Migration of soil microbes may promote tree seedling tolerance to drying conditions

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Abstract. Soil–microbe interactions have the potential to mediate the ability of tree populations to persist in their current location or establish in new areas. Immigration of microbial taxa from drier conditions may promote seedling tolerance to drying climates. In a greenhouse experiment, we determined seedling performance of *Ostrya virginiana* and *Betula nigra* seedlings after experimentally swapping sterilized soils and local and foreign microbial inocula from nine sites over a gradient of precipitation and soil types, in well-watered and water reduced conditions. Swapping microbial inocula relative to abiotic soils along latitudinal, but not longitudinal, gradients resulted in reduced seedling biomass. Additionally, growth in water reduced conditions was maximized when pots were inoculated with microbes from drier sites. These results suggest that extirpation of local microbial taxa, and/or immigration of novel microbial taxa to a site may be detrimental to plant growth due to mismatches between microbes and soil conditions. However, immigration of drought adapted microbial taxa may provide additional drought tolerance to plant populations facing drying conditions. This work contributes to the understanding of how microbial interactions may potentially exacerbate or mitigate challenges to plant populations caused by climate change.

Key words: climate change; drought; range shifts; soil biota; soil microbes; tree migration.

Introduction

Tree populations in the eastern temperate forests are under pressure from increasing temperatures and increased variability in precipitation (Chen et al. 2011, IPCC 2018, Swanston et al. 2018). In response, tree species ranges are predicted to shift northward and westward to track historical climatic conditions (Iverson et al. 2008, Fei et al. 2017). However, these predictions do not consider how soil biotic interactions may promote or interfere with these shifts (van der Putten et al. 2007, Johnson et al. 2010, van der Putten 2012).

Dispersal abilities and climate tolerances vary widely among both plant and microbial species (Finlay 2002, Berg et al. 2010, Peay et al. 2010a,b), which could result in novel associations between plant populations, microbial communities, abiotic soil conditions, and climate conditions. The consequences of these novel interactions in novel environmental conditions for plant establishment are not well understood and could range from beneficial or detrimental to establishment in new areas (van der Putten et al. 2007, Johnson et al. 2010, van der Putten 2012, Valladares et al. 2014, Kaisermann et al. 2017,

Lozano et al. 2017). Plant growth can respond to specific interactions between soil microbes and abiotic soil properties, such that plants may benefit when the soil microbial community is adapted or otherwise matched to the abiotic soil conditions at a site (Johnson et al. 2010, Keymer and Lankau 2017). For example, Keymer and Lankau (2017) found that *Carpinus carolinana* seedlings performed best when the microbial inoculum was sourced from the same site as the background soil, likely because the native ectomycorrhizal fungal communities appeared to be more efficient at transferring nitrogen to host plants compared to those source from different sites.

The plant–soil–microbe community relationship can be conditional (Johnson et al. 2008, Berendsen et al. 2012, Huang et al. 2014, O'Brien et al. 2018). Thus, the outcomes of contemporary or novel plant–soil–microbe community interactions may be altered under new climates. A plant's ability to deal with stress can be facilitated by microbial symbionts (Rodriguez et al. 2008, Lau and Lennon 2012, Kivlin et al. 2013, Gehring et al. 2017). For example, in times of water stress mycorrhizal fungi can expand the plant's absorptive surface area (Smith and Read 2008). Likewise, some root-inhabiting endophytes are more prevalent in stressed conditions (Mandyam and Jumpponen 2005) and can increase root biomass (Alberton et al. 2010, Newsham 2011) and soil structure aggregates (Miller and Jastrow 2000). A recent

study by O'Brien et al. (2018) showed that soil microbes from one site with lower rainfall promoted plant growth in dry conditions more than microbes sourced from a different site with higher rainfall. If soil microbes influence a plant's response to drought, then microbial communities may help plants tolerate novel environments (Lau and Lennon 2012). Moreover, if historically dry sites contain microbial populations with strong effects on host plant drought tolerance, then migration of these microbial populations to newly drying sites may provide additional drought tolerance to the plant populations at those sites, potentially allow persistence of plant populations in sites that are currently outside of the plant populations climate niche (O'Brien et al. 2018).

Here, we report on a greenhouse experiment that manipulated soils, soil microbial communities, and soil moisture to determine seedling biomass to answer two questions: (1) Is plant performance optimized when grown with microbial communities native to the abiotic soil conditions? (2) Could movement of microbes from historically drier areas to newly drying areas improve plant ability to tolerate a new environment?

We collected soils and soil microbial inoculum across nine sites along a latitudinal and longitudinal gradient spanning four states in the Midwestern United States, with the goal of sampling microbial communities assembled under drier and wetter conditions across a range of soil types. We crossed sterilized bulk soils from each site with local or foreign microbial communities sourced from sites either to the south or west of the soil source, which was fully crossed with a water reduction treatment. Our experimental goals were to determine (1) if tree seedling performance increased when microbial communities were native vs. foreign to abiotic soils and (2) to determine whether seedling performance would be maximized when the environmental conditions matched the environmental conditions under which the microbial community was assembled. Specifically, we evaluated whether plant performance in water reduced conditions was maximized when pots were inoculated with microbial communities sourced from drier sites.

Materials and Methods

Soil, microbial inoculum, and seed

We grew tree seedlings in combinations of abiotic soils and microbial inocula designed to simulate climate driven shifts in microbial communities, shifting microbial communities either to the east or to the north to model multiple possible patterns of microbial movements in response changing climatic conditions. We collected soils from nine sites in the current range of *Ostrya virginiana* and mostly within the current range of *Betula nigra* (six of nine sites; Fig. 1, USDA 2015). Sites were arranged as three parallel longitudinal transects across the western portion of the tree species range, ranging from western Missouri to central Illinois and Wisconsin, USA, with

the three sites along each longitude separated by ~3° latitude (Fig. 1). See Appendix S1: Table S1 for site description with environmental variables. Average annual precipitation over the five years prior to sampling (2010–2015) was determined for each site using the PRISM database (PRISM Climate Group 2004). From the precipitation records, there was a larger precipitation gradient from north to south than west to east (Fig. 1). When shifting microbes across longitude (west to east), the novel microbes tended to maintain more similar abiotic soil conditions (e.g., in % organic matter, Appendix S1: Table S2) but tended to move drier sourced microbial communities to abiotic soils sourced from wetter sites (Fig. 1). However, south to north shifts typically involved shifting microbial communities into higher organic matter soils (Appendix S1: Table S2) and the northward shift treatment tended to move microbial communities from wetter and hotter sites to abiotic soils sourced from drier and cooler sites (Fig. 1).

At each site, we collected 5–10 soil cores at the base of five *Ostrya virginiana* trees to a depth of 20 cm in the spring of 2016 (approximately 3–4 L per site). Soil cores were placed in a plastic bag, homogenized, and kept on ice until we returned to Madison, Wisconsin. Soil inoculum was kept at 4°C until planting. We collected approximately 18–19 L of bulk soil per site within a 10 m radius of each tree. All bulk soils were put in five-gallon (1 gallon = 3.79 L) buckets and stored at ambient temperatures until sterilization. The bulk soils were sterilized with γ-irradiation at a dose between 20 and 40 kGy (Steris Isomedix Services, Libertyville, Illinois, USA). Both the soil inoculum and bulk background soils were mixed within sites prior to use in the greenhouse experiment. Data on general soil properties can be found in Appendix S1: Table S2.

Ostrya virginiana is widely distributed throughout eastern United States and Canada, while *Betula nigra* has a more limited distribution to central and mid-eastern United States. Both tree species are associated with ectomycorrhizal fungi and differ in their drought tolerance (Niinemets and Valladares 2006). *Betula* is less drought tolerant than *Ostrya* and is predicted to spread northwest in response to climate change (Prasad et al. 2007) with losses in range in the Midwest compared to *Ostrya* (Goring and Williams 2017). *Ostrya virniniana* seeds were obtained from Sheffield's Seed Company in Locke, New York. Seeds were cold stratified in a 4°C for 90 d. Seeds were then sown on wet soils for germination. We collected *Betula nigra* seeds from naturally established trees located at Possibility Place Nursery in Monee, Illinois, in the spring of 2015. Seeds were immediately put on wet soils for germination.

Experimental design

A combination of two plant species, microbial inocula, two water treatments and sterilized background soils were used in a greenhouse experiment to test effects

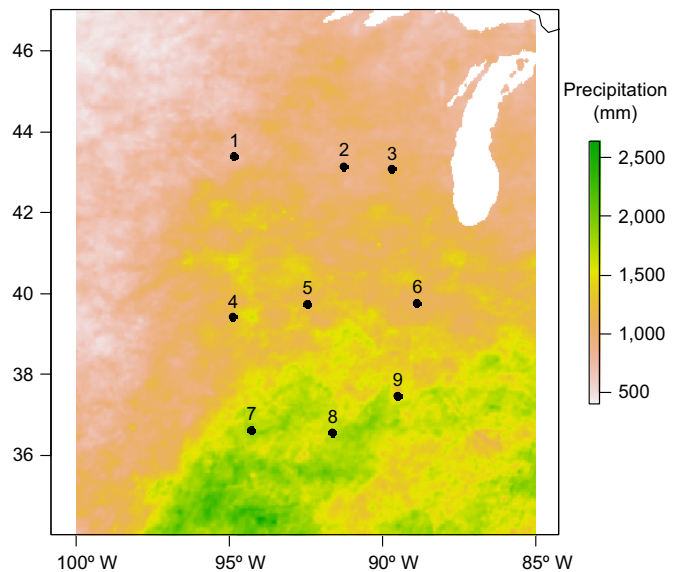| Soil source	Microbial source		
	Status quo	Eastern shift	Northern shift
1	1	X	4
2	2	1	5
3	3	2	6
4	4	X	7
5	5	4	8
6	6	5	9
7	7	X	X
8	8	7	X
9	9	8	X

FIG. 1. Illustration of soil and microbial inocula combinations for treatments and geographic location of sampling sites. Status quo, microbial inoculum collected from same site as background soil; northward shift, microbial inoculum collected from the sites directly south of background soil; eastward shift, microbial inoculum collected from the sites directly west of background soil. Choropleth shows annual precipitation (mm) for 2015, the year of sampling. X refers to combinations of soil and microbial inocula that did not exist in the experiment.

of local vs. foreign (northern or eastern shifted) microbial communities on seedling growth in well-watered or water-reduced conditions. Local microbial treatments (status quo, hereafter) have microbial inocula and sterilized background soils sourced from the same site. The foreign microbial treatments used either microbial inocula sourced from sites one step west of the source of the sterilized background soil (eastern shift, hereafter) or microbial inocula sourced from a site one step south (northern shift, hereafter; see Fig. 1). Seedlings of *Ostrya* and *Betula* were grown in 1.6-L tree pots (10.2 × 10.2 × 24.1 cm; TP-49, Stuewe and Sons, Tangent, OR, USA), filled with 1.0 L of sterile sand combined with 0.5 L of mixed sterilized field soils from each site. A 63-mL inocula (4% of total pot volume) was added to each pot to initiate a microbial community. Each treatment had approximately 10 replications across both seedling species (replication varied according to seedling availability).

Seedlings were planted in a set of three cohorts based on germination timing, over a four-week period in June and July of 2016. No additional nutrients were added to sterilized background soils. To create variation in soil moisture, half of all plants were placed in a well-watered treatment in which pots were watered to saturation once per week. The remaining pots were placed in a water reduction treatment in which pots were watered to saturation once every other week. Mid-way through the experiment, we quantified soil moisture differences between the watering treatments in all pots. We measured the mass of each pot at the end of a two-week watering cycle (when pots would be in their driest state),

and then again, the following day after all pots had been watered to saturation. We determined an index for moisture loss for each water treatment and soil source by calculating the proportion of the saturated pot mass remaining after a two-week period (W[dry]/W[wet] × 100). Well-watered pots (having gone 1 week since watering) retained on average 93.01% ± 0.25% SE of their saturated pot mass, while water reduction pots (having gone 2 weeks since watering) retained on average only 85.08 ± 0.79 SE (estimate = −0.05, SE = 0.003, t_{214} = −16.65, P < 0.0001). In other words, in the well-watered treatment pots lost 7% of their saturated pot mass over 1 week with no watering, while pots in the water-reduced treatment lost 15% of their saturated pot mass over 2 weeks with no watering.

Seedlings were harvested after five months in November of 2016, with the harvest date staggered to reflect the start date for each planting cohort. Aboveground biomass and belowground biomass were separated, dried at 60°C for 48 h, and weighed.

Statistical analysis

Our study employed a hierarchical, but unbalanced, level of replication, with the water treatments and microbial shift treatments replicated unevenly across nine distinct soil sources and replicate pots of each unique combination soil source, microbial inocula, and water treatment (see Fig. 1). To draw conservative conclusions on the effect of our microbial shift and water treatments, independent of general growth differences and hydrodynamics across soil types, we calculated the deviation of

plant biomass from status quo conditions for each seedling in each watering treatment. First, we detrended seedling biomass for the effects of seedling species, planting cohort, and initial height using residuals from a linear model. Then, we calculated the mean seedling biomass (using the detrended data) for the status quo treatment in each watering condition for each of the nine background soil sources. Then, we subtracted this Status Quo mean from the individual detrended seedling biomass in each pot that shared that same background soil source, separately for each watering treatment. This resulted in a metric that ranged from negative to positive values; negative values indicate that the seedling was smaller than the "expected" growth in the status quo condition, while positive values indicate that the seedling was larger than the "expected" growth, with the deviation from expectation isolated to the effects of the microbial inocula. This approach allows us to compare the relative effect of foreign vs. native microbial communities and their interaction with the watering treatment across soil types with different mean growth rates. Because we standardized seedling biomass within each watering treatment separately, this data cannot be used to estimate the main effect of the watering treatment, which we tested using the non-standardized data in a separate model.

We used linear mixed models to compare the seedling biomass deviation from status quo conditions, with the microbial treatment (status quo, eastern shift, or northern shift), watering treatment (well-watered vs. water-reduced), and their interaction modeled as fixed effects. Because we homogenized soil collections from each site prior to planting, our replicate pots of each abiotic soil/microbial source combination are not statistically independent replicates. Therefore, we included the background soil source and the microbial inocula source as random effects to account for this non-independence. Models were fit with the lmer function in the lme4 package in the R statistical language (Bates et al. 2015). P values for individual parameter estimates using t tests and omnibus tests of experimental treatments using F tests were calculated using the Satterthwaite estimated degrees of freedom, implemented through the lmerTest package in R (Kuznetsova et al. 2017). All data followed normal assumptions. We used *a priori* contrasts to test our two research questions.

Is plant biomass optimized when grown with microbial communities native to the abiotic soil conditions?.—We contrasted the seedling biomass deviation from the status quo condition between the status quo treatment (set to 0) and either the eastern shifted or northern shifted microbe treatment, averaged across both watering treatments. A significant positive estimate would indicate that regardless of water conditions, seedlings performed worse when pots were inoculated with microbes from a different site than the sterilized background soil. If a statistically significant effect of microbial treatment was found, we ran an additional model that included the watering treatment and the microbial treatment × watering treatment interaction, to test whether the microbial effect was consistent across both watering conditions.

Could movement of microbes from historically drier areas to newly drying areas improve plant ability to tolerate a new environment?.—To answer this question quantitatively, we calculated the difference in the mean annual precipitation (MAP) between the source of the microbial inocula and the source of the abiotic soil (also the source for the status quo microbial inocula) for each pot, using only those pots with foreign microbial inocula. We used a linear mixed model with seedling biomass deviation from the status quo treatment as the dependent variable, and the difference in MAP, the watering treatment, and their interaction as fixed independent variables. Abiotic soil source and microbial source were included as random factors. Since negative values for precipitation difference indicate that the inoculated microbial community was sourced from an area with less precipitation than the native microbial community, a statistically significant negative estimate would indicate that seedlings perform *better than expected* when inoculated with foreign microbial communities that come from sites drier than the source of the abiotic soil, while seedlings perform *worse than expected* when inoculated with microbial communities source from sites wetter than the abiotic soil source. We additionally performed this regression separately in the well-watered and water-reduced treatments.

Results

Is plant biomass optimized when grown with microbial communities native to the abiotic soil conditions?

Averaging across watering treatments, seedlings were smaller in pots inoculated with foreign microbial communities from sites south of soil source (northern shift), as compared to the status quo treatment (Fig. 2, Appendix S1: Table S3, estimate = 1.040, SE = 0.342, $t_{183.0} = -3.043$, $P = 0.003$). When comparing only northern shifted microbial communities to native ones, there was no significant interaction with the watering treatment (estimate = -0.920, SE = 0.687, $t_{166} = -1.338$, $P = 0.183$). When foreign microbes came from the west of the soil source (eastern shift), there was no difference in plant biomass relative to native status quo treatments (Fig. 2, Appendix S1: Table S3, estimate = 0.429, SE = 0.373, $t_{190.0} = -1.149$, $P = 0.252$), when averaged across water treatments.

Could movement of microbes from historically drier areas to newly drying areas improve plant ability to tolerate a new environment?

Across all pots, final seedling biomass did not differ between our well-watered and water-reduced treatments
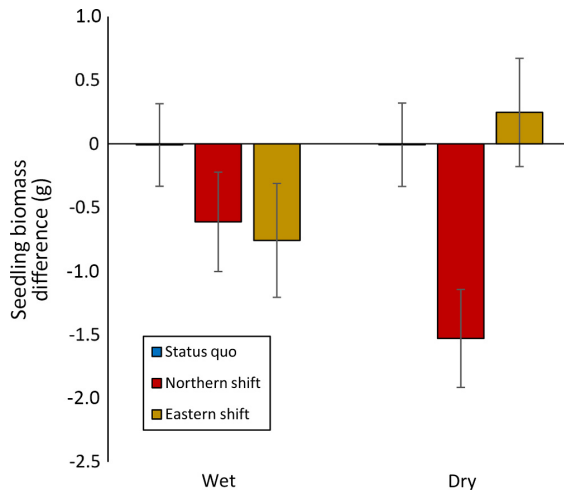
Fig. 2. Seedling biomass (mean ± SE) expressed as the difference from the mean of the status quo treatment for each of the nine soil types in each watering treatment. Blue bars, status quo; red bars, northern shift; gold bars, eastern shift. Mean biomass in the status quo treatment is zero by definition, but is plotted to show the variability within the treatment. See Results: Is plant biomass optimized when grown with microbial communities native to the abiotic soil conditions? for statistical tests.

(estimate = −0.029, SE = 0.288, $t_{203.5}$ = −0.100, P = 0.92). However, the biomass of seedlings with foreign microbial inocula relative to status quo treatments differed across watering treatments and direction of microbial movement.

Regardless of whether microbial communities were shifted east or north relative to the source of the sterilized background soil, microbes form areas with less precipitation tended to promote greater seedling biomass relative to the growth in the status quo treatment for a given soil source (Fig. 3). However, this relationship was only evident in the water-stressed treatment, as evidenced by a significant interaction between precipitation difference and watering treatment (Appendix S1: Table S4, $t_{110.4}$ = −3.724, P = 0.0003). The relationship was significantly negative in the water reduced treatment (estimate = −0.008, SE = 0.002, $t_{26.2}$ = −3.497, P = 0.0017), but not in the well-watered treatment (estimate = 0.004, SE = 0.002, $t_{48.8}$ = −1.463, P = 0.1498).

DISCUSSION

Plants rely on microbial communities to mineralize limiting nutrients from soil organic matter, transport nutrients and water into plant tissue via symbionts, and suppress soil-borne pathogens. Thus, plant biomass may depend on the efficiency with which soil microbes tolerate local soil conditions and process the soil organic matter. In this study, we measured biomass of *Ostrya virginiana* and *Betula nigra* seedlings in pots where microbial communities were native or foreign to the abiotic soil conditions, in well-watered and water reduced conditions to identify if disassociation of historic soil–microbe

interactions altered tree seedling performance, and whether limiting water impacted this interaction. We found that movement of microbial communities from sites south of the abiotic soil source tended to reduce seedling performance, but that this effect was not evident when microbial communities were sourced from sites west of the soil source. However, in reduced water conditions, seedling performance was dependent on the microbial source. We found a quantitative relationship in which plant growth in water-stressed, but not well-watered conditions, was optimized by inoculation with microbial communities sourced from historically drier sites. Together, these results suggest that plants benefit from microbial communities selected by local soil conditions; however, they also benefit from microbial communities assembled in response to the climatic conditions facing the plant.

Is plant performance optimized when grown with microbial communities native to the abiotic soil conditions?

Whether plants performed better when grown with microbial communities native or foreign to the abiotic soil conditions depended on the source of the foreign microbes. When microbial communities were transplanted from sites south of the abiotic soil source, plant biomass was lower, regardless of the watering treatment. However, when microbial communities were transplanted from sites west of the abiotic soil source, plant biomass was similar between the native and foreign microbial treatments. Our experiment does not provide a conclusive mechanism for this difference, but one possibility is that abiotic soil properties change more dramatically across the latitudinal versus the longitudinal gradient, in particular in the amount of organic matter (Appendix S1: Table S2), and so the Northern Shifted microbial communities may have been more maladapted to the experimental soil conditions relative to the native community (Ayres et al. 2009, Johnson et al. 2010).

In a similar study, *Carpinus caroliniana* seedlings were bigger when sterilized soils were inoculated with microbial communities from the same field site, compared to treatments where abiotic soils and microbial communities were collected from different sites (Keymer and Lankau 2017). In that study, in which microbial communities were only shifted along a latitudinal gradient, the benefit of local microbial communities likely derived from more efficient N transfer from local vs. foreign ectomycorrhizal fungi, perhaps due to adaptation of EMF species to the qualities of the local soil organic matter (Keymer and Lankau 2017). Since both tree species studied here form ectomycorrhizal fungal relationships, a similar phenomenon may have occurred in our study. Similar results have been documented for arbuscular mycorrhizal fungi as well; AMF communities collected from P-limited sites promoted greater plant growth than AMF from an N-limited site in P-limited
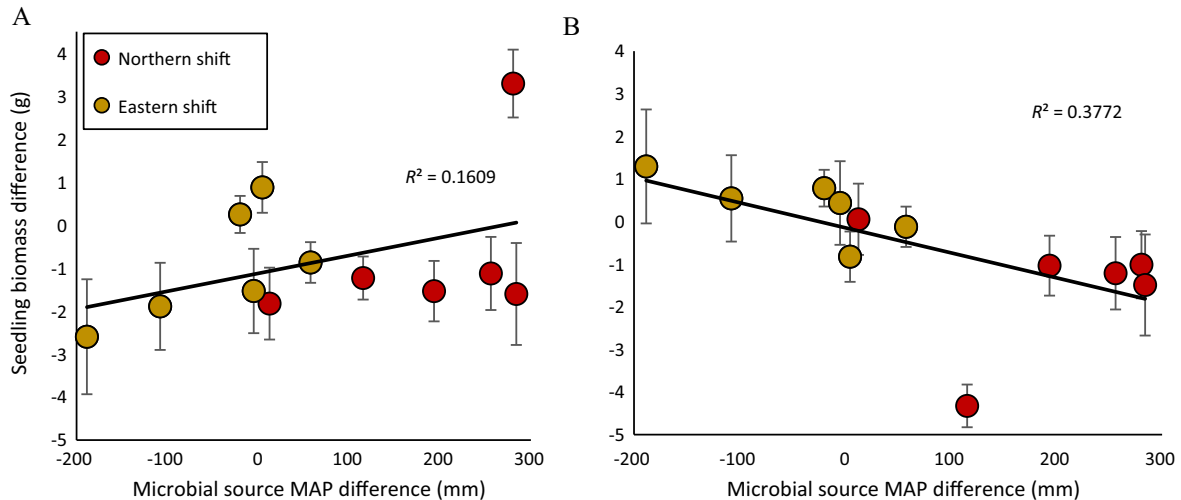
FIG. 3. Seedling biomass (mean ± SE), expressed as the difference from the mean of the status quo treatment for a given soil type, regressed against the difference in mean annual precipitation (MAP) between the soil source site (i.e., status quo site) and microbial source site. Thus, negative values indicate microbial communities sourced from sites wetter than the status quo site, while positive values indicate microbial communities source from sites drier than the status quo site. Only pots receiving foreign microbial inocula (northern shift and eastern shift treatments) are shown. (A) Well-watered treatment; (B) water-reduced treatment. Note that because biomass is standardized within watering treatments, values between panels A and B should not be compared directly. See Results: Can movement of microbes from historically drier areas to newly drying areas improve plant ability to tolerate a new environment? for statistical tests.

conditions, while the reverse was true for plant growth in N-limited conditions (Johnson et al. 2010). Additionally, decomposer communities may have higher efficiency on substrates to which they have had a longer history of exposure, as proposed by the home-field advantage hypothesis (Ayres et al. 2009).

Of course, the importance of maintaining microbial communities adapted to soil conditions must be balanced by the need for plants to have access to specific coevolved microbial partners. In Keymer and Lankau [2017], soil, microbes, and plant seeds were sourced from the same communities. In the current study, seeds were not sourced from the same sites as microbial communities or abiotic soils, which could disrupt any positive or negative plant–microbe coevolution. When plant species are themselves foreign to the soil, cointroduction of microbes from the plant's native range may be necessary for establishment as has been found for the establishment of pine plantations in the southern hemisphere (Nuñez et al. 2009). As both plant and microbial taxa shift in geographic space in response to changing climates or anthropogenic introductions, the consequences for plant performance may be difficult to predict if they depend on the degree of disruption to both the historical plant-microbe and microbe–soil relationships.

Q2: Could movement of microbes from historically drier areas to newly drying areas improve plant ability to tolerate a new environment?

We found that inoculating our experimental pots with foreign microbial communities from historically drier source sites tended to result in greater seedling growth in water-stressed conditions, as compared to pots inoculated with foreign microbial communities from historically wetter areas. In other words, the growth detriment seedlings faced from inoculation with microbes foreign vs. native to the abiotic soil was counteracted in water-stress conditions if the foreign microbial communities came from historically drier locations. Our results suggest that microbial communities assembled under drier conditions possess traits that can help plants tolerate dry soils. Across many studies, fungal symbionts of plants tended to promote plant responses to drought more strongly than other climate change factors (Kivlin et al. 2013). Previous research has shown a similar phenomenon that plant fitness is greatest when the historical environmental conditions matched the current conditions; drier adapted microbial communities increased plant growth in dry conditions when compared to wet adapted microbial communities (Lau and Lennon 2012, O'Brien et al. 2018). The mechanisms behind microbially mediated plant drought tolerance are not clear in our case. Drought conditions may lead to changes in microbial abundance, composition, and function (Drigo et al. 2008). Some soil bacteria, endophytes, and mycorrhizal fungi can increase drought tolerance to plants (di Pietro et al. 2007, Kivlin et al. 2013), for instance through increased absorptive surface area (Egerton-Warburton et al. 2007, Compant et al. 2010). In our experiment, different microbial communities may have led to greater or lesser acquisition of the available soil water, e.g., through different mycorrhizal symbionts, and/or alterations to the soil structure that

affect water holding capacity (Rillig and Mummey 2006, Wilson et al. 2009). While we cannot definitively support any given mechanism, data on water holding capacity do not suggest substantial changes in response to microbial communities, as pot weights during dry-down periods did not vary significantly with either microbial shift treatments (status quo, eastern shift, or northern shift, $P = 0.98$) nor with the mean annual precipitation of the microbial source site ($P = 0.60$). It is important to note that seedling growth in our experiment was not significantly decreased in our water reduced treatment, despite significant reductions in water content in the pots, indicating that the imposed water reduced treatment was relatively mild relative to plant tolerances. It is unclear whether the microbially mediated effects observed here would be more pronounced, or overwhelmed in more severe drought conditions.

In natural settings, unlike our experiment, climates are changing along many axes, in both the means and variances in temperatures and precipitation, and the diverse members of microbial communities may respond to different aspects of climates via both changes in local abundance and dispersal to new communities. Nevertheless, this research provides an initial investigation of how forest communities might be impacted through geographic redistribution of microbial taxa; if drought increases, plants may benefit from the immigration of drought-tolerant microbial populations. Of course, plant species and populations will also be redistributed across landscapes, and so a full understanding of the consequences of these movements must account for disruption of historical plant, microbial community, and soil relationships. Understanding how microbial communities respond to changing climates through both local community shifts and geographic redistribution may prove important to accurately predicting plant population's ability to tolerate novel climatic conditions.

Literature Cited

Alberton, O., T. W. Kuyper, and R. C. Summerbell. 2010. Dark septate root endophytic fungi increase growth of Scots pine seedling under elevated CO_2 through enhanced nitrogen use efficiency. Plant and Soil 328:459–470.

Ayres, E., H. Steltzer, B. L. Simmons, R. T. Simpson, J. M. Steinweg, M. D. Wallenstein, N. Mellor, W. J. Parton, J. C. Moore, and D. H. Wall. 2009. Home-field advantage accelerates leaf little decomposition in forests. Soil Biology and Biochemistry 41:606–610.

Bates, D., M. Mäechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Berendsen, R. L., C. M. J. Pieterse, and P. A. H. M. Bakker. 2012. The rhizosphere microbiome and plant health. Trends in Plant Science 17:478–486.

Berg, M. P., E. T. Kiers, G. Driessen, M. Van der Heijden, B. W. Kooi, F. Kuenen, M. Liefting, H. A. Verhoef, and J. Ellers. 2010. Adapt or disperse: understanding species persistence in a changing world. Global Change Biology 16:587–598.

Chen, I.-C., J. K. Hill, R. Ohlemüeller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Compant, S., M. G. A. Van Der Heijden, and A. Sessitsch. 2010. Climate change effects on beneficial plant-microorganism interactions. FEMS Microbiology Ecology 73:197–214.

di Pietro, M., J.-L. Churin, and J. Garbaye. 2007. Differential ability of ectomycorrhizas to survive drying. Mycorrhiza 17:547–550.

Drigo, B., G. A. Kowalchuk, and J. A. van Veen. 2008. Climate change goes underground: effects of elevated atmospheric CO_2 on microbial community structure and activities in the rhizosphere. Biology and Fertility of Soils 44:667–679.

Egerton-Warburton, L. M., N. C. Johnson, and E. B. Allen. 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. Ecological Monographs 77:527–544.

Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, and C. M. Oswalt. 2017. Divergence of species response to climate change. Science Advances 3:e1603055.

Finlay, B. J. 2002. Global dispersal of free-living microbial eukaryote species. Science 296:1061–1063.

Gehring, C. A., C. M. Sthultz, L. Flores-Rentería, A. V. Whipple, and T. G. Whitham. 2017. Tree genetics defines fungal partner communities that may confer drought tolerance. Proceedings of the National Academy of Sciences USA 114:11169–11174.

Goring, S. J., and J. W. Williams. 2017. Effect of historical land-use and climate change on tree-climate relationships in the upper Midwest United States. Ecology Letters 20:461–470.

Huang, X.-F., J. M. Chaparro, K. F. Reardon, R. Zhang, Q. Shen, and J. M. Vivanco. 2014. Rhizosphere interactions: root exudates, microbes, and microbial communities. Botany 92:267–275.

IPCC. 2018. Summary for policymakers. In V. Masson-Delmotte, et al., editors. Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, Switzerland.

Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management 254:390–406.

Johnson, N. C., J.-H. Graham, and F. A. Smith. 2008. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytologist 135:575–585.

Johnson, N. C., G. W. T. Wilson, M. A. Bowker, J. A. Wilson, and R. M. Miller. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences USA 107:2093–2098.

Kaisermann, A., F. T. de Vries, R. I. Griffiths, and R. D. Bardgett. 2017. Legacy effects of drought on plant-soil feedbacks and plant-plant interactions. New Phytologist 215:1413–1424.

Keymer, D. P., and R. A. Lankau. 2017. Disruption of plant-soil-microbial relationships influence plant growth. Journal of Ecology 105:816–827.

Kivlin, S. N., S. M. Emery, and J. A. Rudgers. 2013. Fungal symbionts alter plant responses to global change. American Journal of Botany 100:1445–1457.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. LmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82:1–26.

Lau, J. A., and J. T. Lennon. 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. Proceedings of the National Academy of Sciences USA 109:14058–14062.

Lozano, Y. M., C. Armas, S. Hortal, F. Casanoves, and F. I. Pugnaire. 2017. Disentangling above- and below-ground facilitation drivers in arid environments: the role of soil microorganisms, soil properties and microhabitat. New Phytologist 216:1236–1246.

Mandyam, K., and A. Jumpponen. 2005. Seeking the elusive function of the root-colonising dark septate endophytic fungi. Studies in Mycology 53:173–189.

Miller, R. M., and J. D. Jastrow. 2000. Mycorrhizal fungi influence soil structure. Pages 3–18 in Y. Kapulnik and D. D. Douds, editors. Arbuscular mycorrhizas: physiology and function. Springer, Dordrecht, The Netherlands.

Newsham, K. K. 2011. A meta-analysis of plant responses to dark septate root endophytes. New Phytologist 190:783–793.

Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecology Monographs 76:521–547.

Nuñez, M. A., T. R. Horton, and D. Simberloff. 2009. Lack of belowground mutualisms hinders Pinaceae invasions. Ecology 90:2352–2359.

O'Brien, M. J., F. I. Pugnaire, S. Rodríguez-Echeverría, J. A. Morillo, A. López-Escoriza, D. J. Aránega, and C. Armas. 2018. Mimicking a rainfall gradient to test the role of soil microbiota for mediating plant responses to drier conditions. Oikos 127:1776–1786.

Peay, K. G., M. I. Bidartondo, and A. E. Arnold. 2010a. Not every fungus is everywhere: scaling to the biogeography of fungal-plant interactions across roots, shoots and ecosystems. New Phytologist 185:878–882.

Peay, K. G., M. Garbelotto, and T. D. Bruns. 2010b. Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91:3631–3640.

Prasad, A. M., L. R. Iverson, S. N. Matthews, and M. Peters. 2007-ongoing. A climate change atlas for 134 forest tree species of the Eastern United States [database]. Northern Research Station, USDA Forest Service, Delaware, Ohio, USA.

Prism Climate Group. 2004. Oregon State University. http://prism.oregonstate.edu

Rillig, M. C., and D. L. Mummey. 2006. Mycorrhizas and soil structure. New Phytologist 171:41–53.

Rodriguez, R. J., J. Henson, E. Van Volkenburgh, M. Hoy, L. Wright, F. Beckwith, Y.-O. Kim, and R. S. Redman. 2008. Stress tolerance in plants via habitat-adapted symbiosis. ISME Journal 2:404–416.

Smith, S. E., and D. J. Read. 2008. Mycorrhizal symbiosis. Third edition. Academic Press, Oxford, UK.

Swanston, C., L. A. Brandt, M. K. Janowiak, S. D. Handler, P. Butler-Leopold, L. Iverson, F. R. Thompson III, T. A. Ontl, and D. P. Shannon. 2018. Vulnerability of forests of the Midwest and Northeast United States to climate change. Climatic Change 146:103–116.

USDA, NRCS. 2015. The plants database. National Plant Data Team, Greensboro, North Carolina, USA.

Valladares, F., et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters 17:1351–1364.

van der Putten, W. H., et al. 2007. Plant-soil feedbacks: the past, the present and future challenges. Journal of Ecology 101:265–276.

van der Putten, W. H. 2012. Climate change, above-ground-belowground interactions and species range shifts. Annual Review of Ecology, Evolution, and Systematics 43:365–383.

Wilson, G. W. T., C. W. Rice, M. C. Rillig, A. Springer, and D. C. Hartnett. 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. Ecology Letters 12:452–461.

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