RESEARCH ARTICLE

Extant species are more responsive than locally extinct species to warming effects on soil communities

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Abstract

Purpose   Climate change may alter interactions between plants and their associated soil microbial communities, including microbe-mediated plant-soil feedbacks (PSF). If PSF influence plant performance and abundance in natural communities, climate-induced changes in soil communities might affect local extinction. Here, we examine whether warming-induced shifts in plant-soil interactions are associated with local species loss in tallgrass prairie.

Methods   We conducted a traditional two-phase PSF experiment. In phase 1, phylogenetic pairs of locally extinct and extant prairie species were grown under ambient or elevated temperature conditions in the field. In phase 2, soil microbial communities were collected from below those plants and inoculated onto conspecific and heterospecific seedlings grown in the greenhouse. We compared warming effects on plant performance in soil conditioned by locally extinct and extant species as well as net-pairwise PSF between phylogenetic pairs.

Results   Locally extinct prairie species were more sensitive to soil biota than extant species, generally performing better when grown in soils cultivated by certain extant species. Meanwhile, extant species were more responsive to warming effects on soil communities than locally extinct species, although the direction and magnitude of temperature effects varied across species. We detected no significant overall effects of warming on net-pairwise PSF.

Conclusion   These findings suggest that soil biota might have affected historical plant species losses via negative effects of locally extinct species' soil on their own growth. Warming-induced shifts in soil communities might influence extant prairie species' performance under climate change, indicating a need to consider plant–microbe interactions in future prairie conservation efforts.

Keywords   Climate change · Extirpation · Plant-soil feedback · Prairie · Soil warming

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Introduction

Climate change will likely alter the composition of plant communities and their interactions with associated soil microbial communities, or microbe-mediated plant-soil feedbacks ("PSF") (van der Putten et al. 2016). PSF occurs when plant species influence

the composition, activity, metabolism, and interactions of microbes in the plant rhizosphere, which in turn impact plant growth of conspecifics and other species (Bever 1994). Such changes to the soil can result in either negative or positive PSF, depending on the balance of antagonistic vs. beneficial interactions between the plant and its resident soil community (Bennett and Klironomos 2019). Reduced survival and growth in a plant species' own conspecific, or "home", soil compared to soil cultivated by other species results in a negative PSF. Negative PSF can potentially increase diversity in the plant community by providing an advantage to rare species and limiting the growth and dominance of a single species. Positive PSF occur when species do best when grown with microbial communities associated with conspecifics rather than heterospecifics, and are expected to reduce diversity. As a result, PSF can affect plant performance, abundance, and community dynamics (e.g., succession, dominance, and invasion) (Klironomos 2002; De Deyn et al. 2003; Kardol et al. 2013; Van Nuland et al. 2016; Luo et al. 2019). Moreover, climate change can influence plant community composition via shifts in PSFs (Bardgett 2018; Wubs and Bezemer 2018). However, we know relatively little about how climate change affects PSF (Pugnaire et al. 2019; Hassan et al. 2022) or how PSF might influence plant rarity and decline (Kempel et al. 2018; Reinhart et al. 2021).

Despite a growing body of literature on how climate, especially drought, affects PSF via changes in soil biota composition and activity (Kaisermann et al. 2017; Fry et al. 2018; Xi et al. 2018; Snyder and Harmon-Threatt 2019; Crawford and Hawkes 2020; Rasmussen et al. 2020), it is still unclear how rising temperatures affect the direction and magnitude of PSF (Duell et al. 2019; Pugnaire et al. 2019; Hassan et al. 2022). Theoretically, rising temperatures could result in either more positive or more negative PSF via three non-mutually exclusive pathways (c.f. Figure 2 in Hassan et al. 2022). (1) Warming may modify soil abiotic properties via changes in plant litter decomposition or root exudates that affect nutrient cycling. Warming might reduce or strengthen interactions with (2) beneficial microbes or (3) pests and pathogens, resulting in either more positive or negative PSF, respectively.

Another challenge is understanding how PSF affects plant abundance (Teste et al. 2017; Reinhart

et al. 2021), which is often examined by correlating PSF with demographic characteristics. For instance, rare native plants often have more negative PSF than more common or invasive species (Klironomos 2002; Reinhart et al. 2003; Reinhart and Callaway 2006; Mangan et al. 2010; McCarthy-Neumann and Ibáñez 2012; Suding et al. 2013; Müller et al. 2016; Rutten et al. 2016; Kempel et al. 2018). However, other studies detect negative PSF in dominant plant species (van der Putten et al. 1993; Olff et al. 2000) or no relationship between PSF and plant abundance (Reinhart 2012). Additionally, we still know relatively little about how PSF affect rare or threatened species despite the increasingly recognized need to understand whether biotic interactions limit plant abundance (Kempel et al. 2018). Specifically, if PSF affect species rarity and local species loss (Kulmatiski 2006; Kulmatiski 2018, 2019), PSF may differ between locally extinct versus extant taxa. We can test this hypothesis by comparing PSF between locally extinct species (i.e., a species that has disappeared from a particular area; Pimm et al. 2014) and closely-related extant species. This approach is akin to comparing PSF in native vs. non-native species, a common approach to test the potential role of PSF in invasion (see above), but instead tests the potential role of PSF in population decline and extirpation (Murray et al. 2014; Kempel et al. 2018).

Moreover, if climate change alters the PSFs driving plant abundance, temperature-mediated shifts in soil communities could affect local extinction events. We can test this hypothesis by comparing how locally extinct vs. extant species respond to soils exposed to experimentally-warmed temperatures. Such experimental approaches can provide strong tests of the hypothesized causes of local extinctions (Cahill et al. 2013). Although a warming experiment will not mimic the historical conditions experienced by locally extinct species during their decline, it can reveal whether a specific threat (here, warming-induced changes in PSF) is associated with decreased performance in locally extinct species, potentially leading to the development of successful reintroduction or management strategies where these species persist (Caughlin et al. 2019). This empirical approach can also address whether warming-induced changes in soil biota represent a contemporary threat to extant species and should be considered in conservation efforts (Averill et al. 2022).

Here, we use a traditional two-phase PSF experiment to examine whether warming-induced shifts in soil microbial communities affect plant-soil feedbacks differently in locally extinct vs. extant prairie species (although PSF can also be mediated by abiotic factors [Ehrenfeld et al. 2005]). We use two approaches to address this question: (1) quantifying plant performance in soils cultivated by a suite of species exposed to warmed vs. ambient temperatures (following Klironomos 2002) and (2) calculating the strength of net-pairwise feedbacks between confamilial pairs of locally extinct and extant species under warmed vs. ambient temperatures (following Bever 1994). Specifically, we ask: (1) Does locally extinct vs. extant species' performance differ when grown in soils conditioned by other species, and does soil warming affect these responses (Approach 1)? (2) Does soil warming affect the strength of net-pairwise PSF in confamilial pairs of locally extinct and extant prairie species (Approach 2)? If rising temperatures' effects on soil communities contributed to extirpation, we expect that locally extinct species' growth might be more negatively affected by the effects of soil warming on soil microbial communities than extant species.

Materials and methods

Experimental design

We conducted a soil transplant experiment to test how warming-induced shifts in plant-soil interactions affect plant performance and net-pairwise PSF in locally extinct and extant prairie taxa. In this approach, soil is conditioned in the field by plants and abiotic conditions (here, temperature), and the effect of those microbial communities on plant performance (e.g., growth and biomass) is subsequently assessed in the greenhouse. This method mirrors the "Phase I" (soil conditioning) and "Phase II" (testing) in a two-generation PSF experiment (Bever 1994). We then calculated PSF as net-pairwise feedback, I_s, between confamilial pairs of locally extinct and extant species. Finally, we estimated the ln-response ratio of each species in each temperature combination, which allows us to examine that species' relative growth in its own vs. its confamilial species' soil under ambient or warmed temperatures.

Phase I: Soil conditioning in the field

Soils were conditioned in the warming array at the W.K. Kellogg Biological Station (KBS). The warming array uses infrared heaters to elevate temperatures 3 °C above ambient temperatures, matching the mean estimate for climate warming in the Midwestern US by the end of the twenty-first century (0.3 °C-4.8 °C) (Stocker et al. 2013). It has run consistently from April through October (the growing season in Michigan) since 2008. Four plots are surrounded by six infrared ceramic heaters that evenly raise temperatures by 3 °C, while an additional four control plots are surrounded by six dummy heaters to control for shading effects. For more details on the warming array design, see Kimball et al. (2008).

In spring 2018, we planted seven species (four locally extinct and three extant; Table 1) into the background early successional old-field community in each plot. Selected species are all native, perennial forbs once found in Michigan prairies and savannas. Each confamilial (same plant family) pair consists of one species that became locally extinct in Kalamazoo County, Michigan, from 1890–2004 (Hanes and Hanes 1947; McKenna 2004), which was paired with the most closely-related species that still persists in the area ("extant") (for pairwise analyses, we treated the triplicate as two pairs). For more detail on historical plant extinctions in Kalamazoo County and species selection for experimental work, see Zettlemoyer et al. (2019, 2021). Seeds were sourced as locally to Michigan as possible and always from the Midwest (nurseries in order of selection: Michigan Wildflower Farm [Portland, Michigan], Naturally Native Nursey [South Bend, Indiana], Agrecol [Edgerton, Wisconsin], Prairie Moon [Winona, Minnesota]). We germinated the seven species in low-nutrient potting media (Sunshine Mix LP5, BFG Supply, Kalamazoo, Michigan) in the greenhouse before transplanting seedlings into random locations within each plot (all 20 cm apart) ($N = 10$ plants/species/plot $\times 8$ plots $\times 7$ species $= 560$ plants). These seedlings established and grew throughout the 2018–2019 growing seasons. The initial goal of this experiment was to test whether warming temperatures had more negative effects on locally extinct species (i.e., did warming play a role in local extirpation?), but also allows us to test whether future warming will have negative impacts on still-extant species.

Table 1 Experimental combinations of confamilial locally extinct (indicated by "LE") and extant prairie Phase II test species, which were each planted into Phase I soils cultivated by a conspecific ("home"), its confamilial pair ("away"), and three extant species common in Michigan prairies ("common"; *Monarda fistulosa, Ratibida pinnata,* and *Penstemon digitalis*). Authority is provided under "Phase II test species". Species abbreviations are provided in parentheses. Pairs of "Phase I home" and "Phase I away" species in a row represent phylogenetically-paired locally extinct and extant species

Family	Phase II test species	Phase I home species	Phase I away species	Phase I common species
Lamiaceae	*Monarda fistulosa* L. (MF)	*Monarda fistulosa*	*Pycnanthemum tenuifolium* (LE)	*Ratibida pinnata, Penstemon digitalis*
Lamiaceae	*Pycnanthemum tenuifolium* Schrad. (PT) (LE)	*Pycnanthemum tenuifolium* (LE)	*Monarda fistulosa*	*Ratibida pinnata, Penstemon digitalis*
Asteraceae	*Ratibida pinnata* (Vent.) Barnhart (RP)	*Ratibida pinnata*	*Ratibida columnifera* (LE)	*Monarda fistulosa, Penstemon digitalis*
Asteraceae	*Ratibida columnifera* (Nutt.) Woot. and Standl. (RC) (LE)	*Ratibida columnifera* (LE)	*Ratibida pinnata*	*Monarda fistulosa, Penstemon digitalis*
Plantaginaceae	*Penstemon digitalis* Nutt. ex Sims (PD)	*Penstemon digitalis*	*Penstemon hirsutus* (LE)	*Monarda fistulosa, Ratibida pinnata*
Plantaginaceae	*Penstemon digitalis* Nutt. ex Sims (PD)	*Penstemon digitalis*	*Penstemon pallidus* (LE)	*Monarda fistulosa, Ratibida pinnata*
Plantaginaceae	*Penstemon hirsutus* (L.) Willd. (PH) (LE)	*Penstemon hirsutus* (LE)	*Penstemon digitalis*	*Monarda fistulosa, Ratibida pinnata*
Plantaginaceae	*Penstemon pallidus* Small (PP) (LE)	*Penstemon pallidus* (LE)	*Penstemon digitalis*	*Monarda fistulosa, Ratibida pinnata*

Phase II: Testing the effects of microbial communities in the greenhouse

In May 2019, we grew 200 seedlings of each of the seven species for use as Phase II test seedlings in the greenhouse in low-nutrient potting media. Greenhouse daytime temperatures were kept within 2° of 27 °C (close to ambient conditions) throughout the summer (pers. comm., M. Hammond) (although warm greenhouse conditions could affect PSF results [Schittko et al. 2016]). After 12 weeks, one Phase II test seedling was subsequently transplanted into individual 40 mL Deepots with a 9:1 combination of sterilized sand and soil inoculum (see below). We did not sterilize potting media, so the potting media microbial community may have contributed to signals from the soil inoculum.

We collected field soil from each combination of species×temperature in June 2019 (N=7 species×2 temperatures (ambient vs. warmed)×4 plots/temperature=56 possible soil inocula). We used a 1.9 cm-diameter core to collect soil from 10 cm beneath three seedlings/species/plot (N=168 cores). Different cores were used to collect soil from each plot (i.e., there was no contamination between ambient vs. warmed treatments). However, between species, excess soil

was scraped off cores but not sterilized, so we note there could be cross-species contamination within a plot. We homogenized the soil by species and plot (i.e., soil from near three *Ratibida pinnata* seedlings from plot 1 was combined to make one soil inoculum). This mixing approach (Reinhart 2012) reduces potential differences in chemical and physical soil properties between plots. We sieved the soil (2 mm mesh) to remove rocks and roots. Soil was stored at 5 °C until planting (one week later).

We sterilized and filled D40 (40 mL) Deepots (Stuewe and Sons, Tangent, Oregon) with a 9:1 mixture of sterilized sand:soil inoculum (Bolin and Lau 2022). Sand (Quickrete All Purpose Sand, Atlanta, Georgia) was sterilized by autoclaving at 121 °C for 16 h. Following transplanting, individual Phase II test seedlings were inoculated with Phase I soil from under their conspecifics ("home" soil), soil from under their confamilial species ("away" soil), and soil from three extant species common to prairies ("common" soils; *Monarda fistulosa, Penstemon digitalis*, and *Ratibida pinnata*), under each temperature treatment (ambient vs. warmed) (Fig. 1, Fig. S1 in Supplementary Material) (N=5 possible inocula [1 conspecific/home, 1 confamilial/away, 3 common]×2 temperatures×4 plots/temperature×3 replicates×7

Phase II test species = 840 pots). We only used three replicates per species per plot because four plots/treatment were then combined to examine the effects of warming and soil species on performance. We tested each Phase II species grown in each common Phase I species' soil to examine plant performance in soil communities that they would likely have experienced in natural populations. For example, if *Ratibida columnifera* is the Phase II test seedling, it was inoculated with soil collected during Phase I from under *R. columnifera* (home), *R. pinnata* (away), *M. fistulosa* (common)*,* and *P. digitalis* (common). Note that for some species, the "common" soil is identical to the "away" soil (e.g., *R. columnifera* would be grown in soil from its confamilial *R. pinnata,* which also represents a common species). Once repeat confamilial and common soil species are accounted for, we had 765 pots.

We measured height (cm) on all seedlings after 10 weeks. We harvested plants and divided above- (stems and leaves) and belowground (roots) biomass.

We dried plants at 70 °C for 48 h before weighing aboveground, belowground, and total biomass (sum of above- and belowground biomass; mg).

Data analysis

Approach 1: Differences in performance between locally extinct and extant species under soil warming

To test whether plant performance is influenced by warming effects on soil microbial communities, we fit linear mixed models using the 'lme4' package (Bates et al. 2015) in R version 3.3.1 (R Core Team 2016). We used four separate response variables: height, total biomass, aboveground biomass, or belowground biomass. Height is positively correlated with all biomass metrics within a given species (Appendix Table S1).

We first examined whether Phase I soil treatments (soil conditioned by a conspecific, confamilial, or
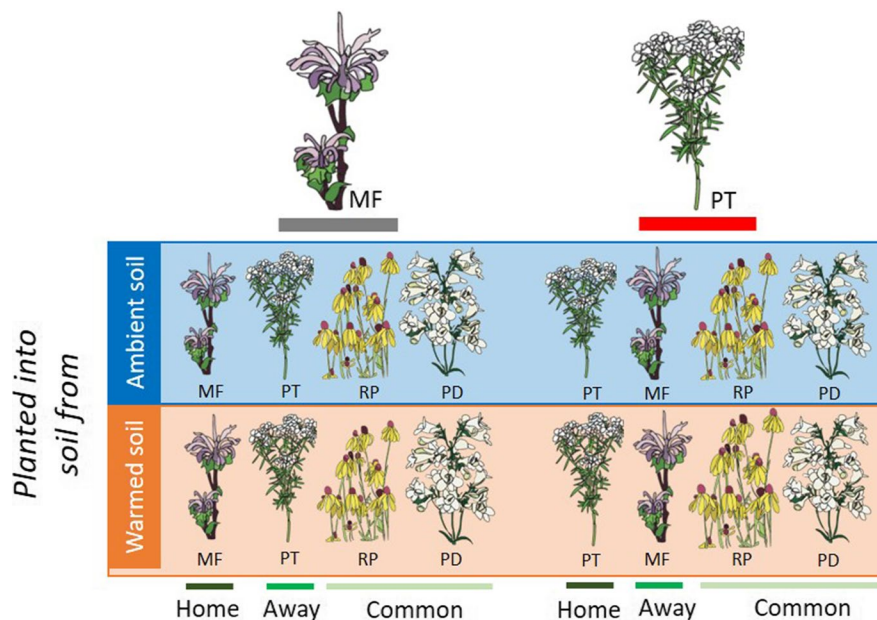

Fig. 1 Experimental design for one confamilial pair (Lamiaceae: extant *Monarda fistulosa* [MF] and locally extinct *Pycnanthemum tenuifolium* [PT]). Phase II test seedlings (top; gray = extant species [here, MF] and red = locally extinct species [here, PT]) were planted into Phase I soils exposed to ambient (blue boxes) or warmed (+3 °C, orange boxes), conditioned by a conspecific ("home", dark green), its confamilial pair ("away", medium green), and three extant species common in Michigan prairies ("common", pale green; common species include *Monarda fistulosa* [MF], *Ratibida pinnata* [RP]*,* and *Penstemon digitalis* [PD]; common species that are already represented as a home or away species within a pair [here, MF] are not included under common species). See Figure A1 for every possible combination of Phase II test species × Phase I soil species. Artwork by Blaire Bohlen

common species) influenced plant performance. Because our design was unbalanced, we confirmed homogeneity of variance between treatments with Fligner-Killeen's test (all $p > 0.2$). We included Phase II test extinction status (locally extinct vs. extant; hereafter "status"), Phase I soil treatment, soil temperature (ambient vs. warmed), and all interactions as fixed effects, and Phase II test species (nested in Phase II test status) and plot (nested in soil temperature) as random effects.

Because soil treatment effects (conspecific vs. away [confamiliar or common] soil) did not differ (Fig. S2) and we wanted to investigate how plant performance was affected by soil conditioned by locally extinct vs. extant species, we conducted similar models to those described above but included Phase I soil status (locally extinct vs. extant) instead of Phase I soil treatment. Here, we were interested in whether the performance of locally extinct vs. extant test seedlings differs in soils conditioned by locally extinct vs. extant species (i.e., a significant two-way interaction of Phase II test status × Phase I soil status) and whether this pattern varies with warming (i.e., a significant three-way interaction of Phase II test status × Phase I soil status × soil temperature).

Finally, because plant performance often depends on the specific species that conditions the soil (Reinhart 2012), we tested for Phase II soil species effects on performance. We included Phase II test status (locally extinct vs. extant), Phase I soil species, soil temperature (ambient vs. warmed), and all interactions as fixed effects, and Phase II test species (nested in Phase II status) and plot (nested in soil temperature) as random effects. Here, a significant two-way interaction of Phase II test status × Phase I soil species indicates that the growth of locally extinct vs. extant species differs between soils conditioned by different species. A significant two-way interaction of Phase II test status × soil temperature indicates that the growth of locally extinct vs. extant seedlings differs in ambient vs. warmed soils. Finally, a three-way interaction of Phase II test status × Phase I soil species × soil temperature suggests that the growth of locally extinct vs. extant species differs in ambient vs. warmed soils, but the direction and/or magnitude of response depends on what soil they were grown in. When the effect of an interaction was significant ($p \leq 0.05$), we used Tukey tests to examine differences between each level of Phase II test status, Phase I soil species, or

soil temperature. We did not examine whether performance of specific Phase II test species differed because this analysis would be confounded with species-specific differences in height or biomass.

Approach 2: Effects of soil warming on net-pairwise plant-soil feedback

We calculated net-pairwise PSF as the coefficient I_s of a significant interaction between confamilial species A and B (Bever et al. 1997):

$$I_s = G(A)_\alpha - G(A)_\beta - G(B)_\alpha + G(B)_\beta$$

where α is soil conditioned by species A, β is soil conditioned by species B, and G represents growth (or biomass). We calculated this separately for each confamilial pair (e.g., extant *Ratibida pinnata* and locally extinct *R. columnifera*). We conducted linear mixed models including Phase II test species, Phase I soil species, and soil temperature as fixed predictors and plot (nested in temperature) as a random effect. A significant two-way interaction of Phase II test species × Phase I soil species indicates a significant pairwise PSF between the two species. A significant three-way interaction between Phase II test species, Phase I soil species, and soil temperature indicates that pairwise PSF differs between ambient and warmed soils. Specifically, a positive pairwise PSF under warming would indicate that extant species likely did not coexist with its confamilial locally extinct species under warming temperatures, implicating pairwise PSF between these two species as a potential determinant of extirpation risk (whereas a negative pairwise PSF under warming implies possible coexistence under climate change). We assessed statistical significance using Type III ANOVA with Satterthwaite's approximation for denominator degrees of freedom using the 'lmerTest' package (Kuznetsova et al. 2015). We then estimated pairwise PSF under each temperature treatment using two separate models: one for ambient soils and another for warmed soils. Here, we included Phase II test species, Phase I soil species, and their interaction as fixed effects and plot as a random factor.

To quantify plant growth responses to conspecific vs. heterospecific soil, we estimated the natural log-response ratio for each species under each

temperature treatment (Bates et al. 2019; Bolin and Lau 2022). We calculated the log-response ratio as:

$$\ln \text{ } Response \text{ } Ratio = \ln(biomass_{conspecific \text{ } soil}) - \ln(biomass_{heterospecific \text{ } soil})$$

We then calculated standard error estimates for the ln-response ratios following Hedges et al. (1999). A positive ln-response ratio indicates that a species performed better in conspecific, or "home", soil.

Results

Does locally extinct and extant species' performance differ when grown in soils conditioned by other species, and do responses vary with warming (Approach 1)?

Phase II test seedlings generally performed better on extant species' soil relative to locally extinct species' soil using all performance measurements (Phase I soil status: biomass metrics all $p < 0.05$, growth $p < 0.1$; Table S2; Fig. 2).

Locally extinct test seedlings tended to grow taller than extant seedlings when planted into soils conditioned by a few specific extant species (Phase II test status × Phase I soil species: height $F_{6,702} = 1.88$,

$p = 0.08$; Table S3; Fig. 3). Specifically, locally extinct test seedlings grew 27% taller than extant test seedlings when grown in extant *Monarda fistulosa* soils (Tukey test for Phase II test status × Phase I soil species, $p = 0.005$), 39% taller in extant *Penstemon digitalis* soils (Tukey test $p = 0.007$), and 22% taller in extant *Ratibida pinnata* soils (Tukey test $p = 0.04$). Locally extinct test seedlings also grew 257% taller, on average, than extant test seedlings in soils conditioned by locally extinct *Pycnanthemum tenuifolium* (Tukey test $p < 0.0001$; Fig. 3). Meanwhile, locally extinct vs. extant test seedlings' height did not differ in soils conditioned by locally extinct *Ratibida columnifera, Penstemon hirsutus,* or *Penstemon pallidus.* Extant test seedlings' height did not differ in response to soil species. Height did not vary with soil temperature (Table S3).

Locally extinct and extant test seedlings differed in their aboveground biomass responses to warming effects on soil communities, but effects depended on the identity of the species that conditioned the soil (Phase II test status × soil temperature × Phase I soil species $F_{6,695} = 2.19$, $p = 0.04$; Table S3; Fig. 4). Extant test seedlings' aboveground biomass was 73% higher in warmed relative to ambient soils when grown in *Pycnanthemum tenuifolium* soil (Tukey test for Phase

Fig. 2 Effect of Phase I soil extinction status (soils conditioned by locally extinct vs. extant species) on (**A**) total biomass (mg), (**B**) aboveground biomass (mg), (**C**) belowground biomass (mg), and (**D**) height (cm) of Phase II test seedlings. Values are least square means ± standard error. *$p < 0.05$; §$p < 0.1$
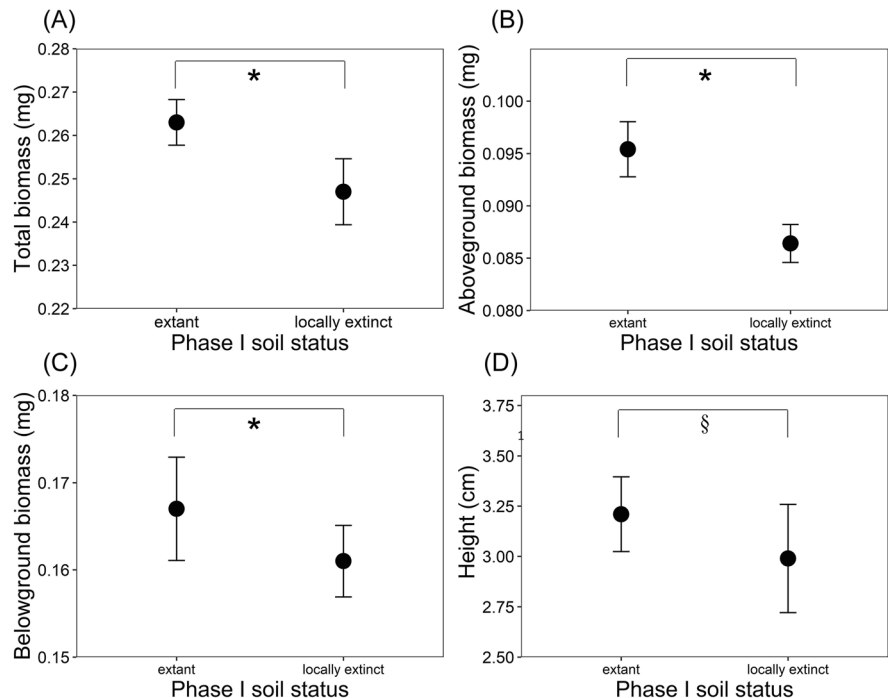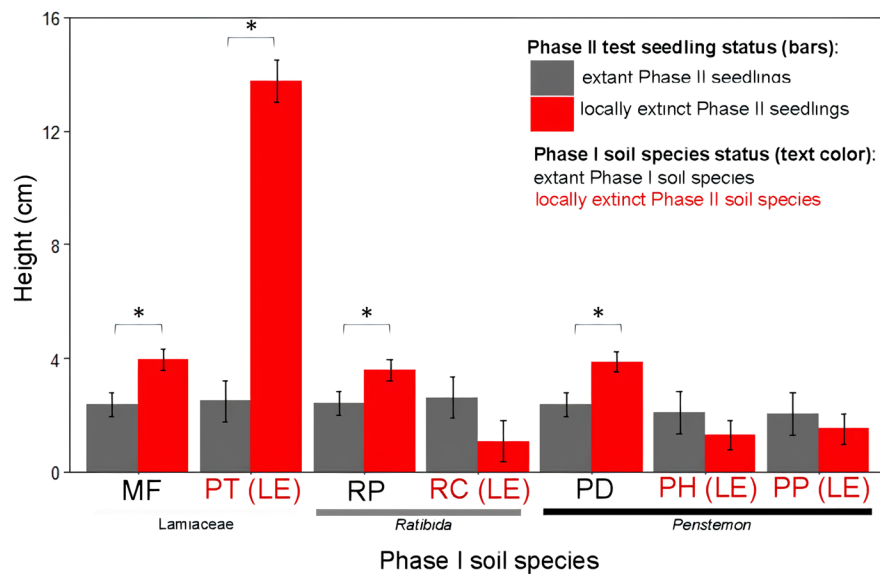
Fig. 3 Height (cm; least square means ± standard error) of locally extinct (red bars) vs. extant (gray bars) Phase II test seedlings (averaged across species) planted into soils conditioned by locally extinct vs. extant species (Phase I species; x-axis). Gray horizonal bars below each panel represent species pairs: Lamiaceae (light gray; MF = *Monarda fistulosa;* PT = *Pycnanthemum tenuifolium*), *Ratibida* (medium gray; RP = *R. pinnata;* RC = *R. columnifera*), and *Penstemon* (black; PD = *P. digitalis;* PH = *P. hirsutus;* PP = *P. pallidus*). LE by a species abbreviation indicates a locally extinct Phase I soil species (also in red text) within a pair. Black text indicates an extant Phase I soil species within a pair. Asterisks above the bars show a significant ($p < 0.05$) difference in height between locally extinct vs. extant Phase II test seedlings grown in a specific Phase I soil species, based on Tukey tests for Phase II test status × Phase I soil species (complete Tukey test results are provided in Supplementary Material 2)

II test status × Phase I soil species × soil temperature, $p = 0.04$). In contrast, extant test seedlings had 18% and 28% lower biomass in warmed relative to ambient soils when grown in *Ratibida pinnata* and *Penstemon pallidus* soils, respectively (Tukey tests both $p = 0.01$). Meanwhile, locally extinct test seedlings' aboveground biomass did not respond to temperature-induced shifts in soil communities, regardless of Phase I soil species.

Temperature influenced belowground and total biomass similarly in locally extinct and extant test seedlings, but effects again depended on the species that conditioned the soil (soil temperature × Phase I soil species: belowground $F_{6,694} = 2.39$, $p = 0.03$; total $F_{6,694} = 2.15$, $p = 0.04$; Table S3; Fig. S3). Belowground biomass increased by 78% in warmed vs. ambient soils conditioned by *Ratibida columnifera (*Tukey test for Phase I soil species × soil temperature, $p = 0.04$) but was 22% lower in warmed vs. ambient soils conditioned by *Penstemon hirsutus* (Tukey test $p = 0.07$). Trends were similar (but not significant) for total biomass.

Does warming affect the strength of net-pairwise PSF in confamilial pairs of locally extinct and extant prairie species (Approach 2)?

Warming did not affect net-pairwise PSF in any of the confamilial pairs studied here (Table S4; Fig. 5). We present net-pairwise PSF estimated using total biomass in the main text; net-pairwise PSF estimated using the other response metrics were qualitatively similar and are included in Appendix Figs. S4-6.

Estimated net-pairwise PSF differed significantly from zero in ambient soils in several cases, although effects were often marginally significant. Under ambient temperatures, *Monarda fistulosa* and *Pycnanthemum tenuifolium* demonstrated positive net-pairwise PSF (Fig. 5a; Fig. S5a). Both species had highest total and belowground biomass when grown in their own soils under ambient temperatures, whereas warmed temperatures resulted in no differences in total or belowground biomass (Fig. 5c; Fig. S5c). *Ratibida pinnata* and *R. columnifera* demonstrated weak negative net-pairwise
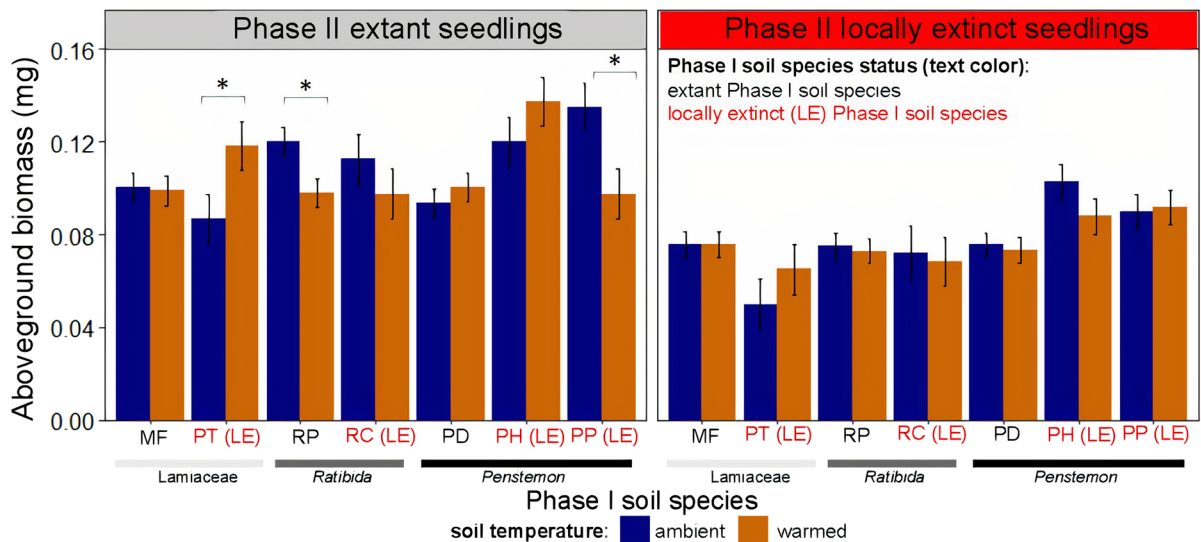
Fig. 4 Effect of Phase I soil species (x-axis) and soil temperature (blue = ambient; orange = warmed + 3 °C) on aboveground biomass (mg; least square means ± standard error) of Phase II extant (left; gray panel) and locally extinct (right; red panel) test seedlings (averaged across species). Gray horizonal bars below each panel represent species pairs: Lamiaceae (light gray; MF = *Monarda fistulosa;* PT = *Pycnanthemum tenuifolium*), *Ratibida* (medium gray; RP = *R. pinnata;* RC = *R. columnifera*), and *Penstemon* (black; PD = *P. digitalis;* PH = *P.* *hirsutus;* PP = *P. pallidus*). LE by a species abbreviation indicates a locally extinct Phase I soil species (also in red text) within a pair. Black text indicates an extant Phase I soil species within a pair. Asterisks above the bars show a significant ($p < 0.05$) difference in biomass between ambient vs. warmed soils conditioned by a specific Phase I soil species, based on Tukey tests for Phase II test status × Phase I soil species × soil temperature (complete Tukey test results are provided in Supplementary Material 2)

PSF under ambient temperatures (Fig. 5d; Fig. S5d). Specifically, extant *R. pinnata* tended to have higher total and belowground biomass in heterospecific soil relative to conspecific soil under ambient temperatures (Fig. 5f; S5f). *Penstemon digitalis* and *P. pallidus* also tended to demonstrate weak negative net-pairwise PSF under ambient temperatures (Fig. S4j), with both species tending toward greater aboveground biomass in heterospecific soils (Fig. S4l). Net-pairwise PSF never differed from zero under warmed temperatures, with one exception. *P. digitalis* and *P. hirsutus* showed weak negative net-pairwise PSF under warmed temperatures (Fig. S4g), largely due to *P. digitalis* having higher aboveground biomass in heterospecific relative to conspecific soil under warming (Fig. S4i).

Discussion

Rising temperatures can affect plant performance, abundance, and interactions with associated soil microbes, but relatively little is known about the effects of temperature on plant-soil feedbacks (Pugnaire et al. 2019; Beals et al. 2020) or the role of plant-soil feedbacks in local extinction events. We find that locally extinct prairie species' height is more responsive to soil biota under ambient temperatures, while extant species' aboveground biomass is more responsive to warming-induced changes in soil biota, although the direction of responses in both cases were species-specific. Warming had no effect on net-pairwise PSF in the prairie species studied here, suggesting that altered net-pairwise PSF between confamilial prairie species under climate change did not influence local extinction events in Kalamazoo County. Our work broadens our understanding of how climate-driven changes in soil conditions might affect plant performance under rising temperatures.

Locally extinct species are responsive to soil biota

Locally extinct species experienced increased growth when planted in several extant species' soil relative to
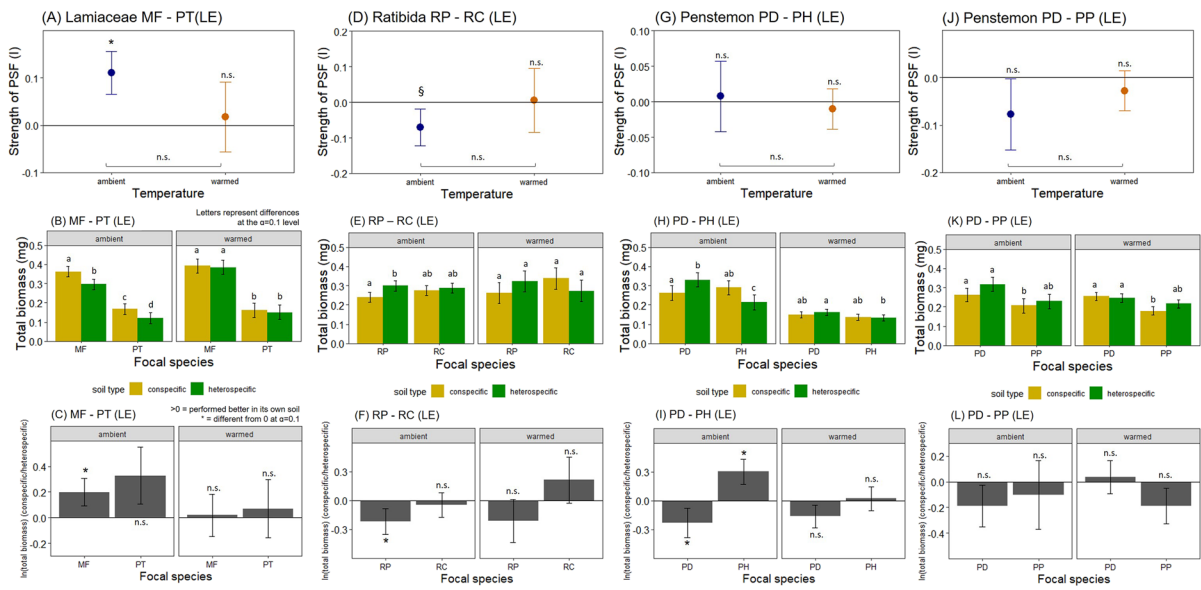
Fig. 5 Strength of net-pairwise plant-soil feedback (PSF), I_s, between (**A-C**) *Monarda fistulosa* (MF) and *Pycnanthemum tenuifolium* (PT) (Lamiaceae), (**D-F**) *Ratibida pinnata* (RP) and *R. columnifera* (RC), (**G-I**) *Penstemon digitalis* (PD) and *P. hirsutus* (PH), and (**J-L**) *P. digitalis* and *P. pallidus* (PP). LE by a species abbreviation indicates the locally extinct species within a confamilial pair. I_s is calculated as the strength of the interaction between confamilial species *A* and *B* under in soils exposed to ambient (blue) vs. warmed (+3 °C; orange) temperatures. Symbols above the points indicate a significant pairwise PSF within that temperature treatment; symbols at the bottom of the panel above brackets indicate a significant difference in pairwise PSF between ambient vs. warmed soil temperatures. *$p < 0.05$; •$p < 0.1$; "n.s." non-significant

($p > 0.1$). Middle row: Total biomass (mg) for each Phase II test species when grown in Phase I soils cultivated by conspecific (gold) vs. heterospecific (green) plants, split by ambient vs. warmed soils. Letters represent differences in total biomass between Phase II test species grown in conspecific vs. heterospecific soils at the $\alpha = 0.1$ level (Tukey tests for Phase II test species × Phase I soil species). Bottom row: ln-response ratio of total biomass when grown in conspecific vs. heterospecific soils and under ambient vs. warmed temperatures. A positive ln-response ratio indicates that a species performed better in its own, or "home", soil. Asterisks indicate that the ln-response ratio differs from zero ($\alpha = 0.1$). However, ln-response ratios do not differ among species or temperature treatments. All values are least square means ± standard error

soil cultivated by other locally extinct species. This is consistent with findings that rare species experience lower growth in their home soil or in soil conditioned by other rare species, possibly via accumulation of pathogens or presence of fewer mutualists (Klironomos 2002; Reinhart and Callaway 2006; Mangan et al. 2010; Kempel et al. 2018). Moreover, locally extinct species grew taller in some extant species' soil (specifically *Monarda fistulosa, Penstemon digitalis,* and *Ratibida pinnata*). This could be due to these extant species' associations with beneficial microbes like mycorrhizae (Vogelsang et al. 2006; Middleton et al. 2015), which could increase plant growth in soils conditioned by those species. Alternatively, species-specific pathogens might be at low abundance or decomposition could

be high in soils associated with these species. Without associated soil microbial community data, we cannot determine mechanisms underlying plant responses. We also note that any specialist soil biota associated with the locally extinct species could have disappeared concurrently (Dunn et al. 2009), potentially resulting in different patterns in our experiment using contemporary soils versus soil conditions when the locally extinct species persisted in this region. However, not sterilizing the potting soil and possible cross-species contamination in soil inocula could have influenced responses to soil biota, so results should be interpreted with caution. Altogether, our results support previous findings that soil biota can influence regional rarity, particularly in endangered (here, locally extinct) plants (Kempel et al. 2018).

Extant species are responsive to warming effects on soil communities

Extant species' aboveground biomass differed between soils exposed to ambient and warmed temperatures. However, the direction of temperature's effect on aboveground biomass depended on the Phase I species that conditioned the soil (Reinhart 2012; Kos et al. 2015). Specifically, extant test seedlings had lower biomass in warmed relative to ambient soils when grown in *Ratibida pinnata* and *Penstemon pallidus* soils. Climate change is generally expected to reduce plant biomass, in part due to reduced plant productivity under lower soil moisture (Zhao and Running 2010; Mora et al. 2015). All seedlings in the greenhouse received regular watering to keep soil moist. However, this region is expected to experience increased precipitation variability, heavier rainfall, and more severe growing season drought (Pryor et al. 2013; Tomasek et al. 2017), so future work might investigate whether moisture levels influence PSF in extant species to quantify future climate risk. Additionally, ongoing work in this system is investigating whether demographic responses to warming temperatures differ between locally extinct and extant species, which will help us determine potential "winners" and "losers" under climate change in this system. Alternatively, any symbionts, decomposers, or pathogens associated with *R. pinnata* and *P. pallidus* could demonstrate responses to warming that affect plant growth. In contrast, extant test seedlings had higher growth in warmed relative to ambient soils when grown in *Pycnanthemum tenuifolium* soil. Meanwhile, belowground biomass showed similarly idiosyncratic responses to soil warming and Phase I soil species, as it increased under warming in soils conditioned by one species (*R. columnifera)* but decreased under warming in soils conditioned by another (*P. hirsutus*). However, belowground biomass responses did not vary between extant vs. locally extinct test seedlings. Ultimately, our finding that warming-induced shifts in soil communities affect plant performance in (some) extant species suggests that climate change can influence the impact of microbial communities on plant growth, but the direction of responses may differ across species.

Notably, no locally extinct species responded to warming-associated shifts in soil biota. Kalamazoo County did not experience significant increases in mean annual temperature between 1890–2004 (Wang et al. 2016; Appendix Fig. S7). Our data suggest that these locally extinct species, which disappeared between 1890–2004, likely did not disappear due to local warming conditions. However, their lack of response to warming temperatures could threaten future population persistence in areas where they still persist. Alternatively, plant performance might vary based on trait differences between locally extinct and extant species (Cortois et al. 2016; Baxendale et al. 2014). The extant species studied here demonstrate traits associated with faster life-history strategies than locally extinct species: they have higher growth rates and thinner leaves (higher specific leaf area) than locally extinct species (unpublished data, M.Z.; Fig. S8; Wright et al. 2004). Such fast-growing species can produce high-quality inputs to soils via decomposition, promoting rapid nutrient cycling and increasing nutrient availability, which can also increase with warming (de Vries et al. 2012) (although warmed plots here do not have significantly higher soil nitrogen content than ambient plots; Fig. S9). Given that plant traits can influence plant competitive ability (Violle et al. 2009) and soil conditions, future studies should investigate whether differences in plant traits influence plant growth responses to climate-driven changes in soil communities (Xi et al. 2021).

Temperature does not affect net-pairwise plant-soil feedback

We detected no overall effect of temperature on net-pairwise PSF (I_s) in the prairie species studied here, similar to previous findings that PSF are insensitive to temperature in the Netherlands (van Grunsven et al. 2010). A recent meta-analysis also found no overall effect of environmental context (including temperature) on PSF (Beals et al. 2020). There are several hypotheses for why we did not find a significant effect of temperature on net-pairwise PSF. First, we transplanted plants as seedlings, but plants may be more susceptible to pathogens earlier in development (Develey-Rivière and Galiana 2007). Alternatively, if the activity of both pathogens and mutualists increases under warming, there may be no detectable net negative or positive effect on PSF (Fry et al. 2018). Here, temperature appeared to weaken net-pairwise PSF (PSF closer to zero) in all four

pairs, although this was not significant, potentially due to limited statistical power to test net-pairwise PSF. Similarly, drought neutralizes negative PSF in two grassland forbs, *Scabiosa columbaria* and *Sanguisorba minor* (Fry et al. 2018), and warming neutralizes positive PSF in *Dactylis glomerata* (Heinze et al. 2017). The weakening effect of temperature on net-pairwise PSF observed here varied in direction across species pairs (i.e., temperature did not consistently make net-pairwise PSF more positive or negative). In the Lamiaceae, net-pairwise PSF under ambient conditions were strongly positive. This is consistent with their rapid growth in the field (pers. obs., M.Z.). Warming weakened positive net-pairwise PSFs in the Lamiaceae, suggesting that temperature might limit the performance and abundance of these two mint species. *Penstemon digitalis* and *P. hirsutus* differed in performance under ambient conditions – *P. digitalis* performed best in heterospecific soil while *P. hirsutus* performed best in its own soil – but temperature weakened these effects in both species, resulting in similar performance in warmed soils. In contrast, increased temperature tended to correlate with somewhat more positive net-pairwise PSFs in the remaining two species pairs. In both extant species within these pairs, *Ratibida pinnata* and *Penstemon digitalis,* performance was highest in heterospecific, ambient soils. However, performance was similarly low in warmed soils, regardless of conditioning by hetero- or conspecific species, suggesting that these extant species could be at risk of decreased performance under warming conditions.

Conclusions

Our results indicate that locally extinct vs. extant species vary in their responses to climate change-mediated shifts in soil communities (although abiotic factors could drive these patterns as well; without microbial or additional soil data, understanding the precise mechanisms underlying weakening net-pairwise PSF under warming is beyond the scope of this study). Extant species' aboveground biomass was sensitive to warming-induced shifts in soil biota, although the direction and magnitude of temperature's effects varied across species. Locally extinct species' height responded to the soil community

cultivated by different species, generally performing worse in soils associated with other locally extinct species. However, they only responded to differences in soil biota under ambient temperatures. Finally, we detected no overall effect of temperature on net-pairwise PSF between confamilial pairs of locally extinct and extant prairie species. Our findings have two key implications for prairie conservation. First, soil biota could have influenced local extinction, independently of temperature. In this case, efforts to reintroduce these extirpated species into local prairie restorations or management in their extant range should consider plant-soil interactions. Second, temperature effects on soil microbial communities might affect contemporary prairie plant performance under climate change, indicating that prairie conservation and restoration efforts may need to consider potential effects of warming-induced shifts in microbial communities when developing conservation priorities.

Author contributions M.A.Z. conceived the study and conducted statistical analyses. K.C.-R. led field work and data collection. Both authors contributed to study design and wrote the manuscript.

Data availability All data for this study are available in the Figshare Repository https://doi.org/10.6084/m9.figshare.19666 392.

Declarations

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