Soil homogenization and microedges: perspectives on soil-based drivers of plant diversity and ecosystem processes

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Abstract. Disturbance caused by agriculture and resource extraction has resulted in widespread homogenization of soils at the local (within-site) scale. Here, we describe how experimental manipulation of heterogeneity at the local scale has had inconsistent effects on plant species diversity. Moreover, we discuss how soil homogenization per se typically has not been accounted for in the study of heterogeneity-diversity relationships, and how disturbance, often viewed as an artifact in soil heterogeneity experiments, can be a key driver of soil homogenization. We propose a conceptual model for describing the relationship between plant size, patch size, and diversity, and we discuss how factors such as disturbance, productivity, and competition among species either should be controlled or accounted for in soil heterogeneity–plant diversity experiments. Finally, we consider the concept of soil patch microedges, which may provide unique microsites for increased plant diversity, and how these biogeochemical and hydrological interfaces could potentially drive ecosystem processes in a manner unique from the adjacent patches. Overall, this synthesis integrates perspectives on the functional links between plant-driven processes, and soil patterns and processes.

Key words: disturbance; diversity; ecosystem processes; ecotone; heterogeneity; niche; patch; soil; spatial scale.

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INTRODUCTION

Understanding the factors that control plant species diversity has been a central goal of plant community ecology, and in the context of global declines in biological diversity, it has become increasingly important to refine this knowledge. Environmental heterogeneity—the spatial and temporal variability of environmental parameters in an ecosystem—has long been recognized as an important driver of plant species diversity (Levin 1974, Ricklefs 1977, Chesson 2000, Stein et al. 2014). Ecological niche theory suggests that a large number of species can coexist, resulting in increased diversity, in an ecosystem where there is high environmental heterogeneity (Tilman and Pacala 1993, Laliberté et al. 2013).

A large body of research has focussed on understanding the influence of heterogeneity in soil and other environmental variables on plant species diversity at the scale of within plant communities (Lundholm 2009). While environmental heterogeneity–plant species diversity relationships are well supported by theoretical work and the majority of observational research, it has been more difficult to successfully demonstrate this relationship experimentally, particularly in soil heterogeneity studies involving nutrient manipulation (Reynolds and Haubensak 2009, Eilts et al. 2011, Tamme et al. 2016). The few experimental
studies that have demonstrated increased local-scale plant diversity with increased soil heterogeneity have involved the manipulation of vertical layers of soil profiles to create distinct microsites within the upper layer of soil (i.e., replacing patches of topsoil with patches of lower strata; Fitter 1982, Williams and Houseman 2014), manipulation of topography in wetland soil (Vivian-Smith 1997), and heterogeneity in disturbance (Wilson and Tilman 2002, Questad and Foster 2008). However, when other soil parameters, such as soil depth to bedrock, physical texture, and chemical properties, have been altered, negative or null effects on diversity have been observed (Grime et al. 1987, Baer et al. 2004). A better understanding of the mechanisms underlying such discrepancies is essential for clarifying the relationship between plant diversity and soil heterogeneity.

A further characteristic of experiments that have explored the relationship between plant diversity and soil heterogeneity is that they have focused predominately on the addition of increased soil heterogeneity to natural soils, above that of the background level of heterogeneity. However, such an approach does not address the full range of environmentally relevant soil heterogeneity scenarios, because it does not include fully homogenized treatments (but see Brandt et al. 2014). In addition, knowledge is lacking regarding the role of disturbance in the study of heterogeneity–diversity relationships. While disturbance often is viewed as an undesirable artifact of soil heterogeneity experiments (Lundholm 2009), soil often becomes more homogeneous and uniform specifically as a result of continuous disturbance from activities such as tillage (Anderson and Coleman 1985, Elliott 1986). Resource extraction, agricultural operations, and other land uses have modified and disrupted the natural soil profile to the extent that an anthropogenic soil order has been proposed (Naeth et al. 2012). The homogenization of soil properties within a site caused by disturbance could result in loss of microsites from the ecosystem, decreasing opportunities for plant species coexistence. Thus, soil homogenization via disturbance may be a significant factor limiting the recovery of plant species diversity and composition in early-successional environments (Grime 1979, Baer et al. 2004).

In this paper, we build on previous work that has addressed the variability observed in heterogeneity–diversity studies (Lundholm 2009, Reynolds and Haubensak 2009, Tamme et al. 2010, Laanisto et al. 2013, Williams and Houseman 2014) by discussing the three critical knowledge gaps introduced above regarding this topic. First, we describe how experimental manipulation of heterogeneity at the local scale has not produced consistent results. Second, we discuss how soil homogenization, unlike increased soil heterogeneity, typically has not been accounted for in the study of heterogeneity–diversity relationships. Third, we consider how disturbance, often viewed as an artifact in soil heterogeneity experiments, nevertheless can be a key driver of soil homogenization. In order to address these knowledge gaps, we propose two conceptual approaches and a suite of methodological approaches. Specifically, we propose a conceptual model for describing the relationship between plant size, patch size, and diversity. To improve the methodology of soil heterogeneity–plant diversity experiments, we explain why factors such as disturbance, productivity, and competition among species need to be either controlled or accounted for. Next, we discuss the concept of soil patch microedges, which may function in a manner analogous to plant community ecotones (albeit at a much smaller spatial scale) by providing unique microsites for increased plant diversity. We conclude by expanding our discussion of microedges, moving beyond the scope of species-level effects, to consider whether microedges can create unique biogeochemical and hydrological interfaces between adjacent soil patches, and how these interfaces could potentially drive ecosystem processes in a manner unique from the adjacent patches. Overall, our discussion of these knowledge gaps and how to address them addresses the functional links between plant-driven processes, and soil patterns and processes.

Sources of Soil Heterogeneity: Ecological Perspectives

A universal property of soils is that they are inherently variable across space and time, but there nevertheless can be substantial variation among sites in the number and variety of
distinct, plant-relevant microsites. At the spatial scale of within plant communities, niche-based sorting may occur among distinct soil patches, roughly the size of an individual rooting zone or the root zone occupied by a small population of a plant species (Day et al. 2003). These patches (i.e., centimeters to meters) are often referred to as microsites by plant ecologists, and they differ from the much smaller scale microsites (i.e., nanometers to micrometers) typically defined by soil scientists (Killham 1994). For example, limestone alvars feature microsites differing in soil depth to bedrock. Differing soil depths in alvar ecosystems have a strong influence on soil moisture levels, which affect the resulting composition and diversity of the plant community, represented by a blend of drought-tolerant and drought-intolerant species in the shallower and deeper microsites, respectively (Lundholm and Larson 2003, Fridley et al. 2011).

A distinction is often drawn between environmentally induced vs. plant-induced heterogeneity. Specifically, heterogeneity can be environmentally induced by geological processes such as weathering and soil formation (Ricklefs 1977), or heterogeneity can be increased by the plants themselves through biotic processes such as colonization, root activity, and decomposition (Gibson 1988, Jackson and Caldwell 1993). The respective contributions of these two sources of heterogeneity can be difficult to extricate (if they are indeed two truly separate entities), but for practical reasons, experimental work often deals with plant-induced and environmentally induced heterogeneity in separate investigations.

Williams and Houseman (2014) proposed that while positive correlations between soil heterogeneity and plant diversity are often attributed to plant-induced soil heterogeneity, neutral processes may instead be the dominant factor (i.e., plant-derived heterogeneity may be detectable, but it does not contribute significantly to the species diversity patterns). However, no studies (to our knowledge) have substantiated this proposition to date, and on the contrary, the results of experiments on this topic appear to suggest that plant-induced heterogeneity promotes coexistence in a manner consistent with niche theory and invasibility criteria (Hendriks et al. 2015, Burns et al. 2017). Nevertheless, the balance between niche and neutral forces likely depends upon the extent of soil heterogeneity present, and neutral forces can dominate when soil heterogeneity at the local scale is low (Williams and Houseman 2014). There are of course many other theories, in addition to niche theory and neutral processes, that have been used to explain plant species coexistence and increased diversity (e.g., pest pressure, allogenic disturbance), but most include at least some component of spatial or temporal variability in plant growth conditions (Wilson 2011).

**Knowledge Gaps Regarding the Relationship Between Plant Diversity and Soil Heterogeneity**

**Variation among diversity–soil heterogeneity studies**

The majority of observational work supports a positive relationship between environmental heterogeneity (e.g., temperature, soil moisture, and nutrient availability) and plant species diversity across a range of natural ecosystems (e.g., grassland, forest, and wetland; Lundholm 2009, Bergholz et al. 2017), with a minority of exceptions that have reported negative and unimodal relationships or no relationship (Loneragan and Moral 1984, Freestone and Harrison 2006, Dufour et al. 2006, Fig. 1b). While, as described above, some experiments also have demonstrated a positive relationship between environmental heterogeneity and plant species diversity, others have found no effect or a negative effect of increased heterogeneity on diversity (Fig. 1c; e.g., Stevens and Carson 2002, Stromberg et al. 2011, Gazol et al. 2013). Although soil heterogeneity simply may not be an important factor driving plant diversity patterns in some experiments, alternatively, the observed variability among experiments could reflect variability in experimental design with respect to the sources of heterogeneity examined and how the treatments were implemented. For example, some heterogeneity treatments, such as nutrient addition, can be confounded by competitive dynamics of the experimental plant community, with the heterogeneity treatment unintentionally favoring a few competitive species, leading to decreased species diversity (Eilts et al. 2011). Moreover, it has been argued that the disturbance associated with the addition of soil patches...
typically results in confounding factors, such as changes in mean resource levels and subsidence, so it is difficult to isolate increased heterogeneity as a causative factor (Lundholm 2009).

Heterogeneity treatments must be implemented at the appropriate spatial scale (discussed further below) and with a high level of replication, because of the inherently high background soil heterogeneity present over multiple spatial scales (i.e., both within and among experimental plots) in most sites (Smith and Lundholm 2012). There also likely has been variation among studies of soil heterogeneity and plant species diversity in their abilities to achieve distinct, plant-relevant microsites. For example, plant roots may overcome local resource differences among microsites by obtaining resources from adjacent microsites through source–sink phenomena, mass flow of water, and diffusion, especially in humid soils (Jones 2012). In addition, while some plant species specialize in distinct niches, others are generalists that can thrive in a variety of microsites (Voss and Reznicek 2012).

**Soil homogenization**

Soil homogenization is a subset of variation in soil heterogeneity; it is the process of soil becoming more homogeneous or uniform across space as a result of continuous mixing from activities such as tillage, erosion, compaction, and displacement (Anderson and Coleman 1985, Elliott 1986). The potential impacts of soil homogenization from legacies of tillage in row crop agriculture deserve specific attention, because cropland under tillage represents a significant proportion of land use worldwide (Vitousek et al. 1997). For example, approximately 40% of Earth’s land area is in agricultural use (Foley et al. 2005). The number of old fields—former croplands abandoned from agricultural land use—has dramatically
increased over the past century to about 200 million hectares globally (Cramer et al. 2008). Tillage or disturbances with similar effects represent a unique type of soil homogenization, because over time the subsoil layer becomes heavily compacted (e.g., hardpan formation), preventing root penetration. This process effectively eliminates the ability of vertical strata to act as microsites.

Chronic disturbance can homogenize the spatial distribution of soil properties (Robertson et al. 1988, 1993, Röver and Kaiser 1997, Celik 2005), which can lead to decreases in plant diversity and changes in community structure and composition (Grime 1979, Coffin et al. 1996). The addition of environmental (soil) heterogeneity to previously cultivated sites has been attempted as a strategy to increase plant diversity with mixed success (Williams and Houseman 2014, Baer et al. 2016, Fig. 1a). In recovering grasslands subject to soil mixing, increased heterogeneity in microtopography and soil chemical and physical properties was associated with increased plant species diversity, and more so in older sites (Deák et al. 2015, Conradi et al. 2016). Soil homogenization also has several non-anthropogenic causes, such as pedoturbation, the vertical mixing of the soil profile caused by soil-dwelling animals, or geological processes (churning clays, cryoturbation, and bioturbation), that occur on a wide variety of spatial scales (Weil and Brady 2016). Other natural causes of soil homogenization can include erosion on steep slopes and sites with weak soil strength (high silt, low organic matter) that experience heavy precipitation.

**Disturbance as a component of plant diversity responses to soil homogenization**

While disturbance is often viewed as an artifact in soil heterogeneity experiments, as described in the previous section, it nevertheless can be a key driver of soil homogenization. Very few studies have examined the effects of soil homogenization on plant diversity directly, but studies of plant diversity as a function of soil disturbance have been more common, and conceivably can be used as a proxy to study the effects of homogenization. We surveyed 19 published studies of sites where soil was mixed through disturbance, then abandoned between 0 and 65 yr prior to the time of sampling (Table 1). In each study, soil properties and plant species composition were compared between a human-disturbed site and a neighboring, undisturbed reference site. In almost all cases (with one exception), plant species diversity or richness was lower in the disturbed site than the reference site, and/or keystone/indicator plant species were absent from the disturbed site. However, when the disturbance effects were assessed in the context of soil properties (i.e., mean coefficient of variation of pH, nutrient concentrations, and organic matter), disturbance only increased soil homogenization in about half of the studies, whereas for the other half, disturbance actually increased soil heterogeneity (Table 1); or alternatively, in the older sites, recovering vegetation and other organisms may have increased soil heterogeneity over time. Overall, these results suggest there may be widespread variability in the relationship between soil disturbance, homogenization, and plant species diversity.

**ADDRESSING THE KNOWLEDGE GAPS**

*Proposed conceptual model for describing the relationship between plant size, patch size, and diversity*

The spatial scale of environmental heterogeneity likely has had a strong influence on the outcome of heterogeneity experiments, and defining the spatial scale of environmental patchiness is crucial for understanding the mechanisms and contexts in which soil heterogeneity interacts with plant diversity. The relationship between patch (microsite) size and plant size has received considerable theoretical (Tilman and Pacala 1993, Chesson 2000) and empirical (Lundholm 2009) attention. Tilman and Pacala (1993) proposed and qualitatively modeled the relationship between resource heterogeneity, plant productivity, and alpha species diversity with three possible outcomes, with the importance of soil heterogeneity in an ecosystem modulated by plant size and productivity. Specifically, if a nutrient-poor system experiences an increased rate of nutrient supply, soil nutrient heterogeneity and plant size are expected to increase. When plant size exceeds patch size, the soil heterogeneity in the environment no longer significantly influences plant species diversity. An example of the latter is that of productive, intermediate-aged soils that host large plants that forage over wide
areas, which reduces variation in resource availability and overall plant diversity (Laliberté et al. 2013). Soil conditions (e.g., pH, porosity) also have a strong influence on root growth and thus can control maximum plant size.

We propose that the relationship between plant size, patch size, and diversity can be modeled in a manner analogous to the dynamic equilibrium model (Huston 1979), which was conceived to describe how the rates of disturbance and growth (productivity) affect plant species diversity. In our adaptation of the model (Fig. 2), termed the patch size–plant size model (PSPSM), if species diversity decreases when plant size exceeds patch size, diversity should be highest when patch size is equal to plant size, and at medium to small patch sizes and plant sizes; when patch size is equal to plant size, individuals can occupy separate niches and coexist in the community, resulting in the highest diversity (Day et al. 2003). As patch size and plant size increase, alpha diversity decreases, because of constraints on space. When patch size exceeds plant size, effective heterogeneity within a local plant community is lost and no longer increases alpha diversity. Despite the logic behind these

### Table 1. Case studies of vegetation and soil characteristics at disturbed sites which have experienced soil homogenization, and their undisturbed reference sites.

| Paper† | Location | Ecosystem | Disturbance | Time since disturbance | Difference in vegetation between undisturbed and disturbed sites | Effect size‡ |
|--------|----------|-----------|-------------|------------------------|---------------------------------------------------------------|-------------|
| (Faber-Langendoen and Maycock 1987, Turner 2001, Stover et al. 2012) | Ontario, Canada | Grassland | Agriculture | 0 | Species richness higher—undisturbed | −0.16 |
| (Puerto et al. 1990) | Spain | Grassland | Erosion | 0 | α-diversity higher at non-eroded sites | −1.16 |
| (Templer et al. 2005) | Dominican Republic | Tropical forest | Agriculture | 0 | Disturbed sites were agricultural (monoculture) | 0.46 |
| (Crisfield et al. 2012) | Alberta, Canada | Grassland | Road/trail construction | 0 | Disturbed sites were trails (bare ground or sparse cover) | 1.52 |
| (Baer et al. 2004, 2005) | Kansas, USA | Grassland | Agriculture | 5 | Restored prairie (disturbed) higher richness and similar Shannon index to native prairie | 4.20 |
| (Jiang et al. 2010) | China | Grassland | Agriculture | 6 | Indicator species absent from disturbed site | −0.52 |
| (DeGrood et al. 2005) | California, USA | Grassland | Road/trail construction | 10 | Bare ground or patchily vegetated with lower species richness | −0.01 |
| (Sánchez-De León and Johnson-Maynard 2009) | Washington, USA | Grassland | Agriculture | 20 | Disturbed site missing indicator prairie species | −5.93 |
| (Scott and Morgan 2012) | Australia | Grassland | Agriculture | 20 | Species richness higher—undisturbed | 0.48 |
| (Stover 2013) | Alberta, Canada | Grassland | Mining | 30 | Species richness higher—undisturbed | −2.54 |
| (Kindscher and Tieszen 1998) | Kansas, USA | Grassland | Agriculture | 35 | Species richness higher—undisturbed | −1.20 |
| (Burke et al. 1995, Coffin et al. 1996) | Colorado, USA | Grassland | Agriculture | 50 | Indicator species absent from disturbed site | 0.48 |
| (Kulmatiski et al. 2006) | Washington, USA | Grassland | Agriculture | 55 | Indicator species absent from disturbed site | 0.71 |
| (Kucharik et al. 2006) | Wisconsin, USA | Grassland | Agriculture | 65 | Species richness higher—undisturbed | 1.95 |

† Out of the 19 papers, some had soil and vegetation data in separate publications.
‡ Effect size is the difference between undisturbed and disturbed sites in mean coefficient of variation of soil properties divided by the pooled standard deviation (Cohen’s d formula). Positive effect size indicates soil heterogeneity was greater in the undisturbed site.
proposed mechanisms, empirical research to properly test the PSPSM is lacking. However, the PSPSM highlights that there are likely only specific conditions under which soil heterogeneity may increase plant species diversity (or under which soil homogenization may decrease diversity), which may help explain why experimenters do not always observe a positive association between the two.

Methodological improvements: controlling or accounting for disturbance, productivity, and competition in soil heterogeneity–plant diversity experiments

In addition to plant size and patch size, other interacting factors, such as disturbance, productivity, and competitiveness of species in the community, will affect diversity levels, and thus should be controlled or accounted for in experiments testing for soil heterogeneity–plant diversity effects. For example, Liu et al. (2017) found higher species richness in heterogeneous soil treatments for a group of species that were all strong competitors under high soil nitrogen levels, but no effect on richness when inferior competitors were considered. This is in line with the prediction that increased similarity of species slows the process of competitive exclusion (Huston 1979).

Patch size may not only interact with plant size, but also with the germination and establishment of plants in a community. Because species can vary in germination requirements, temporal (seasonal) and spatial patchiness may promote the establishment of a diversity of species (Maestre et al. 2003). Certain species favor larger vs. smaller canopy gaps for germination due to the different temperatures and light levels in these microenvironments, which, for example, may help explain the high diversity of plant communities such as chalk grasslands (Grime 1979).

Such a mechanism could be expanded upon to include other aspects of patch size (e.g., volume, distribution, or shape).

The dominant growth form of the colonizing plants also may explain the variability of results observed in studies of soil heterogeneity and plant species diversity (Baer et al. 2016). Specifically, when considering soil homogenization for the disturbed sites discussed above, some were dominated by invasive perennial forage grasses that were planted following the disturbance (Sánchez-De León and Johnson-Maynard 2009). These grasses form a clonal mat and have a large foraging root area—equivalent to a large plant size. Therefore, their effective plant size is large and could counteract any effect of soil heterogeneity, thus decreasing diversity.

Soil patch microedges: potential microsites for increased plant diversity

Causes for ecological variability in the relationship between heterogeneity and diversity may be linked to belowground, small-scale processes, such as microfragmentation (i.e., increased patchiness with increased heterogeneity), which recently has been proposed as a mechanism whereby increased heterogeneity can decrease diversity as a result of increased fragmentation at
a small scale (Tamme et al. 2010, Laanisto et al. 2013). However, research on soil heterogeneity typically has examined its impact as a summative effect of the component microsites in a plant community without considering the interfaces between them. These microsite edges or microedges may act as small-scale ecological transition zones, analogous to the ecotone concept (Clements 1905), but at a smaller scale (the centimeter to meter scale) than is typically considered for plants (i.e., the ecotone concept is typically only considered in the context of adjacent plant communities). Microedges may provide additional niche spaces for increased plant diversity by offering a transitioning blend of the neighboring patches, or by functioning as interfaces with properties distinct from the neighboring patches (Fig. 3). Microedges are also analogous to the transition zones between soil horizons described by soil scientists. Vertical strata found within soil profiles do not have distinct boundaries, but zones of overlap between the upper and lower layer and are named as distinct sublayers in the soil taxonomy hierarchy (Weil and Brady 2016). These two concepts of course can be combined; most research on soil heterogeneity has examined its impact in two dimensions, either vertically or horizontally, but Liu et al. (2017) demonstrated that soil heterogeneity should be examined in three dimensions.

The microedge concept can build upon our proposed PSPSM, with the two concepts linked (in the context of soil homogenization) by the importance of variation in patch size and spatial scale. Specifically, when individual microsites decrease in size during the process of soil homogenization, the overall frequency of microsites increases and microedge surface area increases (Fig. 4a–c). However, with further decreases in microsite size, distinct microsites and their edges become too small to support separate niche spaces in the context of individual plants, and the latter essentially perceive the system as homogeneous (Fig. 4d). Thus, in the transition from very large patch sizes (4a) to very small patch sizes (4d), soil homogenization can alternatively increase or decrease the availability of plant-relevant microsites and alter total microedge area. Similar relationships are present for soil particles at smaller spatial scales (i.e., millimeters to nanometers), with colloids, the smallest of soil particles (<2 μm), exhibiting an extremely high surface area to volume ratio, and imparting unique properties on the colloid particle, such as electrostatic charge for holding nutrients and water (Jones 2012).

Fig. 3. Conceptual diagram illustrating the approach for assessing plant-relevant soil heterogeneity at the local scale (i.e., within sites) (a) based on microsites alone and (b) an approach based on microsites and microedges. In (a), a summative model is depicted where the influence of heterogeneity is modeled by adding up the individual responses of each microsite or patch. In (b), the microsite edges or microedge between patches also are displayed. The microedge interfaces may act as additional microsites where species sorting occurs, and they also could have unique ecosystem properties, such as increased rates of litter decomposition.
SOIL HOMOGENIZATION AND MICROEDGE EFFECTS ON ECOSYSTEM PROCESSES

Soil homogenization and ecosystem processes

Variation in plant species diversity is frequently associated with variation in ecosystem properties and processes such as nutrient cycling, decomposition, and primary production (Tilman 1999, Hooper et al. 2012). It follows that soil heterogeneity can alter ecosystem processes indirectly via its effects on plant species and compositional diversity (e.g., Cardinale et al. 2000, Maestre et al. 2006, Tylianakis et al. 2008) and plant functional traits (García-Palacios et al. 2011, 2013). With respect to soil homogenization, the resulting reduction in plant species diversity could decrease facilitative interactions and niche partitioning among species (decreased overyielding), decreasing nutrient retention and productivity, both above and belowground (Tilman 1999, McKane et al. 2002, Griffin et al. 2009). In addition, loss of functional groups of species due to a reduction in diversity could reduce the complexity of leaf chemistry and phenology, lowering the rate of decomposition (Hector et al. 2000, Zak et al. 2003).

Soil heterogeneity also may influence nutrient cycling directly, as evidenced by the results of split-pot experiments, where plant nutrient acquisition differs among individuals grown with homogenous nutrient availability and those grown with the same amount of nutrients available, but distributed heterogeneously (Hodge et al. 2000, Henry and Jefferies 2002, 2003a, b, Holzapfel and Alpert 2003). Beyond the level of plant–soil interactions, animals may potentially interact with soil microsites to alter ecosystem processes. For example, burrowing mammals and nesting birds can show preferential activity in soil microsites with unique topographical or soil structure properties and altered local disturbance patterns and nutrient deposition (from animal waste) resulting from this activity could alter nutrient cycling locally.

To understand the effects of plant diversity and soil homogenization on ecosystem processes, both the magnitude and variability of processes should be measured (Hooper et al. 2005). Ecosystem processes should be less variable (more consistent over time) in response to environmental fluctuations if plant species diversity is greater (Tilman and Downing 1994). The question of whether soil homogenization, possibly via its influence on plant diversity, can influence the variability of ecosystem processes (i.e., the ability of these processes to remain consistent over time in response to disturbance/stress) may be particularly important in the context of global climate change (García-Palacios et al. 2012). For example, Fridley et al. (2011) described how microrefugia to climate warming can be provided by microsites differing in soil depth; shallow microsites experienced increased species loss in response to climate warming treatments, while the deep microsites gained species lost from the shallow microsites. The high microenvironmental variability in soil depth found within the grassland led to no net species loss in the plant community. The same pattern has been observed in historical climate records at the landscape scale, where pockets of the globe had
environmental characteristics that made them less susceptible to climatic changes and offered climate change refugia to species (Grime and Curtis 1976, Bennie et al. 2006).

Microedges and ecosystem processes
Non-additive interactions among patches along microedges also may apply to ecosystem processes. For example, decomposition rates may be non-additive along patch edges; such a response would be analogous to the results of litter mixture experiments, where the presence of litter from multiple plant species experiences faster decomposition than the litter from the component species in isolation (Gartner and Cardon 2004). These non-additive responses can result from complementarity among microsites (i.e., soil microbial activity limited by a given nutrient in one microsite may be increased by the higher availability of that nutrient in a neighboring microsite, and vice versa). Small-scale processes occurring on a microedge therefore are analogous to larger scale processes that have been observed to be driven by complementarity, such as hot spots and hot moments of elemental cycling at the interface between wetland and upslope areas (McClain et al. 2003).

With respect to soil hydrology and physical properties, there may be important implications of microsites and microedges for soil water movement; the resulting variation in moisture conditions can influence plant community composition and structure. Water movement can be impaired in stratified soils, as can occur with the stratification or layering of microsites in a heterogeneous soil. As water moves between strata or layers (i.e., microsites), it slows down when it reaches the edge of the next distinct layer due to changes in soil composition, especially changes in pore size (Miller and Gardner 1962). The latter results in a longer duration of dry conditions in the adjacent microsite, and a longer duration of wet conditions at the microedge, as water builds up at the boundary.

Conclusions
Plant diversity research has been dominated by plant ecologists, who in many cases have taken a predominately aboveground perspective; the latter studies would be complemented by a more detailed, soil-based perspective regarding the size and composition of belowground microsites. Improving understanding of soil heterogeneity–plant diversity relationships promises to be of great value in elucidating the mechanisms whereby soil disturbance and land use legacies can affect plant communities, as well as ecosystem processes. We have demonstrated that the variability observed in heterogeneity diversity studies may be due to both experimental design and ecological variability. Researchers will likely be able to better test for heterogeneity effects by considering the role of soil homogenization, not only as a control treatment, but as an important potential outcome of disturbance, and by accounting for spatial scale (PSPSM) and other factors such as plant competition. Additionally, consideration of small-scale, belowground processes that are analogous to larger scale processes (e.g., microedges, microfragmentation) may further aid with understanding the discrepancy in results among heterogeneity–diversity studies. The latter studies should then be augmented further by assessing the role of microedges in both promoting increased plant diversity and creating unique interfaces for driving ecosystem processes.

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