Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks

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WE ASSESS THE EVIDENCE FOR CORRELATION BETWEEN ABOVEGROUND AND BELOWGROUND DIVERSITY AND CONCLUDE THAT A VARIETY OF MECHANISMS COULD LEAD TO POSITIVE, NEGATIVE, OR NO RELATIONSHIP—DEPENDING ON THE STRENGTH AND TYPE OF INTERACTIONS AMONG SPECIES

Understanding linkages between the diversity of organisms above ground and that of organisms below ground constitutes an important challenge for our knowledge of how ecological communities and processes are determined at both local and regional scales. Furthering this understanding may render information critical to the

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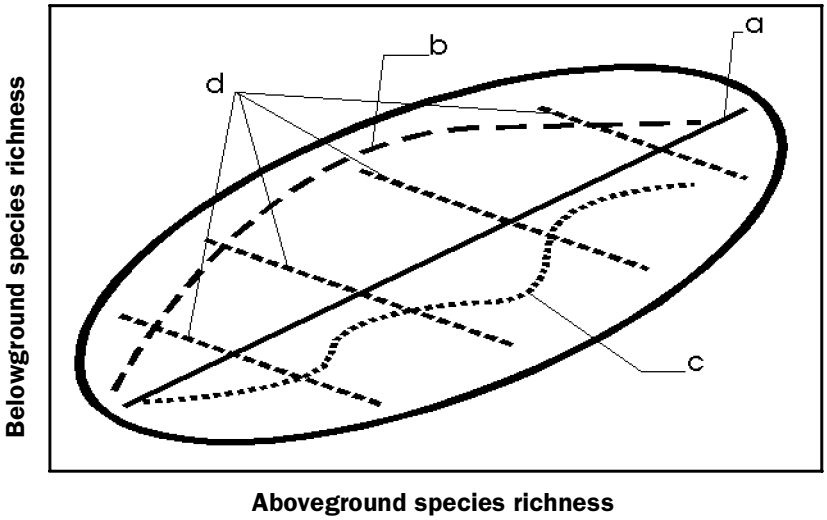

Figure 1. Hypothetical relationships between aboveground and belowground diversity at local and regional scales. A positive correlation between aboveground and belowground diversity across broadscale determinants of climate, soils, and disturbance history includes an envelope of many potential relationships: positive linear correlation (a), asymptotic increase (b), step functions or thresholds (c), or even locally negative correlations despite broadscale positive correlations (d). A better understanding of the underlying mechanisms at both local and regional scales is necessary to understand controls of biological diversity and implement effective conservation efforts.

conservation of species, ecosystems, and the services they provide to humanity. Because belowground diversity is often difficult to measure and many organisms are poorly understood or have yet to be described, discerning patterns of correlation among aboveground and belowground species, and the mechanisms causing these patterns, could provide a proxy for developing approaches for protecting belowground species. In addition, linkages between diversity above ground and below ground may be functionally important at the ecosystem scale in terms of the maintenance and stability of ecosystem processes and the persistence of keystone species or other species with strong ecosystem effects (Chapin et al. 1997, Groffman and Bohlen 1999, Wall and Moore 1999). These are immediate concerns applicable to issues of global change, including tradeoffs between development and ecological sustainability (Wolters et al. 2000).

An international workshop convened in October 1998 under the auspices of the SCOPE (Scientific Committee on Problems of the Environment) Committee on Soil and Sediment Biodiversity and Ecosystem Functioning sought to address such questions about relationships between aboveground and belowground diversity. This article takes a two-step approach to evaluating these relationships. First we review the evidence for correlations between diversity of aboveground and belowground organisms, both on local and across larger biogeographical scales. If correlations exist, we ask whether they result from direct linkages among groups of organisms above and below the surface. Second, where cause-and-effect relationships are apparent, we synthesize what is known about the mechanisms involved in those relationships.

General relationships and explanations

Is high aboveground diversity, either collectively or for specific taxa, correlated with high belowground diversity? Where there are broadscale correlations of aboveground and belowground biodiversity, do these patterns hold at more local scales? For example, because the shape of trajectories for any one habitat or locality that lies within such broad patterns could vary substantially (Figure 1), can we predict the pattern of change in diversity above ground and below ground during natural and anthropogenically imposed disturbances? We review both data that support and data that oppose correlations between aboveground and belowground diversity; we then explore possible explanations for the patterns (or lack thereof). Correlation of aboveground and belowground diversity does not necessarily imply mechanistic linkages, but it is a first step in assessing whether such linkages exist.

Before reviewing the data, however, we need to address several issues raised by the different scales of organisms and processes. The size of various organisms and their spheres of influence vary over several orders of magnitude, temporally and spatially (Beare et al. 1995) (Figure 2). For example, the processes influencing community composition both above ground and below ground might involve daily and other short-term fluctuations in abiotic conditions, seasonal fluctuations in phenology (Strong et al. 1984), yearly variations in climate, decadal or multicentury influences of succession, or geologic (more than a million years) evolutionary relationships (Ricklefs and Schluter 1993). Moreover, the various processes that link aboveground and belowground systems may operate at different scales of biodiversity, influencing, for example, genetic variation within and among populations, species richness and composition, diversity of functional groups, or ecosystem patterns at the landscape scale (Wolters 1997). Belowground, a species approach is not always practical, especially for microbial and many microinvertebrate taxa to which the traditional species concepts are difficult to apply. In such cases, taxanomic groups are commonly lumped into functional groups defined by their role in a community or ecosystem process (de Ruiter et al. 1994, Brussaard et al. 1997, Smith et al. 1997). These issues of scale—spatial, temporal, functional, and phylogenetic—can confound patterns of diversity and the inference of process from those patterns. Together they may negate any single, simple mechanism as the prime determinant of either aboveground or belowground diversity.

Therefore, measurements and mechanisms involved in comparisons among taxa should be closely matched.

Positive correlations

Numbers of species above ground and below ground may be correlated when taxa in both realms respond similarly to the same or correlated environmental driving variables, especially across large gradients of disturbance, climate, soil conditions, or geographic area. In such cases, diversity in the two domains is not necessarily causally linked. Numerous examples illustrate that conversion of natural ecosystems to agriculture decreases both plant diversity aboveground and soil macrofaunal diversity belowground (Lavelle et al. 1994, Lavelle 1996, Wardle and Lavelle 1997). Coffee plantations exhibit a range of plant diversity, depending on management; as plantations are simplified aboveground, they show a significant decline in ant (Perfecto and Snelling 1995) and scarabaeid beetle (Nestel et al. 1993) diversity. Disturbance from land use change decreases species richness and abundance for plants, termites (Eggleton et al. 1997), and nematodes (Freckman and Ettema 1993, Wasilewska 1997). In relict arctic–alpine communities, diversity of endemic and relic plant species is positively correlated with high species richness of endemic soil fauna (Collembola, Acarina, Diplopoda, etc.). These plants and soil animal species persist together because of extreme microclimatic conditions (Rusek 2000). In other cases, as with soil microbes, simplifying the plant community leads to changes in microbial community composition or relative abundance despite little change in microbial diversity at the plot scale (Wardle et al. 1999b).

Similarly, species diversity of different taxa may be correlated across different sites because of island biogeographic effects resulting from the size of suitable habitat fragments and their distance from sources of colonization. Such patterns could arise because of factors associated with a greater sampling area (that is, an increase in the number of individuals sampled, more habitat types, or larger population sizes), in addition to—or instead of—direct ecological interactions and high concentrations of species at certain sites (Rosenzweig 1995). The diversity of various taxa on different islands may also be influenced by island age, with older sites having greater species richness resulting from more time for both immigration and speciation (Borges and Brown 1999).

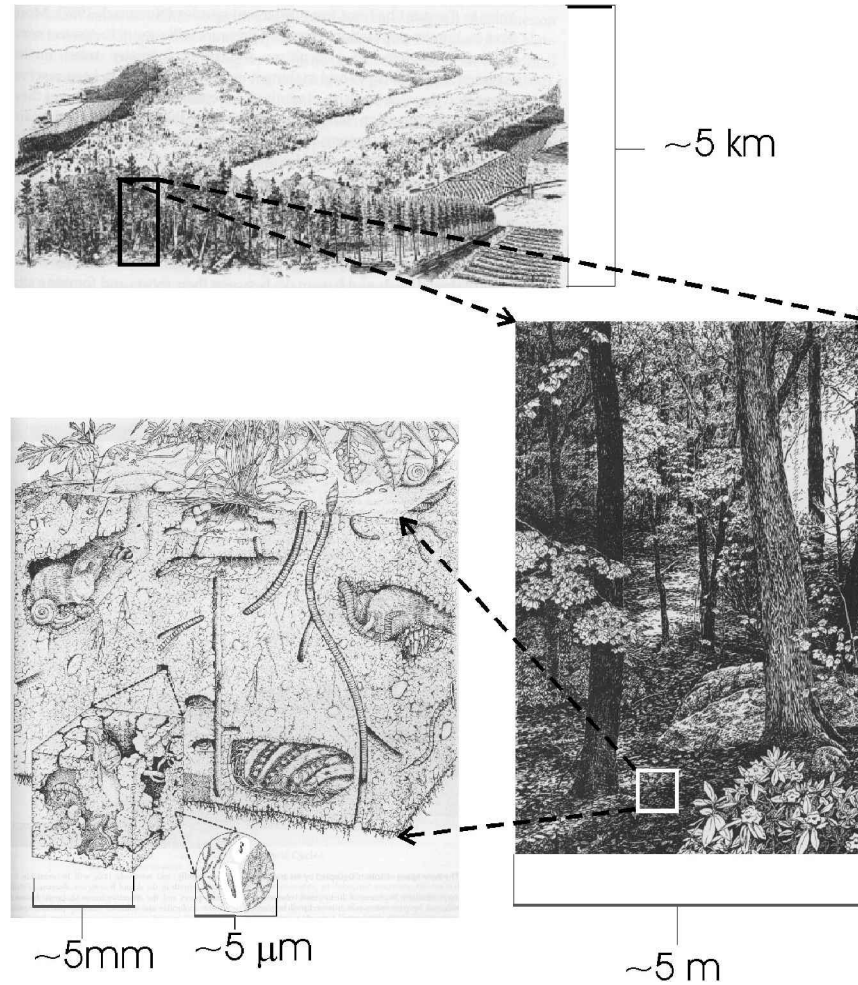

Figure 2. Scales of influence for aboveground and belowground diversity. The scales of organisms and biotic interactions involving aboveground and belowground diversity vary over several orders of magnitude, as do gradients in physical properties. Microscale differences in responses and resources among aboveground and belowground taxa may lead to less correlation between aboveground and belowground diversity at the local scale than there is across broad gradients. To understand patterns of diversity above ground and below ground, it is necessary to keep both spatial hierarchy and hierarchy of determinants explicit. Landscape and forest pictures reproduced with permission of Blackwell Science from Hunter (1996), © 1996, A. Sulzer, artist. Soil profile picture reproduced with permission of **National Geographic**, ***as modified from Gibbons (1984), © 1984, N. Seidler, artist.***

The numbers of species above ground and below ground may be correlated also when direct ecological linkages exist, in which case the diversity is considered to be causally related. For example, aboveground diversity might promote belowground diversity—or vice versa—by increasing the variety of food resources (litter quality and composition), the range of environmental conditions (temperature, humidity), or the structural complexity of the habitat (Anderson 1994).

Aboveground effects on belowground diversity.

High diversity in plant species can result in high diversity of

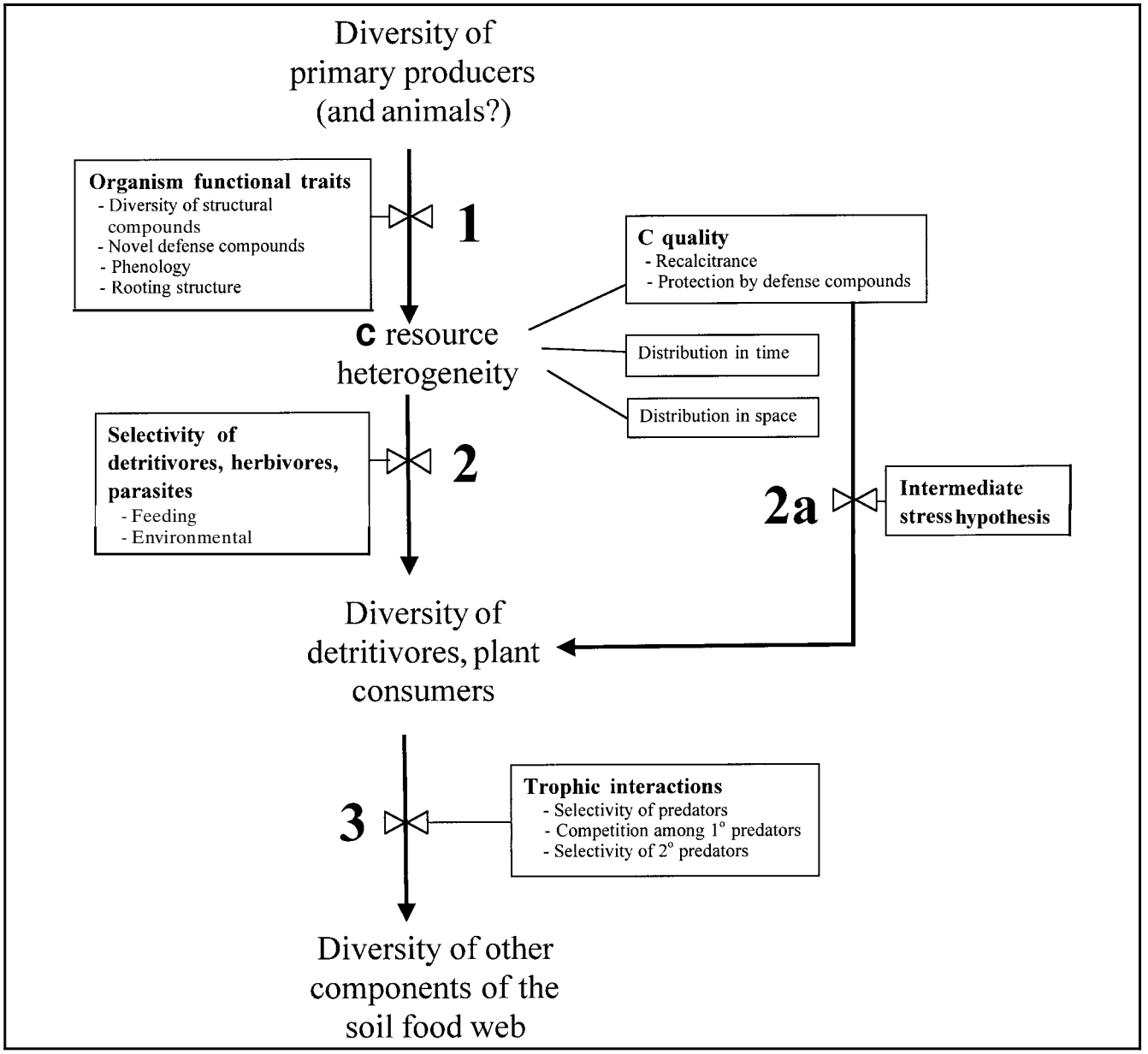

Figure 3. Steps in the hypothesis that increased heterogeneity of carbon (C) substrates from aboveground organisms will positively influence belowground diversity. This mechanism postulates strong bottom-up control of diversity in belowground communities; it should be tested in the context of other potential (e.g., top-down) controls (Hunter and Price 1992).

Step 1. Diversity of primary producers leads to diversity of C inputs belowground. The critical link in this step is how taxonomic diversity maps onto C resource heterogeneity. Except in heavily grazed ecosystems where aboveground herbivores provide large quantities of high quality food for decomposers (McNaughton 1985, Ruess and Seagle 1994, Frank and Groffman 1998), plants dominate aboveground carbon inputs. Aboveground animals could also modify C inputs via herbivory effects on the composition and diversity of plant communities. The relationship between taxonomic diversity and C resource diversity depends on several functional traits of the species present, including chemical composition of live and dead organisms, their distribution in space (e.g., differences in rooting depth; Brown and Gange 1989, Müeller 1989), and their distribution in time (i.e., phenology; Myers et al. 1997).

Step 2. Carbon resource heterogeneity leads to diversity of herbivores and detritivores. The critical link is the selectivity of the primary heterotrophs. Specialization can vary widely. We hypothesize that the degree of specialization of detritivores is roughly bell shaped, with relatively few species showing either high feeding specialization or complete feeding generalization, while the majority show an intermediate level of food selection. Such a distribution may not hold for other groups—e.g., herbivores (Strong et al. 1984) and plant parasites, which tend to be more specific. A bell-shaped distribution of selectivity would preclude a 1:1 mapping of C substrate to species of decomposer or detritivore. However, overall belowground diversity would still be expected to increase with number of C substrates (e.g., McArthur et al. 1988).

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litter quality or litter types entering the belowground subsystem. This resource heterogeneity can lead to a greater diversity of decomposers and detritivores (Anderson 1978, Tian et al. 1997, Sulkava and Huhta 1998) (Figure 3). Selective association of particular species with particular litter types has been shown for fungi (Widden 1986), Collembola (Klironomos et al. 1992), and millipedes (Dangerfield and Telford 1996). A survey of litter-feeding mollusks across forest types indicated a significant correlation between floristic diversity—and, presumably, diversity of carbon inputs—and mollusk diversity (Barker and Mayhill 1999). Root herbivore diversity can be related to the diversity of host plants (House 1989), and genetic diversity of the soil bacterium *Burkholderia cepacia* increases with increasing heterogeneity of organic substrates (McArthur et al. 1988).

The "first link" hypothesis of Lavelle et al. (1995) proposes that plant diversity, because of production of diverse root exudates, can lead to increased diversity of mutualistic soil microflora, the first link of a cascade of effects resulting in increased diversity of other soil animal groups as well. Carbon substrate heterogeneity may be related to plant taxonomic diversity when the presence of important plant defense compounds is linked to particular plant taxa, with consequences for the diversity of selective aboveground (Strong et al. 1984) and belowground (Andersen 1987) herbivores. In other cases, however, belowground diversity is closely linked to the diversity of resource types, independent of plant species richness. For example, a single species of tree could result in greater resource heterogeneity than might several species of grasses (Wardle et al. 1999b).

In addition to responding to heterogeneity of food sources, soil microarthropod diversity can be significantly related to microhabitat diversity (Wardle and Lavelle 1997, Sulkava and Huhta 1998). Where low-quality plant litter decomposes slowly to form deep organic layers with complex structure, this structural heterogeneity in turn promotes the development of diverse surface-living communities (Anderson 1978). In comparisons of single- and mixed-species litter in the southern Appalachian mountains, Hansen and Coleman (1998) observed that certain mites in the family Phthiracaridae were most prevalent in oak litter (especially in the leaf petioles), compared with other litter types, because of enhanced physical protection. They also found that more diverse assemblages of Oribatid mites had significantly faster litter decomposition rates in mixed-species litters than in single-species litters. However, there may be a tradeoff between the food and shelter influences that aboveground litter has on the diversity of belowground organisms: Greater consumption of litter decreases the structural integrity that suits it for use as persistent shelter.

Grazing animals (vertebrate and invertebrate) that affect vegetation diversity may modify insect diversity below ground (Brown and Gange 1989). Holometabolous herbivorous insects are a special case, because the adults of many species feed above ground and the larvae feed on roots. Factors such as plant species and structural diversity above ground, which are often related to diversity of aboveground insect species (Southwood et al. 1979), therefore may have important implications for belowground insect diversity as well.

Belowground effects on aboveground diversity.

A high diversity of resources and species in soil could feed back to a high diversity above ground, where certain species or functional groups are closely linked to groups below ground. For example, van der Heijden et al. (1998) found a positive correlation between the diversity of endomycorrhizal fungal species and plant diversity, potentially because different species of fungi infect different species of plants to different degrees, although alternative explanations exist for the patterns they observed (Wardle 1999). However, this pattern does not hold at the scale of functional types of mycorrhizae: Low-diversity arbuscular mycorrhizal communities can be associated with high diversity of plants, and high-diversity ectomycorrhizal communities can be associated with low diversity of plants (Allen et al. 1995).

Belowground communities also affect nutrient availability and detritus buildup. Feedbacks through these mechanisms could influence the diversity of aboveground communities, although evidence for such feedback is mixed. Laakso and Setälä (1999) found that one of the saprophagous mesofaunal species they manipulated in artificial food webs in microcosms (the enchytraeid *Cognettia sphagnetorum*) stimulated plant growth and was functionally irreplaceable because

Alternative step 2. Carbon resource quality, rather than heterogeneity, leads to diversity of detritivores. The critical link is the analogy of intermediate C resource quality to the intermediate stress hypothesis (Connell 1978, Grime 1979). If diversity is maximized at intermediate levels of environmental stress, then at some intermediate level of C resource quality (decomposability), the diversity of omnivorous detritivores and decomposers will be maximized in any given community. At low digestibility of C resources, only a few species can use the substrate; at high digestibility, a few species are able to outcompete the rest. Application of the intermediate stress hypothesis in this way is speculative, although circumstantial evidence for it exists at the scale of a decomposing leaf for fungal diversity (Frankland 1981). One difficulty is that information on bacterial species richness in most ecosystems is quite limited.

Step 3. Diversity of detritivores or belowground herbivores leads to diversity of organisms at higher trophic levels in belowground food webs. The critical link is trophic interactions. If top-down controls are stronger than bottom-up controls in belowground food webs, patterns of predation in belowground food webs may counterbalance effects of C resource heterogeneity (Hunter and Price 1992, de Ruiter et al. 1995). To further complicate matters, top-down control could arise from predation by aboveground animals because aboveground and belowground food webs can be strongly linked in upper trophic levels.

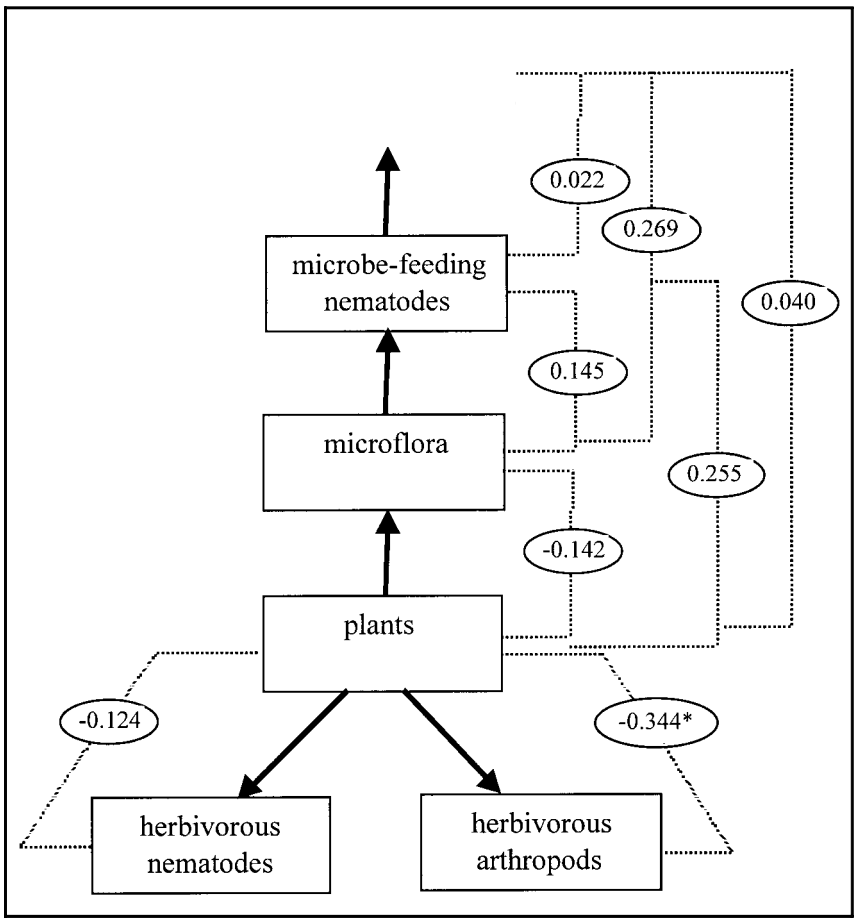

Figure 4. Diagram of a belowground food web showing correlations among Shannon–Wiener diversity indexes of various trophic groups after removal of different plant functional groups. Most correlations are low and not significant because diversity of belowground taxa responded more to changes in plant functional composition than to changes in plant alpha-diversity. The correlation coefficient denoted with a star (*) is significant at* P < *0.05. Reproduced from Wardle et al. (1999a) with permission from the Ecological Society of America.

no other species combinations of mesofauna achieved the same stimulatory effects. In addition, removal of specific belowground top predators can induce a cascade of effects down the food chain that alters the mineralization of available plant nutrients (Santos et al. 1981, Kajak et al. 1993). However, recent microcosm studies failed to find such effects in artificially constructed soil food webs (Mikola and Setälä 1998, Laakso and Setälä 1999). Part of the reason for these mixed results could be that many spheres of biotic influence interact to determine net ecosystem process rates and belowground species composition (Beare et al. 1995). Among these influences are the combined effects of drilling and burrowing by macrofauna, sloughing and exudates in the rhizosphere, decomposition and nutrient turnover in litter and organic layers, and humus and soil aggregate formation, as well as direct trophic interactions. When many interactions among species are weak, variability in the outcome of effects on community composition tends to increase (Berlow 1999).

No or negative correlation

Lack of correlation in diversity among particular groups of organisms can occur for several reasons. First, the species or groups could be responding to different abiotic constraints (e.g., actual evapotranspiration versus potential evapotranspiration; Currie 1991) or to the same abiotic constraints but on different temporal or spatial scales. At a regional scale (across different land-use types), there is often an inverse relationship between earthworm and termite densities because termites adapt better to environments with poor quality or small amounts of organic resources, and with low availability of water (Decaëns et al. 1994). Across broad gradients of abiotic conditions (e.g., arctic to tropics), total diversity (all species in all taxonomic groups) may be correlated between aboveground and belowground compartments, but some taxa may actually become less diverse even though overall diversity is increasing. For example, earthworm (Brussaard et al. 1997, Lavelle et al. 1995), nematode (Boag and Yeates 1998), and mycorrhizal (Allen et al. 1995) diversity does not increase toward the equator (latitudinally), unlike plants and many other organisms.

Second, species or groups could be linked biologically via interactions that decrease diversity in the other compartment. Trophic theory suggests that some belowground species may be less strongly influenced by aboveground diversity because they are regulated by top-down controls within belowground food webs rather than by bottom-up controls, such as heterogeneity of inputs from aboveground vegetation (Wardle and Yeates 1993, de Ruiter et al. 1995). Interactions among trophic levels and different feeding guilds can be complex and sometimes counterintuitive. For example, root-feeding insects can decrease plant species richness in early successional communities (Masters and Brown 1997). This effect, in theory, could decrease aboveground insect diversity if plant diversity determines aboveground herbivore diversity. However, root herbivory can cause a drought stress response within the host plant that increases the performance (often fecundity) of a foliarfeeding insect sharing the same host plant (Masters et al. 1993). Therefore, in plots subjected to root herbivory, the community of foliar-feeding *Hemiptera* was more diverse, and plant species richness and cover were lower, than in soilinsecticide treated plots (Masters and Brown 1997). Similarly, indirect effects of aboveground herbivory on the abundance of belowground organisms

and rates of ecosystem processes, as mediated by root exudates and litter quality, can be either positive or negative. The response depends on the type of herbivore, the plant species being eaten, and the environmental conditions under which it grows (Bardgett et al. 1998). These observations indicate that not all groups within either aboveground or belowground compartments necessarily follow the same diversity trends, even when they are closely linked ecologically.

Third, diversity in one domain could depend on the composition, rather than the diversity, of organisms in the other domain. In local-scale experiments in New Zealand perennial grasslands, belowground diversity did not parallel aboveground diversity. Wardle et al. (1999a) removed different functional groups of the flora and monitored the taxonomic composition of five functional groups of belowground organisms. They found no consistent evidence for the existence of positive relationships between plant diversity and diversity of any of the belowground functional groups (Figure 4). They concluded that soil biodiversity is more likely to be related to the traits of the dominant plant species present (and ultimately to the quality of resource input) than to the diversity of the plant community itself. These results are similar to those seen in studies assessing the effects of plant composition and diversity on ecosystem processes (Hooper and Vitousek 1997).

Fourth, historical, biogeographic, and evolutionary relationships can play a large role in determining species diversity within communities (Ricklefs and Schluter 1993). These factors will not necessarily affect all aboveground and belowground taxa in a similar way, especially across gross differences in size and dispersal ability. For example, adaptive radiation for some soil faunal groups (e.g., New Zealand litter-feeding land snails) occurred before the development of current vegetation patterns (Barker and Mayhill 1999), so diversity of these groups is not necessarily related to the current composition of the plant community.

Fifth, effects of resource quality or quantity may outweigh effects of resource heterogeneity. The intermediate-stress hypothesis suggests a maximum of belowground diversity at intermediate levels of resource quality, independent of aboveground diversity (Cooke and Rayner 1984) (see alternative step 2 in Figure 3 for a fuller explanation). Alternatively, plants may affect belowground diversity through amounts of production rather than just diversity: More resources may sustain a larger and possibly more diverse soil and litter community (Chen and Wise 1999). Indeed, at the continental scale, biogeographical patterns of richness in termite genera correspond more closely to plant net primary productivity than to tree diversity (Eggleton 2000). At the plot scale, soil macrofauna diversity showed no correlation with plant diversity, but it did show a positive correlation with aboveground plant biomass across secondary successional plots in the Amazon Basin (Barros 1999) (Figure 5). Similar patterns may also hold for heterotrophic microorganisms because of the wealth of secondary products and environments created in a resource-rich but physically stable matrix. This mechanism requires more testing, especially because it contradicts observations in plant communities, where high-resource environments often lead to competitive exclusion and lower levels of plant diversity.

Indexes and indicator taxa

Comprehensive comparisons of diversity in aboveground and belowground taxa are almost entirely lacking. However, several intensive research campaigns investigating possibilities for indicator taxa among aboveground species have been made. Because some of the hypothesized mechanisms for aboveground species (e.g., selective feeding preferences) are similar to those for belowground species, these studies suggest what patterns might occur when comparing a wide variety of belowground taxa as well.

Although some studies have reported correlations in diversity among aboveground taxa, no clear evidence emerges for a single taxon that acts as an indicator for the diversity of other taxa at the landscape scale. Higher plant diversity is correlated with greater diversity of aboveground insects in natural (Murdoch et al. 1972) and experimental (Siemann 1998) systems. This pattern may have occurred because insect herbivores are often relatively selective feeders (Strong et al. 1984) or because insect diversity responds positively to plant architectural complexity (Murdoch et al. 1972, Southwood et al. 1979, Lawton 1983). On the other hand, experiments with aboveground indicator taxa in natural ecosystems give variable results, depending on locality, sampling method, and taxa (Gaston 1996b). Preservation of a single location of a single ecosystem type based on the diversity of a single aboveground taxon seems unlikely to preserve the maximal diversity of all aboveground species: Hotspots of diversity for one taxon are not necessarily hotspots for others (Prendergast et al. 1993, Gaston 1996a, Lawton et al. 1998). On the other hand, species turnover across environmental gradients, or beta diversity, can follow similar patterns for multiple taxa (Prendergast et al. 1993, Lombard 1995, Oliver and Beattie 1996, Howard et al. 1998). Therefore, reserves based on changes in species composition of a single taxon across many different ecosystem types may capture much of the regional diversity for many different taxa. This suggests that a simple focus on alpha diversity (within a habitat type), as has been most common, may miss patterns of diversity that are important for implementing effective conservation measures for belowground as well as aboveground species.

Mechanisms and key organisms

Where there are positive correlations among aboveground and belowground taxa, what are the ecological linkages by which aboveground biodiversity affects belowground biodiversity, and vice versa? Do key species or functional groups above or below the surface contribute to maintaining high biodiversity on the other side of the surface?

There are three primary categories of mechanisms by which organisms in one compartment can affect biodiversity

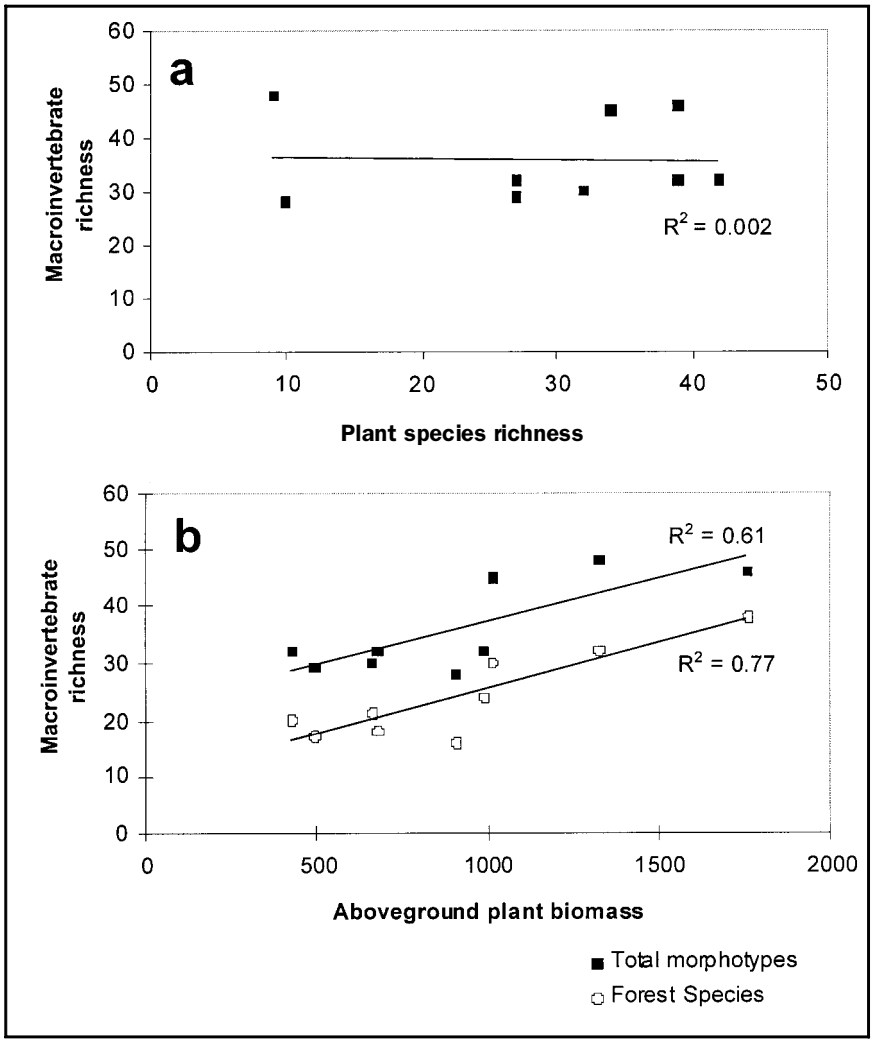

Figure 5. Correlations between soil macrofauna diversity, plant diversity, and plant productivity in nine pastures at Manaus, Brazil. Sites comprise pastures of different ages with different rates of invasion by weeds and regrowth of forest species. Panel A depicts the relationship between species richness of plants and species richness of soil macrofauna, the latter estimated as the number of morphospecies; the regression is not significant. Panel B shows the relationship between aboveground plant biomass and species richness of soil macrofauna; both regressions are significant (P < 0.05), but the correlation is better with species of the original forest than with total richness including grassland species. Both figures reproduced with permission from Barros (1999).

in the other. One category is obligate, selective interactions (one-to-one linkage). An aboveground organism could be so tightly linked to a certain belowground organism (through mutualism, for example) that loss of one guarantees loss of the other. Many such relationships within communities could contribute to correlations in diversity aboveground and belowground. The second category is asymmetric interactions (one-to-many linkage). The effects of a single species or functional group could influence (either promoting or decreasing) richness in the other compartment. The third category is causal richness (many-to-many linkage). Diversity in one compartment causes diversity in the other, so that biotic richness is correlated between aboveground and belowground compartments.

One-to-one species linkages: Obligate and specific. Examples of one-to-one species linkages include species-specific pathogens, herbivores, predators, and mutualists, as well as species or functional groups that provide a key resource for another species or functional group. These linkages occur where the association is both specific and obligate for at least one of the partners, though it need not be for both (for example, a belowground herbivore may depend on a certain species of plant, but the plant is likely to have other herbivores and is not "dependent" on any of them).

The degree of specificity can vary greatly even for symbiotic associations (parasitic or mutualistic). While some parasitic nematodes, such as *Meloidogyne javanica*, have a wide host range, parasitizing many plant species globally (Eisenback and Triantaphyllou 1991), others (e.g., *Heterodera cruciferae* in the Anguinidae) have such narrow host ranges that removal of the plant species, or a change in the physiology of the plant species, could affect the existence of the nematode (Baldwin and Mundo–Ocampo 1991). Ectomycorrhizal fungi exhibit a considerable degree of variation in their host specificities. Whereas many have broad host ranges, some are restricted to a single genus of plants (Molina et al. 1992, Allen et al. 1995, Bruns 1995). On the other hand, the approximately 160 species of Zygomycete fungi that form arbuscular endomycorrhizal associations are obligate symbionts, although none is host specific (Morton 1988, Walker 1992). In both ectomycorrhizae and arbuscular mycorrhizae, a single-host plant may be colonized by more than one species of fungus.

The extent to which associations are obligate can vary also, even for partners in mutualism. Although the degree of host specificity between legumes and their rhizobial symbionts might lead one to assume that the bacteria are dependent on the plant, this is generally not true. The bacteria (*Rhizobium*, *Bradyrhizobium*, and related genera) exist as free-living bacteria in soil, with only a small proportion actually achieving symbiosis with legumes. Rhizobia can survive for long periods in the absence of the host, though their numbers tend to multiply when a compatible legume is present (Giller and Wilson 1991). On the other hand, success for the plant can depend completely on the presence of the bacterium. For this mutualism, the

presence of certain genes, gene clusters, or plasmids is more relevant than species specificity because the genes necessary for nodulation and nitrogen fixation can be readily transferred among bacteria (Young and Haukka 1996).

One-to-many species linkages: Keystones and dominants. Aboveground and belowground taxa can be closely linked functionally, but the relationship does not necessarily lead to correlations of diversity. Certain key species or functional groups can have a large influence on growth, composition, or diversity in the other compartment without necessarily being diverse themselves. Termites are a good example. Specific plant communities are often associated with termite mounds or their immediate environment and may appear in a successional sequence from grasses to shrubs and trees as mounds age and grow (Wood 1996). Long-term exclusion of termites can affect hydrology, soil organic carbon and nitrogen, plant biomass, and the floristic character of plots (Veeresh and Belavadi 1986, Whitford 1991). In the Okavango Delta, the mound-building activities of *Macrotermes michaelseni* affect the spatial arrangement and alpha-diversity of plants as well as landscape structure (Dangerfield et al. 1998, McCarthy et al. 1998). However, the termite community in any given location need not be diverse itself to exert these effects on plant composition and diversity.

Some one-to-many mechanisms could lead to either increased or decreased diversity, depending on the ecological context. Whereas effects of species above ground may clearly influence conditions of growth below ground (or vice versa), the effects on diversity could vary (Jones et al. 1997). Such mechanisms could increase diversity when, for example, they increase habitat heterogeneity or decrease dominance by particularly competitive species. Keystone species—those species whose effects on community or ecosystem dynamics are large relative to their total biomass—often exert their influence by such mechanisms (Power et al. 1996). Given the extensive literature demonstrating that those soil animals that are ecosystem engineers significantly stimulate plant growth by increasing mineralization of nutrients, impacts on plant community structure are likely (Lawton et al. 1996, Lavelle et al. 1997, Folgarait 1998, Mando et al. 1999). However, in light of the complex relationship between nutrient availability and plant diversity, plausible explanations predict that these effects could either increase or decrease plant diversity, depending on circumstances (Jones et al. 1997, Foster and Gross 1998, Brown et al. 1999).

Similarly, multitrophic interactions in the rhizosphere can significantly increase decomposition and mineralization of nitrogen and phosphate, making these elements available for plants (Clarholm 1994, Coleman 1994). Grazing by microarthropods (especially Collembola) can selectively curtail the growth of plant pathogenic fungi, thus aiding plant growth (Lartey et al. 1994). Although all of these interactions clearly influence growing conditions and nutrient availability, modification of growing conditions for organisms on the other side of the soil surface is not necessarily synonymous with increasing their diversity.

Three mechanisms by which asymmetric effects could enhance diversity are through keystone species, direct positive interactions, and environmental modification. Although there may be cases in which one particular species plays the major role in affecting community diversity (e.g., a top predator in trophic interactions; Schoener and Spiller 1996), in other cases, several species could have the same influence, as when effects are mediated by the abiotic environment.

Where keystone species reduce the abundance of otherwise dominant species by selective predation, herbivory, or pathogenesis, they can encourage greater diversity among subordinate species (Power et al. 1996). The extent to which this mechanism operates between aboveground and belowground communities is largely undetermined, but there is strong potential for keystone effects across the soil boundary. For example, belowground herbivory can equal or exceed aboveground herbivory in effects on plant production. The amount of plant biomass consumed by nematodes can be up to three times greater than that consumed by cattle in mixed prairies. Many soil invertebrates are also relatively specific in their feeding preferences (Andersen 1987). If this belowground herbivory reduces dominance by strongly competitive species, it could increase plant diversity. Similarly, selective feeding by aboveground predators could affect diversity of belowground animals through top-down trophic effects.

Direct positive interactions occur when a species or functional group in one domain enables the persistence of many species in the other. At the functional group level, arbuscular mycorrhizae can promote plant diversity (primarily evenness of abundance) by increasing biomass of subdominant species (Grime et al. 1987, Gange et al. 1990).

The third mechanism—altering environmental conditions so that they allow persistence of a greater diversity of organisms in the other domain—is an indirect interaction. Plant canopies and litter deposition have a critical effect on microclimate (insolation, temperature, and relative humidity), affecting soil-dwelling invertebrates (Coleman et al. 1991, Tian et al. 1993, Lavelle et al. 1997), although it can be difficult to distinguish between microclimate and trophic effects. Digging, wallowing, burrowing, and trampling by large animals can change soil temperature, moisture, and nutrient availability (Tardiff and Stanford 1998). To the extent that these disturbances increase environmental heterogeneity, they would most likely increase diversity of belowground organisms as well (Naiman and Rogers 1997), although this relationship remains to be tested.

Similarly, belowground organisms can modify the environment for aboveground species. In soils, termites, earthworms, and ants are ecosystem engineers that may have important aboveground consequences. As these organisms move through soils, they mix organic and mineral materials to form organomineral complexes that influence soil structure and fundamental soil processes such as carbon

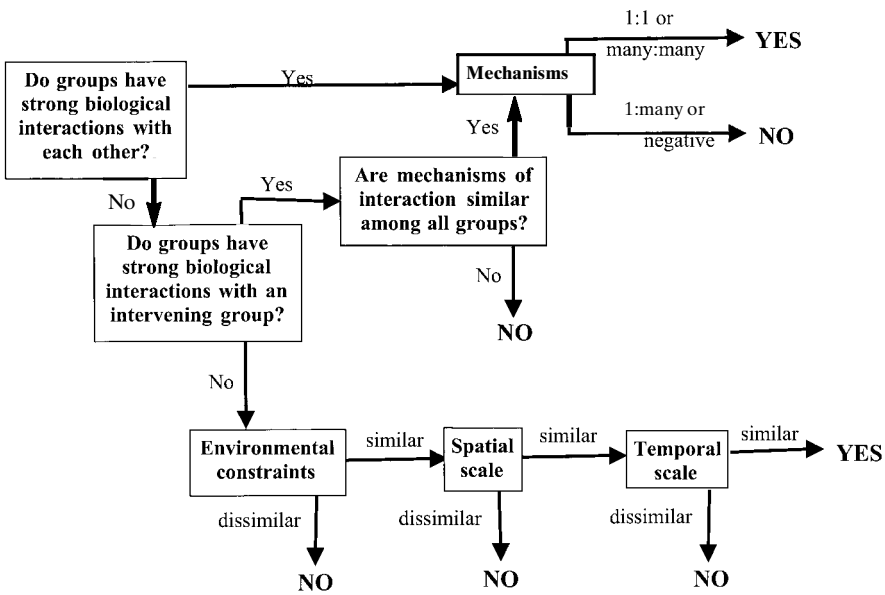

Figure 6. A decision tree asking whether diversities of aboveground and belowground taxa will be correlated. Pathways that lead to no correlation are at least as probable as those that lead to positive correlation. Biological interactions include direct trophic, competitive, or other community interactions (including coevolutionary linkages), or effects on environmental parameters that influence species in the other domain. Spatial scale refers to the distances over which distributions of species within the measured groups vary. Temporal scale refers to the time scales over which species within the measured groups respond to changing conditions.

mineralization, carbon sequestration in stable pools of complex organic matter, nitrogen fixation, nitrification, and other processes that are important determinants of plant growth (Stork and Eggleton 1992, Jones et al. 1994, Beare et al. 1995). These physical, chemical, and biotic modifications lead to environments to which plant roots are attracted or in which seeds may germinate, potentially feeding back to aboveground diversity (Brussaard 1998). Soil disturbance caused by burrowing mammals can also influence plant composition and diversity (Huntly and Reichman 1994, Hobbs and Mooney 1995), though mammals (and other biota) with partial life histories in the soil cannot be cleanly categorized as only aboveground or belowground organisms.

In some cases, the presence of certain species or functional groups could lead to reduced diversity in the other compartment via negative effects. Below ground, the presence of earthworms leads to lower mite diversity in litter in some northern temperate zone ecosystems (Rusek 1985). Above ground, grasses with the C4 photosynthetic pathway have a negative effect on soil herbivorous arthropods and decomposers, probably as a result of poor resource quality (Wardle et al. 1999a). Invasive species can also decrease abundance and diversity of components of the native community.

Many-to-many linkages: Richness causality. The third class of mechanism for aboveground-to-belowground correlations in diversity are those in which greater diversity in one domain leads to greater diversity in the other. A primary pathway postulated for this is that a diversity of carbon inputs from aboveground will lead to a greater variety of food resources for belowground heterotrophs, thus supporting more diverse soil communities through greater niche differentiation (Figure 3). Belowground diversity may influence aboveground diversity as well—for example, in interactions between mycorrhizae and plants (van der Heijden et al. 1998).

Conclusions

Whether correspondence in diversity of aboveground and belowground taxa exists depends on both the nature of the biological interactions among them and the spatial and temporal scales of the ecological factors influencing the biology of the organisms involved. Our basic message is twofold. First, the evidence for correlation between aboveground and belowground diversity is mixed. Across broad gradients in disturbance or environmental conditions, aboveground and belowground diversity may correlate, but the relationships are often much more variable at smaller, more local scales. Where correlations exist, they are not always causal in nature. Second, there are a variety of mechanisms by which organisms above ground could affect community composition and diversity below ground, and vice versa. However, not all of these mechanisms necessarily lead to correlations of species richness in the two domains (Figure 6).

A current difficulty in aboveground-to-belowground comparisons is the lack of information on soil organisms. Ecologists have a far better knowledge of aboveground than belowground organisms, yet a large proportion of global diversity exists below ground. Potentially as much as 99% of soil bacterial and nematode species are still unknown (Wall and Virginia 2000). Species-level comparisons are therefore impossible for these organisms; functional groups are often most useful for describing soil microbial and microfaunal communities. On the other hand, the concept of species works well for describing the diversity of aboveground organisms and soil mesofauna and macrofauna, which have been more studied and better identified. This discrepancy in description further hinders accurate comparisons of aboveground and belowground diversity. Coordination of experiments that assess both aboveground and belowground biodiversity, as well as their effects on ecosystem processes and community dynamics, should be a strong research priority (Brussaard et al. 1997, Wall Freckman et al. 1997, Wall and Moore 1999). Understanding patterns of biological diversity is a matter of renewed urgency because

of the steady anthropogenic destruction of natural ecosystems worldwide. Whether or not we find strong correlations among aboveground and belowground diversity, the search to understand the connections between these two domains will help our understanding of the mechanisms that shape ecological communities, and thus our ability to responsibly manage ecosystems.

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