

Soil fertility, heterogeneity, and microbes: towards an integrated understanding of grassland structure and dynamics

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Abstract

Objective: To highlight the need and the potential for an integrated understanding of three key soil-based drivers of plant community structure and dynamics – soil fertility, soil heterogeneity, and microbes.

Location: European and North American grasslands.

Methods: Review and discussion of conceptual models and empirical literature, including examples of observational and manipulative studies from both natural and restored grassland communities.

Results and Conclusions: In general, the results of empirical studies on soil fertility, soil heterogeneity, and soil microbes in grassland communities do not support expectations of common conceptual models. Ecological theory assumes a unimodal relationship between soil fertility and plant community diversity, yet empirical relationships from grassland communities are variable, the mechanisms underlying these variable patterns are not yet well understood, and there is mixed success at manipulating soil fertility to facilitate restorations. While theory predicts that increased soil heterogeneity will lead to increased plant community diversity, results of experimental manipulations of soil heterogeneity often show the opposite. Of two major conceptual models proposed for how microbes structure plant communities, there is little support for the hypothesis of microbially mediated niche partitioning. Plant-microbe feedbacks do have significant empirical support to date and there is increasing application of positive feedback dynamics in restoration, yet field tests of feedback dynamics remain limited. We suggest that an understanding of interactions between these soil drivers may help to resolve discrepancies between conceptual models and empirical results, improving our understanding of grasslands and our ability to restore them.

Keywords: Microbially Mediated Niche Partitioning; Plant Community Diversity; Plant-Microbe Feedback; Soil Fertility; Soil Heterogeneity.

Introduction

Despite being one of the more challenging environments to study, soil is clearly a critical

ecological arena for plants. Soil is where plants are rooted and from which they draw nutrients and water, it is very heterogeneous, and it teems with microbial life. These three factors – soil fertility, soil heterogeneity, and soil microbes – are well recognized as key drivers of plant community structure and dynamics. Conceptual models about how each of these drivers acts independently to shape plant communities have emerged from histories of empirical and theoretical work. Yet there is limited understanding of how these soil drivers interact with one another to shape plant communities (Fig. 1). There are many tests of how soil fertility affects community diversity, for example, but little examination of how that relationship might alter, or be altered by, soil heterogeneity or soil microbial composition. As another example, there is a growing body of research on feedbacks between plants and soil communities, but little work to date on how feedbacks operate across gradients of soil fertility or in a heterogeneous soil matrix. Our objective is to highlight the need for an integrated understanding of soil fertility, soil heterogeneity, and soil microbes as drivers of plant community structure and dynamics. We tend to focus on plant species diversity, especially plant species richness (i.e., the number of species present in a given area), because it is an aspect of community structure of long interest to ecologists from both basic and applied perspectives, and for which much data exists. We briefly present an overview of the common conceptual models for the relationship between each of the three soil drivers and plant community richness and/or dynamics. We then use examples from both the basic and applied empirical literature to demonstrate that soil fertility, soil heterogeneity, and soil microbes do not consistently shape plant communities in the ways that these conceptual models predict. We suggest that integration of these three soil drivers has the potential to advance understanding of, and success at, restoring grassland diversity. We provide examples of where such integration is beginning to occur, and point out promising avenues for further integration.

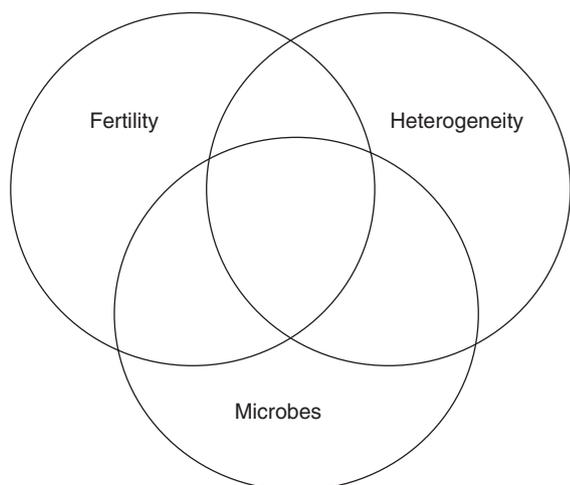


Fig. 1. Conceptual representation of three important soil-based drivers of plant community structure and dynamics, showing areas of two- and three-way overlap. Our understanding of how these drivers interact to shape plant communities in these areas of overlap is currently limited.

Common Conceptual Models

Soil fertility

Soil fertility has long been appreciated as a major driver of vegetation diversity, and the unimodal or humpback relationship is the dominant conceptual model for this driver (Grime 1979). It is generally accepted that system productivity increases with increasing soil fertility, and the humpback model describes a relationship between productivity and plant community diversity for which diversity first increases and then decreases with increasing productivity (see Grace 1999). Many mechanisms have been proposed to explain different segments of the hump, from stress release on the ascending side (Grime 1973, 1979), various competition-related mechanisms on the descending side (total competition, Grime (1977); dynamic equilibrium, Huston (1979); aboveground competition, Newman (1973) and Tilman (1982, 1988); assemblage-level thinning, Oksanen (1996) and Stevens & Carson (1999)), and evolutionary mechanisms that apply to the full gradient (species-pool hypothesis, Taylor et al. (1990)).

Soil heterogeneity

Environmental heterogeneity is a classic driver of species diversity (Hutchinson 1959). According to the heterogeneity-diversity hypothesis, if species differ in their responses to fitness-constraining

environmental factors, then heterogeneity in these factors will favor different species at different times or spatial locations (Tilman & Pacala 1993; Amarasekare 2003). Heterogeneity within the soil environment comprises a suite of dimensions that affect plants. A host of abiotic and biotic factors vary spatially and temporally in soil, including pH, depth, nitrogen and other soil resources, and belowground mutualists, pathogens, or herbivores. The ubiquity of physiological and morphological tradeoffs makes differential species responses to this variation inevitable (Tilman 1990). Soil heterogeneity is thus a commonly accepted mechanism for generating and maintaining plant community diversity (Whittaker & Levin 1977; Tilman 1982, 1988; Gigon & Leutert 1996).

Soil microbes

Soil microbes are increasingly appreciated as important drivers of vegetation structure and dynamics (Reynolds et al. 2003). Two distinct conceptual models of plant-microbe interactions are microbially mediated niche partitioning (Reynolds et al. 2003) and feedback dynamics (Bever et al. 1997). Microbially mediated niche partitioning is an explicitly niche-based model, whereby coexistence of plant species is promoted by associations with microbes that allow different plants species to access different sources of soil N or other soil nutrients (Reynolds et al. 2003). This model recognizes the important role that microbes play, through their enzymatic capacities, in making soil nutrients available to plants. In the case of N partitioning, individual plant species might obtain ammonium from different nitrogenous organic sources, for example urea, proteins, or chitins, via differential associations with such enzymes as ureases, proteases, or chitinases. A similar concept can be envisioned for phosphorus (P) or other limiting soil nutrients.

In contrast to microbially mediated niche partitioning, feedback dynamics require no assumptions of abiotic resource partitioning among plant species. Feedback dynamics can in fact represent alternatives to abiotic niche partitioning and abiotic resource competition as mechanisms of, respectively, coexistence (in the case of negative feedbacks) and exclusion (in the case of positive feedbacks) (Bever et al. 1997). Plant-microbe feedbacks arise from the species-specificity of plant-microbe associations, whereby soil communities respond differently to different plant species and plant species, in turn, can be affected in positive or negative

ways by their associated microbial communities (Bever et al. 1997). Positive feedback dynamics (e.g., from a plant host's accumulation of beneficial soil microbes) can lead to loss of local diversity, as the abundance of the plant species experiencing the greatest positive feedback is continuously reinforced (Bever 2003). In contrast, negative feedback (e.g., from a plant host's accumulation of harmful pathogens) should prevent competitive dominance and increase plant community diversity, as well as cause species replacement over time (Bever 2002, 2003). It has been hypothesized that the relative importance of positive and negative feedbacks changes over succession, with positive feedbacks dominating early in succession, when conditions can be harsher (favoring microbial mutualists) and plant densities lower (inhibiting the spread of negative feedback from pathogens), and negative feedbacks increasing as conditions moderate and plant densities build (Reynolds et al. 2003).

Evaluating the Models

Soil fertility

The relationship between productivity and diversity in grassland communities is far from the simplified hump-shaped curve. A literature survey of observational and experimental studies in a variety of herbaceous plant communities demonstrated that, while most studies were consistent with a hump-shaped relationship between small-scale species richness (i.e., species density, or the average number of species per plot) and total community biomass, the relationship was more often an envelope, suggesting the importance of additional factors (Grace 1999). Furthermore, a review of studies from a variety of relatively natural, unfertilized vascular plant systems, conducted over a range of geographical scales, found that a humpback relationship between species richness and productivity was predominant in only 41-50% of studies, more commonly when productivity gradients crossed a range of community types (Mittelbach et al. 2001). A similar lack of consistency was seen in reviews focusing specifically on grasslands (Gross et al. 2000; Grace et al. 2007). Gross et al. (2000) found a clear humpback relationship between productivity and diversity (here, species density) only at the scale of fields ranging across community types (e.g., short-grass prairie, tall-grass prairie, old fields). Within grassland community types, however, the relationship between productivity and species density is

often highly variable (Gross et al. 2000; Grace et al. 2007).

It should be noted that there is a fairly clear distinction between studies conducted along natural gradients in fertility, such as those analyzed by Mittelbach et al. (2001) or Gross et al. (2000), and studies involving experimental manipulations of fertility. In the latter case, within-community patterns consistently show a decrease in diversity with fertilization (e.g., Tilman 1987; Goldberg & Miller 1990; Huenneke et al. 1990; Wedin & Tilman 1996; Gough et al. 2000; Suding et al. 2005). Declines in diversity with fertilizer addition are expected for sites falling within productivity ranges on the descending side of the humpback relationship (Tilman & Pacala 1993). Yet if the humpback relationship exists, the expectation is also that increases in fertility will increase diversity for sites falling within productivity ranges on the ascending side of the humpback relationship, although this result is not generally observed (Gough et al. 2000).

Nutrient enrichment and non-native dominance are often correlated (Davis et al. 2000). Using the putative hump-shaped relationship as a guide, restoration projects are thus often an attempt to push degraded sites back along the fertility gradient toward a community with less dominance by non-natives and a higher diversity of native species. Soil nitrogen (N) is the primary focus of such manipulations, both because N is the nutrient most limiting to primary productivity in most temperate ecosystems and because N is also fairly manipulable relative to other nutrients. One commonly used technique in soil resource manipulations is the addition of readily available carbon (C, typically sawdust, sugar, or some combination of the two), which has the effect of immobilizing soil N in the microbial biomass, thus making it unavailable (or less available) to plants. Faster-growing annual non-native species are expected to respond more strongly to the decrease in N availability compared to slower-growing native species.

While soil N can be strongly reduced by C addition (e.g., Blumenthal et al. 2003; Prober et al. 2005), responses of plant production and community structure to C addition are variable across studies, suggesting that there is still much to be understood about such manipulations. For example, non-native and native plant species do not always follow the expected pattern of cover or biomass decrease or increase, respectively, with C addition. Some studies report native plant production decreases or neutral responses to C addition (e.g., Reeve Morghan & Seastedt 1999; Alpert & Maron

2000; Haubensak & D'Antonio 2006), while some non-natives appear to be facilitated by C addition (e.g., Blumenthal et al. 2003). Although ruderal or annual species with higher relative growth rates are expected to respond more strongly to nutrient reductions compared to perennial species that are adapted to infertile soils (Chapin 1980), there is evidence that both annual and perennial (non-natives) biomass increase with C addition (Blumenthal et al. 2003). Additionally, some studies have shown a strong plant response to C addition without an accompanying change in soil N (e.g., Paschke et al. 2000; Schultz 2001), calling into question the mechanism of effect. Overall, then, there are a number of exceptions to the simplified expectations of how species should respond to soil fertility. Understanding the causes of these exceptions may prove helpful to restoration efforts in general.

The humpback relationship between soil fertility/productivity and plant community diversity has neither held up well as a basis for interpreting basic studies nor as a useful model for guiding applied studies. While there are many potential factors – from species pool constraints to variable disturbance regimes – that may alter or override the relationship between soil fertility/productivity and plant diversity (e.g., Gough et al. 1994, 2000; Grace et al. 2007), we suggest that soil heterogeneity and soil microbial associations are two particularly key factors that need more attention.

Soil heterogeneity

Compared with research on soil fertility, there have been relatively few tests of the effects of soil heterogeneity on diversity, underscoring the difficulty of both measuring and manipulating this factor. Indirect support for the importance of soil heterogeneity in structuring grasslands comes from demonstrating variation in plant species competitive performance as a function of patch type. For example, using a reciprocal planting design and measuring a suite of plant and soil variables, patches (<0.01–10.0 m²) of different serpentine grassland species were found to be associated with different soil conditions, and plant species often competed best in their 'home' soil patch types (Reynolds et al. 1997). Other indirect evidence of heterogeneity as a driver of diversity comes from observational studies that measure significant positive correlations between heterogeneity in various soil variables, such as soil depth, and the diversity of the overlying plant community (e.g., Lundholm & Larson 2003; Davies et al. 2005).

In contrast to observational studies, evidence from manipulative studies of soil heterogeneity have thus far provided mixed support for the hypothesis that increased heterogeneity leads to greater diversity in grassland communities (Tilman 1993; Steinauer & Collins 1995; Reynolds et al. 1997; Collins & Wien 1998). Application of N in the form of simulated bovine urine to 0.25 m² patches of native prairie resulted in altered vegetation composition in treated versus control patches, increasing overall grassland diversity at the field level (Steinauer & Collins 1995). On the other hand, application of seven different N addition treatments at the scale of 4 m × 4 m plots in nutrient-poor old fields failed to promote species diversity at the field level, a result potentially attributed to colonization limitation by high fertility-adapted species (Tilman 1993). Two other experiments, conducted in old-field (Collins & Wein 1998) and infertile savanna grassland (Reynolds et al. 2007) suggest that nutrient-responsive clonal plant species may come to dominate with soil nutrient addition, regardless of its heterogeneity, resulting in decreased community diversity. At the scales of imposed heterogeneity [0.25 m, Reynolds et al. (2007); ca. 0.5–1.5 m, Collins & Wein (1998)], these clonal species may be able to integrate across patches and thus obviate the heterogeneity-diversity relationship that would otherwise be apparent (Reynolds et al. 2007). Larger scales of heterogeneity (e.g., Steinauer & Collins 1995) may prevent such integration by clonal plants, a possibility that remains to be explicitly tested.

We found only one study that manipulated soil heterogeneity to assess its utility in grassland restoration (Baer et al. 2004). The study was conducted in a formerly cultivated field, where levels of soil nitrate were measured to be five times that of the adjacent native prairie. The investigators manipulated depth heterogeneity and nutrient heterogeneity, creating patch sizes that ranged from 2 m × 2 m to 2 m × 8 m in scale. Consistent with results from other studies (i.e., Collins & Wein 1998; Reynolds et al. 2007), community diversity was depressed by soil N heterogeneity in this study, whereas the dominance of an aggressive, rhizomatous grass, *Panicum virgatum*, was promoted. Baer et al. (2004) concluded that the importance of resource heterogeneity may be dampened by a dominant species that can establish over a wide range of resource availability.

Although the number of studies is limited to date, some patterns in the empirical work on soil heterogeneity are worth noting. Observational studies incorporating natural variation in heterogeneity

generally support the heterogeneity-diversity hypothesis, whereas manipulative studies, which alter heterogeneity via soil nutrient enrichment, often do not. Rather, the results of a number of manipulative studies in both basic and applied systems suggest that soil nutrient enrichment can promote clonal species, regardless of whether the nutrients are applied in a heterogeneous or uniform manner, although the scale of heterogeneity may be important. These results suggest that interactions between soil heterogeneity and soil fertility may be important, an issue that we discuss further below, in the final section on integration.

Soil microbes: microbially mediated niche partitioning

There is accumulating evidence that plants are able to access a variety of forms of soil N and P. For example, temperate grassland, heathland, and arctic and alpine tundra plants have been shown to take up dissolved amino acids (Kielland 1994; Näsholm et al. 2000; Miller & Bowman 2002) or can access organic N in litter (Hodge et al. 2001). A role for ecto- or arbuscular mycorrhizal fungi (AMF) has been demonstrated in some of these studies (Turnbull et al. 1995; Hodge et al. 2001). Furthermore, in otherwise sterile soil, AMF-infected grasses can show increased growth and P uptake compared to non-infected plants when supplied with organic P sources such as RNA (Jayachandran et al. 1992) and phytate (Jayachandran et al. 1992; Tarafdar & Marschner 1994).

Whether microbial associations mediate differential access to forms of N or P among coexisting plant species is still a new and relatively untested model (Reynolds et al. 2003). There is some evidence for partitioning of ammonium, nitrate, and amino acids among coexisting plant species, although, to date, this has been shown only in arctic (McKane et al. 2002) or alpine (Miller & Bowman 2002) tundra systems, and an explicit role for soil microbes has not been established. On the other hand, a study by van der Heijden et al. (1998) demonstrated a role for AMF in generating grassland community diversity, but the mechanism was not identified for this microbial effect.

Manipulations of both N and P substrate diversity and AMF species diversity in experiments with old-field and Midwest prairie species have not found support for microbially mediated niche partitioning (Reynolds et al. 2005, 2006; Vogelsang et al. 2006). Indeed, AMF were found to depress the growth of old-field grassland species grown under limiting N conditions, where partitioning would be

expected (Reynolds et al. 2005). Furthermore, when AMF were beneficial to old-field plant species grown under limiting P conditions, they promoted access to all forms of P rather than specialization of plant species on a single form (Reynolds et al. 2006). A study with Midwest prairie microcosms found that AMF species richness promoted plant community diversity (Vogelsang et al. 2006), a result also found in an earlier grassland study by Van der Heijden et al. (1998). However, Vogelsang et al. (2006) determined that the mechanism was a sampling effect of particular diversity-promoting AMF species, not an effect of P partitioning and AMF diversity per se. We found no studies that examined microbially mediated niche partitioning in a restoration context.

Soil microbes: plant-microbe feedbacks

A growing literature, emerging over approximately the last two decades, has investigated plant-soil feedbacks and their role in plant community structure, successional dynamics, and exotic species invasions. Such feedback studies have typically been conducted in the greenhouse in well-mixed, fertilized soil and find evidence for net negative feedback of the soil community on target plant growth or reproduction (e.g., Bever 1994; Bonanomi et al. 2005). Soil pathogens, parasites, and/or belowground herbivores have been implicated as the agents of negative feedback in these studies (Van der Putten et al. 1990; Bever 1994; Mills & Bever 1998; Olf et al. 2000; Klironomos 2002), as have AMF (Bever 2002; and see Bever 1999). As predicted by conceptual models, negative plant-soil feedback has been linked to oscillatory spatial abundances and coexistence of plant species (Olf et al. 2000; Bonanomi et al. 2005) and to plant species replacement in succession (Van der Putten & Troelstra 1990; Van der Putten et al. 1993; Kardol et al. 2007). Although, in contrast to predictions (Bever 2003; Reynolds et al. 2003), negative feedback has been found to predominate in early-successional, and positive feedback in later-successional communities (Kardol et al. 2006). Plant-microbe feedbacks can also play a significant role in plant species invasions (e.g., Mitchell et al. 2006; Reinhart & Callaway 2006; Van der Putten et al. 2007). For example, invasive, non-native plants may experience 'enemy escape,' or reduced negative feedbacks from pathogens compared to native and rare plants (Klironomos 2002; Kardol et al. 2006, 2007), and may experience positive feedback from AMF or other beneficial soil biota (Klironomos 2002; Callaway et al. 2004; Reinhart & Callaway 2006).

A long-standing question is how soil feedback will be manifest under field conditions (Bever 1994), for example where AMF networks are undisrupted (Van der Putten & Peters 1997). One of the few field-based studies to date, conducted in native serpentine grassland, found limited evidence for negative feedback of three C4 grass species, that interspecific competition was capable of eliminating feedback effects, and that AMF colonization was highest where plant growth was least, implicating a role for AMF in negative feedback (Casper & Castelli 2007).

We found a limited set of studies that had tested the mechanism of plant-microbe feedbacks in a restoration context, half of which were conducted in the greenhouse, and half in the field. The objective of all these studies was to promote the growth of native species either directly by addition of beneficial microbes, or indirectly by decreasing the growth of non-native plants via disruption of their beneficial microbes.

Inoculation of AMF collected from various field sites increased the growth of an edaphic endemic forb, *Erodium macrophyllum* (Gillespie & Allen 2006). However, a mycorrhizal inoculum from a non-native grass-dominated area supported greatest growth of the native forb, compared to growth of the forb inoculated with AMF from the site of its extant population. Seedling emergence of a native grass (*Sporobolus wrightii*) was higher in pots with mycorrhizal inoculation, but there was little effect of inoculation on other measures of plant growth (Richter & Stutz 2002). On the other hand, a separate set of inoculated plants in the field had greater survival, basal diameter, and tiller and panicle production for the first two growing seasons following outplanting.

Field-based experiments may provide more insight into the role of plant-soil feedbacks for restoration. Two studies that added AMF in a field context both suggest that such additions accelerate restoration of native species (Smith et al. 1998; Bever & Schultz 2003). Bever & Schultz (2003) attempted to restore a post-agricultural field where the richness of the AMF community was half that of a nearby prairie remnant, and was dominated by a weedy AMF species. They found that a diverse array of AMF inocula (from whole-soil additions collected from remnant prairie) benefited native species, compared to those plots inoculated with old-field soil or controls (uninoculated). Interestingly, they observed an increase in plant community diversity with prairie soil inoculum only following a prescribed fire, suggesting an interactive effect of restoration treatments. Using a similar approach

with whole-soil inoculations, Smith et al. (1998) found that while inoculation did not change the total percentage cover of plants, percentage cover of native planted grasses was significantly greater in inoculated plots relative to controls. They speculated that such an increase in native plant cover might increase the rate of succession at these sites by allowing natives to outcompete the ruderal non-native species also present at the sites.

Of course, beneficial soil microbes do not only affect native species, and disruption of the positive feedback between soil microbes and non-native species is another strategy. For example, a suite of non-native species including *Centaurea diffusa* and *Bromus tectorum* experienced positive soil history effects (a proxy for plant-soil feedback), in former agricultural fields (Kulmatiski et al. 2006). Here, the researchers hypothesized that positive feedbacks between AMF and non-native species promoted their abundance in former agricultural fields, and found that fungicide treatment reduced cover of non-native species in such fields.

In general, of the two major conceptual models proposed for how microbes structure plant communities, plant-microbe feedbacks have significant empirical support to date, and there is increasing application of feedback dynamics in restoration. Yet, at least for natural or semi-natural grasslands, soil feedback has not been well tested in a field context. We suggest, furthermore, that just as is the case of soil fertility and soil heterogeneity, neither the empirical work nor the conceptual models for soil microbes have thus far paid much attention to the potential for interactions between the three drivers, a subject to which we now turn.

Integration of Fertility, Heterogeneity, and Microbes

Thus far, we have discussed the separate roles of soil fertility, heterogeneity and microbes in determining plant community structure and dynamics. We suggest that a greater emphasis on how these factors interact may enhance our understanding of grasslands and our ability to restore them. We acknowledge that there are many other important drivers of plant community structure and dynamics (e.g., disturbance, aboveground herbivory), and the need for understanding the interaction of multiple drivers (e.g., above- versus belowground processes) is already a well-recognized challenge in ecology (Blomqvist et al. 2000; Bardgett & Wardle 2003; Agrawal et al. 2007). The following discussion is not meant to be exhaustive, but to focus attention on

efforts at integrating across the three important soil drivers and to suggest new experimental approaches.

Soil fertility and soil heterogeneity

The habitat heterogeneity hypothesis (Tilman & Pacala 1993) suggests that the background effect of overall site fertility must be considered when assessing the role of soil heterogeneity. According to this hypothesis, overall plant community diversity may increase, decrease, or remain constant as soil fertility increases, depending on how the effective soil resource heterogeneity experienced by plants changes with soil fertility. Effective soil resource heterogeneity is a function both of plant size and the variation in soil resources from one place to another (point-to-point heterogeneity). Point-to-point resource heterogeneity is expected to increase with soil fertility, simply because the range in a variable necessarily increases with its mean. On this basis alone, the heterogeneity-diversity hypothesis would predict plant community diversity to increase with soil fertility. Fertility gradients are also productivity gradients, however, and so average plant size will also increase with soil fertility, with larger plants having the capacity to forage over larger areas. Depending, then, on the relative rates of increases in point-to-point heterogeneity and plant size, the effective heterogeneity experienced by plants may be greater or less than expected for a given soil fertility. For example, when the increases in point-to-point heterogeneity associated with increasing soil fertility are less than the increases in plant size that generally accompany increased soil fertility, effective heterogeneity will increase with soil fertility. On the other hand, when increases in point-to-point heterogeneity are outweighed by increases in plant size, effective heterogeneity will decrease with soil fertility. While developed with soil nutrient heterogeneity in mind, the habitat heterogeneity hypothesis can also apply to other kinds of environmental heterogeneity, in that the scale of plant size/foraging area relative to the scale of environmental patchiness determines whether patches are potential separate niches or are simply integrated over.

A related hypothesis developed by Rajaniemi (2003) suggests that smaller scale heterogeneity, occurring within the root foraging zone of individual plants, might change over soil fertility gradients and affect the shape of the fertility-diversity pattern via changes in the size symmetry of belowground competition. Size asymmetry in belowground competition might result if larger plants are able to exploit

nutrient patches faster than smaller plants, thus preempting the patches and resulting in disproportionately larger nutrient uptake rates and competitive effects for their size (Schwinning & Weiner 1998). Such belowground asymmetry might constrain diversity at low productivity, where soil nutrients are typically more important in controlling competitive dynamics, or when plant communities are fertilized with granular or organic fertilizers that generate substantial small-scale nutrient heterogeneity (Rajaniemi 2003). While studies of both small- (e.g., Rajaniemi 2007) and large-scale heterogeneity (reviewed above) have been accumulating, it is as yet unclear whether either scale of heterogeneity affects plant interactions and community structure as predicted or which scale is most important in driving patterns of community diversity in nature (Hutchings et al. 2003).

Of course, there are other factors, for example physical disturbances due to animals or abiotic forces, that can also generate local heterogeneity, and not necessarily in any consistent fashion with respect to soil fertility. By themselves, neither the humpback fertility-diversity relationship nor the heterogeneity-diversity hypothesis may provide a satisfactory model for vegetation structure and dynamics. Rather, it may be necessary to consider the joint influence of both soil fertility and heterogeneity in order to understand and predict vegetation pattern. As one example, Tilman & Pacala (1993) illustrate how fertility-heterogeneity dynamics can skew the mode of the humpback productivity-diversity curve between low-, moderate- and high-fertility habitats. These dynamics might help to explain the variability in fertility-diversity relationships that have been observed within communities (Gross et al. 2000). An apparent failure in the heterogeneity-diversity hypothesis might be explained by manipulations of soil heterogeneity that were accompanied by increases in total soil fertility, leading to dominance by a clonal grass species that foraged over a scale greater than the heterogeneity manipulation, which led to decreased community diversity (Reynolds et al. 2007). The study by Baer et al. (2004), as well as the mixed success of carbon addition experiments, likewise suggests that we may need to be aware of interactions between soil fertility and heterogeneity when designing restoration projects.

Soil fertility and soil microbes: microbially mediated niche partitioning

Another area of integration is the effect of soil heterogeneity on the ability of plants, in association

with microbes, to partition soil nutrients. In tests of microbially mediated niche partitioning (Reynolds et al. 2005, 2006; Vogelsang et al. 2006), different forms of nutrients were delivered, such that plants experienced relatively homogeneous and low-level nutrient concentrations. However, in the real world, nutrients occur in 'hot spots,' where the payoff from microbial associations may be locally higher than with a uniform nutrient supply, and thus potentially more detectable. AMF have sometimes been found to enhance plant nutrient capture from patches (Cui & Caldwell 1996; Farley & Fitter 1999; Hodge et al. 2001), although this result is not consistent across studies (Hodge et al. 2000; Hodge 2001, 2003; Smilaurová & Smilauer 2002). Future tests of microbially mediated niche partitioning with AMF and other microbes need to incorporate this kind of spatial heterogeneity in nutrients.

Soil fertility and soil microbes: plant-microbe feedbacks

Plant-microbe feedbacks are known to be influenced by soil fertility. For example, AMF act as parasites or mutualists based on soil P (Johnson et al. 1997) or the dominant form of soil P (Reynolds et al. 2006), as well as host plant and AMF species identity (Klironomos 2003). Furthermore, the identity of AMF species that promote plant diversity may change with level of P (Vogelsang et al. 2006). These studies suggest a complexity and contingency in plant-AMF interactions that could regulate species coexistence, with no one plant-AMF species combination optimal everywhere. Clearly, interactions of plants with other microbes, such as N-fixing bacteria or pathogens, may also exhibit such contingency with environmental variables, including soil fertility. Manipulations of fertility and microbes in grassland microcosms, for example, demonstrated that the effect of increased soil fertility on reductions in plant community evenness due to dominance by fast-growing grasses was contingent on the presence of root-feeding nematodes (De Deyn et al. 2004). Given that plant-microbe interactions change with environmental variables such as soil fertility, we might expect that heterogeneity in nutrients or other soil variables will also influence the outcome of these interactions. As one example, results from a grazed temperate grassland system indicate that negative feedback can vary greatly over relatively small spatial distances (meters, Blomqvist et al. 2000). We currently know relatively little about how plant-microbe feedbacks respond to soil heterogeneity, including whether and at what scale soil

patchiness changes the magnitude and/or sign of positive versus negative feedbacks, the species specificity of such changes, and the consequences for plant species coexistence or other aspects of vegetation pattern.

Integrating all three drivers

Investigating the three-way interaction between soil fertility, soil heterogeneity, and soil microbes will be a challenge that requires a range of approaches, both in the greenhouse and the field. We propose that one fruitful strategy might examine how the interaction of soil microbes with soil heterogeneity affects plant communities at different points along a fertility gradient. In a restoration scenario, for example, experimental manipulations of soil heterogeneity and soil microbes could be implemented at a disturbed site to be restored and at an adjacent undisturbed site, with the former representing the high end of the fertility gradient and the latter site the low end of the gradient. We recommend that soil heterogeneity treatments incorporate fertilization and reverse fertilization patch types, allowing heterogeneity to be manipulated without altering the average level of fertility, which has been a confounding variable in past experimental studies of soil heterogeneity. The soil microbial treatment could include two levels: a diverse native AMF inoculum and a whole soil inoculum. In this way, the relative importance of AMF versus other soil microbes (e.g., pathogens) could be tested, although complementary feedback studies in the greenhouse would be needed to untangle the relative roles of positive versus negative feedbacks.

In conclusion, there is abundant evidence for the roles of soil fertility, heterogeneity, and microbes, by themselves, in driving grassland diversity, composition, and dynamics, yet there is still much unexplained variation and a complete picture is lacking. Explicitly integrating these three factors holds promise in making further progress in our understanding of how grassland communities are structured and how we can best restore that structure.

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