PLANT ECOLOGY

Shifting microbial communities can enhance tree tolerance to changing climates

Cassandra M. Allsup†, Isabelle George†, Richard A. Lankau*

Climate change is pushing species outside of their evolved tolerances. Plant populations must acclimate, adapt, or migrate to avoid extinction. However, because plants associate with diverse microbial communities that shape their phenotypes, shifts in microbial associations may provide an alternative source of climate tolerance. Here, we show that tree seedlings inoculated with microbial communities sourced from drier, warmer, or colder sites displayed higher survival when faced with drought, heat, or cold stress, respectively. Microbially mediated drought tolerance was associated with increased diversity of arbuscular mycorrhizal fungi, whereas cold tolerance was associated with lower fungal richness, likely reflecting a reduced burden of nonadapted fungal taxa. Understanding microbially mediated climate tolerance may enhance our ability to predict and manage the adaptability of forest ecosystems to changing climates.

C limate change is forcing populations outside of their range of climate tolerance, with estimates as high as 16% of species facing extinction in the next century in response (1–3). When faced with changing climates, species must either migrate to track optimal climates or adapt or acclimate to the new conditions; failing that, they face extinction (1, 4). However, species exist within diverse communities, and interactions among species may provide alternative pathways to climate tolerance (5, 6). In particular, macroscopic organisms exist in constant association with diverse communities of microbes (i.e., their microbiome), which shape their phenotypes and their responses to stresses such as climatic change (7, 8).

Plants have repeatedly evolved relationships with microbes to meet essential needs (9, 10). Rhizosphere and endophytic microbes often enhance plant tolerance to a range of stresses when compared with axenic plants (7, 8), including cold (11), heat (12), and drought stress (13–15). Associations with specific microbial taxa can be essential to the adaptation of plant populations to extreme environments (12, 16, 17), and microbial communities sourced from specific environments can affect plant responses to similar environmental stresses in artificial conditions (18–20). Almost all tree species form associations with either arbuscular (AM) or ectomycorrhizal (EM) fungi, which represent phylogenetically and functionally distinct symbioses. Mycorrhizal fungi can enhance plant tolerance to many environmental conditions (7, 21, 22) and are thus prime candidates for microbes responsible for microbially mediated climate tolerance. Such "stress-adapted" microbial communities could influence plant performance by including microbial strains better

able to perform under the stress or by excluding detrimental microbial taxa that cannot tolerate the stressful condition. If microbial associations broadly contribute to determining realized plant-climate niches, then our ability to understand current, and predict future, plant distributions may be incomplete. However, the extent to which variation in microbial communities across climatic gradients can lead to enhancement of host plant tolerance to those same gradients is largely untested in natural conditions. Microbial taxa are likely to adapt faster than their host plants, especially trees (23, 24), and may disperse farther (25, 26). This may provide an alternative source of plant community resistance to climate change through microbial adaptation in place or migration through space.

Increased temperatures and drought are predicted to reshape forests through changes in species abundance (27), redistribution of species ranges (28, 29), and conversions of forest to other biomes (30, 31), with likely feedbacks to the global climate system (32). To investigate how geographic variation in microbial communities could affect tree responses to climate stressors, we first collected microbial communities sourced from 12 locations along gradients of temperature and precipitation. Then, we tested how inoculation with these communities influenced tree seedlings' responses to climate stresses in two locations chosen to represent expanding and trailing range edges, as well as in controlled conditions. At each location, we grew seedlings of several tree genera, including those that associate with either AM or EM fungi, in ambient and reduced rainfall conditions. Across the two sites and the rainfall treatments, this resulted in seedlings experiencing variation in cold, heat, and drought stress. Seedling survival was enhanced by inoculation with microbial communities sourced from areas with climates that best matched the major climate stress facing the seedlings in each field site

or experimental treatment. The microbially enhanced tolerance to heat and drought only occurred for trees associating with AM fungi, whereas cold tolerance occurred across mycorrhizal types. These results indicate that soil and root microbial communities can provide an alternative pathway to climate tolerance for forests.

Matching of microbial community source and climate stress–enhanced survival in field conditions

At our northern site (Fig. 1), we planted a mixture of tree species that were either native to the site (but with range centers south of the site) or had native ranges south of the site (table S1). This experiment simulated the process of range expansion, in which populations expand or establish in areas that have become permissive because of climate change. We expected that survival over winter would be a primary climate stress on seedlings at this site. Therefore, we predicted that seedling survival would be maximized when preinoculated with microbial communities sourced from colder areas (microbially induced cold tolerance). Supporting this hypothesis, in ambient rainfall conditions, seedlings inoculated with soil microbes sourced from areas with colder winters had higher 3-year survival rates [phylogenetic generalized linear mixed model (PGLMM), $P = 0.031$; Fig. 2A and table S2]. This effect was not apparent when seedlings were grown under reduced rainfall conditions (PGLMM, $P = 0.823$; Fig. 2B and table S2). The minimum temperature of the microbial-source site was a better predictor of seedling survival than the mean or maximum temperatures of the source site (33). The aridity of the microbial source was not significantly associated with seedling survival (table S2). Survival was independently influenced by the initial seedling height (table S2). These results did not differ between seedlings associating with AM or EM fungi (Fig. 2, A and B, and table S3).

To examine how microbial-source climate affected survival across the 3-year experiment, we compared survival across distinct seasons ["growing season" spring-to-fall survival versus "overwintering" fall-to-spring survival (fig. S1)]. During the first summer, survival was highest in seedlings inoculated with microbial communities from warmer locations in both ambient and reduced rainfall conditions (PGLMM, $P = 0.064$ and 0.031, respectively; Fig. 2, C and D, and table S4). However, over the first winter period this pattern reversed; overwinter survival was significantly higher for seedlings inoculated with microbial communities from colder sites (PGLMM, $P < 0.0001$ for ambient conditions, $P = 0.019$ for rainfall-reduced conditions; Fig. 2, C and D, and table S4). During the second summer, survival in the ambient versus rainfall-reduced

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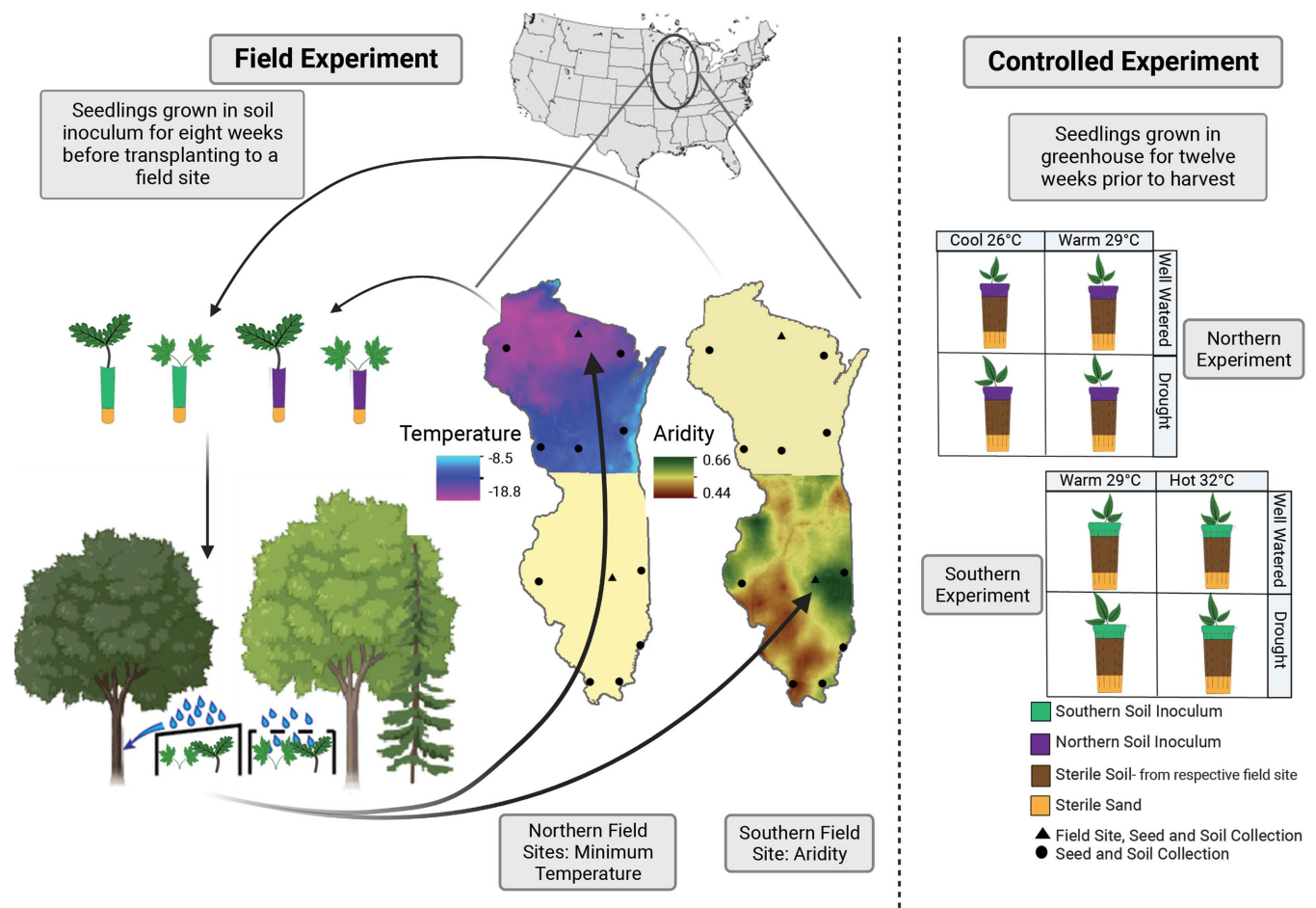†These authors contributed equally to this work.

Fig. 1. Experimental design of linked field and greenhouse experiments. Parallel sets of experiments were performed for the northern sites and soils to simulate range expansion and for the southern site and soils to simulate range contraction. (i) Live soil was collected from six sites in each state. (ii) Seedlings were germinated in sterile conditions and then grown for 8 weeks with live field soil prior to transplantation into experimental sites (triangle symbols). (iii) Seedlings were grown under rainfall-reduction or mock (ambient condition) shelters in field sites for 3 years, with survival monitored seasonally, for each of two cohorts (planted in 2018 and 2019). (iv) Live soil from the same sites was used to inoculate pots for a controlled-environment experiment in which pots were filled with sterilized background soil from the field experiment location. (v) Seedlings were grown for 12 weeks in two temperature conditions crossed with two watering frequencies. The greenhouse experiment was repeated three times, once per year for 3 years, with new soil collections for each repetition.

conditions diverged: survival in ambient conditions reinforced the trend seen in the previous winter, whereas survival in the rainfall-reduced conditions counteracted that trend (PGLMM, rainfall treatment × microbial-source minimum temperature interaction, $P = 0.025$; Fig. 2, C and D, and table S4). That is, under ambient rainfall conditions, seedlings faced one major climatic stress—cold winter temperatures—and survival was optimized by preinoculation with microbial communities from colder sites. But in the rainfall-reduced treatment, seedlings faced multiple climatic stresses (winter cold as well as summer drought), and thus no particular microbial community was able to optimize cumulative survival over the 3-year period.

We chose our southern site in central Illinois to reflect heat and drought stress for our suite of temperate tree species. This location is south of the range center for all of our target species' ranges and near the southern range limit for many. Therefore, this location represented dynamics at a species' trailing edge where climates are becoming too warm or dry for population persistence (table S1). Here, we expected that in the ambient conditions, seedlings would be primarily stressed by high summer temperatures, and we hypothesized that seedling survival would be optimized when they were inoculated with microbial communities sourced from warmer sites (i.e., microbially induced heat tolerance). Alternatively, in our rainfall-reduction treatment, we expected that seedlings would be stressed to a greater relative extent by drought and thus hypothesized that seedling survival would be optimized when inoculated with microbial communities sourced from more arid sites (microbially induced drought tolerance). In partial support of our hypotheses, seedling survival trended toward a positive relationship with the maximum temperature of the microbial-source site for seedlings in our ambient rainfall treatment (PGLMM, $P = 0.093$; Fig. 3A and table S5) but not in the rainfall-reduced treatment (PGLMM, $P = 0.952$; Fig. 3A and table S5). Seeding survival was very strongly promoted by preinoculation with microbial communities from more arid sites in our rainfall-reduced treatment (PGLMM, $P = 0.002$; Fig. 3B and table S5) but not in our ambient rainfall treatment (PGLMM, $P = 0.940$; Fig. 3B and table S5). Qualitatively similar results were found when analyzing survival time with Cox regression at both experimental sites (tables S2 and S5).
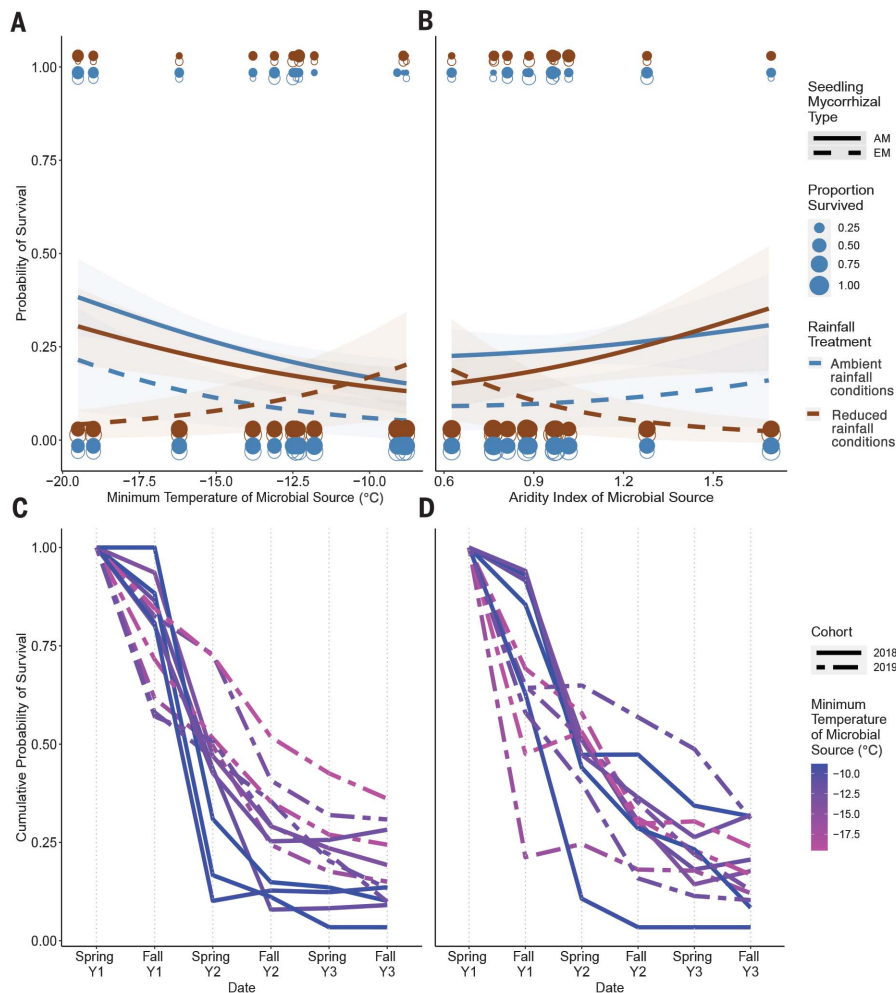
Fig. 2. Seedling survival patterns at the northern field site versus the climatic conditions of the microbial inocula source. (**A** and **B**) Probability of surviving over 3 years versus (A) the minimum temperature or (B) aridity index of the microbial-source site. Aridity index, precipitation/potential evapotranspiration; lower values indicate drier conditions. Blue, ambient rainfall conditions; brown, reduced rainfall conditions. Dashed lines and open symbols, ectomycorrhizal (EM) species; solid lines and filled symbols, arbuscular mycorrhizal (AM) species. (**C** and **D**) Cumulative survival over three years, broken down by spring and fall sampling dates. (C) Ambient rainfall conditions, (D) reduced rainfall conditions. Each line represents the cumulative survival probability for a given microbial inocula source, colored according to the minimum temperature of the microbial-source site. Solid lines, 2018 cohort; dashed lines, 2019 cohort.

Unlike in the northern site, seedlings associated with AM versus EM symbiotic fungi had qualitatively different responses to microbial inoculation sources in our southern site. For AM-associated seedlings, predictions of microbial-induced climate tolerance were strongly supported: AM seedlings survived better when inoculated with microbial communities from hot sources in the ambient, but not reduced, rainfall conditions (PGLMM, P = 0.009 and 0.405, respectively; Fig. 3 and table S6) but showed the opposite pattern with respect to the aridity of the microbial source (PGLMM, P = 0.059 for ambient conditions, P < 0.0001 for rainfall-reduced conditions; Fig. 3 and table S6). Survival of EM-associated seedlings did not display significant relation-

ships in predicted directions with microbial-source climate in any condition (Fig. 3 and table S6).

The impact of microbial-source maximum temperature was broadly distributed across seasonal periods, trending toward a positive relationship in most seasons but not resulting in statistically significant associations with survival for any one seasonal period (PGLMM, P > 0.05 for all; table S7, B and C). By contrast, the effect of microbial-source aridity was concentrated strongly during the second summer. Survival over the second summer depended significantly on the interaction between rainfall treatment and microbial-source aridity (PGLMM, P = 0.014; table S7) because of a strongly significant association in the rainfall-

reduction treatment (PGLMM, P = 0.003; table S7) but no significant relationship in the ambient rainfall treatment (PGLMM, P = 0.493; table S7). Thus, preinoculation with microbial communities from more arid sites led to enhanced drought tolerance for seedlings during the period of most intense drought stress (in rainfall-reduction shelters during the summer months).

Microbially mediated tolerance to drought in controlled conditions

Our field experiments could not separate the climatic conditions that seedlings experienced from the other conditions at our sites, such as soil properties. Additionally, the variation in our inoculated microbial communities could have arisen from many differences among source sites. In particular, among our northern set of microbial inocula, colder microbial-source sites also had soil conditions more similar to those of the field site (e.g., higher levels of soil organic matter) compared with those of the warmer source sites. Because microbial communities can be adapted to local soil conditions in ways that promote plant growth (*34*), if our inoculated microbial communities were differentially adapted to the soil properties at our field sites, this could be mistaken for microbially induced climate tolerance. Additionally, microbial communities may vary in their direct effects on seedling health in ways unrelated to climate tolerance, such as through pathogen load. Therefore, we performed pot experiments using sterilized soil from each field site, inoculated with the same microbial communities used in our field experiment and grown at ambient and elevated summer temperatures with sufficient or restricted watering frequency (*33*). We used this experiment to test whether the patterns observed in our field sites were dependent on specific climate conditions or rather represented nonclimatic relationships between microbial communities, abiotic soil conditions, and seedlings.

In controlled conditions, seedling growth in the soils from our northern experimental site was unaffected by the climate of the microbial inoculum source, unlike our field results. This indicates that the survival patterns observed in our field experiment could not be explained by nonclimatic effects of microbial communities, such as variable pathogen loads or differential adaptation of microbial communities to the soils at our northern site (table S8). This experiment could not directly confirm the pattern of microbially mediated cold tolerance because the seedlings in the pot experiment did not experience winter temperatures.

Seedling growth in the soil from our southern site demonstrated patterns similar to those seen in our field experiment. In particular, seedling growth was enhanced in pots inoculated with microbial communities from drier
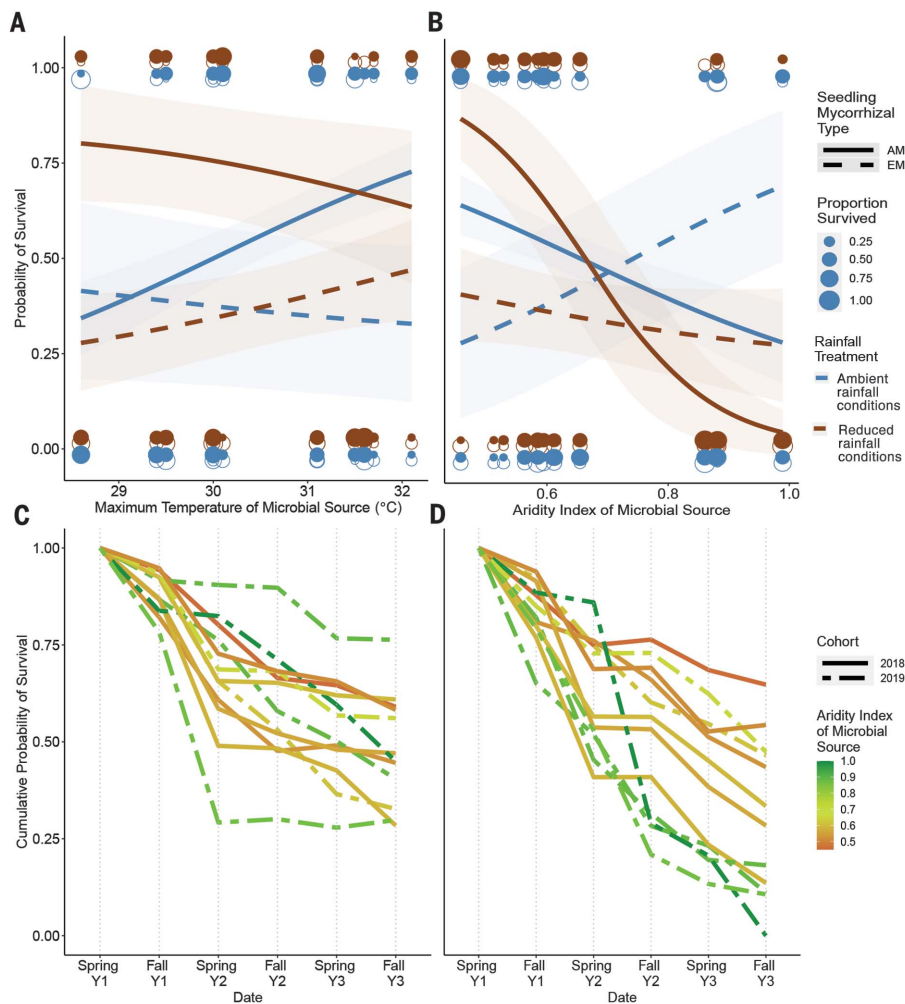
Fig. 3. Seedling survival patterns at the southern field site versus the climatic conditions of the microbial inocula source. Seedling survival at the southern field site. (**A** and **B**) Probability of surviving over 3 years versus the (A) maximum temperature or (B) aridity index of the microbial-source site. Aridity index, precipitation/potential evapotranspiration, measured over the growing season (May to October) prior to soil collection; lower values indicated drier conditions. Blue, ambient rainfall conditions; brown, reduced rainfall conditions. Dashed lines and open symbols, EM species; solid lines and filled symbols, AM species. (**C** and **D**) Cumulative survival over three years, broken down by spring and fall sampling dates. (C) Ambient rainfall conditions, (D) reduced rainfall conditions. Each line represents the cumulative survival probability for a given microbial inocula source, colored according to the aridity index of the microbial-source site. Solid lines, 2018 cohort; dashed lines, 2019 cohort.

sources, but only in the treatment with the greatest drought stress (elevated temperature and restricted watering) (PGLMM, $P < 0.001$; Fig. 4A, table S9, and fig S2). Consistent with the field results, the pattern of microbially mediated drought tolerance was much stronger for AM- compared with EM-associated seedlings (Fig. 4A and table S10).

Microbially mediated climate tolerance is associated with root-associated fungal diversity

Even after 3 years of growth in field conditions, a statistically significant signal of the initial inoculated community remained in the root-associated fungal community composi-

tion for both field sites, and for seedlings of both mycorrhizal types [permutational multivariate analysis of variance (perMANOVA), $P < 0.025$ for all; Fig. 5, A and B, figs. S3 to S6, and table S11]. This indicates that at least some fungal taxa from the initial inoculation were able to persist on seedling roots over 3 years, despite the availability of indigenous fungi for replacement, consistent with strong priority effects documented for both AM and EM fungal symbionts (35, 36). Microbially mediated heat and drought tolerance at our southern site appeared to derive directly or indirectly from the diversity of arbuscular mycorrhizal fungi. This inference relies on three observations. First, the diversity of AM fungi

was higher in the initial inoculum soil from more arid sites (LM, $P = 0.002$; Fig. 4B and table S12B), and this higher diversity persisted in the roots of surviving AM-associated seedlings even after three years of growth at the field site (PGLMM, $P = 0.043$; Fig. 5C and table S13B). These patterns were not evident in EM-associated seedlings. Second, sources of microbial inocula that resulted in a higher diversity of AM fungi on surviving seedlings also tended to have higher survival probabilities for AM seedlings in the rainfall-reduction treatment, but not in the ambient rainfall treatment (GLM, $P = 0.015$; Fig. 5D and table S14B). Third, these results were confirmed in our controlled-environment experiment, where growth of AM-associated seedlings in the warm-dry treatment was positively correlated to the initial diversity of AM fungi in the soil inoculum (PGLMM, $P = 0.001$; Fig. 4D and table S15), and AM fungal diversity acted as a mediator of the effect of microbial-source aridity on seedling growth (table S15). No other aspects of the full fungal community, or other functional guild subsets, met all three conditions (tables S12B, S13B, and S14B).

Alternatively, enhanced cold tolerance at our northern site occurred regardless of mycorrhizal type. Surviving seedlings inoculated with microbial sources from warmer locations (higher minimum temperature) had a higher richness of fungal species after 3 years at the field site (PGLMM, $P = 0.027$; Fig. 5C and table S14A). In contrast to our southern field site, in the northern site, fungal diversity on surviving seedlings was negatively correlated with the survival probability of seedlings with a given inoculum source in ambient conditions (GLM, $P < 0.001$; Fig. 5C and table S16A). This pattern was evident for richness of the pathogen-endophyte guild but not for either mycorrhizal guild analyzed separately (table S16A). Neither total fungal diversity or richness, nor the diversity or richness of any functional guild, in the original inoculum soil correlated with any source-climate variable (LM, $P > 0.07$ for all; table S13A). Thus, the higher fungal diversity in surviving seedlings inoculated with soils from warmer locations may stem from the combination of inoculated fungal taxa with fungal taxa indigenous to the field site. This suggests that the persistence of maladapted fungal species from warmer-site inocula may have acted to inhibit the provision of cold tolerance by the indigenous fungi.

We expect the precise drivers of microbially induced climate tolerance to be idiosyncratic to particular communities and hosts. However, our main conclusion is that the ability to enhance plant-host tolerance is predictable by the climatic history of the microbial community. Our experiments involved a range of tree species and climate variables, indicating that microbially mediated climate tolerance is

Fig. 4. Fungal communities on surviving seedlings reflect initial microbial inocula sources and correlate with seedling survival probabilities. (**A**) Nonmetric multidimensional scaling (NMDS) ordination of fungal communities on surviving seedlings after three years at the northern field experiment, colored according to the minimum temperature of the initial microbial inocula source. Stress = 0.30. (**B**) NMDS ordination of fungal communities on surviving seedlings at the southern field experiment, colored according to the aridity index of the initial microbial inocula source. Stress = 0.28. (**C**) Probability of survival for seedlings in ambient conditions at the northern field site, per microbial inocula source, versus the average fungal richness of surviving seedlings of that same microbial inocula source. (**D**) Probability of survival for AM seedlings in reduced rainfall conditions at the southern field site, per microbial inocula source, versus the average AM fungal diversity of surviving seedlings of that same microbial inocula source.
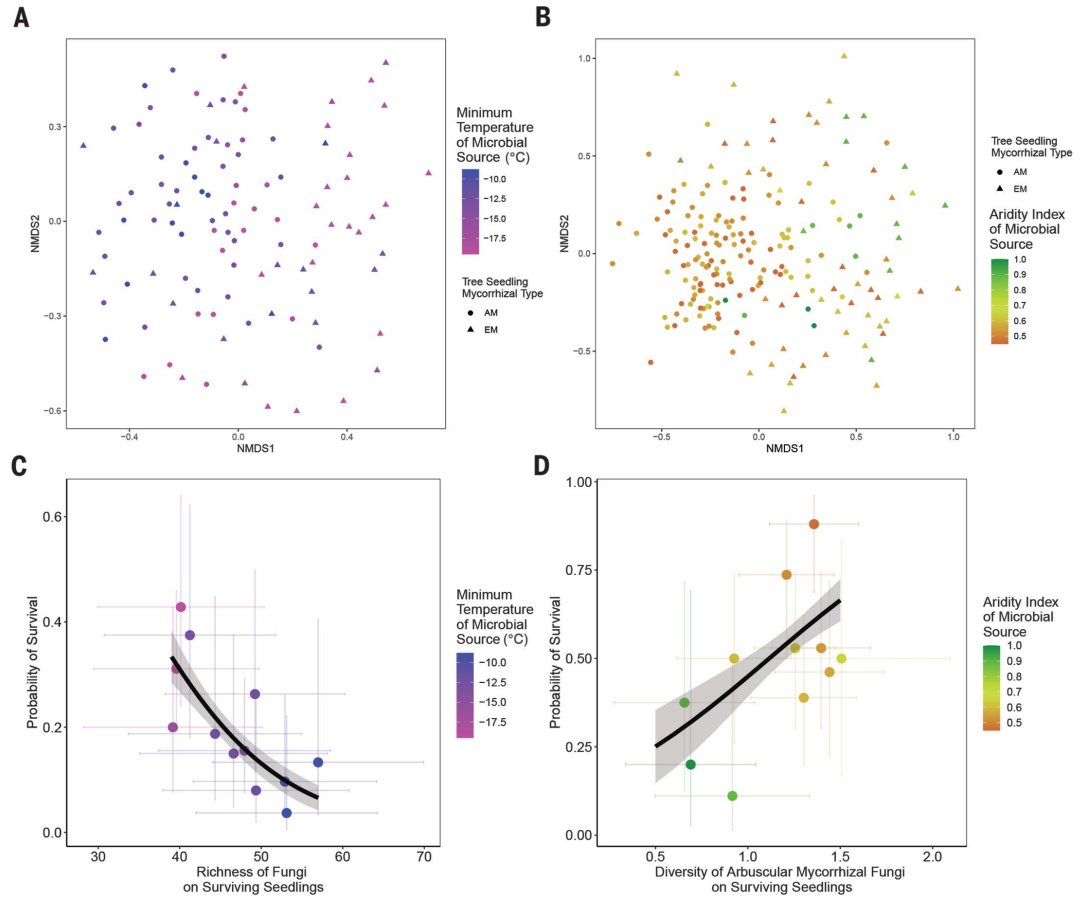
not a rare phenomenon in temperate forests. Future research should seek to determine how widely the phenomenon of microbially mediated climate tolerance occurs across ecosystems, plant species, and climatic stresses regardless of the specific microbial mechanism. Additionally, more research is needed to understand how microbial communities will respond to changing climates through internal resorting of species and redistribution of species across landscapes, and what consequence these shifts will have for host plant climate tolerance. For instance, in situ soil warming and drought experiments have documented shifts in microbial community composition (*37–40*), but it is not clear if the resulting new microbial communities will confer increased tolerance to warming or drying soils for plant species. Our experiments demonstrated that over short time periods, introduction of new microbial taxa (through preinoculated tree seedlings) could lead to higher plant survival than the indigenous community could provide on its own for species at their trailing range edge. This suggests that indigenous microbial communities may not be infinitely flexible in terms of functions for host plants and that movement
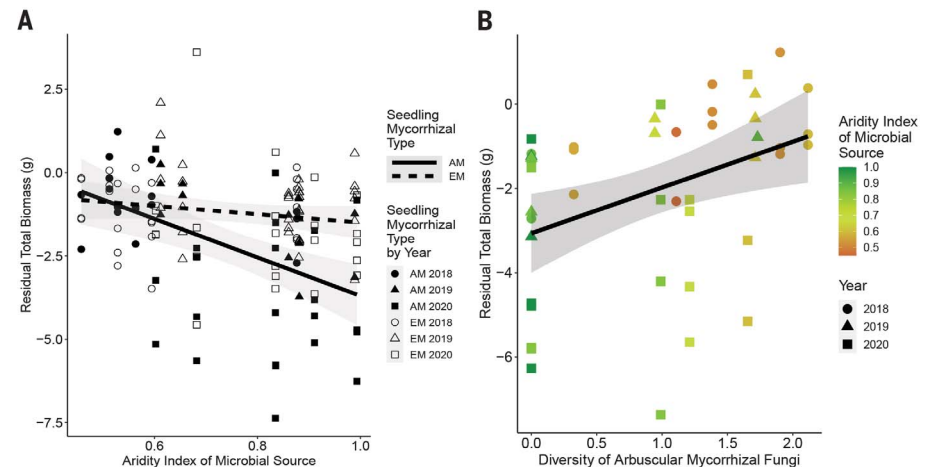

Fig. 5. Seedling growth in water-stressed treatments in controlled conditions reflected microbial-source climate for AM-associated seedlings. Residual seedling biomass in the controlled-condition experiment using southern field-site soil–mirrored patterns seen in the field experiment. Residual values account for differences in growth rate among seedling species and initial size; positive values indicate larger-than-expected biomass for a seedling of that species, whereas negative values indicate a smaller-than-expected biomass. (**A**) Residual biomass of seedlings in the warm-dry treatment versus the aridity index of the initial microbial source, separated by seedling mycorrhizal type. Dashed lines and open symbols, EM species; solid lines and filled symbols, AM species. (**B**) Residual biomass of AM seedlings in the warm-dry condition versus the Shannon-Weaver index of diversity of AM fungi in the original inoculum. Shannon-Weaver diversity of AM fungi in the original inoculum soil was positively correlated with aridity.

of microbial populations across space may be necessary when plants face increasingly stressful conditions. However, the opposite phenomenon may occur at expanding range edges, where conditions are becoming less stressful for a plant species. In this case, introduction of maladapted microbial taxa reduced survival for species in our experiment.

Intentional inoculation of specific microbial taxa into forests is not feasible at scale. However, tree planting is a major component of climate mitigation strategies, with commitments to plant trillions of trees in coming decades (*41*). Trees are typically planted as seedlings after growth in outdoor beds, bringing diverse microbial communities with them to planting sites (*42*). These preinoculated seedlings represent a massive, unintentional movement of rhizosphere taxa across landscapes. However, they may also represent an opportunity for microbially mediated climatic tolerance if tree nurseries were managed to promote colonization by microbial symbionts adapted to specific climatic conditions.

Rapidly changing climates have reshaped ecosystems and driven extinction and will continue to do so. The interconnections in ecosystems, between community members and between communities across space, have the potential to amplify or resist these changes. A better understanding of microbial interactions as an additional strategy for tree populations at expanding and retracting range edges could help inform predictions of forest vulnerability as well as offer new avenues for promoting resilience in managed forests.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adf2027
Material and Methods
Figs. S1 to S6
Tables S1 to 16
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View/request a protocol for this paper from *Bio-protocol*.

Shifting microbial communities can enhance tree tolerance to changing climates

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Editor's summary

As sessile organisms, plants have limited ability to move in response to climate change. However, the microbial communities that help plants access soil nutrients may also increase their tolerance to climate stress. Using field and laboratory experiments, Allsup *et al.* showed that soil microbe communities sourced from colder or drier sites increased the survival of inoculated tree seedlings exposed to cold winters or drought, respectively (see the Perspective by Afkhami). These findings suggest greater potential resilience for trees and highlight the importance of species interactions in determining their response to climate change. —Bianca Lopez

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