Plant-soil feedbacks as drivers of succession: evidence from remnant and restored tallgrass prairies

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Abstract. Plant-soil feedbacks can contribute to the coexistence of plant species and may predict the abundance of plant species within communities. Here, we test if plant-soil feedbacks act as drivers of secondary succession. We found that the strength of feedback experienced by a plant species was positively correlated with that species’ successional stage, indicating that plant-soil feedbacks can contribute to shifts in plant species abundance during succession. We did not observe a significant relationship between strength of feedback and plant species abundance at our study sites, but the positive relationship of feedback and successional stage would generate positive relationships between feedback and the abundance of plant species in communities at equilibrium. This result is supported by spatially explicit simulation models that demonstrate the potential for plant-soil feedbacks to determine changes in species abundance over time and the increasing strength of the relationship between feedback and plant species abundance during succession.

Key words: coexistence; density dependence; diversity; grassland; Janzen-Connell; mycorrhizal fungi; soil pathogens.

INTRODUCTION

Natural enemies have long been hypothesized to allow the coexistence of competing plant species. Although specialist herbivores were originally implicated as the agents of conspecific negative density dependence (Janzen 1970, Connell 1971), increasing evidence indicates that negative density dependence results from feedbacks between plants and soil microbial communities (Bever 1994, Bever et al. 1997, Mangan et al. 2010). These feedbacks occur as soil microbial communities change in association with different plant species, and these changes alter the growth of conspecifics and co-occurring plant species (Bever et al. 1997). This framework has been promoted as an explanation for coexistence of competing plant species (Bever 1994, Packer and Clay 2000, Petermann et al. 2008) and the dominance of invasive species (Klironomos 2002, Callaway et al. 2004, 2008). Building on these successes, further work is needed to determine if plant-soil feedback can explain other patterns and processes in plant communities. In this paper, we test the potential for feedbacks to be altered by land use history, for variation in plant-soil feedbacks to alter plant community structure, and the role of plant-soil feedbacks as drivers of plant succession.

Perhaps the strongest available evidence that soil feedback is important to plant community structure comes from observations of a correlation between strength of feedback and the relative abundance of plant species (Klironomos
Analytic models and spatially explicit simulations using cellular automata models demonstrate that feedback can indeed generate positive dependence of relative abundance on strength of feedback (Mangan et al. 2010, Chisholm and Muller-Landau 2011), providing support that empirical observations of positive correlations between experienced plant-soil feedback and relative abundance is indicative of negative feedbacks structuring plant communities. However, there are examples where the relationship between feedback and abundance is unclear or non-significant (Diez et al. 2010, MacDougall et al. 2011, Reinhart 2012). Theoretical models related to feedback and plant species abundance are based on equilibrium conditions (Mangan et al. 2010), and it is possible that feedback will not predict the abundance of plant species in successional communities. Further work is needed to determine the generality of the feedback-abundance relationship and the conditions under which it occurs.

If plant-soil feedbacks predict abundance under equilibrium conditions, it is also possible that feedbacks underlie other major aspects of plant community dynamics such as species turnover during succession in disturbed plant communities. Some research indicates a potential role for plant-soil feedbacks in succession (van der Putten et al. 1993, Kardol et al. 2006, Kulmatiski et al. 2008, van de Voorde et al. 2012). In general, annuals appear to experience stronger negative feedbacks than perennials (Kulmatiski et al. 2008), and strong negative feedback among early successional plant species is consistent with microbial dynamics facilitating their replacement by other species (van der Putten et al. 1993, Kardol et al. 2007). Further, soils collected from early successional fields appear to inhibit early-successional plant species, whereas soils from late successional fields may promote late-successional plants, suggesting that soil communities may change over time to favor late successional species (Kardol et al. 2006, Middleton and Bever 2012). However, reciprocal feedback tests across a range of early and late successional plant species is needed to demonstrate that plant-soil feedbacks drive successional dynamics.

In this study we tested the role of plant-soil feedbacks in structuring plant communities and as drivers of plant succession. We did this by evaluating the strength and direction of feedbacks, whether they vary with history of anthropogenic disturbance, whether they correlate with relative abundances of plant species across communities of varying land-use history, and whether they vary among plants of different successional stages. We did this with paired greenhouse experiments and field observations in the tallgrass prairies of central North America, in sites that vary from unplowed remnant prairies to prairies replanted on former agricultural fields. To enhance our interpretations of these results, we used a cellular automata model of plant soil feedbacks to demonstrate the pre-equilibrium dynamics of changes in plant species abundance over time and the expected changes in correlation of plant species relative abundance and strength of feedback in a community structured by plant-soil feedbacks.

**Methods**

**Study sites**

Study sites included three remnant and three restored tallgrass prairies located in Northwest Indiana, USA. The three remnant sites were established as nature preserves 30 or more years ago and have been maintained with prescribed fire and selective invasive species removal. However, prior to their protection as nature preserves, these sites have some history of anthropogenic disturbance and alterations to disturbance regimes, including alterations to site hydrology, cattle grazing and fire suppression. The three restored prairies were former agricultural fields with histories of corn and soybean cultivation. These sites were taken out of production and planted with seed mixes containing species representative of mesic tallgrass prairie in this region, including all plant species included within this study (Appendix). Restored sites were planted from eleven to five years before initiation of this study and at the time of this study had well established cover of predominantly native prairie species.

This study system is well suited for testing the role of plant-soil feedbacks in succession since successional trajectories in tallgrass prairie restoration and the composition of undisturbed plant communities.
communities have been well studied so that all of our study species can be categorized by their tolerance to disturbance and relative successional stages. Secondary succession in tallgrass prairie is a continuous process, though in studies of prairie restoration it has been characterized as occurring in three or four stages (Schramm 1990, Betz et al. 1996). This process has been thoroughly described by Schramm (1990) and Betz et al. (1996), and the following describes the expected shifts in plant species abundance with succession in tallgrass prairie, focusing on our study species. The first stage of succession is characterized by ruderal species typical of agricultural fields along with ruderal prairie species, including *Rudbeckia hirta*. This is followed by dominance of short-lived perennials such as *Ratibida pinnata* and *Elymus canadensis*, then longer-lived perennials such as *Panicum virgatum* and *Symphyotrichum novae-angliae*. Schramm (1990) referred to the third stage as the “closeout stage.” During this stage *Andropogon gerardii* increases in abundance to become the dominant plant species. With time, *Andropogon* declines as late successional forbs (e.g., *Parthenium integrifolium*) and the late-successional dominant grass, *Sporobolus heterolepis*, begin to increase in importance. This shift in species abundance is paralleled by these species’ vulnerability to anthropogenic disturbance (Swink and Wilhelm 1994). *Sporobolus* and *Parthenium* are among the most sensitive species. In contrast, *Rudbeckia*, *Ratibida*, and *Elymus* are tolerant of anthropogenic disturbance, and within otherwise undisturbed remnant and restored prairies these species are likely to be most common along the disturbed edges (Schramm 1990, Swink and Wilhelm 1994).

**Feedback experiments**

In each of our six study sites, soil was collected with a 2.5 × 30 cm soil corer from random locations within a 30 × 30 m area. Cores taken within each site were pooled and homogenized, but soils from each site were maintained separately throughout the experiment. Pots (983 mL, 36-cm deep “deepots”; Stuewe and Sons, Tangent, Oregon, USA) were filled with pasteurized soil (Crider silt-loam topsoil mixed 50:50 with sand to improve drainage and root recovery) and inoculated with 100 mL of prairie soil from one of our six study sites. Six replicate pots of inoculated soils were conditioned with single seedlings of each plant species for three months, allowing time for the soil microbial community to respond to the presence of each plant species. Eight prairie species were used to condition the soil including four species of composites (*Asteraceae*: *Rudbeckia hirta* (Black-eyed Susan), *Ratibida pinnata* (Yellow Coneflower), *Symphyotrichum novae-angliae* (New-England Aster), *Parthenium integrifolium* (Wild Quinine) and four species of grasses (*Poaceae*: *Elymus canadensis* (Canada Wild Rye), *Panicum virgatum* (Switchgrass), *Andropogon gerardii* (Big Bluestem), and *Sporobolus heterolepis* (Prairie Dropseed)) (Poaceae). Species were selected that typically occur in remnant and restored tallgrass prairies, represent a range of life histories from ruderal to late-successional species, and can be relatively common within tallgrass prairie at different points in succession (Betz and Lamp 1989, Swink and Wilhelm 1994).

This soil conditioning phase of the experiment included a total of 288 pots (6 sites × 8 plant species × 6 replicates)

After plants conditioned soil for three months, soils and roots were harvested. All roots were cut into fragments 3 cm or smaller and included in the inoculum. New deepots were partially filled with sterile background soil, 100 mL of conditioned soil from one of the site × soil conditioning treatments was added to the pots, and then pots were capped with a layer of sterile soil. Pots were then planted with a recently germinated seedling of one of our eight study species. Each plant species was grown in each plant × soil treatment combination, with five replicates grown in soil previously conditioned by a conspecific and three replicates were grown in the soil of each of the other study species. This experiment consisted of 1248 plants in separate pots (6 sites × conditioned soil from 8 species × 8 plant test species [with 5 replicates grown in conspecific soil and 3 replicates grown in each heterospecific soil]). Plants grew for two months in a temperature controlled greenhouse under ambient light conditions and were watered as needed. Following two months of growth, the above- and belowground portions of the plants were harvested, dried and weighed.

We also tested the mycorrhizal inoculum potential (MIP) of each replicate of conditioned
soil. Fifty milliliters of sterile soil, and this soil was used to fill 115 mL “stubby” cone-tainers (Stuewe and Sons). Cone-tainers were then planted with sorghum (Sorghum bicolor) seedlings and grown for four weeks. Roots were harvested, stained and scored for percent mycorrhizal colonization following standard protocols (McGonigle et al. 1990).

Plant community composition
The abundance of all plant species included in the experiment was estimated at all sites from which soil was collected. Data were collected in late July when plants were near peak biomass. Relative abundance of all species occurring at the site was estimated by recording the percent cover of each species at 35 randomly located 0.5 × 0.5 m plots within the study area.

Data analysis
We used ANOVA to examine main effects of site type (remnant vs. restored prairie), site (nested within site type), “soil conditioning” (plant species used to condition the soil), “plant” (plant species being tested), and their interactions on the log-transformed total biomass of the plants at the conclusion of the experiment. A priori contrasts were used to calculate the average feedback strength experienced by each species following Bever et al. (1997) and Mangan et al. (2010), where feedback is calculated as an interaction coefficient between pairs of plant species (I). Feedbacks have been calculated by comparing a species’ growth in soils associated with conspecifics vs. heterospecifics, or as pairwise interactions comparing two species’ growth in their own and the other’s soils (Bever et al. 1997). Here we focus on the pairwise approach due to its power to predict coexistence or exclusion of competing plant species (Bever et al. 1997) and the previous success of this approach in predicting patterns in plant communities (Mangan et al. 2010, Smith and Reynolds 2012).

Pearson’s correlation coefficients were calculated to determine the relationship between the average strength of feedback experienced by a plant species (mean I) and the log of the average percent cover of each species within each site. Correlation coefficients were also used to test the relationship between plant-soil feedback and successional stage of each plant species. We used ANCOVA to test for differences in these relationships between sites. Successional stages were assigned to our plant species based on coefficients of conservativism (CCs). CCs indicate a species’ dependence on natural areas relatively undisturbed by anthropogenic activities (Swink and Wilhelm 1994), and in our region these values are correlated with the successional stage of the plant species (Spyreas et al. 2012). Minor modifications to these values were made based on studies of secondary succession in tallgrass prairie restorations by Betz et al. (1996) and Schramm (1990) to account for early successional species that are associated with natural disturbances in protected natural areas (Appendix: Table A1), but these changes did not qualitatively impact our results. Response of AMF to different plant species (as indicated by MIP of conditioned soil), the variation in AMF between sites and site types, and interactions between the effects of plant species and site or site type were analyzed using ANOVA. All data were analyzed in SAS 9.4.

Spatial simulation
We developed simulations of plant communities structured by negative feedback to explore changes in relative abundance of species (i.e., succession) and the correlation of relative abundance with strength of feedback across time. In order to separate effects of average strength of feedback from variation between life history strategies, we ran the simulations which explored the consequences of a correlation between average feedback and establishment and mortality rates. We started with no variation in average feedbacks and no variation in life histories (i.e., identical species specific mortality and colonization rates) and with the species initially distributed randomly at equivalent frequencies in saturated communities. Then under similar initial conditions, we randomly assigned differences in average feedback and establishment and mortality rates. We started with no variation in average feedbacks and no variation in life histories (i.e., identical species specific mortality and colonization rates) and with the species initially distributed randomly at equivalent frequencies in saturated communities. Then under similar initial conditions, we randomly assigned differences in average feedback, but again without variation in life histories. Again, under similar initial conditions, we then tested the consequences of a correlation of strength of feedback and life history by assigning species specific background establishment and mortality rates that were proportional to a species’ average feedback such
that a species with a relatively negative average feedback has a relatively high establishment rate and a relatively high mortality rate. As investments in defense would be expected to increase longevity as well as decrease investment in reproduction, thereby decreasing propensity to colonize following disturbance, we allow an advantage to early successional species by starting with a low number of individuals of each plant species and a large proportion of uninhabited space (simulating the consequence of disturbance). We note that this simulation does not fully represent the advantages of weedy species in early succession, as we do not represent lags in colonization by late successional species and the more rapid development time to reproductive maturity of early successional species. We represent these early advantages of early successional species by starting the simulation with each species at a frequency inversely proportional to its rank order of the strength of its average feedback. For the sake of completeness, we also ran simulations with uniform negative average feedbacks across species and variation among life history traits, with both a uniform saturated start and starting at frequencies proportional to their establishment rates, as might be expected in early successional communities.

A detailed description of the model can be found in Mangan et al. (2010) and Mack and Bever (2014). The model is a spatially explicit individual-based stochastic computer simulation. Each cell in a lattice represents an individual plant. The lattice was initially filled at random. In the third set of simulations only 50 plants were initially placed within the community (thus 9950 sites were initially empty). Plants were chosen at random for death in proportion to their mortality rates and the likelihood of each species in the community to be chosen to colonize the empty site was determined by the composition of species within a dispersal neighborhood and an interaction neighborhood around the empty site. Dispersal was uniform across the dispersal neighborhood (24 nearest neighbors) and species more common within the dispersal neighborhood had a higher probability of being chosen for colonization. Soil feedback from neighboring plants is weighted by distance from the empty site (so that plants closer to the empty site exert a stronger feedback effect than plants further away) and species specific feedback values are used to weight the probability that each species will be chosen for colonization. Communities were simulated using 8 species with randomly assigned soil feedback values. The grid size used was 100 × 100 and 2,000,000 death and colonization events were simulated. Pairwise soil feedback effects were assigned randomly within a constrained range of values such that the values more closely resemble empirical measurements following Mangan et al. (2010) and Mack and Bever (2014). Growth in conspecific soil was always less than growth in heterospecific soil to ensure negative feedback and therefore coexistence. MATLAB was used to run all simulations. We analyzed the differences between the correlation coefficients for the correlation of abundance and feedback after 100,000 and 1 million replacements using a GLM in order to measure the change in the relationship between average feedback and abundance over the course of succession.

RESULTS

Greenhouse experiments

Overall, we found significant plant-soil feedbacks (Appendix: Table A1). Follow-up contrasts indicated that these feedbacks were generally negative (Fig. 1), with seven of the eight study species experiencing negative feedback. Strength and direction of feedbacks varied between sites for Andropogon, Panicum and Parthenium (Fig. 2), but feedbacks did not differ significantly between sites for the other five species included in our study. Despite differences between sites, feedbacks were not significantly different between remnant and restored prairies (Fig. 1).

Feedback experienced by a plant species and the successional stage of that species were significantly correlated (Fig. 3A). This relationship was consistent across all of our study sites (ANCOVA successional stage × site interaction; \( F_{5,36} = 0.74, p = 0.6 \); Appendix: Fig. A2). However, feedback was not correlated with plant species abundance. This was consistent when considering mean feedbacks and abundance averaged across all sites, within sites (Appendix: Fig. A1), or for feedbacks averaged across remnant or restored prairies (Fig. 3B).
The abundance of mycorrhizal fungi, as measured by mycorrhizal inoculum potential, varied among sites ($F_{4,228} = 7.13, p < 0.0001$) and in their response to different plant species ($F_{7,228} = 2.25, p = 0.03$), but not between remnant and restored prairies ($F_{1,228} = 0.04, p = 0.8$). Although species varied in their effect on mycorrhizal fungi, there were no clear associations between a species’ effects on AMF and the feedbacks they experienced or their successional stage. However, the mean MIP of soils originating from a site was positively correlated with the mean feedback experienced by plant species at that site ($r^2 = 0.89, p = 0.02$; Appendix: Fig. A3).

**Spatial simulation**

Other than the simulation condition with uniform average feedback, the other four simulation conditions resulted in a positive correlation between abundance and average feedback after 10 million replacement events (Fig. 4). However, early in succession, the correlation may be negative or insignificantly different from zero (Fig. 4A, D, G, J, and M). The correlation coefficients measured after 100,000 replacements were
significantly less than the correlation coefficients measured after 1 million replacements (GLM; $F_{75} = 16.4, p < 0.0001$; Fig. 4B, E, H, K, and N). Note that even without life history trade-offs, the species with weak negative feedbacks behave like late successional species in that they became more abundant over time (Fig. 4C, F, I, L, O). These shifts in species abundance became more prominent as we represent the advantages to early successional species in colonization by either initiating the simulations with low number of individuals (Fig. 4L) or with initial frequencies inversely proportional to their average feedback (Fig. 4O). There was no obvious pattern of abundance in any of the runs with uniform negative average feedback. In this model, only neutral coexistence can result from the trade-off between establishment and mortality. Therefore, any variation from that trade-off that could produce differences in abundance are either strong enough to overcome the uniform negative average feedback and cause the community to go to fixation, or are too weak and are drowned out by them.

**DISCUSSION**

Prevailing views of succession build on evidence of a tradeoff between colonization and competitive ability (Huston and Smith 1987, Tilman 1990). Classic characteristics of weedy species, such as small seed size, abundant seed production, wind dispersal, and fast growth rates are clearly important for species that initially colonize disturbed land. Our results provide evidence that trade-offs between these life-history characteristics and plant-soil feedbacks can be important drivers of succession. While studies of a few species have found strong negative feedback in early successional species (van der Putten et al. 1993, Kardol et al. 2006, van de Voorde et al. 2012), ours is the first study to demonstrate a positive correlation between the strength of feedback and successional stage of plant species. This result supports an important role of the soil community as a driver of shifts in plant species abundance during succession. Our simulation models show that the correlation of plant life-history with experienced feedback will result in the initially abundant rapid-colonizing plant species early in succession being replaced over time by the late successional species, which are more tolerant of their own soil microbial communities.

The shift from negative feedbacks in early successional plant species to weak or positive feedbacks among late successional species provides evidence of a tradeoff of colonization ability and rapid growth rates with investment in plant defense and mutualism, which then mediates shifting relative importance of pathogens and mutualists. Early successional plant species generate strong negative feedbacks, likely because they are weakly defended against pathogens (van der Putten 2003) and also because they are relatively unresponsive to microbial mutualists (Reynolds et al. 2003, Hoeksema et al. 2010). In contrast, late-successional plant species are generally more dependent on microbial mutualists (Janos 1980), which
Fig. 4. Panels A–C represent simulations with initial conditions where all species start at equal frequencies and the environment is fully saturated with average feedback, establishment and mortality rates equal for all species. Panels D–F represent simulations with initial conditions where all species start at equal frequencies and the environment is fully saturated with establishment and mortality rates equal for all species, but species specific differences in average feedback. Panels G–I represent simulations with initial conditions where all species start at equal frequencies and the environment is fully saturated as before, but now with species specific differences in average feedback, establishment, and mortality rates. Panels J–L represent simulations with initial conditions where all species start at equal frequencies, but the environment is only filled to 10% of saturation and again with species specific differences in average feedback, establishment, and mortality rates. Panels M–O represent simulations with initial conditions where species start with frequencies correlated with the rank order of their establishment rate with differences in average feedback. Panels A, D, G, J and M plot the change of the correlation coefficient over time of the relationship between relative abundance and average feedback for each of the four
likely accumulate in the soils associated with their root systems (Bever et al. 2012), and late-successional plant species are better defended against pathogens (van der Putten et al. 1993, van der Putten 2003). As a result, the accumulation of soil pathogens and of soil mutualists within the soil during succession may both inhibit early successional species and facilitate late successional species. It is possible that the dependence of late successional species on soil mutualists and their defense against pathogens may be associated with other traits that allow their persistence late in succession. Our simulations demonstrate that a tradeoff between establishment rates and mortality is not sufficient to explain shifts in species abundance over time, but variation in the strength of plant-soil feedbacks is sufficient to produce these changes. However, other traits, including strong competitive ability (Tilman 1990), may be important, and further work is required to determine the relative importance of tradeoffs of colonization ability with investment in defense and mutualism versus tradeoffs with competitive ability as drivers of shifts in species abundance during succession.

An unresolved conceptual issue in ecology is whether the same processes that drive shifts in species abundance over time during succession also generates other commonly observed changes in plant communities, including increasing species diversity with succession (Bazzaz 1975, Dale and Adams 2003, Gross and Emery 2007). Should this be the case, evidence of the most important trade-offs during succession could be found from evidence of the most important drivers of coexistence in late successional communities. Our results are consistent with soil community dynamics contributing to plant species coexistence within the prairie as most feedbacks were negative, which can stabilize competitive interactions between plant species (Bever et al. 1997, Bever 2003).

However, we did not observe evidence of a positive correlation of strength of feedback and relative abundance, which has been identified as a signature of a primary role of feedbacks in structuring plant communities (Klironomos 2002, Comita et al. 2010, Mangan et al. 2010, Johnson et al. 2012). Previous models predicting a positive association between feedback and abundance are based on equilibrium conditions (Mangan et al. 2010, Chisholm and Muller-Landau 2011), however, our simulation results demonstrate that a positive correlation of relative abundance and strength of feedback is not expected in non-equilibrium communities. In fact, early in succession, the simulations produce a negative relationship as the rapid colonizing plant species are initially most abundant (Fig. 4). This shift in the correlation of the strength of feedback and relative abundance is consistent with our empirical results, and may explain previously published insignificant correlations of relative abundance and strength of feedback (Diez et al. 2010, MacDougall et al. 2011, Reinhart 2012). For example, in MacDougall et al. (2011), native species abundance, but not invasive species abundance, was predicted by the strength of plant soil feedback. This is consistent with our results, as invasive species would not be expected to have reached equilibrium with the invaded community. The restored prairies in our study were planted within the last eleven years, and therefore were not expected to be at equilibrium.

The remnant sites also have recent histories of anthropogenic disturbance and this land use history may have prevented them from being at equilibrium. However, we note that our simulations suggest that plant-soil feedbacks will be a good predictor of future change in these plant communities and that relative abundance of individual species will be correlated with the average strength of their feedback at equilibrium. Consistent with this expectation, we note that Sporobolus was found to consistently experience positive feedback values, regardless of initial conditions.
source of the soil community, and in our region, *Sporobolus* often dominates the least disturbed remnant prairies sites. However, this species is highly sensitive to anthropogenic disturbance (Swink and Wilhelm 1994), which likely explains its rarity at our study sites. If we treat *Sporobolus* as an outlier and remove this sensitive species from the regressions, the relationship between plant-soil feedbacks and plant species abundance becomes significant in remnant prairies ($r^2 = 0.75$, $p = 0.011$), but the relationship in restored prairies remains non-significant ($r^2 = 0.08$, $p = 0.54$). This indicates that these remnant prairies are approaching equilibrium conditions, and as *Sporobolus* recovers from past anthropogenic disturbances, the abundance of plant species within these communities will be correlated with the plant-soil feedbacks experienced by these species.

While we did not see consistent differences in plant-soil feedbacks between remnant and restored prairies, our results suggest that host-specific changes in soil microbial communities may alter species relative abundance, which would increase the mean successional stage of plant communities. Consistent with this expectation, previous work has indicated the potential for soil microbial inoculations to accelerate succession in ecological restoration (Bever et al. 2003, Carbajo et al. 2011, Middleton and Bever 2012). We find that feedback strength is generally similar across variation in soil communities from sites with differing land use histories. As agricultural disturbance produces large changes in soil community composition (Fitzsimons et al. 2008, Fierer et al. 2013), the robustness of plant-soil feedbacks to variation in initial composition of soil microbial communities is notable and is consistent with there being multiple complimentary microbial mechanisms generating negative feedback (Bever 2003, Bever et al. 2012). However, we observed significant variation in the strength and direction of feedback between sites for three plant species. This variation in feedbacks was related to the abundance of arbuscular mycorrhizal fungi (AMF). Average mycorrhizal inoculum potential of trained soils was positively correlated with the average feedback experienced by all species at a site, indicating that AMF have an important role in plant soil feedback (Fitzsimons and Miller 2010, Bever et al. 2012).

Our observation of a consistent relationship between the strength of plant soil feedback experienced by a plant species and plant life histories that determine a plant species’ relative position in succession provides evidence that shifts in plant species abundance during succession can be caused by changes in soil microbial communities. This shift in the relative abundance of plant species is reproduced in simulated plant communities. Moreover, the simulations confirm that following disturbance, communities structured by plant soil feedbacks will progress from negative correlations between relative abundance and strength of feedback to a positive correlation at equilibrium. Thus our results provide support for plant-soil feedbacks simultaneously contributing to shifts in plant species abundance during succession and the maintenance of plant diversity at equilibrium.

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Supplemental Material

Ecological Archives

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