variable.

Earlier, we summarized evidence that the relationship between local and regional diversity changes as local richness is defined for increasingly large scales. One of the simplest ways to predict this change is to resample species–area curves corresponding to saturated and unsaturated communities at increasing "local" scales. The response variable in this analysis is the degree of linearity between local and regional richness, which can be assessed by the exponent of the power function (b) between the two variables ($b=1$ indicates linearity, $b < 1$ indicates various degrees of downward curvilinearity; see Hillebrand and Blenckner (2002) for justification). The steps in constructing the model are illustrated in Figure 17.2, and the proof is outlined in Appendix 17.1. The key point is that, based on species–area curves alone, b is predicted to be a

logarithmic function of the ratio of local area to regional area for saturated communities, but unrelated to this ratio in unsaturated communities (Figure 17.2e, Appendix 17.1). One can now ask which pattern communities follow. Hillebrand and Blenckner's (2002) meta-analysis allows us to address this issue. In this meta-analysis, the exponent (b) is significantly related to the ratio of local to regional area, and follows a logarithmic relationship (H. Hillebrand, pers. comm.; Figure 17.3). The implication is that many of the observed linear patterns between local and regional richness may actually represent saturated communities sampled at too large a local area. This conclusion is contrary to previous reviews that, without taking scale into account, showed the predominance of unsaturated patterns (Cornell and Lawton 1992; Srivastava 1999). Thus, although many studies concluded that communities show unsaturated patterns, the literature on local and regional richness collectively shows scale-dependent patterns that are more consistent with saturated, curvilinear patterns at some scales. Although overall the relationship between b and the ratio of local to regional scale is consistent with saturated *patterns*, the relative roles of local and regional *processes* cannot be deduced from this result for the reasons discussed above.

Since the relationship between local and regional diversity is influenced by scale, it is evident that beta diversity (the slope of the local–regional curve) must also be related to scale. There has been some use of hierarchical statistics to quantify how beta diversity changes across scales (e.g., Gering and Crist 2002). Such an approach may be useful in cases where there are strong predictions about the importance of different scales in the hierarchy. However, in the absence of such mechanistic models, results cannot be generalized beyond the particular discrete scales that the researcher chooses to examine. Scale can be incorporated as a continuous variable by considering beta diversity in nested quadrats (Kunin 1998; Harte et al. 1999; Arita and Rodriguez 2002) or between point counts (Condit et al. 2002).

In summary, we argue for a continuous treatment of space in examining patterns of diversity over approaches that depend on untestable definitions of discrete categories such as local and regional. Such patterns can provide critical tests of the importance of different mechanisms provided they are explicitly tied to models of underlying processes (e.g., Condit et al. 2002). However, the distinction between saturated and unsaturated patterns will always provide at best weak tests of the importance of local and regional processes in structuring communities, because many alternate hypotheses can often generate the same patterns (Shurin and Allen 2001). Instead, discontinuities or constancy in patterns of diversity across scales can generate hypotheses that are then subjected to more mechanistic studies (Kunin 1998; Harte et al. 1999; Condit et al. 2002).

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<A> Empirical evidence—interactions between local and regional processes

Patterns of local and regional diversity have been investigated in a wide range of systems (reviewed in Srivastava 1999; Hillebrand and Blenckner 2002). More mechanistic studies have been conducted in several systems and reveal interesting consequences arising from the joint effects of local and regional processes. Many of these studies indicate that dispersal and local processes are not mutually exclusive, but rather that the two can interact in interesting ways to generate community patterns.

Much of the most compelling evidence for the importance of regional processes comes from studies of sessile species such as terrestrial plants and intertidal invertebrates. A sessile lifestyle poses the problem of dispersal as each individual requires a propagule that colonizes a suitable microsite. However, because of the potential for space and resource competition, biotic interactions can also be of major importance in communities of sessile organisms. Experimental

studies indicate that seed limitation in terrestrial plants is a major constraint on species distributions and local diversity (reviewed in Turnbull et al. 2000). Adding seeds of many species, even ones that are present within relatively small regional scales (e.g., 1 km), often results in dramatic increases in diversity and biomass production at small local scales (e.g., within 1 m^2 plots; Tilman 1997; Turnbull et al. 2000). These studies show strong dispersal limitation of local diversity even though more species often fail than succeed in colonizing when introduced as seed (Tilman 1997). Disturbing the local community also results in greatly enhanced invasion (Burke and Grime 1996), indicating that interactions with local species repels many potential invaders. Further evidence for interesting interactions between local competition, dispersal, and environmental heterogeneity comes from metapopulation/metacommunity models discussed in the Theory section, above.

The predictions of neutral theories with localized dispersal and pre-emptive competition have been most extensively tested with tropical forest trees. Although empirical patterns of relative abundance are well described by neutral theories (Hubbell 2001), whether data indicate that the mechanisms envisioned by the model describe the natural processes remains unknown (see Chase et al., Chapter 14). Patterns of beta diversity are often inconsistent with neutral models, and instead, similarity among sites appears to correspond to variation in the physical environment more than to the scale of local dispersal. A further complication is that theoretical studies have also shown that neutral and non-neutral models can produce virtually indistinguishable patterns of relative abundance (Chase et al., Chapter 14).

Investigations in intertidal invertebrates suggest a shift from strong local interactions to recruitment limitation along an oceanographic gradient of decreasing larval supply along the Pacific coast of North America. A gradient in upwelling and onshore transport results in an

increase in recruitment by larval barnacles from California to the Pacific Northwest (Connolly et al. 2001), an increase in cover of adults, and perhaps greater intensity of local competitive and predatory interactions as well (Connolly and Roughgarden 1998). Clear evidence has been shown for both strong local interspecific interactions (e.g., Wootton 1997) and larval supply (Roughgarden et al. 1988) in Pacific intertidal invertebrates. Connolly and Roughgarden (1999) showed in theory that the strength of species interactions increases with greater levels of larval dispersal. They propose that competition and predation are more important at higher latitudes where larval supply is greatest due to onshore advection from oceanic currents. Comparative field experiments to estimate the intensity of species interactions along gradients of larval supply would be extremely valuable in showing such an interaction between processes at local and regional scales.

Fewer examples of mechanistic studies of the roles of local and regional processes are available in communities of motile organisms. Several studies of freshwater micro-organisms suggest that the outcome of local interactions depends on the supply of colonists from the surrounding region. Shurin (2001) found that effects of predators on zooplankton diversity and composition varied with the degree of habitat connectivity to the regional pool. In isolated ponds, predator invasion reduced local diversity as a number of large-bodied resident species were unable to coexist with zooplanktivorous fishes and insects. When a diverse group of zooplankton from the region was introduced as rare invaders, a number of small-bodied species invaded in the presence of predators, but not in their absence. This indicates that the occurrence of some species was indirectly facilitated by predators. Fish enhanced local diversity in connected communities, indicating that more species were facilitated than excluded. The results suggest that spatial heterogeneity in predator densities is an important factor promoting regional coexistence in

zooplankton, and that effects of predators on local communities are contingent upon habitat connectivity and regional context (see also Cottenie and De Meester, Chapter 8). By contrast, in inquiline communities of pitcher plants, invasion by protozoan species is either unaffected or reduced by mosquito predators (Miller et al. 2002). There is evidence that the occurrence of protozoan species in pitcher plants is limited by both dispersal and local interactions (resources and predation; Miller and Kneitel, Chapter 5). The persistence times of protozoan and rotifer species in pitcher plants are affected by the interaction of detrital resources (a local process) and mosquito colonization (a regional process; M.K. Trzcinski, S.J. Walde and P.D. Taylor unpubl. results). Results from freshwater communities thus suggest that feedbacks between local and regional processes play important roles in regulating species diversity and composition.

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<A> Conclusions

Recent conceptual and empirical advances in understanding local and regional diversity indicate that the distinction between saturated and unsaturated patterns of richness is not a reliable means for estimating the strength of local and regional processes. Current theory suggests that local and regional processes are not mutually exclusive, but may interact in interesting ways to generate patterns in communities (Ricklefs 2004). Empirical examples show that communities that show linear local–regional patterns can be nearly closed to invasion (Shurin 2000; Shurin et al. 2000). A number of reviews have concluded that most communities show linear relationships between local and regional richness; however, these patterns are highly scale dependent. If linear patterns dominate, then the slope of the local-regional curve should be independent of the relative sizes of the local and regional scales. Yet data from the literature survey of Hillebrand and Blenckner (2002) show that the slope increases with the ratio of local to

regional area (Figure 17.3). Thus, the overall picture from the literature on local and regional diversity is more consistent with saturation, or divergence in species–area relations among areas of different regional richness (Figure 17.2). Whether ecological communities are "saturated" with species or open to invasion from the regional pool remains an important unanswered question. We argue that space should be treated as a continuous variable rather than assigned to discrete categories such as local and regional, as illustrated in Figure 17.3. Linking continuous space with models of specific mechanisms of species interactions and dispersal offers much stronger inference than an approach that depends on untestable assumptions about spatial scale.

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<A> Acknowledgments

<A> Appendix 17.1

Consider two regions, each with a characteristic species–area relationship. In region 1, arbitrarily the richer of the two regions, the local richness (S_{L_1}) and regional richness (S_{R_1}) can be predicted from knowledge of the local area (A_L) and region area (A_R) as follows:

$$S_{L_1} = c_1 A_L^{Z_1}$$

$$S_{R_1} = c_1 A_R^{Z_1}$$

where c_1 and Z_1 are constants specific to region 1. In region 2, the appropriate equations are:

$$S_{L_2} = c_2 A_L^{Z_2}$$

$$S_{R_2} = c_2 A_R^{Z_2}$$

with c_2 and z_2 being constants specific to region 2.

The relationship between local and regional richness can be expressed as a power function with constants b and k:

$$S_L = k S_R^{b}$$

Substitution and rearrangement between the above five equations yields the following relationship:

$$b = \frac{(Z_1 - Z_2)\log A_L + \log c_1 - \log c_2}{(Z_1 - Z_2)\log A_R + \log c_1 - \log c_2}.$$

We first examine the form of this relationship for saturated and unsaturated communities. If the community is unsaturated, we expect the species–area curves to be parallel in log–log space, that is, $Z_1 = Z_2$ (Figure 2b; Srivastava 1999). In this case $b = 1$, indicating a linear relationship between local and regional richness irrespective of local or region area (Figure 17.2d, e). If the community is saturated, then $Z_1 > Z_2$ and $\log c_1 \geq \log c_2$ (Figure 17.2a; Srivastava

1999). In this case, $0 \geq b > 1$, indicating a curvilinear relationship between local and regional richness (Figure 17.2c).

The relationship can be simplified by considering the two ways in which the ratio of local to region area can be changed. If we change local area but keep region area fixed, and make the further simplifying assumption that a saturated community will have $c_1 \approx c_2$, then the relationship can be written as:

$$b = m \, \log(A_L / A_R) + 1$$

where m is a constant equivalent to $\log (A_R)^{-1}$. This simple logarithmic relationship is depicted in Figure 17.2e. Alternatively, if we change region area but keep local area fixed, then the relationship becomes:

$$b = n \log (A_R)^{-1},$$

where n is a constant equivalent to $\log A_L$. In practice, this inverse logarithmic relationship, when plotted on a $\log (A_L/A_R)$ axis, is very similar in shape to the variable local area equation.

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Table 17.1. A summary of theories for understanding the relationship between local and regional diversity and their predictions regarding the shape of the relationship between local and regional diversity.

Theory	Predictions for local vs. regional diversity
Island biogeography--simple metapopulation	Unsaturated at all levels of dispersal (non-interactive).
Metapopulation competition, global dispersal	Unsaturated at low dispersal, saturated at high dispersal if patch is considered "local."
Metapopulation competition, local dispersal	Saturated if patches are considered local, possibly unsaturated if the neighborhood is the local scale.
Source-sink ("super-saturation")	Unsaturated at low and high dispersal rates, saturated at intermediate levels (a hump-shaped relationship).
Food-web, keystone predation	Depends on predator and prey dispersal, predator effects on prey extinction and coexistence.

Figure legends

Figure 17.1. A conceptual model of the effects of dispersal rates on patterns of local and regional diversity. The left side of the graph represents patch dynamic models where local interactions occur much faster than dispersal. When local sites have no limits on potential diversity (as in a simple metapopulation), we expect positive relationships between local and regional diversity for all levels of dispersal, although the slope of the function will vary with connectivity. In models with local competitive exclusion, increasing dispersal frequency leads to saturated local–regional functions as local interactions become more intense when more species are supplied from the region. On the right side, dispersal occurs on a similar time scale to demographic rates such that immigration plays an important role in local population dynamics. In this case, low dispersal rates lead to relatively few sink populations and communities are saturated in the patch dynamic sense. Increasing dispersal creates more sink populations and local communities may become regionally enriched, leading to unsaturated patterns of diversity (the "low exclusion" curve). However, if sink populations exert large competitive influence on non-sink populations, then enhanced dispersal may lead to reduced local diversity due to exclusion. In the "high exclusion" case, high dispersal rates may lead to saturation as species in sinks reduce local diversity.

Figure 17.2. Saturated and unsaturated communities can be represented by two different types of log–log species–area plots, (a) and (b). In both cases, regions are shown with more (open circles) and less species (closed circles) at every spatial scale. In the saturated community, local richness should be similar in both regions, whereas regional richness should be divergent, yielding non-parallel species–area curves (a). In the unsaturated community, an identical ratio of local to regional richness creates parallel species–area curves in log–log space (b) (Srivastava 1999).

Now consider sampling the species–area curves at three different sizes of a "local" area, denoted A, B and C, but keeping region area (R) fixed. The local–regional plots are predicted to vary between these various local areas, as shown in (c) and (d). In the saturated community (c), local richness will be a power function of regional richness with the exponent $b<1$. However, as the local area approaches the regional area, local and regional richness will become highly correlated, and b will approach one (linearity). In fact, as local area is increased, b will increase as a logarithmic function of the proportion of local area to regional area (e) (Appendix 17.1). By contrast, in the unsaturated community, all local-regional plots will remain linear ($b=1$) even though the slope of this line will depend on local area (d), because the difference between log local and regional richness will be identical for both regions as seen in graph (b). The numerical examples illustrated use the following values: A = 10, B = 30, C = 90, R = 100 area units. The species–area curves for the saturated community are $S = 0.5A^{0.35}$ and $S = 0.5A^{0.5}$. The species–area curves for the unsaturated community are $S = 0.5A^{0.35}$ and $S = 0.8A^{0.35}$. The results can be generalized to multiple regions and any combination of local and regional areas (Appendix 17.1).

Figure 17.3. Estimates of b, the exponent of a power function between local and regional richness, from 63 published studies analyzed by Hillebrand and Blenckner (2002), as a function of the ratio of local to region area (A_L/A_R) in each study. There is a significant logarithmic relationship between b and A_L/A_R (Hillebrand and Blenckner 2002). This is consistent with the theoretical prediction for a saturated community, but not that for an unsaturated community (Figure 17.2). The y-intercept of the fitted function is 1, identical to the theoretical prediction (see Appendix 17.1). Data were provided by H. Hillebrand.
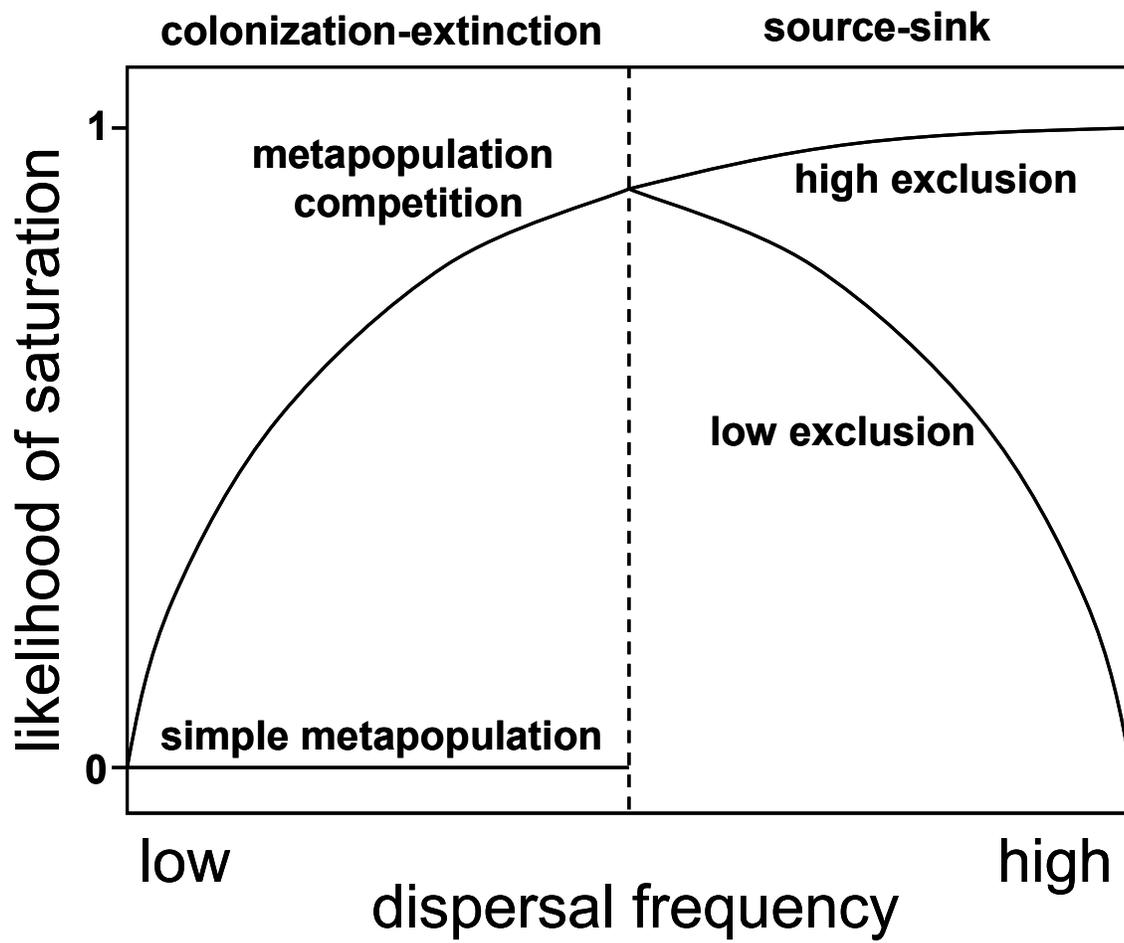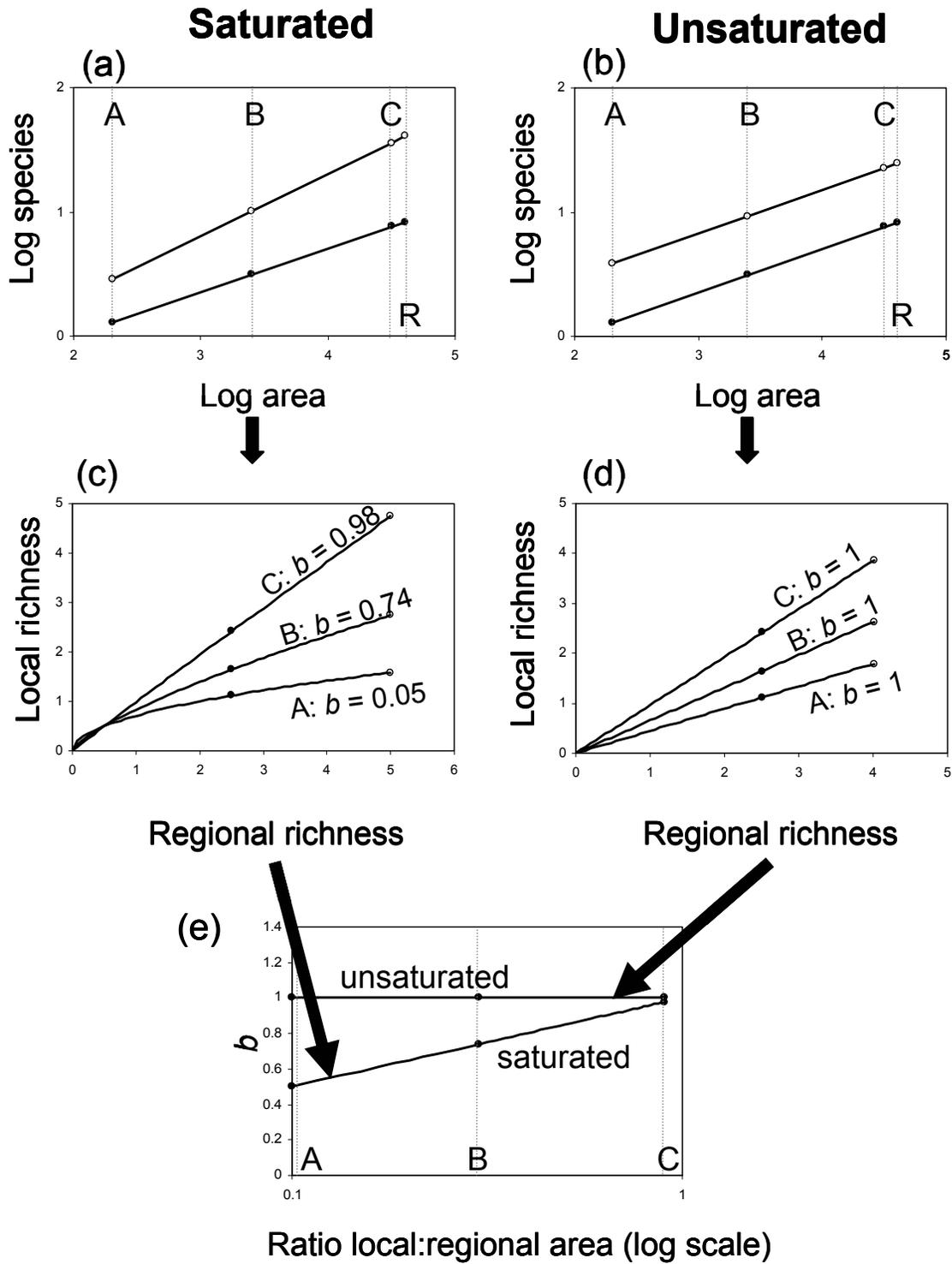
Fig. 1

Fig. 2

Fig. 3