

Are communities saturated? On the relationship between α , β and γ diversity

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Abstract

A popular way to suggest a regional influence on local species diversity has been to plot local *versus* regional diversity. The form of these curves has been interpreted as evidence for or against “community saturation” due to species interactions. This interpretation, however, is unwarranted. Using the concepts of α , β and γ diversity, I show that local–regional richness curves are determined by the way total diversity is partitioned between its α and β components, which itself is a matter of scale. Changing the scale of the local community amounts to changing the scale at which the heterogeneity of the interactions between organisms and their environment manifests itself, and hence the balance between α and β diversity. Community saturation may occur because of physical limitations, but there are no theoretical grounds for the belief that species interactions set an absolute upper limit to diversity at any scale. A distinction between different meanings of the concept of “saturation” is proposed to clarify this issue. I argue that the challenge now is to understand the relationship between α and β diversity at multiple scales, and the processes that determine it.

Keywords

Community saturation, competition, dispersal, local richness, regional richness, scale, species diversity, species interactions.

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Understanding why there are so many – or so few – species, over the whole range of scales from that of a local community to that of the biosphere, has been one of the major focuses of interest in ecology since its beginnings. An important shift in paradigm in community ecology has occurred during the last 15 years or so with the recognition that local communities are not governed solely by local processes, but that regional, biogeographical processes are also important (Ricklefs 1987; Ricklefs & Schluter 1993). A popular way to suggest this regional influence has been to plot local *versus* regional species richness for matching sites (Terborgh & Faaborg 1980; Ricklefs 1987; Cornell & Lawton 1992; Cornell 1993; Cornell & Karlson 1997; Srivastava 1999). Typically, these graphs have shown that local diversity increases with regional diversity, in most cases linearly, as if local communities were obtained by proportional sampling from the corresponding regional pool. Saturating curves in which local diversity becomes independent of regional diversity are a minority, and probably even a small minority taking into account statistical and methodological problems associated with their detection (Cornell &

Karlson 1997; Lawton 1999). These works do suggest that local diversity and regional diversity cannot be understood in isolation. But these graphs have also been given a much stronger interpretation: unsaturating curves would be typical for – though not exclusive to – “unsaturated”, “noninteractive” communities, whereas saturating curves would indicate “saturated”, “interactive” communities (Terborgh & Faaborg 1980; Cornell & Lawton 1992; Cornell 1993). And, despite warnings that patterns alone are not sufficient to infer processes (Cornell & Lawton 1992; Cornell 1993; Lawton 1999), many ecologists have continued to interpret them in that way. In this paper I show that this interpretation is unwarranted, and that saturation of local–regional richness curves does not tell us anything about community saturation due to species interactions, but is more fundamentally related to the scale at which a local community is defined. I argue that a more promising challenge now is to understand the relationship between α and β diversity at multiple scales, and the processes that determine it.

The total diversity in a region may be partitioned into two components: a local, within-community component,

called α diversity (D_α), and a between-community component, called β diversity (D_β), following Whittaker's (1972, 1977) terminology. The total, regional diversity is then γ diversity (D_γ). These diversity levels can be related by additive partition as follows (Lande 1996):

$$D_\gamma = \bar{D}_\alpha + D_\beta \quad (1)$$

Note that this additive partition differs from the classical, multiplicative approach (Whittaker 1972), but it has a greater potential in terms of both consistency (Lande 1996) and application to multiple scales (see below). In what follows, only species richness will be considered, but equation (1) can be applied to other measures of diversity as well (Lande 1996). Equation (1) shows clearly that, if α diversity stays constant while γ diversity increases, as is the case with saturating local–regional richness curves, this implies a corresponding increase in β diversity (Fig. 1). This mutual dependency of local and regional diversity through β diversity has been recognized in theory (Cornell & Lawton 1992; Cornell 1993; Rosenzweig 1995; Srivastava 1999); yet it has been ignored in practice in the interpretation of local–regional richness curves. Both the empirical hypotheses and the models (Caswell & Cohen 1993; Morton & Law 1997) have considered regional diversity as an independent variable in the form of a fixed “species pool” and local diversity in an isolated community as a dependent variable. Assuming that α diversity were constant because of local saturation, the question then is: what allows γ diversity, and hence β diversity, to increase while α diversity is kept constant?

This is fundamentally a matter of how diversity is partitioned between its α and β components, which itself

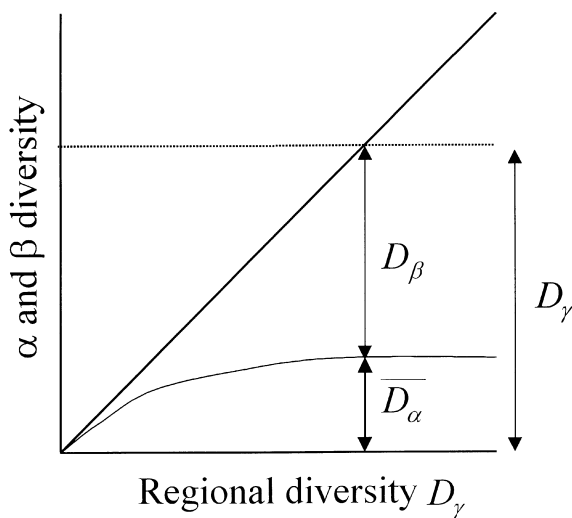


Figure 1 The relationship between α , β and γ diversity on a classical graph of local (α) versus regional (γ) diversity, in a case where α diversity is a saturating function of γ diversity.

is a matter of scale. Although Whittaker's (1972, 1977) concepts of α , β and γ diversity were originally based on a consideration of the spatial scales at which different processes might dominate, it has proved extremely difficult to identify these scales in operational terms. There is essentially no prescription in ecology on how to define the spatial scale of a local community. At one extreme, if the local community is defined at the scale of a few individuals, α diversity will be minimal and almost constant since it cannot be greater than the number of individuals (actually, much less than that since species usually differ markedly in abundance). One advantage of a small scale is that strong direct interactions among organisms can occur at that scale (Huston 1999). But the “saturation” of species richness at such a scale also becomes an inevitable consequence of the physical limitation of the entity considered, irrespective of interactions among species. Simply, the environmental heterogeneity that is responsible for the bulk of diversity has been transferred from the local to the regional scale, hence from α to β diversity. At the other extreme, if the local community is defined at a scale close to that of the entire region, α diversity will incorporate almost all of γ diversity and obviously increase parallel to the latter, also irrespective of interactions among species. At intermediate scales, all intermediate cases are possible, without there being any particular reason for species interactions to determine the pattern more than at extreme scales. Caley & Schluter (1997) have shown that the local–regional richness curve is expected to change gradually from a saturating to a linear curve as a simple consequence of increasing the size of the local habitat, without any species interactions involved. Srivastava (1999) presented other scenarios in which differences in the size of the regions can lead to changes in the shape of the curve. Generally speaking, changing the scale of the local community amounts to changing the scale at which the heterogeneity of the interactions between organisms and their environment manifests itself, and hence the balance between α and β diversity.

This can be generalized by noting that the division between the “local” and “regional” scales is an idealization for a more complex reality. For most organisms, there is a nested hierarchy of multiple scales characterized by different patterns and processes, from a small neighbourhood to the biosphere, through the patch, “community”, landscape, regional and continental scales. Whittaker (1977) already recognized this, and suggested a provisional extended classification with seven diversity levels. However, he also acknowledged that the α and β concepts could be applied to different scales, an alternative that seems more appropriate given that spatial scales intergrade along a continuum and differ among

organisms. At each scale, diversity can then be partitioned using equation (1), such that total (or γ) diversity in a spatial unit becomes within-unit (or α) diversity at the next higher scale. The total diversity at a scale is thus determined by diversity at the next lower scale (α component) and the between-unit diversity (β component) maintained as the result of environmental heterogeneity (in space, time or food resources) and niche differences among species (which define different ways to respond to environmental heterogeneity) at that scale. Movements between spatial units (dispersal, migration...), however, act as a homogenizing force, which tends to reduce the β component of diversity but at the same time to increase the α component because immigration contributes to maintain local coexistence (Loreau & Mouquet 1999). Thus, the various scales interact, with both bottom-up and top-down effects which affect the balance between the α and β components of diversity at all scales.

All this in no way implies that species interactions are unimportant. But, even when they are strong, their effect is scale dependent and mixed with the effects of other scale-dependent factors in such a way that they are unlikely to set diversity at a particular scale to a constant level across regions that are subject to different constraints. To take a simple example as an illustration, consider a set of species competing for the same limiting resource in a mosaic of n patches. Each patch is homogeneous enough to lead to competitive exclusion of all but one species, but is different enough from the other patches so that a different species is competitively dominant in each patch. In this scenario, local diversity is constrained to a minimum by competition ($D_\alpha = 1$), and the total species richness in the mosaic ($D_\gamma = n$) is determined by the environmental heterogeneity between patches, which finds expression in a maximum β diversity ($D_\beta = n - 1$). Now consider a similar mosaic of patches in another region where dispersal is allowed among patches. If dispersal is high enough, it can counteract local competitive exclusion and maintain the coexistence of all species in each patch (Loreau & Mouquet 1999; Mouquet and Loreau, unpublished results). In this case, total diversity is still determined by the environmental heterogeneity between patches ($D_\gamma = n$), but the homogenizing force of dispersal has transferred its effect from the β to the α component of diversity ($D_\alpha = n$, $D_\beta = 0$). Thus, dispersal may interact with local competition to control the balance between α and β diversity in completely different ways in different regions. The same can be shown to be true for patch size: for a given level of dispersal, smaller or less productive patches sustain fewer individuals on average, which tends to decrease local diversity by stochastic extinction of inferior species

maintained by dispersal in a patch, and hence to increase β diversity correspondingly.

Given these complex interactions among scales, is it reasonable to expect such a thing as “community saturation”? Clearly, as discussed above, “saturation” can occur because of physical limitations. If the environment is used in the form of discrete units at a scale, the absolute number of units sets an absolute upper limit to diversity at that scale. Stochastic processes may further contribute to reduce this upper limit. But, once these physical limitations are accounted for, there are no theoretical grounds for the widespread belief that species interactions set an absolute upper limit to diversity at any scale. They may set a limit, but only a limit relative to a given species pool. Take for instance MacArthur’s (1972) classical model of exploitation competition. I choose this example not because it is the most general and robust model of competition (e.g. Abrams 1998 for some of its limitations), but because the body of theory developed by MacArthur (1972) on competition and limiting similarity is usually interpreted as implying that communities are saturated with species (Cornell & Lawton 1992; Cornell 1993). Given a fixed pool of species with fixed traits such as niche breadth and overlap, MacArthur’s (1972) theory predicts that a single community emerges as a globally stable equilibrium configuration—the community that best utilizes available resources. But the composition and diversity of this equilibrium community are shaped by the particular species pool and resource availability distribution chosen. Although the species that coexist at equilibrium must be sufficiently dissimilar in the way they use resources, there is no absolute “limiting similarity” (Abrams 1983). Accordingly, communities may saturate through time for a given initial species pool, but they do not generally saturate with species with respect to changes in the species pool, as determined by evolutionary or historical processes. Evolutionary adjustments of local diversity have been recognized previously (Cornell & Lawton 1992; Cornell 1993); yet their obvious implication is that there should be no “hard limit” to local diversity when regions with different evolutionary histories are compared. As Whittaker (1972) already emphasized, “There is no evident intrinsic limit on the increase in species number, with increased packing and elaboration of axes of the niche hyperspace” (p. 217).

The same conclusion could be shown to hold for any other mechanism of coexistence. Thus, a clear distinction needs to be made between different meanings of the concept of community saturation: saturation through time should be distinguished from saturation with respect to the species pool (Morton & Law 1997), and saturation of species richness should be distinguished from saturation of total density, biomass or other measures of community-

level performance related to resource use. Competition for limiting resources obviously implies some form of saturation of total community density under equilibrium conditions, it may also lead to saturation of species richness through ecological time provided sufficient temporal and spatial homogeneity, but it is not expected to lead to saturation of species richness with respect to the species pool unless physical limitations come into play. These theoretical conclusions suggest that local species diversity should usually increase with regional diversity except for small-scale communities, a pattern that seems consistent with empirical data (Lawton 1999).

The identification of patterns is often a useful step in the scientific investigation to raise new questions. These questions, however, can only ultimately find an answer in the study of processes. Patterns of local *versus* regional species richness have played their role in pointing to a link between local and regional diversity. I suggest that it is now time to shift attention to the processes that control diversity over the whole range of scales (see also Huston 1999). Recognizing the relationship between the α and β components of diversity at these multiple scales may help in bringing us a little closer to that objective.

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BIOSKETCH

Michel Loreau has a broad interest in population ecology, community ecology, ecosystem ecology, theoretical ecology and evolutionary ecology. His current theoretical work is focused more especially on biodiversity and ecosystem functioning, and on the ecology and evolution of indirect species interactions mediated by material cycling in ecosystems.

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