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CHAPTER 10

# *Diversity Emerging: Toward a Deconstruction of Biodiversity Patterns*

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## Introduction

Life is about diversity, heterogeneity, and novelty. The understanding of how these properties interact, emerge, are maintained, and eventually destroyed is at the core of the research programs of biogeography, ecology, and evolution. Diversity (or more properly, biodiversity), although present at all levels of organization, is most commonly measured by ecologists and biogeographers as the number of species found at a particular point in time or space (species richness). For more than two centuries ecologists, paleontologists, and biogeographers have been quantifying the number of species found in almost all imaginable places on the Earth, from the deep ocean to mountain tops, from soil to canopies, and foremost, along gradients in the physical environment, such as those along latitude, longitude, altitude, salinity, aridity, and depth (Brown 1988). We can certainly be assured that diversity changes and that it does so in a non-random way. However, our understanding of the principles underlying those changes has remained elusive. Thus, although the task of enumerating species at a given location might be simple (given the required time and funding), understanding the processes and underlying mechanisms is not.

Why are there more species of trees in a 0.1-ha plot in the Peruvian Amazon than in a plot of similar area in the temperate forest of Chile? To answer questions involving differences in diversity between places or along geographic gradients, it is tempting to resort to changes in the external environment that are associated with available energy, area, or temperature; or to changes in the intensity of ecological

interactions such as predation, competition, or disease; or to historical reasons that might have affected dispersal, speciation, or extinction rates (Hutchinson 1959; Pianka 1966; Schall and Pianka 1978; Diamond 1988; Rohde 1992; Rosenzweig 1995; Brown and Lomolino 1998; Waide et al. 1999; Gaston 2000). A good example in this regard is the latitudinal pattern in species diversity, for which around 25 or so hypotheses have been proposed (e.g., Brown and Lomolino 1998; Roy et al., this volume; Turner and Hawkins, this volume; Whittaker, this volume).

In this chapter, we argue that part of the difficulty in achieving a grand unified theory for patterns in species richness resides in the nature of the response variable itself. Species richness is an aggregated variable that subsumes, in a single number, the variety of life at the species level found in a particular place and time. Further, because each species counts the same when computing richness, all species are in practice considered equivalent (see also Lomolino 2000a,b), but of course, they are not. We all know that the only variety that the concept of species richness captures well is that contained in Latin binomials. Diversity indices (e.g., Shannon's  $H$ ) go a step further by weighting species by their abundance. But these indices still assume that, other than their sheer abundance, species are essentially equivalent. We do not attempt to trivialize the concept of species richness; our aim is simply to show that in order to understand patterns in species richness we need a deeper understanding of the quality and nature of the units that are being measured.

In this chapter, we will try to deconstruct richness patterns. We use the word *deconstruction* in its etymological sense, as a "turning to the roots" of what is being measured, or "disaggregation," to make apparent what is hidden. As shown here, deconstructing biodiversity patterns or examining other expressions of biodiversity (see also Roy et al., this volume) can sometimes open easier paths because the biological attributes of species are more tangibly related to their ecological and evolutionary implications. Interestingly, deconstruction is usually done but not pursued consciously as a methodological strategy to analyze richness patterns, for we usually do not work with richness per se but with richness of a particular group of organisms. This widespread practice usually goes unnoticed and is taken to reflect our own taxonomic expertise. On the contrary, we claim that deconstruction should be consciously performed as a methodological strategy for at least four reasons:

1. To understand the causes underlying patterns in species richness
2. To reconcile seemingly disparate explanations of richness patterns that emphasize an overriding importance to a given environmental factor, such as area or energy (e.g., Rosenzweig and Sandlin 1997; Rhode 1998; Chown and Gaston 2000)
3. To make apparent the need to overcome current methodological restrictions on the way richness data are collected and analyzed
4. To restate the question of richness in a comparative framework

As is usually the case in science, most of the time we realize that the wheel was already in place when we discovered it. In this sense we pay due recognition to the work of Michael Huston, who in his book stressed (1994:2):

One of the central premises ... is that biological diversity can be broken down into components that have consistent and understandable behavior. The other central premise is that the various components of biological diversity are influenced by different processes, to the extent that one component may increase, while another decreases in response to the same change in conditions.

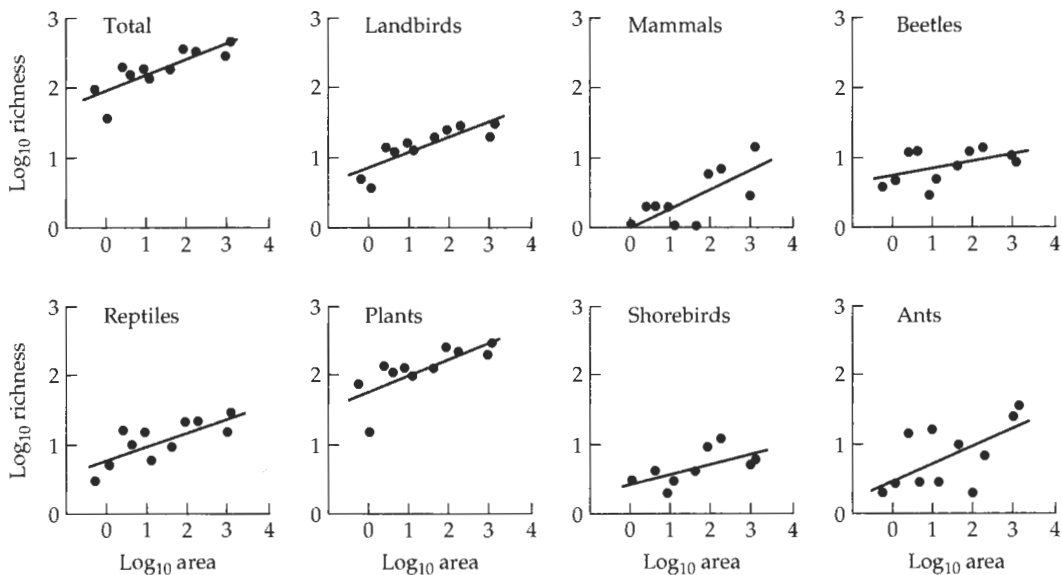
In this context, our attempt here is to emphasize some key issues and develop these ideas further, showing both their theoretical foundations as well as their empirical appeals.

## The Deconstructive Approach to Species Richness

The basic assumption behind deconstructing patterns in species richness is that assessing diversity as richness does not adequately characterize the way in which species differ from each other, and which cause them to respond in different ways to changes in the environment. Further, as we show below, by decomposing richness into smaller subsets of species that are internally homogeneous, in terms of sharing a particular attribute, we can gain better insight into the causes that underlie richness changes in time and space. As pointed out by Huston (1994), the more types of organisms that are included in a sample of species richness, the more mechanisms are likely to influence the observed richness.

A simple example can help illustrate our point. In Figure 10.1, we plot the relationship between area and the total number of species for 11 islands within the archipelago of the Sea of Cortés (Cody and Velarde 2002), as well as the same relationship on the same islands for different groups of organisms distinguished according to taxonomic affiliation (i.e., a taxonomic deconstruction). Note that we use only those islands for which complete inventories of all taxa under study have been conducted. We would like to make three obvious points about this figure. First, as observed anywhere in the world, the number of species that different groups attain in a given area differs by more than one order of magnitude (e.g., plants versus mammals). Second, while in general species richness in different groups increases with area, it does so at very different rates. Third, the amount of variance in species richness explained by area varies among groups, from 75% in land birds to 24% in tenebrionid beetles (Figure 10.2).

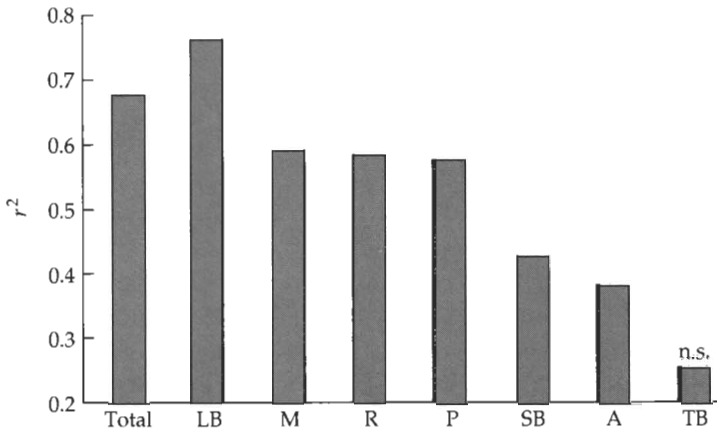
The differences in the effect of area on richness likely result from differences in dispersal abilities or opportunities, energetic demands, and in general, from differences in the characteristics that define a group of organisms as different from one another in the first place, and which determine that they have different readings of the environmental text. However, we can continue



**FIGURE 10.1** Relationship between richness (number of species) and area on 11 islands in the Sea of Cortés.

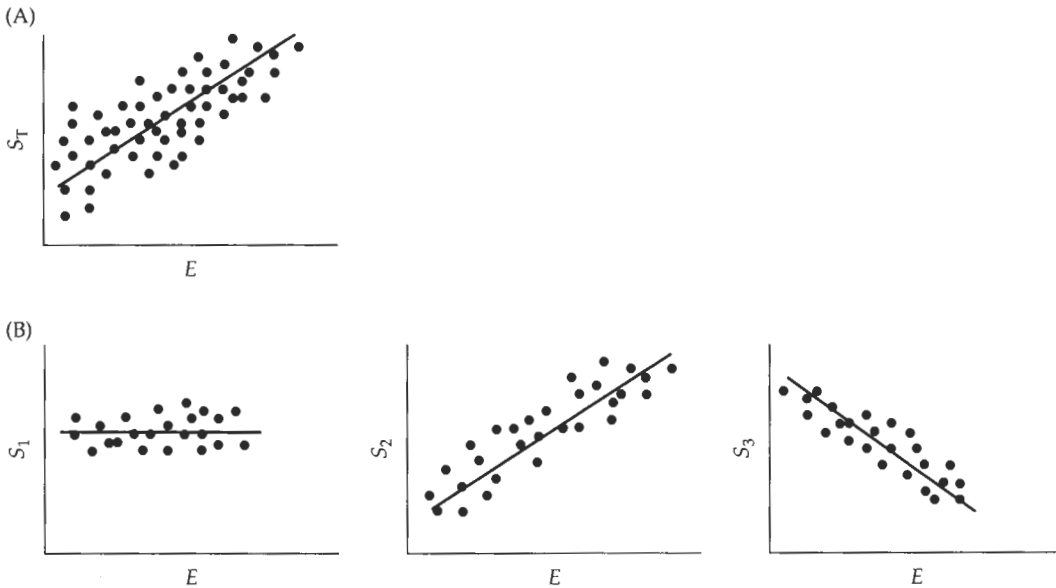
this deconstruction even further, for even within taxonomic groups (e.g., plants) we can distinguish different kinds of organisms characterized by a suite of life history traits that will likely cause them to respond differently to changes in their external environment. We could also deconstruct total species richness on the basis of physiological attributes of taxa (such as endotherms versus ectotherms) or other taxonomic distinctions (such as vertebrates versus invertebrates), or on ecological attributes such as food web position (decomposers, producers, primary consumers, and secondary consumers).

What is the right way to deconstruct richness patterns and where or when should we stop deconstructing? We will postpone discussion of these issues until the end of this chapter; meanwhile we would like to emphasize several important conclusions derived from the preceding example. First, species richness can be decomposed in many different ways. Second, depending on the criteria used to make this decomposition, we will likely arrive at different answers regarding the importance of a given environmental factor such as area (see the above example). Third, deconstruction opens the way to a comparative approach to richness patterns by allowing one to ask why there are more species of one type than of another in a given place or time, and why some groups of species respond in different ways to the same environmental gradient. Notice that this is possible because the data in this example are derived from the survey of several groups of species on the same set of islands. This might not be a necessary requirement for deconstruction, but it certainly might constrain its full application.



**FIGURE 10.2** The importance of area in affecting richness of different taxa expressed as the amount of explained variance in number of species ( $r^2$ ). LB, landbirds; M, mammals; R, reptiles; P, plants; SB, shorebirds; A, ants; TB, tenebrionid beetles.

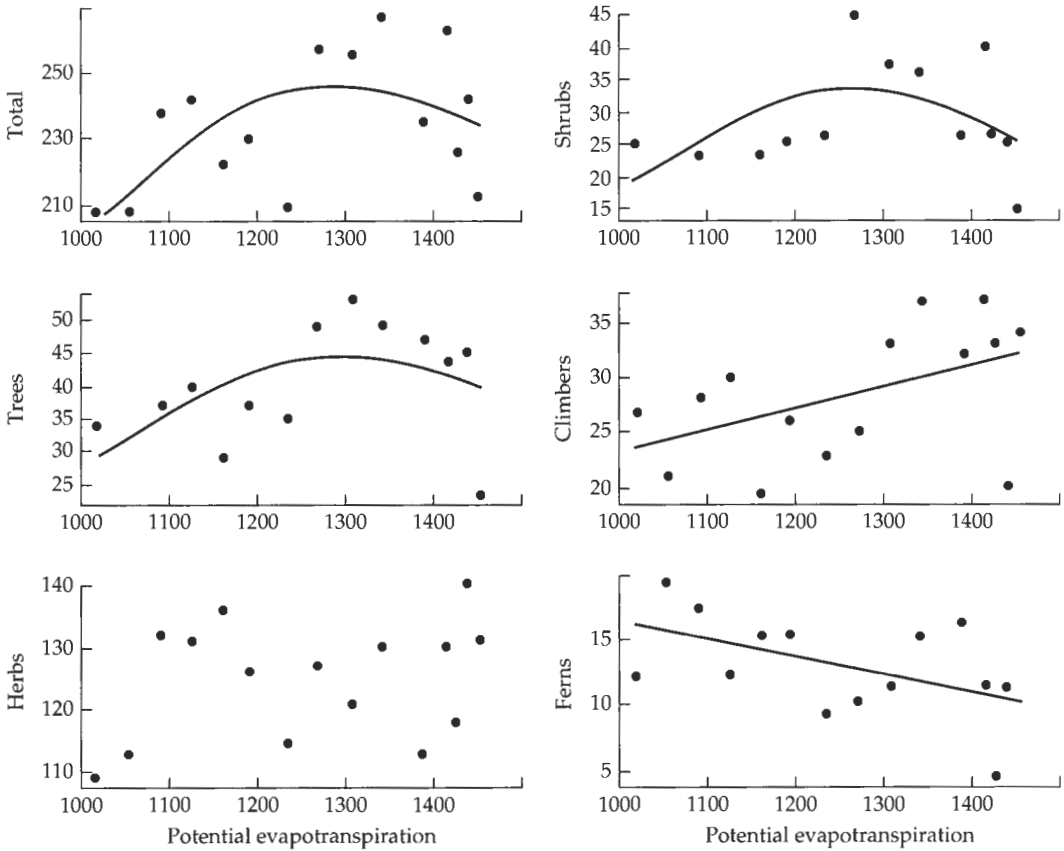
At the risk of being redundant, thus far we have argued that to analyze how the total number within a group of species (e.g., vascular plants) changes across an environmental gradient, assumes that all species are equal or ecologically equivalent, but they are not. On this point, we concur with Lomolino (2000a,b) in that non-random variation in species characteristics is of fundamental importance in understanding biogeographic patterns. To further illustrate the use of deconstruction, we show a hypothetical example in Figure 10.3. The traditional method of analyzing patterns in richness treats all species as equivalent and assesses the relationship between the response variable (i.e., total richness,  $S_T$ ) and an explanatory variable (i.e., environmental factor,  $E$ ). However, this procedure masks the real complexity of the pattern, for a large amount of error variance in the relationship between  $S_T$  and  $E$  can be explained by further disaggregating  $S_T$  in species groups ( $S_1$ ,  $S_2$ , and  $S_3$ ) that show qualitatively different responses to changes in  $E$ . Thus there is a diversity of diversity patterns. A recent paper by Bhattarai and Vetaas (2003) illustrates this point (Figure 10.4). These authors studied the elevational gradient in plant species richness in the Himalayas and tested for the effect of several environmental variables upon total species richness, as well as across five groups of species defined on the basis of their life form (e.g., ferns, herbs, climbers, trees, and shrubs). As shown in Figure 10.4, the relationship between species richness and potential evapotranspiration (PET) changes, depending on life form (see also Arroyo et al. 1996 for a similar analysis along a latitudinal gradient). The pattern is unimodal for shrubs and trees, positive and monotonic for climbers, and negative and monotonic for ferns, while herbs show no pattern. Thus in order to answer the question of why the total number of plant species increases nonlinearly with PET, one should first



**FIGURE 10.3** Schematic representation of the deconstructive approach. (A) An illustration of how total richness ( $S_T$ ) relates to environmental factor  $E$ . (B) Total richness can be decomposed or dissected by analyzing how different groups of species ( $S_1$ ,  $S_2$ , and  $S_3$ ) respond to the same factor  $E$ .

answer the question of why trees, shrubs, and climbers increase in richness with PET, but herbs and ferns do not.

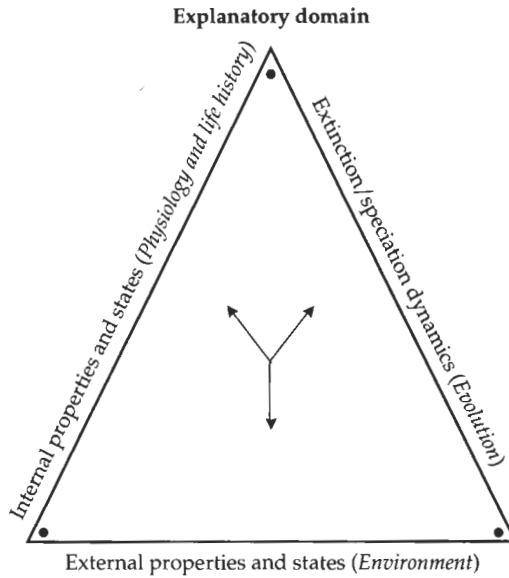
As we have already emphasized, and will continue to develop further, comparing and analyzing ecological systems in terms of numbers of species does not capture adequately the heterogeneity of the system and, in some situations, it might obscure instead of foster, understanding. Richness variation across geographic gradients can be meaningfully decomposed so as to shed light upon the underlying causes. Most current explanations of the geographic variation in species richness consider species as equivalent and emphasize the causal role of the external environment (e.g., area, productivity, water availability), but these explanations, as well as the mechanisms that they invoke, fail to recognize that the processes that control species diversity at any particular location (i.e., migration, extinction, and diversification) are not independent of the life history or physiological and ecological attributes of a species, for these attributes determine what aspects of the outside world are relevant to them. Thus further understanding of the dynamics of species diversity requires an expanded conceptual framework where differences among species are emphasized and explicitly considered in order to understand species richness patterns. Although it might seem old-fashioned to speak of deconstruction when unifying theories are becoming trendy (e.g.,



**FIGURE 10.4** Relationship between species richness of different life forms and potential evapotranspiration (PET). (After Bhattarai and Vetaas 2003.)

Hubbell 2001), we think it is a logical imperative to properly qualify the complexity of patterns before unification is attempted. Deconstruction capitalizes on the differences among organisms and explores how patterns change depending on the criteria used to disaggregate richness.

At the most basic level, deconstruction is possible because the number of species in a given time and place emerges from the interaction between an organism's strategies and attributes and the environment wherein it exists and has been embedded. This, in turn, affects the extinction and diversification dynamics of the lineages to which it belongs. In Figure 10.5, we illustrate this approach by depicting an explanatory domain for species richness patterns as the space contained within a triangle formed by three major axes: one, accounting for the internal properties and states of organisms (i.e., their physiological, ecological, and life history traits); another, depicting the external properties and states of the external environment wherein the organisms are embedded



**FIGURE 10.5** Conceptual model delimiting the explanatory domain for species richness patterns. The black dots indicate that most current explanations of richness patterns have privileged explanations along one single explanatory axis (see text for discussion).

(e.g., temperature, precipitation, productivity) including the effects of other co-occurring species (e.g., competitors, predators, parasites); and a final axis depicting extinction/speciation dynamics that largely result from the long-term interaction between organisms and their environment. Within this explanatory domain, patterns emerge as the result of the interaction among the characteristics of species, their environments, and their evolutionary dynamics, emphasizing that species differences do affect the patterns we observe, thus rendering possible the use of a deconstructive approach. Eventually, deconstruction could be performed along each of these three axes.

For the sake of simplicity, in this contribution we emphasize deconstruction with a focus on how traits of organisms affect patterns in richness. We present two case studies that illustrate potential interactions among these axes. The first example makes the point that the persistence of species in a particular landscape depends on the interaction between the attributes of the species and those of the environment wherein the species is embedded. The second example illustrates that the differential persistence of species with particular life history traits along environmental gradients can give rise to the differential proliferation of taxa, and thus to the emergence of diversity patterns. In this case, it is shown that only by deconstructing richness patterns according to life history traits is it possible to further understand the emergence of richness gradients.



### *Interaction between Species Traits and Environmental Characteristics*

Landscapes are not homogeneous. In fact, we can discern a landscape pattern, represented, for example, by the distribution of attributes such as patch size, patch shape, and connectivity; and a landscape dynamic, represented by the rate of change in landscape pattern. Because species are not equal in terms of their sensitivity to landscape patterns and dynamics, persistence is a function of species attributes. Typically, species with restricted dispersal will be more sensitive to connectivity, while wide-ranging species might be more sensitive to amount of habitat. In recent contributions (Keymer et al. 2000; Marquet et al. 2003), a rigorous treatment of this idea was attempted. Using a simple metapopulation model that represented the pattern of patch occupancy by a given species, Keymer et al. (2000) coupled this model to a dynamic landscape model that included patch dynamics, where the proportion of available habitat patches changed dynamically. In this model, the landscape dynamic is represented by the rate of patch creation ( $\lambda$ ) and destruction ( $e$ ), where  $\tau = 1/e$  gives the mean lifespan of a patch that can be colonized, and  $s = \lambda / (e + \lambda)$  gives the expected amount of available patches in the landscape (Figure 10.6). The species dynamic is given by the rate of propagule production ( $\beta$ ) and the intrinsic species-specific extinction rate in patches ( $\delta$ ). Following Keymer et al. (2000), the non-spatial version of this model or mean field approximation can be written as

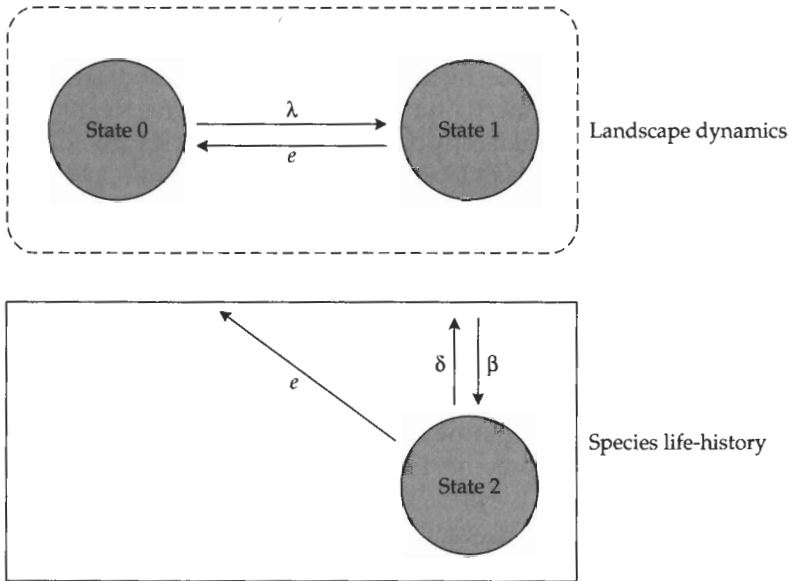
$$\frac{d}{dt} p_0 = e(p_1 + p_2) - \lambda p_0$$

$$\frac{d}{dt} p_1 = \lambda p_0 - \beta p_1 p_2 + \delta p_2 - e p_1$$

$$\frac{d}{dt} p_2 = \beta p_1 p_2 - (\delta + e) p_2$$

As is typical of patch occupancy metapopulation models of the Levin's type, metapopulation persistence can be assessed by the reproductive number ( $R_0$ ) (Marquet and Velasco-Hernández 1997), which in analogy with its use in epidemiology (Anderson and May 1991) measures the number of secondary colonizations that an occupied patch will accrue during its lifetime, or in our case, the "infective" properties of a particular life history. Clearly, persistence will be achieved whenever  $R_0 > 1$ , at which point a species invading a landscape will persist and reach a positive equilibrium abundance. As shown by Keymer et al. (2000), this model can be expressed as

$$R_0 = \frac{\beta s}{\delta + \tau^{-1}}$$



**FIGURE 10.6** Schematic representation of the model developed by Keymer et al. (2000). State 0 = destroyed patch; State 1 = habitable empty patch; State 2 = habitable occupied patch (see text for discussion).

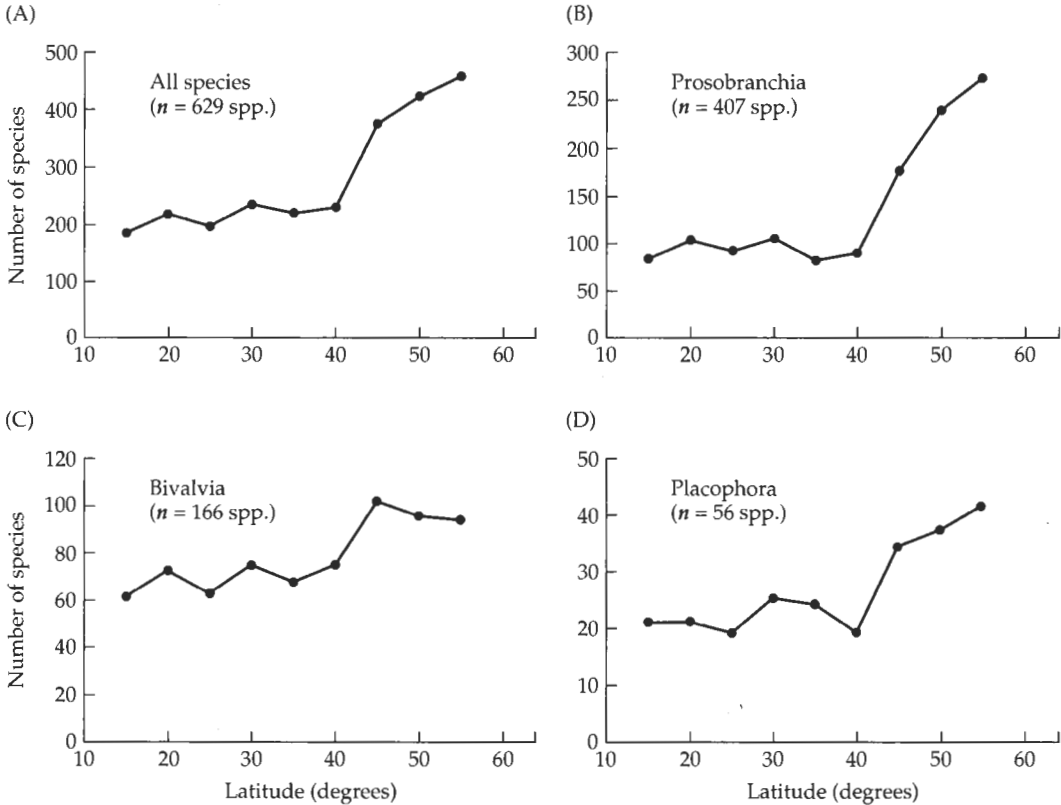
As shown by this expression, persistence depends both on the life history of the species inhabiting the landscape (given by  $\beta$  and  $e$ ), as well as on the properties of the landscape itself, which in this case are represented by the amount of available habitat ( $s$ ) and its average lifetime ( $\tau$ ). Thus, persistence of species depends on the interaction between external (environmental) and intrinsic (life history) factors. In a multispecies case, those species whose life history traits allow them to achieve  $R_0$  greater than 1 will persist and will become more represented in a given landscape (i.e., they will attain higher richness). Similarly, along a gradient in landscape characteristics (i.e.,  $s$  and/or  $\tau$ ), a gradient in richness will emerge as a result of the interaction between species traits and landscape features.

### *Of Species Traits, Environmental Contexts, and Speciation–Extinction Dynamics*

As shown above, the characteristics of the environment do affect species persistence. Thus, environments with different combinations of biotic and abiotic attributes will be dominated by species showing different sets of adaptive strategies, some of which will do better than others and will tend to predominate by increasing persistence (i.e., reducing extinction rate). This

would result in a progression in the dominance of different strategies along a sequence of environments, or an environmental gradient. The ability of a species to persist is a necessary cause, although not a sufficient one, for further species proliferation via speciation. In this context, it is expected that both extinction and speciation rates will not be random, but will be correlated with several species traits (e.g., Owens et al. 1999) as has been shown for traits such as body size (e.g., Maurer et al. 1992), geographic range (e.g., Cardillo et al. 2003; Jablonski and Roy 2003; Jones et al. 2003), fruit type (Smith 2001), sociality (Muñoz-Duran 2002), type of larvae (Jablonski and Lutz 1983), habitat use (Crame 2002), and growth form (de Queiroz 2002), among others. Ecological requirements related to habitat or resource use are correlated with speciation and extinction rates within a lineage (Rensch 1959; Eldredge 1979; Jackson 1974). In particular, generalist species capable of using different resources in alternative environments (such as a lineage might encounter through time), or specialist species whose resource patches are abundant, widespread, and persist through time, are subjected to less directional selection, and their lineages subjected to low speciation and extinction rates, as exemplified by large African mammals (Vrba 1980, 1987). Dispersal mode and ability also affect macroevolutionary dynamics. For example, weak dispersal in marine gastropods that lack planktotrophic larvae results in narrow geographic ranges, and consequently, in higher rates of extinction, as well as of speciation. In contrast, species with planktotrophic larvae and high dispersal abilities have low extinction and speciation rates and, correspondingly, large geographic ranges (Valentine and Jablonski 1983). A similar but opposite pattern has been documented for herbs as compared to woody plants (Levin and Wilson 1976). Thus, characteristics of species can be associated with their differential speciation and extinction or, more generally, species-sorting (Vrba and Gould 1986; Vrba 1989). In this scenario, and with everything else being equal, species richness along a large-scale environmental gradient is expected to be dominated by different proportions of species with different traits. If species-sorting were to be compounded by traits promoting higher speciation or lower extinction rates in some environments, then gradients in diversity would be observed. As explained below, these mechanisms might account for contrasting gradients in the richness of marine invertebrates of the southeastern Pacific (Valdovinos et al. 2003; Astorga et al. 2003).

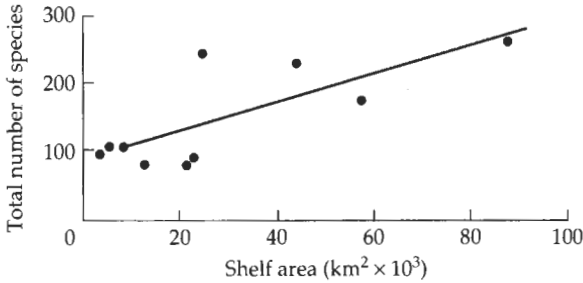
Valdovinos et al. (2003) analyzed the diversity and distribution of 629 shelled molluscs along the Pacific South American shelf, from 10°S to 55°S, including only those known to live in waters more shallow than 200 m, corresponding approximately to 95% of all described mollusc species for this continental shelf (Valdovinos 1999). Strong latitudinal changes in mollusc species diversity exist along the Peru–Chilean shelf for all major mollusc taxa studied and especially for the most diverse group within molluscs, the prosobranchs (Figure 10.7A). However, the change in species diversity is not



**FIGURE 10.7** Relationship between total number of mollusc species and latitude in the southeastern Pacific. (After Valdovinos et al. 2003.)

monotonic across latitudes. Diversity of prosobranch species per latitudinal band remains relatively low and constant around a value of 100 between 15°S and 40°S, and then sharply increases to the south, reaching around 300 species per band in the area around Cape Horn (Figure 10.7B). This general pattern is similar for all taxonomic groups (Figures 10.7B–D). Thus along the Peru–Chilean coast, mollusc species richness does not follow the typical decline toward the poles that is observed in several other marine and terrestrial groups (Brown and Lomolino 1998; Roy et al. 1998; Rhode 1999).

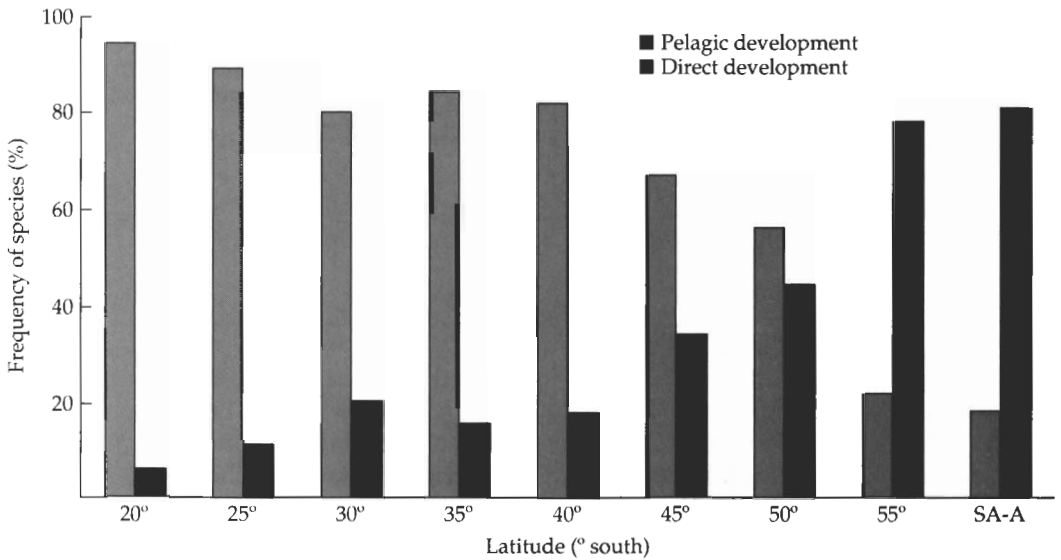
Discordant latitudinal diversity gradients have previously been documented for other marine taxa in different regions of the world, for which different causal factors have been proposed (Thorson 1965; Gaines and Lubchenco 1982; Santelices and Marquet 1998; Clarke 1992). However, the present case is particularly intriguing, since Roy et al. (1998) have shown that prosobranch species richness in the northeastern Pacific increases toward



**FIGURE 10.8** Relationship between total number of mollusc species and shelf area in the southeastern Pacific. (After Valdovinos et al. 2003.)

tropical latitudes; this pattern is positively correlated with sea surface temperature, thus lending support to the energy input hypothesis (Currie 1991). On the contrary, Valdovinos et al. (2003) show that shelf area, but not temperature, explains a significant portion (59%) of the variance in species richness (Figure 10.8). This significant relationship was produced by the large increase in area south of about  $42^\circ\text{S}$  to  $45^\circ\text{S}$ , a region dominated by large archipelagoes, fjords, and convoluted interconnected channels (see Castilla et al. 1993). Thus, while the solar-energy input hypothesis (Currie 1991) does seem to be a good explanation for diversity patterns in the Northern Hemisphere, it clearly does not account for mollusc diversity in the Southern Hemisphere. This analysis suggests that toward high latitudes along the southeastern Pacific, there may be a shift in the relative importance of the factors controlling diversity, with available shelf area playing a more prominent role. Valdovinos et al. (2003) hypothesize that the observed trend in mollusc diversity has been the result of higher diversification of molluscs at higher latitudes (south of  $42^\circ\text{S}$ ) triggered by the use of discrete refugia that might have enabled taxa to survive repeated glacial advances over the past 40 million years. This, coupled with fragmentation and isolation of mollusc distributional areas as a consequence of range shifts, could have actually favored the diversification of species in southern latitudes (Crame 1997, and this volume), conforming a pocket of high taxonomic diversity. This fragmentation of distributions and consequent allopatric speciation created a taxonomic diversity pump (Valentine 1984; Clarke and Crame 1997). As predicted by this model, there is a higher proportion of congeneric species south of  $42^\circ\text{S}$  (3.3 species per genus) than on the central coast of Chile (1.6 species per genus), suggesting that the increased diversity was produced by local radiation and not by recent colonization of species from other areas, such as New Zealand or the Antarctic Peninsula (Powell 1973; Dell 1990; Crame 1997).

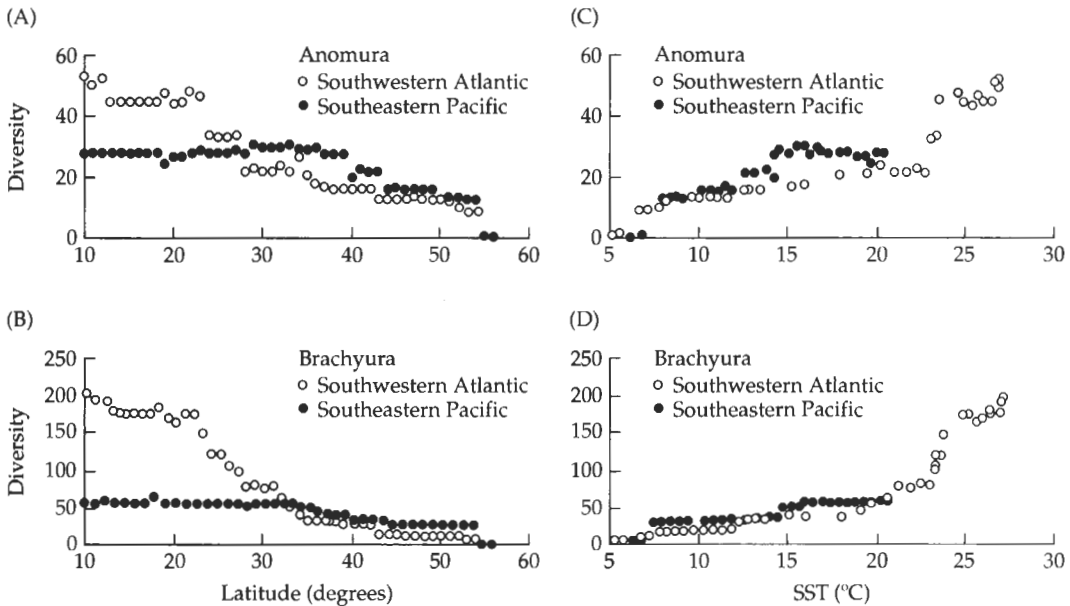
From a deconstructive perspective, it is tempting to ask whether all species are, on average, equivalent in terms of their response to changes in area. If this were the case, no further knowledge regarding causal factors could be obtained by deconstructing the pattern since under deconstruction this pattern would stay the same. Available data suggest that this is not



**FIGURE 10.9** Relationship between latitude and frequency of mollusc species with pelagic versus direct development in the Southern Hemisphere. (After Gallardo and Penchaszadeh 2001.)

the case, for this latitudinal trend in species richness is paralleled by a trend in mollusc mode of development, which suggests that deconstructing along this life-history axis could increase our knowledge of the causes behind richness patterns. This phenomenon, which has been known for a long time, has been dubbed Thorson's rule. Basically, this rule states that, as latitude increases, most marine invertebrate species tend to show a direct mode of development, while as latitude decreases, species tend to show indirect development with a well-defined planktotrophic phase (Thorson 1946, 1950). Although originally proposed for the northeast Atlantic Ocean, the Mediterranean, and the Persian Gulf (Thorson 1936, 1950; Mileikovsky 1971), Gallardo and Penchaszadeh (2001) have extended Thorson's rule to include marine gastropods in the southeastern Pacific (Figure 10.9). This latitudinal gradient in developmental mode lends further support to the mechanisms proposed by Valdovinos et al. (2003) to explain the higher diversity of mollusc species toward high latitudes in the southeastern Pacific.

Species with restricted dispersal (i.e., brooders or direct developers) are more likely to suffer range fragmentation and become isolated as a consequence of repeated glacial advances and climate change, thereby enhancing the probability of speciation. Astorga et al. (2003) recently proposed this link between gradients of developmental strategies and diversity. Having compared latitudinal diversity patterns for brachyuran and anomuran



**FIGURE 10.10** Relationship between number of species, latitude (top two panels), and sea surface temperature (SST; bottom two panels) for anomuran and brachyuran crustaceans in the southeastern Pacific and southwestern Atlantic. (After Astorga et al. 2003.)

crustaceans, which share the same mode of development (planktotropic) in two oceans (southeastern Pacific and southwestern Atlantic), Astorga et al. found that both groups of species show the typical decrease from tropical to high latitude areas (Figure 10.10). Further, these authors showed that sea surface temperature correlates positively and significantly with species richness (see Figure 10.10) in contrast with the finding of Valdovinos et al. (2003) for mollusc species, and demonstrates that a decrease in richness is usually found for species with planktotropic development, whereas anomalous or inverse patterns are usually found in groups with direct development.

It is clear that at least in this case, and likely in most cases, deconstruction not only provided better insights on the determinants of species richness gradients, but helped to reconcile divergent hypotheses and patterns regarding its generation. Diversity patterns depend on the interaction between species properties and the environmental contexts wherein they are embedded, highlighting the complexity inherent in attempts to explain patterns in species richness. As this example makes clear, the deconstruction of richness patterns is essential to understanding the causes that underlie species richness patterns in marine environments (see also Gaines and Lubchenco 1982; Roy et al. 2000).

## Frontiers: Toward a Relational Theory of Biodiversity

In his presidential address to the American Society of Naturalists, Hutchinson (1959) appointed Santa Rosalia as the patroness of evolutionary studies. Given the current state of the art in our understanding of *Why are there so many kind of Animals?*, a skeleton encrusted in a stalactite of whom little is reliably reported seems an adequate choice. Our attempt in this chapter has been to elaborate on the importance of the components of species richness based on early ideas put forward by Huston (1994). Although we cannot claim devotion to Santa Rosalia, we think that this recognition is essential to free her from her cave and her encrusted state.

Throughout this chapter we have advanced what we called a deconstructive approach to the analysis of species richness patterns. By this we mean the analytical strategy of disaggregating species richness into smaller subsets of species that share a particular characteristic such as mode of development or other phylogenetic, ecological, or life-history trait. We claim that this procedure allows a better understanding of changes in richness in space and time to the extent that it makes explicit how the environment interacts with the biological attributes of species, subsequently giving rise to richness patterns. Ideally, we should start with the most comprehensive dataset possible, then deconstruct it and pose the question of richness in comparative terms, or why a group with trait  $x$  has more species than one with trait  $y$  (where  $x$  and  $y$  are alternative ecological, physiological, or life-history traits). This method is in contrast to the usual approach of measuring the number of species of a given taxon, for example along a spatial gradient, and comparing the numbers of the same taxon at different positions along the gradient. When measuring species number in this manner, species are treated as equivalent, and comparisons are relative to the same taxa; the observed differences are thought to be driven by changes in an external environmental factor affecting all species equally. In this context, the ultimate causes of richness changes are taken as external and independent of the species themselves (because they are all treated as equivalent). However, we should realize that the response variable—the number of species—is internally heterogeneous, in such a manner that it can be decomposed in different groups of species, each affected in different ways by the same environmental factor. Therefore, what is causing the pattern is neither external nor independent to the species being considered, but resides in the interaction between species traits and the external factor being investigated.

At a more fundamental level, the deconstructive approach is a relational approach to diversity, asserting that the number of species in a particular place or time depends on the relationships that exist between the environment and the characteristics of species—interaction that, in the long term, is expressed in extinction/diversification dynamics (see Figure 10.5). As emphasized in our examples, we cannot speak of the effect of an external environmental factor without making reference to a particular type of



species in comparison with others, for each type specifies its own relevant environment and interacts differently with it.

In theory, deconstruction can be iterated down to single species, because each species is unique. However, before reaching this level, we will likely lose the pattern (or the statistical power to detect the pattern). Similarly, deconstruction can be performed in many different ways, but to do so requires knowledge of how much deconstruction is enough and what attributes should be used to carry out deconstruction. We do not have a definitive answer to these questions. Suffice it to say that deconstruction should be guided both by theory and by empirical knowledge of the species under analysis and should stop, at least in theory, whenever internally homogeneous and equivalent sets are achieved (i.e., they fulfill the symmetry assumption; see Hubbell 2001), because for these sets, further deconstruction would be impossible to carry out. If our interest is to test for the effects of energy availability, then a sensible way to carry out deconstruction would be by disaggregating richness on the basis of energy metabolism, distinguishing endotherms from ectotherms, body size, or diet. However, this procedure will ultimately be constrained by data availability.

Notwithstanding these limitations, we think that deconstruction can help to test and refine current hypotheses on the factors controlling species richness to the extent it focuses on the interaction between an environmental factor and the biological attributes of species, which most of the time have well-known consequences upon species distribution and abundance. As emphasized by Huston (1994:69), acknowledging that organisms are functionally different within ecological systems allows the partitioning of richness into different components that might be influenced by completely different processes. However, in contrast with Huston (1994), we do not see this as a problem that can be solved by carefully selecting the group of species to be analyzed but as an opportunity to disentangle, through deconstruction, the mechanisms that underlie richness patterns. In this regard, deconstruction should be a common methodological strategy to be fostered in order to reduce the complexity and increase our understanding of the pattern itself.

For the sake of simplicity, we have treated the interaction between the organisms and the environment as static. However, recent theoretical work suggests that this interaction is dynamic and involves a two-way process whereby the organisms, while themselves affected, also affect their local environment by modifying biotic and abiotic components. This operates through a process whose ecological consequences are reflected in the modification, creation, maintenance, and destruction of habitat for other organisms (i.e., engineering) (see Jones et al. 1994) and in the modification of the sources of natural selection acting upon themselves (i.e., niche construction) (see Lewontin 1983; Odling-Smee et al. 1996; Laland et al. 1999; and Kitchell 1990). This means that the axes of the explanatory domain depicted in Figure 10.5 are not independent but interact with each other creating a dynamic process whose

end result is the emergence of diversity. These propositions, as well as our deconstructive approach, are built on the fact that species are not equivalent, and they stress that further development in our understanding of ecological, evolutionary, and biogeographic patterns and process should focus on the relational aspects underlying the interaction among organism properties, environmental contexts, and resulting evolutionary dynamics.

The deconstructive approach is not limited to the analysis of species diversity patterns. In fact, it can be applied to any ecological, evolutionary, or biogeographic pattern based on the analysis of a large number of species or ensembles. Examples include patterns in body size distributions (e.g., Marquet and Cofre 1999; Gaston et al. 2001), species abundance distributions (e.g., Magurran and Henderson 2003), the analysis of patterns in geographic ranges (e.g., Gaston 2003), and in general, the patterns usually analyzed by macroecologists (e.g., Brown 1995; Blackburn and Gaston 2003). However, there are two major challenges that prevent this approach from becoming widespread and useful. The first is related to the availability of data, for deconstruction requires knowledge of the ecological traits and life-history characteristics of the majority of the species under analysis, because these traits provide the axes for deconstruction. The second relates to the development of statistical procedures, on the one hand, to assess the relative contribution of the different axes used for deconstructing patterns and, on the other hand, to deal with the issue of non-independence among them. Because the axes for deconstructing a pattern are multiple, it is essential to have a statistical procedure to identify useful axes in terms of how much new information they provide. However, besides these problems, strategic deconstruction is a useful approach to understanding biodiversity patterns, to discovering new ones, and to refining our expectations on how they will change in the face of global changes in the environment.

Before closing, a final digression is in order. As noted by some reviewers, we managed to write a paper on species diversity without discussing two major recent approaches that have made great advances in this field: macroecology (e.g., Brown 1995; Brown et al. 2003), and the statistical-mechanical, symmetric, neutral, grand unified theory of biodiversity (Hubbell 2001). From a deconstructive perspective, Hubbell's symmetric theory could be called a tropically deconstructed symmetric theory of biodiversity because its domain of applicability is restricted to tropically similar species, which are envisioned as equivalent in terms of each having on average equal fitness, as well as experiencing the same per capita demographic processes. Thus this theory assumes that once trophic deconstruction is performed, no further deconstruction is possible because we arrive at a set composed of equivalent entities. While we think that this theory holds great promise for the scientific advancement of the fields of ecology and biogeography, it is not clear why it should be restricted to tropically similar species. It is somehow a contradiction for a unified theory to be so restrictive in its application. Further, even tropically similar species may differ in many significant ways that render them non-equivalent, violat-

ing the symmetry assumption, and paving the way for further deconstruction. However, it should be emphasized that Hubbell's theory identifies a criterion that might be useful as a stopping rule for the deconstructive process: symmetry. Thus, deconstruction should stop when species are grouped into categories that satisfy the symmetry assumption.

Finally, macroecology envisioned as the research program whose aim is the search for general law-like principles underlying the emergence of ecological patterns, structure, and organization (e.g., Brown 1999; Marquet 2002; Brown et al. 2003) takes, at first glance, a completely opposite perspective from deconstruction to the extent that it aims to find the minimum set of principles (e.g., metabolic scaling; Brown et al. 2003), whose application would put all species on a common ground because it cues on attributes that are general to all living systems. In this context, macroecology holds the promise of coming out with a truly unifying perspective on the diversity of life: one where the deconstructive approach will be meaningless. However, because deconstruction capitalizes on the differences among organisms and explores how they affect the emergence of ecological patterns and structures, it complements unified theories by pointing out the functionally important and different pieces of the ecological puzzle that should be eventually unified.

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