Limnol. Oceanogr., 49(4, part 2), 2004, 1269–1277

Biodiversity and ecosystem functioning: A complex adaptive systems approach

Jon Norberg
Department of Systems Ecology, Stockholm University, 10691 Stockholm, Sweden

Abstract

Environmental factors regulate biodiversity through species sorting processes. Species distributions in communities affect ecosystem processes and environmental factors. These dynamics are determined by the properties (traits) of species in the community. The optimal temperatures for growth, the minimal amount of resource that sustains positive mass balance, and the amount of energy allocated to predator defenses are examples of such traits. Over time, the trait distributions in communities may change in response to environmental changes, which, in turn, changes the processes and consequently the structure of the system. The result of such processes is the focus of complex adaptive systems (CAS) theory. This paper gives an overview of how CAS theory can contribute to understanding the role of biodiversity on the ability of functional groups that make up the ecosystem to change their species compositions in response to changes in the environment. Any trait that requires investment of energy, mass, or time is subjected to a tradeoff for alternative use of this resource. Such interspecies tradeoff relationships can be used to make predictions about past environmental conditions, as well as the response of the properties of a group of species, e.g., total productivity and species distributions, to future changes in the environment. The trait-based framework presented here makes explicit predictions regarding the relation between the environment, trait distributions, and ecosystem processes. Trait variance, a measure of the width of the distribution of traits in the community, is proportional to the rate at which species within functional groups can replace each other in response to environmental changes. This adaptive capacity is crucial for the ecosystem's ability to maintain certain processes under times of change. Examples of empirical tradeoffs are given as well as how to formalize them to use in the CAS framework.

Until recently, most research on the role of biodiversity for ecosystem functioning has focused on the general relationship between species richness and some ecosystem process, irrespective of the environmental factors determining species richness in the first place. The random sampling of species, which served to pose the question of whether species diversity in general would affect ecosystem functioning, has recently been challenged to be of limited relevance for natural conditions (Huston 1997; Vinebrooke et al. 2004); as put by Grime (1997), ''There are obvious conflicts with published evidence from work on natural rather than synthesized ecosystems.'' In most experimental studies of the role of biodiversity and ecosystem functioning, species were randomly drawn from a species pool regardless of their traits, and experiments with biodiversity gradients caused by an environmental factor such as nutrient load (Tilman and Downing 1994) have been heavily criticized for having confounded effects (Huston 1997). Essentially all mechanistic explanations for why species richness should matter for ecosystem functioning are based on differences in traits (Loreau et al. 2002; Schmid et al. 2003), which leads to the conclusion that species richness will not matter (for ecosystem functioning) unless species differ in their properties (traits). Therefore, the general question of whether species richness matters needs to primarily address (1) how species richness relates to trait distributions in communities in general (Walker et al. 1999; Petchey and Gaston 2002), (2) what the processes relating regional to local species abundances are, i.e., metacommunity/ecosystem dynamics (Bond and Chase 2002; Loreau et al. 2003; Leibold and Norberg 2004) and species area relationships (Plotkin et al. 2000; Hubbel 2001) (3) how species sorting processes affect local trait distributions (Chase and Leibold 2003), and (4) how trait distributions in the community, i.e., dominant and subdominant traits, relate to ecosystem functioning (Norberg at al. 2001). Any natural community will already have undergone selective processes (species sorting), and, assuming that extinctions are correlated with the traits of importance for ecosystem functioning, the set of species will undoubtedly already have a bias with regard to which traits are represented. Thus, a more complete picture must involve the environment affecting ecosystem functioning both directly (the individual species response to the environmental factor) and via changes in the trait distribution in the community. That is, species richness is more a result of the selection processes acting on traits than a causal variable affecting ecosystem functioning. Even though many of these aspects have been analyzed separately in earlier studies, few studies have related environmental factors directly to dynamics of biodiversity and aggregate properties such as ecosystem processes in a single framework. In the present paper I provide a theoretical approach inspired by complexity theory that addresses this issue.

Complex adaptive systems

One of the greatest challenges to science is to understand the role of diversity in form and function of organisms in creating an almost infinite number of possible combinations of organisms. Not only are organisms themselves complex,

[1] Corresponding author (Jon.Norberg@ecology.su.se).

Acknowledgments

Jon Chase, Mathew Leibold, Jan Bengtsson, Beatrice Crona, Stanley Dodson, Mona Johansson, Björn Naeslund, and one anonymous reviewer gave valuable comments that improved the manuscript. The research was funded by grants from the Swedish research council.

but they interact with each other over time in communities, and different sorting processes cause self-organization into distinct structures such as food webs, ecosystems, biomes, zonations along gradients, and repeating temporal patterns (transformational evolution sensu Lewontin 1977). Given similar environmental constraints, similar emergent structures and patterns may develop in different regions on earth even though the components, the species, may differ. Such self-organizing processes are the focus of studies in complex adaptive systems theory (Holland 1996). In the present paper I will try to outline how this theory might prove useful in ecology and especially for the debate on the role of biodiversity for ecosystem functioning.

Theories for complex adaptive systems (CASs) have emanated from many disciplines including economics (Arthur et al. 1997), social science (Langton 1995; Janssen 1998), and biology (Holling 1992; Levin 1998). A main focus of CAS theory is to understand the dynamics of aggregate patterns that result from the interaction of system components. In a recent review Levin (1998) identified the following three criteria as the basic ingredients of CASs:

1. Sustained diversity and individuality of components
2. Localized interactions among those components
3. An autonomous process that selects from among those components, based on the results of local interactions

Thus, CASs result from three main processes: one that creates diversity (or disorder in general terms), one of interactions between species (components), and one that selects on the gradient created by the diversity in form and function. The net result is that the assemblage of species continuously changes toward a dominance of those best suited to deal with the selective forces of the environment. The most well-known example of CASs is evolution of species, but biology is a nested set of CASs acting on different levels, from evolution by natural selection to succession within local communities to biogeographical aspects of metacommunities, any of which may take place on many spatial scales (Holling 2001; Leibold and Norberg 2004). Any community that exhibits the ingredients of CASs, i.e., sustained diversity by immigration from a regional species pool or resting stages, local interactions such as competition for resources, and a selective process such as competitive exclusion based on, for example, lowest resource levels for sustaining positive growth (R^*, Tilman 1982), will show continuous succession and an ability to change its composition in response to changes in the selective processes. It needs to be pointed out clearly that CAS theory is not something new and alternative to, e.g., evolutionary or ecological theory, but provides a useful tool to understand common processes causing organization across many disciplines. Also, CAS theory does not imply group selection or optimization at the ecosystem level, but rather focuses on the consequences of sorting processes acting on components of a group for the aggregate properties such as total abundances, productivity, and species dominance patterns. As such, it is particularly useful for studying the relationship between biodiversity and ecosystem functioning.

A species-trait perspective

As noted above, similar structures and patterns arise on different parts of earth even though the components, the species, are not the same. For example, the seasonal succession of temperate lakes, exhibiting spring and autumn blooms with a summer period dominated by zooplankton control, is found globally, and the succession of phytoplankton species is relatively predicable in terms of the general characteristics, albeit not on a species level (PEG [Plankton Ecology Group] model in Sommer 1989). These temporal patterns are the result of a dynamic interplay of selective forces acting on the community resulting in predictable patterns of aggregate group properties such as total biomass, average growth rates, or average edibility. In order for a change of such aggregate community properties to occur, the diversity in species is expressed as a gradient of traits on which selective processes may act. Quantitative traits, as used in genetics, are physical or physiological aspects that have a continuous and measurable range. If such traits correlate to the fitness of individuals, there exists a tradeoff gradient on which selection can act (Fisher 1958). This notion can be extended to interspecies comparisons of traits (Grime et al. 1997; Reynolds 1997; Norberg et al. 2001). If traits correlate with specific growth rate, we can think of them as interspecies tradeoff relationships. If a set of species compete, species with the most competitive set of traits will shape the average properties of the community due to succession. Examples of such traits are species response functions to temperature or pH, or the amount of energy that is allocated to mitigate some limiting factor such as nutrients or predators. An important conclusion from these arguments is that species traits and trait diversity are of more importance than species numbers or taxonomic identity. In the following paragraphs I will outline how a focus on trait distribution rather than species richness may improve our understanding.

Which traits to focus on and what are traits really?

We assume that species make a difference in the functioning of the ecosystem because of their differences in traits. We define traits here as species characters that are quantifiable. There are obviously a large number of possible traits within species, and which traits matter for ecosystem functioning is a question that depends on which traits determine the processes that are of interest for a given ecosystem process and which traits are crucial in the species sorting and assemblage processes. The effect of the sorting process driven by the environmental variable(s) represents the link between the environment and the trait distributions in the community. The link between the resulting trait distributions and ecosystem functioning thus depends on how the sorting process affected the relevant traits for the ecosystem process. These traits may be, but do not necessarily have to be, the same traits. For example, the ability to exploit a resource at low concentrations will be crucial if this resource is a limiting factor at least temporarily. If this trait is correlated to, e.g., body size, the species sorting process due to resource limitation can cause a change on the average community

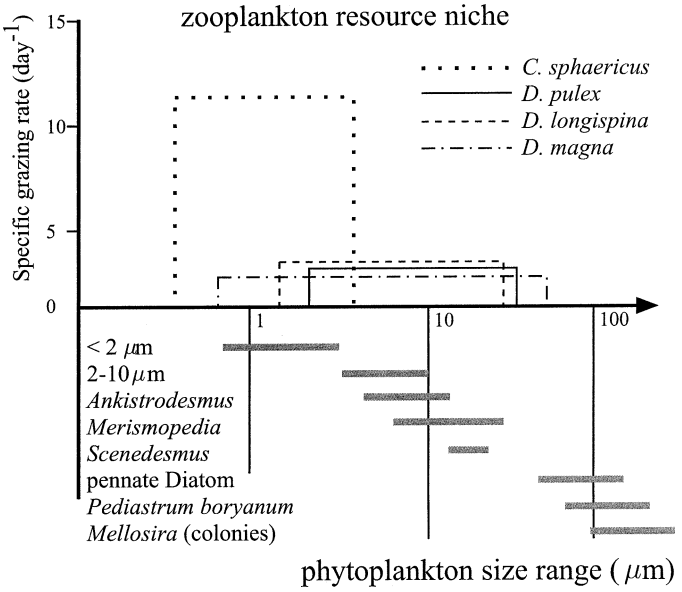

Fig. 1. Feeding traits of four Cladoceran zooplankton (*Daphnia magna*, *Daphnia longispina*, *Daphnia pulex*, and *Chydorus sphaericus*) and their approximate prey sizes. Note that the complementary differences in prey size may facilitate coexistence even though there are large differences in prey capture efficiencies (redrawn from Norberg 1999).

body size and thus affect trophic level interactions (Brooks and Dodson 1965). Often traits on which taxonomic classifications are based are morphological rather than physiological, but Petchey and Gaston (2002) presented a method to calculate functional diversity, an analogy of phylogenetic diversity, based on species traits relevant for ecological processes. Similar approaches to classify species according to traits were proposed earlier (Walker et al. 1999). Both of these approaches involved a set of traits that were related to some ecosystem process, but this relationship was not made explicitly. By formulating the relationships between factors that determine competitive outcomes in communities and the traits involved, we may make such explicit statements and derive understanding for how aggregate measures of groups of species change depending on the environmental drivers.

Classification of traits

Traits may be classified into at least two categories having distinct ecological consequences (Tilman et al. 1997; Loreau et al. 2002). First, traits may be related to the range of substitutable resources, such that species with complementary traits (partly not overlapping) may theoretically coexist (*see* theories on limiting similarity; MacArthur and Levins 1967). Such complementarity may, for example, be different rooting depths in terrestrial plants, territorial ranges, ability to use different forms of nitrogen (e.g., by nitrogen fixation), or the range of prey body sizes shown in Fig. 1 for four different Cladocerans.

Second, traits may be related to the efficiency of uptake of essential resources, such that in the case of only one homogenous resource and a constant environment, the most efficient species will exclude others by competition (sampling effect sensu Tilman et al. 1997). In this case there is no complementarity, and for any given environmental condition there exists only one single optimal value of the trait (for example the lowest resource level that sustains positive growth, i.e., zero net growth isoclines) such that species with this trait would come to dominate the community in a stable environment. In many experiments an initial sampling effect was evident because of the way the experiment was set up, but over time as competition takes place complementarity effects become more pronounced (Pacala and Tilman 2003). Furthermore, some traits relate the efficiency to environmental parameters such as temperature or pH (Norberg et al. 2001). Functional groups, commonly used as the unit of ecosystem networks, are here defined as a group of species having similar resource requirements (i.e., sharing essential resources) and thus potentially competing for them (Steneck 2001). This means that over time succession can take place by means of competition that alters the composition and thus the overall functioning of the group. In an ecosystem model this would mean that the parameters change in relation to the environmental parameters that affect competition within these groups. Functional groups can be assemblages of species within one trophic level, such as green, blue-green, and diatom algae for autotrophs, or cladocerans and copepods for zooplankton. Thus, by definition, a higher number of functional groups would mean a higher degree of complementarity (higher range of different resources being used), and a higher number of species within functional groups would mean a higher probability for sampling effects, i.e., more efficient use of the resources that are essential for this functional group (Tilman et al. 1997; Hooper 1998). It is important to distinguish these two categories of traits, since the complementarity-related traits may be part of the process that sustains trait diversity of the sampling-related traits by decreasing the effect of competition. For example, in the pelagic there might only be one optimal set of traits with regard to light harvesting properties for any given mixed layer depth and light profile. However, because different functional groups of phytoplankton, i.e., greens, blue-greens, and diatoms, have different pigments and light harvesting properties (blue-greens being better dark adapted) in addition to different resource requirements (N_2 or Si), the diversity of light harvesting responses in the community can be higher than in monocultures due to complementary use of resources of different functional groups, i.e., coexistence of three functional groups results from the different resource requirements according to resource theory (Tilman 1982). A similar argument is made by Leibold (1995) regarding the related concept of the niche. Any other process that decreases competition or delays the effect of competition, such as spatial heterogeneity and dispersal, will have an effect on sustaining the diversity of traits that relate to competition for essential resources.

Examples of tradeoffs and quantitative traits

In Fig. 1, a combination of traits is presented for a guild of Cladoceran zooplankton as an example of complementary

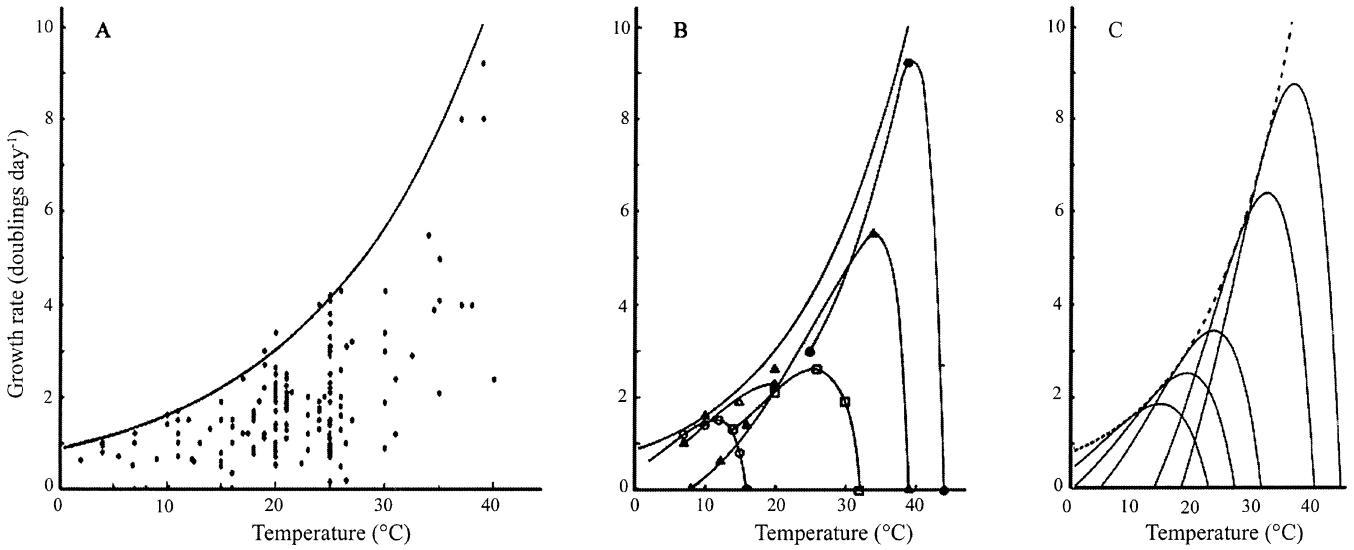

Fig. 2. (A) An envelope function for temperature-dependent growth rates in unicellular phytoplankton (line) and all data points used in the study (dots) (redrawn from Eppley 1972). (B) Examples of single species responses to temperature (redrawn from Eppley 1972). Note that high growth rates at one temperature trade off with growth rates at other temperatures, so that species are predicted to replace each other. (C) A mathematical formulation of an interspecific temperature response function. The graph shows species responses for different values of temperature optima traits, *Z*, (solid lines) and the envelope of the tradeoff function (dashed line) from Eq. 1. The width, *w*, of the response function parameter is here set to 12.

traits (resource use range) and efficiency traits (filtration rate). The *x* axis is the resource use range, given as the range of prey body sizes the species can ingest, and the efficiency at which these prey are filtered is given on the *y* axis. In laboratory experiments (Norberg 1999), *Daphnia magna* typically outcompeted all other species except *Chydorus sphaericus*. Thus, even though *C. sphaericus* had a higher filtration rate per capita (i.e., is more efficient), *D. magna* could coexist because of complementary resource use. *D. longispina* and *D. pulex* typically were outcompeted by *D. magna* but coexisted with each other and with *C. sphaericus*. In a situation with one single prey species (and thus size) one would expect only the zooplankton species with the highest filtration efficiency to outcompete all others, yielding lower trait diversity in filtration efficiency and consequently lower species richness.

Other examples of traits related to process efficiency are those that relate the growth of species to abiotic conditions such as pH and temperature. Eppley (1972) presented a compilation of temperature responses for unicellular algae (Fig. 2A,B). His data make two important points. First, there is an obvious tradeoff in temperature optima such that species that grow well at high temperature do less well at lower temperatures compared to species that have a lower temperature optima. Second, there exists an interspecific limit on maximum growth rate, which Eppley (1972) described as an envelope function. An envelope function gives the present evolutionary limit of maximum growth for any temperature. Similar interspecies functions for temperature and body mass have now been developed for a variety of processes (Gillooly et al. 2001), but note that these studies do not focus on the upper limit of process rates (envelopes) but rather on the mean.

By describing a tradeoff relationship mathematically we can later use it to predict dynamics of aggregate community properties such as total biomass, average trait, and trait distributions. The following function describes the temperature response of growth for all possible species by defining a continuum in the trait *Z*, as

$$f_{\text{Temperature}}(Z, T, w) = \left[1 - \left(\frac{T - Z}{w}\right)^2\right] 0.59e^{0.0633T} \quad (1)$$

where the trait $Z[^\circ C]$ gives the temperature where the growth rate is equal to the maximum determined by the envelope. The parameter $T[^\circ C]$ is the environmental temperature, and $w[^\circ C]$ is the width of the temperature response function. The envelope function is given as the term $0.59e^{0.0633T}$ following Eppley (1972). For any temperature, *T*, a species with an optimal growth at $Z_{\text{opt}} = T$ will have the maximum possible growth rate determined by the envelope function and will thus be the competitive dominant. The function is shown in Fig. 2C for five different traits together with the envelope. Note that the formulation of the individual species temperature response as a quadratic function is a simplification and many other schemes have been proposed (Ahlgren 1987).

Other typical examples of tradeoffs in ecology are opportunist–gleaner, or *r–K* strategies (Reynolds 1997; Litchman and Klausmeier 2001) and different kinds of predator-defense mechanisms that decrease competitive/exploitative abilities (Chase et al. 2000). Below I present how resource-uptake/growth and predator-defense/growth tradeoffs might hypothetically be formulated mathematically as general interspecies tradeoff functions. The value of the trait of a species is given as parameter *Z*. The resulting growth rate then depends on the value of the trait, *Z*, and the resource (*Q*) or

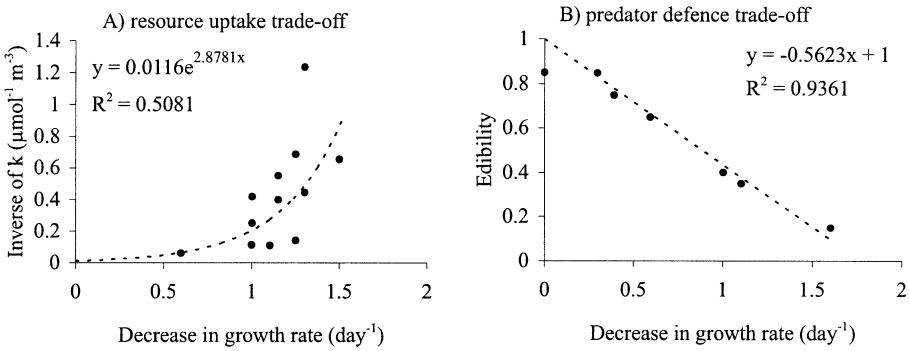

Fig. 3. Two examples of interspecies tradeoffs were allocation of energy for growth into biochemical or physical structures results in (A) increased resource-uptake efficiency at low concentrations (decreases the value of the half-saturation constants, here shown as the inverse $1/k$ for silica uptake) or (B) decreased edibility (unitless) by zooplankton (data compiled by Wirtz and Eckhardt 1996, only species from Lake Constance). The tradeoff cost is here estimated as the reduction in growth rates compared to the fastest growing species in the study ($\sim$2.1 d^{-1}). These tradeoff relationships can be described by mathematical functions and used in the framework described in the text to predict dynamics of aggregate community properties.

predator (P) abundances, respectively.

$$f_{\text{Resource uptake}}(Z, Q) = r\frac{Q}{k(Z) + Q} - (bm + cZ) - d \quad (2)$$

$$f_{\text{Predator defense}}(Z, P) = r - (bm + cZ) - d - pe(Z)P \quad (3)$$

Parameters used are r (time^{-1}) for intrinsic growth rate; bm (time^{-1}) for basal metabolism; d (time^{-1}) for dilution rates; p for predation rate (time^{-1}) for nonmetabolic loss rates; and c (time^{-1}) for the energetic cost associated with trait Z (unitless). The functions $k(Z)$ and $e(Z)$ relate the investment in the trait, Z, to the parameters determining resource-uptake kinetics and edibility, respectively. Empirical examples for such functions are shown in Fig. 3A,B. The reduction in growth is an estimate of the energetic cost expressed in the formulas as a metabolic investment, cZ, and the functions $k(Z)$ and $e(Z)$ can be calculated from the fitted curves shown in Fig. 3. Such interspecies tradeoff functions provide information about the processes of species sorting and thus the dynamics of community attributes such as trait distributions and total productivity as described below.

Other notable compilations of numerical traits for different functional groups can be found for phytoplankton in Reynolds (1997), phytoplankton and zooplankton in Andersen (1997), for a variety of taxa Petchey and Gaston (2002), and for British grassland plants in Grime et al. (1997).

What are the optimal traits and envelopes?

A tradeoff is a very powerful concept because it is based on general physical principles of conservation of mass and energy as well as the laws of thermodynamics. Any use of energy for some purpose other than reproduction and growth will decrease the intrinsic growth rate of the species. The three types of tradeoff functions presented above all share a common property that for any value of the environmental constraint, temperature, resource, or predator density, respectively, there exists only one optimal trait, Z_{opt}. Mathematically, Z_{opt} is found by setting the first derivative of the tradeoff function to zero and solving for Z as a function of the environmental constraint. Substituting Z_{opt} back into the tradeoff function yields the envelope function, i.e., the maximum performance of any species given the tradeoff relation. This envelope does not have to be a fixed function in evolutionary time. Different body designs (key innovations) that have evolved historically have had the effect of pushing this envelope. For example, the appearance of endotherms distinctively changed the conditions for the temperature-related growth envelope, and different morphologies in zooplankton show up as different envelopes for the relation between filtering rate and body size (Peters and Downing 1984). Species have arrived at their suite of traits by path-dependent evolution, meaning that certain traits or combinations of traits may not be realized or some traits may be correlated. The use of envelopes and species distributions within them may allow us in the future to study evolutionary and ecological processes simultaneously.

Trait distributions in communities

The distribution of traits in natural communities is a result of past environmental conditions. Consider, for example, the hypothetical distribution of temperature response function parameters (optima and width) in phytoplankton in temperate and tropical regions. Even though the relation between diversity and latitude is unclear for phytoplankton, one might speculate that the range of temperature optima found in the tropics (Fig. 4B) is far lower due to a very stable temperature regime, while temperate areas may have a much larger range in temperature optima (Fig. 4A) represented by species in the community. A disturbance is an environmental condition that falls outside the community's ability to cope, which is reflected by the trait distribution. Trait distributions thus reflect the environmental variability in the community, but note that species richness does not necessarily have to correlate with trait diversity. Just as species abundance distributions are of more importance than mere species numbers,

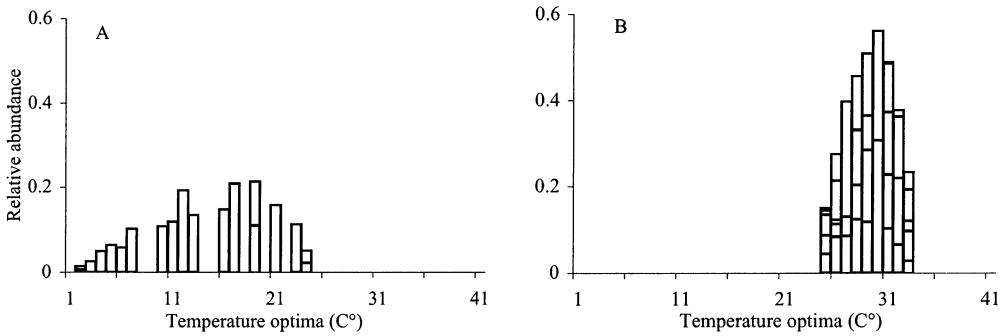

Fig. 4. An illustration of how distributions of traits in communities, here exemplified by the optimal temperature for growth, may result from different environments such as (A) temperate and (B) tropical regions. I hypothesize that this particular trait may have a wider distribution in temperate areas compared to tropical ones because the environmental temperature is more variable. Although the number of species in tropical areas might be much higher, the trait variance, V, a measure of trait diversity, may be much less. This illustrates that species richness and trait diversity do not necessarily correlate. The average optimal temperature in the community, $\hat{Z}$, reflects the average in environmental temperatures.

the distribution of traits is of greater interest than the number of species or traits, respectively. Some traits represented in species dominating in the community will have larger effects on how the community as a whole performs than traits represented in rare species. Thus, instead of rank distributions, for example, as measured by the Shannon index, the average and the variance of traits better describe the community attributes. In the following I will use trait variance around the average trait as the definition for trait diversity.

Dynamics of group properties

Understanding natural ecosystems requires additions to simple theoretical population models in order to encompass issues of spatial as well as species heterogeneities. Also, aggregated measures such as total group biomass and productivity, dominant traits, and trait distribution in the system may be more important to study than the precise composition of all the components. Norberg et al. (2001) developed an approach for approximating the dynamics of such aggregated measures. The theory relies on the idea that tradeoff functions are an inherent constraint on the distribution of traits in species and that species sorting causes the average properties of the community to change in a predictable way based on the environmental constraints. Species sorting simply means that through the openness of the system, species enter communities and persist there when the conditions are right, and do not do so when they are not right (Chase and Leibold 2003). In essence the CAS approach presented below is an abstract, but mathematically convenient, way to present the species sorting concept, which makes it very useful for understanding its role in the relationship between biodiversity and ecosystem functioning.

During events of strong competition where a certain trait aspect determines the competitive outcome, it is possible to make fairly detailed predictions regarding the succession of the community. We can describe the dynamics of biomass for any species C_i in the community as

$$\frac{dC_i}{dt} = f(\boldsymbol{Z}_i, \boldsymbol{E})C_i + m(\boldsymbol{Z}_i, \boldsymbol{E}, t) \tag{4}$$

where $\boldsymbol{Z}_i$ is the vector (a list) of traits of species i and could potentially also involve multiple traits. The function $f(\boldsymbol{Z}_i, \boldsymbol{E})$ gives the growth rate of a species with traits $\boldsymbol{Z}_i$ under the environmental conditions $\boldsymbol{E}$, which is a vector of environmental constraints affecting the growth rates of the species (note that $\boldsymbol{E}$ also may contain the abundances of other species or resource densities). The function $m(\boldsymbol{Z}_i, \boldsymbol{E}, t)$ describes rates that are density-independent changes in abundance such as immigration from other sources or hatching from resting stages. This function could in principle be an independent function of local conditions (e.g., dispersal from other systems), determined by the internal environment (for hatching), or modeled spatially explicitly in a metacommunity framework (Leibold and Norberg 2004). Multiple traits, as indicated by the vector notation, involve the problem of correlation between traits. This issue can be handled, but I will not develop it here; thus, in the following text, I will omit vector notations for clarity.

The aggregate properties, such as total biomass, average trait, and trait variance, of the general formulation above can be approximated. The following equations provide insight into the relationship between these aggregate properties. For a community with mean trait $\hat{Z}$, the dynamics of total biomass, C_T, is given as

$$\frac{dC_T}{dt} \approx \left(f + \frac{f''}{2}V\right)C_T + M \tag{5}$$

(I will here simplify the notation by writing f instead of $f(\hat{Z}, E)$), and the equation for the average trait, $\hat{Z}$, follows

$$\frac{d\hat{Z}}{dt} \approx f'V + \frac{M}{C_T}(\hat{Z}_M - \hat{Z}) \tag{6}$$

where the right-hand terms describe dynamics related to mi-

gration. M is the net change in biomass due to migration, and $\hat{Z}_M$ is the average trait of the migrating community.

Translated to nonmathematical language, Eq. 5 states that the growth of the group is determined by the growth of the average trait but that this growth is reduced proportionally to the trait variance, V (since f'' is usually negative for any function with one single optimum in the vicinity of this optimum). Since the tradeoff function has the property that only one trait is optimal for each environmental condition, E, all other traits in the system are suboptimal and thus decrease the growth rate of the whole group. Equation 6 describes how the rate of change in the average trait of the community is affected by the process of succession; the equation states that the rate at which the average trait in the community $\hat{Z}$ moves toward the optimal trait Z_{opt} is proportional to trait variance (the first derivative of the tradeoff function with respect to Z always has the same sign as $Z_{\text{opt}} - \hat{Z}$). Thus, trait variance, V, is a good estimate of the adaptive capacity of the community. Furthermore, we were able to approximate the dynamics of trait variance, which gives us a closed system for these three aggregated measures (C_T, $\hat{Z}$, and V) of a group of species. There are many ways by which one could approximate the trait variance, and I will below present a version that illustrates its characteristics more intuitively, but refer to the original paper (Norberg et al. 2001) for a mathematically better justified approach. The dynamics of the trait variance is roughly approximated by

$$\frac{dV}{dt} \approx \beta(Z_{\text{opt}} - \hat{Z})^2 - \alpha V + \frac{M}{C_T}[(\hat{Z}_M - \hat{Z})^2 + (V_M - V)] \tag{7}$$

where β and α are parameters that need to be estimated by simulations, and V_M is the variance in traits of the migrating community. This equation shows that trait variance increases as the difference between the current optimal trait and the current average trait in the community increases. If the environment is stable, $\hat{Z}$ will approach Z_{opt}, and thus the first term will become zero and the variance will decline exponentially due to competitive exclusion.

The above provides a formalized and explicit framework for describing interactions of the different processes that make up a CAS. Not surprisingly, Eq. 6 is the ecological analog of Fisher's fundamental theorem of natural selection (Fisher 1958). The different processes of a complex adaptive system approach are here formalized by the mathematical equations described above and the relations shown in Fig. 5. Note how the environment interacts with the trait distribution in affecting ecosystem functioning in an active community and the importance of the immigrating/resting community in sustaining traits distributions. Leibold and Norberg (2004) give more detail on the role of immigration in terms of the metacommunity concept.

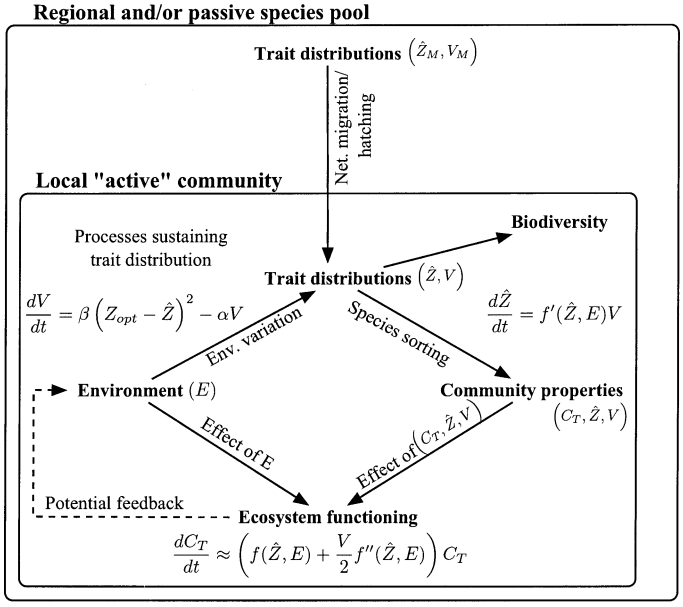

Fig. 5. The framework for ecosystems as complex adaptive systems provides a useful tool for understanding the interaction between the environment, diversity, and ecosystem functioning. Ecosystem functioning is determined by the state of the environmental factors as well as the aggregated properties of the community. Trait diversity (trait variance, V) in communities is sustained by environmental variability and/or immigration from the regional species pool or by hatching from resting stages. The properties of the community change as a result of species sorting processes, thereby affecting the dominant trait in the group, x_{avg}. The adaptive capacity of the group is the ability of group properties to change in response to changes in the environment, i.e., dx_{avg}/dt, which is proportional to the trait diversity (V). Thus, the environment affects ecosystem functioning by direct effects, e.g., temperature regulates the process rates, or indirect effects by changing the conditions for the species sorting and thus the trait distributions in the community. For simplicity, terms relating to the effect of immigration are not shown in this figure but are presented in the text and analyzed further in Leibold and Norberg (2004). All variables except total biomass, C_T, can be thought of as vectors of multiple traits and environmental factors (*see text*).

Outlook

Looking at trait distributions in communities has had an important role in ecology, such as the distributions of body sizes (Holling 1992; Havlicek and Carpenter 2001) in communities. Another field that relies on the fact that environmental factors structure communities based on their traits is paleoclimate reconstruction. With the knowledge of species distributions as well as the environmental conditions in a set of 100 training lakes, it is possible to predict the environmental history of a set of independent lakes (Bigler and Hall 2002) by estimating the mean of the distributions of species traits. Furthermore, they also calculated estimated optima and tolerances both for pH and temperature for a large fraction of the species but did not provide any information on the distribution (diversity) of optima in the community. Nevertheless, such studies may be useful when making historical analyses of the dynamics of community attributes such as trait distribution and relate them to the environmental changes by, for example, independent data sets of pH or temperatures.

Macroecology is a branch of ecology that deals with finding patterns among species, which hint at larger processes that drive these (Brown 1999). Allometric relationships are

among these patterns (Gillooly et al. 2001). However, most of the literature of allometry focuses on finding the average slope between body size and processes. To look at the evolutionary constraints, one needs also to focus on the envelope function of these processes, i.e., not only at the mean rates but also the maximum rates. Statistically this poses a bigger problem, since methods for detecting the envelopes are less well developed than traditional statistics focusing on mean and variances. In fact, the existence of a true envelope for processes would in a way invalidate the assumption of normality. Quartile statistics would only provide an estimate since it assumes a normal distribution. Development in this field would have to look at alternative distributions that have definite limits.

Trait distributions in communities both provide information for past environmental fluctuation regimes as well as give an indication of the ability to cope with future response to environmental changes. While local trait distributions are limited by many factors, such as environmental history, past extinction, and colonization events, at the macroecological scale we may expect to find the relationships under which the evolution of species has been constrained historically. These envelope functions provide the current limits of possible traits. The theoretical framework proposed here allows us to use these envelope functions to make predictions regarding how environmental fluctuations may determine local trait distributions and the adaptive capacity of the community in the face of change. Most importantly, this framework will allow us to investigate the processes of species sorting and the resulting effects of species abundances on ecosystem functioning simultaneously in relation to environmental factors.

References

AHLGREN, G. 1987. Temperature response functions in biology and their application to algal growth constants. Oikos **49:** 177–190.

ANDERSEN, T. 1997. Pelagic nutrient cycles. Ecological studies. Springer.

ARTHUR, W. B., S. DURLAUF, AND D. LANE. 1997. The economy as an evolving complex system II, series in the sciences of complexity. Addison-Wesley.

BIGLER, C., AND R. I. HALL. 2002. Diatoms as indicators of climatic and limnological change in Swedish Lapland: A 100-lake calibration set and its validation for paleological reconstructions. J. Paleolimnol. **27:** 97–115.

BOND, E. M., AND J. M. CHASE. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. Ecol. Lett. **5:** 467–470.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size and composition of plankton. Science **150:** 28–35.

BROWN, J. H. 1999 Macroecology: Progress and prospect. Oikos **87:** 3–14.

CHASE, J. M., AND M. A. LEIBOLD. 2003. Ecological niches: Linking classical and contemporary approaches. Univ. Chicago Press.

———, ———, AND E. SIMMS. 2000. Plant tolerance and resistance in food webs: Community level predictions and evolutionary predictions. Evol. Ecol. **14:** 289–314.

EPPLEY, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. **70:** 1063–1085.

FISHER, R. A. 1958. The genetical theory of natural selection. Dover.

GILLOOLY, J. F., J. H. BROWN, G. B. WEST, V. M. SAVAGE, AND E. L. CHARNOV. 2001. Effects of size and temperature on metabolic rate. Science **293:** 2248–2251.

GRIME, J. P. 1997. Biodiversity and ecosystem functioning: The debate deepens. Science **277:** 1260–1261.

———, AND OTHERS. 1997. Integrated screening validates primary axes of specialisation in plants. Oikos **79:** 259–281.

HAVLICEK, T., AND S. R. CARPENTER. 2001. Pelagic species size distributions in lakes: Are they discontinuous? Limnol. Oceanogr. **46:** 1021–1033.

HOLLAND, J. 1996. Hidden order: How adaptability creates complexity. Perseus.

HOLLING, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecol. Monogr. **62:** 477–502.

———. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems **4:** 390–405.

HOOPER, D. U. 1998. The role of complementarity and competition in ecosystem response to variation in plant diversity. Ecology **79:** 704–719.

HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monogr. in Pop. Biol. Princeton Univ. Press.

HUSTON, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. Oecologia **110:** 449–460.

JANSSEN, M. 1998. Use of complex adaptive systems for modeling global change. Ecosystems **1:** 457–463

LANGTON, C. G. 1995. Artificial life: An overview. MIT Press.

LEIBOLD, M. A. 1995. The niche concept revisited—mechanistic models and community context. Ecology **76:** 1371–1382.

———, J. NORBERG. 2004. Biodiversity in metacommunities: Plankton as complex adaptive systems? Limnol. Oceanogr **49:** 1278–1289.

LEVIN, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. Ecosystems **1:** 431–436.

LEWONTIN, R. C. 1977. Adaptation. Encicl Einaudi Turin **1:** 198–214.

LITCHMAN, E., AND C. A. KLAUSMEIER. 2001. Competition of phytoplankton under fluctuating light. Am. Nat. **157:** 170–187.

LOREAU, M., N. MOUQUET, AND R. D. HOLT. 2003. Meta-ecosystems: A theoretical framework for spatial ecosystem ecology. Ecol. Lett. **6:** 673–679.

———, AND OTHERS. 2002. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science **294:** 804–808.

MACARTHUR, R. H., AND R. LEVINS. 1967. The limiting similarity, convergence and divergence of coexisting species. Am. Nat. **101:** 377–385.

NORBERG, J. 1999. Resource-niche complementarity and autotrophic compensation determines ecosystem-level responses to increased cladoceran species richness. Oecologia **122:** 264–272.

———, D. P. SWANEY, J. DUSHOFF, J. LIN, R. CASAGRANDI, AND S. A. LEVIN. 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. Proc. Natl. Acad. Sci. U.S.A. **98:** 11376–11381.

PACALA, S., AND D. TILMAN. 2003. The transition from sampling to complementarity, p. 151–166. *In* A. Kinzig, S. W. Pacala, and D. Tilman [eds.], The functional consequences of biodiversity. Monogr. Pop. Biol. Princeton Univ. Press.

PETCHEY, O. L., AND K. J. GASTON. 2002. Functional diversity (FD) and species richness and community composition. Ecol. Lett. **5:** 402–411.

PETERS, R. H., AND J. A. DOWNING. 1984. Empirical analysis of zooplankton filtering and feeding rates. Limnol. Oceanogr. **29:** 763–784.

PLOTKIN, J. B., AND OTHERS. 2000. Predicting species diversity in tropical forests. Proc. Natl. Acad. Sci. U.S.A. **97:** 10850–10854.

REYNOLDS, C. S. 1997. Vegetation processes in the pelagic: A model for ecosystem theory. Excellence in ecology. Ecological Institute, Oldendorf.

SCHMID, B., J. JOSHI, AND F. SCHLÄPFER. 2003. Empirical evidence for biodiversity-ecosystem functioning relationships, p. 120–151. *In* A. Kinzig, S. W. Pacala, and D. Tilman [eds.], The functional consequences of biodiversity. Monogr. Pop. Biol. Princeton Univ. Press.

SOMMER, U. 1989. Plankton ecology. Science Tech. Publishers.

STENECK, R. S. 2001. Functional groups, p. 121–139. *In* S. A. Levin [ed.], Encyclopedia of biodiversity. Academic.

TILMAN, D. 1982. Resource competition and community structure. Monogr. Pop. Biol. Princeton Univ. Press.

———, AND J. A. DOWNING. 1994. Biodiversity and stability in grasslands. Nature **367:** 363–365.

———, C. L. LEHMAN, AND K. T. THOMSON. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Natl. Acad. Sci. U.S.A. **94:** 1857–1861.

VINEBROOKE, R. D., K. COTTINGHAM, J. NORBERG, M. SCHEFFER, S. I. DODSON, S. C. MABERLY, AND U. SOMMER. 2004. Cumulative impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. Oikos **104:** 451–457.

WALKER, B., A. KINZIG, AND J. LANDERIGE. 1999. Plant attribute diversity, resilience and ecosystem function: The nature and significance of dominant and minor species. Ecosystems **2:** 95–113.

WIRTZ, K.-W., AND B. ECKHARDT. 1996. Effective variables in ecosystem models with an application to phytoplankton succession. Ecol. Model. **92:** 33–53.

Received: 1 February 2003
Accepted: 23 October 2003
Amended: 17 November 2003