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Interactions of the Major Biogeochemical Cycles

Global Change and Human Impacts

Edited by
Jerry M. Melillo, Christopher B. Field,
and Bedrich Moldan

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Biogeochemical Interactions and Biodiversity

Valerie T. Eviner and F. Stuart Chapin III

There has been considerable recent interest in the ecosystem consequences of global and regional shifts in biogeochemical cycling and the loss of species diversity. Since biogeochemical cycling is the result of an interaction of numerous organisms, the link between diversity and biogeochemistry is a natural one. Changes in either diversity or biogeochemical cycling can dramatically influence one another, and the large human impact on both has the capacity to compromise the ecosystem functions on which society relies.

A number of significant changes are occurring in the Earth's biogeochemistry (Austin et al., Chapter 2, this volume; Galloway, Chapter 14, this volume; Chapin et al. 2000). Because of these shifts in global and regional biogeochemistry, as well as land use changes and the introduction of exotic species, we are in the midst of one of the largest extinction events in the history of life on Earth, with extinction rates 100–1,000 times greater than prehuman rates. The ecosystem response to these multiple biogeochemical shifts depends largely on the response of the biotic community. For example, shifts in vegetation in response to these human-induced changes can have ecosystem impacts that are larger and different in direction than the direct biogeochemical response to these changes (Hobbie 1996; Shaw and Harte 2001). Beyond a shift in composition, loss of diversity can compromise the capacity of a community to perform ecosystem functions, particularly in response to multiple stresses (Griffiths et al. 2000; Degens et al. 2001; Muller et al. 2002).

In this chapter we explore the feedbacks between changes in biogeochemical interactions and biodiversity. Plant species richness is the component of biodiversity that is most frequently studied in relationship to ecosystem function, but we include other examples where they are available.

Effects of Changes in Biogeochemical Cycling on Diversity

Shifts in the biotic community in response to a variety of biogeochemical changes have been well documented (Table 8.1). Deposition of toxic levels of heavy metals and SO_2 can decrease the diversity of plants, soil microbes, and several other types of organisms. These decreases in species richness are directional changes through selection for species that can tolerate levels of pollutants that are potentially toxic to many organisms (Table 8.1). The differential responses of components of the biotic community to these pollutants can have significant impacts on biogeochemical cycling. For example, heavy metals suppress N_2O production more than NO production (Holtan-Hartwig et al. 2002).

Plant diversity substantially decreases in response to chronic N inputs across a large number of ecosystems through selection for fast-growing plant species and canopy dominants and selection against legumes and small-statured species. N deposition also causes shifts in microbial community composition and diversity (Table 8.1). Additions of other limiting nutrients in terrestrial systems do not have as strong an effect on community diversity as does N. For example, even though P was the most limiting nutrient to plant growth, P additions did not alter plant species richness in a chalk grassland, whereas N additions substantially decreased plant species diversity (Willems, Peet, and Bik 1993). Similarly, in an annual grassland, additions of P and K had very little effect on plant community composition, whereas additions of N decreased species richness (Goldberg and Miller 1990). These results show that N additions tend to have strong impacts on plant species diversity, whereas community composition has variable responses to additions of other nutrients, even if they are limiting.

Eutrophication by N and P in aquatic systems also tends to decrease the diversity of aquatic organisms and selects for plants that are good competitors at high nutrient levels and for animals that tolerate low oxygen levels. In both aquatic and terrestrial habitats, these directional changes in community composition are likely to determine the ecosystem effects of resource additions (Fridley 2002).

The effects of elevated CO_2 on plant and microbial community composition are variable. Elevated CO_2 often results in a change in plant and microbial species composition, but there are no generalizable responses in the nature of species that are selected for. Several studies, however, have found that elevated CO_2 increases plant species evenness (proportionate distribution of species) (Table 8.1).

Although climate is not specifically a biogeochemical change, increased fluxes of CO_2, CH_4, and N_2O into the atmosphere are resulting in warming and possible changes in precipitation patterns that will likely impact the biological community. Changing weather patterns will cause directional shifts in species composition and diversity, based on the life history of the species (Sternberg et al.

Table 8.1. Shifts in the biotic community in response to a variety of biogeochemical changes

Biogeochemical change	*Diversity change*	*Selection for species*
SO_2 deposition	Decreased species richness of:	Selection against sensitive species
	plants[1]	
	soil microarthropods[2]	
	macroinvertebrates[3]	
	ants[4]	
Heavy metals	Decreased species richness of:	
	plants[5]	Selection for tolerant plants[6]
	microbes	Selection for resistant microbes with fast growth[7]
		Change in microbial community structure and function[8]
	aquatic macroinvertebrates[9]	Selection for tolerant dominants[10]
N additions	Terrestrial plants—decreased richness[11]	Selection for fast-growing, tall species[12]
		Selection against short-statured species, legumes[13]
	Aquatic organisms—decreased plant diversity[14]	Select for fast-growing plants and against native species
		Select for animals that tolerate low oxygen[15]
	Mycorrhizal diversity decreases [16]	Select for species that are small-spored, less mutualistic, do well at high N[16]
	Soil microbes	Increase fungi[17]
		Selection for microbial communities dependent on plant compositional shifts [18]

(continued on next page)

Table 8.1. *(continued)*

Biogeochemical change	*Diversity change*	*Selection for species*
Elevated CO_2	Plants—increased evenness, but no change in richness[19]	Shifts in plant species composition, but no consistent groups of species selected for, some evidence of selection against dominants[20]
	Microbes	Larger effects on composition than diversity Shifts in composition but not consistent[21]
Warming	Plants	Shifts in plant composition, selection for species depends on other environmental conditions[22]
	Microbes—increased diversity[23]	Preferential stimulation of methanogens over methane-oxidizers[24]
	Soil mesofauna—increased diversity if moisture is not limiting[25]	

[1] Singh, Agrawal, and Narayan 1994; [2] Bressan and Paoletti 1997; [3] Carcamo and Parkinson 2001; [4] Hoffman, Griffiths, and Andersen 2000; [5] Salemaa, Vanha-Majamaa, and Derome 2001; [6] Del Rio et al. 2002, Lasat 2002; [7] Muller et al. 2001; [8] Kozdroj and van Elsas 2001, Muller et al. 2001, Muller et al. 2002; [9] Clements and Kiffney 1995; [10] Clements 1994, Clements et al. 2000; [11] Reed 1977, Inouye et al. 1987, Tilman 1988, Goldberg and Miller 1990, Huenneke et al. 1990, Wilson and Tilman 1991, Berendse, Aerts, and Bobbink 1993, Willems, Peet, and Bik 1993, Inouye and Tilman 1995; [12] Dukes and Mooney 1999; [13] Jones and Winans 1967, Willems, Peet, and Bik 1993; [14] Tilman 1999, Mosier et al. 2001; [15] Byers 2002; [16] Arnolds 1991, Egerton-Warburton and Allen 2000, Lilleskov, Fahey, and Lovett 2001, Egerton-Warburton et al. 2001, Lilleskov et al. 2002; [17] Arnolds 1991; [18] Bardgett et al. 1999; [19] Leadley et al. 1999, Niklaus et al. 2001a, He, Bazzaz, and Schmid 2002; [20] Leadley and Korner 1996, Chiariello and Field 1996, Potvin and Vassuer 1997, Owensby et al. 1999, Dukes and Mooney 1999; [21] O'Neill 1994, Kandeler et al. 1998, Hungate et al. 2000, Phillips et al. 2002, Dhillion, Roy, and Abrams 1996, Rillig et al. 1997, Grayston et al. 1998; [22] Harte and Shaw 1995, Chapin and Korner 1996, Hobbie 1996, Saleska, Harte, and Torn 1999, Price and Waser 2000; [23] Andrews et al. 2000; [24] Schlesinger 1997; [25] Harte et al. 1995.

1999). Several studies have shown that warming influences plant species composition through selection for certain plant species (Harte and Shaw 1995; Chapin and Korner 1996; Hobbie 1996), although this is not always the case (Price and Waser 2000). These shifts in vegetation composition are largely responsible for ecosystem responses to warming (Hobbie 1996; Saleska, Harte, and Torn 1999; Shaw and Harte 2001). Similarly, an increase in microbial diversity in response to warming increases soil C respiration (Andrews et al. 2000), while preferential stimulation of methanogenic bacteria over methane-oxidizers could stimulate increased CH_4 flux from wetland soils (Schlesinger 1997).

Clearly, changes in biotic diversity in response to biogeochemical factors are not random additions or deletions of species; they are selective changes in species composition. Resulting changes in biogeochemical processes may be better explained by these changes in species composition than by changes in species richness.

The Ecosystem Effects of Species Diversity

Mechanisms

Many components of biological diversity could be important in determining ecosystem processes. Most studies have focused on the ecosystem consequences of species richness within a group of organisms (e.g., plant species diversity or microbial diversity). The most commonly proposed mechanism for a diversity effect on ecosystem function is complementarity. Organisms differ in their niches, including how, when, and where they play their role, and the combination of species with different niches can affect ecosystem function in ways that differ from the effects of any single species. For example, species differences in the type, timing, or spatial zone of resource uptake can enhance overall community resource utilization, leading to an increase in plant production. The more unique the niches of the species are, the greater the diversity effect.

The observed relationships between diversity and ecosystem functions may also be explained by the "sampling effect" (Aarrsen 1997; Huston 1997). The sampling effect is based on one or a subset of species with strong ecosystem effects. In this case, the relationship between species richness and ecosystem function is not a mechanistic effect of diversity per se, but rather, it is due to an increased statistical probability of including a particular species in a community of higher diversity.

A third mechanism, "interspecific facilitation" (Cardinale, Palmer, and Collins 2002), has received less attention in the literature. Like complementarity, this ecosystem effect is a result of the activity of multiple organisms. Whereas complementarity is a function of the accumulated independent effects of the component species, in interspecific facilitation, the function and sometimes the existence

of these species complexes rely on close interactions among the component species. Some examples include symbiotic N fixation and substrate degradation that can only be achieved by a closely associated community of microbes (consortia). Extreme examples are eukaryotic cells and their intracellular units that are endosymbiotic prokaryotes or the descendents of these (e.g., mitochondria, chloroplasts, S-oxidizing bacteria, methanogens, methane-oxidizing bacteria) (Caldwell et al. 1997).

A fourth alternative is that there is no mechanistic effect of diversity on particular ecosystem processes; rather diversity and an ecosystem process co-vary because they are controlled by the same environmental factor. This is not a mechanism that can explain direct experimental manipulations of diversity, but it can be an important consideration when comparing natural systems or experimental treatments in which species richness is manipulated through a change in environmental factors (e.g., Huston 1997; Wardle 2001). For example, when comparing community diversity and productivity in unmanipulated natural plots in very low-productivity environments, the correlation between productivity and diversity may not be causative but due to the fact that both are limited by the same resources (Wardle 2001).

At a mechanistic level, sampling effects, complementarity, and interspecific facilitation all depend on a mixture of species that differ in a key trait or combinations of traits. These mechanisms are not mutually exclusive, and the importance of these multiple mechanisms highlights a critical feature of biological diversity: a given function can be attained through multiple pathways.

The Effects of Biological Diversity on Different Ecosystem Functions

Species diversity can influence many ecosystem processes, but ecosystem processes differ in their relationships to diversity and/or composition of the biotic community. The strongest relationships between species richness and ecosystem processes are for those processes that are directly related to resource utilization (reviewed in Eviner and Chapin, in review). A number of studies have observed a positive relationship between plant richness (Naeem et al. 1994; Tilman et al. 1997; Hooper and Vitousek 1998; Mulder, Uliassi, and Doak 2001) or mycorrhizal richness (van der Heijden et al. 1998) and plant productivity. Increased productivity in response to increased plant species richness can be mediated through complementarity in the use of various resources, but this relationship is often weak and is usually better explained by the presence of highly productive species (Naeem et al. 1994; Tilman et al. 1997; Hooper and Vitousek 1998; Spehn et al. 2000a; Mulder, Uliassi, and Doak 2001). Plant species richness also contributes to nutrient and water retention, but again, species composition usually plays a

larger role than species number (Naeem et al. 1994, 1995; Tilman, Wedin, and Knops 1996; Tilman et al. 1997; Hooper and Vitousek 1998).

Much as plant species richness can enhance productivity through complementarity of resource use, a diverse microbial community may enhance decomposition of litter or soil organic matter through the same mechanism (Solanius 1981; McGrady-Steed, Harris, and Morin 1997; Dobranic and Zak 1999). Decomposition rates are not, however, always enhanced by increased diversity of microbial communities because the identity of species plays a larger role than their number (Finlay, Maberly, and Cooper 1997). For example, selection for certain microbes can enhance decomposition of plant residues despite decreases in microbial community diversity (Griffiths et al. 2000). Microbial community composition can also affect the degradation of specific compounds (Janzen, Dormaar, and McGill 1995; Colombo, Cabello, and Arambarri 1996; De Boer, Klein Gunnewiek, and Parkinson 1996). There are many substrates, particularly environmental contaminants, that cannot be degraded by isolated populations of microbes, but only by consortia (Rozgaj and Glancersoljan 1992; Caldwell et al. 1997), particularly in anaerobic environments (Palmer et al. 1997). Composition of the microbes within consortia can dramatically alter degradation rates (Wolfaardt et al. 1994), indicating that the effects of a community on degradation are due not only to the number of species, but also to their composition.

Similar to decomposition, rates of nitrification, denitrification (Martin, Trevors, and Kaushik 1999; Griffiths et al. 2000), and methane oxidation (Willison et al. 1997; Griffiths et al. 2000) relate to microbial diversity and are also strongly influenced by the composition of the microbial community (Landi et al. 1993). Overall, it is clear that microbial community composition can have strong impacts on ecosystem function (Colombo, Cabello, and Arambarri 1996; De Boer, Klein Gunnewiek, and Parkinson 1996; Balser, Kinzig, and Firestone 2001).

While microbial diversity can enhance decomposition and nutrient cycling, plant composition generally has a stronger effect on these processes, because the species composition of the plant community determines the substrates available for microbial utilization. Although the identity of plant species has strong effects on these processes, there is little reason to hypothesize an effect of plant species richness on these processes. All experimental evidence indicates that decomposition rates are not related to plant species richness, but to plant composition (Naeem et al. 1995; Wardle, Bonner, and Nicholson 1997; Bardgett and Shine 1999; Hector et al. 2000; Spehn et al. 2000b; Knops, Wedin, and Tilman 2001). Several of these studies found that decomposition rates of litter mixtures could not be predicted based on rates of the component species alone (nonadditive effect), suggesting the importance of substrate mixtures, but these were both positive and negative effects and were largely due to specific combinations of substrates

(species composition), not an increase in the number of litter types (Wardle and Nicholson 1996; Wardle, Bonner, and Nicholson 1997; Hector et al. 2000). There have been a few mechanistic hypotheses linking plant species richness and decomposition rates. Higher diversity treatments tend to have higher percent cover and soil water use, resulting in lower temperature and moisture for decomposition. Although these directional microclimate changes would be predicted to have a negative effect on decomposition, the magnitude of these microclimate effects on decomposition rate was extremely small (Hector et al. 2000). Similarly, plant substrate quality has a larger impact on nutrient mineralization than does plant richness. Although plant species richness can stimulate N cycling through an increase in substrate quantity (Spehn et al. 2000b) or decrease nitrification rates through higher plant NH_4 uptake (Niklaus et al. 2001b), these effects tend to be weaker than the influence of substrate quality on N cycling. This accounts for the frequent observation that the role of richness in ecosystem function is overwhelmed by species composition and environmental factors (Fridley 2002; Loreau 1998; Loreau 2000; Wardle, Bonner, and Barker 2000).

Although species composition is key to a mechanistic understanding of the role of the biotic community in determining ecosystem processes, diversity per se is important to ensuring stability of these species effects. Different functions and environmental tolerances are usually distributed independently among species. There may be redundancy in a function, but it is unlikely that there will be overlap in the suite of functions associated with any species, including functional roles, environmental tolerances, physiological requirements, and microhabitat preferences (Beare et al. 1995). Species diversity is critical for the maintenance of these roles under fluctuating conditions. Diversity provides a community with multiple ways of performing a function, providing stability in biogeochemical processes despite shifts in environmental conditions (McNaughton 1977; Rao and Willey 1980; Chapin and Shaver 1985; McGrady-Steed, Harris, and Morin 1997; Naeem and Li 1997; Griffiths et al. 2000; Degens et al. 2001).

Effects of Species Composition on Interactions among Biogeochemical Cycles

Biogeochemical cycling is largely mediated through the biotic community, which both supplies and metabolizes substrates. Species composition largely controls the ratios at which elements cycle in systems and the potential of these element cycles to interact as a result of the suite of traits, functions, and environmental preferences of the species present in a community.

C, N, S, and P are not cycled in simple stoichiometric ratios because these elements are mobilized and stabilized by different mechanisms (McGill and Cole

1981). N is bonded directly to the C skeleton of organic compounds, and thus mineralization of N is a by-product of the intracellular breakdown of organic compounds by microbes for energy (C). This accounts for the strong relationship between litter C:N and rates of decomposition and net N mineralization. Because P is not directly bonded to the C skeleton of organic matter but is associated with C through ester bonds, mineralization of P occurs through enzymatic activity, which cleaves P from organic matter. Thus mineralization of P from organic matter is not directly related to litter C:P ratio but is controlled more directly by plant and microbial need for P. P can also be accessed by organisms through production of charged organic compounds that can free PO_4 from binding sites in the soil or through accumulation of calcium oxalates that increase P availability by decreasing soil calcium. The control of sulfur release from organic matter is intermediate between N and P because it occurs in organic matter in both C-bonded and ester-bonded forms. Thus, organic S can be released through both microbial C metabolism and directly by biotic demand for S.

Because these elements are stabilized by different mechanisms, the effect of an organism on any one of these elements can be independent of its effect on other elements. For example, grassland plant species with very similar effects on N cycling can differ substantially in their effects on P cycling (Hooper and Vitousek 1998; Eviner 2001), water fluxes, and soil C (Eviner and Chapin 2001). Similarly, the influence of the plant community on nutrient retention differs for different elements (Naeem et al. 1994, 1995). The functions of species can also vary independently from their environmental tolerances (Eviner and Chapin 2001), so shifts in environmental conditions are not likely to select for species with specific suites of functional effects. A notable exception to this is that soil fertility levels often select for plant species that reinforce these levels of fertility (Chapin 1980). Species not only differ in their effects on multiple elements, but also in how they couple multiple elements. The ratios of elements required for optimal growth can differ among species, and many organisms can store nutrients that are in excess at one time and later use them for growth.

The stoichiometry of decomposers can greatly influence rates of N mineralization. Fungi, with a high C:N ratio (15:1–45:1), will mineralize relatively more N than bacteria, which have a low C:N ratio (3:1–5:1) and higher requirement for N (Paul and Clark 1995). For both herbivores and decomposers, the ratio of nutrient release from a given substrate will be determined by the requirements of those organisms for the different nutrients. A species with a higher N:P requirement will recycle N at a relatively lower concentration than a species with a lower N:P requirement (Sterner, Elser, and Hessen 1992; Elser et al. 2000). The balance of nutrients released will change because of shifts in both the species providing the substrate (producers) and the consumers.

The ratios of element uptake and resorption by plants can have substantial effects on biogeochemical interactions, since plant litter is the major substrate for element recycling and fuels many biogeochemical processes. Plant species differ in the ratios of elements taken up to produce new biomass and resorbed prior to litter fall (Aerts and Chapin 2000), so species differences in these properties alter rates at which different elements cycle. For example, many studies have linked plant species effects on decomposition and N cycling to litter C:N ratios (Taylor, Parkinson, and Parsons 1989; Wedin and Tilman 1990; Scott and Binkley 1997; Maithani et al. 1998; Mueller et al. 1998; Mafongaya, Barak, and Reed 2000).

Species differences in C quality of litter also have strong effects on rates of decomposition and mineralization (Melillo, Aber, and Muratore 1982; Aber, Melillo, and McClaugherty 1990; Palm and Sanchez 1991; Taylor et al. 1991; Stump and Binkley 1993; Schimel et al. 1996), because secondary compounds can inhibit microbial activity (Lodhi and Killingbeck 1980; Thibault, Fortin, and Smirnoff 1982). These secondary compounds can be more important than C:N ratios in explaining plant species effects on biogeochemical cycling (Eviner 2001).

Although plant regulation of N and C dynamics has largely focused on litter quality, up to a tenfold difference in rates of net N mineralization can occur because of a threefold difference in labile C inputs by different species (Wedin and Pastor 1993). These labile C inputs are generally simple C compounds that are readily available as an energy source to microbes and can accelerate decomposition of recalcitrant litter and soil organic matter (Sallih and Bottner 1988; Mueller et al. 1998; Bottner, Pansu, and Sallih 1999). These recalcitrant C compounds are often not used as an energy source, and microbes often require labile C to provide energy for the metabolism of these recalcitrant compounds in their search for N. Labile C will stimulate decomposition of a recalcitrant compound under N-limited conditions but not under high N availability (van Ginkel, Gorissen, and Van Veen 1996). These examples clearly demonstrate that the biogeochemistry of C is affected not only by an interaction of nutrients, but also by the interaction of different types of C compounds that are produced by different plant species.

Plant composition can also influence biogeochemical cycling by altering microclimate conditions such as temperature, pH, soil moisture, and O_2 concentrations (van Vuuren et al. 1992; Mack 1998; Eviner 2001; Caraco and Cole 2002). For example, in waterlogged soils or sediments, plant species that enhance soil O_2 concentrations have been responsible for enhanced decomposition of organic matter (Allen et al. 2002), increased nitrification rates (Engelaar et al. 1995), decreased CH_4 formation (Grosse, Jovy, and Tiebel 1996), and lower consumption of SO_4, leading to decreased mobilization of Fe and mineralization of P (Christensen 1999). Interactions of plant inputs also determine the fate of nitrate in anaerobic environments by regulating the concentrations of NO_3 and

organic C available to denitrifiers. The amount of C in relation to NO_3 is positively correlated to the amount of N_2 versus N_2O produced by denitrification. At high levels of labile C, however, the fate of NO_3 can shift from denitrification to dissimilatory nitrate reduction to ammonium (DNRA) (Fazzolari, Nicolardot, and Germon 1998; Silver, Herman, and Firestone 2001; Yin et al. 2002).

Ultimately, a plant species effect on biogeochemical cycling reflects its suite of traits. For example, an interaction of litter, microclimate effects, and labile C inputs determines plant species effects on net N mineralization and nitrification, soil C dynamics, and decomposition, and these traits vary independently among species (Eviner 2001). This independent distribution of multiple ecosystem functions among species is a key driver of the effect of the biotic community on biogeochemical interactions.

Biogeochemical interactions are also related to species-specific responses of microbes to combinations of substrates and environmental conditions. For example, the effect of N in limiting lignin decomposition depends on the species of white rot fungus present, because N inhibits some species less than others (Schimel 1995). Similarly, variation in methane oxidation with N concentrations depends on the composition of the microbial community (Groffman and Bohlen 1999). Ultimately, the suite of functions and environmental tolerances of a given species will determine the interaction of elements, their stoichiometry, and the interactions of biogeochemical cycling with environmental conditions. By altering environmental conditions and the ratios of available elements, any given species can also influence the distribution and activity of other organisms, further altering biogeochemical interactions. Thus, it is not surprising that the stoichiometry of elements is highly uncoupled in both terrestrial and aquatic ecosystems.

Biogeochemical Interactions and Species Mixtures

The interactions between biogeochemical cycles are mediated by the suite of organismal traits being expressed, and the nature of traits has a much larger role in determining biogeochemical cycling than does the diversity of traits. There is no clear relationship between species richness and biogeochemical interactions because the organismal traits that determine the dynamics of different elements do not consistently occur together when species are compared. The ecosystem effects of species mixtures often cannot be predicted based on the patterns of species effects in monocultures (nonadditive effects), as seen in processes ranging from decomposition (Naeem et al. 1995; Wardle and Nicholson 1996; Wardle, Bonner, and Nicholson 1997) to N cycling (Blair, Parmelee, and Beare 1990; Wardle, Bonner, and Nicholson 1997; Finzi and Canham 1998; Nilsson, Wardle, and

Dahlberg 1999; Eviner 2001) to plant growth (Newman et al. 1979; Lawley, Newman, and Campbell 1982; Lawley, Campbell, and Newman 1983; Nilsson, Wardle, and Dahlberg 1999). Just as the ecosystem effects of a species depends on an interaction of traits that a given species exhibits, these trait combinations have the same effect on biogeochemical cycling when they are due to the mixture of multiple species, each of which exhibits some of these traits (Eviner 2001). Some trait combinations, however, are unique to species mixtures, seldom occurring within a single plant species (e.g., litter with recalcitrant C and high N content). Nonadditive effects of species mixtures are mediated by an interaction of particular traits of particular species, not simply by a diversity of traits. Nonadditive effects of species mixtures can also be due to shifts in species traits resulting from the identity of the neighboring species. For example, nonadditive effects of plant mixtures on N cycling in California annual grasslands relate to shifts in litter quantity and quality, labile C inputs, and microclimate effects when species are grown in mixture versus monoculture (Eviner 2001). Nonadditive effects of plant mixtures can also be mediated through shifts in the activity and distribution of other organisms that play key roles in biogeochemical cycling (Blair, Parmelee, and Beare 1990; Williams and Alexander 1991). For example, N and C dynamics in plant mixtures were nonadditive functions of the component monocultures because earthworms responded nonlinearly to the plant mixtures (Saetre 1998).

All of these examples demonstrate that the rates and interactions of biogeochemical cycles can best be understood by focusing on the composition of organisms and the traits they exhibit, not simply on species number, because combinations of specific organismal traits mediate elemental fluxes.

Interactions between Biodiversity and Biogeochemical Interactions

Ultimately, an interaction of species and biogeochemical cycles determines ecosystem processes, and species diversity can influence ecosystem responses to biogeochemical changes by influencing the pool of species that can respond to varying conditions. For example, high-diversity plant communities have a higher enhancement of net primary production (NPP) in response to elevated CO_2 (Niklaus et al. 2001a; Reich et al. 2001; He, Bazzaz, and Schmid 2002) and N (Fridley 2002; He, Bazzaz, and Schmid 2002) than do low-diversity communities. Plant richness, however, does not always enhance ecosystem CO_2 assimilation (Stocker et al. 1999), and species composition plays an important role in determining these responses. The diversity-induced enhancement of NPP in response to elevated CO_2 in a calcareous grassland only occurred in the early years of the experiment, when CO_2 increased growth of stress-tolerant, noncompetitive

species. These species decreased over time in the elevated CO_2 plots (Niklaus et al. 2001a), and with this shift in plant composition, the diversity-CO_2 interaction disappeared.

These studies clearly show that communities with high species richness are more likely to contain species that can positively respond to enhanced resource availability. A natural extension of this logic would suggest that a loss of species richness could compromise ecosystem function in response to environmental stresses owing to the presence of fewer species able to tolerate the stressful conditions. Many studies have shown that decreases in diversity in response to a single environmental stress do not compromise ecosystem function, because of the ability of other species to compensate for the function of the lost species. Several studies have shown, however, that these less diverse microbial communities cannot maintain ecosystem function in response to additional environmental stresses (Griffiths et al. 2000; Degens et al. 2001; Muller et al. 2002) and are also less able to respond to subsequent positive changes, such as additions of labile substrates (Muller et al. 2002). These results are particularly striking because all three of these examples are from soil microbial communities, which are assumed to contain ample diversity to buffer any change and still maintain function.

These studies emphasize that, although several species may be able to play the same ecosystem role under stable conditions, a diversity of organisms is critical for maintaining that ecosystem role under changing conditions, and loss of diversity can dramatically compromise ecosystem function. This decreased function occurs because species that have similar functions can have very different environmental tolerances. Thus one environmental stress can decrease diversity through selection for species with specific tolerances, compromising the ability of the remaining community to respond to another stress.

It is essential to consider the relative importance of changes in biogeochemical processes versus shifts in diversity on ecosystem processes. For example, there has been much debate over the importance of plant species richness to productivity. Although experimental evidence has indicated that species richness can positively affect production, cross-site comparisons of natural communities usually indicate that the productivity-diversity relationship is a bell-shaped curve (Huston 1997; Wardle 2001). In extreme resource-limited environments, both productivity and species richness tend to be low and are limited by the same resources. Both species richness and productivity increase in ecosystems with moderate resource availability. In systems with extremely high resource availability, productivity is high, but species richness tends to be low. In low-resource or extreme environments, there are not many organisms that can cope with the conditions that limit production. At the other extreme, high N availability in terrestrial environments strongly selects for species that are fast growing and highly com-

petitive. A similar trend would be expected in many aquatic systems in response to P availability. Over fluctuating conditions, a diversity of plants allows production to be somewhat stabilized by providing species that can tolerate these varying conditions. Sustained differences in environmental conditions, however, can strongly select for species that are best adapted to those conditions, decreasing diversity. These communities may be optimized to their current conditions but may also have less flexibility in the face of other environmental changes.

Conclusion

In this chapter we have given numerous examples where species composition and richness alter biogeochemical processes. In processes influenced by resource use, complementarity of species functions can account for the effects of species richness, but the strength of this effect is determined by the extent to which species differ in their functional traits. Overall, the composition of the biotic community plays a much stronger role than species richness in determining biogeochemical cycling. The importance of composition is further highlighted because shifts in the biotic community due to biogeochemical changes alter species richness through selection for certain species. Suites of organismal traits determine elemental stoichiometry and environmental tolerances of species, which then determine how element cycles interact. For example, plant species can differ significantly in their effects on environmental conditions and the stoichiometry of elements. These suites of traits greatly affect the activity and composition of the consumer communities. The elemental composition of the consumer community dictates the stoichiometry and rates of nutrient release from plant litter, and the processes mediated by the microbial community are sensitive to the relative availability of elements. Thus, organism-induced variation in nutrient forms and concentrations can differentially affect almost every biogeochemical flux.

The vast majority of research linking species diversity and ecosystem processes has focused on this relationship under a relatively constant set of conditions. In these experimental communities the effect of species richness on ecosystem processes saturates at a low species number, and species composition tends to have a larger effect than species richness. Ecological theory, and a handful of experiments that have tested it, show that over changing conditions, the maintenance of ecosystem processes depends on a diversity of species. Species have unique combinations of functions, environmental preferences, and species interactions, and this suite of traits determines how a species responds and maintains itself, its functions, and its interactions under different conditions. There is very little true redundancy in the overall role played by species when accounting for these suites of traits.

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Literature Cited

Aarssen, L. 1997. High productivity in grassland ecosystems: Effected by species diversity or productive species? *Oikos* 80:183–184.

Aber, J., J. Melillo, and C. McClaugherty. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Canadian Journal of Botany* 68:2201–2208.

Aerts, R., and F. S. Chapin. 2000. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research* 30:1–67.

Allen, W. C., P. B. Hook, J. A. Biederman, and O. R. Stein. 2002. Temperature and wetland plant species effects on wastewater treatment and root zone oxidation. *Journal of Environmental Quality* 31:1010–1016.

Andrews, J. A., R. Matamala, K. M. Westover, and W. H. Schlesinger. 2000. Temperature effects on the diversity of soil heterotrophs and the delta C-13 of soil-respired CO_2. *Soil Biology and Biochemistry* 32:699–706.

Arnolds, S. 1991. Decline of ectomycorrhizal fungi in Europe. *Agriculture Ecosystems and Environment* 35:209–244.

Balser, T., A. P. Kinzig, and M. K. Firestone. 2001. Linking microbial communities and ecosystem function. Pp. 265–357 in *The functional consequences of biodiversity*, edited by A. Kinzig, S. Pacala, and D. Tilman. Princeton: Princeton University Press.

Bardgett, R. D., J. L. Mawdsley, S. Edwards, P. J. Hobbs, J. S. Rodwell, and W. J. Davies. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. *Functional Ecology* 13:650–660.

Bardgett, R. D., and A. Shine. 1999. Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. *Soil Biology and Biochemistry* 31:317–321.

Beare, M., D. Coleman, D. Crossley, P. Hendrix, and E. Odum. 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant and Soil* 170:5–22.

Berendse, F., R. Aerts, and R. Bobbink. 1993. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. Pp. 104–121 in *Landscape ecology of a stressed environment*, edited by C. Vos and P. Opdam. London: Chapman and Hall.

Blair, J., R. Parmelee, and M. Beare. 1990. Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology* 71:1976–1985.

Bottner, P., M. Pansu, and Z. Sallih. 1999. Modelling the effect of active roots on soil organic matter turnover. *Plant and Soil* 2166:15–25.

Bressan, M., and M. G. Paoletti. 1997. Leaf litter decomposition and soil microarthropods affected by sulphur dioxide fallout. *Land Degradation and Development* 8:189–199.

Byers, J. E. 2002. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia* 130:146–156.

Caldwell, D. E., G. M. Wolfaardt, D. R. Korber, and J. R. Lawrence. 1997. Do bacterial communities transcend Darwinism? *Advances in Microbial Ecology* 15:105–191.

Caraco, N. F., and J. J. Cole. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecological Applications* 12:1496–1509.

Carcamo, H. A., and D. Parkinson. 2001. Localized acidification near sour gas processing plants: Are forest floor macro-invertebrates affected? *Applied Soil Ecology* 17:199–213.

Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–429.

Chapin, F. I., and C. Korner. 1996. Arctic and alpine biodiversity: Its patterns, causes, and ecosystem consequences. Pp. 7–32 in *Functional role of biodiversity: a global perspective*, edited by H. A. Mooney, J. Cushman, E. Medina, O. Sala, and E. Schulze. New York: John Wiley and Sons.

Chapin, F. I., E. Zavaleta, V. Eviner, R. Naylor, P. Vitousek, H. Reynolds, D. U. Hooper, S. Lavorel, O. Sala, S. Hobbie, M. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.

Chapin III, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233–260.

Chapin, F. S., and G. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66:564–576.

Chiariello, N., and C. Field. 1996. Annual grassland responses to elevated CO_2 in multiyear community microcosms. Pp. 139–155 in *Carbon dioxide, populations, and communities*, edited by C. Korner and F. A. Bazzaz. San Diego: Academic Press.

Christensen, K. K. 1999. Comparison of iron and phosphorus mobilization from sediments inhabited by Littorella uniflora and Sphagnum sp. at different sulfate concentrations. *Archiv für Hydrobiologie* 145:257–275.

Clements, W. 1994. Benthic invertebrate community responses to heavy metals in the upper Arkansas River basin, Colorado. *Journal of the North American Benthological Society* 13:30–44.

Clements, W., and P. Kiffney. 1995. The influence of elevation on benthic responses to heavy metals in Rocky Mountain streams. *Canadian Journal of Fisheries and Aquatic Science* 52:1966–1977.

Clements, W., D. Carlisle, J. Lazorchak, and P. Johnson. 2000. Heavy metals structure benthic communities in Colorado mountain streams. *Ecological Applications* 10:626–638.

Colombo, J., M. Cabello, and A. Arambarri. 1996. Biodegradation of aliphatic and aromatic hydrocarbons by natural soil microflora and pure cultures of imperfect and lignolitic fungi. *Environmental Pollution* 94:355–362.

De Boer, W., P. Klein Gunnewiek, and D. Parkinson. 1996. Variability of N mineralization and nitrification in a simple, simulated microbial forest soil community. *Soil Biology and Biochemistry* 28:203–211.

Degens, B. P., L. A. Schipper, G. P. Sparling, and L. C. Duncan. 2001. Is the microbial community in a soil with reduced catabolic diversity less resistant to stress or disturbance? *Soil Biology and Biochemistry* 33:1143–1153.

Del Rio, M., R. Font, C. Almela, D. Velez, R. Montoro, and A. D. Bailon. 2002. Heavy metals and arsenic uptake by wild vegetation in the Guadiamar River area after the toxic spill of the Aznalcollar mine. *Journal of Biotechnology* 98:125–137.

Dhillion, S. S., J. Roy, and M. Abrams. 1996. Assessing the impact of elevated CO_2 on soil microbial activity in a Mediterranean model ecosystem. *Plant and Soil* 187:333–342.

Dobranic, J. K., and J. C. Zak. 1999. A microtiter plate procedure for evaluating fungal functional diversity. *Mycologia* 91:756–765.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135–139.

Egerton-Warburton, L., and E. Allen. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10:484–496.

Egerton-Warburton, L., R. Graham, E. Allen, and M. Allen. 2001. Reconstruction of historical changes in mycorrhizal fungal communities under anthropogenic nitrogen deposition. *The Royal Society of London Proceedings B. Biological Sciences* 1484:2479–2848.

Elser, J. J., R. W. Sterner, E. Gorokhova, W. F. Fagan, T. A. Markow, J. B. Cotner, J. F. Harrison, S. E. Hobbie, G. M. Odell, and L. J. Weider. 2000. Biological stoichiometry from genes to ecosystems. *Ecology Letters* 3:540–550.

Engelaar, W. M. H. G., J. C. Symens, H. J. Laanbroek, and C. W. M. Blom. 1995. Preservation of nitrifying capacity and nitrate availability in waterlogged soils by radial oxygen loss from roots of wetland plants. *Biology and Fertility of Soils* 20:243–248.

Eviner, V. T. 2001. Linking plant community composition and ecosystem dynamics: Interactions of plant traits determine the ecosystem effects of plant species and plant species mixtures. Ph.D. diss., Department of Integrative Biology, University of California, Berkeley.

Eviner, V. T., and F. I. Chapin. 2001. The effects of California grassland species on their ecosystems: Implications for sustainable agriculture and rangeland management. *California Agriculture* 55:254–259.

———. 2003. The role of species richness and composition in determining ecosystem processes. *American Naturalist,* in review.

Fazzolari, E., B. Nicolardot, and J. C. Germon. 1998. Simultaneous effects of increasing levels of glucose and oxygen partial pressures on denitrification and dissimilatory nitrate reduction to ammonium in repacked soil cores. *European Journal of Soil Biology* 34:47–52.

Finlay, B., S. Maberly, and Cooper J. I. 1997. Microbial diversity and ecosystem function. *Oikos* 80:209–213.

Finzi, A., and C. Canham. 1998. Non-additive effects of litter mixtures on net N mineralization in a southern New England forest. *Forest Ecology and Management* 105:129–136.

Fridley, J. D. 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia* 132:271–277.

Goldberg, D., and T. Miller. 1990. Effects of different resource additions on species-diversity in an annual plant community. *Ecology* 71:213–225.

Grayston, S. J., C. D. Campbell, J. L. Lutze, and R. M. Gifford. 1998. Impact of

elevated CO_2 on the metabolic diversity of microbial communities in N-limited grass swards. *Plant and Soil* 203:289–300.

Griffiths, B. S., K. Ritz, R. D. Bardgett, R. Cook, S. Christensen, F. Ekelund, S. J. Sorensen, E. Baath, J. Bloem, P. C. de Ruiter, J. Dolfing, and B. Nicolardot. 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: An examination of the biodiversity-ecosystem function relationship. *Oikos* 90:279–294.

Groffman, P. M., and P. J. Bohlen. 1999. Soil and sediment biodiversity: Cross-system comparisons and large-scale effects. *BioScience* 49:139–148.

Grosse, W., K. Jovy, and H. Tiebel. 1996. Influence of plants on redox potential and methane production in water-saturated soil. *Hydrobiologia* 340:93–99.

Harte, J., M. S. Torn, F. Chang, B. Feifarek, A. Kinzig, R. Shaw, and K. Shen. 1995. Global warming and soil microclimate—results from a meadow-warming experiment. *Ecological Applications* 5:132–150.

Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community—results of a climate-warming experiment. *Science* 267:876–880.

He, J. S., F. A. Bazzaz, and B. Schmid. 2002. Interactive effects of diversity, nutrients and elevated CO_2 on experimental plant communities. *Oikos* 97:337–348.

Hector, A., A. J. Beale, A. Minns, S. J. Otway, and J. H. Lawton. 2000. Consequences of the reduction of plant diversity for litter decomposition: Effects through litter quality and microenvironment. *Oikos* 90:357–371.

Hobbie, S. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* 66:503–522.

Hoffman, B. D., A. D. Griffiths, and A. N. Andersen. 2000. Responses of ant communities to dry sulfur deposition from mining emissions in semi-arid tropical Australia, with implications for the use of functional groups. *Austral Ecology* 25:653–663.

Holtan-Hartwig, L., M. Bechmann, T. R. Hoyas, R. Linjordet, and L. R. Bakken. 2002. Heavy metals tolerance of soil denitrifying communities: N_2O dynamics. *Soil Biology and Biochemistry* 34:1181–1190.

Hooper, D., and P. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* 68:121–149.

Huenneke, L., S. Hamburg, R. Koide, H. A. Mooney, and P. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71:478–491.

Hungate, B. A., C. H. Jaeger, G. Gamara, F. S. Chapin, and C. B. Field. 2000. Soil microbiota in two annual grasslands: Responses to elevated atmospheric CO_2. *Oecologia* 124:589–598.

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

Inouye, R., N. Huntly, D. Tilman, J. Tester, M. Stillwell, and K. Zinnel. 1987. Old-field succession on a Minnesota sand plain. *Ecology* 68:12–26.

Inouye, R., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 years of nitrogen addition. *Ecology* 76:1872–1887.

Janzen, R., J. Dormaar, and W. McGill. 1995. A community-level concept of controls on decomposition processes: Decomposition of barley straw by *Phanerochaete chrysosporium* or *Phlebia radiata* in pure or mixed culture. *Soil Biology and Biochemistry* 27:173–179.

Jones, M. and S. Winans. 1967. Subterranean clover vs. nitrogen-fertilized annual grasslands: Botanical composition and protein content. *Journal of Range Management* 20:8–12.

Kandeler, E., D. Tscherko, R. D. Bardgett, P. J. Hobbs, C. Kampichler, and T. H. Jones. 1998. The response of soil microorganisms and roots to elevated CO_2 and temperature in a terrestrial model ecosystem. *Plant and Soil* 202:251–262.

Knops, J. M. H., D. Wedin, and D. Tilman. 2001. Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia* 126:429–433.

Kozdroj, J., and J. D. van Elsas. 2001. Structural diversity of microorganisms in chemically perturbed soil assessed by molecular and cytochemical approaches. *Journal of Microbiological Methods* 43:197–212.

Landi, L., L. Badalucco, F. Pomare, and P. Nannipieri. 1993. Effectiveness of antibiotics to distinguish the contributions of fungi and bacteria to net nitrogen mineralization, nitrification, and respiration. *Soil Biology and Biochemistry* 25:1771–1778.

Lasat, M. M. 2002. Phytoextraction of toxic metals: A review of biological mechanisms. *Journal of Environmental Quality* 31:109–120.

Lawley, R., E. Newman, and R. Campbell. 1982. Abundance of endomycorrhizas and root-surface microorganisms on three grasses grown separately and in mixtures. *Soil Biology and Biochemistry* 14:237–240.

Lawley, R., R. Campbell, and E. Newman. 1983. Composition of the bacterial flora of the rhizosphere of three grassland plants grown separately and in mixtures. *Soil Biology and Biochemistry* 15:605–607.

Leadley, P. W., and C. Korner. 1996. Effects of elevated CO_2 on plant species dominance in a highly diverse calcareous grassland. Pp. 159–175 in *Carbon dioxide, populations, and communities,* edited by C. Korner and F. A. Bazzaz. San Diego: Academic Press.

Leadley, P. W., P. A. Niklaus, R. Stocker, and C. Korner. 1999. A field study of the effects of elevated CO_2 on plant biomass and community structure in a calcareous grassland. *Oecologia* 118:39–49.

Lilleskov, E., T. Fahey, and G. Lovett. 2001. Ectomycorrhizal fungi aboveground community changes over an atmospheric deposition gradient. *Ecological Applications* 11:397–401.

Lilleskov, E., T. Fahey, T. Horton, and G. Lovett. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology* 83:104–115.

Lodhi, M., and K. Killingbeck. 1980. Allelopathic inhibition of nitrification and nitrifying bacteria in ponderosa pine (*Pinus ponderosa* Dougl.) community. *American Journal of Botany* 67:1423–1429.

Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model. *Proceedings of the National Academy of Sciences of the United States of America* 95:5632–5636.

Loreau, M. 2000. Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos* 91:3–17.

Mack, M. C. 1998. Effects of exotic grass invasion on ecosystem nitrogen dynamics in a Hawaiian woodland. Ph.D. diss., University of California, Berkeley.

Mafongoya, P., P. Barak, and J. Reed. 2000. Carbon, nitrogen, and phosphorus mineralization of tree leaves and manure. *Biology and Fertility of Soils* 30:298–305.

Maithani, K., A. Arunachalam, R. Tripathi, and H. Pandey. 1998. Influence of leaf litter

quality on N mineralization in soils of subtropical humid forest regrowths. *Biology and Fertility of Soils* 27:44–50.
Martin, T. L., J. T. Trevors, and N. K. Kaushik. 1999. Soil microbial diversity, community structure, and denitrification in a temperate riparian zone. *Biodiversity and Conservation* 8:1057–1078.
McGill, W., and C. Cole. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* 26:267–286.
McGrady-Steed, J., P. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390:162–165.
McNaughton, S. 1977. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. *American Naturalist* 111:515–525.
Melillo, J., J. Aber, and J. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
Mosier, A. R., M. A. Bleken, P. Chaiwanakupt, E. C. Ellis, J. R. Freney, R. B. Howarth, P. A. Matson, K. Minami, R. Naylor, K. N. Weeks, and Z. L. Zhu. 2001. Policy implications of human-accelerated nitrogen cycling. *Biogeochemistry* 52:281–320.
Mueller, T., L. Jensen, E. Nielsen, and J. Magid. 1998. Turnover of carbon and nitrogen in a sandy loam soil following incorporation of chopped maize plants, barley straw, and blue grass in the field. *Soil Biology and Biochemistry* 30:561–571.
Mulder, C. P. H., D. D. Uliassi, and D. F. Doak. 2001. Physical stress and diversity-productivity relationships: The role of positive interactions. *Proceedings of the National Academy of Sciences of the United States of America* 98:6704–6708.
Muller, A. K., K. Westergaard, S. Christensen, and S. J. Sorensen. 2001. The effect of long-term mercury pollution on the soil microbial community. *Fems Microbiology Ecology* 36:11–19.
Muller, A. K., K. Westergaard, S. Christensen, and S. J. Sorensen. 2002. The diversity and function of soil microbial communities exposed to different disturbances. *Microbial Ecology* 44:49–58.
Naeem, S., L. Thompson, S. Lawler, J. H. Lawton, and R. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–737.
Naeem, S., K. Hakansson, J. Lawton, M. Crawley, and L. Thompson. 1995. Biodiversity and plant productivity in a model assemblage of plant species. *Oikos* 76:259–264.
Naeem, S., and S. B. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–509.
Newman, E., R. Campbell, P. Christie, A. Heap, and R. Lawley. 1979. Root microorganisms in mixtures and monocultures of grassland plants. Pp. 161–173 in *The soil-root interface,* edited by J. Harley and R. Russell. London: Academic Press.
Niklaus, P. A., P. W. Leadley, B. Schmid, and C. Korner. 2001a. A long-term field study on biodiversity x elevated CO_2 interactions in grassland. *Ecological Monographs* 71:341–356.
Niklaus, P. A., E. Kandeler, P. W. Leadley, B. Schmid, D. Tscherko, and C. Korner. 2001b. A link between plant diversity, elevated CO_2, and soil nitrate. *Oecologia* 127:540–548.
Nilsson, M., D. Wardle, and A. Dahlberg. 1999. Effects of plant litter species composition and diversity on the boreal forest plant-soil system. *Oikos* 86:16–26.
O'Neill, E. 1994. Responses of soil biota to elevated atmospheric carbon dioxide. *Plant and Soil* 165: 55–65.

Owensby, C. E., J. M. Ham, A. K. Knapp, and L. M. Auen. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Global Change Biology* 5:497–506.

Palm, C., and P. Sanchez. 1991. Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. *Soil Biology and Biochemistry* 23:83–88.

Palmer, M., A. Covich, B. Finlay, J. Gilbert, K. Hyde, R. Johnson, T. Kairesalo, S. Lake, C. Lovell, R. Naiman, C. Ricci, F. Sabater, and D. Strayer. 1997. Biodiversity and ecosystem processes in freshwater sediments. *Ambio* 26:571–577.

Paul, E., and F. Clark. 1995. *Soil microbiology and biochemistry.* San Diego: Academic Press.

Phillips, R. L., D. R. Zak, W. E. Holmes, and D. C. White. 2002. Microbial community composition and function beneath temperate trees exposed to elevated atmospheric carbon dioxide and ozone. *Oecologia* 131:236–244.

Potvin, C., and L. Vassuer. 1997. Long-term CO_2 enrichment of a pasture community: Species richness, dominance, and succession. *Ecology* 78:666–677.

Price, M. V., and N. M. Waser. 2000. Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications* 10:811–823.

Rao, M., and R. Willey. 1980. Evaluation of yield stability in intercropping: Studies on sorghum/pigeonpea. *Experimental Agriculture* 16:105–116.

Reed, F. 1977. Plant species number, biomass accumulation, and productivity of a differentially fertilized Michigan old-field. *Oecologia* 30:45–53.

Reich, P. B., J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S. Naeem, D. Bahauddin, G. Hendrey, S. Jose, K. Wrage, J. Goth, and W. Bengston. 2001. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. *Nature* 410:809–812.

Rillig, M. C., K. M. Scow, J. N. Klironomos, and M. F. Allen. 1997. Microbial carbon-substrate utilization in the rhizosphere of Gutierrezia sarothrae grown in elevated atmospheric carbon dioxide. *Soil Biology and Biochemistry* 29:1387–1394.

Rozgaj, R., and M. Glancersoljam. 1992. Total degradation of 6-aminonapthalene-2-sulfonic acid by a mixed culture consisting of different bacterial genera. *Fems Microbiology Ecology* 86:229–235.

Saetre, P. 1998. Decomposition, microbial community structure, and earthworm effects along a birch-spruce soil gradient. *Ecology* 79: 843–846.

Salemaa, M., I. Vanha-Majamaa, and J. Derome. 2001. Understory vegetation along a heavy-metal pollution gradient in SW Finland. *Environmental Pollution* 112:339–350.

Saleska, S. R., J. Harte, and M. S. Torn. 1999. The effect of experimental ecosystem warming on CO_2 fluxes in a montane meadow. *Global Change Biology* 5:125–141.

Sallih, Z., and P. Bottner. 1988. Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biology and Fertility of Soils* 7:67–70.

Schimel, J. 1995. Ecosystem consequences of microbial diversity and community structure. Pp. 239–254 in *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences,* edited by F. Chapin and C. Koerner. Berlin: Springer-Verlag.

Schimel, J., K. Van Cleve, R. Cates, T. Clausen, and P. Reichardt. 1996. Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on

microbial activity in taiga floodplain soil: Implications for changes in N cycling during succession. *Canadian Journal of Botany* 74:84–90.
Schlesinger, W. H. 1997. *Biogeochemistry.* San Diego: Academic Press.
Scott, N., and D. Binkley. 1997. Foliage litter quality and annual net N mineralization: Comparison across North American forest sites. *Oecologia* 111:151–159.
Shaw, M. R., and J. Harte. 2001. Control of litter decomposition in a subalpine meadow-sagebrush steppe ecotone under climate change. *Ecological Applications* 11:1206–1223.
Silver, W. L., D. J. Herman, and M. K. Firestone. 2001. Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. *Ecology* 82:2410–2416.
Singh, J., M. Agrawal, and D. Narayan. 1994. Effect of power-plant emissions on plant community structure. *Ecotoxicology* 3:110–122.
Solanius, P. 1981. Metabolic capabilities of forest soil microbial populations with reduced species diversity. *Soil Biology and Biochemistry* 13:1–10.
Spehn, E. M., J. Joshi, B. Schmid, M. Diemer, and C. Korner. 2000a. Aboveground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology* 14:326–337.
Spehn, E. M., J. Joshi, B. Schmid, J. Alphei, and C. Korner. 2000b. Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. *Plant and Soil* 224:217–230.
Sternberg, M., V. K. Brown, G. J. Masters, and I. P. Clarke. 1999. Plant community dynamics in a calcareous grassland under climate change manipulations. *Plant Ecology* 143:29–37.
Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers, and nutrient cycling in pelagic ecosystems. *Biogeochemistry* 17:49–67.
Stocker, R., C. Korner, B. Schmid, P. A. Niklaus, and P. W. Leadley. 1999. A field study of the effects of elevated CO_2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology* 5:95–105.
Stump, L., and D. Binkley. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. *Canadian Journal of Forest Research* 23:492–502.
Taylor, B., D. Parkinson, and W. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology* 70:97–104.
Taylor, B., C. Prescott, W. Parsons, and D. Parkinson. 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. *Canadian Journal of Botany* 69:2242–2250.
Thibault, J., J. Fortin, and W. Smirnoff. 1982. In vitro allelopathic inhibition of nitrification by balsam poplar and balsam fir. *American Journal of Botany* 69:676–679.
Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities.* Monographs in Population Biology. Princeton: Princeton University Press.
Tilman, D., D. Wedin, and J. Knops. 1996. Effects of biodiversity on nutrient retention and productivity in grasslands. *Nature* 379:718–720.
Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
Tilman, D. 1999. Global environmental impacts of agricultural expansion: The need for

sustainable and efficient practices. *Proceedings of the National Academy of Sciences of the United States of America* 96:5995–6000.

van der Heijden, M., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability, and productivity. *Nature* 396:69–72.

van Ginkel, J. H., A. Gorissen, and J. A. Van Veen. 1996. Long-term decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Journal of Environmental Quality* 25:1122–1128.

van Vuuren, M., R. Aerts, F. Berendse, and W. de Visser. 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. *Biogeochemistry* 16:151–166.

Wardle, D. A., K. I. Bonner, and G. M. Barker. 2000. Stability of ecosystem properties in response to aboveground functional group richness and composition. *Oikos* 89:11–23.

Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invisibility: Evidence of a biological mechanism or a consequence of sampling effect? *Oikos* 95:161–170.

Wardle, D., and K. Nicholson. 1996. Synergistic effects of grassland plant species on soil microbial biomass and activity: Implications for ecosystem-level effects of enriched plant diversity. *Functional Ecology* 10:410–416.

Wardle, D., K. Bonner, and K. Nicholson. 1997. Biodiversity and plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79:247–258.

Wedin, D., and D. Tilman. 1990. Species effects on nitrogen cycling: A test with perennial grasses. *Oecologia* 84:433–441.

Wedin, D., and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia* 96:186–192.

Willems, J. H., R. K. Peet, and L. Bik. 1993. Changes in chalk grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science* 4:203–212.

Williams, B., and C. Alexander. 1991. Interactions on mixing litters from beneath sitka spruce and scots pine and the effects on microbial activity and N-mineralization. *Soil Biology and Biochemistry* 23:71–75.

Willison, T. W., M. S. O'Flaherty, P. Tlustos, K. W. T. Goulding, and D. S. Powlson. 1997. Variations in microbial populations in soils with different methane uptake rates. *Nutrient Cycling in Agroecosystems* 49:85–90.

Wilson, S. D., and D. Tilman. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* 88:61–71.

Wolfaardt, G. M., J. R. Lawrence, R. Robarts, and D. E. Caldwell. 1994. The role of interactions, sessile growth, and nutrient amendments on the degradative efficiency of a microbial consortium. *Canadian Journal of Microbiology* 40:331–340.

Yin, S. X., D. Chen, L. M. Chen, and R. Edis. 2002. Dissimilatory nitrate reduction to ammonium and responsible microorganisms in two Chinese and Australian paddy soils. *Soil Biology and Biochemistry* 34:1131–1137.