

Ecosystem Consequences of Changing Biodiversity

Experimental evidence and a research agenda for the future

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The earth is currently in the midst of the sixth major extinction event in the history of life. The causes of earlier extinction events (e.g., the extinction of dino-

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saur) are uncertain but probably reflected changes in the physical environment caused by such factors as meteor impacts or pulses of volcanism. By contrast, the current extinction event is biotically driven—specifically by human impact on land use, species invasions, and atmospheric and climatic change. Scientists are increasingly concerned about the global extent of the environmental impacts of human activities (Vitousek 1994). However, the loss of species diversity is unique among major anthropogenic changes because it is irreversible. Thus, understanding the consequences of species loss is critical.

Current extinction rates are 100–1000 times higher than prehuman levels, and the expected extinction of currently threatened species could increase this rate by a factor of 10 (Pimm et al. 1995). Many of the species that have been driven extinct by humans were rare species that were endemic to small or isolated habitats, such as islands (Pimm et al. 1995). For example, the spread of

Polynesians across the Pacific Islands during the past 1000–4000 years resulted in the extinction of approximately 2000 bird species (Pimm et al. 1995, Steadman 1995)—15% of the world's avian diversity. Similarly, European settlement in the Hawaiian Islands eliminated 84 plant species, almost 10% of the native flora of the islands, and an additional 133 plant species are threatened with extinction (Sohmer 1994). Significant extinctions have also occurred on mainlands. For example, the fynbos vegetation of South Africa has lost 36 species, and an additional 618 species are threatened with extinction (Pimm et al. 1995).

There are clear winners and losers among species as a result of human activity. In countries with modest human population densities, such as Scotland, there are no consistent ecological differences between those plant species that have increased in abundance over the past 50 years and those that have decreased (Figure 1). However, in countries such as England and The Netherlands, where high human population densities have caused more extensive habitat alteration and eutrophication, fast-growing, nutrient-demanding plant species are increasing in abundance, whereas the slow-growing plants that formerly occupied much of this region are decreasing (Figure 1; Thompson 1994). Other “weedy” species associated with humans include some species of rats, deer, and geese. Thus, changes in human activity alter the types as well as the numbers of species.

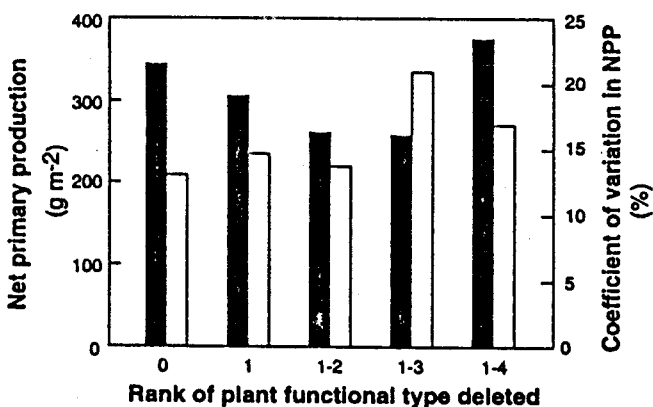
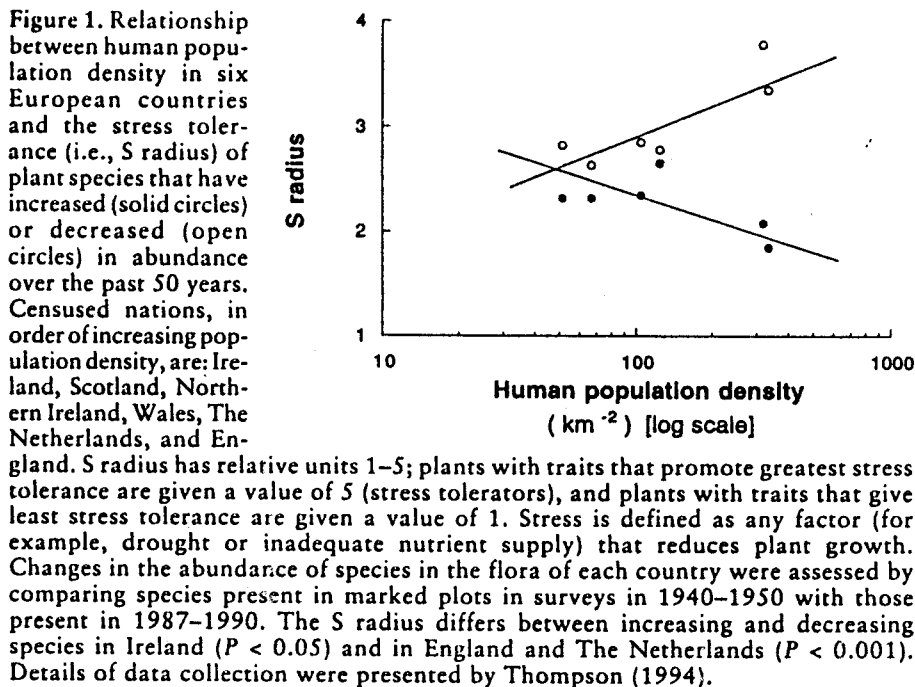


Figure 2. Simulations of net primary production (NPP; solid bars) and the annual coefficient of variation of NPP (CV; open bars) in a short-grass steppe in response to successive deletion of the four most abundant plant functional types, based on a simulation model of grassland NPP (Coffin and Lauenroth 1990). The four most abundant functional types, in order of decreasing abundance, were: shallow-rooted C_4 grasses (rank 1), medium-rooted C_4 grasses (rank 2), deep-rooted C_4 grasses (rank 3), and medium-rooted C_3 grasses (rank 4). The model was first run until species reached equilibrium under conditions of stochastic weather and no species deletions, producing a steady-state pattern of functional-type abundance typical of a short-grass steppe (Lauenroth and Milchunas 1992). Each deletion was implemented by removing the most abundant functional type and preventing this type from regrowing during the next 200 years, by which time the modified community had reached steady state. Four successive deletions were implemented, in order of decreasing functional-type abundance. Results for each replicate simulation were averaged over the last 50 years of the simulation (William K. Lauenroth, unpublished results).

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In response to the documented rapid changes in biotic diversity, there has been an international effort to understand and predict the consequences of these changes (Schulze and Mooney 1993, Mooney et al. 1996). Although several hypotheses postulate plausible ecosystem impacts of altered biotic diversity, there is a paucity of concrete evidence to test these ideas. Such evi-

dence could be important in convincing governments to abide by the International Biodiversity Convention, which seeks to maintain global biotic diversity. In this article, which is based on a recent workshop (Steffen et al. 1996), we summarize evidence about the ecosystem consequences of changes in species diversity and present a research agenda to ad-

dress these consequences. The workshop was sponsored by Global Change and Terrestrial Ecosystems (GTCE), an international group of researchers whose goal is to design research that will improve understanding of the role of terrestrial ecosystems in the functioning of the earth system.

Ecosystem consequences of changing species diversity

Simulation models provide a venue for conducting long-term "thought experiments" that are difficult to carry out in practice. We combined a model of the presumed relationship between plant diversity and ecosystem processes (Sala et al. 1995) with a grassland ecosystem model (Coffin and Lauenroth 1990) to explore how changes in the number of "functional types" of plants might affect total net primary production (NPP). We define functional types as groups of species that have similar effects on ecosystem processes. We deleted functional types from the model one at a time, beginning with the most abundant functional type, allowed the model community to recover to a stable community composition between deletions, and asked how NPP was affected (Figure 2).

The most striking result from this modeling exercise was that removal of the most abundant functional type, the shallow-rooted C_4 grasses that constituted 90% of the original community NPP in the model, reduced NPP by only 10% because other functional types increased their production by using the new resources that became available. Subsequent removal of medium-rooted C_4 grasses reduced NPP by an additional 15%. Removal of the third functional type (deep-rooted C_3 grasses) produced no further changes in NPP, but interannual variation in NPP increased dramatically, suggesting that the ability of the depauperate community to compensate for stochastic fluctuations in weather was reduced. When a fourth functional type (medium-rooted C_3 grasses) was removed, deep-rooted C_4 grasses, which are normally a small component of the community, greatly expanded, increasing NPP to the pre-deletion level and creating an entirely different community.

This modeling exercise suggests several possible consequences of species loss. Initially, there may be little detectable effect of species loss on NPP if the remaining species increase to compensate for species removal. This prediction is consistent with results of field experiments in both tundra and grassland, in which community NPP was relatively insensitive to large changes in production by individual species (Lauenroth et al. 1978, Chapin and Shaver 1985, Chapin et al. 1995).

A second implication of the results is that NPP of low-diversity communities may be less well buffered against natural variation in weather than that of high-diversity communities. Again, there is supporting experimental evidence for this prediction: Diverse plots in a Minnesota grassland showed a lower decline in aboveground biomass than less diverse plots during a severe drought (Figure 3; Tilman and Downing 1994). This field experiment is complicated, however, by the fact that the low-diversity plots were the result of long-term addition of nitrogen fertilizer, which probably caused rapidly growing species to outcompete, and ultimately eliminate, drought-resistant species. The loss of drought-resistant species thus provides an alternative explanation for the greater vulnerability of high-nitrogen, low-diversity plots to drought (Sala et al. 1995). Regardless of the mechanism by which productivity was buffered during drought in low-nitrogen diverse plots—that is, high diversity or the presence of drought-resistant species—the result has important implications because many ecosystems are declining in diversity in response to anthropogenic nitrogen deposition.

These modeling simulations and correlative field observations, although they suggest strong effects of species diversity on ecosystem processes, cannot provide definitive proof of these relationships. To more directly test the effects of species diversity on ecosystem processes, several recent experiments have directly manipulated the number of species in a community (i.e., species richness) and measured resulting changes in ecosystem processes. For example, in a Minnesota grassland,

Figure 3. Relationship between drought resistance of vegetation in a Minnesota grassland and plant species richness prior to the drought. Drought resistance was measured as the log of the ratio of plant biomass at the height of the drought to plant biomass before the drought. Data are shown as means \pm SE (redrawn from Tilman and Downing 1994).

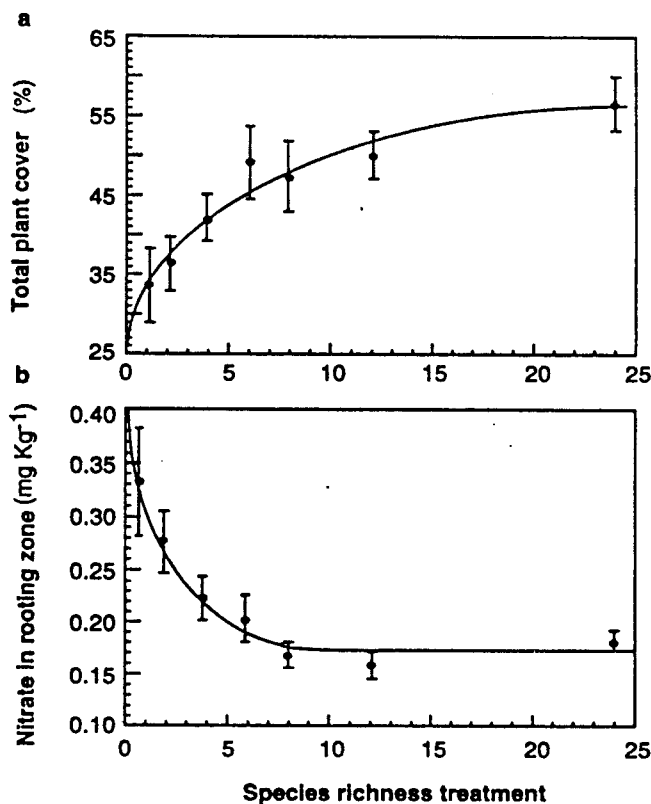
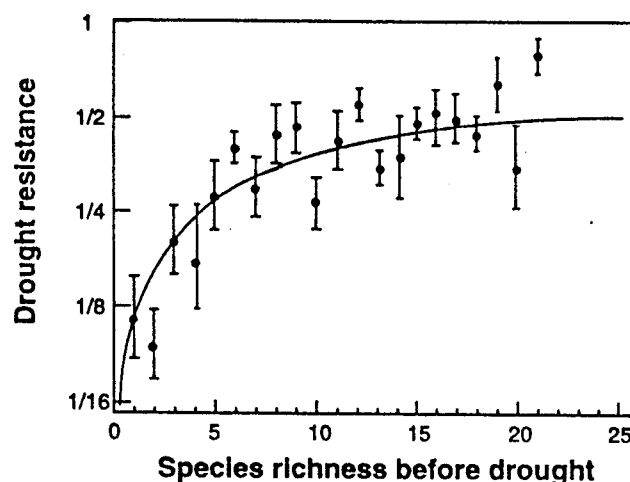


Figure 4. Effect of the number of plant species (1, 2, 4, 6, 8, 12, or 24 species) sown on a plot (species richness treatment) on total plant cover (a) and nitrate concentration in the rooting zone (b). Measurements were made three years after plots were sown. Data are shown as means \pm SE (redrawn from Tilman et al. 1996).

Tilman et al. (1996) sowed plots with seven levels of plant diversity (1–24 species). Each level of diversity was replicated 20 times, with each replicate being a separate random draw from a pool of 24 experimental species. This study found plant cover to be an increasing function of plant species richness (Figure 4a). The more diverse plots had lower concentrations of inorganic soil nitrogen (Figure 4b), presumably reflecting greater plant uptake of nitrate in the more diverse plots (Tilman et al. 1996).

Although this experiment provides a convincing demonstration of the effects of species richness on productivity and soil nitrogen concentration, the underlying mechanisms for these effects are not known. Do more species simply increase the probability of having a single productive species? Or do more species allow the community to tap more resources because these species differ in the timing or rooting depth at which they acquire resources (i.e., complementary resource use)? The relative importance of these alternative explanations for the effects of diversity on ecosystem processes is not yet known for this experiment, much less for the hundreds of other ecosystems that remain to be studied.

In another grassland experiment, in California, the number of plant functional types (for example, nitro-

Figure 5. Response of resource use to the number of plant functional types in a plot. Relative resource use is an index that integrates plant effects on pool sizes of available resources (nitrogen, phosphorus, and water) across all growing seasons. The index measures the extent that potentially limiting resource pools (inorganic nitrogen and available phosphorus in all seasons, and water in September) were reduced in vegetated treatments compared with nonvegetated treatments, as described by Hooper and Vitousek (in press). Functional type treatments are early-season annuals (E), late-season annuals (L), and perennial bunchgrasses (P). Data are shown as means \pm SE. The line is the best-fit regression line.

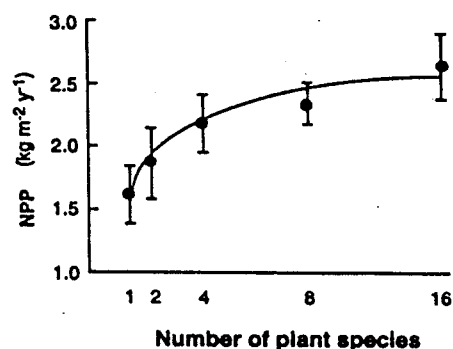
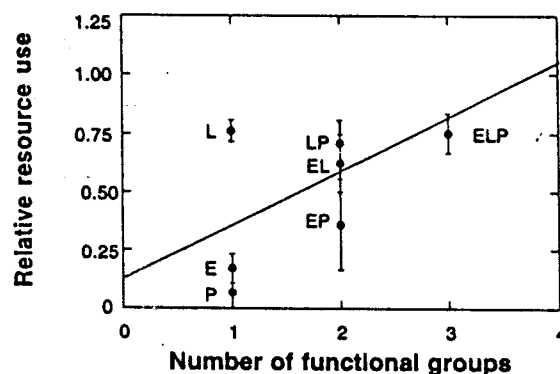


Figure 6. Net primary production (NPP) in experimental communities that differ in plant species richness. Data are shown as means \pm SE (redrawn from Naeem et al. 1994).

gen-fixing species and non-nitrogen-fixing spring annuals) was manipulated (Hooper in press, Hooper and Vitousek in press). In this experiment, differences among types of plants that were present had at least as large an effect on primary productivity, nutrient losses, and microbial nitrogen retention as did differences in the number of functional groups. Within a given season, soil inorganic nitrogen pools were lowest in the more diverse plots, suggesting greater uptake. However, direct measurement of nitrogen accumulation by each species showed that the greater uptake of nitrogen in the more diverse plots resulted primarily from a greater likelihood of including early season annuals, a highly competitive functional group, in the more di-

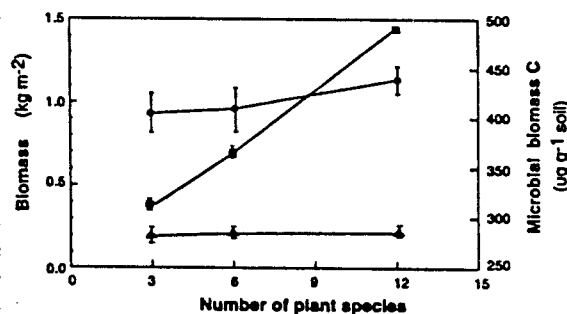
verse treatments, rather than from spatial complementarity of nutrient use (e.g., different rooting depths of different functional types). Across the entire growing season, however, phenological differences among functional types led to temporal complementarity, because different plant types were better competitors for different resources at different times of year. Therefore, the more diverse plots showed greater overall resource use, although some treatments with only a single functional type still had resource-use values equivalent to those in the most diverse treatments (Figure 5).

Ecosystems consist not only of plants, which initially assimilate energy, but also of herbivores, carnivores, and decomposer organisms,

which consume and process this energy, releasing nutrients to support further carbon assimilation. Increasing the number of species from one to four in each of four trophic levels (plants, herbivores, parasitoids, and decomposers) in experimental mesocosms revealed a positive correlation between diversity and productivity (Naeem et al. 1994, 1995). Altering only plant diversity had the same effect on productivity as did altering diversity at all four trophic levels (Figure 6), suggesting that changes in plant diversity were primarily responsible for the productivity response in the four-trophic level experiment. However, in these experiments each level of diversity had a predefined species composition, so it may have been the addition of a more productive plant species in the most diverse treatment that accounted for the results. Indeed, many experiments show no relationship between diversity and productivity or show declining productivity with increasing diversity (Johnson et al. 1996).

In one experiment in which plant species richness had no effect on plant parameters (architecture, photosynthesis, or plant biomass), it nevertheless had a strong impact on soil biological activity (microbial biomass, hyphal length, and enzyme activity; Figure 7). As a result, high levels of plant diversity enhanced organic matter decomposition and reduced nitrogen leaching. Whether these effects of plant diversity on microbial processes contribute to the

Figure 7. Biomass of plant shoots, roots, and soil microorganisms in old-field Mediterranean ecosystems planted with different numbers of plant species (Jacques Roy, Shivcharn Dhillian, Jean-Louis Guillermin, and Laurence Béguier, manuscript submitted). Data are shown as means \pm SE. Ecosystems were 0.5 m² intact soil monoliths 30 cm deep that had been collected in the field following the summer drought. After the few remains of vegetation were removed, monoliths were planted with mixtures of annual grasses, composites, and legumes. Species diversity was altered by planting one, two, or four species of each of these three different plant families into the experimental community. Ecosystems were maintained in a greenhouse for one year with environmental conditions closely matching the natural environment and were harvested at time of peak aboveground biomass, at which time the biomass of roots (triangles), shoots (circles), and microorganisms (squares) were determined by harvest (for plants) or by chloroform fumigation and extraction (for microorganisms).



inverse relationship between plant diversity and soil nitrogen concentration in the Minnesota grassland (Figure 4) remains to be determined.

Plant species diversity may also influence the response of ecosystems to global environmental change. A computer simulation of the response of a deciduous forest to elevated carbon dioxide showed that a diverse community of nine tree species, each with a different photosynthetic response to carbon dioxide, exhibited a 30% greater photosynthetic response to elevated carbon dioxide than did a second model community composed of a single species with the average carbon dioxide response of the more complex community (Figure 8; Bolker et al. 1995). Thus, ecosystem models that neglect physiological diversity in a community may fail to capture both the magnitude and the mechanism of ecosystem response to environmental change.

The studies described above provide intriguing hints that species diversity could affect many ecosystem processes, including photosynthetic carbon gain, productivity, and nutrient cycling. However, the nature and magnitude of these effects varies with ecosystem type, functional response measured, and experimental conditions (Johnson et al. 1996). At present, too few experiments have been conducted to draw convincing generalizations. Moreover, all studies so far have been conducted on relatively simple systems, in which the gain or loss of a few species is more likely to have detectable effects than in more complex systems. Alternatively, as ecologists study ecosystems with more species, disruption of complex webs of biotic interactions could initiate a cascade of effects that might not occur in simple systems. To determine how general the linkages between species number and ecosystem processes may be, diversity effects must be studied in more complex systems.

Ecosystem consequences of landscape diversity

Just as species richness is important to the functioning of an ecosystem, the diversity of ecosystems in a landscape may be critical to understand-

ing the functioning of landscapes and regions (Burke and Lauenroth 1995). Landscape diversity is defined by the number of ecosystem types and their spatial distribution. These attributes determine water quality, sediment yield, carbon balance, and trace gas flux. Moreover, human impacts are ubiquitous at large scales, making it appropriate to consider commodity production and economic processes as functions of most current landscapes.

The simplest question about landscape processes is this one: Under what circumstances do regional processes simply reflect the properties of the most common ecosystems? For example, land-use heterogeneity has significant influences on regional trace gas flux in northeastern Colorado (Alvin Mosier and Ingrid Burke, unpublished data). This region supports three major land-use types: native rangeland, dryland farming, and irrigated cropland; native rangeland is the most abundant but least intensively managed land-use type (Figure 9). Regional methane consumption is greatest in the most abundant land-use type (rangelands) and least in irrigated croplands (Bronson and Mosier 1993). By contrast, ni-

trous oxide flux is highest from irrigated croplands—so high that irrigated croplands constitute the major regional source of nitrous oxide to the atmosphere, despite their small areal extent (Figure 9). To understand the regional impacts of landscape units, it is clearly necessary to know their properties as well as their areal extents. Ecosystems that cover a small area may have large impacts on regional properties; for example, beaver ponds are hot spots for methane production (Bridgman et al. 1995), and riparian areas and wetlands collect sediments and nutrients (Peterjohn and Correll 1984).

Under some circumstances, the sizes, shapes, and interdigitation patterns of ecosystems in a landscape profoundly affect their functioning. For example, in fire-prone ecosystems, such as Yellowstone National Park, the pattern of fire spread is usually determined by both the landscape pattern in ecosystems of differing flammability and the climatic conditions at the time of the fire (Turner et al. 1993). However, unusually intense fires, which occur approximately every 300 years, spread across the landscape without

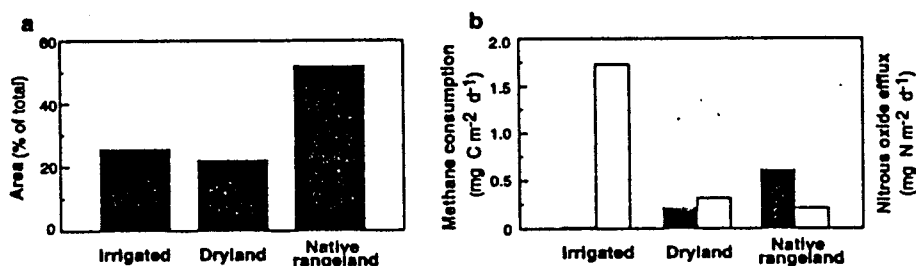


Figure 9. Effects of land use (irrigated cropland, dryland wheat, and native rangeland) on regional trace-gas flux in northeastern Colorado. (a) Areal extent of each ecosystem type (% of total area). (b) Unit-area fluxes of methane (solid bars) and nitrous oxide (open bars). Methane flux from irrigated croplands is nearly undetectable. Arvin R. Mosier and Ingrid C. Burke, unpublished data.

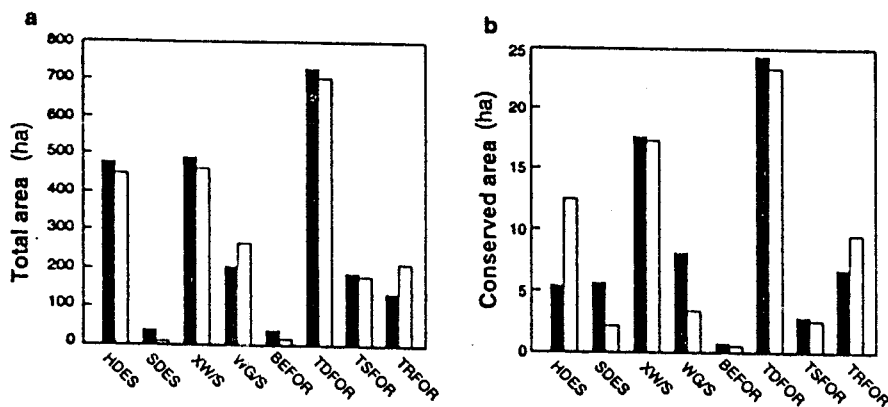


Figure 10. Area of major African biomes estimated for vegetation at equilibrium with the current climate (solid bars) and with a climate characteristic of tripled atmospheric carbon dioxide (open bars; Prentice et al. 1992). (a) Biome distributions for the total African continent. (b) Biome distributions for the area conserved within national parks. The biome types are hot desert (HDES), semidesert (SDES), xerophytic woodland/scrubland (XW/S), warm grassland/shrubland (WG/S), broadleaved evergreen forest (BEFOR), tropical dry forest (TDFOR), tropical seasonal forest (TSFOR), and tropical rain forest (TRFOR; Amanda Lombard, unpublished results.)

regard for differences in flammability among ecosystems. Thus, the importance of landscape heterogeneity to fire spread depends on fire intensity. In other instances, where controls over a process differ qualitatively between the edges and the centers of patches—for example, seed dispersal into a burned patch—patch size and shape will influence the average rates of the process when these rates are summed at the regional level.

Landscape pattern and heterogeneity have important implications for the usefulness of protected areas for species conservation in the face of climatic change. Models that project changes in the distribution of vegetation in response to climatic change (Prentice et al. 1992) suggest that the relative abundance of biomes would change dramatically in response to a tripling of atmospheric carbon dioxide (Figure 10). The most notable change in African biomes simulated by the model was an increase in the relative abundance of warm grassland/shrubland and tropical rain forest at the expense of all other biomes. The two biomes that are currently most rare, semidesert and broadleaved evergreen forest, are projected to decrease by 81% and 69%, respectively (Figure 10a), particularly in national parks (Figure 10b), in response to this simulation of climatic change.

These projections of biome shifts in Africa are based on the equilibrium distributions of vegetation with climate; they ignore migration of organisms in response to climatic change (Bond and Richardson 1990). Barriers to migration are increasing as the land between African national parks becomes more fragmented and transformed. Wise management of the land matrix between existing protected areas to allow the movement of organisms is, thus, essential to future preservation of species diversity in protected areas. One way to minimize the hazards of migration as organisms move in response to the changing climate is to protect new areas that have a high altitudinal diversity. Such areas would allow organisms to migrate altitudinally over short distances within the same park in response to climatic change. Of existing national parks in Africa, 60% span less than 500 m elevation. Thus, a priority for future planning of protected areas is to conserve the connectivity among these areas and to establish new protected areas in places that are presently climatically diverse.

Research agenda for the future

The evidence presented in this article indicates that both species and landscape diversity have important ecosystem consequences and that land-

scape diversity will influence the conservation of future species diversity. However, there have been too few studies to provide rigorous generalizations. Given the rate at which natural biotic diversity is changing, it is imperative that scientists develop a more predictive understanding of the ecosystem consequences of these changes. Based on the GCTE workshop (Steffen et al. 1996), we recommend a multipronged research agenda that develops a theoretical framework for more rigorous predictions. This agenda includes both providing for a network of laboratory and field experiments and observations that explicitly test these predictions and developing an applied program that explores the consequences of biodiversity changes for the sustainability of both natural and managed ecosystems. The following four hypotheses provide an initial focus for research on the relationships between biodiversity and ecosystem processes.

- High species richness maximizes resource acquisition at each trophic level and the retention of resources in the ecosystem. If plant species differ in the timing or vertical distribution of absorption of a growth-limiting nutrient or in the form of the nutrient (e.g., nitrate, ammonium, or organic nitrogen) that they absorb, an increase in the number of species would increase the probability of having species that can tap resources of different types and locations and at different times. Similar arguments apply to microorganisms, herbivores, and organisms at higher trophic levels. If a larger proportion of available resources is acquired by organisms, these resources should be less prone to loss from the ecosystem. One way to test this hypothesis is by carrying out field and laboratory experiments that alter species richness and measuring the temporal and spatial use of resources by component species in relationship to total community production.

If this hypothesis proves to be correct, extremely simple ecosystems such as agricultural monocultures and forestry plantations may have an inherently low resource-use efficiency at certain times of the year or under certain climatic conditions.

Without external inputs, they may also be less sustainable over the long term than more diverse ecosystems. Low-diversity managed ecosystems provide another effective venue for testing the diversity-acquisition hypothesis and for exploring its societal consequences.

- High species diversity reduces the risk of large changes in ecosystem processes in response to directional or stochastic variation in the environment. Species whose effects on ecosystem processes are similar often differ in their responses to environmental variations, or they would be unlikely to coexist in the community. Consequently, if this hypothesis is correct, a high species diversity would increase the probability that the processes will be sustained even if a particular species is lost in response to some extreme event or to a directional change in the global environment. In this case, the co-occurrence of species in a community with similar ecological effects does not necessarily imply that these species are "redundant" (Walker 1992, Lawton and Brown 1993), especially over long time scales. We suggest that diversity experiments be monitored carefully during extreme events or that extreme circumstances (e.g., droughts) be imposed artificially.

The concept of diversity as an insurance policy against radical ecosystem change can be assessed through risk analysis, which considers the economic costs and benefits of maintaining crop genotypes, species, or landscapes. For example, risk analysis can identify the ecological and economic consequences of alternative scenarios of future biotic changes in managed or natural systems. Ecologists should seek to define the circumstances and probabilities associated with these alternative scenarios. Just as one would not choose to eat in a restaurant that had a 1% probability of food poisoning, explicit identification and assessment of the ecological and societal consequences of alternative biodiversity changes could prove useful in convincing the public and governments of the values of biotic diversity and the potential dangers of its loss.

- High species diversity reduces the probability of large changes in eco-

system processes in response to invasions of pathogens and other species. A high species diversity makes it less likely that a newly arrived species of pathogen, plant, or animal will be highly different from some species in the extant community and thus be a successful invader with an ecosystem impact that differs from that of extant species. Thus, a high species diversity may provide insurance against large ecosystem changes in response to biological invasions. We suggest that ecologists study the susceptibility of diversity experiments to invasion by newly introduced species of pathogens, plants, and animals and document the ecosystem consequences of successful invasions. Islands of varying distances from continents often differ in species diversity and history of invasion. These archipelagos therefore serve as "natural experiments" to study the effects of diversity on invasibility.

The validation of this hypothesis would confirm the advantages of maintaining genetic diversity in crop monocultures and would suggest that the use of multi-cropping systems in agriculture be expanded (Vandermeer and Schultz 1990). This hypothesis also suggests that human-aided invasion of new species is most likely to occur in low-diversity managed landscapes.

- Landscape heterogeneity most strongly influences those processes or organisms that depend on multiple patch types and are controlled by a flow of organisms, water, air, or disturbance among patches. Some regional processes are the simple area-weighted average of process rates observed in individual patches (Figure 9) and will not be strongly influenced by landscape heterogeneity. However, other processes are affected in a nonlinear fashion by interactions among landscape patches because they depend strongly on conditions found at interfaces among patches. We recommend a research agenda that uses first principles to identify these landscape-dependent processes and that studies the controls over these processes in managed landscapes with different patch sizes or edge-to-area ratios. For example, forest regeneration following clear-cutting should be most sensitive to landscape fragmentation

in species with limited range of seed dispersal. The results of research of this type are critical to predicting the regional impact of current trends in land-use change.

Conclusions

There are ethical and esthetic arguments for conserving biodiversity, regardless of its functional importance. In addition, biodiversity is critical to species interactions and the persistence of diversity in communities, an important issue that we have not addressed. However, the experiments and observations that we have summarized in this article suggest that changes in biodiversity can have significant impacts on ecosystem and landscape processes, both on a day-to-day basis and during extreme events. Ecosystem processes, in turn, determine services, such as clean water and air, that are required by society (Ehrlich and Mooney 1983). Given the current rapid rates of environmental change, it seems wise to conserve the present levels of diversity as insurance against an uncertain future. As our understanding of the functional consequences of biodiversity improves, it should be possible to pinpoint situations in which its conservation is particularly critical.

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ASSISTANT PROFESSOR - Two Positions - begin 16 August 1998

Michigan State University, East Lansing, Michigan 48824

The Department of Geography at Michigan State University is continuing a major expansion of personnel and resources for a **Basic Science and Remote Sensing Initiative**, which will focus on the use of earth observation satellites, geographic information systems, field studies, and models for global change research. Strong emphasis is being placed on the study of land use and cover change, including its global and regional aspects, with a focus on using satellite observations from existing and planned earth observing systems.

The Department and University have invested considerable resources to build this new initiative, including laboratory and office space and new tenure-track positions. The Initiative is an integral part of MSU's overall emphasis on increasing research capacity, and meshes with existing departmental programs in cartography/GIS, land use and cover change, human-environment interaction, economic geography, geomorphology and climatology.

The Initiative is seeking applicants to two tenure-track positions at the level of Assistant Professor. Successful candidates will be expected to conduct and manage externally funded research, and will have demonstrated expertise in some combination of the following: application of earth observation satellites to global change research; GIS technology applied to environmental problems; and land use and cover change models. Expertise with microwave sensors will be required for one position.

All candidates should have experience and expertise in the basic science of global environmental change, and have a Ph.D. in geography or a related field. Successful candidates for both positions will be expected to teach introductory, advanced, and graduate courses. Inter-departmental and Inter-college collaborative research and grant activities are expected.

Salary will be competitive and commensurate with qualifications and experience. Review of applications begins 15 January 1998 and continues until appointment is made. Please send letters of application discussing research and teaching interests, curriculum vitae, pertinent publications, and three letters of reference to: Professors Richard Groop or David Skole, Department of Geography, Ph: (517) 355-4649, Email: groop@pilot.msu.edu or skole@pilot.msu.edu

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