Species Composition, Species Diversity, and Ecosystem Processes: Understanding the Impacts of Global Change

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Summary

Invasions by exotic species, climate change, increased atmospheric CO₂, deposition of N, habitat destruction and fragmentation, predator decimation, and many other anthropogenic perturbations to ecosystems can have both direct impacts on ecosystem processes and indirect effects mediated through changes in ecosystem composition and diversity. The work reviewed in this chapter suggests that the long-term effects of global change will depend on the changes in ecosystem composition and diversity that occur in response to global change. If this is so, the discipline of ecology faces its greatest challenge to date: to discover how to predict the effects of global change on ecosystem composition and diversity and how to predict the joint impacts of all these changes on a variety of ecosystem processes.

Introduction

Humans are having unprecedented impacts on the ecosystems of the earth. Atmospheric concentrations of such greenhouse gases as carbon dioxide and nitrogen dioxide are increasing, leading to predictions of rapid climate change for many parts of the globe (e.g. Raval and Ramanathan 1989; Schneider 1989, 1990, 1993; Sellers et al. 1996). Humans now dominate the global nitrogen (N) cycle via production of N fertilizer, cultivation of legumes as crops, and production of nitrogenous gases via fossil fuel combustion (e.g. Vitousek 1994; Galloway et al. 1995; Vitousek et al. 1997). Humans have already directly appropriated, and degraded, about 43% of the land surface of the Earth (Daily 1995), thus impacting the future utility of this land. This habitat modification, destruction, and fragmentation is leading to a marked increase in the rate of species extinction and to great changes in the species composition and diversity of many ecosystems (e.g. Prescott-Allen and Prescott-Allen 1978; Simberloff 1984;
Groom and Schumaker 1993; Tilman et al. 1994; Moilanen and Hanski 1995). Similarly, humans now use 54% of all accessible freshwater runoff and 26% of total terrestrial evapotranspiration (Postel et al. 1996). Human movements of species within and among major biogeographic realms are allowing exotic species to replace native species in many aquatic and terrestrial ecosystems (e.g. Elton 1958; Fox and Fox 1986; Drake et al. 1989; Vitousek 1990; D’Antonio and Vitousek 1992). Humans also release into the environment a wide array of biologically active organic compounds, including pesticides that may mimic endocrine hormones (Colburn et al. 1996).

As Vitousek (1994) emphasized, we are certain that human society is causing increased atmospheric CO$_2$, dominating the global N cycle, appropriating land and water, fragmenting habitats, and causing massive invasions by exotic species. However, we are uncertain of the impacts of these actions. There is an increasingly urgent need to know what the long-term impacts of these human activities, loosely called global change, will be on the composition, structure, functioning, sustainability, and stability of Earth’s aquatic and terrestrial ecosystems. The need to understand and accurately predict the impacts of various scenarios of global change, and to find ways to alleviate such impacts, is undoubtedly the greatest challenge facing the discipline of ecology, and one of the greatest needs of society. We will meet this challenge only if we make major advances in our knowledge of the fundamental processes that determine ecosystem structure, dynamics, and functioning.

It seems highly improbable that such understanding will come from simple extrapolations of correlational patterns observed in natural ecosystems. Correlation is not causation. Such extrapolations would have to assume that correlation is causation, that the basic processes structuring ecosystems would not be altered by the forces of global change, and that the responses of presently intact systems to small-scale natural variation in temperature, precipitation, nitrogen availability, and so forth, would also occur even after the major changes in ecosystem species composition that are apt to result from global change.

I suggest that we consider a different approach. I hypothesize that the largest effects of global change may be modifications of the biotic composition, biodiversity, and trophic structure of ecosystems, and that these changes will cause both qualitative and quantitative shifts in a variety of ecosystem processes. To predict these shifts will require knowledge of how the forces of global change influence ecosystem species composition and diversity, and how composition and diversity influence ecosystem processes. Thus, this view suggests that the impacts of particular global change scenarios will depend both on how these modify the structure and composition of an ecosystem, and on how the novel ecosystem consequently created functions. For instance, is it worthwhile to extrapolate from correlational data on the effects of normal climatic variation on a
Minnesota oak forest to predict how a 4°C increase in temperature might affect it, especially if the long-term impact of such a temperature increase would be to replace the forest with grassland? And, would it be appropriate to use knowledge of native prairies to predict the behavior of grasslands created by such temperature increases if they have novel species compositions and lower species diversity than native prairie? It seems plausible that climate change would create novel grasslands because few native prairie species would be able to invade such a region given the slow rate of migration of such species and the difficulty of migration through the fragmented landscapes that now exist in much of North America. Indeed, the dominant native bunchgrasses of Minnesota prairies often require ten to twenty years to invade an abandoned field that is directly bordered by prairie (Inouye et al. 1987; Tilman 1990, 1994), and another twenty to forty years to attain dominance. How long would be required if they had to move ten to 100 km through an inhospitable and fragmented landscape?

I raise these questions because much work suggests that the species and functional group composition and diversity of ecosystems may be an important determinant of ecosystem processes, which are formally defined later in this chapter. The forces of human-caused global change directly impact ecosystem functioning by changing the physical parameters that an ecosystem experiences. However, larger, long-term impacts may be through change in species composition and diversity. In some cases, the resultant ecosystems may bear little resemblance to any that exist today. If the rates of ecosystem processes are highly dependent on species composition and diversity, then a major challenge facing us is to understand how composition and diversity will respond to global change, and how the resultant ecosystems will function.

Although ecosystem ecology, evolutionary ecology, population ecology, and community ecology have not developed in isolation from each other, many of the advances in these disciplines have been achieved by making a series of simplifying assumptions about the other three. One of the central assumptions of modern ecosystem ecology, which traces many of its roots to the pioneering work of Lindeman and the Odums, is that the functional composition of an ecosystem is a greater determinant of ecosystem processes than its species composition or diversity. This simplifying assumption began when initially quantifying the flow of energy and the cycling of materials in ecosystems. Both to make this work practical and to emphasize the roles of trophic structure, organisms were grouped by their trophic roles (e.g. primary producers, primary consumers, secondary consumers, decomposers, and so on), sampled, and analyzed as units. This approach has provided many significant insights into the functioning of ecosystems. Indeed, it seems difficult to imagine how an ecosystem could have been treated as an interactive system, complete with feedback, had this simplifying assumption not been made.
The past half-century has been an era of concomitant advances in population and community ecology, which have revealed many of the details of the interactions among species that determine the location of species and their abundance. Work in ecosystem ecology has shown that ecosystem processes often are controlled by a few key species, and that variation in species composition can cause large differences in these ecosystem processes. As important as this, the accelerating effects of humans on ecosystems via destruction, fragmentation, intensive ecosystem management, introduction of exotic species, predator decimation, and domination of nutrient cycling have led to greatly increased public and scientific concern. This brings to the forefront a series of questions that represent a new conceptual frontier for ecosystem ecology. The questions center on that which controls ecosystem species and functional group composition and biodiversity, and on how and why composition and diversity affect ecosystem processes.

The ability of the discipline of ecology to address these issues will influence our impact on environmental policy during a time when humans are having unprecedented, massive, and potentially irreversible effects on the ecosystems of the earth. To address these issues will require a series of fundamental conceptual, theoretical, observational, and experimental breakthroughs. The groundwork for these has been laid during the past two decades, but the intellectual challenge—the greatest our discipline has ever faced—lies before us.

**Ecosystem Processes**

There are many different ecosystem processes. Among the most fundamental are rates of primary and secondary production, the stores and rates of cycling of carbon (C), N, and other elements in an ecosystem, and the rates of gain and loss of these elements from an ecosystem. Additionally, the stability of each of these, including both its resistance to disturbance and its resilience after disturbance, are important (Pimm 1979, 1984; King and Pimm 1983). Collectively these will be called *ecosystem processes*. (They also are appropriately called “ecosystem functioning,” a term that need not imply any notion of teleology.)

In this chapter, I will use a review of the literature and conceptual speculation to explore three related questions: (1) What impacts may global change have on the composition and diversity of ecosystems? (2) Do changes in composition influence ecosystem processes? and, (3) Do changes in species diversity impact ecosystem processes, and why? Although there are not yet answers to these questions, I hope to show that they are critically important questions that are answerable if we dedicate sufficient intellect and effort.
Global Change and the Composition and Diversity of Ecosystems

Although there are uncertainties about the rate and magnitude of climate change caused by the assimilation of greenhouse gases, most global circulation models (GCMs) predict climatic changes that are of greater magnitude than has occurred naturally within the past several thousand years (e.g. Schneider 1993). There is an immense literature speculating on the possible impacts of such changes in climate on species abundance, geographic distributions, and biodiversity (e.g. Webb and Wigley 1985; Davis 1986; Cronin and Schneider 1990; Huntley 1991; Schwartz 1991; Peters and Lovejoy 1992; Chapin et al. 1995). The climatic changes predicted by most GCMs are sufficiently great that large changes in species composition are expected. However, because of limitations on rates of species migrations (e.g. Schwartz 1992) and slow changes in soil C and N, it seems improbable that there will be a simple mapping of the present relationships between climate and composition. Many species that are currently dominant in areas with a given climate and soil may not remain dominant after certain climate changes and may not become the dominants of new areas that approach the physical conditions of their former natural habitats. Rather, other species—probably those that are presently rare but happen to be present in a region and have traits similar to those that would dominate were dispersal not limiting—may become the new dominants of a region. Well-dispersed, weedy species should also increase in abundance (e.g. Nee and May 1992; Tilman et al. 1994). The number of species in these new ecosystems is apt to be much lower because of dispersal limitation. Thus, if the future were to be painted with bold broad brush strokes, the Picasso-like scene would be one of domination by many fewer species than at present, with many habitats dominated by species, perhaps weedy species, that presently may not be dominant in any habitat.

This same qualitative scenario of changes in ecosystem composition and diversity may occur because of global impacts on the N cycle. Human-caused doubling of global N fixation is causing great increases in N deposition in many areas of the world (e.g. Vitousek 1994; Galloway et al. 1995). Numerous fertilization experiments suggest that increased rates of N deposition will lead to the loss of many native species and to dominance by once-rare species, often non-natives. Similarly, habitat fragmentation also leads to the biased extinction of species (e.g. Diamond 1972, 1973; Terborgh 1974; Lovejoy et al. 1984; Laurance 1991; Tilman et al. 1994; Steadman 1995). In general, top carnivores, rare species, and poor dispersers are preferentially lost following habitat fragmentation and destruction.

The loss of species and changes in species, functional groups, and trophic composition may change a variety of ecosystem processes. Such effects are illustrated by the following three case studies. These are a biased subset of
a much larger number of possible studies, chosen because of my greater familiarity with them.

Case 1. Impacts of Nitrogen Addition

Nitrogen addition can cause dramatic shifts in plant composition and declines in plant diversity (e.g. Lawes and Gilbert 1880; Thurston 1969; Silvertown 1980; Bobbink et al. 1987; Tilman 1987, 1996; Aerts and Berendse 1988; Huenneke et al. 1990). A long-term experimental study in Minnesota illustrates several of the impacts of high rates of N deposition (Tilman 1987, 1988, 1994, 1996; Tilman and Downing 1994; Wedin and Tilman 1996). Nitrogen is the major soil resource limiting growth of plant species and determining primary productivity (Tilman 1987). In 1982, a series of 207 plots were established to which various amounts of ammonium nitrate were added. The experiment, replicated in four different fields, had nine different nutrient treatments including controls that received no nutrients, plots that received phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and trace metals but no N, and plots that received P, K, Ca, Mg, and trace metals and one of seven different rates of N addition. The rates of N addition were 0, 1, 2, 3.4, 5.4, 9.5, 17, and 27 g m$^{-2}$ yr$^{-1}$ of N added in two equal applications. Present rates of N deposition (wet and dry fall) in the region are about 0.8 g m$^{-2}$ yr$^{-1}$, whereas rates in the Ohio valley are about 2 to 4 g m$^{-2}$ yr$^{-1}$, and rates in parts of Europe and 10 to 15 g m$^{-2}$ yr$^{-1}$. The rates of experimental addition span these, and include some higher rates that may give results indicative of long-term effects of deposition at lower rates.

Composition and Diversity

This experiment has shown that N addition led to major changes in the plant species composition (Figure 19.1), plant functional group composition, insect species composition, and mycorrhizal fungal species composition (Johnson 1993) of these grasslands. In particular, higher rates of N addition led to the loss of native plant species, especially C-4 grasses, and to greatly increased abundances of non-native plant species, especially C-3 grasses. At the highest rates of N addition, all plots converged on dominance by Agropyron repens, a European perennial C-3 grass and a dominant agricultural weed. Plant species diversity declined with increasing rates of N addition, with a detectable decline in plant species richness even for addition of 1 g m$^{-2}$ yr$^{-1}$, and with species richness declining to 35% of its original value at the highest rate of N addition (Figure 19.2).
Composition and Nitrogen Dynamics

Ecosystem processes in this grassland were impacted by these changes in species composition and diversity. In particular, the shifts in species composition caused by N addition led to sharp declines in litter and root C/N ratios (Wedin and Tilman 1996). Because high C/N ratios tend to cause slow rates of decomposition and net N immobilization, and low C/N ratios tend to cause high rates of decomposition and net mineralization of nitrogen, the shifts in plant species composition caused by N addition could greatly impact N cycling in these grasslands. Wedin and Tilman (1996) found just such impacts. Soil nitrate (NO$_3$) concentrations increased by over an order of magnitude and in situ N mineralization rates increased four- to six-fold. The change in soil NO$_3$, however, was highly dependent on the C/N ratio of above- and belowground biomass (Wedin and Tilman 1996; Figure 19.3a). Only plots with low C/N ratios in plant biomass had high concentrations of soil nitrate. These were the plots that either initially were dominated by C-3 grasses or that became dominated by C-3 grasses after N addition. Be-
cause of the high motility of NO\textsubscript{3} through the soil, it might be expected that plots with high concentrations of soil NO\textsubscript{3} would also lose more of their total N. This occurred (Figure 19.3b; Wedin and Tilman 1996) and consequently, much of the N added at high rates was lost from these plots. This loss of N occurred whenever the rates of N addition were sufficient to cause the replacement of C-4 grasses by C-3 grasses, which occurred within about twelve years for plots receiving about 5 g m\textsuperscript{-2} yr\textsuperscript{-1} of N.

**Composition and Carbon Storage**

Changes in plant species composition caused by N addition also had a significant impact on C storage in these ecosystems. It has been hypothesized that atmospheric N deposition may increase plant growth, and thus terrestrial C storage, by a sufficient amount to explain the “missing C” issue (Peterson and Melillo 1985; Schindler and Bayley 1993; Hudson et al. 1994; Townsend et al. 1996). It was found that net C storage in the plots depended on plant species composition. In areas initially dominated by C-4 grasses, about 20 to 25 g of C was stored for every g of N added, when N was added at a sufficiently low rate to minimize shifts in species...
composition. However, there was no net C storage at these rates of N addition in areas initially dominated by C-3 grasses. At higher rates of N addition, the rates of C storage converged in both types of areas on a low rate of C storage (Figure 19.4; Wedin and Tilman 1996). This corresponded to having their species composition converge on dominance by non-native C-3 grasses.
Figure 19.4. Effect of the rate of N addition in the Cedar Creek N fertilization plots on the net amount of carbon stored per unit of N added. Note that the fields converged on similar storage when their compositions converged on dominance by C-3 grasses at high rates of N addition. Figure modified from Wedin and Tilman (1996).

Composition, Diversity, and Stability

These same plots have provided insights into the relationships between biodiversity, species and functional group composition, and stability. In 1987 and 1988, this region experienced the third-worst drought of its 150-year recorded meteorological history. On average, this drought caused peak aboveground living standing crop (henceforth, total plant biomass) to decrease to less than half of its former level. However, the actual magnitude of the change in total plant biomass depended on the plant species richness of the plots. On average, plots containing one or two plant species had a decrease in total plant biomass about one-fifth to one-tenth of their predrought levels, whereas plots with from fifteen to twenty-six species fell to about one-half of their predrought levels. This dependence of drought resistance on plant species diversity remained highly significant even when a large number of potentially confounding variables were statistically controlled in a series of multiple regressions (Tilman and Downing 1994; Tilman 1996). Interestingly, of the twenty potentially confounding variables entered into a multiple regression, those that were retained as significant in a backward elimination procedure were mainly measures of changes in plant species composition or plant functional group composition. The rate of N addition, which caused plant composition to change, was not retained, but the biomasses of Agropyron repens, the dominant C-3 grass of plots receiving high rates of N addition, of Schizachyrium scoparium, the dominant C-4 grass of control plots, and of forbs, legumes, and woody plants
were all retained. This indicates that changes in their abundance better explained changes in drought resistance than did the actual rate of N addition. In total, this suggests that the stability of this ecosystem is dependent both on its species richness and on its composition, and that the effect of N addition on stability was mediated through the effects of N on composition and diversity.

**Composition, Diversity, and Variability**

A similar pattern was observed when year-to-year variation in total plant biomass within individual plots during nondrought years was analyzed (Tilman 1996). Higher levels of plant species richness within a plot was associated with lower year-to-year variation in plant biomass, and this dependence held in multiple regression analyses in which a series of potentially confounding variables were controlled. Nine of eighteen candidate variables were retained in backward elimination multiple regressions as significant, with five of these being measures of plant compositional differences among plots (biomasses of *Agropyron repens*, *Schizachyrium scoparium*, *Poa pratensis*, C-3 grasses, and legumes). As before, both diversity and composition were significant controllers of stability in these plots, but the rate of N addition was not.

**Case 2. Effects of Species Composition on Nutrient Cycling**

The rate of nutrient mineralization, which is an important determinant of ecosystem productivity, depends on the species composition of an ecosystem. For instance, Pastor et al. (1984) found that never-logged forest stands on Blackhawk Island in the Wisconsin River, differed in their in situ rates of N mineralization in ways that corresponded with their species composition. The highest rates of N mineralization occurred in a stand dominated by sugar maple; the lowest in a stand dominated by red pine. Annual above ground production increased with the rate of N mineralization. These differences in N mineralization corresponded with differences in the quality of the litter produced by the tree species that dominated these eight stands, suggesting that species composition controlled N mineralization. A direct test of this possibility was provided by a well-replicated experiment in which five grass species were planted into initially identical soils (Wedin and Tilman 1990). In situ rates of N mineralization diverged through time, with marked differences corresponding to interspecific differences in litter quality (Wedin and Pastor 1993; Wedin et al. 1995). Similarly, the invasion of Hawaii by an exotic legume greatly changed N dynamics (Vitousek and Walker 1989; Walker and Vitousek 1991), as have other plant invasions.
(Vitousek 1990). In total, changes in species and functional group composition are apt to impact the rates of supply of limiting nutrients, which, in turn, could feedback on composition.

Case 3. Trophic Structure

Ecosystems differ in their trophic structure, which can be measured as the proportion of the total living biomass that occurs on each trophic level. In both terrestrial and aquatic ecosystems, this can be highly dependent on the presence or absence of one or a few predator species (e.g. Paine 1969; Oksanen et al. 1981; Carpenter and Kitchell 1988, 1993; Leibold 1989; Hairston and Hairston 1993). For instance, at the time of Neolithic settlement, most of the British Isles was covered by dense, productive forests, but much of this was converted within Neolithic times into grassland (Tansley 1949). Similar shifts occurred in Europe (Ellenberg 1988). Tansley, Ellenberg, and others contend that this dramatic shift was caused more by large mammal grazing and by predator decimation by Neolithic people, than by direct clearing of forests. The high densities of goats, sheep, cattle, and other herbivores resulting from human pastoral practices increased seed and seedling mortality on trees and slowed tree recruitment, causing grasslands to replace forests. Predator decimation is a hallmark of human expansion, and is effecting trophic structure in other areas, as in portions of the United States where geese and deer densities are unusually high. Similarly, the presence or absence of some species of predatory fish can greatly impact the trophic structure of lakes (Carpenter and Kitchell 1988, 1993). For instance, in lakes in which large *Daphnia* are the major herbivore on planktonic algae, the absence of a top predator can shift a lake toward high algal abundances, whereas the presence of a top predator can greatly decrease algal biomass. Early work by Darwin (1859), in addition to work by Paine (1966, 1988) in the intertidal have also clearly demonstrated the effects of predators on the trophic structure of food webs.

Changes in trophic structure could impact many ecosystem processes. Consider the impacts of deer on the savannas of Cedar Creek Natural History Area in Minnesota. For a variety of reasons, deer populations have increased greatly at Cedar Creek and in its vicinity since settlement. In 1982, a series of deer exclosures was established at Cedar Creek (Inouye et al. 1994). These exclosures have shown some surprising effects of deer herbivory on primary productivity and soil total N (Ritchie and Tilman 1995; Ritchie et al. 1997; Knops et al. unpublished manuscript). Inside of deer exclosures, peak plant standing crop of oak savanna has increased during the past fifteen years, whereas it has remained about constant outside the deer exclosures (Figure 19.5). This increase in plant biomass corresponds with an increase in total soil N in the plots from which deer were excluded. Why, though, did deer exclosure cause soil total N to increase?
Figure 19.5. Effect of deer browsing (broken line) and of deer exclosure (solid line) on total plant biomass of otherwise unmanipulated plots in a field of native oak savanna. High biomass of plots without deer is caused by legumes, especially *Lathyrus*, which became much more abundant when deer were excluded. Figure modified from Knops et al. (in review).

The cause was a dramatic shift in plant community composition resulting from reduced deer herbivory. Deer feed preferentially on the fast-growing legume *Lathyrus venosus*, which has high tissue N levels. After twelve years, the deer exclosures had caused *Lathyrus* abundance to increase six- to eight-fold. Especially in years with cool, moist springs, *Lathyrus venosus* dominated the deer exclosures. By late summer, when the peak standing crop was measured, *Lathyrus* often had died and entered the decomposition loop. The long-term net effect of deer exclosure was the increased primary productivity caused by the increased rates of N fixation associated with a change in plant species composition.

Separating the Effects of Composition and Diversity

The following are but a few of the numerous examples that illustrate that changes in both species composition and diversity that result from global change have the potential to have major impacts on ecosystem processes. These changes in composition and diversity may be a major cause of shifts in ecosystem processes. On one level, it seems impossible for species composition not to matter for ecosystem processes. After all, ecosystem processes are driven by the lives, deaths, and interactions of organisms. One of the tenets of population ecology is that no two species are identical, and that it is the differences among species that allow coexistence
in multispecies ecosystems. However, does this imply that ecosystem processes must depend on both the identity and abundance of every species in an ecosystem? Surely not. There may be many species of viruses, bacteria, fungi, vascular plants, insects, and so forth, that are sufficiently similar to other members of their group that they could be substituted for each other with no discernible impact on ecosystem processes (Lawton and Brown 1993; Vitousek and Hooper 1993). Additionally, most species are rare, and, with the exception of keystone species (e.g. Paine 1966; Power et al. 1996), the loss or addition of most rare species may have little detectable effect on ecosystem processes. Those species that should matter, and the reason they should matter for ecosystem processes, will depend on the ecosystem process of interest.

Although it has long been clear that species composition influences ecosystem processes, it has been less clear whether ecosystem processes also would depend on biodiversity, and how the effects of composition can be separated from those of biodiversity. Recent papers suggest that ecosystem processes may depend on biodiversity (Ewel et al. 1991; McNaughton 1993; Vitousek and Hooper 1993; Naeem et al. 1994, 1995; Tilman et al. 1996). Specifically, primary productivity or plant standing crop became larger with increasing diversity, as did nutrient use, and nutrient leaching losses decreased with increasing diversity in these studies.

To experimentally determine the effects of species diversity on ecosystem processes, it is necessary to ensure that all species are represented in an unbiased manner at all levels of diversity. This requires that there be a defined species pool, and that various species combinations be drawn from this pool. For a small species pool, it might be possible to choose all possible combinations of species taken one, two, three, four, and so forth, at a time. This would mean that a given species will compose the same proportion of the total species mix used at each level of diversity. When this occurs, tests for the effects of diversity on ecosystem processes merely involve comparing average responses among the different levels of diversity. This design can be expanded to determine the effects of species or functional group composition by having replicate plots for each unique combination of species or functional groups. Analysis of variation (ANOVA) or regression then could be used to separate the effects of diversity and composition. This same design can be used in a slightly modified form when the species pool is too large to allow use of all possible species combinations. In this case, the species compositions of plots with a given level of diversity would be determined by random draws of that number of species from the species pool, with each plot being a separate random draw. To minimize effects caused by species compositional differences among various sets of random draws, it is necessary to have a relatively large number of plots, for example twenty to forty, at each level of diversity. Even within this design it is possible to distinguish between effects of diversity and composition by having replicates of each particular randomly drawn species combination. By having many random species combinations, the mean response among replicate
ecosystems at a given level of diversity becomes independent of particular species combinations, and differences among means measure the effect of diversity. The variance among the various species combinations at a given diversity level measures the effects of alternative species compositions. This is the design used in the Cedar Creek biodiversity experiments (Tilman et al. 1996), which have shown that both functional composition and functional diversity are significant determinants of plant community biomass and other ecosystem processes (Tilman et al. 1997).

It is also possible to impose this experimental design on various models of interspecific interactions to determine how these interactions depend on diversity (Tilman et al. 1997). The resulting theories of the effects of biodiversity on ecosystem processes predict that plant standing crop should be an increasing function of diversity, and that nutrient leaching loss should decrease with diversity. The predicted effects of diversity are the logical outcome of a few simple processes and assumptions. It is assumed that species differ in their abilities to compete for one or more limiting resources. In the simplest case, in which all species compete for the same limiting nutrient, increased diversity leads to increased productivity simply because better, more productive species are more apt to be present at higher levels of diversity. The highest productivity occurs when the single best species is present, but the probability of this occurring increases with diversity. Thus, this effect is a probabilistic effect that only requires that species compete and that they differ in productivity. When species compete for two limiting resources, or when there are two or more niche axes along which species are differentiated, increased diversity leads to increased productivity because of species complementarities, that is, on average, increased diversity leads to a fuller coverage of niche space, allowing a more complete utilization of resources and, therefore, higher productivity. At any given level of diversity, different combinations of species can lead to different productivities or levels of nutrient utilization and loss. The differences among these different species combinations are a measure of the effects of species composition, whereas the differences in mean responses among different levels of diversity measure the effect of diversity. Within the three models in Tilman et al. (1997), of the total variance in productivity, from about one-third to two-thirds was explained by diversity, with the remainder explained by composition. Thus, even in these simple models, both composition and diversity are major determinants of ecosystem processes.

The Challenge

These examples illustrate the challenge before us. There is not yet adequate understanding of what controls species diversity, species composition, or trophic structure, nor how these influence ecosystem processes and
vice versa, and yet such understanding is essential if the impacts of present-day and future alternative trajectories of global change are to be predicted.

In other words, we do not yet know that which explains the broad patterns of the natural world. What allows thirty species of phytoplankton to coexist in a few liters of lake water, or 300 species of tropical trees to coexist in a hectare, or 4,500 species of insects to coexist in a few square kilometers at Cedar Creek? What causes latitudinal gradients in diversity? What controls C, N, P and other element cycles on local, continental, and global scales? What causes changes in composition, diversity, life-history, and life-forms along continental gradients in productivity, elevation, or disturbance? What causes the worldwide convergence of traits within a given type of biome?

If a step is taken back from the Earth and the broad, general, repeatable patterns that occur are viewed, most of these have not yet been rigorously described or explained (Lawton 1996). The problem is not that we lack explanations for these, it is that we have too many explanations, and these are conceptual outlines rather than rigorous predictive theory. What is lacking are rigorous tests tied to mechanistic theory that allow us to distinguish among competing hypotheses and establish workable theory. If the actual forces structuring natural ecosystems are not understood, how are we to understand how these ecosystems will change in response to the forces of global change? We need to develop and test simple, mechanistic theories that can explain what we see, and then use these as our tools to predict that which various futures may hold.

This is not just an academic goal. If we fail to achieve this level of knowledge, we will have missed the most important contribution that our discipline could have given to society. We live in an era of unprecedented human impacts of the Earth's ecosystems. Ecology must develop into a predictive science if we are to realistically and honestly inform society of the future consequences of the present patterns of human environmental behavior. The more rigorous and well-tested the conceptual basis for ecology becomes, the greater will be our ability to predict the alternative futures that lie before the Earth and how they depend on the actions that society takes.

How can we achieve as ambitious a goal as this? In addition to using existing resources at an optimum level, we must articulate society's need for major new research programs directed at a predictive understanding of the elements of global change. Such programs should attract and train the next generation of ecologists, a generation dedicated to fundamental advances in ecological understanding and the application of this knowledge to the environmental issues that face the globe. The long-term viability and sustainability of our society depends on advances in ecological knowledge as fundamental as those that led to the dawn of the nuclear age. These can be achieved only by appropriate investments.
References


