

REPORT

FOREST ECOLOGY

Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics

Jonathan A. Bennett,^{1*} Hafiz Maherali,² Kurt O. Reinhart,³ Ylva Lekberg,^{4,5} Miranda M. Hart,¹ John Klironomos^{1*}

Feedback with soil biota is an important determinant of terrestrial plant diversity. However, the factors regulating plant-soil feedback, which varies from positive to negative among plant species, remain uncertain. In a large-scale study involving 55 species and 550 populations of North American trees, the type of mycorrhizal association explained much of the variation in plant-soil feedbacks. In soil collected beneath conspecifics, arbuscular mycorrhizal trees experienced negative feedback, whereas ectomycorrhizal trees displayed positive feedback. Additionally, arbuscular mycorrhizal trees exhibited strong conspecific inhibition at multiple spatial scales, whereas ectomycorrhizal trees exhibited conspecific facilitation locally and less severe conspecific inhibition regionally. These results suggest that mycorrhizal type, through effects on plant-soil feedbacks, could be an important contributor to population regulation and community structure in temperate forests.

Tree species diversity is critical for the maintenance of forest biodiversity and associated ecosystem functions (such as nutrient cycling and carbon storage) (1, 2), yet the factors regulating tree diversity remain unclear. One important factor is conspecific density dependence, in which adult trees can have density-dependent positive or negative effects on conspecific recruitment and population growth (3–5). Conspecific density dependence is influenced by plant-soil feedbacks, in which adult plants modify the soil so that it affects the performance of conspecific individuals (6). For example, the accumulation of antagonists (such as soil-borne herbivores and pathogens) near adult plants can increase local diversity by reducing recruitment for abundant species (7–9). Alternatively, the accumulation of mutualists can facilitate conspecific recruitment and increase the dominance of abundant species, reducing diversity (10, 11). Given the potentially large effects of these feedbacks on plant performance, any factor affecting plant-soil feedback may also affect conspecific density dependence and plant diversity (6).

Symbioses between plant roots and fungi (mycorrhizas) are an important component of plant-

soil feedbacks (12, 13); the fungi provide the plant with nutrients and protection from antagonists in exchange for sugars derived from photosynthesis (9, 14, 15). However, the benefit derived from mycorrhizas may depend on the type of mycorrhiza formed, particularly between the dominant arbuscular mycorrhizas (AMs) and ectomycorrhizas (EMs). Adult EM trees more

consistently facilitate seedling recruitment than AM trees do (16). This effect could be caused by greater access to and transfer of nitrogen by EM to their hosts, which makes them more beneficial than AM in nitrogen-limited systems such as forests (17, 18). In addition, EM fungi form a physical sheath around young feeder roots, offering greater protection from antagonists than that by AM fungi (9, 19). Either of these mechanisms may increase survival of young EM trees relative to AM trees. Consequently, plant-soil feedbacks may be more positive for EM trees relative to AM trees, resulting in damped conspecific inhibition for EM trees relative to AM trees. Differences in feedback between mycorrhizal types have been hypothesized to lead to reduced tree diversity in EM-dominated stands relative to AM stands within tropical forests (9, 18, 20) and may also affect temperate forest diversity. Here, we present the results of three studies testing (i) whether plant-soil feedback differs between AM and EM temperate tree species, (ii) whether AM and EM fungi alter the extent of root damage and consequently seedling survival, (iii) whether mycorrhizal type alters local conspecific density dependence, and (iv) whether mycorrhizal type and plant-soil feedback correlate with large-scale forest population regulation. We use the results of these tests to infer the importance of mycorrhizal types for plant-soil feedback and their influence on temperate forest population dynamics.

To test whether plant-soil feedbacks differ between AM and EM trees, we sampled 55 North American temperate tree species (30 EM and 25 AM) from a total of 550 geographically distinct populations located mainly in mixed forests (Fig. 1). In each population, we collected roots and soil from beneath a focal conspecific tree

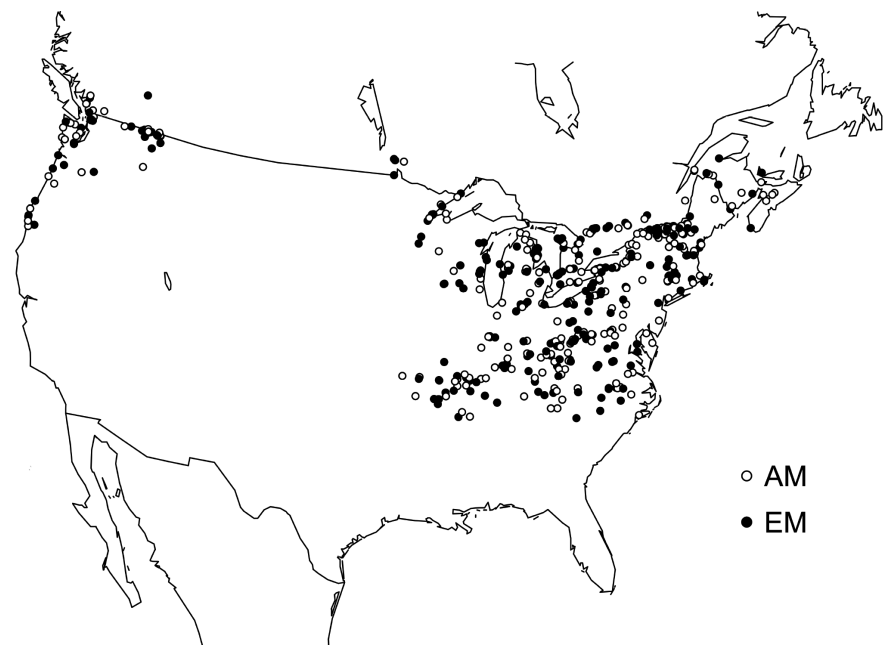


Fig. 1. The distribution of AM and EM tree populations in North America sampled for plant-soil feedbacks. AM, white; EM, black.

¹Department of Biology, University of British Columbia—Okanagan Campus, Kelowna, BC V1V 1V7, Canada.

²Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada. ³Fort Keogh Livestock and Range Research Laboratory, U.S. Department of Agriculture—Agricultural Research Service, 243 Fort Keogh Road, Miles City, MT 59301–4016, USA. ⁴MPG Ranch, Missoula, MT 59801, USA. ⁵Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA.

*Corresponding author. Email: jon.a.bennett@gmail.com (J.A.B.); john.klironomos@ubc.ca (J.K.)

and a randomly selected heterospecific tree of no particular mycorrhizal type (21). For each population, we quantified plant-soil feedbacks as log-response ratios comparing seedling growth between soils inoculated with conspecific or heterospecific soil. To isolate the effects of root-associated microbes and soil chemistry on plant-soil feedback, we also compared seedling growth between soils inoculated with conspecific and heterospecific roots or between sterilized conspecific and heterospecific soils; these tests used only five AM and five EM species. Plant-soil feedback was positive for most EM species and negative for most AM species (Fig. 2). This difference was not affected by the mycorrhizal type of the heterospecific tree, how closely related the conspecific and heterospecific tree were, or soil chemical properties (table S1). Phylogenetic influences on plant-soil feedback appear to be determined by the phylogenetic distribution of mycorrhizal types (fig. S1), although that may not be the case in all systems (22). Plant-soil feedbacks remained positive for EM trees and negative for AM trees using whole-soil inoculum and root inoculum, but not sterile soil (Fig. 2 and table S1). Combined, these results indicate a strong biotic effect of mycorrhizal type on plant-soil feedback. However, it remains possible that some unmeasured soil properties, such as the availability of different forms of nitrogen (18), also influence variation in plant-soil feedback between mycorrhizal types.

Differences in both nutrient benefits and protection from antagonists likely contributed to the variation in plant-soil feedback between mycorrhizal types. EM roots had greater mycorrhizal colonization but similar root lesions (a measure of root damage) in conspecific relative to heterospecific soils (Fig. 2C). This pattern was unaffected by the mycorrhizal type of the heterospecific tree, indicating some specificity in the EM association (fig. S2). Conversely, AM roots had similar mycorrhizal colonization in conspecific soil but more root lesions (Fig. 2C). We also observed negative relationships between mycorrhizal colonization and lesion density for both mycorrhizal types, possibly because of competition for root space or resources—although lesion densities remained high for AM species in conspecific soil for all but the most mycorrhizal AM trees (fig. S3). Combined, these results suggest that (i) EM seedlings benefit from a greater abundance of specific EM fungi near conspecifics, whereas compatible AM fungi appear ubiquitous (23), and (ii) AM seedlings are harmed more than EM seedlings by antagonists accumulating near conspecifics, possibly because AM colonization offers less protection.

To experimentally test whether colonization by different mycorrhizal types alters density dependence by preventing root damage by antagonists, we transplanted 10 uninoculated seedlings and 10 seedlings preinoculated with mycorrhizal fungi into soil beneath conspecific and heterospecific individuals. We used four tree species varying in feedback responses (two per mycorrhizal type) and five populations per species. Uninoculated seedling survival was drastically reduced

beneath mature conspecifics relative to heterospecifics for both EM (630%) and AM (1070%) trees (Fig. 3A). Roots of the surviving seedlings had 60% fewer lesions when they were planted beneath heterospecifics relative to conspecifics for both mycorrhizal types (Fig. 3B). These results show a strong potential for conspecific inhibition irrespective of mycorrhizal type, potentially because of increased root damage by antagonists. Seedlings preinoculated with EM fungi had 840% higher survival and 75% lower lesion densities than those of uninoculated seedlings when planted beneath conspecifics, but inoculation had no effect beneath heterospecifics (Fig. 3, A and B, and table S3). In contrast, AM seedlings did not benefit from preinoculation, nor did preinoculation affect lesion densities, regardless of transplant location (Fig. 3, A and B, and table S3). These

patterns were highly consistent among species within mycorrhizal type (fig. S4), indicating that antagonist pressure is greater near conspecifics and that EM, but not AM, reduce root damage and improve survival. However, more expansive testing would be required to determine whether this pattern extends to all species within mycorrhiza type. The precise mechanism also remains unclear because these effects may result from direct protection from antagonists by EM or through indirect effects mediated through improved nutrition (10, 19).

If mycorrhizal type alters the magnitude and direction of density dependence, then it should affect recruitment near conspecific trees. To identify such differences, we counted individuals <2.54 cm in diameter (multiple years of seedlings) beneath a focal conspecific and beneath a

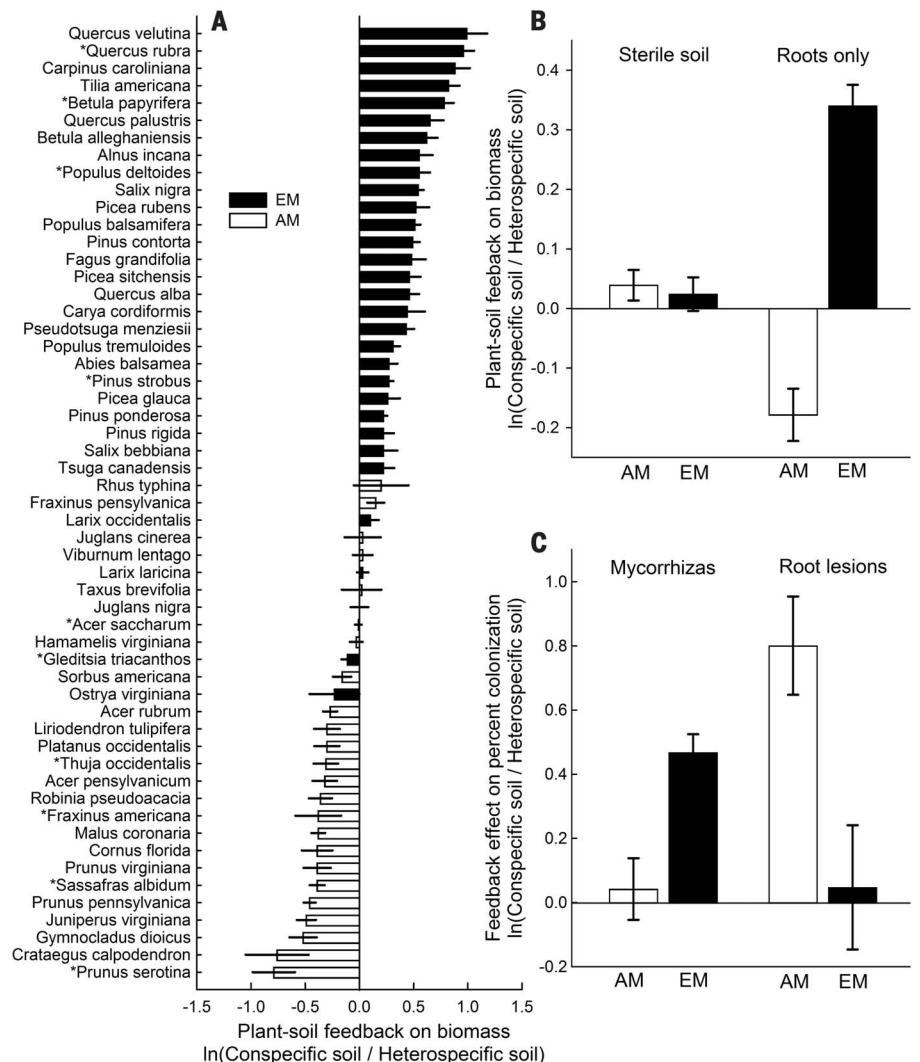


Fig. 2. Plant-soil feedbacks for EM and AM species. EM, black; AM, white. (A to C) Experiments compared conspecific versus heterospecific soil effects on growth between mycorrhizal types by using (A) whole-soil inocula; (B) sterile soil, or only the roots; and (C) the effects of whole-soil inoculum on mycorrhizal colonization and root lesion densities. Only 10 species (asterisks) were used for (B) and (C). Values represent mean log response ratios and associated standard errors and are based on either (A) 10 tree populations or [(B) and (C)] all species and populations (100 populations).

heterospecific individual 5 to 10 m away for five tree species per mycorrhizal type (10 populations per species). EM trees had 40% more conspecific seedlings beneath their canopy than beneath heterospecific trees, whereas AM trees had 30% fewer

conspecific seedlings beneath their canopy than beneath heterospecific trees (Fig. 3C and table S3). Additionally, we found no effect of seedling location on root lesion densities for EM trees, but AM seedlings near conspecifics had twice the

number of lesions than those near heterospecifics (Fig. 3D and table S3). These results support our previous findings that adult EM trees facilitate conspecific seedlings by providing compatible EM fungi that can inhibit antagonist damage, whereas AM seedlings experience conspecific inhibition (9, 10, 20) because AM fungi are less effective at preventing antagonists, despite the ubiquity of compatible AM fungi (Fig. 1 and fig. S3).

To test whether mycorrhizal type affects density dependence and forest dynamics at larger scales, we tested whether there was a correlation between our greenhouse estimates of feedback (Fig. 2A) and published estimates of conspecific density dependence from forests in the eastern United States (3). We found that mycorrhizal type or plant-soil feedbacks explained a small but statistically significant portion of the variation in regional conspecific density dependence (table S4). EM species (and species with positive feedback) exhibited less conspecific inhibition (Fig. 4). Given the strong association between conspecific inhibition and both population abundance and community diversity (3), these results suggest that mycorrhizal type may influence temperate forest structure through effects on plant-soil feedback. Similar effects of mycorrhizal type on population dynamics have been observed within tropical forests and shrublands, occasionally resulting in monodominance of EM species, despite the prevalence of AM associations in these forests (9, 10). In herbaceous communities, plant-soil feedbacks remain an important determinant of plant population and community dynamics, despite limited variation in mycorrhizal type (11, 24, 25). Regulation of plant populations and communities through plant-soil feedback may therefore be a general feature of plant communities, although any effect of mycorrhiza type is likely limited to woody systems.

Forest diversity is frequently regulated by conspecific density dependence (3, 4), which in turn can be influenced by both species functional traits and environmental variation among sites (5, 7, 26). Given the wide taxonomic and geographic scope of our studies, each of these factors likely affected the outcome. Specifically, plant traits and local environmental conditions can affect plant-soil feedbacks by altering the benefits of mutualists and susceptibility to antagonists (6, 27, 28), which may explain some of the variation in plant-soil feedback and density dependence within mycorrhizal type. Despite this variation, our findings indicate that mycorrhizal type and plant-soil feedbacks alter conspecific density dependence at multiple scales in temperate forests.

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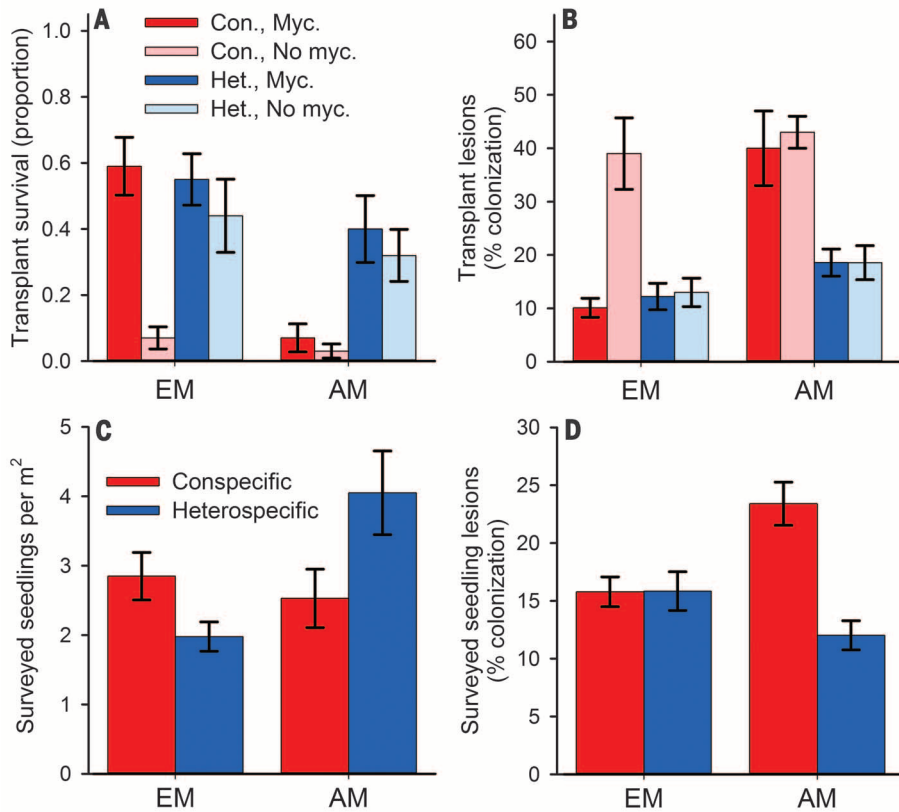
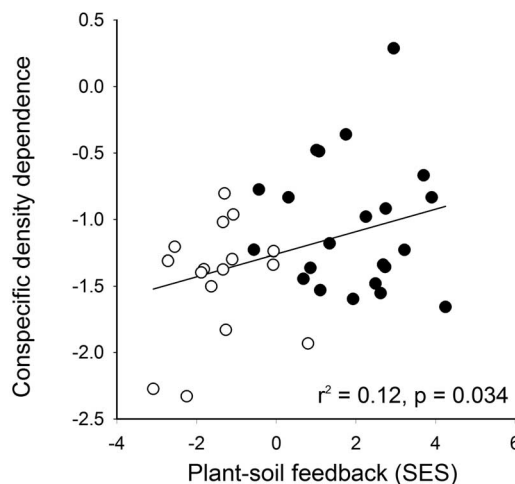


Fig. 3. A comparison of the relative effect of conspecific and heterospecific trees on seedling survival and lesion densities between EM or AM tree species. (A to D) Shown are (A) seedling survival and (B) lesion densities for transplanted seedlings, and (C) natural seedling and (D) lesion densities. Seedlings were located beneath either conspecific (red) or heterospecific (blue) trees. For the transplant experiment, seedlings were preinoculated with their associated mycorrhizal fungi (dark colors) or not (light colors). Transplants included five populations of four tree species [two EM (*Betula papyrifera* and *Pinus strobus*) and two AM (*Acer saccharum* and *Fraxinus americana*)], whereas surveys included 10 populations of 10 tree species (Fig. 2A, asterisks). Error bars represent 1 SE.

Fig. 4. Regional conspecific density dependence as a function of plant-soil feedback and mycorrhizal type.

Shown is a partial residual plot (adjusted to the mean) after accounting for phylogeny. Both plant-soil feedback and density dependence (3) represent standardized effect sizes (supplementary materials, materials and methods), resulting in a different scale than that of Fig. 1. EM tree species are in black, and AM tree species are in white ($n = 38$ tree species). Lines and regression statistics are based on linear regression of the partial residuals.



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ACKNOWLEDGMENTS

We thank the Natural Sciences and Engineering Research Council (NSERC) of Canada (Discovery Grant, and Discovery Accelerator

Award) for financial support. J.A.B. was supported by a NSERC postdoctoral fellowship. Y.L. was supported by MPG Ranch (<http://mpgranch.com>). We also thank K. Botev, J. Coughlin, A. Dunger, L. Evans, J. Hale, M. Hemley, R. Juliano, H. King, L. Kunze, Y. Ling, W. Liou, E. Mason, M. Murata, J. Newton, H. Singh, M. Thompson, K. Ralph, and P. Veloso for field and laboratory assistance. Data have been uploaded as supplementary materials.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/355/6321/181/suppl/DC1
Materials and Methods

Figs. S1 to S4

Table S1 to S5

References (29–47)

Data S1

16 August 2016; accepted 25 November 2016
10.1126/science.aai8212

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Science **355** (6321), 181-184.
DOI: 10.1126/science.aai8212

Soil biota and plant diversity

Soil biota, including symbionts such as mycorrhizal fungi and nitrogen-fixing bacteria, as well as fungal and bacterial pathogens, affect terrestrial plant diversity and growth patterns (see the Perspective by van der Putten). Teste *et al.* monitored growth and survival in Australian shrubland plant species paired with soil biota from plants of the same species and from other plants that use different nutrient acquisition strategies. Plant-soil feedbacks appear to drive local plant diversity through interactions between the different types of plants and their associated soil biota. Bennett *et al.* studied plant-soil feedbacks in soil and seeds from 550 populations of 55 species of North American trees. Feedbacks ranged from positive to negative, depending on the type of mycorrhizal association, and were related to how densely the same species occurred in natural populations.

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