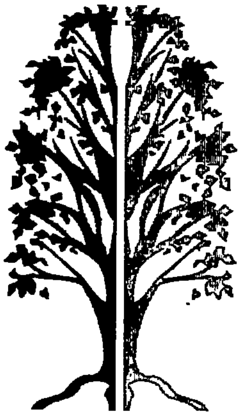

FUNCTIONAL DIVERSITY

David Tilman
University of Minnesota, St. Paul

GLOSSARY

diversity-productivity hypothesis The proposal that greater diversity would lead, on average, to greater total biomass or productivity.

diversity-stability hypothesis The proposal that ecosystems containing more species would be more stable.

ecosystem composition The list of species or functional groups that are present in a given ecosystem.

ecosystem functioning The rate, level, or temporal dynamics of one or more ecosystem processes such as primary production, total plant biomass, or nutrient gain, loss, or concentration.

functional diversity The range and value of those species and organismal traits that influence ecosystem functioning.

functional group A set of species that have similar traits and that thus are likely to be similar in their effects on ecosystem functioning.

niche differentiation Differences in the morphology, physiology, or behavior of species that can influence their abundances, dynamics, and interactions with other species, including the ability of various competing species to coexist.

sampling effect The hypothesis that diversity might influence an ecosystem process because of the greater chance that a given species trait would be present at higher diversity, and the effect of its presence on ecosystem functioning.

FUNCTIONAL DIVERSITY refers to those components of biodiversity that influence how an ecosystem operates or functions. The biological diversity, or biodiversity, of a habitat is much broader and includes all the species living in a site, all of the genotypic and phenotypic variation within each species, and all the spatial and temporal variability in the communities and ecosystems that these species form. Functional diversity, which is a subset of this, is measured by the values and range in the values, for the species present in an ecosystem, of those organismal traits that influence one or more aspects of the functioning of an ecosystem. Functional diversity is of ecological importance because it, by definition, is the component of diversity that influences ecosystem dynamics, stability, productivity, nutrient balance, and other aspects of ecosystem functioning.

Encyclopedia of Biodiversity, Volume 3

I. MEASUREMENT OF FUNCTIONAL DIVERSITY

Because of the large number of traits that each species possesses, the large number of different species that exist in most habitats, and the incomplete knowledge of which species traits influence various ecosystem processes, there is, as yet, no simple way to measure functional diversity. Rather, items that are more easily measured than functional diversity are used as indices or correlates of functional diversity. The most common of these indices is the number of species present in a habitat, which is called the species richness or species number of the habitat. All else being equal, habitats with greater species richness should also have greater functional diversity. This occurs because species differ in their traits. Sites that contain more species should thus also contain, on average, a greater range of species traits, which is greater functional diversity. Species diversity indices, such as the Shannon diversity index, are similarly used as indirect measures of functional diversity. Another commonly used index of functional diversity is the number of different functional groups (defined later) that exist within a given community or ecosystem. This is also called functional group diversity. Assuming that organisms can be categorized as belonging to groups that differ in traits relevant to ecosystem functioning, greater functional group diversity should correlate with greater functional diversity. However, variations among species within a given group could also contribute to functional diversity. Observational, experimental, and theoretical studies indicate that functional diversity, as measured by any of these three means, is one of several important factors that determine ecosystem functioning. Because there is, as yet, no clear way to measure functional diversity, one or more of these three indices will be used as a proxy for functional diversity in this chapter. Before reviewing the research linking functional diversity to ecosystem processes, which is the focus of the remainder of this chapter, it is important to introduce and define some terms.

II. EXPLANATION OF CONCEPTS AND TERMINOLOGY

A. Functioning

As they are used by ecologists, the words *function*, *functional*, and *functioning* are not meant to imply that an ecosystem process has any underlying goal or purpose. Indeed, to try to minimize any such implications, it has become standard practice to refer to "ecosystem functioning" or "ecosystem process" rather than the "function of an ecosystem." The latter might be misinterpreted as meaning that an ecosystem exists to perform a given function, which is inconsistent with our knowledge of the process of evolution. Rather, functioning refers solely to the way in which an ecosystem operates.

B. Ecosystem Processes

Ecologists study many different aspects of the functioning of communities and ecosystems. The three most frequently considered ecosystem processes are productivity, stability, and resource dynamics. Productivity refers to the rate of production of biomass within a given trophic level. The production of plant biomass is called primary production, the production of biomass of herbivores is called secondary production, and that of predators is called tertiary production. Stability has a wide range of definitions, including the degree to which an item is resistant to change when experiencing a single perturbation, the degree to which an item fluctuates in response to an ongoing suite of small-scale perturbations, and the dynamics of return to its prior state after a single perturbation. Stability can be measured at the level of populations, communities, or ecosystems. The resource dynamics of an ecosystem are measured by the rates of supply and loss of limiting nutrients, by the efficiency with which organisms use limiting resources, and by the proportion of limiting resources that the organisms living in an ecosystem are able to capture.

C. Functional Groups

Each species has a large number of morphological, physiological, and behavioral traits, many of which might influence the abundance of species and ecosystem functioning. One way to deal with such complexity has been to identify traits that seem more likely to influence ecosystem processes. Chapin *et al.* (1997) suggested that the species traits with the greatest effects on ecosystem functioning were those that (a) controlled the acquisition, use, and availability of limiting resources; (b) modified the feeding structure of food webs; and (c) affected the occurrence and magnitude of disturbances. Such traits can be used to classify organisms into different functional groups. For instance, species can be divided, first, into functional groups based on their position in a food web: photosynthetic plants, herbivores, predators, parasites, parasitoids, decomposes, and so on. Organisms within each of these groups can be further subdivided based on their acquisition and use of their limiting resources. For grassland plants, for instance, this might be based on the time, within the growing season, when each plant was maximally active (cool-season versus warm-season plants), and on its carbon (C-3 or C-4 photosynthetic pathway) and nitrogen physiology (high nitrogen use efficiency, low nitrogen use efficiency, ability to fix atmospheric nitrogen). Such considerations might lead, for instance, to the classification of grassland plants into six functional groups: C-3 grasses, C-4 grasses, C-3 forbs, C-4 forbs, legumes, and woody plants. The assumption inherent in making such a classification is that species within a class are highly similar, and those in different functional groups differ markedly from one another.

D. Diversity versus Composition

It has long been recognized that the functioning of an ecosystem depends on which species the ecosystem contains (i.e., on it species composition). Interest in species diversity as an alternative or additional explanation for ecosystem functioning means that it is necessary to define species diversity, especially functional diversity, in a way that distinguishes diversity from species composition. This requires a definition that is more restricted than that traditionally used. In particular, effects should be attributed to diversity only once there has been simultaneous control for effects of composition, and effects should be attributed to composition only once there has been simultaneous control for effects of diversity. To achieve this in an experimental, theoretical, or observational study, it is necessary (a) to hold composition constant via randomization (numerous communities with randomly-chosen compositions) while changing diversity, (b) to hold diversity constant while changing composition, (c) to simultaneously vary both in an appropriately randomized and replicated design, or (d) to control for each statistically, such as via multiple regression, which is most appropriate for observational studies.

III. EARLY WORK ON FUNCTIONAL DIVERSITY AND ECOSYSTEM PROCESSES

Effects of diversity on ecosystem processes were first recognized by Darwin in *The Origin of Species*. Darwin noted that it was well-known that increased plant diversity led to greater primary productivity in pastures. The British ecologist, Charles Elton, hypothesized in his 1958 book titled *The Ecology of Invasion by Animals and Plants* that diversity would impact many aspects of ecosystem functioning. In particular, he suggested that greater diversity would lead to greater ecosystem stability, an idea that was further developed by the leading ecologists of that era, including Robert MacArthur, Gene Odum, and Ramon Margalef. Elton also suggested that greater diversity would decrease the susceptibility of an ecosystem top invasion by other species and would decrease the incidence of outbreaks by diseases and pests.

Elton's diversity-stability hypothesis was called into question, though, by the mathematical theory of May (1972), which predicted that the linear stability of communities of competing species would, in general, decrease as the diversity of the communities increased. The general consensus reached after publication of May's book was that other factors were likely to be more important than diversity as determinants of ecosystem processes. This view led ecologists to focus more of their attention on other issues, with much of that effort dedicated to better understanding the mechanisms of species interactions and the effects of species composition on ecosystem processes.

Recent explorations of the potential effects of diversity on ecosystem processes were inspired, to a great extent, by the publication of *Biodiversity and Ecosystem Functioning* (Schulze and Mooney, 1993). In a chapter in that book, Vitousek and Hooper hypothesized that many ecosystem processes, like primary productivity, should increase as diversity increased, and they stressed that the most important component of diversity might be functional group diversity. Agricultural studies were reviewed in a chapter by Swift and Anderson, who noted that mixed crops, especially those containing a legume and a grass, were often more productive than either crop species growing alone, supporting the diversity-productivity hypothesis. A chapter by McNaughton reviewed and evaluated a large number of observational and small-scale experimental studies in which stability was greater for ecosystems containing more species and highlighted data supporting Darwin's diversity-productivity hypothesis. These and other contributions in this book set the stage for a burst of work that has included development of additional mathematical theories, field and laboratory experiments, and observational studies.

IV. THE EFFECTS OF FUNCTIONAL DIVERSITY

A. Functional Diversity, Productivity, and Nutrient Dynamics

1. Theory and Concepts

The potential effects of functional diversity on productivity have been described by two qualitatively different models, reviewed in Tilman (1999). The first is the sampling effect model, simultaneously proposed in 1997 by three different authors (L. Aarssen; M. Huston; and D. Tilman, C. Lehman, and K. Thomson). The sampling effect model hypothesizes that species differ in their competitive abilities, and that species that are better competitors are also more productive. Given these assumptions, communities that have greater diversity should, on average, be more productive because they are more likely to contain one or more species that are more productive.

A formal mathematical treatment of the sampling effect, provides some deeper insight into the way that functional diversity can impact ecosystem processes. For this treatment, let R^* be the level to which a limiting resource is reduced by a species when growing alone. As shown both theoretically and in numerous competition experiments (Grover 1997), the best competitor would be the species with the lowest R^*. The R^* value of the species can be used to rank them from good to poor competitive ability (i.e., from the lowest to the highest R^* value). Assume that the species composition of a community is determined by random draws (sampling) from the infinite pool of species with all possible R^* values between a minimum ($R^*_{\min}$) and maximum ($R^*_{\max}$). On average, the functional diversity of a community would depend on the number of species drawn, N, which is the initial diversity. The number of species in a community, N, is a good measure of functional diversity in this model because the range in the values of the relevant species trait (R^*) is higher in communities containing more species. These assumptions of sampling effect yield a simple equation that relates the long-term average biomass of a plant community, $B_{(N)}$, to its original plant species diversity, N:

$$B_{(N)} = aQ\left(S - \left(R^*_{\min} + \frac{R^*_{\max} - R^*_{\min}}{N+1}\right)\right) \qquad (1)$$

Here a is the rate of resource mineralization, Q the coefficient of resource conversion into biomass, and S is the rate of resource supply in the habitat.

The sampling effect model predicts that total community biomass, a measure of primary productivity, increases with plant diversity, as shown in Fig. 1a. The trend predicted is one in which added diversity leads to large increases in productivity when diversity is low, but has progressively smaller impacts when diversity is higher. This simple model demonstrates that the magnitude of the effect of functional diversity, as measured by N, on ecosystem functioning depends on the range of interspecific differences in the species pool—that is, on the term ($R^*_{\max} - R^*_{\min}$) in Equation 1. This gives basis to the intuitive concept that diversity effects ecosystem processes because ecosystems with greater diversity have a greater range in those species traits that influence functioning.

The sampling effect model also predicts that the average quantity of unconsumed resource should decrease as diversity increases (Fig. 1b). Indeed, in the sampling effect model, the increased biomass at higher diversity is caused solely by the more complete utilization of the limiting resource that occurs, on average, at higher diversity.

The model also illustrates the importance of species composition. Each point in the two graphs of Figure 1 represents the response of a community with a different randomly determined species composition. Thus, the variability among plots with the same diversity measures the impact of composition, and the variability among diversity levels represents the impact of diversity. Both diversity and composition are strong determinants of productivity and resource levels in the sampling effect model.

The other major type of models that have been proposed to relate productivity to diversity are niche differentiation models. In essence, such models assume that a habitat is spatially or temporally heterogeneous, that species differ in the traits that determine their response to this heterogeneity, and that each species is a superior competitor, and thus is more productive, for some subset of the heterogeneous habitat conditions. These assumptions can allow a large number of species to coexist and assure that ecosystem productivity increases, on average, as diversity increases. For instance, two factors, such as soil pH and temperature, might limit plant abundance. Each species could have some combination of these factors at which it performed best. Such niche

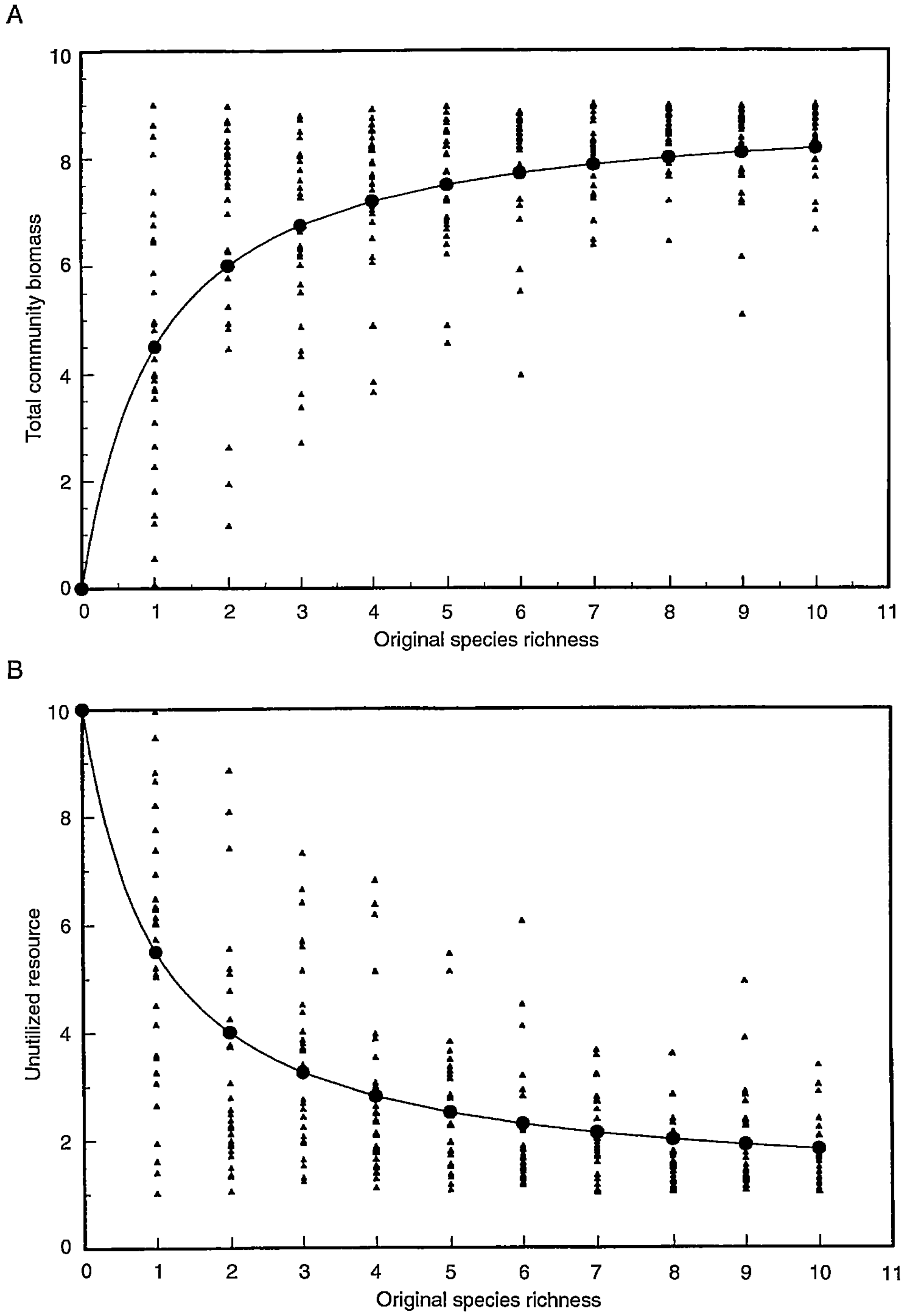

FIGURE 1 (A) The sampling effect model predicts that productivity should be greater at greater functional diversity, here measured by the number of species present. The variation within a given level of species richness is caused by different species compositions. (B) Productivity is higher in plots with greater functional diversity because of greater capture of the limiting resource. The concentration of unutilized resource is predicted to decline as diversity increases.

differentiation would mean that each species did best in a part of the habitat, but that no species could fully exploit the entire range of conditions.

The essence of such niche models can be captured by making the simple assumptions that each species has a circular area of radius r in which it can live and be a good competitor (Fig. 2a), that all species attain comparable abundances per unit habitat occupied, and that competition similarly reduces abundances of all overlapping species. If the values for one limiting factor range from 0 to $a\ r$ and the other from 0 to $b\ r$, where a and b measure habitat heterogeneity for factors 1 and 2, and if species are drawn at random from all those that could live at some point in the habitat, then total community biomass (i.e., the proportion of environmental conditions "covered" by one or more species) would be

$$B_{(N)} = 1 - \left(1 - \frac{\pi}{ab + 2(a + b) + \pi}\right)^N \qquad (2)$$

Here N is species diversity. $B_{(N)}$ is an increasing function of species diversity (Fig. 2b). The amount of unused habitat decreases as diversity increases, much as the concentration of unutilized resource was decreased for the sampling effect model. As for the sampling effect model, the variance within a given level of diversity is caused by differences in species composition, and differences between diversity levels is caused by diversity.

In addition, the niche model predicts that greater habitat heterogeneity (i.e., greater values of a and b) requires greater diversity in order to achieve a given level of productivity. In general, heterogeneity should increase with habitat size, leading to the prediction that greater biodiversity is required to attain a given level of productivity in larger habitats. For instance, for small, relatively homogeneous habitats ($a = b = 1$), only six species are needed to attain 95% of maximal productivity. However for spatially heterogeneous habitats ($a = b = 10$), a diversity of 135 plant species is needed to achieve this level.

A comparison of the sampling effect model with the niche differentiation model reveals a major difference in the expected pattern of the dependence of productivity on diversity. For the sampling effect model, there are no higher diversity plots that are more productive than the most productive monoculture. In contrast, for the niche model, there are two-species plots that are more productive than the most productive monoculture, three-species plots that are better than the best two-species plot, and so on. For ecosystems that meet the assumptions of the sampling effect model, which might occur for highly productive agricultural fields, there might be situations in which judicious choice of the right species and variety could lead to as great productivity from a monoculture as would be possible for a highly diverse mixture of species. In contrast, for habitats with spatial or temporal heterogeneity, which should occur for almost all natural ecosystems and for all but the most intensively managed ecosystems, niche differentiation models are more likely to hold. In such cases, increased diversity is expected to lead to greater productivity and to more complete use of limiting resources.

Although these models, and the models of Michel Loreau, have predicted that greater diversity can lead to greater ecosystem productivity, this need not always be the case. For instance, if the assumptions of the sampling effect model were modified to have progressively better competitors be progressively less productive, productivity would be a decreasing function of diversity. This suggests a more general principle: if species differ in their competitive abilities, and if higher competitive ability is correlated with some other traits, then these traits will, on average, be better represented in more diverse communities, thus biasing the functioning of these communities in the direction determined by these correlated traits.

2. Experimental Studies

Darwin suggested that it was common knowledge among farmers that a greater diversity of pasture plants would lead to a greater production of herbage in pastures. In his 1993 chapter, McNaughton cited this and presented more recent examples in which greater plant diversity led to greater productivity, as did Swift and Anderson. Indeed, earlier work reviewed in Harper's 1977 book showed that pairs of coexisting species often yield more than either species did when living by itself. As reviewed in the 1993 chapter by Vitousek and Hooper, some of the first evidence linking higher plant diversity to greater retention of soil nutrients came from a field experiment in Costa Rica by Ewel as collaborators. They found that communities planted to many tropical species generally retained more soil fertility than those planted to monocultures.

The first published direct test of the diversity-productivity hypothesis came from a greenhouse experiment by Naeem *et al.* (1995). By growing various randomly chosen combinations of 16 plant species 1, 2, 4, 8, or 16 at a time in a greenhouse, they found that community biomass was greater at higher plant diversity (Fig. 3a). This team performed another experiment in a series of growth chambers and also had results

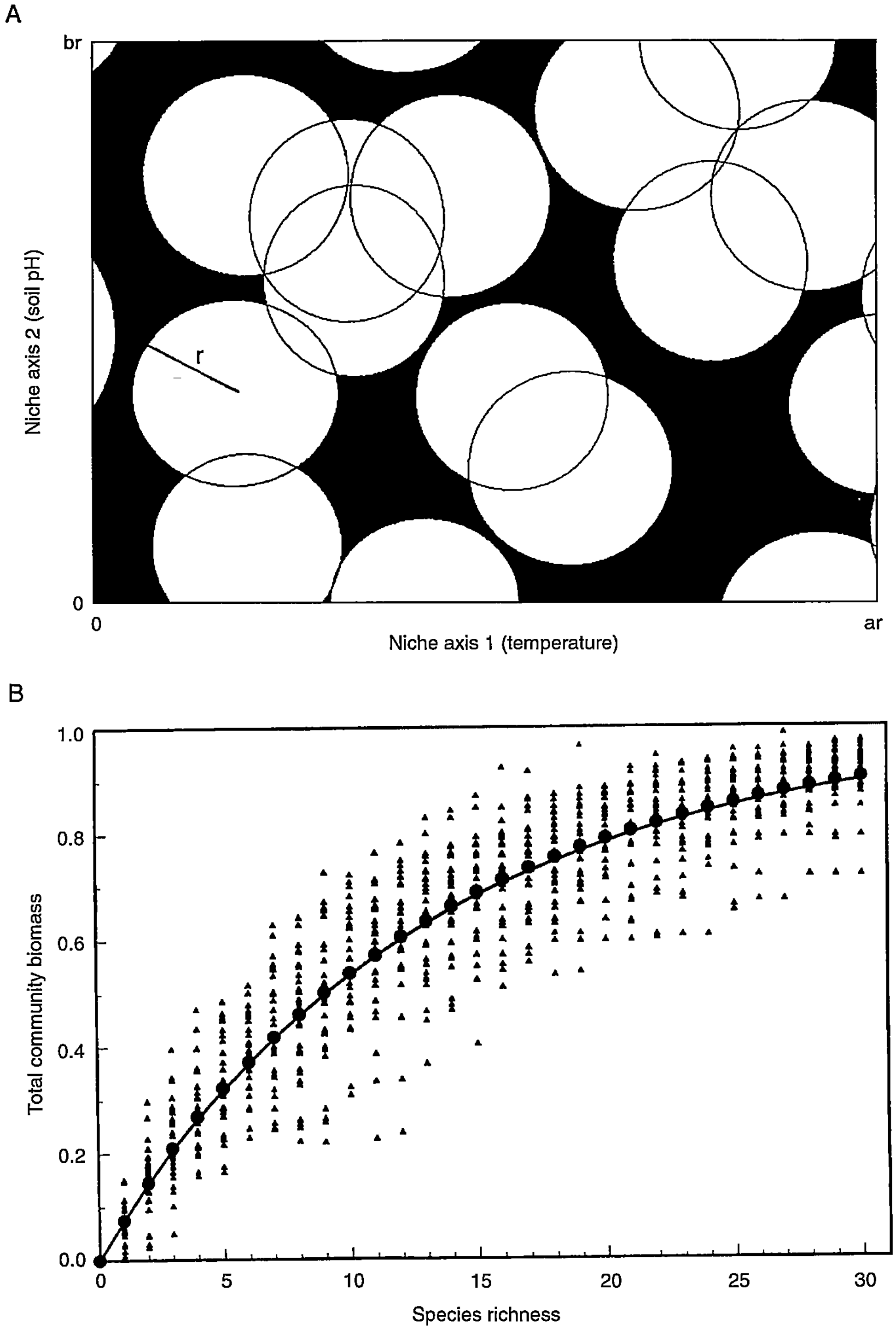

FIGURE 2 (A) A graphical illustration of a niche differentiation model. Here each circle represents the range of environmental conditions in which a given species can live, and the full rectangle shows the range of environmental conditions that occur in a given habitat. This model and similar niche differentiation models predict that productivity should be an increasing function of diversity. (B) The predicted effects of diversity on productivity for the model illustrated in part (A).

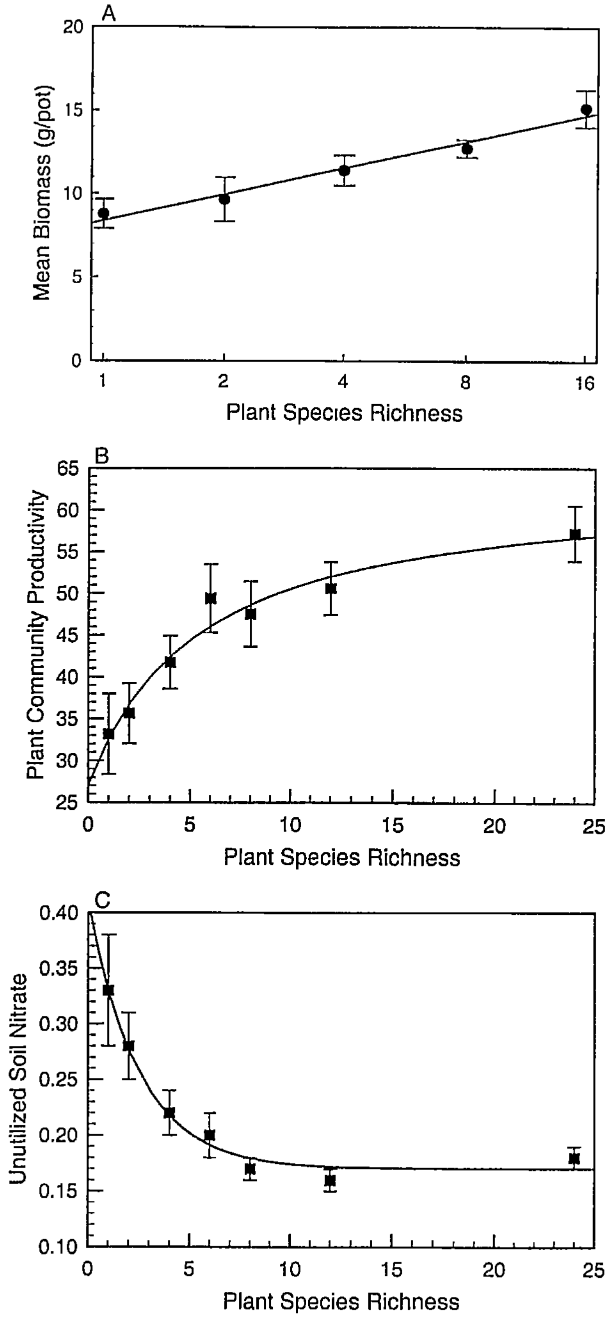

FIGURE 3 (A) The observed effect of plant diversity on the productivity of plant communities in the greenhouse experiment of Naeem and collaborators. (B) Effects of diversity on productivity for the Minnesota field experiment in which grassland diversity was experimentally controlled in 147 plots. (C) Effects of diversity on the concentration of unutilized soil nitrate for the Minnesota experiment.

suggesting that greater diversity leads to higher productivity (Naeem *et al.*, 1994). Next came results from a large-scale field experiment begun in Minnesota in 1993 (Fig. 4). Its 147 plots, each 3 m × 3 m, were planted to contain 1, 2, 4, 6, 8, 12, or 24 plant species randomly and independently chosen from a set of 24 prairie-grassland species (reviewed in Tilman, 1999). It found highly significant effects of plant diversity on both productivity (Fig. 3b) and on the soil concentration of the limiting resource, nitrate (Fig. 3c). By the fifth year of this experiment, its results supported niche differentiation models more than the sampling effect model as the major cause of the effects of diversity on the measured ecosystem processes. Indeed, the most productive plot in 1998 was a 24-species plot that had 65% greater total biomass than the most productive monoculture. A second experiment, adjacent to this Minnesota exper-

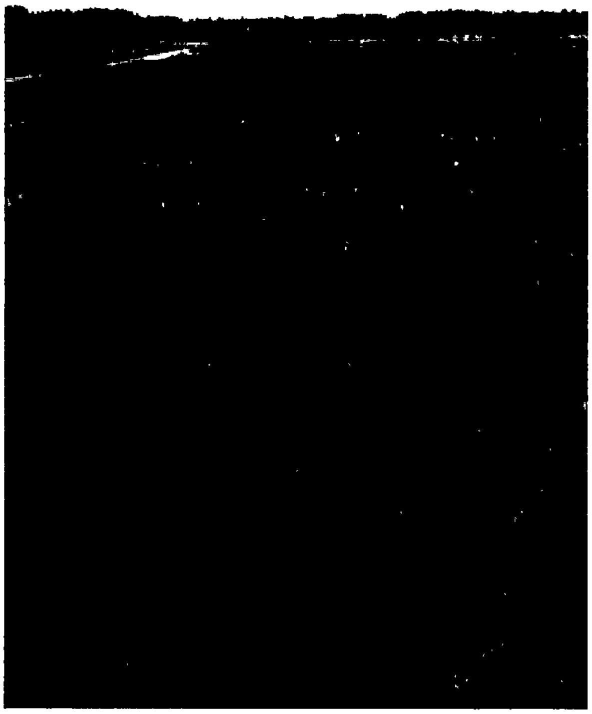

FIGURE 4 The smaller of the Minnesota biodiversity experiments, shown here, has demonstrated that plant diversity has a strong effect on ecosystem productivity and nutrient dynamics. The experiment has 147 plots, each being 3 m × 3 m (about 10 feet by 10 feet) in size. See also color insert, Volume 1.

iment (reviewed by Tilman, 1999), controlled for both species diversity and functional group diversity (Fig. 5). Its results were similar to those of the first experiment and showed highly significant effects of species diversity, functional group diversity, and functional group composition on primary productivity and nutrient dynamics. In both of the Minnesota grassland diversity experiments, the vast majority of species coexisted in all plots to which they had been added, further supporting niche differentiation models.

Knops *et al.* (2000) recorded the number of nonplanted species that invaded the Minnesota diversity experiment plots, and their biomass at the time when they were removed from the plots. They found that significantly fewer species invaded higher diversity plots and that the total biomass of invading species was lower in higher diversity plots. Further analyses suggested that the effect of diversity on invasions was caused by the lower levels of soil nitrate in higher diversity plots. This provides one simple mechanism whereby diversity may influence the extent to which an ecosystem is invaded by other species and suggests that levels of unconsumed limiting resources may, in general, be an important determinant of the success of an invading species.

For native, undisturbed grasslands close to the two Minnesota biodiversity experiments, plant abundances were greater and soil nitrate was lower in more diverse plots (see Tilman, 1999), which is consistent with the experimental results and with the predictions of theory. However, correlational patterns must be interpreted carefully because they could be confounded by other correlated variables. Michel Loreau used a model that linked environmental factors, biodiversity, and ecosystem functioning to explore this point. The model illustrated that correlational field data could be misinterpreted easily because of a confusion of cause-and-effect relationships. Just such issues cloud the interpretation of the possible effects of island diversity on ecosystem processes for a study of 50 Swedish islands. In an intriguing study that showed links between island size and the frequency of wildfire, David Wardle and collaborators found that a suite of ecosystem traits were correlated with both island size and plant diversity. However, it is unclear if diversity caused the observed differences in ecosystem processes or if both these processes and diversity were controlled by fire frequency.

Hooper and Vitousek (1998) performed a field experiment, planted in 1992, in which they controlled plant functional group diversity and composition using plants common to California grasslands. After a year of growth, they found that functional group composition had a much greater effect on plant community biomass than functional group diversity, but that the utilization of soil nutrients increased significantly as diversity increased.

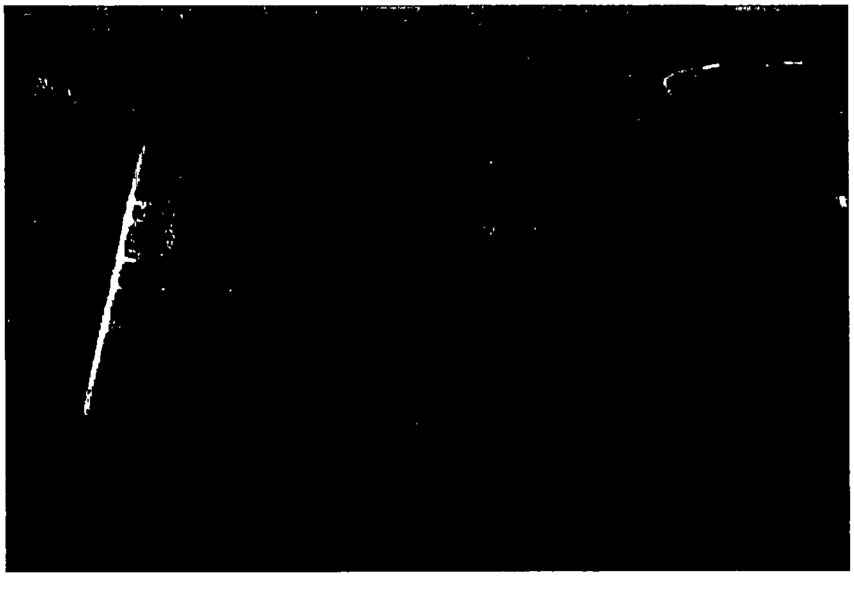

FIGURE 5 The larger of the Minnesota biodiversity experiments uses about 270 of the 342 plots shown It has shown strong effects of plant species richness, plant functional group richness, and plant functional group composition on ecosystem processes. Each plot is 13 m × 13 m (about 40 feet by 40 feet). See also color insert, Volume 1.

In a 4-month greenhouse experiment, Symstad *et al.* (1998) found that total plant biomass was significantly higher at higher diversity and that most of this effect was attributable to the presence of legumes. They also determined the effects of the deletion of individual species on total biomass and found that the strength and direction of these effects depended on which species were present and which was deleted.

In an experiment that was replicated at eight different sites across Europe, ranging from Scotland and Ireland to Portugal and Greece, Hector *et al.* (1999) found that greater plant diversity led to greater primary productivity. An important finding of this unique experiment was that the quantitative effect of diversity on primary productivity was the same across all eight sites. In combination with the other field and laboratory experiments, the European experiment suggests that there is a general, repeatable effect of grassland diversity on primary productivity.

In total, these studies show that plant productivity is greater at greater diversity and that this also corresponds with greater utilization of limiting soil resources. In general, short-term experiments showed weaker effects of diversity on productivity and soil nutrients than longer-term experiments. This is expected because diversity should impact ecosystem processes via changes in plant abundances mediated by competition, and such interactions can require several years to occur. Further work is needed on other trophic levels and in other communities to determine the extent to which the patterns observed to date apply to other trophic levels (e.g., herbivores, predators) or to other communities (e.g., marine fisheries, forest ecosystems, coral reefs).

B. Functional Diversity and Stability

1. Theory and Concepts

A large number of authors, including Charles Elton, Robert May, Stuart Pimm, and Sam McNaughton have contributed considerable insights into the effects of diversity on stability. May (1972), for instance, showed that the abundances of individual species become progressively less stable as the diversity of the community in which they live increases. Several recent papers have explored the effects of diversity on the stability of communities of competing species (Doak *et al.*, 1998; Ives *et al.*, 1999; Tilman, 1999). The first two of these papers showed that the temporal variability of an ecosystem process, such as ecosystem productivity, is expected to be lower when the ecosystems contain more species. This can occur for the same reason that a portfolio composed of many different types of stock tends to be more stable than one containing stock of a single company. An additional factor that can cause ecosystem functioning to be more stable for more diverse ecosystems is competition. When some disturbance harms one species, the species with which it interacts experience less competition. This allows these competitors to increase in abundance. Their greater abundance partially compensates for the decreased abundance of the first species, thus stabilizing the functioning of the ecosystem. Ives *et al.* (1999) showed that increased diversity only led to increased stability when the species differed in their responses to habitat fluctuations and disturbances. Because such differences are a direct measure of functional diversity, the work of Ives *et al.* (1999) showed that increases in functional diversity lead to greater stability. For a thorough treatment of theory relating diversity and stability, see "Stability, Concept of."

2. Experimental and Observational Studies

The evidence that led Elton to propose the diversity-stability hypothesis was anecdotal. In his 1993 chapter, and in earlier papers, McNaughton defended the diversity-stability hypothesis by citing several observations and experiments in which greater diversity was associated with greater stability. A variety of other studies, summarized in Tilman (1999), also have found effects of diversity on stability. For instance, a study by Frank and McNaughton of eight grassland sites within Yellowstone National Park found that those with greater plant species diversity had smaller shifts in plant community compositions during a severe drought. Two British ecologists, Taylor and Woiwod, performed a long-term project in which they monitored the abundances of hundreds of insect species at a large number of sites. The data they collected provide evidence that supports the hypothesis that more diverse insect communities should be more stable. The greater stability is expected because of the statistical averaging (or portfolio) effect pointed out by Doak *et al.* (1998). Specifically, because the temporal variances in the abundances of individual species in this community scales as their abundance to a power of about 1.6, the portfolio effect should cause more diverse insect communities to have lower temporal variability.

Several authors have found that greater oak tree diversity stabilizes the population density of an animal, the acorn woodpecker, that feeds on the seeds of the trees (see Koenig and Haydock, 1999). Acorn woodpeckers are highly dependent on acorns as a source of food, but oaks produce acorns as a mast seed crop. Masting means that there is great year-to-year variability in the rate of acorn production. There is a striking decrease in the year-to-year variability of acorn woodpecker abundances for woodpeckers living in habitats containing a greater diversity of oaks. Thus, greater oak diversity led to more stable acorn woodpecker populations. Moreover, acorn woodpecker densities were much lower for areas with a single oak species than for those with several.

A long-term experiment in Minnesota provides additional evidence suggesting that greater plant diversity leads to greater stability (reviewed in Tilman, 1999). In a series of 207 plots annually monitored from 1982 to 1999, total plant community biomass was found to be more stable in plots containing more species. Both in response to a major disturbance, a severe drought (Fig. 6), and in response to normal year-to-year variation in climate (Tilman, 1999), plots with greater diversity had lower year-to-year variability in their total plant biomass. In particular, the severe drought caused plant biomass to fall to half of its predrought level in plots with about 15 or more species, but caused it to fall to 1/8 to 1/12 of its predrought levels in plots containing one or two plant species (Fig. 6). Similarly, year-to-year variation in total biomass fluctuated about twice as much in low diversity as in high diversity plots (Tilman, 1999). Although total community biomass was more stable at higher diversity, analyses of the stability of individual species showed that these declined slightly but detectably, at higher diversity. Thus, diversity stabilized total community biomass at the same time that it destabilized the abundances of individual plant species. Plant diversity and composition were confounded in this experiment because both changed in response to nitrogen addition. Multiple regression, used to control for this confounding, found highly significant effects of diversity on stability for both cases. These analyses also showed that species composition and functional group composition also had significant effects on stability.

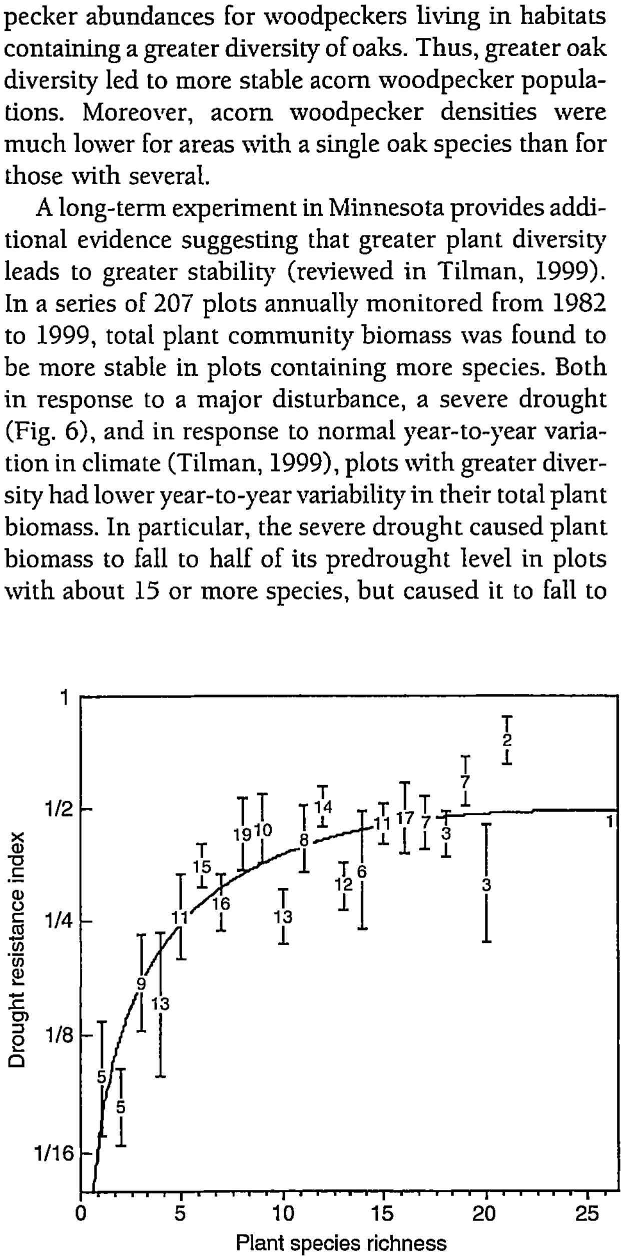

FIGURE 6 The resistance of Minnesota grassland ecosystems to drought was highly dependent on their plant biodiversity. Ecosystems containing a large number of plant species had their productivity fall to about half of its predrought levels during a severe drought, but those containing only one or two plant species had it fall to about 1/8 to 1/12 of the predrought level.

McGrady-Steed, Harris, and Morin (1997) found, in a laboratory study of the effects of diversity in microbial communities, that the temporal variability was significantly smaller at higher diversity. Indeed, a four-fold increase in diversity led to about a three-fold decrease in the temporal variability of whole-community net respiration, a measure of ecosystem activity. The rate of microbial decomposition of particulate organic matter also increased with diversity in this study. Finally, they found that greater diversity led to lower susceptibility to invasion by another species, but that invader success was highly dependent on community composition. Naeem and Li (1997) similarly found that greater diversity led to greater reliability, which was measured as the lower variability in total community biomass among communities of identical diversity. This effect was also apparent in the greenhouse experiment that Naeem and collaborators had performed earlier.

In total, these studies provide strong evidence that communities with greater diversity are more stable and suggest that individual species in such communities may be less stable. Theory, experiment, and observation are in general agreement, but this topic merits additional exploration.

V. CONCLUSIONS

The research performed to date illustrates that a variety of different ecosystem processes are impacted by the number and kinds of species living in the ecosystem.

This work illustrates that species differ in traits that influence ecosystem functioning and suggests that ecosystem processes depend on the range in those traits represented in the ecosystem. However, there are, as yet, no clear demonstrations of the specific traits that are relevant to particular ecosystem processes and no simple ways to directly measure functional diversity. Rather, correlates of functional diversity, such as species richness or functional group richness, remain the best, albeit indirect, way to measure functional diversity.

See Also the Following Articles

C_4 PLANTS • ECOSYSTEM FUNCTION, PRINCIPLES OF • FUNCTIONAL GROUPS • HABITAT AND NICHE, CONCEPT OF • STABILITY, CONCEPT OF

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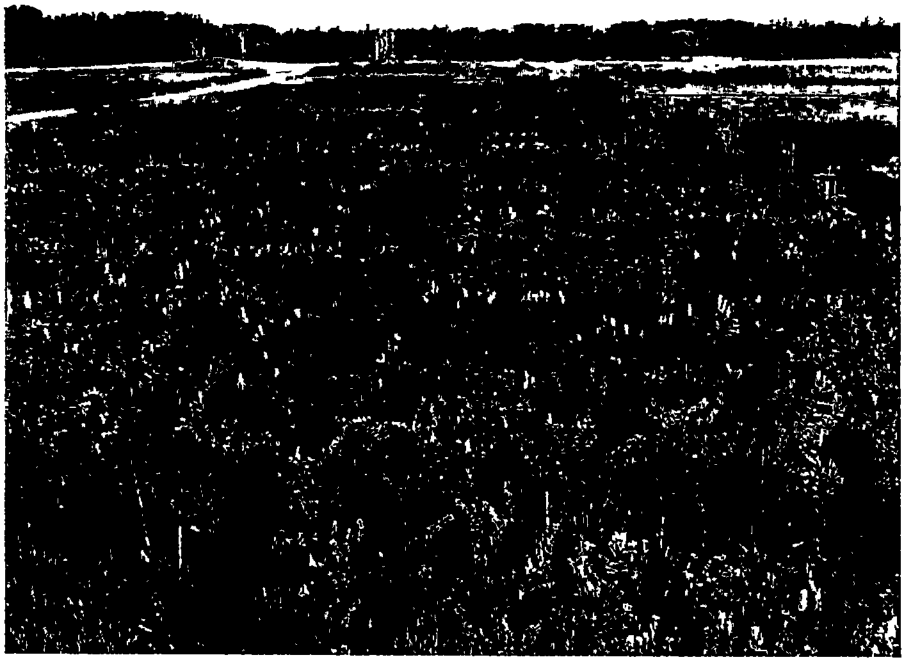

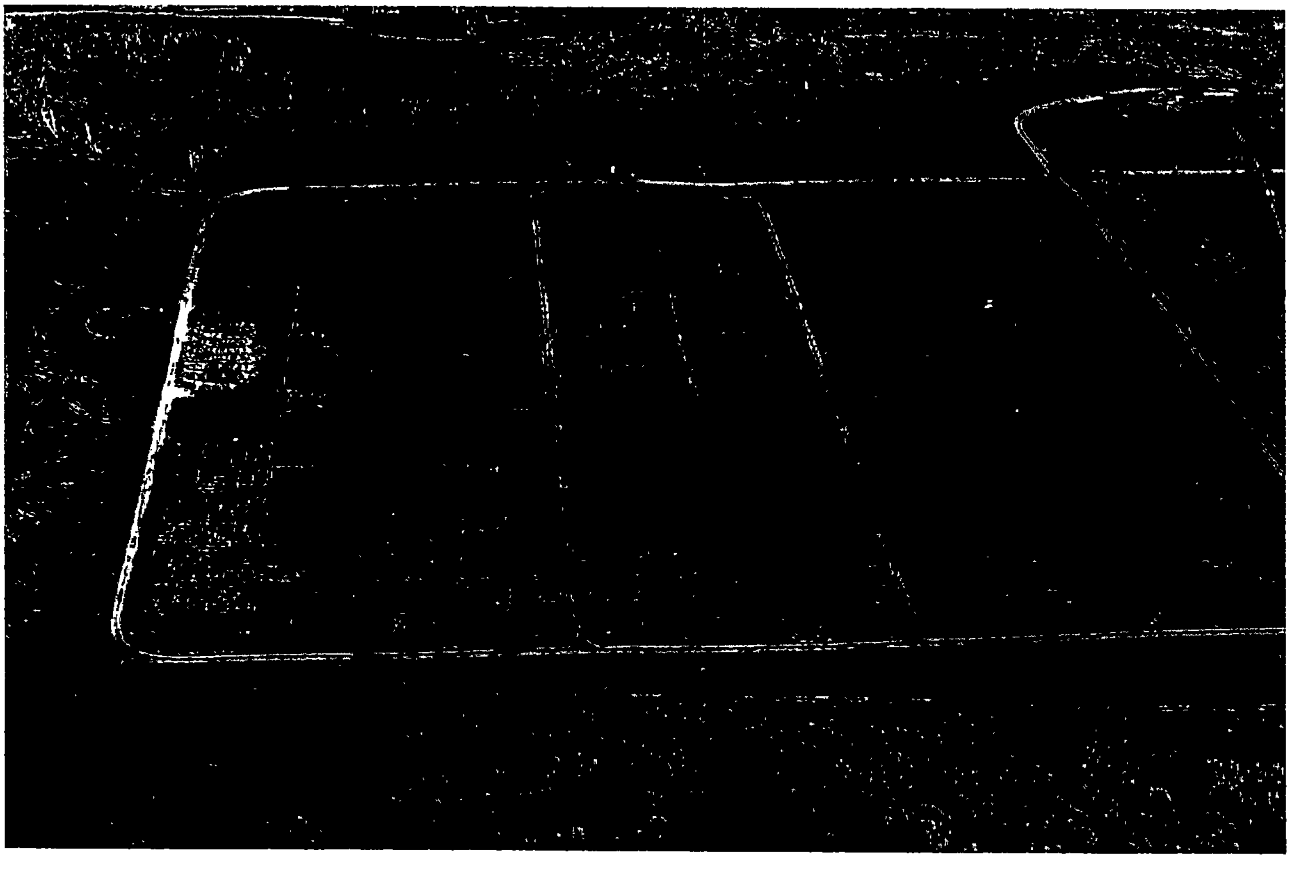

FUNCTIONAL DIVERSITY. Functional diversity, those components of biodiversity that influence how an ecosytem operates or functions, has been examined in a notable set of ongoing field experiments in Minnesota. Top: The smaller of the Minnesota biodiversity experiments has demonstrated that plant diversity has a strong effect on ecosystem productivity and nutrient dynamics. The experiment has 147 plots, each being 3 m × 3 m (about 10 feet by 10 feet) in size. Bottom: The larger of the Minnesota biodiversity experiments uses about 270 of the 342 plots visible here. It has shown strong effects of plant species richness, plant functional growth richness, and plant functional group composition on ecosystem processes. Each plot is 13 m × 13 m (about 40 feet by 40 feet). See article FUNCTIONAL DIVERSITY (Vol. 3).