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**EMBRACING VARIABILITY IN THE APPLICATION OF PLANT-SOIL
INTERACTIONS TO THE RESTORATION OF COMMUNITIES AND
ECOSYSTEMS**

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Abstract

Plant-soil interactions are the foundation of effective and sustained restoration of terrestrial communities and ecosystems. Recent advances in ecological science have greatly contributed to our understanding of the effects of soil conditions on plant community dynamics, and our understanding of plant composition impacts on almost every aspect of soil structure and function. While these theories provide important guidelines for the practice of restoration, they often fall short of providing the level of information required to make effective site-specific management decisions. This is largely because of ecology's search for simple unifying theories and the resulting tendency to generalize from studies at one or only a few sites. An average effect or broad-scale simple relationship tends to provide a "one size fits all" (or none) prescription for managers. Plant-soil interactions can vary greatly depending on their context (e.g. environmental conditions, management practices, time, neighboring community, interaction with other organisms). The ability to predict these context-dependent interactions between plants and soils can be developed by building upon existing general frameworks for understanding plant-soil interactions. Collaborations between researchers and managers can develop conceptual tools that allow us to understand and manage the variability and complexity of plant-soil interactions, simultaneously advancing theory and applicability.

Keywords

plant-soil interactions, plant traits, restoration, species effects, context-dependence, microbial communities, soil nutrients

Introduction

Ecological restoration embraces a broad range of goals, ranging from amelioration of highly degraded abiotic conditions (e.g., toxic pollutant levels and the absence of topsoil on old mine sites), to the reinstatement or enhancement of key ecosystem functions (e.g., production, erosion control, water flow and quality), to the reestablishment of a target biotic community (e.g., rare species, native species, high diversity, few invasive species). In terrestrial ecosystems, plant-soil interactions are the foundation for effective and sustained achievement of any of these goals. Soil conditions constrain plant performance and community composition (Grime 2001, Pywell et al. 2003), and attempts to restore plant communities are likely to fail if they don't consider the limitations imposed by soil conditions. On the other hand, plant composition can impact almost every aspect of soil structure and function (Wardle 2002, Eviner and Chapin 2003), so that restoration of soil conditions is often best achieved by using plants as tools to alter soils (Sarrantonio 1994, Ingels et al. 1998, Whisenant 1999, Eviner and Chapin 2001). Bidirectional feedbacks between plants and soils have the potential to be major tools for restoration (e.g., initial colonizing plants ameliorating poor soil conditions) or major obstacles to restoration (e.g., invasive species altering soil conditions to benefit themselves) (Suding et al. 2004, Ehrenfeld et al. 2005, Vinton and Goergen 2006, Levine et al. 2006, Krueger-Mangold et al. 2006).

While ecological theory can provide useful guidelines for multiple restoration goals, it often falls short of providing the level of information required by managers to

develop and implement a successful restoration project (Table 1). In a review of 87 restoration projects, Lockwood and Pimm (1999) found that 19.5% were completely unsuccessful, an additional 48% of the projects only met some goals, and 13% met all goals, but required continued management to sustain these goals. Fewer than 1 in 5 projects were viewed as successful, and most of these had relatively modest goals. Many restoration failures can be attributed to site-specific issues that haven't been taken into account (Wassenaar et al. 2007), an inevitable outcome when restoration success from a handful of sites is used as a broad-scale prescription, and when the inherent variability and complexity that dominate many of our data sets are minimized in favor of simple ecological principles (Hildebrand et al. 2005). For example, management practices that successfully increased native plant diversity at some dune sites resulted in increased exotic plant diversity when applied to other dune sites (Mason and French 2007).

Currently, restoration failures are often dismissed as “problem sites” (Wassener et al. 2007), but it is critical to incorporate these failures into our conceptual understanding (Hackney 2000) by fitting the results of individual restoration projects into a mechanistic framework that accounts for site-specific conditions— allowing us to focus on *why* responses are variable, rather than just pointing out that a site differs from the average response. In this paper we:

(1) Review recent advances in our understanding of plant-soil interactions, focusing on plant traits to explain plant responses to and effects on soils, and how these can be used as tools for effective restoration.

(2) Cite examples of context-dependence that highlight the need to move beyond broad-scale generalizations to an understanding of site-specific conditions.

(3) Lay out mechanistic frameworks that can be used to develop a predictive understanding of how plant-soil interactions vary across sites, time, biotic communities, and management practices.

Incorporating context-dependence into predictive, mechanistic frameworks has the potential to result in a level of understanding that will improve the ability of managers to implement effective site-specific restoration efforts.

Ecological Frameworks as Management Tools: Moving from Broad-Scale Generalizations to Site-Specific Recommendations

Ecological science has made great strides in advancing our understanding of soil impacts on plants (response traits) and plant impacts on soils (effect traits). However, these advances have primarily been generalizations at the broad-scale, which can be useful tools at some level, but have limited ability to guide decisions at the site-level (Table 1).

Plant Response Traits

Plant Response Traits – General Frameworks

Plant ‘response traits’ determine the response of a plant to its environment (Keddy 1992, Lavorel and Garnier 2002) (Table 2). These traits allow restoration practitioners to determine the habitat conditions needed to support a given species, select which species are

best suited to site conditions, or predict which species will be competitively superior under a given set of conditions.

The probability of restoration success will increase by selecting species most suitable to the environmental conditions at the site. Grime's C-S-R approach (Table 2) allows us to select species for restoration sites based on traits that make them more suitable to tolerate conditions of competition, stress, or disturbance (Grime 1986, 2001, reviewed in Whisenant 1999). Similarly, Chapin (1993) has shown that different suites of traits are associated with plants growing at low fertility versus high fertility sites (Table 2). Other studies have identified traits that determine species response to aboveground grazing or fire, with different disturbances leading to selection for different suites of traits (Grime 2001, Rusch et al. 2003, Lloret and Vila 2003, Diaz et al. 2007), which are critical for understanding how species will respond to management practices often employed in restoration projects.

These trait-based approaches also allow us to identify mismatches between current site conditions and those required by the species we'd like to restore, providing an understanding of how site conditions must be altered to promote a target species for restoration. For example, Chapin's fertility framework (Table 2) allows us to determine if sites need to be fertilized or have nutrients removed in order to promote a given species. Based on this type of understanding, carbon (C) additions to soil are increasingly being used to sequester nitrogen (N) in the microbial biomass, thus decreasing the fertility of a site to promote species that are more successful under low nutrient conditions (Blumenthal et al. 2003, Krueger-Mangold et al. 2006).

The study of response traits also provides us with a reality check of what is possible by demonstrating that there are some inevitable constraints and trade-offs in our selection of plant species at restoration sites. For example, we might desire fast-growing plants to establish at abandoned mine sites or at sites that have lost most of their topsoil, but the species that can tolerate these toxic or low fertility soils are generally slow-growing plants and in most cases, stress tolerant plants will be the best (or only) choice for the current conditions. Response traits and their tradeoffs are the basis for state and transition models used to understand ecosystem degradation and potential for restoration (Gondard et al. 2003, Suding et al. 2004).

Site-Specific Response Traits

As discussed above, response traits provide a powerful tool for determining which species are suitable for sites that differ broadly in environmental conditions, or which broad conditions must be achieved in order to favor a target species or community. While these are powerful frameworks at this broad scale, they are less useful when trying to manage community composition among plants that are all suited to a given set of conditions. This is often the case with restoration projects that focus on replacing exotic communities with native communities at a given site. In many instances, both sets of species are well-suited to the same broad set of conditions (e.g., high fertility), so there's a need to determine which response traits explain species distributions at local scales. We will explore local response traits related to resource use in some detail, because these are likely to provide useful and effective targets for management. A parallel approach can be

used for other mechanisms underlying local restoration success, such as response to disturbances or management practices.

Species prevalence may be a function of key soil characteristics or functions in relation to response traits that determine resource use:

- *How much* resource is required
- *When* resources are used (e.g., are invasives exploiting a phenological niche that the natives do not?)
- *Where* resources are obtained spatially (e.g., differences in rooting distribution)
- *Which* resource forms are used (e.g., differences in preference for NH_4 vs. NO_3)
- *What* balance of multiple resources is required (e.g., stoichiometry)
- *What* associations are exploited to access resources or alter resource states (e.g., mycorrhizal fungi, nitrifiers)

Understanding these differences across species allows us to target management actions to alter resource conditions in a way that promotes the desirable species. In some systems, much of this information is already available and could be used to modify current restoration approaches – here we discuss California grasslands as a detailed example.

Restoration efforts in California grasslands that endeavor to establish native perennial grasses and oust exotic annual grasses may be able to take advantage of differences in the timing, location, and form of resources used (Fig 2). Nutrient uptake by native perennials occurs throughout the growing season and into the summer, as well as at deeper soil levels, compared to shallow-rooted annuals that access fall and early-spring nutrient pulses (Heady et al. 1991, Brown 1998). Exotic annuals and native perennials in

California grasslands also differ in the form of N they take up, with exotics taking up proportionally higher NO_3 than NH_4 (Davidson et al. 1990). Restoration efforts have exploited the phenological differences in resource use by adjusting the timing of controlled burns or herbicide applications targeting exotics, with varying success in California grasslands (reviewed in Stromberg et al. 2007, DiTomaso et al. 2007). Because exotic annuals have a slight tendency to out-compete native perennials under higher nutrient conditions (reviewed in Corbin et al. 2007), reducing soil nutrient availability may also promote successful restoration. To shift competitive outcomes based on phenological differences in nutrient uptake, attempts to decrease soil nutrients should be made in the fall and early spring, when exotics take up most of their N (Fig 2).

Manipulation of soil resources aimed at a reduction of site nutrient levels is usually attempted through C additions to soil in the form of sugars or sawdust. Even when local response traits are considered, however, the effectiveness of C additions greatly varies across projects. This method has had mixed results in California grassland restoration (reviewed in Corbin et al. 2007), as well as in restoration of a number of different systems (Blumenthal et al. 2003, Krueger-Mangold et al. 2006). The type and amount of C required to reduce N levels depends on both site conditions and plant species, with no clear, consistent relationship between C added and N sequestered (Blumenthal et al. 2003, Rowe et al. 2006). Despite a rich literature exploring the interactions between C and N in the soil (van de Geijn and van Veen 1993, Kuzyakov 2002, Hyvonen et al 2007, Blagodatskaya et al. 2007), there is still relatively little ability to predict how these interactions change across sites, highlighting the need to carefully consider context-dependence. An alternative

approach in the case of California grasslands, where the exotic annual grasses prefer NO_3 and also promote larger populations of ammonium oxidizing bacteria (Hawkes et al. 2005), might be to add nitrification inhibitors to reduce the amount of NO_3 in soil.

Clearly, an understanding of site-specific response traits (where, when, what, etc.) is a critical step towards improving our restoration strategies, but some key questions that need to be addressed include:

- (1) Does successful restoration require attainment of all of these resource conditions (what, where, how much, who, etc.), or only a subset?
- (2) What are the factors that govern which resource conditions are the most important, and how their relative importance changes under shifting environmental conditions and across scales?

Both successful and failed restoration projects can be used to increase our understanding of how these resource traits shape community interactions, and thus successful restoration strategies.

Similar to response traits to soil resources, response traits to management impacts (e.g., grazing, fire) can show strong general patterns, but also important changes across sites (Pakeman 2004, Fynn et al. 2005, Diaz et al. 2007). Diaz and colleagues (2007) found that a number of conceptual frameworks differ in their predictions of plant community response to aboveground grazing, because they were based on local or regional studies that varied in which traits determine plant response to grazing. By analyzing a global database of plant-grazing interactions, they found that across a global scale, key traits that are favored by grazing are: annual growth habit, short-stature, prostrate growth, and

stoloniferous or rosette architecture (as opposed to tussock). However, the strength of these traits in predicting responses to grazing can change depending on precipitation and grazing history. For example, in most grassland sites across the globe, grazing can be used to favor annual over perennial plants, but this will not be an effective management tool in dry regions with a long evolutionary history of grazing (Diaz et al. 2007). Their approach sets the stage for a trait-based framework that can bridge both global generalizations and site-specific conditions.

Plant Effect Traits

Plant Effect Traits – General Framework

Plants not only respond to soil conditions, they can also shape them. Plant ‘effect traits’ (Violle et al. 2007) can predict the effect that different plant species have on a wide variety of soil conditions and processes (Table 3, Wardle 2002, Eviner and Chapin 2003). Manipulation of vegetation composition is a traditional tool for providing key ecosystem services to agriculture and restoration (Sarrantonio 1994, Ingels et al. 1998, Eviner and Chapin 2001), and is the most effective long-term method for soil restoration (Whisenant 1999). When comparing species across a broad range of environmental conditions, species are often found to have suites of related traits which maintain the current flux of nutrients (Chapin et al. 1993, Lavorel and Garnier 2002). For example, the species that can tolerate low fertility sites also tend to have traits that foster slow rates of nutrient recycling (e.g., lower litter quantity and quality) (Chapin et al. 1993). Thus, just as the conventional approaches to response traits are powerful at broad scales, the use of functional groups or

single traits such as litter chemistry can predict plant species effects on soil processes such as N cycling at regional scales across steep gradients of abiotic conditions (Taylor et al. 1989, Scott & Binkley 1997) because at such a coarse scale, environmental conditions select for certain suites of plant traits (Chapin et al. 1993, Diaz and Cabido 1997, Diaz et al. 1999, reviewed in Eviner and Chapin 2003).

As with response traits, there are tradeoffs among the effect traits that a species may have—limiting the options of multiple soil conditions that can be restored with a given plant species. For example, species with quickly decomposing litter may enhance nutrient cycling, but their decreased litter layer will provide poor insulation for soil during cold periods (Eviner 2004). The restoration of multiple soil conditions can be achieved, however, by planting a mixture of species with different effect traits (but see mixture section below). The effects of plants on ecosystems can also be used as a tool for restoring target plant communities, by using particular species to shift soil conditions to a state more suitable for the desired species (Krueger-Mangold et al. 2006). For example, Herron and colleagues (2001) increased the presence of the native blue bunch wheatgrass (*Pseudoroegneria spicata*) ten-fold over the exotic spotted knapweed (*Centaurea maculosa*) by seeding in annual rye (*Secale cereal*) to draw down soil N.

Context Dependence of Plant Effects on Ecosystems - Abiotic Conditions

While single traits or functional groups can be powerful predictors of plant effects on N and C cycling at large scales, traits that strongly co-vary over steep environmental gradients may vary independently across species at local scales, so that variation of traits

within a site can be substantial (Lavorel and Garnier 2002, Ackerly and Cornwell 2007). Relationships between litter quality and N cycling are often weak within a given site (Steltzer & Bowman 1998, Eviner et al. 2006) because the other mechanisms that determine plant effects on N can vary independently from litter chemistry (Eviner 2004). The use of multiple traits is better than one-dimensional functional groups for predicting site-level differences in functions among species (Shock et al 1983, Wedin and Tilman 1990, Cheng and Coleman 1991, Steltzer and Bowman 1998, Bottner et al. 1999, Eviner and Chapin 2003, Mack and D'Antonio 2003, Eviner et al. 2006) and can be the basis of a local-scale functional effect framework (Eviner and Chapin 2003).

A functional effect framework could be critical not only in discerning differences across species locally, but also to account for shifts in the effects of a given species across changing conditions. For example, legumes are frequently planted to increase soil N availability in agriculture and restoration (Eviner and Chapin 2001), but when *Lupinus bicolor* was planted into similar plots, some plots showed high enhancement of soil N cycling rates, while other plots showed little to modest increases in N mineralization -- no plot provided the average value for this species (Figure 1). It is far more useful for a manager to know the conditions under which this legume will provide N, than it is to know the average effect of the species. Similarly, the restoration of native California grasses is often justified based on the ecosystem services they provide - such as decreasing N leaching. However, different studies in California have shown opposite patterns of whether exotic versus native grasses are more effective at minimizing N leaching (reviewed in

Eviner and Firestone 2007). Similarly, the effects of native grass restoration on soil properties in the Midwestern US change with soil type (Kucharik 2007).

Many studies have demonstrated that the ecosystem effects of a given species are not constant (reviewed in Ehrenfeld 2003). Both the values and relative ranking of species effects on N and C cycling can change across sites (Lovett and Rueth 1999, Scheffer et al. 2001, Kalburtji and Mamolas 2000, Verchot et al. 2001, Bridgham and Richardson 2003). These variations in the soil effects of a given species can be as great as the variation across different species coexisting at a site (Eviner 2001, Bridgham and Richardson 2003, Eviner et al. 2006). Shifts in the absolute and relative effects of plant species on soil due to environmental changes have been documented for a wide variety of soil characteristics and processes, including microbial biomass (Johnson et al. 1998, Priha et al. 1999, Zak et al. 2000), microbial resistance and resilience (Orwin and Wardle 2005), fungal colonization of roots (Rillig et al. 1998), methane consumption (Menyailo and Hungate 2003), formation of humus (Berg 2000), and fluxes of many soil nutrients (Raulund-Rasmussen and Vejre 1995, McKenzie et al. 1995). It will be invaluable for restoration managers to predict which species will provide specific services at a given site, or how the services provided by a given species will change as conditions vary within a site or across the landscape.

Functional context-dependent predictions can be made by incorporating existing approaches that predict species effects based on multiple plant traits (Eviner and Chapin 2003), with an understanding of how environmental conditions determine:

- (1) the relative importance of which traits impact ecosystem processes,
- (2) individual trait values, and

(3) the ecosystem effect of a given trait.

These three mechanisms are discussed below, and an understanding of the relative importance of these mechanisms will enable us to identify the key factors that will predict the context-dependence of species effects.

1. The relative importance of these traits may change across abiotic gradients

Seasonal and site-dependent effects of species can be due to fundamental shifts in which traits control soil processes (Bradley and Fyles 1996, Hobbie 1996, Eviner 2001, Evans et al. 2001, Scott et al. 2001, Scheffer et al. 2001, Mack and D'Antonio 2003, reviewed in Ehrenfeld 2003). For example, the importance of litter C/N in determining plant species effects on N cycling decreases as soil moisture becomes limiting (Vinton and Burke 1997, Steltzer and Bowman 1998, Burke 1989). Similarly, in unfertilized watersheds, net N mineralization is strongly influenced by soil moisture and soil temperature, but fertilized sites are less sensitive to changes in microclimate (Gilliam et al. 2001).

2. Individual traits change in response to environmental conditions

Environmental conditions can have large effects on many plant traits that are key regulators of soil characteristics (Table 4). The magnitude of trait variation within a species under different environmental conditions can be as great as the variation in plant traits known to determine differences in the ecosystem effects of different plant species (Olf 1992, van der Krift et al. 2001, Hobbie and Gough 2002, Westoby et al. 2002).

3. The effects of traits change depending on environmental conditions

The ecosystem effects of a species can vary by site because the relationship between traits and ecosystem functions may change under different environmental conditions (Meetenmeyer 1978, McTiernan et al. 2003, Donnelly et al. 1990, Hobbie 2000, Vesterdal 1999). For example, at nutrient poor sites, species with high initial litter N have a greater amount of litter that becomes stable humus, but this relationship is not seen at nutrient-rich sites (Berg et al. 2003). Similarly, labile C can stimulate decomposition of recalcitrant litter and soil organic C under low nutrient conditions, because microbes use labile C as an energy source to metabolize recalcitrant C in search of N. With high N availability, labile C decreases decomposition because microbes utilize the labile C and N and do not need to break down recalcitrant substances (Sparling et al. 1982, Reid and Goss 1983, Billes et al. 1988, Liljeroth et al. 1994, Cheng 1996, van Ginkel et al. 1996). This interaction of labile C, litter chemistry, and nutrient availability likely is responsible for the fact that increasing soil N availability can stimulate (Hunt et al. 1988, Berg and Tamm 1994, Hobbie 2000) or inhibit decomposition (McClaugherty and Berg 1987, Prescott 1995, Magill and Aber 1998), with some of this variation depending on species or site (Aerts and De Caluwe 1997, Hobbie 2000).

Context Dependence of Plant Effects on Ecosystems - Time

When plants are used in restoration to promote certain soil processes and characteristics, we must consider that plant-soil interactions can vary over time, ranging from seasonal cycles to long-term trends. The mechanisms that account for time-dependent effects include short- to long-term changes in plant traits and their relative importance in

mediating an ecosystem process, accumulation of trait effects, and persistence of trait effects, even after the species has been removed.

1. Plant effect traits and their relative importance change with time

Both the values and relative importance of plant species effects on N and C cycling can change seasonally (Harris and Safford 1996, Mack and D'Antonio 2003, Eviner et al. 2006). Seasonal changes in species effects are largely phenological, but are also partially due to changes in the controls of N cycling over the growing season, similar to shifts in abiotic conditions described above (Bradley and Fyles 1996, Eviner 2001, Mack and D'Antonio 2003). Long-term changes in species effects may be observed (reviewed in Strayer et al. 2006), as some traits shift with plant age and other trait effects accumulate to detectable levels (e.g. gradual build-up of soil organic matter). For example, restoration of native tallgrass prairie species into former agricultural land have marked effects on soil C and N cycling, but these effects change over time, with storage of soil C increasing over the first 5-10 years, and then varying in its trajectory as the restored stands age (Baer et al. 2002, Camill et al. 2004, Kucharik 2007).

2. Plant trait effects on soils are persistent through time

Species effects on soil processes and properties can persist for years after the species have been removed. Agricultural rotations are the best evidence that such effects can persist after one plant species has been replaced with another. Specific plants are grown in order to rebuild soil fertility or suppress soil pathogens, with the goal of affecting subsequent crop performance (Magdoff & van Es 2000; Larkin 2003; Newton et al. 2004). Similarly, the effects of invasive plants on microbial communities, soil characteristics, and

nutrient cycles are likely to persist even after removal of the exotics. These legacy effects can influence growth and successional pathways of the new plant community (Larkin 2003). In California grasslands, plant legacies of total soil N and net N mineralization persisted for three years, while legacy effects of nitrification persisted for over five years, *but only were detectable during wet growing seasons* (Eviner personal communication).

Plant Mixtures- Integration of Response and Effect Traits

Using Plant Mixtures to Provide Multiple Effect and Response Traits in Time and Space – General Framework

Species mixtures have long been used to provide multiple functions. For example, in agricultural systems, crops can provide productivity, while other key services are provided by covercrops (e.g., legumes for soil fertility, mustards to control harmful nematodes) (Eviner and Chapin 2001). By considering both response traits and effect traits, mixtures of species can be selected so that, collectively:

1. Multiple services are provided by selecting species with different effect traits
2. These services are provided consistently over time and across changing conditions because within each functional group, multiple species are included that differ in their response traits.

Restoration strategy can capitalize on the substantial advances made in the field of biodiversity and ecosystem function. In general, when diversity is manipulated *at the plot-level*, increased species richness is associated with increased production and increased resistance to invasions. This is largely due to species differing in their response traits, so

that multiple species can more effectively consume resources, and explains why the identity of species in the mixtures have a stronger impact than simply species richness (reviewed in Levine et al. 2002, Bengtsson et al. 2002). In instances where the roles that individual species play in productivity and invasion resistance are not known (which is many cases of management), these plot-scale studies suggest an important benefit to including multiple species in a planting. The relationship between species richness and production or invasion resistance is different when looking at unmanipulated distributions of these factors across landscapes. In this case, sites that are diverse tend to be lower-productivity sites and also tend to have a higher richness of invaders present (reviewed in Levine et al. 2002, Bengtsson et al. 2002). This landscape-level correlation can be a useful tool in site selection for restoration projects, or in understanding the constraints to what goals are possible at a given site.

Non-additive Interactions in Plant Mixtures- Neighbor-specific Changes in Plant Effects and Responses

While much attention has been given to the effects of plant diversity on ecosystem functions and stability (Naeem et al. 1999, Loreau et al. 2001), these studies largely tend to overlook that the effects and responses of a given species in mixture can greatly differ from the species in monoculture. The ecosystem effects of species mixtures can sometimes be predicted based upon the component species in monoculture (Blair et al 1990, Klemmedson 1992, Thomas 1968, Staaf 1980), but also can be lower (Saetre 1998, Finzi and Canham 1998) or higher (Morgan et al. 1992, Taylor et al. 1989, Anderson and

Hetherington 1999, Robinson et al. 1999) than would be predicted based on monoculture results. Non-additive effects are very common (Wardle et al. 1997, Briones and Ineson 1996) and can depend on the species in mixture (McTiernan et al. 1997, Nilsson et al. 1999, Fyles and Fyles 1993, Briones and Ineson 1996) or change over time, even for a given species mixture (McTiernan et al. 1997, Fyles and Fyles 1993, Wardle et al. 1997). While non-additive effects are prevalent, there is little insight into when to expect additive effects versus positive or negative non-additive effects. This is a critical point when trying to restore plant-soil interactions or specific soil attributes.

Again, a mechanistic trait-based understanding of these non-additive effects will be essential to both enhancing and applying our ecological understanding. Non-additive effects of mixtures can be due to:

1. Changes in a species trait due to neighbors

Many traits are known to change when a given species is grown in mixtures versus monoculture, including nutrient concentrations (Welker et al. 1991, Thornton & Millard 1996), root:shoot allocation (Theodose & Bowman 1997, Ba et al. 2006), plant architecture (Ikeda et al. 1994, D'Antonio et al. 1998, McConnaughay & Bazzaz 1992, Rodriguez & Brown 1998), water use efficiency (Burton & Bazzaz 1995, Szente et al. 1993), and timing of nutrient uptake (van den Boogard et al. 1995). Differences in litter C:N ratios and labile C in species grown in mixtures versus monocultures account for the non-additive effects of mixtures on N cycling (Eviner 2001). Such neighbor-induced changes in species traits can also impact competitive interactions and species' responses to management practices and shifts in environmental conditions.

2. Unique combinations of traits in mixtures not present in individual species

Trait combinations can result in unexpected effects of species mixtures. For example, labile C inputs (e.g. through root exudation) can prime microbial breakdown of more recalcitrant substrates (Seastedt 1984). Similarly, nutrient additions can prime microbial utilization of other substrates (Vestgarden 2001, Ehaliotis et al. 1998). In contrast, plant secondary compounds can inhibit microbial activity, decreasing microbial utilization of more labile substrates, leading to overall decreases in C and N cycling (Handayonto et al. 1997, Swift et al. 1979).

Restoration managers need to consider not only the identity of plants, but also their density. Neighbor density can greatly impact plant traits and plant-soil feedbacks. Grasses in high density stands can have increased forage quality due to higher allocation to leaves than to stems (Pyke & Archer 1991). Density can also greatly impact plant allocation, biomass production, nutrient content and concentration, and litter chemistry (Eviner and Uriarte, personal communication).

A mechanistic understanding of non-additive interactions in species mixtures is critical for managing both the effects and responses of diverse restoration plantings. These neighbor-induced changes in both resource and effect traits are likely to interact with other site-dependent factors reviewed above.

Soil-Plant Interactions as Impacted by Soil Microbial Communities

At the heart of plant-soil interactions lies the microbial community. Microbial communities:

- are ultimately responsible for most biogeochemical transformations in soil,
- can play a significant role in impacting soil structure, and
- can have strong effects on plant growth and competitive dynamics.

Restoration success can require the presence of key microbial groups, particularly those microbes that are obligate or facultative symbionts with plant roots. Plant seedlings grow substantially better when planted into a community with established mycorrhizal connections than in disturbed sites or in isolation (reviewed in Whisenant 1999). In some cases, such as with pine trees, establishment requires simultaneous introduction of plants and ectomycorrhizal fungi if these root symbionts are not already present. Addition of symbiont inoculum can also facilitate restoration efforts when microbial communities have been disturbed or altered. Mycorrhizal inoculations, for example, have been shown to increase plant establishment and growth (Cuenca and Lovera 1992), increase soil organic matter, nitrogen, and aggregation (Requena et al. 2001), and alter succession by shifting competitive interactions between plants (Allen and Allen 1990). In addition, inhibiting microbial symbiont establishment can be used as a tool to reduce establishment and growth of unwanted species. For example, in the absence of AMF and actinorhizal *Frankia*, native oleaster shrub growth decreased by four-fold (Visser et al 1991), while growth of an invasive leguminous shrub decreased by five-fold in the absence of specific *Bradyrhizobium* strains (Parker et al. 2006).

The role of microbes in restoration isn't just restricted to the presence or absence of broad functional groups—microbial community composition can greatly impact soil conditions and plant establishment. The diversity of arbuscular mycorrhizal fungi (AMF)

can have large impacts on plant community composition and diversity (van der Heijden et al. 1998). The composition of AMF communities can also be an important determinant of plant dynamics. Restoration of late-successional plant seedlings was more successful with early-successional mycorrhizae than late-successional mycorrhizae, likely because seedlings are more carbon-limited than adult plants and form mycorrhizal associations that reflect a tolerable carbon cost (Allen et al. 2003). Caravaca et al. (2003) found additional specificity of AMF during restoration, with greater restoration success using native AMF compared to allocthonous species. This can be of concern in the reestablishment of native plants in habitats with non-native plants, because exotic plant species can shift AMF communities by as much as 80% (Hawkes et al. 2006), and such invader-induced shifts in microbial composition can benefit the invasive plant over the natives (Callaway et al. 2004).

Plant species can foster distinct free-living and root-associated microbial communities in soils (Jaworski, 1971, Olf et al. 2000, Marschner et al. 2001, Vandenkoornhuyse et al. 2003) that can have positive (Requena et al. 1997, Bever et al. 2001) or negative (Bever 2002, Kollmorgen et al. 1985, Packer and Clay 2004) feedbacks to host plant performance. These effects are especially evident in agricultural systems where specific crop plants are actively used to stimulate microbial disease suppression (see reviews in Weller et al. 2002, Garbeva et al. 2004, Mazzola 2004). The effective use of cropping strategies to increase populations of soil microbes, such as fluorescent pseudomonads, that are antagonistic to plant pathogens implies similar approaches could be used to restore microbial communities outside of agricultural systems. However,

success in simplified agricultural monocultures may not easily transfer to more complex natural communities.

Microbial communities and their interactions with plants exhibit context dependence much like what we see in plant communities. For example, plant effects on soil microbial communities depend on the site and soil type, and these changes in plant-microbial interactions across sites have very different feedbacks to plant performance (Bezemer et al. 2006). Similarly, the identity, phenology, and density of neighbors in a mixed plant community can impact the composition and structure of soil microbial communities (Hausmann and Hawkes, in preparation, Hawkes et al. 2005, Hawkes et al. 2006, Lawley et al. 1982, Lawley et al. 1983, Hartnett et al. 1993, Jastrow and Miller 1993, Westover 1997, Whisenant 1999), which again, has the potential to alter soil properties and processes and plant performance. Microbial community composition, biomass, and function can also vary with soil type, environmental conditions, and land management independently of plant species composition and dynamics (Hawkes et al 2007, Williamson and Wardle 2007, Garbeva et al. 2004). The context dependence of microbial communities suggests that restoration efforts are unlikely to foster desired microbial communities simply by providing the plants.

Because microbial communities can directly and indirectly affect plant success and ecosystem processes such as SOM formation, decomposition, CO₂ production, and N cycling (Balsler and Firestone 2004, De Boer et al. 1996, Schimel et al. 1995, Treseder and Allen 2000, Hawkes et al. 2005), successful restoration may need to actively target both plant and microbial communities, and their interactions. As with the other examples

discussed above, a focus on the traits of both plants and microbes will allow us to better understand the effects of plants on microbes, the effects of microbes on plants, how plant-microbial interactions impact soil properties and processes, and how all of these interactions change with changing conditions (e.g. Orwin and Wardle 2005, Orwin et al. 2006). There is far less known about the details of what controls interactions between plant communities and microbial communities, so that a context-dependent framework is not presented here, as it had been for the other sections. However, data from restoration projects can greatly enhance our understanding of these interactions.

Conclusion

Restoration practitioners are faced with considerable challenges. To effectively restore an ecosystem or ecological community, it is often critical to consider multiple species, multiple functions, and their interactions. Furthermore, the restoration of self-maintaining systems is increasingly requiring the consideration of human-induced local- to global-scale environmental changes. The study of plant-soil interactions provide an important foundation for restoration, but the application of these principles often fails the “acid test” proposed by Bradshaw (1987). This is largely because broad-scale generalizations and “average effects” fail to provide managers with the information they need to address site-specific conditions. In order to help managers with the challenge of designing successful restoration techniques at a specific site, we need to embrace the variability of ecological studies and develop frameworks to understand this variability (rather than having physics envy). “It depends” may very well be the one unifying simple principle of ecological science, making studies of context-dependence a critical frontier in

both the theory and application of ecological science. Current conceptual frameworks of plant-soil interactions provide a strong foundation to build upon, and in this paper, we present a number of mechanistic frameworks that can advance our understanding of plant-soil interactions. Collaborations between researchers and restoration practitioners will provide the most rapid development of an understanding of context-dependence, by coupling such theoretical frameworks with the critical data of the conditions underlying successes and failures in individual restoration projects.

Implications for Managers

- Ecological theory on plant-soil interactions provides a critical foundation for restoration strategies
 - Predictions of plant responses to soil conditions are critical in choosing sites, determining which species can thrive at a given site, and predicting which species will out-compete others at a site
 - Selection of plant species can be an important tool to impact almost every aspect of soil conditions
- Most current theories on plant-soil interactions focus on broad-scale generalizations or “average effects”, but interactions between plants and soil can change with environmental conditions, management practices, time, and the identity and density of neighboring species. This context-dependence limits the ability to apply current ecological theory to site-specific conditions

- A predictive understanding of how plant-soil interactions vary can be developed by building on existing theory, but requires collaborations between managers and researchers to link the theoretical frameworks with the on-the-ground data of the conditions underlying success or failure in individual restoration projects.

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Table 1: Ecological principles as tools for restoration practice, and conceptual tools needed to better predict context-dependence.

Restoration Goal	Tools provided by generalized ecological concepts	Strengths and limitations of generalized framework	What we need to know to develop a framework of context-dependence
Plant composition	<p>Response traits provide:</p> <ul style="list-style-type: none"> - Selection of species suitable for a given site - How to alter a site to be suitable for a given species - How environmental shifts or management will impact competitive interactions - Limitation /tradeoffs of what's possible <p>Diversity theory provides:</p>	<p>Works well across sites that differ greatly, does not provide insight into species responses or interactions within a given set of conditions at a site</p> <p>Works well across broadly different</p>	<ul style="list-style-type: none"> - Specifics of resource use (who, what, where, when, how much) - Do all of these resource conditions need to be addressed, or are there key conditions that are most important? - What are the factors that determine which resource traits are most important and how their relative importance changes under different biotic and abiotic conditions?

	<p>- An understanding of sites/environmental conditions are conducive to fostering high plant diversity, or thwarting invasions</p> <p>Plant-microbe interactions provide:</p> <p>- Identification of key microbial groups or specific microbes necessary for fostering the desired plant community</p>	<p>sites, requires an understanding of context-dependent response traits (see above) to address specific sites and species combinations</p> <p>The basic understanding of plant-microbial interactions is still incomplete. Basic questions include:</p> <p>- How do plant and microbial traits predict plant effects on microbes and microbe effects on plants?</p> <p>- To what extent are plant and microbial responses to biotic and abiotic changes coupled?</p>	<p>- How do neighbors affect response traits, thereby altering plant interactions?</p> <p>Once this basic understanding increases, the same types of questions listed above, can be addressed for plant-microbial interactions.</p>
Ecosystem	Effect traits provide:	Works well for species from sites that	- How do the relative importance of

<p>function</p>	<ul style="list-style-type: none"> - Selection of species that are likely to provide a given service - Limitations/ tradeoffs of what's possible <p>Diversity and ecosystem function theory provides:</p> <ul style="list-style-type: none"> - General pattern of increased diversity enhancing productivity, decreasing nutrient leaching, and protecting against invasions - General pattern of providing ecosystem services over time and 	<p>differ greatly, does not provide insight into species effects within a given set of conditions at a site, or how a given species changes its affect across sites or time</p> <p>Provides a general fallback method for restoration when little is known about the specific attributes of species.</p> <p>Specific understanding of species' site-specific effect and response traits provide stronger tool. Does not account for non-additive effects, which are strong determinants of the effects of</p>	<p>traits in determining ecosystem processes change with environment?</p> <ul style="list-style-type: none"> - How do trait values change in response to the environment? - How do the effects of a given trait change with environment? - How do species traits change due to neighbors? - How do interactions of different traits (from different species) affect ecosystem processes?
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	<p>changing conditions due to functional redundancy</p> <p>Plant-microbial interactions provide:</p> <ul style="list-style-type: none"> - The need for key microbial groups or specific microbes to provide given ecosystem functions 	<p>species mixtures.</p> <p>The basic understanding of plant-microbe interactions is still incomplete, and limitations in microbial community analyses and links between structure and function limit the type of understanding we have for plant-ecosystem interactions. Basic questions include:</p> <ul style="list-style-type: none"> - How do plant communities, microbial communities, and plant-microbial interactions impact ecosystem processes? 	<p>Once the basic understanding increases, the same types of questions listed above, can be addressed for plant-microbial interactions.</p>
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Table 2. Response traits are a guide to predict which species are most suited to broad-scale differences in site conditions.

Site conditions	Traits of species suited to site conditions	Reference
<i>Competitive</i> - low stress, low disturbance (sites with potential for rapid growth)	Rapid growth Low reproductive allocation Little storage Long or short lived	Grime 1986, 2001
<i>Stressful</i> - Harsh abiotic conditions, resource limited, potentially exposed to toxins, extreme temperatures	Long-lived Occasional flowering Slow growth Low reproductive allocation Storage of carbon and nutrients	
<i>Disturbance</i> - frequently disturbed sites, sites with unpredictable growing conditions	Very short-lived Frequent flowering Rapid growth High reproductive allocation Storage in seeds	
<i>High fertility site</i>	High growth rate High tissue N	Chapin et al. 1993

<i>Low fertility site</i>	High water use High nutrient uptake Low C-based defenses Low root:shoot ratio High leaf turnover rate Low growth rate Low tissue N Low water use Low nutrient uptake High C-based defenses High root:shoot ratio Low leaf turnover rate	
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Table 3. Multiple traits that influence plant species effects on soil properties and processes (reviewed from Eviner and Chapin 2003).

SOIL PROPERTY	PLANT TRAITS THAT INFLUENCE THIS PROPERTY
Soil temperature	aboveground biomass, shoot morphology, aboveground litter persistence (litter chemistry and structure) and color
Soil moisture	biomass, shoot morphology, litter persistence (litter chemistry and structure), water uptake, rooting area, leaf area, phenology, species effects on soil structure and water holding capacity
Soil pH	cation pumping, form of N uptake, organic acids in exudates/litter
Soil C/N Soil organic matter	litter & tissue chemistry, biomass, allocation (particularly to roots), exudate quantity and quality, species effects on microclimate and microbes
Available inorganic N	litter and exudate quantity and quality, root turnover, plant uptake, phenology, species effects on organic matter, pH and microclimate
Available inorganic P	litter and exudate quantity and quality, root turnover, plant uptake, phosphatases, phenology, species effects on organic matter, pH and microclimate
Net N cycling	litter and exudate quantity and quality, root turnover, plant uptake, phenology, species effects on organic matter, pH, microclimate, and total and active microbial biomass
Microbial biomass	litter and exudate quality and quantity, plant nutrient uptake,

C,N,P	species effects on organic matter, pH, microclimate, microbial community composition
Water infiltration	root characteristics and turnover, hydrophobic substances, species effects on organic matter and soil aggregation
Water holding capacity	species effects on organic matter, soil aggregation, and pore size
Soil aggregation	litter and exudate quantity and quality, rooting characteristics, species effects on microbes
Soil cohesion	root morphology (particularly surface area, rooting area), C inputs, species effects on organic matter and microbes

Table 4. Environmental conditions that impact the values of plant traits.

Trait	Conditions that alter trait	References
Tissue/litter chemistry	Soil fertility	Crews et al. 1995, Ostertag and Hobbie 1999
	Soil moisture	Del Arco et al. 1991, Pugnaire and Chapin 1992, Vitousek et al. 1994, Austin and Vitousek 2000
	Plant age	Fenner et al. 1999
	Season	Riipi et al. 2002
Root exudation	Soil fertility	Liljeroth et al. 1991, van Veen et al. 1989, Bremer and Kuikman 1997, van der Krift et al. 2001
	Herbivory	Wardle 2002
	Plant age	Smith 1970
	Microenvironment	Martin 1977, Janzen and Bruinsma 1993
	Rhizosphere microbes	Marschner 1995
Phenology	Soil fertility	Nomura and Kikuzawa 2003
Rooting patterns	Soil moisture	Abdul-Jabbar et al. 1982
Tissue allocation	Temperature	Hobbie 1996
	Plant age	Gleeson and Tilman 1994
	Soil moisture	Kalapos et al. 1996
	Soil fertility	Olsthoorn et al. 1991

Figure 1. Most ecological data is inherently variable, but we tend to concentrate on simple summaries of the data—averages or simple relationships between variables. Management prescriptions are usually based on these simple generalizations, which often do a poor job of informing about site-specific conditions. For example, when looking at the effects of *Lupinus* on rates of net N mineralization, no sites produce an average effect (based on data from Eviner et al. 2006).

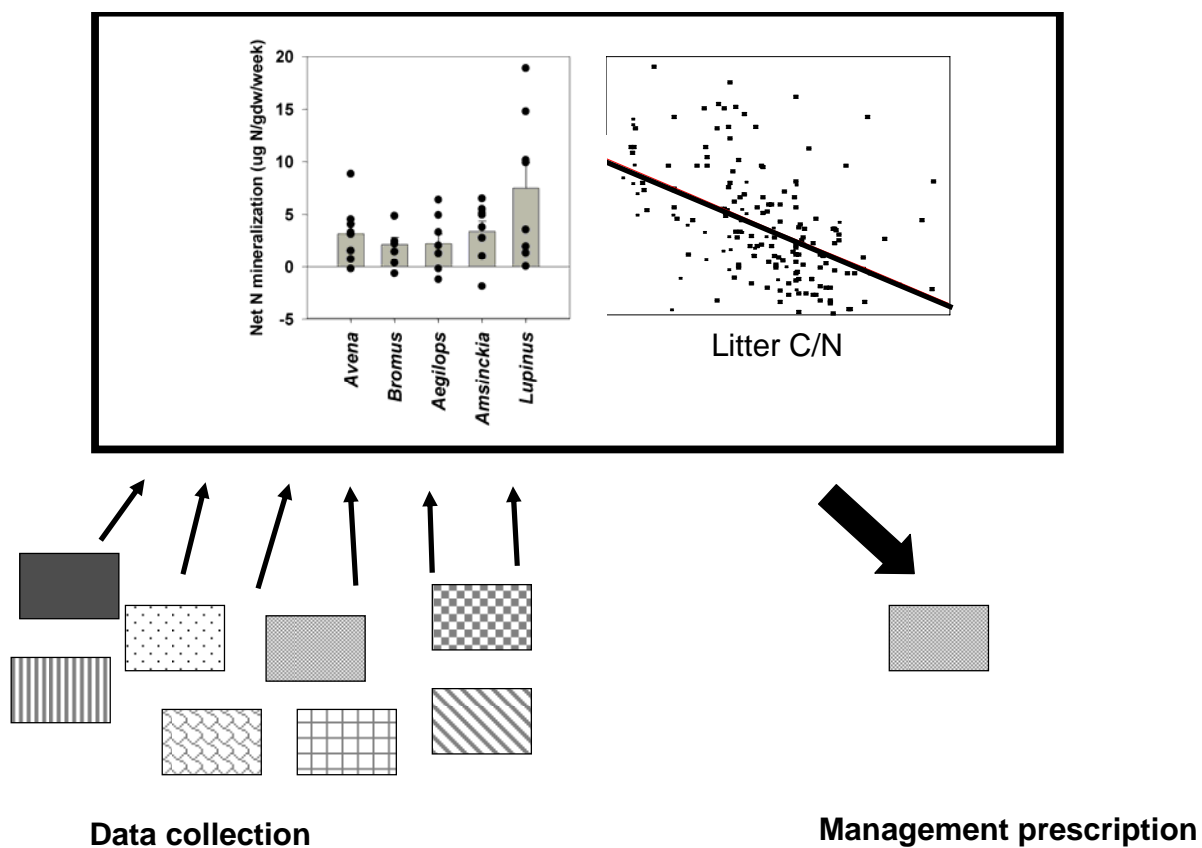


Figure 2. Differences in resource traits among exotic annual and native perennial grasses in California grasslands. These resource differences can inform promising restoration tools (see text for details).

