

# Developing Unified Theories in Ecology as Exemplified with Diversity Gradients

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*Submitted September 16, 2004; Accepted June 2, 2005;  
Electronically published August 5, 2005*

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**ABSTRACT:** A scientific field matures as its theoretical underpinnings consolidate around unified theories: conceptual structures consisting of a few general propositions that encompass a wide domain of phenomena and from which can be derived an array of models. We demonstrate this process with a synthetic theory of ecological gradients and species richness. Our unified theory rests on four propositions. First, variation in some environmental factor effects variation in the number of individuals creating a gradient. Second, in a uniform environment of fixed area, more individuals lead to more species. Third, the variance of an environmental factor increases with its mean for sites of equal area. Fourth, all nonmonotonic relationships (i.e., hump shaped or U shaped) require a trade-off in organismal performance or in population characteristics with respect to the environmental gradient. We identify 17 models that link environmental gradients with diversity, show their relationship to our framework, and describe issues surrounding their empirical testing. We illustrate how a general theory can be used to build new models such as that for the U-shaped productivity-diversity relationship. Finally, we discuss how our theory could be unified further with other theories of diversity and indicate other areas of ecology that are ripe for unification. By providing an example of the process of theory unification, we hope to encourage such efforts throughout ecology.

*Keywords:* diversity, gradient, productivity, scale, species richness, theory, unification.

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Scientific truths are tentative and partial, and subject to continual revision and refinement, but as we tinker with truth in

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Am. Nat. 2005. Vol. 166, pp. 458–469.

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science—amending here, augmenting there—we always keep our ear attuned to the timbre of the web. (Raymo 1991, p. 145)

Theory is the keystone to understanding. It evolves as its components (e.g., framework, facts, concepts, models, hypotheses) and related theories change and become associated in new ways (Pickett et al. 1994). A mature theory consists of well-defined models that represent or simplify reality and show the relationships between the parts of a theory and their causal mechanisms. These models generate hypotheses. Using empirical data, we then can reject or confirm constituent hypotheses, leading to elimination, modification, or acceptance of the models, and thereby arrive at an understanding of how mechanisms affect patterns in nature. One characteristic of a mature theory is that it unifies a set of models or subsidiary theories that were previously treated as disparate or conflicting.

Our notion of a unified theory provides an answer to the problem posed by Lawton (1999) and Simberloff (2004). They decry the lack of general laws in community ecology. We agree with them; community ecology, by its very nature, will not have simple, general laws, as in physics. Rather, community ecology has unified theories within which it is possible to develop models for particular, contingent systems.

## Unified Theory: Definition and Illustration

A unified theory is a conceptual structure consisting of a few general propositions that characterize a wide domain of phenomena and from which can be derived an array of models. This definition of a unified theory differs somewhat from how the concept is used in the field of physics, in which a unified theory is a single mathematical framework. This difference is inherent to the types of entities studied in biology versus physics. The latter consists of a few universal objects that interact through a limited set of universal processes. In contrast, biology consists of an extremely large set of unique objects (e.g., genes, species) that interact through many different types of processes. Even items like the genetic code are not completely uni-

versal. Because of this inherent heterogeneity, unified theories in biology must comprise general conceptual structures that accommodate a variety of objects and processes.

A theory is an overarching entity of which models are one component (Pickett et al. 1994, box 3.2). A theory indicates the necessary components that characterize a complete model. These components are more general elements than any particular mechanism. Theories go through various stages of development before they are mature (Pickett et al. 1994, fig. 4.1). Our effort is part of the consolidation phase, which occurs midway through the maturation processes. Most, if not all, theories in ecology are not unified or mature. Therefore, we provide an illustration from evolutionary biology. This example clarifies our intent regarding a unified theory of diversity gradients. We end this article with a consideration of other areas of ecology that may be ripe for unification.

The theory of evolution by natural selection was first put forward by Darwin (1859). In its modern understanding, the theory posits that evolution by natural selection requires three components: phenotypic variation in a trait, a relationship between variation in that trait and fitness, and a genetic basis for variation of the trait (Endler 1986). If these three conditions are met, then the trait will evolve.

This general theory is not a mathematical model that can be applied to any particular situation. Rather, many particular models are derived from it. For example, from those propositions, one instantiation of the theory is the familiar breeder's equation,  $\Delta\bar{z} = sh^2$ , in which the change in the mean phenotype of a trait ( $\Delta\bar{z}$ ) is a function of the strength of selection ( $s$ ) and the heritability of that trait ( $h^2$ ). This is a quantitative genetics model. A completely different instantiation is a genic, single-locus, two-allele model,  $\Delta p = [sp(1-p)^2]/[1-s(1-p)^2]$ , in which the change in the frequency of an allele ( $p$ ) is a function of the strength of selection and the current allele frequency. Both equations are valid, both contain a long list of overlapping but different background assumptions, and they can be linked if additional assumptions are made. The general propositions are the unified theory, while the equations are particular applications. In turn, this more restricted theory of natural selection is one component of a more general theory of evolution in which other processes cause evolution (e.g., genetic drift) or retard it (e.g., genetic linkage). Each of the components of the general theory encompasses a multitude of mechanisms, and particular models depend on particular combinations of those mechanisms.

### Theory Unification: An Ecological Example

#### *Approaches to Unification*

A unified theory can arise in two ways. In the first approach, many specific models are proposed to explain a

general phenomenon. Unification comes by recognizing common elements of those models and using them as the basis for the unified theory. In the second approach, a general theory is proposed, and particular instantiations are created for consideration. Each approach represents ends of a continuum of ways to advance unification. Any particular unified theory likely develops through a combination of such agglomerative and deductive approaches.

We developed our unified theory of diversity gradients through an agglomerative process by examining an array of current models. Nonetheless, for clarity, our presentation starts with the general propositions. We then examine two particular models in light of that theory to show how the general propositions manifest. Finally, we show how all of the current 17 models fit within our unified theory.

Understanding broad-scale patterns of species richness is a central focus of the science of ecology and biogeography. A variety of mechanisms have been posited to cause environmental gradients of species richness. Current models consist of various combinations of these mechanisms. By providing guidance in making such combinations, unification within a single general theory can point to novel combinations of mechanisms that may affect pattern. The next phase of the unification process is to determine the relative importance of the various mechanisms or to identify conditions under which particular mechanisms operate or dominate. Once fully developed models are in place, hypotheses or predictions about patterns of diversity along ecological gradients can be posited and tested, thereby advancing ecological understanding. In addition, a fully assembled theory can be integrated more easily within a larger theory of diversity.

#### *State of the Theory*

Models of diversity date to Baron von Humboldt's attempts to explain the then newly discovered latitudinal gradient (von Humboldt 1808; Hawkins 2001). Today, we recognize that diversity changes along a variety of types of gradients, some primarily spatial (e.g., latitude, depth, elevation; Willig et al. 2003) and some primarily ecological (e.g., disturbance, salinity, succession; Grace 1999). Gradients of productivity have been of particular interest and are characterized by strong opinion and controversy (e.g., Grime 1973, 1979; Huston 1979; Tilman 1982; Rosenzweig 1992; Huston and DeAngelis 1994; Grace 1999; Waide et al. 1999; Mittelbach et al. 2001). Along gradients of productivity, species richness may increase, decrease, or assume a hump shape or evince a U shape, and the pattern changes with geographic and ecological scale (Mittelbach et al. 2001). A large number of observational (Waide et al. 1999; Mittelbach et al. 2001) and manipulative (Dodson

et al. 2000; Gough et al. 2000) tests have been conducted to confirm patterns or infer causal mechanisms.

Because of this rich literature, an exploration of the theory of ecological gradients is sufficiently complex that we excluded considerations of the equally rich literature on spatial gradients (e.g., latitudinal, elevational, bathymetric) even though these are inextricably linked to environmental gradients (Willig et al. 2003). Within ecological gradients, we concentrate on productivity gradients because they are the focus of nearly all mechanistic models. Regarding diversity, our focus is on species richness because that is the component of diversity addressed by virtually all models.

We present a unified theory of species richness as it relates to ecological gradients as an exemplar of the unification process. The current bewildering array of models are in various stages of development. We show that all models share a few common premises. Our proposed structure unifies these models, can be applied to most environmental gradients of species richness, and accommodates the variety of empirical patterns. In addition, our structure shows how to construct a model to explain U-shaped patterns, which hitherto have not received theoretical treatment.

Theory relating species richness to productivity is ripe for unification. Most or all of the components of theory are in place, but their refinement, exactitude, and interconnections are not sufficient, consequently leading to a perplexing and contentious literature that does not permit confidence in the application of theory to practical situations. Improvements in the empirical content of studies relating productivity and species richness as well as incisive testing of hypotheses are needed for further consolidation. Equally if not more important, identification of the common mechanistic bases that underlie current models should lead to improved generality as well as direct future empirical studies and development of theory.

#### Toward a Unified Theory

Our unified theory rests on four propositions. First, a gradient implies one or more limiting resources or conditions. Second, in a uniform environment of fixed area, more individuals lead to more species. Third, the variance of an environmental factor increases with its mean for sites of equal area. Fourth, all nonmonotonic relationships (i.e., hump shaped or U shaped) require a trade-off in organismal performance or in population characteristics with respect to the environmental gradient. We begin with a description of and justification for each of these four propositions and subsequently show that models of gradients in species richness are predicated on some or all of them. All models include the first two propositions,

whereas some include one or both of the last two propositions. We do not claim that all of these propositions hold under all circumstances. We endeavor to unify current models rather than test the empirical truth of any of them. Future work is needed to test the generality of our propositions.

Our four propositions are of different kinds. The first proposition is a definition, establishing when a gradient exists. The second proposition encompasses several mechanisms that can be derived from the first principles. The third proposition is a formalization about a common empirical pattern. The fourth proposition comprises a heterogeneous mix of mechanisms that derive from other domains and theories. Such variability in the bases for the propositions reinforces the contention that our theory is an agglomeration of a variety of types of models.

#### *Gradients*

Our first proposition is that there is variation in some environmental factor that effects variation in the number of individuals creating a gradient. This proposition is part of all gradient models of species richness, although it is often implicit. The environmental factor could be resources or some condition such as stress or disturbance. For the purposes of our presentation, the exact mechanism creating that link does not matter and will differ for each particular situation. Importantly, not all environmental variation creates variation in numbers of individuals, thereby constraining the domain to which our theory applies.

If the gradient exists with respect to a single limiting resource, then each species restricts itself more than it restricts other species, thereby minimizing competitive exclusion and creating a richness gradient. Otherwise, species richness would be the same everywhere. If there are multiple resources associated with the gradient, the minimum (limiting) resource dominates (Liebig's Law of the Minimum; van der Ploeg et al. 1999), but the identity of that resource may be species specific and may change along the gradient.

#### *Individuals $\propto$ Species*

The proposition that the number of species rises with the number of individuals was developed by Fisher et al. (1943) and Preston (1962a, 1962b) and has been termed the "more individuals hypothesis" (Srivastava and Lawton 1998). Three mechanisms have been invoked to account for this pattern: random placement, local extinction, and speciation. Random placement (also called passive sampling) creates a relationship between the number of individuals and the number of species if local species richness

is determined by random sampling from a regional species pool (Coleman 1981; Coleman et al. 1982) or metacommunity (Hubbell 2001). As the number of individuals in a local area increases, the number of species should increase because the likelihood of including a rare species increases as a result of chance alone. That the relationship between local and regional richness is positive and monotonic does not depend on the abundance distribution at either scale, although those distributions determine the exact form of the relationship.

Local extinction is the mechanism invoked by Preston (1962*a*, 1962*b*) and highlighted most often as part of MacArthur and Wilson's (1967) theory of island biogeography. This mechanism assumes that any local population will persist only above some minimum size. As an area holds more individuals, more populations can attain their species-specific minimum viable sizes. Although details matter about the exact form of the relationship between numbers of individuals and numbers of species, the core assumption is simply that the relationship is positive and monotonic.

Some models posit a positive relationship between the number of individuals and the rate of speciation (VanderMeulen et al. 2001). This mechanism most appropriately deals with species richness patterns at large spatial scales, as an explanation for the diversity of the regional species pool. Thus, mechanisms giving rise to a relationship between the number of individuals and the number of species can operate at a variety of scales in space and time.

Given a gradient in the number of individuals, each of these mechanisms can lead to a gradient in the number of species. All models of species richness gradients invoke at least one of these mechanisms. In many cases, the models often focus on causes of gradients in the number of individuals and assume a mechanism whereby more individuals give rise to more species.

#### *Mean $\propto$ Variance*

The proposition that the mean and the variance of environmental characteristics are related positively is based, in part, on the recognition that most environmental factors are bounded by zero (i.e., have a theoretical minimum). Such a bound predisposes a positive relationship, although it need not exist empirically. If the magnitude of an environmental factor is zero, or close to zero, at one end of the gradient, then perforce the variance will rise initially. A continued rise in the mean allows for the possible continued rise in the variance unless an upper bound also exists (e.g., water saturation of soil). Thus, this proposition is limited to those environmental gradients that have such bounds.

This mean-variance relationship is invoked in models that focus on patch dynamics (e.g., Abrams 1988). More specifically, species richness is measured at some unit area within which exists multiple patches. The patches may be only big enough to contain a single individual, or they may be larger. For some models, the heterogeneity is generated by interactions among individuals (e.g., Tilman 1988; Huston and DeAngelis 1994; Currie et al. 2004). Most commonly, the invoked mean-variance relationship is spatial, but some models invoke temporal heterogeneity (Chesson and Huntly 1988; Rosenzweig 1995). Regardless, increases in environmental heterogeneity lead to increases in the number of species because species specialize on distinct environmental conditions and outcompete other species within that ecological space. Thus, a wider range of environmental conditions facilitates coexistence of a greater number of species.

#### *Trade-Offs and Inflexion Points*

Many models posit that a trade-off leads to a hump-shaped pattern. The models differ with regard to the specifics of the invoked trade-off but share the basic proposition that an inflexion point arises as a consequence of two mechanisms acting in concert but in different directions. Commonly invoked trade-offs are competitive ability for various resources or versus a variety of other abilities (e.g., stress tolerance, colonizing ability).

Trade-offs can occur at different levels. In some cases, the trade-off involves the characteristics of an individual, such as competitive ability versus stress tolerance (Grime 1973). In other cases, the trade-off is a characteristic of the populations in a community, such as the intensity of competition versus the intensity of predation (Oksanen et al. 1981). In yet other cases, the trade-off involves characteristics of entire species, such as speciation rates versus extinction rates (VanderMeulen et al. 2001).

The inflexion point arises because of a change in the relative importance of two environmental factors in controlling the number of individuals. This trade-off can be conceptualized as gradients in each of two factors that run in opposite directions (i.e., evince a negative spatial association). Along one portion of the combined gradient, the first factor limits the number of individuals. At some other point, the second factor becomes limiting. This switch results in the number of individuals increasing along one portion of a gradient and decreasing along another. For many models, this switch in importance is controlled by inherent properties of species. For example, Tilman (1988) theorized that nitrogen limitation creates a productivity gradient in terrestrial plant communities until plant density is great enough that light becomes limiting. Although trade-offs are invoked by models accounting for

a hump-shaped pattern, this mechanism can explain U-shaped patterns as well (see “Using the Theory to Build New Models”).

Often the identities of interacting mechanisms that determine the number of individuals are not stated explicitly. Similarly, the unique contributions of each mechanism to total abundance rarely are quantified with respect to an underlying gradient. As a result, the mechanistic trade-off is not emphasized in conceptual models or detailed in quantitative models. The absence of mathematical rigor enhances the likelihood that such concealment persists, diminishing an appreciation for the similarities of form that the details obscure. Indeed, much ink has been spilled in arguments for and against various models. Those arguments often boil down to a preference for one trade-off versus another. We take a more catholic position by not advocating any particular trade-off. Rather, we embrace all of them as theoretical possibilities.

Perhaps most critically, the array of posited mechanisms often is not mutually exclusive. Our unified framework invokes a variety of particular mechanisms. Although mechanisms may be mutually exclusive in a particular instance, they are not universally exclusive and may not even be exclusive in a particular setting. We should not expect the same trade-off to be ubiquitous across all species in a guild, community, or trophic level. Phylogenetic history within particular clades almost guarantees that constraints differ among taxonomic groups. From the perspective of the ontology of theory, a more mature science investigates the identity, interaction, and relative importance of various mechanisms and trade-offs in different ecological, geographic, or taxonomic settings.

### Applying the Unified Theory

#### *Examining the Details of Two Models*

To see how our unified theory relates to current models of productivity-diversity relationships, consider the energy model (Connell and Orias 1964; Wright 1983). We follow the formal presentation of Wright (1983), which is couched in terms of the relationship of species richness and area. A brief section in that article’s “Discussion” indicates that the model can be applied to latitudinal gradients, and it has subsequently been invoked to account for positive relationships between productivity and species richness (e.g., Mittelbach et al. 2001; Hawkins et al. 2003). Our explication of this model does not include terms for area as in the presentation of Wright (1983) because we are interested in models that explain changes in species richness along an environmental gradient containing equal focal areas (i.e., species density).

The model explicitly invokes our first proposition that

the number of individuals ( $N$ ) is proportional to the total production of available energy ( $E = N/\rho$ , where  $\rho$  is an empirical constant for a given taxonomic group relating the number of individuals supported per unit of available energy; Wright 1983, p. 498). Next, Wright invokes our second proposition through reference to the model of Preston (1962a), relating the number of individuals to the number of species ( $S = a(N/m)^z$ , where  $m$  is the population size of the rarest species and  $a$  and  $z$  are constants). By substitution, the model becomes  $S = a(E\rho/m)^z$ , a monotonic positive relationship between productivity ( $E$ ) and species richness ( $S$ ), in which the exact shape of the relationship depends on a set of empirical constants. The model requires our first two propositions and nothing more than those propositions. Further assumptions are needed to support the instantiations of each proposition. Although the first proposition is straightforward, the second rests on a complex argument by Preston (1962a) concerning the distribution of species abundances and how population size relates to extinction probability. Other mechanisms could be invoked that yield the same qualitative relationship while differing in details (e.g., Hubbell 2001). The energy model does not explain the source of the available energy or its relationship to climate, which is the domain of other theories (e.g., O’Brien et al. 2000).

Our second example relating a particular model to our unified theory is that of Oksanen (1996). This model predicts a hump-shaped relationship between plant species richness and productivity by invoking our first, second, and fourth propositions. The model implicitly assumes our first proposition, that there is an environmental gradient that creates a gradient in productivity (i.e., biomass). It explicitly associates the number of individuals in a plot with biomass. This part of the model is not quantified. Next, the model invokes our second proposition that species richness ( $S$ ) always is associated positively with abundance ( $N$ ), using the formula developed by Fisher et al. (1943):  $S = \alpha \log [1 + (N/\alpha)]$ , where  $\alpha$  is a constant determining the exact form of the relationship.

The hump-shaped pattern arises because of a trade-off in individual characteristics (proposition 4). From low to intermediate levels of productivity, plots are uncrowded, and the number of individuals increases with productivity. In contrast, at higher levels of productivity, the plots become crowded, and individuals preempt space. Some unstated mechanism causes a change in individual growth characteristics so that further biomass increases come about via an increase in the sizes of individuals, leading to a concurrent reduction in the number of individuals ( $N$ ), a process known as self-thinning and expressed as  $B = cN^{-3/2}$ , where  $B$  is biomass and  $c$  is a constant (Yoda et al. 1963). Oksanen’s (1996) model differs conceptually from that of Stevens and Carson (1999) with respect to

whether larger individuals or larger species (or both) predominate under conditions of crowding.

The benefit of analyzing this model within the context of our unified theory is to highlight the missing components of the model. The Oksanen (1996) model fails to quantify the relationship between biomass and number of individuals and to specify the mechanism causing the change in size with crowding. As such, this model is incomplete.

#### *All Models*

We now consider our unified theory more generally. We identified 17 models of species richness gradients (table 1). We note that other tallies may differ depending on criteria for grouping publications. Our list of models is likely not complete. Our contention is that any additional model that we have failed to identify also will fit within our structure. Such a challenge can be considered a test of our claim to have identified the key components of a unified theory of species richness gradients.

Ten of the models are verbal. Verbal models are difficult to test because they fail to make quantitative predictions and suggest only qualitative ones. Our unification will facilitate the quantification of qualitative models by showing their relationships with analytic models and by highlighting the essential components of the latter models. Several of the analytic models (models 2–4 of table 1) are of the form 1, 2, many; that is, they show the conditions necessary for the coexistence of two species and then assume that such conditions are sufficient to account for the coexistence of many species. Clearly much work is needed to make such models sufficient for predicting species richness patterns along empirical gradients.

The models differ in the types of gradients to which they have been applied. All but three models (4, 16, and 17) are based on productivity. Model 4 applies to any resource gradient, and models 16 and 17 concern a gradient in a particular environmental condition, temperature. For nearly all models involving trade-offs, one part of that trade-off involves competitive ability or the results of interspecific competition.

In general, the mechanisms linking numbers of individuals to numbers of species can be divided into three types: limiting resources and interspecific competition, trophic interactions, and responses to abiotic stresses or other gradients. Only five models explicitly included the proposition that the number of species increases with the number of individuals, and consequently most were not precise about the mechanistic basis for the relationship. For models involving competition, we classified the mechanism as local extinction because competitive exclusion

leads to a reduction in species richness (e.g., models 2 and 10).

We classified models 1 and 5 as random placement because they are based on the assumption that greater productivity results in more individuals, which then results in more species. Model 5, unlike most of the others, predicts a pattern of strictly increasing species richness along the gradient. For models involving large spatial scales (i.e., grain, focus, or extent), we classified the mechanism as speciation (e.g., model 12). These models either explicitly (models 13–17) or implicitly (model 12) invoke evolutionary time and mechanisms.

Five models include environmental heterogeneity: four spatial (models 3, 7, 10, and 17) and one temporal (model 4). For three of the models (3, 4, and 10), the cause and pattern of environmental heterogeneity are unspecified. For the other two models (7 and 17), heterogeneity is caused by biotic interactions.

All but three of the models (5, 16, and 17) invoke trade-offs to explain hump-shaped species richness patterns. In some cases, the model was not presented originally in that context but was modified later. For example, Rosenzweig (1995) showed that the temporal covariance model of Chesson and Huntly (1988) can be applied to produce a hump-shaped pattern in richness by assuming a negative covariance between the environment and competition (model 4). Four models (2, 4, 6, and 8) invoke trade-offs with growth rate and assume that species richness is maintained at low levels of productivity because disturbance or temporal variability in resource levels prevents communities from reaching equilibrium. All other models assume equilibrium conditions.

Trade-offs involving competition explicitly are invoked by seven models (3, 4, and 6–10). The models differ in what factor evinces a trade-off with competition, which could involve competition for different resources, herbivory or predation resistance, or stress tolerance. Three models invoked a more general trade-off of adaptation to different resources or portions of a gradient (models 11, 12, and 15). The distinctiveness of these models is that the sorting of species along the gradient occurs via evolutionary mechanisms, in effect assuming that the realized niches of the species are equivalent to their fundamental niches. The other models (1, 3, 4, and 6–10) assume that the fundamental niche of any particular species comprises the entire gradient or at least more of the gradient than the realized niche.

Nearly all of the models concern the species richness of a single guild or trophic level. Even models that involve predation or herbivory focus on the species richness of the trophic level being consumed. We know of only one model that predicts species richness patterns of entire communities through the effects of interactions among mul-

**Table 1: Models of diversity gradients and their components and mechanisms**

Model			Proposition 2					Sources
No.	Name	Type	Proposition 1	Explicit	Mechanism	Proposition 3	Proposition 4	
1	Space preemption	Analytic	Productivity	Yes	Random placement	N/A	Density-dependent body sizes	Oksanen 1996; Stevens and Carson 1999
2	Dynamical instability	Analytic	Productivity	No	Local extinction	N/A	Growth rate vs. chaotic dynamics	Rosenzweig 1971; Wollkind 1976
3	Resource competition and resource heterogeneity	Analytic	Productivity	Yes	Local extinction	Spatial	Competitive ability for different resources	Tilman 1982, 1988; Abrams 1988
4	Temporal covariance	Analytic	Resource	No	Local extinction	Temporal	Growth rate vs. competitive ability	Chesson and Huntly 1988; Rosenzweig 1995
5	Energy	Analytic	Productivity	Yes	Random placement	N/A	N/A	Connell and Orias 1964; Wright 1983
6	Disturbance and competition	Simulation	Productivity and disturbance	No	Local extinction	N/A	Competitive ability vs. growth rate	Huston 1979; Huston and Smith 1987
7	Transport limitation	Simulation	Productivity	No	Local extinction	Spatial	Competitive ability for resources with different effect radii	Tilman 1988; Huston and DeAngelis 1994
8	Humpback	Verbal	Productivity, stress, and disturbance	No	Local extinction	N/A	Competitive ability vs. growth rate vs. stress tolerance	Grime 1973, 1979
9	Predator-victim ratios	Verbal	Productivity	No	Local extinction	N/A	Competitive intensity vs. herbivory/predation intensity	Oksanen et al. 1981; Rosenzweig 1995
10	Predation/herbivory vs. competition	Verbal	Productivity	No	Local extinction	Spatial	Competitive ability vs. resistance to herbivory/predation	Leibold 1996, 1999
11	Intertaxon competition	Verbal	Productivity	No	Local extinction	N/A	Clade-level specialization on different resources	Rosenzweig and Abramsky 1993; Tilman and Pacala 1993
12	Available habitat	Verbal	Productivity	No	Speciation	N/A	Adaptation to different resources	Denslow 1980; Rosenzweig and Abramsky 1993
13	Speciation rates	Verbal	Productivity	Yes	Speciation	N/A	Speciation rate vs. extinction rate	VanderMeulen et al. 2001
14	Evolutionary rates	Verbal	Productivity	Yes	Speciation	N/A	Adaptive ability vs. genetic drift	VanderMeulen et al. 2001
15	Adaptive trade-offs	Verbal	Productivity	No	Speciation	N/A	Adaptation to different resources	VanderMeulen et al. 2001
16	Temperature and evolutionary rates	Verbal	Temperature	No	Speciation	N/A	N/A	Rohde 1992
17	Biotic interactions and evolutionary rates	Verbal	Temperature	No	Speciation	Spatial	N/A	Currie et al. 2004

Note: Proposition 1: type of gradient; proposition 2: mechanism linking the number of individuals and number of species; proposition 3: environmental heterogeneity; proposition 4: type of trade-off.

multiple trophic levels (J. Moore, unpublished data). Two evolutionary models (16 and 17) that do not involve productivity or resources could be applied to species richness patterns for entire communities.

#### *Using the Theory to Build New Models*

A unified theory provides a structure for building new models. Currently no model exists to explain U-shaped relationships between productivity and species richness. On the basis of a literature survey, Mittelbach et al. (2001) found that U-shaped relationships accounted for 27% of all nonmonotonic relationships (17 data sets in 13 studies including terrestrial plants, mammals, birds, reptiles, amphibians, butterflies, and marine gastropods). More recently, Scheiner and Jones (2002) found a U-shaped pattern for terrestrial plants in Wisconsin. Although generally weak, U-shaped relationships are not an aberration and need to be understood from a theoretical perspective.

Here we sketch the basics for such a model. A more complete, formal treatment awaits further development. Our effort is designed only to demonstrate how such model building would proceed. We emphasize that this model is not general. The models contained within a unified theory can range from quite general to very specific. The value of the unified theory comes from identifying the components that must exist in any model, thus guiding model development.

Our model is built on several conclusions derived from our propositions. First, in a U-shaped relationship, species richness initially decreases and subsequently increases along the gradient. From this we infer that the number of individuals along the gradient must change in a similar fashion. That is, we are treating our second proposition as an assumption and inverting the direction of inference from the observed species richness gradient to an unobserved density gradient. Second, we again invert the direction of inference and from our fourth proposition infer that the inflexion point represents a trade-off or change in the dominating mechanism that controls the number of individuals. Consideration of an example clarifies this process.

The empirical example involves terrestrial plants in Wisconsin (Scheiner and Jones 2002). The data consist of a heterogeneous mix of community types, with prairie sites having lower productivities and many forest sites having higher productivities. Our model invokes all four propositions. First, we invoke propositions one and two, which relate the gradient to the number of individuals and the number of species, respectively. Along a gradient from prairies, through savannas to forests, the life-forms that dominate in forests are larger, so increasing productivity results in fewer individuals—one tree rather than dozens

or hundreds of herbs and grasses. As the gradient extends beyond the ecotone, however, greater productivity favors more trees and thus more individuals. Next we invoke our fourth proposition concerning trade-offs. The trade-off involves the ability to compete for limited water and tolerate periodic fires at one end of the gradient versus the ability to compete for limited light at the other end. Finally, we invoke the third proposition regarding environmental heterogeneity. With increases in spatial grain, the observed pattern changes from U shaped to hump shaped. An increase in the spatial grain permits an increase in environmental heterogeneity within each sample. As might be expected, heterogeneity increased to a greater extent in ecotonal areas at intermediate productivities than in areas of high or low productivity.

At this stage, the model is tentative and clearly post hoc. It can be tested by examining the hypothesized mechanisms. We could see whether the numbers of individuals change along the gradient in the assumed manner. We could examine species for fire tolerance and competitive ability at low light levels. We could directly measure environmental heterogeneity at different parts of the gradient and at different grain sizes.

This exercise emphasizes that particular models within a unified theory need not be general. Any model is a compromise that balances realism, generality, and precision (Levins 1968). Many of the models of productivity–species richness relationships, especially for hump-shaped relationships, were promulgated as if the theory encompassed only one model, igniting disagreements among those promoting particular models. We recognize that particular models usually are limited in their domains, whereas an overarching theoretical framework provides the generality needed to accommodate a variety of models. Past practice treated these models as representations of rival theories. Instead, we treat them as instantiations of the same underlying theory. Future explorations of these models may show that they make contradictory predictions under similar circumstances. In such a case, a test of the models will result in discarding or restricting the domain of at least one of them. Such tests are beyond the scope of this article.

#### *Models and Hypotheses*

One utility of a model is in its ability to be falsified (Popper 1959). Such falsification can assume two forms: evaluation of assumptions or assessment of predictions (i.e., tests of hypotheses). Regardless of the form of falsification, the variables to which a model relates and the domain to which the model applies need to be defined explicitly so as to guide empiricists in the proper formulation of tests. Unfortunately, many of the current models that apply to gra-

dients of species richness are sufficiently imprecise so that the formulation of meaningful tests is compromised (but see Currie et al. 2004). Sometimes, models fail to explicate the form of the expected relationship between species richness and productivity or identify the particular metrics of diversity (e.g., richness vs. Shannon's diversity) and productivity between which a relationship is posited. In addition, models may fail to indicate whether systematic or ecological attributes should delimit groups of species for consideration. For example, most analyses focus on all species within a particular level in the systematic hierarchy (e.g., a family), functional guild (e.g., diurnal foliage-gleaning insectivores), or trophic level (e.g., herbivores). It is unclear whether subsets of such groups may be examined without compromising the validity of the test. Moreover, models may fail to state the ecological or spatial scale at which proposed mechanisms operate and thereby fail to give guidance for study designs. In addition, some models predict multiple patterns—linear increases, linear decreases, or unimodal relationships—depending on the scale of analysis (i.e., considerations of grain, focus, and extent; *sensu* Scheiner et al. 2000). Finally, the majority of models are verbal and thus make only qualitative predictions. In general, models that do not give rise to precise predictions about well-delimited groups of organisms at specified spatial and temporal scales invite results that are controvertible and can stymie the development of ecological understanding.

Even if a model gives rise to precise predictions without ambiguity concerning scale or metrics that estimate the characteristics of interest, the design of empirical tests may fail to ensure that analyzed data correspond to the biological domain of the model. For example, most models concern entire guilds or trophic levels, whereas most empirical studies have examined only the response of a particular taxonomic group or ensemble (*sensu* Fauth et al. 1996). Sample sizes are small, considerations of spatial and temporal scale are infrequent, and patterns often are considered with respect to only a narrow range along an environmental gradient. Many times, an observed pattern has been associated with a mechanism that operates at a spatial or temporal scale that is quite different from the focal scale of the analysis. Equally important, rarely have experimental analyses of the relationship between species richness and productivity been designed to identify the relative importance of competing mechanisms in the sense of strong inference (Platt 1964).

As a consequence of such limitations, the list of possible models has grown over time, without appreciable synthetic evaluation. Indeed, the most recent reviews of the state of the theory of productivity and species richness (Rosenzweig and Abramsky 1993; Rosenzweig 1995) nicely set the stage for the integration of ideas but could not achieve

a comprehensive synthesis because of shortcomings in the body of theory with respect to concepts, data, hypotheses, and framework. Similarly, recent reviews and meta-analyses of data concerning the relationship between productivity and species richness have not been undertaken within the context of assessing the merits of competing mechanisms or processes thought to cause patterns (e.g., Waide et al. 1999; Mittelbach et al. 2001; Hawkins et al. 2003). Such critiques are not limited to discussions concerning environmental gradients such as productivity. A recent comprehensive evaluation of latitudinal gradients in diversity (Willig et al. 2003) grappled with similar conceptual and empirical issues.

### The Next Level of Unification

Mature theories are characterized by clear frameworks, well-considered models, and strong bodies of data. Equally important to maturation of a theory is the extent to which it articulates with related theories and frameworks. The theory of gradients outlined here is not connected strongly to other theories concerning aspects of diversity. Such integration will require considerable conceptual development and empirical study.

For example, the role of chance in effecting biological patterns has received increasing attention in ecological, biogeographic, and evolutionary studies. Stochastic mechanisms can give rise to patterns that appear as general and quantifiable as those produced by deterministic mechanisms. Chance may play an important role in determining many patterns of diversity such as those regarding area (e.g., Coleman et al. 1982), latitude (e.g., Colwell and Lees 2000; Willig et al. 2003), nestedness (e.g., Roberts 2002), range size (Lyons and Willig 1997), or community structure (Stevens and Willig 2000*a*, 2000*b*). Understanding the role of chance in effecting environmental gradients of diversity is in its infancy.

By analogy with latitudinal gradients of species richness, Willig and Lyons (1998) posited that a hump-shaped species richness gradient could be produced by chance alone. More specifically, if the fundamental niche of each species with respect to an underlying environmental gradient is characterized by a randomly determined median and range along that gradient, then the number of species able to occupy the central portion of an empirical gradient should be high and should decrease monotonically toward the terminus of the gradient in either direction, producing a hump-shaped pattern. Two different evolutionary processes may give rise to such a phenomenon. First, the location of allopatric barriers affecting speciation processes within a clade might be random with respect to environmental characteristics. Hence, site-specific local adaptation may give rise to pools of species whose fundamental niches

with respect to any particular environmental gradient are stochastic. Alternatively, if the spatial association between two gradients is weak, then the location and breadth of species niches with respect to one gradient may give rise to a hump-shaped species richness gradient even if niche characteristics evolve in a deterministic fashion regarding the other gradient.

The challenge to ecology is to extend the integration of theories of diversity gradients to include a variety of perspectives. Other factors that need to be incorporated into a truly universal theory of diversity include stochastic processes, local community interactions, evolutionary origins, and biogeographic contingencies. The development of a richer body of analytic models for all of these factors would make such connections easier to forge. Such unification would herald a comprehensive understanding of the factors that interact to determine environmental and spatial variation in all aspects of diversity.

### Unification and the Status of Ecological Theories

Ecology currently has no unified theories that are mature (i.e., broad theories that are complete, with well-developed and well-integrated components). Nonetheless, several broad theories may be ripe for unification and further maturation. Indeed, the vitality of the entire discipline depends on the extent to which the process of unification proceeds for each of the broad theories that constitute the conceptual foundations of ecology, as well as the extent to which these broad theories interact to form a grand framework for understanding. To further this goal, we briefly describe several theories that have characteristics that indicate they are candidates for unification.

The first example illustrates the second approach to unification, deduction from a general theory to specific models. Brown et al. (2004) present a metabolic theory of ecology (MTE) that links metabolic rate with body size, temperature, and resource stoichiometry. In turn, these factors are linked to survival, growth, reproduction, and controls on ecological processes. This theory consists of a few general propositions—that characteristics of organisms vary predictably with body size, temperature, and chemical composition—and is built on a general model that describes how materials are transported through space-filling fractal networks of branching tubes (West et al. 1997). The theory covers a wide domain of phenomena (e.g., population dynamics, species richness, trophic dynamics). Brown et al. (2004) are accompanied by a forum (Agrawal 2004) featuring an array of responses that point to how the MTE can become the basis of a unified theory. As proposed by Brown et al. (2004), the MTE consists of a single mathematical model. However, several authors (Cyr and Walker [2004]; Harte [2004]; Li et al. [2004];

Sterner [2004]; Tilman et al. [2004]) note that considerable variation in the assumed constants characterize that model, suggesting that a fruitful strategy for further development of the MTE would be to treat the components as general propositions from which to derive alternative, specific models.

The second example illustrates the first approach to unification, aggregation of individual models to a general structure. Willig et al. (2003) put forward a general theory that the latitudinal species richness gradient is a consequence of the manner in which four primary factors (energy, temperature, geometric constraints, and area) directly or indirectly affect  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity. The process of unification began in the mid-1960s with Pianka's (1966) review of the six extant models. The number of models continued to increase, 10 by the mid-1980s (Brown and Gibson 1983) to well over a score today (Willig et al. 2003). A number of substantive efforts at consolidation (e.g., Rohde 1992; Rosenzweig 1995; Schemske 2002) have advanced the maturation of this theory.

An area seemingly not ripe for unification is one that both Lawton (1999) and Simberloff (2004) claim contains no general laws: competition-induced community structure. The view that competition structures local communities has been among the most controversial subjects in ecology, with vocal proponents (e.g., Bowers and Brown 1982; Tilman 1982) and detractors (e.g., Connor and Simberloff 1979; Strong et al. 1979; Simberloff and Boecklen 1981). However, it is an area with a rich history of quantitative and conceptual models. The models of Lotka (1925) and Volterra (1926) have been amplified and refined by 80 years of further model development that have identified the components of a theory of competition-induced community structure (e.g., MacArthur 1972; Cody and Diamond 1975; Morin 1999; Chase and Leibold 2003). The necessary mechanisms include size assortment, size adjustment, and density compensation. These mechanisms must be integrated along a spectrum from pairwise competition through diffuse competition and must consider scenarios involving equilibrial and nonequilibrial conditions. A clear set of propositions are needed to abstract these mechanisms into a hierarchical framework that forms the foundation of the unified theory.

The above examples are not meant to be exhaustive. Rather, they illustrate that ecology is rapidly becoming a mature science characterized by a limited number of unified theories. We encourage others to continue this process.

### Acknowledgments

We thank D. DeAngelis, G. Mittelbach, R. Whittaker, and three anonymous reviewers, whose reactions to various versions of this manuscript stimulated improvements in

content and exposition. Our collaboration is an outgrowth of activities by a working group (An Analysis of the Relationship between Productivity and Diversity Using Experimental Results from the Long-Term Ecological Research Network) undertaken at the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (NSF; DEB-9421535, DEB-0072909), the University of California, Santa Barbara, and the State of California. This manuscript is based on work done while serving at the NSF. The views expressed in this article do not necessarily reflect those of the NSF or the U.S. government.

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