

Positive and negative feedbacks drive aboveground traits in rare plant species

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Abstract

Microbially mediated plant-soil feedbacks drive patterns of plant growth, competitive ability, succession, and community composition. Although rare plant species maintain unique functional traits that often facilitate negative feedbacks, there is not a consensus on the belowground drivers nor the effects of phylogenetic origin of previously plant-conditioned soil on aboveground traits associated with rare species. Using a common garden, we connect belowground fungal colonization to aboveground traits in species varying in rarity, and soil conditions varying in the phylogenetic relatedness of conditioning plant species, to demonstrate the mechanistic relationship between belowground ectomycorrhizal fungal (ECM) colonization and aboveground total plant biomass in 14 *Eucalyptus* species varying in their rarity status. Specifically, we found that while the rarest species displayed 88% less total biomass than common species, the rarest species also maintained 62% greater ECM colonization than common counterparts. Further, negative feedbacks resulted in reduced biomass coupled with positive feedbacks that resulted in increased ECM colonization that varied on the basis of phylogenetic relatedness. The rarest species decreased by 71% - 94% in total biomass but increased by 96% - 114% in ECM colonization in phylogenetically similar and distant soil compared to conspecific soil conditions. The effect size of ECM colonization directly affected the effect size of total biomass in phylogenetically distant conditions with a significant negative correlation ($r^2 = -0.83$) to show that biomass may be a function of ECM colonization acting differently among species varying in rarity. Consequently, rare plant species may utilize stronger associations with belowground mycorrhizal mutualists than common plant species, to facilitate geographic, competitive, and functional persistence, even while maintaining lower biomass.

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soil conditions. The effect size of ECM colonization directly affected the effect size of total biomass in phylogenetically distant conditions with a significant negative correlation ($r^2 = -0.83$) to show that biomass may be a function of ECM colonization acting differently among species varying in rarity. Consequently, rare plant species may utilize stronger associations with belowground mycorrhizal mutualists than common plant species, to facilitate geographic, competitive, and functional persistence, even while maintaining lower biomass.

Introduction

Plant-soil feedbacks are major drivers of plant growth, long-term survival, and patterns of biodiversity in plant communities, that are especially important in an era of global change (van der Putten et al. 2013, Van Nuland et al. 2017, Semchenko et al. 2022). Through unique alterations in the biological and chemical properties of soil due to plant traits and inputs that lead to changes to the microbial community composition and function, the conditioning effects of plant communities drive patterns of productivity, composition, and succession in future plant communities through soil legacy effects (Li et al. 2023; Lu et al. 2023; Qu et al. 2023). Although plant-soil feedbacks can range from facilitative to inhibitory, microbially mediated legacy effects can persist in the soil for long periods of time after the conditioning plant species have disappeared (Kulmatiski & Beard 2011; Schmid et al. 2021). Therefore, patterns of plant growth, reproduction, and competitive ability in current plant communities may be driven by soil-microbial changes induced by previous species no longer present or prevalent (Bever 2003, van der Putten et al. 2013). Specifically, mutualistic ectomycorrhizal (ECM) fungi play an integral role in mediating the productivity and diversity of aboveground plant communities through facilitating shifts in nutrient availability as well as soil structure and stability across early, mid-, and late successional stages (Kaľucka & Jagodziński 2017; McMahan et al. 2022; Zhao et al. 2023 Wang et al. 2023). For example, Hannula et al. (2021) found that while bacterial communities quickly respond to alterations in plant community composition, microbially mediated soil legacy effects remain after five months of succession. Similarly, McMahan et al. (2022) found that plant succession is highly influenced by mycorrhizal dependence, with ECM plant hosts demonstrating higher seedling survival and biomass in early succession. Additionally, other belowground root-colonizing fungi such as dark septate endophytes (DSE) can enhance aboveground plant growth through increased nitrogen (N) and phosphorus (P) root absorption as well as increased root surface area (He et al. 2019; Xie et al. 2021). However, Reininger & Sieber (2012) suggests that a trade-off exists between DSE and ECM communities, such that increased allocation to ECM fungi can create physiological barriers preventing the colonization of beneficial DSE with extended effects on future plant community dynamics. Furthermore, plant community composition and variation in plant functional groups can also drive unique changes in soil-legacy effects not seen in species-specific monocultures (Schmid et al. 2021). While species-specific legacy effects exist in grasslands, Heinen et al. (2020) demonstrated that a marked dominance in functional group (grasses versus forbs) within a conditioning community leads to negative feedbacks on the same functional group in future plant communities. Moreover, these community-driven legacy effects often exhibit subsequent effects on plant-herbivory, plant-pollinator, and plant-plant interactions, all of which can determine changes to ecosystem function (Wurst & Ohgushi 2015; Heinen et al. 2018; Li et al. 2023).

Although legacy effects work in tandem with other ecological and evolutionary processes shaping communities, the conditioning effects of previous plant communities in soil are often recognized as major determinants of above- and belowground plant success in widespread grassland communities consisting of common species (Kulmatiski et al. 2008; van de Voorde et al. 2011; Cortois et al. 2016). For example, Kulmatiski et al. (2008) found that 83% of the 315 experiments at that time were focused on grassland systems that informed patterns in plant-soil feedback strength and direction. Patterns in grasslands, however, may not be applicable to other systems varying in growth form, habitat, or rarity such as trees, forests, or plants with rare status (Rabinowitz 1981). However, the consideration of plant-soil feedbacks is paramount to understanding rare species persistence in community mixtures due to unique and wide variation of specialized functional traits in rare species, such as specific leaf structures, root systems, growth forms and rates, and microbial mutualisms, often not seen in common species (Dee et al. 2019; Xi et al. 2021; Zhang et al. 2022). For

example, rare species have been found to exhibit low biomass (Kempel et al. 2018; Vincent et al. 2020), high specific root length (SRL) (Poot & Lambers 2003), and increased phenotypic plasticity (Munson & Sher 2015; Boyd et al. 2022). Although ecological studies of rare plant species are often focused on the geography and population traits of rare species, rather than the context of growing conditions, studies have demonstrated the role of plant-soil feedbacks in driving patterns of rarity and commonness in plant communities on the landscape (Klironomos 2002; Maron et al. 2016; Kempel et al. 2018). For example, Maron et al. (2016) suggested that abundant common species may suffer from increasingly negative plant-soil feedbacks, while rare species may persist in a geographically limited space due to positive plant-soil feedbacks. Moreover, van der Putten et al. (2013) proposed that rare plant species may have the potential to become invasive outside of their native range due to favorable, positive plant-soil feedbacks in non-native ranges. Further, the relationship between unique plant functional traits and belowground mycorrhizal fungi can range from mutualistic to parasitic dependent on temporal and spatial variation in soil nutrient conditions; however, the expected relationships between plant traits and soil factors, such as N enrichment, are inconsistent and often lack predictability (Treseder 2004; Hoeksema et al. 2010). For example, Treseder (2004) found that mycorrhizal abundance decreased by 15% under N fertilization, while Johnson et al. (2010) suggested that the prominence of mycorrhizal parasitism decreased under nitrogen-limiting conditions. However, Hoeksema et al. (2010) and Wooliver et al. (2018) both demonstrated a marked reduction in mycorrhizal dependence under high N conditions. Taken together, these studies suggest that unique interactions take place between plant functional traits and variation in soil conditions, such that plants either carefully manipulate the allocation of carbon (C) to belowground symbionts or are parasitized by them under higher N conditions. Whether and how N enrichment affects plant host reliance on mycorrhizal fungi on the basis of species rarity to affect the outcome of plant-soil feedbacks is unknown, to our knowledge.

Although plant community composition is crucial to the development of unique plant-soil feedbacks, the phylogenetic relatedness underpinning plant communities provides a mechanistic driver of plant soil feedback strength and direction (Jiang et al. 2022). There is a strong phylogenetic signal to the degree in which plant species share their belowground biotic partners, such that more closely related species have more similar microbiomes (Wandrag et al. 2020). Although some plant species have demonstrated increased growth in phylogenetically similar communities due to the utilization of closely related co-evolved microbial communities (Anacker et al. 2014), others have demonstrated positive feedbacks in plant growth in communities of increasing phylogenetic distance (Kempel et al. 2018; Jiang et al. 2022). The beneficial relationship between phylogenetically distant species and their associated microbial communities may be mediated by species-specific mutualists and negative feedbacks in pathogen colonization (Crawford et al. 2019). For example, Kempel et al. (2018) found that regionally rare plant species demonstrated increased soil biota coupled by decreased biomass in genetically similar mixtures. Similarly, plant-soil feedbacks also drive divergence in community trait optimums on a phylogenetic basis, such that phylogenetic patterns in plant-soil feedbacks can be partially explained by phylogenetic conservatism in plant traits (Senior et al. 2018). Consequently, plant-soil feedbacks can be explained by plant traits, many under selection evolutionarily, and are reflected in phylogenetic patterns of plant co-existence (Kut'áková et al. 2018). For example, Münzbergová & Šurinová (2015) and Fitzpatrick et al. (2017) both demonstrated that the intensity of plant-soil feedbacks were affected by physical plant traits such as height, specific leaf area (SLA), and leaf N and P concentration, as well as temporal traits such as plant life stage. Further, Jiang et al. (2022) suggested that divergent, phylogenetically dependent, plant-soil feedbacks exist among rare versus common species, such that rare species persist in phylogenetically distant communities, while common species perform best in phylogenetically similar communities. These phylogenetically based plant-soil feedbacks are thought to effect spatial and temporal patterns of rare versus common species differently on the basis of functional trait response (Jiang et al. 2022). For example, Reijenga et al. (2021) found that priority effects, which can include plant-soil feedbacks in which early arrival species condition soils in a way that exerts inhibitory or facilitative control on secondary communities (Chappell et al. 2022), can facilitate the persistence of rare species due to improved resistance to competitive displacement through traits promoting longevity operating in rare but not common species (McKinney 1997), leading to higher levels of metacommunity diversity. These results suggest that local plant-soil feedbacks may facilitate the phylogenetically dependent persistence of rare spe-

cies in community mixtures, even with lower biomass and abundance in a given community (Kempel et al. 2020; Vincent et al. 2020; Nytko et al. *in review*). Taken together, the phylogenetic relatedness of a community, as well as species' rarity must be considered under varying soil nutrient conditions when analyzing the mechanistic drivers and evolutionary processes shaping plant-soil feedbacks across the landscape.

To understand how the evolution of performance traits interacts with the rarity and phylogenetic relatedness of species to drive variation in plant-soil feedbacks, we analyzed the above- and belowground biomass and associated ectomycorrhizal (ECM) and dark septate endophyte (DSE) colonization of 14 species of native Tasmanian *Eucalyptus* of known evolutionary relatedness under two N treatments (low vs. high) (data from Wooliver et al. 2018). Previous work has demonstrated that rare species have low biomass coupled with high SLA, late onset and short duration of flowering, and high tissue nutrient content (N and P), potentially caused by critically important interactions and trade-offs with mycorrhizal symbionts (Cornwell & Ackerly 2010; Holdaway et al. 2011; Ames et al. 2017; Kempel et al. 2020; Vincent et al. 2020; Lachaise et al. 2021; Nytko et al. *in review*). Moreover, common ECM plant hosts demonstrate significant variation in leaf, root, dispersal, and vegetative functional traits such as SLA, specific root length (SRL), seed mass, plant height, and life span (Friesen et al. 2011). Thus, belowground mycorrhizal colonization and aboveground trait expression in rare plant species via plant-soil feedbacks may be connected. By connecting belowground fungal colonization to plant traits associated with species rarity, across soils conditioned by species varying in phylogenetic relatedness, we can utilize evolutionary history within a common garden framework to understand the connection between, and the mechanisms underlying, differing aboveground trait expression and belowground legacy effects in rare versus common species. Understanding the mechanistic role of belowground microbially mediated legacy effects in determining the persistence of rare species is a significant advance because it allows for eco-evolutionary informed predictions of rare species performance not only at a geographic level, but also at a functional level across communities varying in composition and relatedness. We hypothesized that: 1) Total plant biomass, ECM colonization, and DSE colonization vary based on the rarity of plant host; 2) Plant species inoculated by conditioned soil varying in phylogenetic relatedness (conspecific, similar, distant) from phase one, demonstrate differences in total plant biomass, ECM colonization, and DSE colonization. To understand potential mechanistic drivers of hypotheses 1 and 2, we also hypothesized that: 3) The difference between the total plant biomass of species in conspecific soil versus same lineage or opposite lineage soil is related to differing rates of ECM and DSE colonization. Our results not only confirm that rare species maintain lower levels of biomass, but also demonstrate increased ECM colonization in rare versus common species, particularly in low N conditions. These results suggest that ECM fungi may play a mechanistic role in maintaining rare species persistence, even with lower aboveground biomass, across the landscape. Microbial mechanisms underlying differences in plant-soil feedbacks of rare and common species will become increasingly important in a changing world for understanding species persistence, as well as facilitating necessary range expansion and succession.

Methods

Study Species & Experimental Design

To measure the above- and belowground traits and mycorrhizal colonization of eucalypts associated with varying levels of rarity and relatedness, we reanalyzed data from a previously published study (Wooliver et al. 2018). Fourteen species of Tasmanian eucalypts belonging to subgenera *Symphomyrtus* were used due to their known variation in above- and belowground functional traits and mycorrhizal associations. Ranging in above- and belowground functional traits representative of resource acquisition and use strategies, such as growth form, biomass, SLA, and leaf nutrient content (Wooliver et al. 2018; Liu et al. 2023), eucalypt species depend on belowground ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) communities for sufficient nutrient acquisition and growth (Adjoud et al. 1996; Qin & Yu 2021). Moreover, Tasmanian eucalypts not only vary in functional trait expression, but also in species rarity, in accordance with Rabinowitz (1981). Consequently, eucalypt species found in small ranges, endemic to Tasmania, favoring specific habitats, and occurring in small local populations are considered to be the most rare, while species found in large ranges across ubiquitous habitat, and large local populations are considered to be common. Based on these stan-

wards, 14 species of Tasmanian *Eucalyptus* were categorized into ordinal ranked levels of rarity using the percent of Tasmanian bioregions inhabited, as well as measures of range size and population aggregation in accordance with Williams & Potts (1996). Rarity types five and seven are not represented in the data due to a lack of seed availability and absence in the sampled arboretum (details below). Soil inoculum used in this study were collected under individuals in both an arboretum in northern Tasmania (41.2265S, 146.3022E) and a forestry trial in southeastern Tasmania (43.3350S, 146.9451E). Soil inocula were pooled within species replicates as well as across sampling locations. Wooliver et al. (2018) conducted a fully factorial common garden study constituting of species that were grown in soils conditioned by 1) conspecific (“monoculture”) soil, 2) same lineage (“closely related”) soil, and 3) opposite lineage (“distantly related”) soil, under varying levels of N enrichment and fungicide application. Performance traits such as aboveground, belowground, and total biomass were measured, along with the proportion of roots colonized by ECM and DSE fungi after five months of growth at the end of the experiment. See details of this experiment in Wooliver et al. (2018). Reanalysis of these data in the context of rarity allows for a deeper understanding of the strength and direction of plant-soil feedbacks in rare versus common species as well as the mechanisms driving these above-belowground feedbacks in rare species.

Statistical Analyses

All statistical analyses were performed using R Statistical Software (version 4.2.1, R Core Team 2022). Linear mixed models (LMM) were first used to examine the effects of rarity, phylogenetic relatedness of conditioned soil (soil origin), N enrichment, and fungicide application on total plant biomass, ECM colonization, and DSE colonization (“lmer” function in “lme4” package, R) (**S1 Table**). The LMM yielded an interactive effect between rarity and soil origin, however, there was no main effect of fungicide nor interactive effects between rarity/soil origin and other fixed effects on total biomass. On the other hand, fungicide demonstrated a main effect on ECM colonization and DSE colonization. To account for the effects of N enrichment (low vs. high) and fungicide (live cultures vs. fungicide) application on total biomass, ECM colonization, and DSE colonization, N enrichment was utilized as a fixed effect and fungicide application was accounted for in the error structure of all linear mixed models as a random effect. Specifically, to address Hypothesis 1 and 2 that total plant biomass, ECM colonization, and DSE colonization vary based on the rarity of plant host species and the phylogenetic origins of conditioned soil inoculum under different levels of N enrichment, linear mixed models were used to determine the singular and interactive effects of rarity, soil origin, and N enrichment on the total biomass, ECM colonization, DSE colonization of eucalypts accounting for a blocked design in the error structure of the model. Tukey HSD post-hoc analyses were completed for all significant results (“ghlt” and “cld” functions in “multcomp” package, R).

Additionally, standardized plant-soil feedback mean effect sizes (Hedges’ *g*) were calculated for the total biomass and percent ECM colonization of plant species grown in conspecific versus same lineage soils, and conspecific versus opposite lineage soils (i.e., the soils include rare and common species within and across lineages) on the basis of the 2nd generation of plants that varied in level of rarity, described above. Effect sizes were calculated using the Hedges’ *g* statistic as it accounts and corrects for variance that may be introduced by unequal or small sample sizes (Hassan et al. 2022). Positive values of Hedges’ *g* indicated positive plant-soil feedbacks in which the total biomass or percent ECM colonization was greater in soils conditioned by similar or opposite lineages compared to conspecific soils. These types of positive feedbacks in biomass and mycorrhizal colonization mediated by phylogenetically similar soil conditions represent a home-field advantage in which phylogenetically similar plant species readily share microbial mutualists due to a shared evolutionary history and symbiosis of host-associated microbial communities (Anacker et al. 2014; Fitzpatrick et al. 2018; Kohl 2020; Kazarina et al. 2023). On the other hand, negative values of Hedges’ *g* indicate negative plant-soil feedbacks in which the total biomass or percent ECM colonization was lower in soils conditioned by similar or opposite lineages compared to conspecific soils. These types of negative feedbacks in biomass and mycorrhizal colonization mediated by phylogenetically similar or dissimilar soil conditions are indicative of a disruptive effect on plant growth and inform the maintenance of trait variation within plant communities. Hedges’ *g* values that were not significantly different than 0 were representative of a neutral or lack of plant-soil feedback. Therefore, the Hedges’ *g* values associated with each comparison

along the rarity gradient represented a measure of both the strength and direction of microbially mediated plant-soil feedbacks. The strength of plant-soil feedbacks was assessed by the magnitude of the effect size, while the direction of the feedbacks was determined by the sign of the effect size. Pearson product-moment correlations between the effect sizes of total biomass and ECM colonization along a rarity gradient were also analyzed to further understand the significance and direction of feedbacks.

Results

In support of Hypothesis 1 that total plant biomass, ECM colonization, and DSE colonization are related to the rarity of plant host, rare species displayed significantly lower biomass, but higher rates of ECM colonization than common counterparts when grown in a common garden environment across all soil conditions. (**Table 1 ;Figure 1**). For example, the rarest species had 62% more ECM colonization while maintaining 88% less total plant biomass than common counterparts (Figure 1). The rarest species also demonstrated 64% greater DSE colonization in soil than common species, however, this difference was not significant at $\alpha=0.05$. Further, the relationship between total plant biomass and ECM colonization was significantly dependent on soil N enrichment (Table 1). Eucalypt species across all rarity levels grown in high N conditions demonstrated a 37 % increase in biomass but 11 % decrease in ECM colonization than species under low N conditions (**Figure 2**). Consequently, high N conditions significantly facilitated higher levels of plant biomass but lower ECM colonization, while low N conditions significantly supported lower levels of plant biomass but higher ECM colonization. Additionally, rarity and N treatment demonstrated a significant interaction to affect the ECM colonization of Tasmanian eucalypts (Table 1; Figure 2). The disparity between rare versus common biomass and ECM colonization was more prevalent under high N enrichment, as demonstrated by a 166% increase in biomass and a 64% decrease in ECM colonization from rare to common species under high N conditions, compared to a 149% increase in biomass and a 27% decrease in ECM colonization from rare to common species under low N conditions.

In support of Hypothesis 2 that total plant biomass, ECM colonization, and DSE colonization are related to the phylogenetic origin of conditioned soil, there was a significant interaction between plant rarity and soil origin; rare species maintained significantly lower biomass but higher rates of ECM colonization in same lineage and opposite lineage soils compared to conspecific soils (Table 1;**Figure 3**). For example, the rarest species, grown in soil conditioned by phylogenetically similar species demonstrated a 114% increase in ECM colonization, but a 94 % decrease in total biomass compared to conspecific conditioned soils. These patterns were also consistent in species grown in phylogenetically distant soil which demonstrated a 96 % increase in ECM colonization, but a 71 % decrease in total biomass compared to conspecific conditioned soils. On the other hand, common species displayed similar patterns, however, to a much lesser extent; ECM colonization increased by 26%-78% and total biomass decreased by 25%-52% in conspecific relative to distantly related soil inoculum and conspecific to closely related soil inoculum, respectively. DSE colonization did not vary significantly by phylogenetic origin of conditioned soil across all rarity levels. These results from a common garden suggest that rare species may maintain distinct and critical tradeoffs between aboveground performance traits and belowground associations with fungal mutualists not prevalent in common species (i.e., there is reduced performance but increased reliance on ECM in any different soil than that conditioned by the same species in rare eucalypts).

Consistent with Hypothesis 3, that the divergence in plant total biomass in conspecific versus soils conditioned by other species is driven by rates of ECM colonization, biomass exhibited strong negative plant-soil feedbacks in conditioned soil relative to conspecific soil, while rates of ECM colonization demonstrated simultaneous strong positive plant-soil feedbacks (**Figure 4**). These results suggest that species grown in soil conditioned by other species maintain lower biomass but stronger associations with mycorrhizal mutualists when compared to the same species grown in monoculture. Furthermore, the effect size of ECM colonization directly affected the effect size of total biomass in phylogenetically distant conditions with a significant negative correlation ($r^2 = -0.83$) to show that performance traits, such as biomass, may be a function of ECM colonization acting differently among species varying in rarity (**Figure 5 & Table 2**).

Further, the strength of the relationship between belowground mycorrhizal feedbacks and aboveground plant traits was significantly affected by the phylogenetic relatedness of conditioned soil. While both conspecific to same lineage and conspecific to opposite lineage treatments demonstrated similar patterns in the relationship between total biomass and rates of ECM colonization, the differences in feedbacks in conspecific to same lineage treatments displayed a moderate negative relationship ($r^2 = -0.58$). Differences underlying the significance of conspecific to same lineage and conspecific to opposite lineage feedbacks may be due inadequate sample size. These results suggest that differences in ECM colonization not only drive aboveground feedbacks differently in rare versus common species, but also more strongly in distantly related species. Taken together, these results suggest that microbially mediated belowground feedbacks function to drive aboveground feedbacks in performance traits critical for species survival. Furthermore, if the continued survival of rare species is dependent on the maintenance of low biomass via belowground microbial associations, then the legacy effects of soil conditioned by species varying in rarity and phylogenetic relatedness are expected to exert strong control over future plant community phenology, composition, and biodiversity at the population level.

Discussion

Species rarity is often considered an unfavorable ecological response to environmental factors (Wamelink et al. 2014; Irl et al. 2017). Recent studies, however, have demonstrated that ecological and evolutionary factors interact to drive divergent patterns in aboveground traits between rare and common species (Boyd et al. 2022; Nytko et al. *in review*). Much less consideration has been given to potential belowground mechanisms driving the aboveground divergence of traits and subsequent plant-soil feedbacks in rare species. This omission is important as species do not live in isolation; community context and soil legacy affects are meaningful and likely have important feedbacks that can reinforce rarity over time. Our results show that 1) the total biomass and ECM colonization of a species is dependent on the rarity of the plant host; 2) the total biomass and ECM colonization of a species is also affected by the phylogenetic relatedness and N enrichment of conditioned soil; and 3) differences in belowground ECM colonization drive aboveground trait divergence and larger plant-soil feedbacks in rare versus common species. Taken together, the results suggest that rare plants may more heavily utilize mycorrhizal associations in phylogenetically distant communities under low N conditions, than common species, even while maintaining lower biomass levels for continued persistence across the landscape. Overall, rare plant species, while having reduced biomass aboveground, may maintain rich belowground mycorrhizal, rather than non-mycorrhizal, fungal communities conducive to nutrient acquisition and high potential for adaptation under climatic change. Results such as these have not commonly been considered for rare species.

Plant performance is often measured using a variety of functional traits such as life-form, dispersal, seed biology, and phenotypic response to environmental conditions (Pywell et al. 2003, Bragion et al. 2018; Hanisch et al. 2020). However, without an understanding of the mechanisms underlying functional trait expression, predictions of trait response to climate and associated changes in ecosystem function are limited. For example, our results demonstrate that rare species overall maintain lower biomass than common species across all soil conditions. Under current measures of plant species' success, lower productivity is often considered ecologically unfavorable due to associations between lower biomass and decreased fecundity (Poorter et al. 2015; Younginger et al. 2017). However, our results also indicate that the aboveground trait values of rare species may not be representative of an unsuccessful survival strategy, as is often seen in common species. Instead, lower biomass in rare species may reflect a unique tradeoff in which more resources are allocated to belowground mycorrhizal symbionts for nutrient uptake and pathogen protection that allow for continued persistence (Poot & Lambers 2003; Bothe et al. 2010; Soudzilovskaia et al. 2019; Tedersoo & Bahram 2019). Furthermore, the trade-off between ECM fungal colonization and aboveground biomass is dependent on the phylogenetic relatedness of conditioned soil in which plants were grown and the rarity level of plant host, such that the rarest species experience the strongest negative feedbacks in growth but strongest increase in ECM colonization when grown in soil conditioned by phylogenetically distant species. These conclusions support and expand upon the findings of Kempel et al. (2018) and Jiang et al. (2022)

to demonstrate the microbial mechanisms underlying plant-soil feedbacks in plant communities varying in rarity and phylogenetic distance.

While these patterns may be mediated by the unique functional traits of rare species varying in phylogenetic relatedness, an alternative hypothesis may suggest that the characteristic low biomass of rare species is a function of ECM parasitism in low N environments. While these results are consistent with parasitic patterns in belowground fungi, as well as the functional equilibrium model of resource allocation under N enrichment (Johnson et al. 2008), it is also unusual to observe parasitism of mycorrhizal fungi in low N environments in which mutualisms are necessary for nutrient acquisition (Johnson 1993; Johnson et al. 2008). Consequently, the biomass of rare plant species may be representative of: 1) N-limitation; 2) allocation to belowground resources for limiting micronutrients; 3) the maintenance of valuable functional traits rather than biomass production in nutrient-lacking environments. Although the effects of soil nutrient conditions on productivity in rare versus common plant species need to be studied further, these results suggest that the ability of a rare species to survive and persist in expanding range and niche space may be microbially mediated, particularly via previous plant communities. Specifically, rare plant species may benefit geographically, competitively, and functionally from mycorrhizal mediated soil legacy effects, to facilitate the persistence and potential expansion of rare species in phylogenetically distant, and to a lesser extent phylogenetically similar, communities rather than common species under climate change.

Predicting the future spatial and temporal persistence of rare species is key to conservation and management, as well as maintaining ecological function (Kunin & Gaston 1997). Species' rarity can be predicted by prominent negative plant-soil feedbacks (Ke et al. 2015; Klironomos 2002), however, predictions of rare species persistence are limited without a mechanistic understanding of these plant-soil feedbacks. Studies examining the mechanistic causes of rarity are often ecological in focus, however, recent research has demonstrated that the phylogenetic origin of plant species and the microbial community of previously conditioned soil can interact to affect the strength and direction of mycorrhizal mediated feedbacks (Segnitz et al. 2020). For example, Woolbright et al. (2014) suggested that novel interactions with ECM fungi may influence the ability of relict species to migrate, persist, or outperform common counterparts, while maintaining lower levels of genetic variability, in atypical habitats (Chung et al. 2015). Our results not only confirm that rare species on average suffer stronger negative plant-soil feedbacks on biomass when grown in conspecific soils, but also show that the strength and direction of plant-soil feedbacks in rare species are mediated by positive feedbacks in ECM colonization in both closely and distantly related plant-conditioned soils. These results suggest that conspecific-conditioned soils may be lacking adequate levels of mycorrhizal mutualists, while incurring high levels of plant pathogens (Hannula et al. 2021). Consequently, rare species productivity is inextricably tied to belowground mycorrhizal colonization, making rare species more susceptible (both positively and negatively) to soil conditioning effects such as legacy and priority effects as well as above- and belowground species interactions (Nytko et al. *in review*). Therefore, long-lasting microbially mediated legacy effects of previous plant communities may drive patterns of rare species abundance, as demonstrated by low abundant species in Anacker et al. (2014), Maron et al. (2016), and Yan et al. (2022), as well as patterns of rare species productivity and composition in successional communities.

Biotic interactions shape species' distributions, functional traits, and rarity (Cosentino et al. 2023; Kempel et al. 2020; Nytko et al. *in review*; Wisz et al. 2013); however, biotic interactions are commonly underrepresented in conservation, leading to errors in the estimation of rare species occurrence and future persistence (Flores-Tolentino et al. 2020). Although the majority of literature regarding the causes and consequences of rarity is dedicated to the response of species to abiotic factors, Woolbright et al. (2014) demonstrated the critical importance of biotic interactions in understanding both the geographic occurrence and genetic underpinnings of isolated relict species. Our results expand on the hypotheses proposed in Woolbright et al. (2014), to demonstrate the critical importance of above- and belowground interactions in understanding rarity as well as determining functional trait expression (Kempel et al. 2020). These results suggest that the expression of phenotypes among populations within the same species are the consequence of previous plant communities and current feedbacks with belowground symbionts. Moreover, biotic interactions may drive patterns of geographic mosaics in rare species by shaping the direction of co-evolution to establish

differences in trade-off strength and subsequent trait expression not seen in common species. Consequently, geographically based differences in the availability and abundance of mycorrhizal symbionts may result in population-related variation in the expression of traits, long-term species persistence, and conservation priority. As such, the phenotypes of rare species that we consider to be a conservation priority may be a consequence of microbially mediated plant-soil feedbacks.

Conclusions & Implications : The majority of plant species are rare in any given plant community. Furthermore, the conservation of rare populations are often characterized by geographic and genetic parameters, such that a rare population is one of small size, located in an uncharacteristically atypical area, with limited genetic diversity (Rabinowitz 1981; Cole 2003) without consideration of the community context or past evolutionary history of that species. Rare species are rare for a variety of reasons, but some may maintain lower levels of biomass and higher rates of ECM colonization to persist. If the microbially mediated plant-soil feedbacks seen in rare species are representative of a unique trade-off between allocation to ECM colonization versus aboveground biomass when growing in intermediately related plant-conditioned soils, then there are likely to be significant implications for conservation practices. Although abiotic factors are important proponents of functional trait expression (Lavorel et al. 2011; Caruso et al. 2020), the long-lasting microbial impacts of previous plant communities, especially ones that may not strongly alter soil communities in positive or negative ways for the next generation of plants, may exert more control over the phenotypic appearance and persistence of rare species than originally hypothesized. As legacy effects become increasingly pronounced under climate change, accounting for above- and belowground biotic interactions will become increasingly important in spatial distribution modeling (SDM) and predictions of rare species occurrence in changing communities. Additionally, if species rarity is dependent on microbial counterparts for the successful maintenance of lower biomass, rare species management may be improved through the consideration of belowground colonization via mycorrhizal mutualists at the population level. These greenhouse results suggest that the aboveground traits of rare species are not indicative of an unsuccessful plant strategy, but rather a consequence of previous plant conditioning effects as well as interactions with current fungal mutualists that vary by previous plant community inhabitants that need to be field-tested. Accordingly, the low abundance and biomass characteristic of rare species may disguise a rich belowground world of beneficial mutualists, worthy of further investigation into the contribution of belowground feedbacks to aboveground functional traits in rare species around the world.

Tables

Table 1. Plant rarity and phylogenetic origin of soil inoculum interact to significantly affect aboveground biomass and belowground Ectomycorrhizal (ECM) colonization of plant hosts. Nitrogen (N) treatment also significantly affects the total biomass and ECM colonization of eucalypts across all rarity levels. Rarity is characterized by the range size, habitat specificity, and local population size of a species; rarity level 1 represents the rarest species. Soil origin represents the phylogenetic relatedness of conditioned soil (conspecific, same lineage, opposite lineage within the Tasmania eucalypts).

Response	Effects	DF	Chisq	P value
Total Biomass	Rarity	5	149.007	< 2.2e-16*
	Soil Origin	2	108.234	< 2.2e-16*
	Nitrogen (N)	1	29.448	5.744e-08*
	Rarity x Soil Origin	10	22.388	0.013*
	Rarity x N	5	4.484	0.482
	Soil Origin x N	2	0.271	0.873
	Rarity x Soil Origin x N	10	6.949	0.730
	ECM Colonization	Rarity	5	116.983
Soil Origin		2	40.994	1.254e-09*
Nitrogen (N)		1	5.654	0.017*
Rarity x Soil Origin		10	24.225	0.007*
Rarity x N		5	18.354	0.003*

DSE Colonization	Soil Origin x N	2	1.291	0.524
	Rarity x Soil Origin x N	10	14.037	0.171
	Rarity	5	9.447	0.093
	Soil Origin	2	0.667	0.717
	Nitrogen (N)	1	3.206	0.074
	Rarity x Soil Origin	10	14.847	0.138
	Rarity x N	5	2.510	0.775
	Soil Origin x N	2	0.903	0.637
	Rarity x Soil Origin x N	10	10.408	0.405

Table 2. Belowground feedbacks affecting Ectomycorrhizal (ECM) colonization drive aboveground feedbacks in total biomass, dependent on the phylogenetic relatedness of conditioned soil. Hedges’ g represents the effect size of differences between the biomass and ECM colonization of plants conditioned by their own soil (conspecific) versus plants conditioned by phylogenetically similar species’ soil (same lineage), or plants conditioned by phylogenetically dissimilar species’ soil (opposite lineage).

Response	Effect	Effect Between	DF	F value	P value
Total Biomass (Hedges’ g)	ECM Colonization (Hedges’ g)	Conspecific – same lineage	1	2.0671	0.2239
		Conspecific – opposite lineage	1	9.0525	0.0396*

Figure Legends

Figure 1. Total biomass (a) and Ectomycorrhizal (ECM) colonization (b), are significantly affected by the rarity level of plant host across all soil conditions in a common garden environment (Wooliver et al. 2018). Dark septate endophyte (DSE) colonization does not vary by the rarity level of plant host (c). Rarity level 1 represents the rarest species.

Figure 2. Total biomass (a) and Ectomycorrhizal (ECM) colonization (b) of rare and common eucalypts are significantly affected by Nitrogen (N) treatment (low vs. high) and rarity level. Plants conditioned in high N have higher total biomass, but significantly lower ECM colonization than counterparts conditioned in low N across all rarity levels. The negative relationship between total biomass and ECM colonization is however, most prevalently displayed in the rarest species compared to common species.

Figure 3. Total biomass (a) and Ectomycorrhizal (ECM) colonization (b) of rare and common eucalypts are significantly affected by the phylogenetic origin of conditioned soil treatments (soil origin) in which they are growing. Dark septate endophyte (DSE) colonization (c) does not vary by the phylogenetic origin of conditioned soil. Conspecific soil inoculum is conditioned by the same species, similar lineage soil inoculum is conditioned by phylogenetically similar species, and opposite lineage soil inoculum is conditioned by phylogenetically dissimilar species on the Tasmanian *Eucalyptus* phylogeny (Wooliver et al. 2018). Rarity level 1 represents the rarest species.

Figure 4. Belowground feedbacks in Ectomycorrhizal (ECM) colonization drive aboveground feedbacks in plant biomass. The total biomass of rare species display strongly negative plant-soil feedbacks, while the ECM colonization of rare species display strongly positive plant-soil feedbacks. The strength of these feedbacks are further affected by the phylogenetic origin of soil inoculum and rarity level of plant host. Conspecific to same lineage treatments represent differences in plant biomass and ECM colonization between plants conditioned by their own soil versus plants conditioned by phylogenetically similar species’ soil. Conspecific to opposite lineage treatments represent differences in plant biomass and ECM colonization between plants conditioned by their own soil versus plants conditioned by phylogenetically dissimilar species’ soil. Rarity level 1 represents the rarest species.

Figure 5 . The correlation between total biomass and Ectomycorrhizal (ECM) colonization are dependent

on plant host rarity and the phylogenetic relatedness of conditioned soil (soil origin). As ECM colonization increases, total biomass significantly decreases across rarity levels in phylogenetically distant soil, such that the rarest species display lower biomass but higher ECM colonization than common species.

References

- Ames, G.M., Wall, W.A., Hohmann, M.G., Wright, J.P. (2017). Trait space of rare plants in a fire-dependent ecosystem. *Conserv. Biol.* , 31(4): 903-911. doi: 10.1111/cobi.12867.
- Anacker, B.L., Klironomos, J.N., Maherali, H., Reinhart, K.O., Strauss, S.Y. (2014). Phylogenetic conservatism in plant-soil feedback and its implications for plant abundance. *Ecol. Lett.* , 17(12): 1613-1621. doi: 10.1111/ele.12378.
- Bever, J.D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol.* , 157(3): 465-473. doi: 10.1046/j.1469-8137.2003.00714.x.
- Bothe, H., Turnau, K., Regvar, M. (2010). The potential role of arbuscular mycorrhizal fungi in protecting endangered plants and habitats. *Mycorrhiza* , 21: 445-457. doi: 10.1007/s00572-010-0332-4.
- Boyd, J.N., Anderson, J.T., Brzyski, C., Cruse-Sanders, J. (2022). Eco-evolutionary causes and consequences of rarity in plants: a meta-analysis. *New Phytol.* , 235(3): 1272-1286. doi: 10.1111/nph.18172.
- Boyd, J.N., Odell, J., Cruse-Sanders, J., Rogers, W., Anderson, J.T., Baskauf, C., Brzyski, J. (2022). Phenotypic plasticity and genetic diversity elucidate rarity and vulnerability of an endangered riparian plant. *Ecosphere* , 13(14), e3996. doi: 10.1002/ecs2.3996.
- Bragion, E.F.A., Coelho, G.A.O., de Siqueira, F.F., Uriarte, M., van den Berg, E. (2018). Sharp differentiation on the performance of plant functional groups across natural edges. *J. Plant Ecol.* , 12(1): 186-198. doi: 10.1093/jpe/rty009.
- Caruso, C.M., Maherali, H., Martin, R.A. (2020). A meta-analysis of natural selection on plant functional traits. *Int. J. Plant Sci.* , 181(1). doi: 10.1086/706199.
- Chappell, C.R., Dhimi, M.K., Bitter, M.C., Czech, L., Paredes, S.H., Barrie, F.B., Calderón, Y., Eritano, K., Golden, L.A., Hekmat-Safe, D., Hsu, V., Kieschnick, C., Malladi, S., Rush, N., Fukami, T. (2022). Wide-ranging consequences of priority effects governed by an overarching factor. *eLife* , 11: e79647. doi: 10.7554/eLife.79647.
- Chung, Y.A., Miller, T.E.X., Rudgers, J.A. (2015). Fungal symbionts maintain a rare plant population but demographic advantage drives the dominance of a common host. *J. Ecol.* , 103(4): 967-977. doi: 10.1111/1365-2745.12406.
- Cole, C.T. (2003). Genetic variation in rare and common plants. *Annu. Rev. Ecol. Evol. Syst.* , 34: 213-237. doi: 10.1146/annurev.ecolsys.34.030102.151717.
- Cortois, R., Schröder-Georgi, T., Weigelt, A., van der Putten, W.H., De Deyn, G.B. (2016). Plant-soil feedbacks: the role of plant functional group and plant traits. *J. Ecol.* , 104(6): 1608-1617. doi: 10.1111/1365-2745.12643.
- Cosentino, F., Seamark, E.C.J., Van Cakenberghe, V., Maiorano, L. (2023). Not only climate: The importance of biotic interactions in shaping species distributions at macro scales. *Ecol. Evol.* , 13(3): e9855. doi: 10.1002/ece3.9855.
- Cornwell, W.K. & Ackerly, D.D. (2010). A link between plant traits and abundance: evidence from coastal California woody plants. *J. Ecol.* , 98(4): 814-821. doi: 10.1111/j.1365-2745.2010.01662.x.
- Crawford, K.M., Bauer, J.T., Comita, L.S., Eppinga, M.B., Johnson, D.J., Mangan, S.A., Queenborough, S.A., Strand, A.E., Suding, K.N., Umbanhowar, J., Bever, J.D. (2019). When and where plant-soil feedbacks

may promote plant co-existence: a meta-analysis. *Ecol. Lett.* , 22(8): 1274-1284. doi: 10.1111/ele.13278.

Dee, L.E., Cowles, J., Isbell, F., Pau, S., Gaines, S.D., Reich, P.B. (2019). When do ecosystem services depend on rare species? *Trends Ecol. Evol.* , 34(8): 746-758. doi: 10.1016/j.tree.2019/03/010.

Enquist, B.J., Feng, X., Boyle, B., Maitner, B., Newman, E.A., Jørgensen, P.M., Roehrdanz, P.R., Thiers, B.M., Burger, J.R., Corlett, R.T., Couvreur, T.L.P., Dauby, G., Donoghue, J.C., Foden, W., Lovett, J.C., Marquet, P.A., Merow, C., Midgley, G., Morueta-Holme, N., Neves, D.M., Oliveira-Filho, A.T., Kraft, N.J.B., Park, D.S., Peet, R.K., Pillet, M., Serra-Diaz, J.M., Sandel, B., Schildhauer, M., Šímová, I., Violle, C., Wieringa, J.J., Wiser, S.K., Hannah, L., Svenning, J.C., McGill, B.J. (2019). The commonness of rarity across land plants. *Sci. Adv.* , 5(11), eaaz0414. doi: 10.1126/sciadv.aaz0414.

Fitzpatrick, C.R., Gehant, L., Kotanen, P.M., Johnson, M.T.J. (2017). Phylogenetic relatedness, phenotypic similarity and plant-soil feedbacks. *J.Ecol.* , 105(3): 786-800. doi: 10.1111/1365-2745.12709.

Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., Johnson, M.T.J. (2018). Assembly and ecological function of the root microbiome across angiosperm plant species. *Proc. Natl. Acad. Sci. U.S.A.* , 115(6): 1157-1165. doi: 10.1073/pnas.1717617115.

Flores-Tolentino, M., García-Valdés, R., Saénz-Romero, C., Ávila-Díaz, I., Paz, H., Lopez-Toledo, L. (2020). Distribution and conservation of species is mismatched if biotic interactions are ignored: the case of the orchid *Laelia speciosa* . *Sci. Rep.* , 10: 9542. doi: 10.1038/s41598-020-63638-9.

Friesen, M.L., Porter, S.S., Stark, S.C., von Wettberg, E.J., Sachs, J.L., Martinez-Romero, E. (2011). Microbially mediated plant functional traits. *Annu. Rev. Ecol. Evol. Syst.* , 42: 23-46. doi: 10.1146/annurev-ecolsys-102710-145039.

Hanisch, M., Schweiger, O., Cord, A.F., Volk, M., Knapp, S. (2020). Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *J. Appl. Ecol.* , 57(8): 1535-1550. doi: 10.1111/1365-2664.13644.

Hannula, S.E., Heinen, R., Huberty, M., Steinauer, K., De Long, J.R., Jongen, R., Bezemer, T.M. (2021). Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. *Nat. Commun.* , 12: 5686. doi: 10.1038/s41467-021-25971-z.

Hassan, K., Dastogeer, K.M.G., Carrillo, Y., Nielsen, U.N. (2022). Climate change-driven shifts in plant-soil feedbacks: a meta-analysis. *Ecol. Process.* , 11: 64. doi: 10.1186/s13717-022-00410-z.

He, C., Wang, W., Hou, J. (2019). Characterization of dark septate endophytic fungi and improve the performance of liquorice under organic residue treatment. *Front. Microbiol.* , 10:1364. doi: 10.3389/fmicb.2019.01364.

Heinen, R., van der Sluijs, M., Biere, A., Harvey, J.A., Bezemer, M. (2018). Plant community composition but not plant traits determine the outcome of soil legacy effects on plants and insects. *J. Ecol.* , 106(3): 1217-1229. doi: 10.1111/1365-2745.12907.

Heinen, R., Biere, A., Bezemer, T.M. (2020). Plant traits shape soil legacy effects on individual plant-insect interactions. *Oikos* , 129(2): 261-273. doi: 10.1111/oik.06812.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabin-ski, C., Bever, J.D., Moore, J.C., Wilson, G.W.T., Klironomos, J.N., Umbanhowar, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.* , 13(3): 394-407. doi: 10.1111/j/1461-0248.2009.01430.x.

Holdaway, R.J., Richardson, S.J., Dickie, I.A., Peltzer, D.A., Coomes, D.A. (2011). Species- and community-level patterns in fine root traits along a 120,000-year soil chronosequence in temperate rain forest. *J. Ecol.* , 99(4): 954-963. doi: 10.1111/j.1365-2745.2011.01821.x.

- Irl, S.D.H., Schweiger, A.H., Medina, F.M., Fernández-Palacios, J.M., Harter, D.E.V., Jentsch, A., Provenza, A., Steinbauer, M.J., Beierkuhnlein, C. (2017). An island view of endemic rarity - Environmental drivers and consequences for nature conservation. *Divers. Distrib.* , 23(10): 1132-1142. doi: 10.1111/ddi.12605.
- Johnson, N.C. (1993). Can fertilization of soil select less mutualistic mycorrhizae? *Ecol. Appl.* , 3(4): 749-757. doi: 10.2307/1942106.
- Johnson, N.C., Rowland, D.L., Corkidi, L., Allen, E.B. (2008). Plant winners and losers during grassland N-eutrophication differ in biomass allocation and mycorrhizas. *Ecology*, 89(10): 2868-2878. doi: 10.1890/07-1394.1.
- Johnson, N.C., Wilson, G.W.T., Bowker, M.A., Miller, R.M. (2010). Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proc. Natl. Acad. Sci. U.S.A.* , 107(5): 2093-2098. doi: 10.1073/pnas.0906710107.
- Jiang, Y., Wang, Z., Chu, C., Kembel, S.W., He, F. (2022). Phylogenetic dependence of plant-soil feedback promotes rare species in a subtropical forest. *J. Ecol.* , 110(6): 1237-1246. doi: 10.1111/1365-2745.13879.
- Kaluka, I.L. & Jagodziński, A.M. (2017). Ectomycorrhizal fungi: A major player in early succession. In: Varma, A., Prasad, R., Tuteja, N. (eds) *Mycorrhiza – Function, Diversity, State of the Art*. Springer, Cham. doi: 10.1007/978-3-319-53064-2_10.
- Kazarina, A., Sarkar, S., Thapa, S., Heeren, L., Kamke, A., Ward, K., Hartung, E., Ran, Q., Galliard, M., Jumpponen, A., Johnson, L., Lee, S.T.M. (2023). Home-field advantage affects the local adaptive interaction between *Andropogon gerardii* ecotypes and root-associated bacterial communities. *Microbiol. Spectr.* , 11(5). doi: 10.1128/spectrum.00208-23.
- Ke, P.J., Miki, T., Ding, T.S. (2015). The soil microbial community predicts the importance of plant traits in plant-soil feedback. *New Phytol.* , 206(1): 329-341. doi: 10.1111/nph.13215.
- Kempel, A., Rindisbacher, A., Fischer, M., Allan, E. (2018). Plant soil feedback strength in relation to large-scale plant rarity and phylogenetic relatedness. *Ecology* , 99(3): 597-606. doi: 10.1002/ecy.2145.
- Kempel A, Vincent H, Prati D, Fischer M. (2020). Context dependency of biotic interactions and its relation to plant rarity. *Divers. Distrib.* , 26(6): 758-68. doi: 10.1111/ddi.13050.
- Klironomos, J.N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* , 417(6884): 67-70. doi: 10.1038/417067a.
- Kohl, K.D. (2020). Ecological and evolutionary mechanisms of underlying patterns of phyllosymbiosis in host-associated microbial communities. *Philos. Trans. R. Soc. B.* , 375(1798). doi: 10.1098/rstb.2019.0251.
- Kulmatiski, A., Beard, K.H., Stevens, J.R., Cobbold, S.M. (2008). Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.* , 11(9): 980-992. doi: 10.1111/j.1461-0248.2008.01209.x.
- Kulmatiski, A. & Beard, K.H. (2011). Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure. *Soil Biol. Biochem.* , 43(4): 823-830. doi: 10.1016/j.soilbio.2010.12.018.
- Kunin, W.E. and Gaston, K.J. (1997). The biology of rarity: causes and consequences of rare-common differences. Springer Dordrecht. doi: 10.1007/978-94-011-5874-9.
- Kučáková, E., Herben, T., Münzbergová, Z. (2018). Heterospecific plant-soil feedback and its relationship to plant traits, species relatedness, and co-occurrence in natural communities. *Oecologia* , 187: 679-688. doi: 10.1007/s00442-018-4145-z.
- Lachaise, T., Bergmann, J., Rilling, M.C., van Kleunen, M. (2021). Below-and aboveground traits explain local abundance, and regional, continental and global occurrence frequencies of grassland plants. *Oikos* , 130(1): 110-120. doi: 10.1111/oik.07874.

- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J., Pellet, G., Douzet, R. (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *J. Ecol.* , 99(1): 135-147. doi: 10.1111/j.1365-2745.2010.01753.x.
- Li, K., Veen, G.F., ten Hooven, F.C., Harvey, J.A., van der Putten, W. (2023). Soil legacy effects of plants and drought on aboveground insects in native and range expanding plant communities. *Ecol. Lett.* , 26(1): 37-52. doi: 10.1111/ele.14129.
- Lu, W., Bi, X., Zheng, Y. (2023). Soil legacy effects on biomass allocation depend on native plant diversity in the invaded community. *Sci. Prog.* , 106(1): 368504221150060. doi: 10.1177/00368504221150060.
- Maron, J.L., Smith, A.L., Ortega, Y.K., Pearson, D.E., Callaway, R.M. (2016). Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology* , 97(8): 2055-2063. doi: 10.1002/ecy.1431.
- McKinney, M.L. (1997). How do rare species avoid extinction? A paleontological view. In: Kunin, W.E. & Gaston, K.J. (eds) *The biology of rarity. Population and community biology series*, 17. Springer, Dordrecht. doi: 10.1007/978-94-011-5874-9-7.
- McMahen, K., Guichon, S.H.A., Anglin, C.D., Lavkulich, L.M., Grayston, S.J., Simard, S.W. (2022). Soil microbial legacies influence plant survival and growth in mine reclamation. *Ecol. Evol.* , 12(11): e9473. doi: 10.1002/ece3.9473.
- Munson, S.M. & Sher, A.A. (2015). Long-term shifts in the phenology of rare and endemic Rocky Mountain plants. *Am. J. Bot.* , 102(8): 1268-1276. doi: 10.3732/ajb.1500156.
- Münzbergová, Z. & Šurinová, M. (2015). The importance of species phylogenetic relationships and species traits for the intensity of plant-soil feedback. *Ecosphere* , 6(11): 1-16. doi: 10.1890/ES15-00206.
- Nytko AG, Senior JK, Wooliver RC, O'Reilly-Wapstra J, Schweitzer JA, Bailey JK. An evolutionary case for rarity. [Preprint]. (2023). In review at *Ecol. Evol.* , doi: 10.21203/rs.3.rs-3369472/v1.
- Nytko, A.G., Senior, J.K., O'Reilly-Wapstra, J., Schweitzer, J.A., Bailey, J.K. [Preprint]. (2023). Evolution of rarity and phylogeny determine above- and belowground biomass in plant-plant interactions. In review at *PLOS One* , doi: 10.1101/2023.11.10.566621.
- Peay, K.G., Belisle, M., Fukami, T. (2012). Phylogenetic relatedness predicts priority effects in nectar yeast communities. *Proc. Biol. Sci.* , 279(1729): 1749-758. doi: 10.1098/rspb.2011.1230.
- Poorter, H., Jagodzinski, A.M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usoltsev, V.A., Buckley, T.N., Reich, P.B., Sack, L. (2015). How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* , 208(3): 736-749. doi: 10.1111/nph.13571.
- Poot, P. & Lambers, H. (2003). Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. *J. Ecol.* , 91(1): 58-67. doi: 10.1046/j.1365-2745.2003.00738.x.
- Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J., Rothery, P. (2003). Plant traits as predictors of performance in ecological restoration. *J. Appl. Ecol.* , 40(1): 65-77. doi: 10.1046/j.1365-2664.2003.00762.x.
- Qin, F. & Yu, S. (2021). Compatible mycorrhizal types contribute to a better design for mixed *Eucalyptus* plantations. *Front. Plant Sci.* , 12: 616726. doi: 10.3389/fpls.616726.
- Qu, Q., Xu, H., Liu, G., Xue, S. (2023). Soil legacy effects and plant-soil feedback contribution to secondary succession processes. *Soil Ecol. Lett.* , 5: 220131. doi: 10.1007/s42832-022-0131-9.
- Reijenga, B.R., Murrell, D.J., Pigot, A.L. (2021). Priority effects and the macroevolutionary dynamics of biodiversity. *Ecol. Lett.* , 24(7): 1455-1466. doi: 10.1111/ele.13766.

- Reinhart, K.O., Bauer, J.T., McCarthy-Neumann, S., MacDougall, A.S., Hierro, J.L., Chiuffo, M.C., Mangan, S.A., Heinze, J., Bergmann, J., Joshi, J., Duncan, R.P., Diez, J.M., Kardol, P., Rutten, G., Fischer, M., van der Putten, W.H., Bezemer, T.M., Klironomos, J. (2021). Globally, plant-soil feedbacks are weak predictors of plant abundance. *Ecol. Evol.* , 11(4): 1756-1768. doi: 10.1002/ece3.7167.
- Reininger, V. & Sieber, T.N. (2012). Mycorrhiza reduces adverse effects of dark septate endophytes (DSE) on growth of conifers. *PLOS One* , 7(8): e42865. doi: 10.1371/journal.pone.0042865.
- Schmid, M.W., van Moorsel, S.J., Hahl, T., De Luca, E., De Deyn, G.B., Wagg, C., Niklaus, P.A., Schmid, B. (2021). Effects of plant community history, soil legacy and plant diversity on soil microbial communities. *J. Ecol.* , 109(8): 3007-3023. doi: 10.1111/1365-2745.13714.
- Segnitz, R.M., Russo, S.E., Davies, S.J., Peay, K.G. (2020). Ectomycorrhizal fungi drive patterns of plant-soil feedbacks in a regionally dominant tropical plant family. *Ecology* , 101(8): e03083. doi: 10.1002/ecy.3083.
- Senior, J.K., Potts, B.M., O'Reilly-Wapstra, J.M., Bissett, A., Wooliver, R.C., Bailey, J.K., Glen, M., Schweitzer, J.A. (2018). Phylogenetic trait conservatism predicts patterns of plant-soil feedback. *Ecosphere* , 9(10), e02409. doi: 10.1002/ecs2.2409.
- Soudzilovskaia, N.J., van Bodegom, P.M., Terrer, C., van't Zelfde, M., McCallum, I., McCormack, M.L., Fisher, J.B., Brundrett, M.C., César de Sá, N., Tedersoo, L. (2019). Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nat. Commun.* , 10, 5077. doi: 10.1038/s41467-019-13019-2.
- Tedersoo, L. & Bahram, M. (2019). Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev. Camb. Philos. Soc.* , 94(5): 1857-1880. doi: 10.1111/brv.12538.
- Treseder, K.K. (2004). A meta-analysis of mycorrhizal responses to nitrogen, phosphorous, and atmospheric CO₂ in field studies. *New Phytol.* , 164(2): 347-355. doi: 10.1111/j.1469-8137.2004.01159.x.
- van de Voorde, T.F.J., van der Putten, W.H., Bezemer, M. (2011). Intra- and interspecific plant-soil interactions, soil legacies and priority effects during old-field succession. *J. Ecol.* , 99(4): 945-953. doi: 10.1111/j.1365-2745.2011.01815.x.
- van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., van de Voorde, T.F.J., Wardle, D.A. (2013). Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* , 101(2): 265-276. doi: 10.1111/1365-2745.12054.
- Van Nuland, M.E., Bailey, J.K., Schweitzer, J.A. (2017). Divergent plant-soil feedbacks could alter future elevation ranges and ecosystem dynamics. *Nat. Ecol. Evol.* , 1, 0150. doi: 10.1038/s41559-017-0150.
- Vincent, H., Bornand, C.N., Kempel, A., Fischer, M. (2020). Rare species perform worse than widespread species under changed climate. *Biol. Conserv.* , 246. doi: 10.1016/j.biocon.2020.108586.
- Wamelink, G.W.W., Goedhart, P.W., Frissel, J.Y. (2014). Why some plant species are rare. *PLOS One* , 9(10), e111293. doi: 10.1371/journal.pone.0111293.
- Wandrag, E.M., Bates, S.E., Barrett, L.G., Catford, J.A., Thrall, P.H., van der Putten, W.H., Duncan, R.P. (2020). Phylogenetic signals and predictability in plant-soil feedbacks. *New Phytol.* , 228(4): 1440-1449. doi: 10.1111/nph.16768.
- Wang, X., Kou, Y., Liu, J., Zhao, W., Liu, Q. (2023). Soil microbial legacy determines mycorrhizal colonization and root traits of conifer seedlings during subalpine forest succession. *Plant Soil* , 485: 361-375. doi: 10.1007/s11104-022-05835-1.
- Woolbright, S.A., Whitham, T.G., Gehring, C.A., Allan, G.J., Bailey, J.K. (2014). Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends Ecol. Evol.* , 29(7): 406-416. doi: 10.1016/j.tree.2014.05.003.

- Wooliver, R.C., Marion, Z.H., Peterson, C.R., Potts, B.M., Senior, J.K., Bailey, J.K., Schweitzer, J.A. (2017). Phylogeny is a powerful tool for predicting plant biomass responses to nitrogen enrichment. *Ecology* , 98(8): 2120-2132. doi: 10.1002/ecy.1896.
- Wooliver, R.C., Senior, J.K., Potts, B.M., Van Nuland, M.E., Bailey, J.K., Schweitzer, J.A. (2018). Soil fungi underlie a phylogenetic pattern in plant growth responses to nitrogen enrichment. *J. Ecol.*, 106(6): 2161-2175. doi: 10.1111/1365-2745.12983.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Formann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.C. (2013). The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biol. Rev. Camb. Philos. Soc.* , 88(1): 15-30. doi: 10.1111/j.1469-185X.2012.00235.x.
- Wurst, S. & Ohgushi, T. (2015). Do plant-and soil-mediated legacy effects impact future biotic interactions? *Funct. Ecol.* , 29(11): 1373-1382. doi: 10.1111.1365-2435.12456.
- Xi, N., Adler, P.B., Chen, D., Wu, H., Catford, J.A., van Bodegom, P.M., Bahn, M., Crawford, K.M., Chu, C. (2021). Relationships between plant-soil feedbacks and functional traits. *J. Ecol.* , 109(9): 3411-3423. doi: 10.1111/1365-2745.13731.
- Xie, L., Bi, Y., Ma, S., Shang, J., Hu, Q., Christie, P. (2021). Combined inoculation with dark septate endophytes and arbuscular mycorrhizal fungi: synergistic or competitive growth effects on maize? *BMC Plant Biol.* , 498. doi: 10.1186/s12870-021-03267-0.
- Yan, X., Levine, J.M., Kandlikar, G.S. (2022). A quantitative synthesis of soil microbial effects on plant species coexistence. *Proc. Natl. Acad. Sci. U.S.A.* , 119(22), e2122088119. doi: 10.1073/pnas.2122088119.
- Younginger, B.S., Sirová, D., Cruzan, M.B., Ballhorn, D.J. (2017). Is biomass a reliable estimate of plant fitness? *Appl. Plant Sci.* , 5(2): 1600094. doi: 10.3732/apps.1600094.
- Zee, P.C. & Fukami, T. (2018). Priority effects are weakened by a short, but not long, history of sympatric evolution. *Proc. Biol. Sci.* , 285(1871): 20171722. doi: 10.1098/rspb.2017.1722.
- Zhang, S., Zang, R., Sheil, D. (2022). Rare and common species contribute disproportionately to the functional variation within tropical forests. *J. Environ. Manage.* , 304, 114332. doi: 10.1016/j.jenvman.2021.114332.
- Zhao, W., Wang, X., Howard, M.M., Kou, Y., Liu, Q. (2023). Functional shifts in soil fungal communities regulate differential tree species establishment during subalpine forest succession. *Sci. Total Environ.* , 861, 160616. doi: 10.1016/j.scitotenv.2022.160616.







