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Review paper

Plant–soil interactions in metal contaminated soils

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A B S T R A C T

The legacy of industrialization has left many soils contaminated. However, soil organisms and plant communities can thrive in spite of metal contamination and, in some cases, metabolize and help in remediation. The responses of plants and soil organisms to contamination are mutually dependent and dynamic. Plant–soil feedbacks are central to the development of any terrestrial community; they are ongoing in both contaminated and healthy soils. However, the theory that governs plant–soil feedbacks in healthy soils needs to be studied in contaminated soils. In healthy soils, negative feedbacks (*i.e.* pathogens) play a central role in shaping plant community structure. However to our knowledge, the nature of feedback relationships has never been addressed in contaminated soils. Here we review literature that supports a plant–soil feedback approach to understanding the ecology of metal-contaminated soil. Further, we discuss the idea that within these soils, the role of positive as opposed to negative plant–soil feedbacks may be more important. Testing this idea in a rigorous way in any ecosystem is challenging, and metal contamination imposes an additional abiotic constraint. We discuss research goals and experimental approaches to study plant–soil interactions applicable to metal-contaminated soils; these insights can be extended to other contaminated environments and restoration efforts.

1. Introduction

Recent decades have seen a growing interest in the role of facilitation on plant community development and composition with respect to stressful environments (Stachowicz, 2001; Kivlin et al., 2013). Twenty years ago, Bertness and Hacker (1994) demonstrated that the success of a salt-marsh plant community was determined by facilitation from neighbor plants in stressful or anoxic sediments. Since then, the role of facilitation from neighboring plants has been tested along environmental stress gradients (Espeland and Rice, 2007), and the use of 'nurse plants' in facilitating plant community development has been applied to restoration in limiting and harsh environments (Padilla and Pugnaire, 2006; Eränen and Kozlov, 2007). Moreover, recent evidence has shown that facilitation between species within the plant community can enhance phytoremediation of metals in contaminated soils (Wang et al., 2014). The mechanisms of facilitation and remediation are rooted in soils, and this review is focused specifically on plant–soil interactions in metal-contaminated-soils. The contributions by soil microorganisms to remediate metal contamination and the biology of the microbes and their host plants have been well documented (Ma et al., 2011; Sessitsch et al., 2013); this topic is not covered here. However, the dynamic relationships among plants, soil organisms, and metal contamination have not been sufficiently explored. Plant–soil feedbacks, the bidirectional relationships between plants and their soils, can be affected by abiotic factors (Clarholm and Skyllberg, 2013) that pose a selective force on the community. Research has shown that major drivers like climate change (van der Putten et al., 2010; Rajkumar et al., 2013) can affect the plant–soil relationship. Metal contamination, another important stressor on soils, has also been found to alter the nature of plant and soil community interactions (Pawlowska et al., 1997; Zhang et al., 2007).

The global increase in human development and land use is rapidly changing our world (DeFries et al., 2004). When soils accumulate contaminants, the health of the ecosystem is influenced (Effland and Pouyat, 1997). Soil ecologists have well-developed theories of plant–soil feedbacks (Wardle, 2002; Bardgett and Wardle, 2010). Traditionally, plant–soil feedback theory suggests that negative feedbacks, such as pathogens or nematode and insect pests from the soil, drive plant community

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structure and diversity. This idea has been studied extensively and recently reviewed (Bever et al., 2012; van der Putten et al., 2013). Indeed, experiments in many different systems, including a meta-analysis of grassland soil data, have shown that negative feedbacks from soil are the primary force affecting plant community succession, distribution, composition and diversity (Packer and Clay, 2000; Engelkes et al., 2008; Kulmatiski et al., 2008; Mangan et al., 2010). In contrast, facilitation, a positive feedback from the soil to the plant, is frequently associated with biological invasions (van der Putten et al., 2013). When soil metal contamination exerts an abiotic stress on a biotic community, selection will favor organisms with resistance traits over those with strong competitive ability. Relationships within these communities tend toward facilitation (Bertness and Callaway, 1994; Wagner, 2004).

Contamination can mean many things; this review is focused on soils contaminated with metals. Soil organic matter (SOM) is central to metal remediation and nutrient cycling and must be considered in the context of soils with metal contaminants. However, studying SOM levels can be complicated for two reasons. First, many sites contaminated with metals are also contaminated with organic pollutants complicating accurate measurements of SOM in the field. Second, as contaminated sites become re-vegetated, SOM will naturally accumulate in the soil, affecting the relationship between the plants, soil microbes and metals. It is undeniable that SOM plays an important role in mediating the interactions of plants, soil microbes and metals. In this review however, we focus only on the literature and our experiences with metal contamination, rather than organic pollution, as we tie a recent and relevant case study to literature surrounding plant and microbe community responses to metals in soils.

As an introduction, we highlight an ongoing case study from Liberty State Park (LSP) in Jersey City, New Jersey, USA, a previously industrial site affected by metal and organic contamination that is now undergoing natural succession. We then review the literature on the response of soil organisms to metal contamination, and make the argument that contaminated systems must be studied within the context of feedbacks, among plants, soil organisms and soil metals (Fig. 1). We also suggest that facilitation, within the context of metal-contaminated soils, may be more important than historical paradigms focused on negative plant–soil feedbacks would suggest. This is a hypothesis in need of testing. Bruno et al. (2003) have identified the role of facilitation in the succession and establishment of plant communities in stressful environments that result from naturally occurring ecological changes. Metal contamination in soils, on the other hand, is likely not caused by naturally occurring ecological changes. Studying effects of metals on plant and soil communities is important and has applications to restoration and natural recovery of disturbed or postindustrial land. We review literature here that describes metal-contaminated soil with respect to both mono-specific experiments or plots and whole diverse plant communities and at various stages of succession (van der Putten et al., 2013). We conclude by describing some possible approaches to address this increasingly important and highly relevant question in soil ecology, and discuss methodologies to increase our understanding of the mechanisms driving succession, remediation and community composition.

2. Liberty State Park – a case study in the ecology of metal-contaminated soils

Postindustrial landscapes are increasingly providing the opportunity for restoration and adaptive reuse. However, developing long-term solutions to metal-contaminated soils requires a deep understanding of the ecology of the site. The state of the plant and soil communities with respect to their contaminant is dynamic. Metal contamination may serve as a direct and negative filter on both the soil and plant communities. At the same time, the bottleneck of this filter results in a community that is resilient to metals

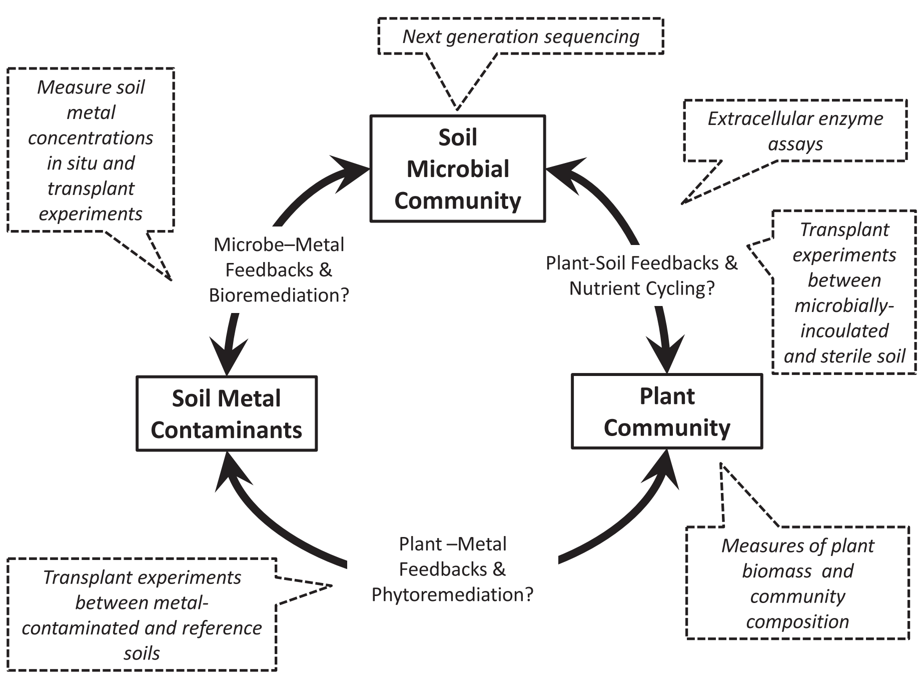

Fig. 1. Scheme showing the dynamic three way relationship among plants, soil organisms and metal contamination. Boxes with solid lines contain the three pools (plants, soil metals, and soil organisms) connected by two-way arrows indicating feedback relationships. Important research questions are noted across the arrows between the pools. Possible experimental methods to address the questions are marked in dashed-line call-out-boxes. These methods, when applied to a well designed experiment or field study along a concentration gradient, will resolve the mechanisms of interaction among plants, soil microbes and metal contamination in soils. Some of the questions that can be answered include, but are not limited to: 1.) Does a unique microbial community form as a result of contamination; 2.) Does the unique microbial community lead to increased nutrient cycling or remediation? and 3.) At what levels of contamination do we see changes in the plant and soil communities?

and likely capable of mitigation, lowering effective metal concentrations in the soil (Gallagher et al., 2011). The time scales of community development and mitigation can vary with conditions, resulting in a time-dependence of the effects of facilitation and feedbacks. These phenomena, and others, are currently under investigation at LSP. There, the soil is heavily contaminated by metals and organic pollutants, and yet, a seemingly healthy deciduous forest is naturally regenerating without human intervention or restoration.

2.1. Liberty State Park in Jersey City, New Jersey, USA

LSP is a designated brown field (defined as a former industrial land with contaminated soils or waters) and now on the site of what was an extensive rail yard connecting metropolitan New York City to the rest of the country (Fig. 2). Rail operation began in 1863 and continued until abandonment in 1969. Park soils historically have been heavily contaminated with metals (such as V, As, Pb, Cu, Zn) and organic pollution (not yet defined). Major portions were remediated in the 1970s, when the New Jersey Department of Environmental Protection's Division of Parks and Forestry took control, but one large portion (approx 104 ha) was fenced-off from human access and remains un-mitigated. After extensive investigation and characterization by the USDA Natural Resource Conservation Service, the soils in the fenced site have been given their own series designation, the Ladyliberty Series (National Cooperative Soil Survey, 2012). For over 150 years, abiotic conditions at the site were limiting to life, and soil formed through the accumulation of debris and urban fill from New York City as well as industrial pollution associated with the rail traffic. Successful establishment of plant propagules was likely limited. When rail use stopped and the land was abandoned (over 40 years ago), succession and community development began. The legacy of contamination remains and the concentrations of soil metals have been mapped, revealing gradients in metal loads (Gallagher et al., 2008a).

2.1.1. The complications of combined metal and organic contamination

The relationship between soil metals and SOM at LSP is quite complex. SOM is accumulating with the succession of the forest, but diverse organic pollution is also present. Lumps of coal can be found littered on the ground. It has been known for some time that soil metals are often adsorbed or occluded by carbonates, organic matter, Fe–Mn oxides, and primary or secondary minerals (Adriano, 1986; Ross, 1994). In addition, organic matter, particularly leaf litter, can provide a sink for metals, which bind passively to surfaces or actively through the physiological activity of the microbial colonizers (Gadd, 1993; Ledin, 2000). Conversely, organic matter can also act as a source when microbial activity mobilizes the metals (Gadd, 1993) or through the action of deposit feeders (Weis and Weis, 2004). Hence, soil metal sequestration or adsorption by SOM is dependent upon the rates of uptake and retention by the various tissue types, translocation to deposit feeders and release through decomposition. Such a feedback system creates a complex dynamic between stable and biologically available fractions of the various soil metal species, an area of current research at LSP.

Interestingly, in the case of LSP, the correlation between total organic content and the various soil metals was only significant for two species, As and V. The concentrations of these metals were generally below residential standards, but above ecological soil screening criteria (Gallagher et al., 2008a). However it is important to note, that total organic content in this soil was measured by loss on ignition (LOI), and it does not account for origin of the organic carbon or its bioavailability. The data from this site also suggest that as the rate at which metals were metabolized (and presumably bound) increased, (i.e. As < Cr < Cu < Pb < Zn) the rate of attenuation, the difference between soil metal concentration of 1995 and 2005, also increased (Gallagher, 2008). In this young terrestrial system, the continued addition of organic material as a result of plant growth appears to be acting as a sink for the examined soil metals. However, far more research studying the species of organic carbon (pollutants versus plant products) and their interaction with soil microbes, metals and eventually the plants is needed.

2.1.2. Succession at LSP

As with any case of succession, the first pioneers at this site primed the soil and facilitated the success of later arrivals. In the case of un-impacted soils through successional time, theory states that positive feedbacks will eventually give way to negative feedbacks that dominate community dynamics (Fig. 3a, Reynolds et al., 2003). In contrast, in metal-contaminated soil that imposes a stress on the community, he hypothesize that positive feedbacks will play a persistent role, dominating community composition, and becoming increasingly important as the stress or contamination increases (Fig. 3b). In the case of LSP, a naturally-occurring temperate deciduous forest has been developing since abandonment. Early successful colonizers of the park are pioneer tree species: *Betula populifolia* Marsh. (35% cover), *Populus deltoids* Marsh. (16% cover) and *Populus tremuloides*, Michx. (14% cover). Their success may be the result of both soil metal tolerance and metal translocation (Gallagher et al., 2011). Specifically, metal savaging by Fe plaque (Feng et al., 2013) or sequestration within the plant tissue (especially the root) (Gallagher et al., 2008a; Qian et al., 2012) may all be facilitating the long term competitive success of *B. populifolia*.

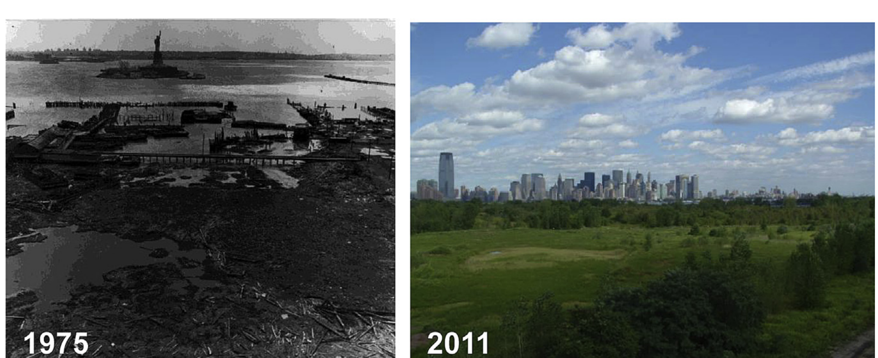

Fig. 2. Images of Liberty State Park, Jersey City, NJ, USA from 1975 recently after rail use abandonment (credit: Robinson Aerial Surveys, Inc.), and from 2011 after 36 years of succession and naturally occurring plant community regeneration (credit: Sean Gallagher).

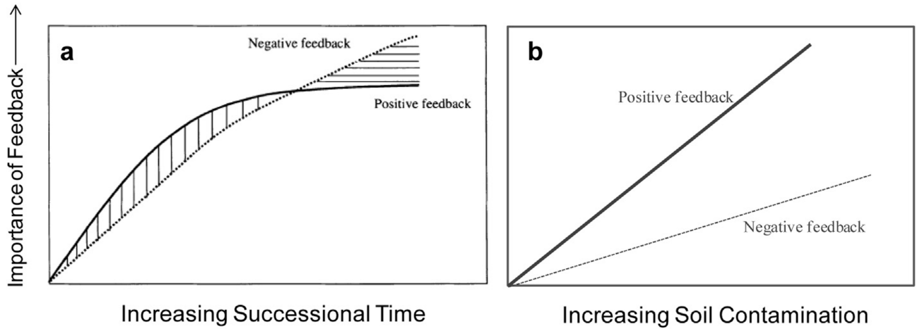

Fig. 3. The hypothesized relative importance of positive versus negative feedbacks with respect to a.) increasing successional time (adapted from Reynolds et al., 2003) and b.) increasing metal contamination load (stress) in soils.

In similar environments, selective uptake within the mycorrhizal assemblages facilitates primary production in spite of high metal loads (Krpata et al., 2008). The ability of plants to tolerate metals on their own or accept facilitation through soil microbial symbionts will affect the composition of the community. With respect to LSP, different metals have different concentration distributions across the site. The exact relationship between plant community distributions with respect to metal loads in the soils has been mapped (Gallagher et al., 2008b). Investigating the relationship of metal concentrations to the distribution of soil microbial communities (both fungal and bacterial) is an ongoing and interesting next step.

Disturbed sites like LSP, by definition, lack an ecological legacy and often do not respond predictably to traditional vegetation management practices (Hobbs and Harris, 2001). Work at LSP has demonstrated that the anthropogenic legacy of industrialization can produce an environmental stress gradient associated with metal contamination in the soil, resulting in distinct plant communities with different functional guild representation (Gallagher et al., 2011). The ecological communities at LSP are high functioning and include diverse bird (Hofer et al., 2010) and plant assemblages (Gallagher et al., 2008b). However, the composition of the forest community seems to be in a state of arrested succession, where late successional species are not establishing as might be seen in a comparable forest of this region. In addition to the species listed above, *Acer rubrum* is only occasionally found in wet areas, and three species of *Rhus* sp. dominate the shrub community. However there are virtually no climax forest tree species present, with only a rare *Quercus rubra* seedling occurring in spite of this species' presence in the regional pool. Researchers working at the site hypothesize that such a community trajectory is tied to, if not driven by, plant–soil feedbacks. As in un-contaminated ecosystems, when positive, plant–soil feedbacks (facilitation) should lead to a mitigation of the abiotic stressors and result in succession, though sometimes atypical. When negative, they should reinforce the stress and lead to arrested succession or an unpredictable trajectory and plant community end point within the context of the surrounding biome. In the case of LSP, we suspect that both processes are occurring simultaneously, but whether positive or negative feedbacks dominate likely depends on immediate circumstances and should be investigated.

3. Response of biota in metal-contaminated soils

3.1. Support for the feedback perspective

On contaminated soil, the role of microbial community functioning cannot be isolated from plant community composition, and the activity of the microbial community is intertwined with soil abiotic properties (Schimel et al., 2007) (Fig. 1). Phytoremediation, the capacity of specific fast-growing plants to accumulate and sequester metals from soil, has been exploited in recent decades as a cost effective means of remediating metal-contaminated soils (McIntyre, 2003). In some cases, plant taxa themselves translocate metals as in the case of *B. populifolia* at LSP (Gallagher et al., 2008a), but most often, the ability of a plant to tolerate and remediate metals is directly tied to the presence of organisms in its rhizosphere (Kuiper et al., 2004). Such interactions are receiving more attention in the phytoremediation literature (Khan, 2005; Sessitsch et al., 2013). However, a greater understanding of the ecology of plant–soil feedbacks in disturbed or, with respect to this article, metal-contaminated soils (Bissett et al., 2013) is needed and will reveal the mechanisms that will ultimately ameliorate metal contamination stress and facilitate the restoration of entire plant communities and not just one plant taxa.

In metal-contaminated soil, microbial communities are experiencing and responding to contamination together with the above ground plant community, and likewise the microbes, fungi and bacteria, are altering the soil environment as they translocate, absorb or sequester, and remediate contaminants (*sensu* Clarholm and Skyllberg, 2013). Moreover, as a community develops over time, what is true about the plant and soil relationship in contaminated systems at one time point may no longer hold true at a later successional stage. Frey et al. (2006) tested this idea over a period of four years in a factorial experiment within young forest soil plots. They combined metal contamination with acid deposition. After repeated measurements, they found that the effects of metal contamination and low pH on the microbial community composition (fatty acid analysis and DNA fingerprinting) and functioning (respiration) changed through time with forest development.

3.2. The special role of facilitation within feedbacks

The evidence supporting the role of facilitation from soil organisms to the plant community in metal-contaminated soils is growing, but the relationship among arbuscular mycorrhiza (AMF), plants and metals in soil varies (Khan, 2005). For instance, in metal-contaminated soils, the infection rate by AMF was dependent on the successional state of the plant community and lower in the unremediated compared to remediated soils (Pawlowska et al., 1997). In contrast, we know that primary production is inhibited in metal-laden soils, but growth can be remediated by the protective and positive effects of mycorrhiza (Krpata et al., 2008). Bacteria and fungi however, occupy very different niches.

Metal resistant bacteria, including Cr resistant bacteria capable of reduction of more harmful Cr(VI) to less harmful Cr(III), have been isolated in sites contaminated with metals (Das et al., 2014). Metal resistant bacteria have been isolated from the rhizosphere of plants found on copper mine wasteland, and those microbes can enhance root elongation in the presence of copper (He et al., 2010). Under highly experimental conditions, tomato plants were exposed to metal contamination and plant growth promoting bacteria that either did or did not produce siderophores. Tomato plant growth benefitted from the additional bacteria, but those inoculated specifically with the bacteria capable of sequestering iron were most successful (Burd et al., 2000). These results demonstrate that microbial facilitation can be conducive for plant growth on metal-contaminated soil. However, the identity and functional role of the microbes (*i.e.* fungi vs. bacteria) are likely very important to the outcome of facilitation and different metals have varying effects in a given soil.

Though their role in facilitation and remediation is indirect, micro-fauna and meso-fauna play an important role in facilitating plant growth (Bonkowski, 2004; Wardle et al., 2004; Ekelund et al., 2009; Krumins, 2014) even under metal contamination (Korthals et al., 1996; Neher, 2010). As in any diverse community, not all taxa are equally sensitive to disturbance, metal contamination in this case. This makes micro- and meso-fauna very important indicators of soil health. The composition of soil nematode communities (from all trophic groups) have been used to indicate soil health (Bongers, 1990; Fiscus and Neher, 2002), and other taxa have been evaluated as well (Ellis et al., 2002). Enchytraeid communities in particular can be surprisingly sensitive to metal contamination (Kapusta et al., 2011). This is important to the trajectory and restoration of contaminated sites; one of the important feedbacks to primary production and plant community composition is the presence and metabolism of a diverse soil fauna (De Deyn et al., 2003).

As shown in Fig. 1, there are bidirectional effects between metals and soil organisms, soil organisms and plants, and metals and plants that have been reported. With respect to plants and soil organisms, these responses occur at both the population and community level. These individual effects imply a multidirectional set of interactions (Fig. 1) where, for example, metals influence soil organisms, which influence plants, and where metals also influence plants directly. Some of these effects facilitate plant life in metal-contaminated soils. One way metals indirectly affect plants is through microbial population shifts that result in altered soil metabolism. The metabolic activities of all soil organisms can either directly or indirectly facilitate plant growth and community development on any soil but this facilitation may be particularly important on metal-contaminated soils where metals can be toxic to soil organisms and plants. If metals did not foster metabolic, microbial, and resistance changes, they would simply reduce biomass as a result of their toxicity. Functions like nitrogen mineralization can help release plants from nutrient limitation, and they are easily measured as soil enzymatic activities (Burns et al., 2013). There is a great need to study the mechanisms of these interactions to understand the feedback relationships in more depth.

In research studies testing the hypothesis that metal induced changes in soil metabolism facilitate plant growth, enzymatic functional responses have been mixed from metal-contaminated soils. Some studies highlight toxic effects of metals on microbes and metabolism, others reveal metal induced microbial population shifts and development of microbial metal resistance. For example, when microbial communities from soils adjacent to industrialized sites were analyzed, both decreased soil community diversity (He et al., 2010) and decreased enzymatic function (Hinojosa et al., 2004; Wang et al., 2007) were found with increasing metal load. Likewise, in a study conducted in mixed community grassland soils from a site contaminated with metals and other pollutants for approximately 50–60 years, both microbial biomass and enzymatic activity markedly declined with increasing metal load in the soil (Kuperman and Carreiro, 1997). However in a different study, increased soil metal loads were associated with increased enzymatic activities (Pascual et al., 2004). When soil microbial community structure and function was measured in metal-contaminated soils, shifts in the microbial community composition and functioning were associated with plant community successional age and composition (Zhang et al., 2007).

These mixed results are likely due to sometimes overlooked differences in study sites and design. For example, long term versus short term effects of metals can be very different, especially because facilitation mediated through development of resistance or microbial community shifts can take place over a long period of time while metal toxicity on plants and microbes can typically be observed on a much shorter time scale. It is also likely that the response (could be many responses, *i.e.* primary production, fecundity or community composition) of the biotic community to metal concentration is not linear. It is likely that both the length of time the contamination has been present in the soil and the duration of the study have important implications for the microbial composition and enzymatic activity data. Furthermore, results from studies where metals are added to soils in a lab may not correspond to results in the field. Finally, the concentrations of individual metals in the soil are different between sites and concentration and the identity of the metals are significant factors that must be carefully evaluated. For example, Cd, Hg, and Pb are necessary trace elements for many microbes but toxic at higher concentrations. To advance the understanding of plant–soil feedbacks in metal-contaminated soil, it is important to study different sites under different conditions to reach more generalizable conclusions.

4. Goals and suggested approaches

The goal of many studies in community ecology is to determine mechanisms of interaction and develop theory that can help predict outcome. Here, we have reviewed literature supporting the hypothesis that plant–soil feedbacks are central to the dynamic relationship among plants (at the population and community level), soil organisms and soil metal contamination (Fig. 1). Then by definition, within this interaction, there are three feedback relationships: 1.) Plants and soil organisms; 2.) soil metals and soil organisms and 3.) soil metals and plants (Fig. 1). We suggest experiments and methodological approaches that will help resolve the mechanisms of interaction between the three dynamic pools. The mechanisms of interaction drive metal remediation and community succession, and this relationship must be better understood to help metal-contaminated soils recover. The framework we suggest in Fig. 1 is just that, a simplified framework. In reality, different metals will interact with plants and soil organisms in very different ways. Further, though beyond the scope of this article, SOM that is very likely integrated with the soil organisms (especially microbes) is also an important part of these relationships. Ideally field studies will be partnered with manipulative experiments to resolve differences and account for variability in metal load and the interactions of SOM.

4.1. Experimental approaches

The basic approach to investigate the relationship between plants, soil metals and soil organisms is not daunting, but the scale of replication must be large and coupled to field studies. Greenhouse transplant experiments using plant communities in microcosm plots and manipulative experiments using sterile/non-sterile and contaminated/un-contaminated soils will be initial experiments that reveal the role of feedbacks among plants, soil organisms and contamination. These experiments are manageable (Brinkman et al., 2010), but a major challenge is in achieving the necessary replication when researchers scale up to the 'field level'. In addition to problems of replication with field studies, the nature of the relationships among soil organisms, plants and contamination are dynamic (Bissett et al., 2013), and greenhouse or "bench studies" may not accurately represent *in-situ* conditions. Field studies should include comparisons between control or reference sites and metal-contaminated sites. True reference sites, those that lack the contaminant in question, for any field study can be challenging to find. Likewise, long term data sets that reveal patterns of succession and community dynamics are very rare. However, even in highly disturbed areas (*i.e.* urban New Jersey), sites that lack the contaminant, but have similar geography and climatic influences can be found. Though not perfectly controlled, the results of these studies will reveal whether facilitation by beneficial organisms is occurring when greater increases in plant biomass and/or enzyme function on the contaminated soils is found compared to uncontaminated soils. Field results will inform empirical work that includes sterilized controls and can confirm the role of beneficial soil organisms.

An additional approach that helps solve the problems of replication is to examine trends along contamination gradients (Pouyat et al., 1995; Gallagher et al., 2008a). Using site specific methods, the critical thresholds of ecological structure and function can be identified. Following this, analysis can begin with ordination techniques to describe multivariate community and abiotic factors followed by correlation and regression, to determine relationships among any one of the three interacting pools (plants, soil organisms and soil metals). Most of the research findings from LSP have been achieved this way. Yet another approach is to increase the scale of study, combine experiments and examine meta-data allowing for inclusion of reference sites and long term studies. The urban Long Term Ecological Research (LTER) sites of Baltimore (Pickett and Cadensasso, 2008) and Phoenix (Grimm et al., 2000) are providing a foundation of data from urban brown fields and contaminated lots. However, more small scale research studying the virtually limitless number of naturally assembling brown fields, frequently contaminated, will provide the replication and references needed to arrive at meaningful generalizable theory.

4.1.1. The value of a case study

There is high scientific value in studying systems affected by contamination for extended periods of time that are more realistically reflective of long-term trends. Because of the instability of these systems and the dynamic nature of interactions between plants and the soil community, the data that drives development of theory may depend on the successional stage of the site studied. Many of the effects of metals in soil are not immediate and the resulting changes take place over different time-scales, depending on the effect in question. Different sites can be arrested at different stages of succession depending on the nature and duration of contamination (Gallagher et al., 2011). Specific studies must, in time, identify factors that provide predictive information about the trajectory of a particular site. However, to develop ecological theories that can be generalized to all metal-contaminated soils, it is important to understand a significant number and variety of contaminated environments with respect to relatively uncontaminated controls or reference sites (Pouyat et al., 2007). Finding true reference sites can be challenging for several reasons. First, the majority of disturbed or contaminated sites do not have the longevity to establish an ecological legacy, and second, reference sites are often established with the cultural and research bias of the investigator who chooses the ecological characteristics to be used as a metric. That said, reference sites that lack the contaminant of interest can be identified when the nature of the contamination in the study site is known.

4.2. Methodologies

Through rapidly increasing technological advances, we have valuable tools to study biotic and abiotic interactions in soils (Fig. 1). The phylogeny of microbial taxa in soil can now be resolved in great detail with next generation sequencing technology (Rousk et al., 2010). These tools provide a way to assess differences in microbial community composition at very high levels of resolution. Rare taxa, whose presence was never documented in the past, are now counted and their role in plant–soil feedbacks appreciated (Hol et al., 2010). Extracellular enzymes, in soil solution, attached to clay surfaces, or adsorbed to humic compounds, are generally assumed to be of microbial origin with those that originate from plants and animals only playing a minor role (with the exception of rhizosphere soil that is in the most close association with roots) (Haider and Schaffer, 2009).

The composition of the soil microbial community is likely to significantly influence the level of enzymatic turnover in specific soils. Hydrolases and transferases play a role in decomposing organic compounds and simple enzymatic assays can be used to determine their relative activities in different soils to get an estimate of nutrient cycling and formation of soil organic matter (Burns et al., 2013). A large number of assays have been developed, most use substrate analogs and rely on spectrophotometric analysis of reaction products. A special consideration of applying these assays to contaminated soils is that the ability of the soil and its associated contaminants to inhibit or activate its enzymatic activity should be assessed to ensure a controlled understanding of the relationship between microbial community composition and enzymatic turnover. One must keep in mind that great variation is often seen in the responses of different enzymes to the same contaminant/s (He et al., 2010). When measures of enzymatic potential are coupled to measures of plant or microbial community composition and soil metal characterization, the mechanisms of interaction can be resolved.

These methodologies are limited to exploration unless carried out within the context of manipulative and replicated field or greenhouse experiments that can be conducted on a gradient or compared to suitable references and controls. In this situation, next generation sequencing, especially when tied to measures of enzymatic activity, will reveal changes in microbial community structure that can inform functioning. Likewise, enzymatic assays can directly reveal the functional potential of the soil community. Measures of enzymatic activities associated with carbon, phosphorus and nitrogen cycling will indicate indirect facilitation of primary production and may provide information about nutrient limitation. Next generation sequencing may reveal resistance genes and genes coding for proteins with functions associated with the amelioration of metal contamination.

5. Conclusion and perspectives

A large fraction of the earth is impacted by human use and development (Pickett and Cadensasso, 2008), leading to substantial increases in contamination and abiotic stressors that affect whole ecosystems. Not all contaminated or human impacted soils function equally (Pouyat et al., 2006), and the relationship between plants and their soil community is likely to evolve with different human-induced environmental changes (Miki, 2012). As ecologists, we do not know how theories of community assembly and succession can be applied to human impacted landscapes, and it is possible that experimental results in such environments may significantly differ from those predicted based on established ecological paradigms. Here, we do not suggest a new ecological paradigm for contaminated soils, but we do argue that a more holistic approach to studying plants and their soils interacting with contamination will reveal useful data that can inform restoration of degraded soils. This is an ambitious goal; though we still do not understand all the mechanisms of interaction, the role of soil biota in plant community structure and ecosystem functioning is well appreciated (Coleman and Whitman, 2005).

The null argument to the premise we have developed in this article is that contaminated soils function exactly as healthy soils, but they are merely subject to additional abiotic drivers; they are not special. This is an important question for investigation, and may turn out to be true; we hope this review inspires investigators to explore further. Indeed, ecosystems exposed to highly varied contamination and disturbance can often be highly productive (Suding et al., 2004) as we have documented at LSP (Gallagher et al., 2008b). However, the mechanisms are yet to be resolved, and the results are highly mixed. We know a great deal about soil microbe remediation of metal contaminated soil (Giller et al., 2009), and we know a great deal about phytoremediation (McIntyre, 2003), but these processes will be maximized when a holistic feedback approach is applied (Fig. 1). Defining the roles of soil biota in the structure and function of plant communities in contaminated soils and the mechanisms by which facilitation takes place is essential to understanding fundamental and certainly restoration ecology in a human dominated world. Such an understanding may foster an improved assessment of the current practice of restoration within degraded environments, which are presently evaluated using metrics of species composition built upon traditional concepts of competitive exclusion and plant–herbivore or plant–pathogen interactions. Deeper insights to the problems discussed here will challenge plant–soil feedback theory and inform our understanding of plant community ecology on metal contaminated soils – a highly relevant next frontier in the ecology of disturbed environments (Grimm et al., 2000).

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