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FORUM

Placing local plant species richness in the context of environmental drivers of metacommunity richness

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Summary

1 Ecologists seem poised to reap the benefits of recent work examining the effects of energy and resources on plant taxonomic richness in local communities. My goal here is to present a qualitative model to further our understanding about the driving forces of plant taxonomic richness across spatial scales.
2 The model attempts to predict local plant species richness based on previous work regarding (i) correlations between temperature, precipitation and richness, (ii) correlations between soil nutrient availability and richness derived from both descriptions and experimental manipulations, and (iii) empirical demonstrations of the importance of the species pool in regulating local species richness.
3 The model consists of a phenomenlogical submodel of the multiplicative effects of temperature, water and mineral nutrients on plant species richness, with a spatially implicit submodel of immigration and extinction of species in local communities.
4 The model makes the following five testable predictions. (i) Local richness increases linearly with immigration rate of new species and curvilinearly with local extinction rate. (ii) The effects of altered local immigration and extinction rates will be most apparent in local communities embedded in species-rich metacommunities. (iii) Local communities are not saturated, but rather increase in richness directly with increasing metacommunity richness. (iv) Unimodal or hump-shaped productivity-richness relations arise when low water or temperature limit diversity at low productivity and mineral nutrients limit diversity at high productivity. (v) An apparent scale-dependence of the effect productivity on richness should arise when there exists a matching scale-dependence of the underlying environmental drivers. These predictions do not contrast sharply with available data, but remain largely untested.
5 I suggest that continued attempts to synthesize the most predictive patterns emerging from the burgeoning global data bases of both taxonomic and genetic diversity will guide us toward mechanistic explanations of the determinants of species richness, suggest why special cases differ from general patterns, and provide additional novel predictions not currently apparent.

Key-words: metacommunity, species pool, scale-dependence, scale, latitudinal gradient, diversity, productivity, hump-shaped, competition, source–sink, shifting limitation

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Introduction

Patterns of biodiversity along latitudinal and productivity gradients are some of our most dramatic patterns in the living world (Wallace 1878; Waide *et al*. 1999), and there seems to be renewed interest in explaining such large scale patterns (Ricklefs & Schluter 1993; Brown 1995; Currie *et al*. 2004; Ricklefs 2004). Recent empirical and theoretical studies have examined patterns of plant diversity in relation to specific environmental drivers such as water, temperature and mineral nutrients (Allen *et al*. 2002; Francis & Currie 2003; Davies *et al*. 2004; Suding *et al*. 2005), which all correlate to some degree with latitude and productivity. In addition, it is widely recognized that local plant communities can be strongly influenced by the regional species pool (Partel *et al*. 2000; Foster 2001; Grace 2001). Here

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my objectives are to combine existing environment-biodiversity relations into a simple coherent framework, to link local and metacommunity scales and to describe the resulting predictions for local species richness.

Predictive relations exist between environmental factors and plant taxonomic richness. O'Brien (1998), Francis & Currie (2003), and Davies *et al*. (2004, 2005) have shown that water and energy can explain as much as 80% of the variation in plant taxonomic richness within regions ranging in size from biomes to the globe. Allen *et al*. (2002) have shown that biochemical kinetics of metabolism can predict, from first principles, large scale temperature-richness patterns of endotherms and ectotherms, including tree species richness in both North America and Costa Rica. Temperature can also vary at small scales, with consequences for local communities. In alpine communities, plant aggregation, snowpack, microtopography, aspect and elevation can influence temperatures experienced by individuals, influencing both individual fitness and species diversity (Callaway *et al*. 2002; Kammer & Mohl 2002; Korner 2002; Kikvidze *et al*. 2005). In deserts and intertidal zones, established plants and dominant algae can reduce air and surface temperatures, reducing direct heat stress, soil drying and salinization, and thereby enhance fitness and diversity (Shreve 1931; Turner *et al*. 1966; Bertness *et al*. 1999; Hacker & Bertness 1999). Small scale variation in water availability can also cause variation in plant fitness, total biomass and species richness (Briggs & Knapp 1995; Goldberg & Novoplansky 1997; Novoplansky & Goldberg 2001; Maestre *et al*. 2005), even in generally mesic environments (Stevens *et al*. 2005; Bunker & Carson 2005).

Several mechanisms have been proposed to explain these environment–richness relationships. Mechanistic models of physiological tolerance indicate that a wider variety of physiological configurations can survive in benign (warm and wet) conditions than in harsh (cold or dry) conditions (Hall *et al*. 1992; Kleidon & Mooney 2000; VanderMeulen *et al*. 2001). Increased speciation rate in warmer environments, due to increases in metabolic rate (including per locus mutation rate) and decreased generation time has also been suggested to enhance diversity (Rohde 1992; Allen *et al*. 2002). While debate exists concerning these mechanisms (Currie *et al*. 2004; Huston *et al*. 2003; Davies *et al*. 2004), they nonetheless remain plausible explanations of plant diversity gradients.

In addition to water and temperature, soil nutrients also have important impacts on plant species richness. Both broad scale patterns (Tilman & Pacala 1993; Huston 1993, 1994) and experiments (DiTomasso & Aarssen 1989; Gough *et al*. 2000a; Suding *et al*. 2005) show that plant species richness declines with increasing mineral nutrients. Many hypotheses have been proposed to explain this pattern (for review see Rajaniemi 2003), and competition-based explanations seem promising (Foster & Gross 1998; Rajaniemi *et al*. 2003; Stevens *et al*. 2004).

The above patterns and mechanisms suggest that these relations are scale independent, with very small scale (i.e. neighbourhood) processes driving environment–richness patterns at larger scales (Huston 1999). Predictive relations between temperature, water and richness seem to occur across a wide range of spatial scales. Of the proposed mechanisms for all of these patterns, all operate at the individual (physiological tolerance, mutation rate) or neighbourhood (competition) level. Huston (1999) suggested that the consequences of these small scale processes controlling diversity scale up to larger regions. This is not to say that other, larger scale phenomena do not influence regional patterns of richness (Silvertown 1985; Latham & Ricklefs 1993; Qian & Ricklefs 2000), but rather that small scale processes lead to a coherent set of mechanisms and patterns that are scale-independent and do not depend on historical contingencies.

Toward a heuristic model

Below, I first create a simple model for metacommunities that combines the phenomenological patterns of species richness and temperature, water and nutrients observed at large spatial scales. I begin with patterns at large spatial scales for two reasons. First, the species pool at large spatial scales forms the metacommunity that provides the ecological context for local communities (Ricklefs 2004; Huston 1999; Leibold *et al*. 2004). Second, related phenomenological models have already been proposed to describe some of the large scale patterns. Following this model for metacommunities, I draw on a metapopulation model to embed the richness of a local community into the metacommunity species pool.

Environmental determinants of metacommunity species richness

The effects of temperature, water and mineral nutrients on plant species richness in large areas seem relatively straightforward. Combining the above patterns in a functional form, we have the basis for a qualitative model for species richness,

$$S_M \propto T(1 - T + W)\cdot\frac{W}{(\alpha + W)}\cdot\frac{e^{-N}}{\beta + e^{-N}} \qquad \text{eqn 1}$$

where S_M, T, W and N are species richness in the metacommunity, temperature, water supply rate and nutrient supply rates, respectively, of a metacommunity, and α and β are positive constants (Fig. 1). The values of the constants are not particularly important for generating the qualitative shapes of the patterns of richness. The forms of the expressions for T, W and N were selected for their simplicity, and because they have strong empirical support. The polynomial term for the temperature effect depends on water availability and derives directly from O'Brien (1998), O'Brien *et al*. (2000) and Francis & Currie (2003). The Michaelis–Menten

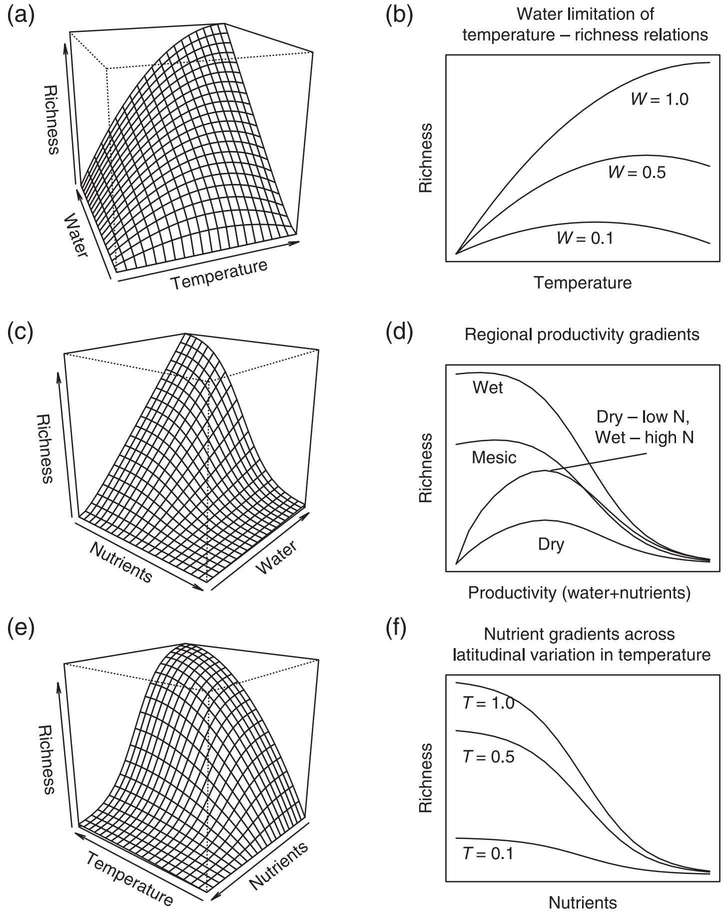

Fig. 1 Qualitative effects of temperature, water and limiting mineral nutrients on plant species richness ($\alpha = 0.1$, $\beta = 1$). Figures (b), (d) and (f) are vertical cross sections of Figures (a), (c) and (e), respectively. (a–b) Effects of temperature and water on richness ($N = 0.1$). (c–d) Effects of water and nutrients on richness ($T = 1.0$). The x axis in (d) represents various diagonal cross sections (generally left to right) through (d). It represents both a nutrient gradient (0–1) and a covarying water gradient that differ for each case (Dry, $W = 0–0.33$; Mesic, $W = 0.34–0.67$; Wet, $W = 0.68–1.0$; Dry-LowN/Wet-High, N & $W = 0–1.0$). (e–f) Effects of temperature and nutrients on richness ($W = 1.0$).

form of the water term was selected to describe the form of the precipitation–richness relationship in Francis & Currie (2003). The logistic form of the nutrient term was selected because it does not result in negative values as nutrients increase, and because it results in proportional loss of species with increasing nutrients, consistent with empirical observation (Gough *et al*. 2000a). Unlike the models of O'Brien (1998) and Francis & Currie (2003), or Huston (1994), this model attempts to combine and reconcile the patterns associated with water and temperature and those associated with soil nutrient availability. Equation 1 reproduces the dominant patterns of plant species richness (Fig. 1), and in doing so, allows direct comparison of the contrasting roles of temperature, water and nutrients. Further, it has implications for effects of productivity on richness.

Equation 1 does not explicitly include several environmental factors that have been shown to influence plant richness and composition, such as disturbance (Connell 1978; Huston 1994), herbivory (Collins *et al*. 1998; Carson & Root 2000; Chase *et al*. 2000; Fine *et al*. 2004; in press) and additional soil characteristics (Crawley *et al*. 2005; Gough *et al*. 1994, 2000b; Grace 1999; Grace *et al*. 2000; Weiher 2003). pH may be especially important, influencing richness at several spatial scales (Gough *et al*. 2000b; Partel 2002; Crawley *et al*. 2005). It might be readily incorporated into a physiological tolerance model or included for its effects on nutrient availability. For the time being, however, parsimony suggests that we can put off consideration of these factors for a later time.

Embedding a local community into the regional metacommunity

Species richness in a local community changes through immigration or local extinction, and is capable of changing much more rapidly than the richness of a metacommunity. For this reason, I place species richness of a particular local community into a metacommunity framework, presenting one possible derivation below. My representation of the state variable P_j is inspired by and directly analogous to metapopulation models of species distributions among sites (Gotelli 1991; Levins 1969; Hanski 1982). In the model presented here, let the variable of interest, P_j, be the proportion of the species in the metacommunity found in a particular local community j, and let each local community j be embedded in the metacommunity, where metacommunity richnessn S_M is scaled to 1. Let propagules (species) derive from the metacommunity in which richness changes relatively slowly and is determined by temperature, water and nutrient availability (metacommunity richness is, therefore in this sense, independent of local species richness), i.e.

$$\frac{dP_j}{dt} = i_j(1 - P_j) - e_jP_j(1 - P_j) \qquad \text{eqn 2}$$

This is simply a metapopulation model with propagule rain and rescue effect (Gotelli 1991). Total immigration rate of new species (first term in equation 2) has a maximum at $P_j = 0$, and decreases linearly with increasing P_j. Gotelli (1991; Gotelli & Kelley 1993) refers to this as propagule rain, where, in this case, per species immigration rate, i_j, does not otherwise depend on the richness of other local communities, but merely on the regional pool. Total extinction rate (second term in equation 2) has a maximum at $P_j = 0.5$. Increasing P_j decreases total extinction rate by increasing the importance of the rescue effect, $1 - P_j$ (Brown & Kodric-Brown 1977; Hanski 1982). Decreasing P_j merely decreases the likelihood of an extinction, eP_j.

The equilibrium solution for this model is

$$P_j^* = \frac{i_j}{e_j} \qquad \text{eqn 3}$$

This solution shows an infinite number of stable equilibria of local richness values P_j which depend on specific rates of immigration and extinction in that local community j (equation 3); richness saturates at 1.0 when $i > e$. This also shows that the effect of i on P_j^* is linear, whereas the effect of e on P_j^* is curvilinear, related directly to e^{-1}. This difference between the incremental effects of i and e constitute the first prediction of this model.

We then place this within the metacommunity context, where, combining equation 1 and 3 gives,

$$S_j \infty \frac{i_j}{e_j}\left(T(1 - T + W) \cdot \frac{W}{(\alpha + W)} \cdot \frac{\exp^{-N}}{\beta + \exp^{-N}}\right) \qquad \text{eqn 4}$$

Equation 4 represents the effects of the average environmental conditions in a metacommunity and the rates of immigration and extinction in the local community in determining the number of species in that local community. Ecologists recognize that the richness of a local community depends in part on the richness of the surrounding matrix (e.g. Cantero *et al.* 1999; Partel *et al.* 2000; Foster & Tilman 2003), and equations 2–4 derive and specify a relation between local community richness and total immigration rate into a local site.

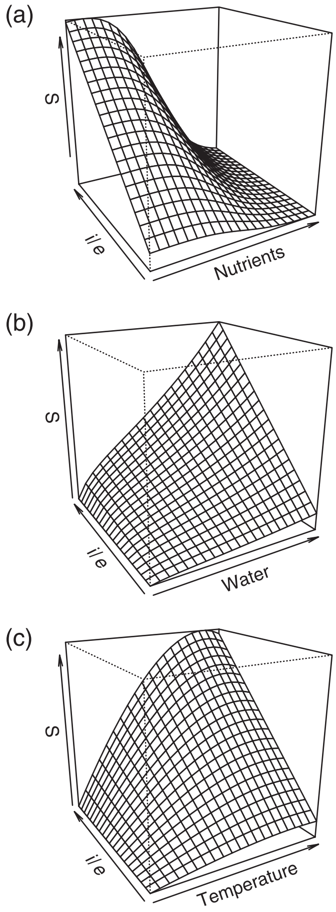

Fig. 2 Predicted responses of local species richness to variation in environmental variables and local immigration and extinction rates. (a) Effects of average nutrient supply rates and local immigration and extinction. (b) Effects of average water supply rates and local immigration and extinction. (c) Effects of average temperature and local immigration and extinction. Note that i and e vary linearly along the i/e axis (increasing $i = 0.01, \ldots, 0.1$; $e = 0.15, \ldots, 0.1$; $i/e = 0.067, \ldots, 1.0$).

Variation among local communities in any factor or process, such as area or herbivory, that influences local immigration or extinction rates is thus predicted to influence local richness, and this influence should thus be directly proportional to the richness of the metacommunity (Huston 1999). This means that the effects of i/e on richness will be most pronounced and measurable in the most diverse metacommunities (Fig. 2). This constitutes the second prediction of the model.

Another prediction of equation 4 is that local communities are never truly saturated: local richness, S_j, increases linearly with metacommunity richness. This constitutes the third prediction of the model. This is conceptually similar to neutral models which assume that a local community is a random sample of the metacommunity (MacArthur & Wilson 1963; Hubbell 1997, 2001; Bell 2000; Bell 2001). In principle, local communities can saturate if they are sufficiently small. The precise nature of this sampling curve will depend on the size of the local community, and the species abundance distribution of the metacommunity. However, simulations (not shown) indicate that the relation may be indistinguishable from linear for local communities composed of at least several thousand individuals, roughly equivalent to a few millilitres of pond water containing phytoplankton, a hectare of grassland, or 10 hectares of mature forest.

Productivity–richness patterns

Water, nutrients and temperature control plant productivity, and thus it seems warranted to address what equation 4 might predict about patterns of plant species richness along productivity gradients. Equation 4, however, does not include an explicit representation of productivity. I excluded measures of the environment that include plant performance, such as actual evapotranspiration (cf. Francis & Currie 2003) because of the complex relations between plant biomass, density and richness (Enquist *et al*. 1998; Stevens & Carson 1999) and on the basis of parsimony (Peters 1991): I would like to see how far we can get in relating the environment to richness, even if there exist intermediate mechanistic linkages (Grime 1979; Huston 1994, 1999).

Data suggest that the effects of productivity on plant species richness are various, and may be positive, negative, unimodal or U-shaped (Waide *et al*. 1999; Mittelbach *et al*. 2001, 2003). Equation 1 predicts unimodal patterns of richness along productivity gradients, which are widely cited in the literature (Waide *et al*. 1999; Mittelbach *et al*. 2001, 2003; Chalcraft *et al*. 2004) and arise when nutrients covary positively with either water (Fig. 1c–d) or temperature. In such cases, either low temperature or low water limit both richness and productivity, and high nutrient availability limits richness at high productivity. This constitutes the fourth prediction of the model, and arises in part because of the assumed multiplicative rather than additive effects of nutrients and water or temperature. Other parameter combinations resulting in productivity gradients (e.g. a nutrient gradient with constant water and temperature) predict monotonic productivity–richness relations. The underlying cause of any particular natural productivity gradient is not always clear. For example, either soil moisture or temperature can regulate soil microbial dynamics and create variation in plant available nutrient concentrations (Atlas & Bartha 1998; Chapin III *et al*. 2002), thereby causing in a natural productivity gradient.

Several studies have also suggested that spatial scale may dictate the form of the productivity–richness relation (Pastor *et al*. 1996; Waide *et al*. 1999; Gross *et al*. 2000; Mittelbach *et al*. 2001, 2003; Chase & Leibold 2002; Chalcraft *et al*. 2004). Some investigators have proposed that different mechanisms that control diversity operate at different spatial scales (Shmida & Wilson 1985; Latham & Ricklefs 1993; Qian & Ricklefs 2000; Scheiner *et al*. 2000; Hubbell 2001; Chase & Leibold 2002). Nothing in equation 4, however, inherently predicts scale dependence of productivity–richness relations. Nevertheless, equation 4 does predict such scale dependence if temperature, water and nutrients each vary widely, but at different spatial scales. In such cases, random samples of plant communities at different spatial scales could result in different productivity–diversity relations at different scales (Scheiner *et al*. 2000). This constitutes the fifth prediction of the model.

Conclusions

HOW DO THE PREDICTIONS ARISING FROM EQUATION 4 FIT WITH EXISTING HYPOTHESES AND THE AVAILABLE DATA?

The first prediction, that local richness increases linearly with immigration rate of new species and curvilinearly with local extinction rate, contrasts with predictions of Loreau & Mouquet (1999). They show that richness increases as a sigmoidal function of immigration, although this may appear linear over a wide range of immigration intensities. To my knowledge, these ideas have not been evaluated with any data (cf. Tilman 1993; Stevens *et al*. 2004).

Second, it predicts that the effects of altered local immigration and extinction rates will be most apparent in local communities embedded in species-rich metacommunities. This was suggested previously by Huston (1999) and Foster (the shifting limitation hypothesis, 2001), with regard to effects of productivity on immigration, extinction and the resulting richness. Specifically, equation 4 predicts that the slope of the richness–biomass relation should be steeper in plots with added seeds (an experimentally enriched species pool). Foster (2001) and Foster *et al*. (2004) found this to be the case in undisturbed, but not disturbed vegetation. In contrast, Stevens *et al*. (2004) found no such differences in slopes, and this may have been due to the higher productivity and light interception at their site. Such contrasting findings might be better understood with direct measurement of both immigration and extinction rates.

Third, equation 4 predicts that local communities are not saturated, but rather increase in richness directly with increasing metacommunity richness. This seems consistent with some data sets (Cantero *et al*. 1999; Partel *et al*. 2000), but testing this prediction at larger scales is problematic (Huston 1999), and in small enough communities (e.g. a neighbourhood of one individual), it must be false. In practice, we need to look at scales small enough so that competition could limit richness (Huston 1999), but not so small as to be trivial (Munzbergova 2004). Null models may help make quantitative predictions in competition-limited vs. competition-unlimited conditions such as equation 4.

Fourth, equation 4 predicts that unimodal or hump-shaped productivity–richness relations arise when low water or temperature limit diversity at low productivity and mineral nutrients limit diversity at high productivity. This extends Foster's (2001) shifting limitation hypothesis to include very low productivity conditions.

This prediction is largely untested, as the large-scale studies that have identified unimodal patterns in plant communities have not generally performed the necessary manipulations across sites.

Fifth, equation 4 predicts that the apparent scale-dependence of the effect of productivity on richness, now widely discussed in the literature, should arise only if there exists a matching scale-dependence of the underlying environmental drivers. This does not seem to have been considered among the hypotheses to explain unimodal patterns in plant communities (Chalcraft *et al*. 2004). Assessing the spatial scale-dependence of relevant environmental factors seems important to further our understanding of scale-dependent patterns of species richness.

In addition to a growing appreciation and understanding of scale effects (Leibold *et al*. 2004; Ricklefs 2004), two additional avenues seem promising. First, there exist direct parallels between the control of genetic and taxonomic diversity (Vellend 2005). While the study of these types of diversity has taken largely separate paths (Vellend & Geber 2005), the study of plant taxonomic diversity may benefit from an infusion of theory and data on genetic diversity. Second, diversity research has been limited by the amount of data available (Huston 1999), but progress is being made in this area with increasing amounts of data, analysis and synthesis at a wide variety of temporal and spatial scales (see, for example, www.salvias.net, palaeodb.org, knb.ecoinformatics.org, www.nceas.ucsb.edu, www.neoninc.org, www.lternet.edu, www.mobot.org/MOBOT/Research/APweb, and data appendices or 'data papers' in major ecological journals). Large data bases have been essential for the progress of molecular biology (e.g. www.ncbi.nlm.nih.gov), and now seem necessary for understanding taxonomic diversity at multiple scales as well.

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