Received: 28 January 2024 | Accepted: 5 October 2024

DOI: 10.1111/1365-2745.14443

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Climate-driven shifts in plant–soil feedback of a perennial grass species

Anna Florianová[1] | Zuzana Münzbergová[1,2]

[1]Institute of Botany of the Czech Academy of Sciences, Průhonice, Czech Republic

[2]Department of Botany, Faculty of Science, Charles University in Prague, Praha 2, Czech Republic

Correspondence
Anna Florianová
Email: anna.florianova@ibot.cas.cz

Funding information
Grantová Agentura České Republiky, Grant/Award Number: GAČR 22-00761S

Handling Editor: Paul Kardol

Abstract

1. Plant–soil feedback (PSF) plays a key role in determining the composition of plant communities, and understanding the impact of the ongoing climate change on PSF is thus crucial for predicting the consequences of climate change for ecosystems.
2. Here, we conducted a growth-chamber experiment to examine possible climate-driven shifts in PSF of a perennial grass, *Festuca rubra*, originating from two climatically distinct sites, by using all factorial combinations of soil biota origin, plant origin, and cultivation climate.
3. Soil biota generated more negative PSF effects when grown under the climatic conditions of their origin. This observation suggests that soil biota, especially soil pathogens, are well adapted to their local climate, exhibiting greater efficiency in suppressing plant growth within their climatic conditions.
4. All plants, regardless of their origin, exhibited less negative PSF (expressed as relative performance in live vs. sterilized soil) when grown under warmer climate than under colder climate, likely due to positive effects of increased activity of soil decomposers and enhanced nutrient cycling.
5. Plants showed negative PSF when grown with local soil biota under home climate, and the negative PSF disappeared when plants were grown with foreign biota or in away climates. This suggests that any disruption of the established plant-soil-climate interactions may lead to the release of plants from negative PSF, potentially destabilizing plant communities.
6. *Synthesis*. Our results highlight the adaptions of soil biota to their native climate as key drivers of plant–soil feedback interactions and suggest that climate change could significantly alter these interactions, potentially leading to new plant community dynamics. These findings emphasize the need for further investigations to unravel the mechanisms driving these responses and evaluate their consequences for ecosystem resilience in the face of climate change.

KEYWORDS
global climate change, grasslands, nitrogen cycle, plant–soil interactions, precipitation gradient, soil microbial communities

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Author(s). *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Plant–soil feedback (PSF)—a process where plants alter the biotic and abiotic properties of soil they grow in, which subsequently influences the performance of plants grown in that soil in the future (Bever et al., 1997)—has been recognized as an important driver of plant community assembly and ecosystem functioning (Bardgett & van der Putten, 2014; Reynolds et al., 2003). High rates of recently observed as well as expected changes in temperature and precipitation regimes (IPCC, 2014) are likely going to affect the distribution of soil microbes and plants and modify the ways plants and soil interact (van der Putten et al., 2016). Understanding the impact of climate change on PSF is thus crucial for predicting the consequences of climate change for ecosystems and for providing avenues to mitigate its consequences in natural and applied systems.

Plants exhibit local adaptations to specific climatic conditions (Anderson & Song, 2020; Nicotra et al., 2010; Sammarco et al., 2022) and their associated soil biota (Crémieux et al., 2008; Johnson et al., 2010; Pánková et al., 2014). At the same time, soil biota can adapt to specific climate and to local plant genotypes (Johnson et al., 2010; Tack et al., 2012). These adaptations, along with changes in the composition of soil biota communities in response to genetic or species composition of local plant communities, shape the outcome of plant–soil interactions (Blanquart et al., 2013; Hoeksema & Forde, 2008; Kulmatiski et al., 2008; van der Putten et al., 2013). The distribution of both plants and their associated soil biota is largely driven by spatial variation in climatic conditions (Blankinship et al., 2011; Zhou et al., 2020). It may thus be expected that climate change will affect PSF as well (van der Putten et al., 2016). Indeed, Hassan et al. (2022) in their meta-analysis showed that drought and warming can induce context-specific shifts in PSF, which are dependent on plant functional groups, life history traits and experimental conditions.

Climate change may lead to novel or altered interactions between plants and soil biota (Bardgett & Wardle, 2010) due to differences in their respective rates and mechanisms of adaptation to novel conditions (van der Putten et al., 2009). For example, in case of asynchronous range shifts, that is in a situation when soil biota migrate faster to the new environment than plants (or oppositely), plants of a certain climatic origin encounter soil biota of a different climatic origin. This can disrupt established negative PSF caused by specialized antagonistic microbes in the plant's original range (Engelkes et al., 2008; van Grunsven et al., 2007), while a lack of adapted mutualistic organisms in new ranges can constrain plant growth (Nunez et al., 2009). The environmental context also plays a crucial role in shaping PSF (De Long et al., 2019; van der Putten et al., 2016). Previous studies manipulating cultivation conditions have shown that temperature and moisture levels can affect soil biota composition and activity (Deveautour et al., 2018; Heinze et al., 2017; Siebert et al., 2019), as well as plant biomass allocation and root architecture (Bergmann et al., 2016; Cortois et al., 2016), thereby altering the intensity with which plant roots interact with the soil (Aldorfova & Munzbergova, 2019; Duell et al., 2019; Florianova & Munzbergova, 2018; Fry et al., 2018; Kaisermann et al., 2017). Importantly, individual groups of soil biota may differ in their sensitivity to climatic conditions as well as in the degree of co-adaptation with plants. Generally, soil pathogens are more specialized and show a higher degree of co-adaptation with plants than soil mutualists (Molina & Horton, 2015; Smith & Read, 2008). It can thus be expected that disrupting established plant–soil interactions will lead to less negative overall PSF.

To comprehend how climate change affects plants through changes in soil biota, it is essential to simultaneously manipulate soil origin, plant origin and climatic conditions in all factorial combinations. Several double interactions within this triple framework have been explored, such as the genetic differentiation and phenotypic plasticity of plant populations in response to climate (Hamann et al., 2016; Munzbergova et al., 2017; Nicotra et al., 2010; Valladares et al., 2014), the specificity of soil biota (Cardinaux et al., 2018; Koorem et al., 2020; Pankova et al., 2011; Van Nuland et al., 2017) or climate dependency of soil biota (von Holle et al., 2020). However, very few studies (to our knowledge only Remke et al., 2022 and Aares et al., 2023) have so far manipulated all three components of the climate-plant-soil framework.

In this study, we investigated the interaction between soil biota origin, plant origin, and cultivation climate using *Festuca rubra*, a perennial grass dominating alpine grasslands in large parts of Europe, as a model. We conducted a two-phase growth chamber experiment, examining the PSF (here in two versions as recommended by Brinkman et al. (2010)—biotic PSF defined as relative performance of plants when grown in live vs. sterile soil, and whole-soil PSF as relative performance of plants when grown in self-conditioned vs. community-conditioned soil) of *F. rubra* originating from two climatically distinct sites, when grown with local or foreign soil biota (i.e. soil biota originating from either the 'home' or 'away' site), cultivated in climate representing the climate of either the 'home' or 'away' site. We assessed *Festuca's* PSF under all treatments and investigated the changes in soil chemistry following soil conditioning to explain the observed differences in the PSF. We tested the following hypotheses:

- H1: Soil pathogens are more strongly adapted to their climate of origin compared to soil mutualists, and therefore soil biota generates more negative PSF effects in their home than in away climate.
- H2: Plants are adapted for growth in their respective climates of origin, therefore perform better and show less negative PSF in home than in away climate.
- H3: The degree of co-adaptation between plants and soil pathogens is higher than between plants and soil mutualists, making PSF effects more negative when plants are grown with their local soil biota (i.e. soil biota originating from the same site as the plants) than when grown with foreign soil biota (i.e. biota from the other site).
- H4: Due to the above-mentioned mutual adaptations of plants and soil and adaptations of both of these components to climate,

PSF is expected to be most negative when plants are grown with their local soil biota under their home climate.

2 | MATERIALS AND METHODS

2.1 | Study system and material collection

We used a predominantly clonally reproducing grass species, *Festuca rubra* L., forming a dominant part of alpine grasslands in large parts of Europe, as a model species. Thanks to being dominant in ecosystems highly threatened by climate change, studying this species is likely to provide important knowledge on functioning of whole alpine grassland systems. This species is a perfect model also because it is known to strongly interact with soil biota (Henneron et al., 2020; Kut'akova et al., 2023; Wubs & Bezemer, 2018) and its populations are strongly adapted to climatic conditions and also show high levels of phenotypic plasticity (Kosova et al., 2022; Munzbergova et al., 2017). In addition, we previously used *F. rubra* as a model species to study species adaptations to changing climate in the same area (e.g. Munzbergova et al., 2017, 2019; Munzbergova & Hadincova, 2017; Stojanova et al., 2019; Surinova et al., 2019). There is thus considerable background knowledge of the study system that provides an important basis for interpretation of our results.

The study material was sampled at two calcareous grassland sites in southern Norway with contrasting climates, here referred to as a cold, wet site (mean summer temperature 7.5°C, annual precipitation 2700 mm) and a warm, dry site (mean summer temperature 11.5°C, annual precipitation 600 mm). Even though the warm, dry site is significantly drier than the cold, wet site and is on the very end of the precipitation gradient within the studied area, it has sufficient moisture levels and the plant communities there are not drought limited. Both sites have similar grazing regime and history, bedrock, slope and exposure, and host grazed intermediate-rich grassland communities dominated by *F. rubra* (Klanderud et al., 2015; Meineri et al., 2014).

In July 2020, we collected plant and soil material at each of the sites and transported them to the Czech Republic where we immediately started the experiments. At each site, we collected 10 individuals of *F. rubra*, at least 1 m apart from each other to avoid collecting plants belonging to the same clone. Within close proximity of each clone, we collected a soil sample of approximately 2 L to serve as soil inoculum after sieving on a 5 mm mesh. In total we thus had 20 individuals of *F. rubra* and 20 samples of field soil inoculum, 10 from each site.

In addition, we selected three other species from each site to grow a control community and collected 10 individuals of each of the species. The selected species were one grass species per site (*Anthoxanthum alpinum* at the cold, wet site, and *A. odoratum* at the warm, dry site) and two forb species per site (*Alchemilla* sp. at each site, *Veronica alpina* at the cold, wet site, and *V. officinalis* at the warm, dry site). We used different species of the same genera for the communities from each site as *F. rubra* is one of the very few species occurring in large abundance at both sites.

2.2 | Experimental design

We performed a two-phase growth-chamber PSF experiment. In the first (conditioning) phase, soil conditioned by *Festuca* and soil conditioned by a grassland community without *Festuca* (consisting of *Anthoxanthum*, *Alchemilla* and *Veronica* species) were prepared. The soil was always conditioned by plants from a given site in soil containing live inoculum from the same site when cultivated under climate corresponding to the same site ('home' climate). In the second (feedback) phase, we studied performance of *F. rubra* originating from each of the sites when grown with soil biota from the same ('local') or the other ('foreign') site, in self-conditioned or community-conditioned soil, in the 'home' and 'away' climate, either in sterile or in live soil (Figure 1).

2.2.1 | Conditioning phase

The aim of the conditioning phase was to prepare the soil, conditioned by the species, for the upcoming feedback phase. The conditioning phase ran from August 2020 to May 2021, that is 10 months. To set up the conditioning phase, we used a 2:2:1 mixture of topsoil, sand and compost as background soil (see Appendix S1, Table S1.1 for particle size and chemical composition of the soil). The topsoil was collected at a mesic grassland in the Czech Republic because the needed amount of soil could not be transported from Norway. We, however, tried to find soil with as similar characteristics to the soil at the study sites as possible. The background soil was sterilized by gamma-irradiation, mixed with soil inoculum from our study sites in a 9:1 ratio and used to fill 4-L pots (16 × 16 × 16 cm). Each of our 10 inoculum samples per site was used in two pots—one to be *Festuca*-conditioned and one to be community-conditioned. For each site, we thus had 20 pots, in total resulting in 40 4-L pots. The pots to be *Festuca*-conditioned were planted with three ramets (single tillers originating from the same genotype, able of independent existence) of *F. rubra*. The pots to be community-conditioned were planted with a community of *Anthoxanthum*, *Alchemilla* and *Veronica* (one individual each). We always used plants originating from the same site as the soil inoculum, and we placed the pots in a growth chamber simulating climate of the same site.

We used two growth chambers (Growth Unit 550, PSI—Photon System Instruments) which were set to simulate field conditions at the two sites throughout the vegetative season to cultivate the plants. The regimes in the growth chambers were derived from the temperature course at the two sites as described by Munzbergova et al. (2017), but avoiding night frosts due to technical limitations of the growth chambers. The regime corresponded to conditions of the peak of the vegetation season. The maximum temperature in the cold, wet growth chamber was set to 15°C, and in the warm, dry

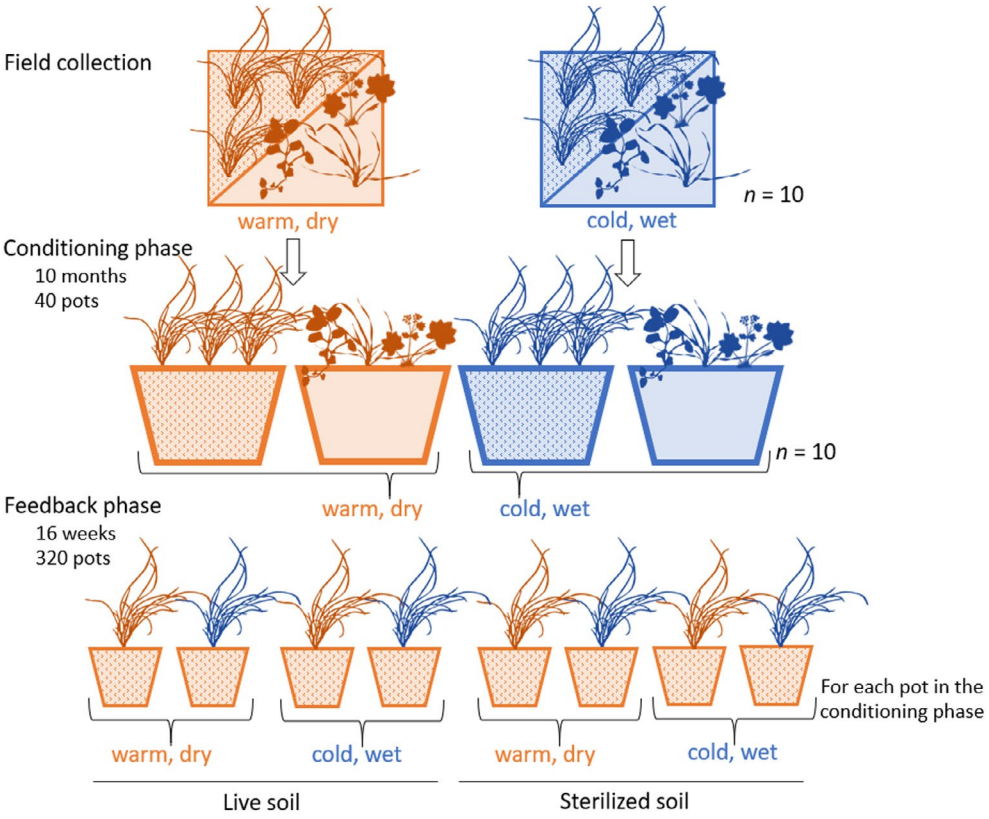


FIGURE 1 A schematic diagram of the experimental design. Soil and plants were collected from a cold, wet (blue) and a warm, dry (orange) site, and conditioned by *Festuca* (thin grass silhouettes; dotted soil) or by a community (*Anthoxanthum*, *Alchemilla* and *Veronica*; forb and thick grass silhouettes; unpatterned soil). In the feedback phase, *Festuca* from each site was grown in *Festuca*-conditioned or community-conditioned soil from each site, sterilized or live, under cold, wet or warm, dry climate.

growth chamber to 25°C. Minimum temperature in both chambers was set to 8°C. Both regimes had 16 h of full light (06.00–22.00 h) and 4 h of full dark with a gradual change in light availability in the transition between the light and dark period over 2 h. The plants were watered twice a week with 200 mL of tap water. The amount of water was determined so that soil in the pots in the warmer chamber was moderately wet most of the time and the plants did not suffer from drought stress, while soil in the colder chamber was constantly moist, on the verge of being waterlogged. The pots were weeded when needed.

After 10 months, the conditioning phase was terminated. From each pot, we took a soil sample for analysis of soil available nitrogen to assess possible differences in nitrogen cycling among the two systems. Each sample consisted of soil collected from each of the four corners of the pot in full depth using a tubular soil sampler with diameter of 6 mm. Soil samples were kept at −20°C until the analyses. Concentration of plant available nitrogen (NH_4^+, NO_3^- and NO_2^-) was recorded in the filtrate of 5 g of soil with 50 mL of 0.5 M K_2SO_4 solution by flow injection analysis with spectrophotometric detection (Ammerman, 2001; Egan, 2001). The analyses were performed by the Analytical Laboratory of the Institute of Botany, Czech Academy of Sciences.

In each *Festuca*-conditioned pot, we cut 20 single ramets of similar size, each with three leaves and without visible signs of initiating flower buds from the tussocks, and placed them into small plastic cups filled with water to set roots, to get plant material to be used in the feedback phase. The remaining above-ground biomass, as well as the biomass of the three species in the community-conditioned pots, was then harvested and larger roots were manually removed from the soil. The remaining above-ground biomass, as well as the biomass of the three species in the community-conditioned pots, was then harvested and larger roots were manually removed from the soil and washed. Both above- and below-ground biomass was dried and weighed. For *Festuca*-conditioned pots, we calculated the average dry mass of one ramet and used this value for estimating the total above-ground biomass of *Festuca* including the 20 ramets that were cut prior to weighing. Soil left in each pot after harvesting the plants was divided into two halves, one half was sterilized using gamma irradiation and the other half was left intact.

2.2.2 | Feedback phase

Following the harvest of the conditioning phase, the soil from each pot from the conditioning phase was used to fill eight 200 mL pots (5 × 5 × 8 cm) used in the feedback phase, four with sterilized and four with live soil. The pots with sterilized soil were excessively watered (5 × 200 mL of water within 3 days) before planting any plants

into them to wash out nutrients that were released into the soil during sterilization. This method of washing out nutrients was chosen so that the levels of available nitrogen did not significantly differ between sterilized and non-sterilized soils (tested prior to setting up the feedback phase). While the pots may seem quite small, our model species is a tussock grass of small stature and slow growth. According to our previous experiments on *F. rubra* (e.g. Kosova et al., 2022; Munzbergova et al., 2017) we know that this pot size is suitable for experiments of a similar duration. Also, the pots were not filled by the plant at the time of harvest, and we are thus confident that the results of the experiment are not affected by pot size.

The feedback phase was initiated by planting into each pot a single ramet without any rhizomes and with roots developed in water over 2 weeks prior to planting. In such a way, we were able to use the same genotypes in the feedback phase as in the conditioning phase, but not transfer any soil biota on plant roots among the treatments. Ramets that died within the first 2 weeks were replaced.

Each of the pots in the feedback phase was planted with a single ramet of *F. rubra*. Half of the eight pots originating from one large pot from the conditioning phase, specifically two pots with sterilized and two pots with live soil, were planted with a plant originating at the same site as the soil inoculum and as the plants used to condition the soil. The other two pots with sterilized and two pots with live soil were planted with a plant originating at the other site than the inoculum and conditioning plants. One of each two pots was then always placed into a growth chamber simulating the home climate and one into a growth chamber simulating the away climate. From each large pot in the conditioning phase, we thus had 8 small pots in the feedback phase: 2 soil sterilizations × 2 plant origins × 2 cultivation climates. The conditions in the growth chambers corresponded to the conditions of the peak vegetation season used in the conditioning phase and were retained over the whole period. In total, we had 320 pots in the feedback phase: 2 soil origins × 2 conditioning species (*Festuca* vs. community) × 2 soil sterilizations × 2 plant origins × 2 cultivation climates × 10 replicates.

The feedback phase lasted for 16 weeks, from May 2021 to September 2021. After the 16 weeks, right before the harvest of the feedback phase, we measured maximum photosystem II efficiency (*Fv*/*Fm*) to assess the physiological status of the plants. The *Fv*/*Fm* value provides information on overall photosynthetic efficiency (Jahns & Holzwarth, 2012; Tang et al., 2007). In healthy leaves, the value is usually close to 0.8, lower value indicates that a proportion of PSII reaction centre is damaged or inactivated, so called photoinhibition, and is commonly observed in plants with reduced vitality under stress (Baker & Rosenqvist, 2004; Jahns & Holzwarth, 2012). *Fv*/*Fm* was measured on three fully developed undamaged leaves of each plant using FluorPen FP-100 MAX/USB (Photon System Instruments, Drásov, Czech Republic) in dark-acclimated (1 h) plants (Maxwell & Johnson, 2000). All plants were measured between 12 AM and 2 PM to minimize differences between plants due to daytime. An average value of the three measurements per plant was used in further analyses. After measuring the Fv/Fm, we harvested the plants and carefully washed their roots. We recorded the number of ramets, divided the plants into above-ground and below-ground biomass, dried them at 60°C for 48 h and weighed them.

After the harvest, we determined the concentrations of carbon, nitrogen, and phenolic compounds in root biomass of eight out of the 10 replicates per treatment to assess changes in plant chemistry. Carbon and nitrogen concentrations were determined by the Analytical Laboratory of Institute of Botany, Czech Academy of Sciences, by methods of Ehrenberger and Gorbach (1973) using CHN catalyst (Carlo Erba NC 2500). The concentration of total phenolic compounds was determined spectrophotometrically by the Folin–Ciocalteu method similarly as in Ainsworth and Gillespie (2007). We homogenized 0.03 g of root biomass and incubated it in 1.5 mL 80% methanol overnight. We incubated supernatant with Folin–Ciocalteu reagent for 10 min in the darkness, then we added 700 mM Na_2CO_3 and incubated for 10 min. We measured the absorbance of the reaction mixture at 765 nm in a microplate reader in Multiskan SKY (Thermo Fisher). We calculated total phenolics as gallic acid amount in the supernatant solution/the amount of gallic acid (mg) in a unit of dry weight (g) using a regression curve of gallic acid standards and absorbance at 765 nm.

2.3 | Data analyses

To assess the effect of treatments on *Festuca* performance in the feedback phase, we calculated two PSF indices. The first index, further referred to as biotic PSF index, was calculated as $\ln\frac{x_{live}}{x_{sterile}}$, where x_{live} is performance of each plant when grown in live soil and $x_{sterile}$ is performance of a plant grown in a paired pot with identical treatment (i.e. plant and soil of the same origin, the same conditioning species, and the same cultivation climate), but sterilized soil, as recommended by Brinkman et al. (2010). An index value of less than zero indicates a negative biotic PSF, meaning the plant performs worse in live soil than in sterilized soil, while a value greater than zero indicates a positive biotic PSF, meaning the plant performs better in live soil than in sterilized soil. The other PSF index, further referred to as whole-soil PSF index, was calculated as $\ln\frac{x_{Festuca}}{x_{community}}$, where $x_{Festuca}$ is performance of each plant when grown in *Festuca*-conditioned (i.e. conspecific) soil and $x_{community}$ is performance of a plant grown in community-conditioned (i.e. heterospecific) soil under the same treatment. Both indices were calculated separately for number of ramets (used here as a proxy for plant fitness), biomass (sum of above-ground and below-ground biomass), root-shoot ratio, *Fv*/*Fm*, root phenols, root nitrogen (N), and root carbon to nitrogen ratio (C:N). All analyses were performed separately on the two indices as well as directly on *Festuca* performance data from the feedback phase.

The data on *Festuca* performance in the feedback phase and the two PSF indices were analysed using linear mixed effect models [R-package lme4 (Bates et al., 2015), R-package lmerTest (Kuznetsova et al., 2017) for estimating *p*-values] with blocks (i.e. eight pots in the feedback phase that were derived from one inoculum sample) as random effects. Each measure of plant performance as well as both biotic and whole-soil PSF indices for each measure of plant

performance were used as dependent variables. To directly test our hypotheses, we used the following as explanatory variables: Soil-Climate (i.e., climatic conditions of the soil biota's home vs. away climate site), Plant-Climate (i.e., climatic conditions of the plants' home vs. away site), and Plant–Soil (i.e., plants grown with local vs. foreign soil biota). In addition, soil conditioning (*Festuca* vs. community-conditioned soil), soil sterilization and their interactions with the above-mentioned explanatory variables were considered as independent fixed factors where applicable (only soil conditioning in analyses of biotic PSF indices, only soil sterilization in analyses of whole-soil PSF indices, both in analyses of raw plant performance data). We also repeated the analyses with soil origin (warm, dry site vs. cold, wet site), soil conditioning (conditioned by *Festuca* vs. community), soil sterilization, plant origin (warm, dry vs. cold, wet), cultivation climate (conditions in the growth chamber simulating climate of the warm, dry vs. cold, wet site), and their interactions as explanatory variables. These analyses provided qualitatively the same results as the first analyses but were harder to interpret in context of our hypotheses, and we therefore only present them in the appendix (Appendix S3, Table S3.1, Figures S3.1–S3.5). Similarly, we present results of the analyses on raw plant performance data and whole-soil PSF indices in the appendix (Appendices S2 and S4), and only refer to them throughout the manuscript when needed. Only the results of the analyses on biotic PSF indices are shown in full in the main results section of the paper.

To test for differences in soil NH_4^+, NO_3^- and NO_2^- levels after the conditioning phase between the treatments we used a linear mixed effect model with square-root transformed values of NH_4^+, NO_3^- and NO_2^- as dependent variables. Conditioning species (*Festuca* vs. community), site (i.e. origin of soil inoculum and conditioning plants grown under their home climate), and their interaction were used as explanatory variables. Inoculum sample (i.e. soil from one spot at the natural site used as field inoculum in one pot conditioned by *Festuca* and one pot conditioned by the community) was used as a random effect.

All analyses were performed using R ver. 4.1.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Plant performance after the feedback phase

3.1.1 | H1: Adaptations of soil biota to climate

Soil-Climate (i.e. soil biota grown in their home vs. away climate) had a marginally significant effect on biotic PSF index for biomass and significant for root-shoot ratio (Table 1). Both PSF for biomass and PSF for root-shoot ratio were more negative when soil biota were in their home climate than in the away climate (Figure 2). We also detected a marginally significant effect of the interaction between Soil-Climate and soil conditioning on number of ramets (Table 1). Under soil's biota home climate, *Festuca* showed a higher biotic PSF

TABLE 1 Results of linear mixed effect models testing the effect of soil conditioning (*Festuca* vs. community-conditioned soil), Soil-Climate (soil biota grown under home vs. away climate), Plant-Climate (plants grown under home vs. away climate), Plant-Soil (plants grown with local vs. foreign soil biota) and their interactions with soil conditioning on biotic PSF index (ln performance in live soil/in sterilized soil) for number of ramets, biomass, root-shoot ratio, *Fv/Fm*, root phenols, root N and root C:N.

	Biotic PSF index (ln performance in live soil/in sterilized soil)													
	Number of ramets		Biomass		Root-shoot ratio		Fv/Fm		Root phenols		Root N		Root C:N	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Soil conditioning	0.02	0.893	2.53	0.114	**9.77**	**0.002**	**5.40**	**0.022**	0.82	0.367	0.00	0.995	0.06	0.801
Soil-Climate	2.49	0.117	***2.94***	***0.089***	**4.30**	**0.040**	0.11	0.743	0.09	0.761	0.70	0.405	0.03	0.866
Plant-Climate	1.21	0.273	1.28	0.260	0.66	0.417	0.19	0.664	0.00	0.985	0.13	0.716	0.00	0.961
Plant-Soil	0.52	0.472	0.00	0.980	0.13	0.719	1.90	0.170	0.51	0.477	0.15	0.698	0.07	0.792
Plant-Climate × Plant-Soil	1.46	0.223	***1.65***	***0.081***	**3.42**	**0.044**	0.67	0.573	0.22	0.883	0.32	0.812	0.03	0.993
Conditioning × Soil-Climate	***3.35***	***0.070***	0.37	0.546	0.56	0.457	0.28	0.596	0.06	0.804	0.18	0.668	0.03	0.854
Conditioning × Plant–Soil	0.97	0.327	0.16	0.688	0.18	0.673	0.63	0.428	0.28	0.598	0.61	0.438	1.94	0.167
Conditioning × Plant-Climate	1.04	0.310	0.72	0.396	0.95	0.331	0.82	0.368	0.04	0.846	0.94	0.335	0.07	0.787

Note: Identity of the original inoculum sample used as a random effect. Significant results ($p \leq 0.05$) are in bold, marginally significant ($p \leq 0.1$) in bold and italic. df effect = 1, df error = 128 for number of ramets, biomass, root shoot ratio, and *Fv/Fm*, df error = 100 for root phenols, root N and root C:N; df represents Satterthwaite approximation for degrees of freedom.

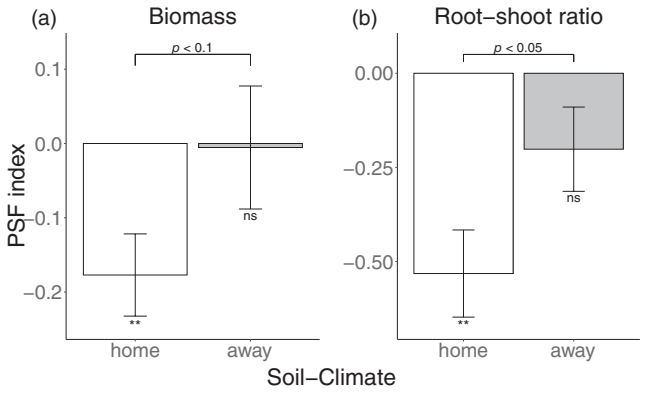


FIGURE 2 Effect of Soil-Climate (i.e. soil biota grown under home vs. away climate) on *Festuca* PSF index for (a) biomass and (b) root-shoot ratio. Bars and error lines represent mean ± SE. Asterisks at individual bars indicate whether the PSF index for given combination significantly differs from zero after individual *t*-tests; ns $p > 0.05$, $^{**}p < 0.01$.

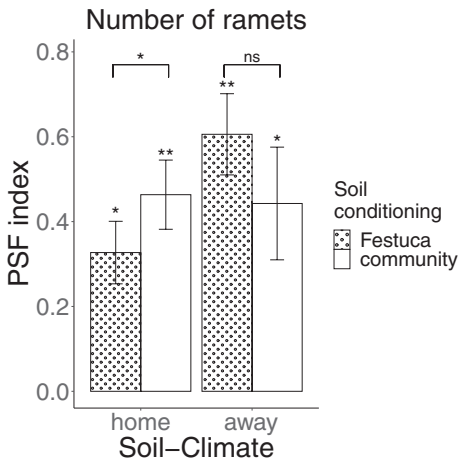


FIGURE 3 Effect of Soil-Climate (i.e. soil biota grown under home vs. away climate) and soil conditioning (i.e. *Festuca*- vs. community-conditioned soil) on *Festuca* PSF index for number of ramets. Bars and error lines represent mean ± SE. Asterisks at individual bars indicate whether the PSF index for given combination significantly differs from zero after individual *t*-tests; ns $p > 0.05$, $^{*}p \leq 0.05$, $^{**}p < 0.01$.

index for number of ramets when grown in community-conditioned soil than in *Festuca*-conditioned soil. On the contrary, under soil's biota away climate, the PSF was higher in *Festuca*-conditioned soil compared to community-conditioned soil (Figure 3). Similar patterns were shown using the alternative analyses [significant effects of interaction between soil origin and cultivation climate (Soil × Clim) on biotic PSF (Appendix S3, Figure S3.4 and Table S3.1), significant effect of soil origin × soil sterilization × cultivation climate (Soil × Ster × Clim) on root-shoot ratio (Appendix S2, Table S2.1) and significant effects of soil sterilization × Soil-Climate on biomass and root-shoot ratio (Appendix S2, Figure S2.5, Table S2.2)]. No effect of Soil-Climate, alone or in interaction, was detected for whole-soil PSF (Appendix S4, Table S4.1).

3.1.2 | H2: Plant adaptations to climate

Plant-Climate (i.e. plants grown in their home vs. away climate) had no significant effect on biotic PSF index for any of the studied performance measures (Table 1), meaning there was no overall difference in PSF of plants when grown in their home vs. in away climate. Contrary to this, all plants had higher biotic PSF for biomass (less negative) and root N (more positive) and lower (more negative) biotic PSF for root-shoot ratio and root C:N ratio under the warm, dry climate compared to the cold, wet climate [Figure 4, significant effect of cultivation climate on biotic PSF, no interaction between plant origin and cultivation climate (Plant × Clim) (Appendix S3, Table S3.1)]. The same patterns were shown when using raw biomass data [significant effect of interaction between soil sterilization and cultivation climate (Ster × Clim), but no significant effect of interaction between plant origin and cultivation climate alone (Plant × Clim) or in interaction with soil sterilization (Ster × Plant × Clim) or soil conditioning (Cond × Plant × Clim) (Appendix S2, Table S2.1, Figure S2.4); no significant effect of Plant-Climate alone or in interaction with soil sterilization (Ster) or soil conditioning (Cond) in Appendix S2, Table S2.2]. No effect of Plant-Climate, alone or in interaction, was detected for whole-soil PSF (Appendix S4, Table S4.1).

3.1.3 | H3 & H4: Co-adaptations of plants, soil biota and climate

The main effect of Plant-Soil (i.e. plants grown with local vs. foreign soil biota) on biotic PSF index was not significant for any of the measures of plant performance (Table 1). However, the interaction between Plant-Soil and Plant-Climate (i.e. plants grown under home vs. away climate) was marginally significant for biotic PSF index for biomass and significant for biotic PSF index for root-shoot ratio (Table 1). When the plants were grown with their local soil biota, their PSF for both biomass and root-shoot ratio was more negative in the plants' home climate than in the away climate. On the contrary, when the plants were grown with foreign soil biota, there was no difference in their PSF when grown in home vs. away climate (Figure 5). The pattern was, however, not confirmed by the alternative analyses [no significant effect of soil origin × plant origin (Soil × Plant) on biotic PSF index (Appendix S3, Table S3.1) and no significant effect of soil origin × soil conditioning or soil sterilization × plant origin (Soil × Cond × Plant or Soil × Ster × Plant) on raw plant performance data (Appendix S2, Table S2.1)]. No significant effect of Plant–Soil, alone or in interaction, was detected for whole-soil PSF (Appendix S4, Table S4.1).

3.2 | Soil available nitrogen after the conditioning phase

Soil with inocula from the cold, wet site conditioned under the cold, wet climate had nearly seven times lower levels of soil

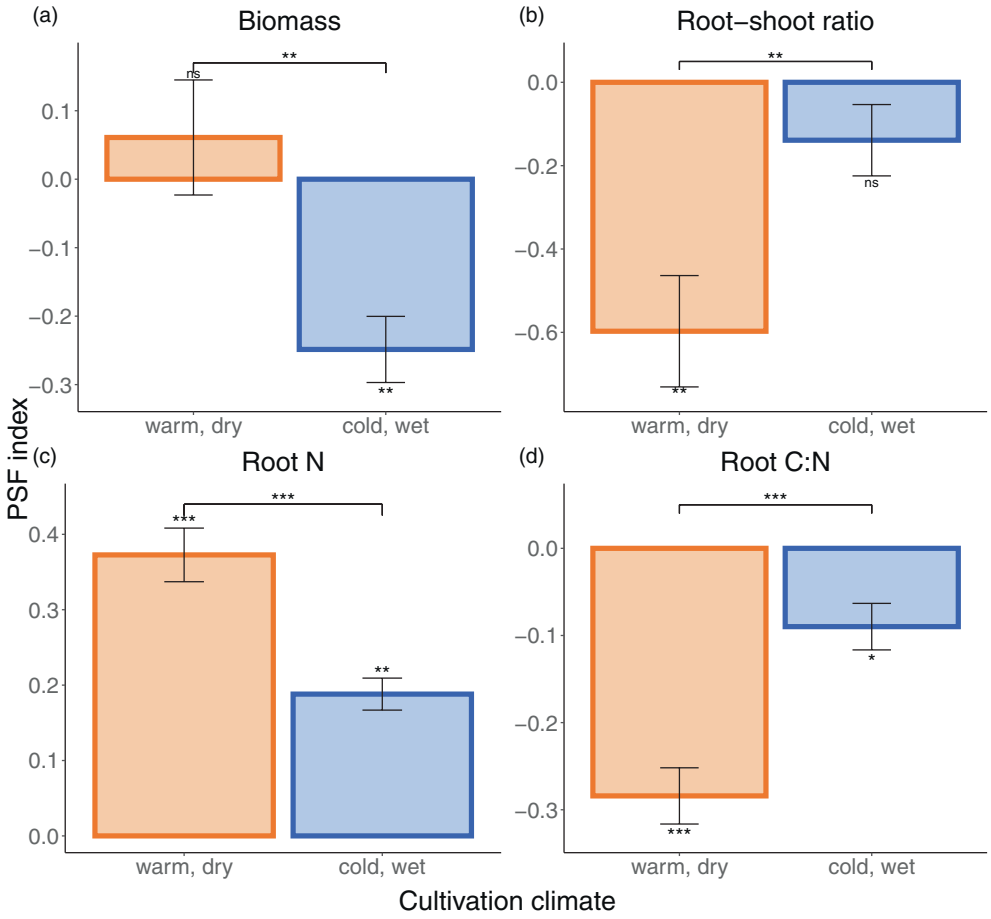


FIGURE 4 Effect of cultivation climate (warm, dry vs. cold, wet) on *Festuca* biotic PSF index for (a) biomass, (b) root-shoot ratio, (c) root N, and (d) root C:N. Bars and error lines represent mean ± SE. Asterisks at individual bars indicate whether the PSF index for given site of plant origin significantly differs from zero after individual *t*-tests; ns $p > 0.05$, $^{*}p \leq 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

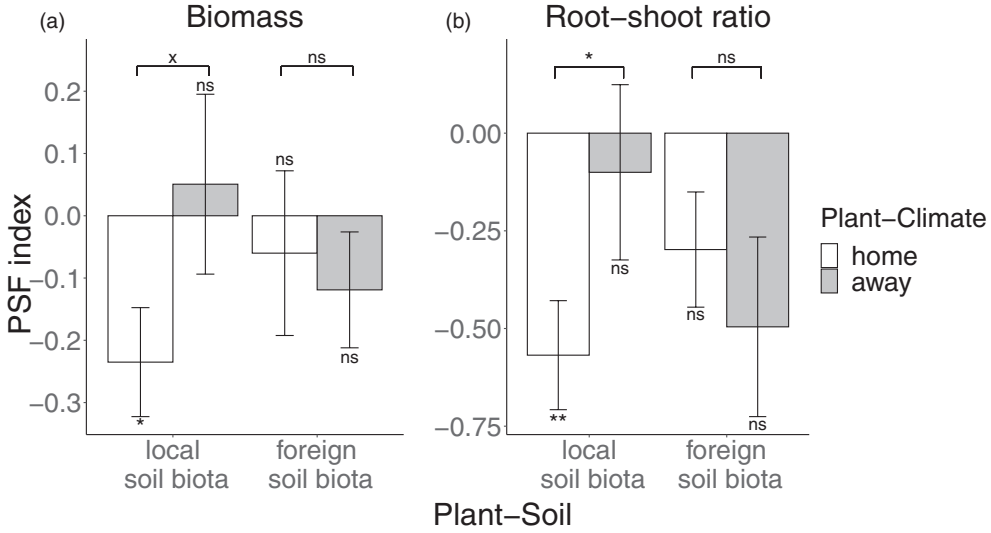


FIGURE 5 Effect of Plant-Climate (i.e. plants grown under home vs. away climate) and Plant-Soil (i.e. plants grown with local vs. foreign soil biota) on *Festuca* PSF index for (a) biomass, and (b) root-shoot ratio. Bars and error lines represent mean ± SE. Asterisks at individual bars indicate whether the PSF index for given combination significantly differs from zero after individual *t*-tests; ns $p \geq 0.1$, x $p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$.

NO_3^- than soils with inocula from the warm, dry site conditioned under the warm, dry climate (effect of site, $F_{1,29}=59.23$, $p<0.001$, Appendix S5, Figure S5.1), but did not differ between *Festuca*- vs. community-conditioned soils ($F_{1,29}=0.01$, $p=0.991$). In contrast, soil NH_4^+ did not differ between sites ($F_{1,29}=1.03$, $p=0.320$), but soils conditioned by *Festuca* had nearly two times lower levels of soil NH_4^+ than community-conditioned soils ($F_{1,29}=21.80$, $p<0.001$, Appendix S5, Figure S5.2). No interaction between conditioning species and site, as well as no differences in soil NO_2^- were found ($F_{1,29}<3.09$, $p>0.087$).

4 | DISCUSSION

In this study, we investigated possible climate-driven shifts in PSF of a perennial grass species *Festuca rubra*. By using soil and plants originating from two climatically distinct sites, grown in growth chambers simulating climates of the two sites, we studied PSF of *Festuca* (as its performance in live vs. sterilized soils, and as its performance in *Festuca*-conditioned vs. community-conditioned soil) in its home versus away climate when grown with its local versus foreign soil biota. We found evidence for soil biota, but not for plants, being adapted to their native climate, which was demonstrated by stronger (more negative) PSF effects in soil biota's home than in away climate. Overall, our results suggest that rapid climate changes may lead to less effective regulation of plant growth via soil biota effects, and therefore destabilization of plant communities.

In line with our first hypothesis, we showed that *Festuca*'s biotic PSF was consistently more negative when grown with soil biota that were exposed to their home climate, than when grown with soil biota that were exposed to their away climate (Figure 2; Figure B.5). In addition, we found an interactive effect of Soil-Climate (i.e. soil biota grown under home vs. away climate) and soil conditioning (*Festuca* vs. community conditioned soil) on PSF for number of ramets (Figure 3), showing that presence of self-conditioned soil biota has less positive effect on number of ramets than community-conditioned soil biota under the home climate, but more positive under the away climate. These findings suggest that soil biota, and soil pathogens in particular, are adapted to their native climate, resulting in a more efficient regulation of plant performance when the soil biota occurs in their home climate. Previous studies have indicated differential adaptations of various groups of soil biota (reviewed in Blankinship et al., 2011) and even distinct bacterial ecotypes (Chase et al., 2021) to local climates. However, a meta-analysis of Blankinship et al. (2011) has been inconclusive regarding the impact of altered climate on different trophic groups of soil biota due to a lack of such investigations. Our findings imply that rapid climate changes without sufficient time for soil biota to adapt to novel conditions can, at least in our model system, lead to the release of plants from negative plant–soil interactions, enabling them to increase their dominance and destabilize plant communities.

Contrary to our second hypothesis, we have not shown any adaptations of plants to their local climate, neither in terms of their direct performance (Appendix S2, Tables S2.1 and S2.2) nor in terms of their PSF (Table 1). Regardless of plant origin, all plants performed better (higher number of ramets and biomass, Appendix S2, Figures S2.3 and S2.4) under the cold, wet climate than under the warm, dry climate. The lack of significant adaptation effect to the local climate compared to our previous studies on *F. rubra* in the same study area (e.g. Kosova et al., 2022; Munzbergova et al., 2017; Stojanova et al., 2019; Thakur et al., 2023) could be given by the fact that here we studied only two populations differing in both temperature and moisture, while the previous studies showed strong interactions between these two climatic factors.

In terms of PSF, all plants regardless of their origin showed a higher biotic PSF for biomass (less negative) and root N (more positive) and more negative PSF for root-shoot ratio and root C:N ratio under the warm, dry climate compared to the cold, wet climate (Figure 4), showing that under the warm, dry climate, plants benefited more (or suffered less) from presence of soil biota than in the cold, wet climate. These results are in line with results of Rutten and Gómez-Aparicio (2018) who showed that PSF ranges from positive in dry sites to negative in wet sites on a natural precipitation gradient. In our experiment, there was much higher soil NO_3^- in the warm, dry than in the cold, wet climate after the conditioning phase (Appendix S5, Figure S5.1), suggesting higher activity of decomposers and therefore faster nutrient cycling in the warm, dry than under the cold, wet climate. This is consistent with other research showing that, as long as the communities do not get limited by water availability, warming leads to increased nitrogen mineralization and nitrification, and thus increased plant available N in soil (Andresen et al., 2010; Butler et al., 2012; Chen et al., 2020; Dijkstra et al., 2010). Similarly as suggested in a review of Pugnaire et al. (2019), enhanced nutrient cycling in our study allowed the plants to benefit more from presence of soil biota and therefore develop less negative biotic PSF under the warm, dry (but not water-limited) climate than under the cold, wet climate.

We only found limited support for our third hypothesis that plants are adapted to their local soil biota. The main effect of Plant-Soil (i.e. plants grown with local vs. foreign soil biota) on *Festuca* PSF was not significant (Table 1), but we detected a weak, yet significant effect of its interaction with Plant-Climate (i.e. plants grown under home vs. away climate) (Figure 4). This result suggests that there is co-adaptation between plants and soil biota, but that the consequences of this co-adaptation depend on climatic context. This aligns with our fourth hypothesis in which we expected that PSF is adapted to climate, and thus most negative when both plants and soil biota are under their home climate. Indeed, we showed that with their local soil biota, plant's PSF for biomass was more negative in plant's home climate than in the away climate, while with foreign biota, there was no difference in PSF among the climates (Figure 4). Our results are in line with those of Aares et al. (2023) who showed that plant performance improved in home climate compared to away climate only when plants were placed in foreign soil, as well as it improved in home soil compared to away soil only when in foreign climate. Previous

studies showed that presence of local mycorrhizal fungi and rhizobacteria positively affect the ability of plants to deal with altered climate, for example by ameliorating drought stress (Hoeksema et al., 2018; Remke et al., 2020, 2021; Rubin et al., 2018). Our results suggest that when considering all groups of soil biota, the positive effect of locally adapted soil mutualists may be counteracted and even outweighed by enhanced negative effects of locally adapted pathogens. These findings altogether demonstrate the complicated nature of plant–soil responses to environmental novelty and stress the need for further studies in this field.

Most climate-dependent effects on PSF were observed only in case of the biotic PSF index, that is when comparing plant growth in live versus sterilized soil, not when comparing plant performance between *Festuca*-conditioned and community-conditioned soil. This finding suggests that the climate dependent PSFs are mostly driven by generalist microbes, and it is thus unlikely that they affect those PSF that are responsible for plant species coexistence. Similarly, an overall weak degree of co-adaptation between plants and their local soil biota in our study system do not indicate that possible asynchronous range shifts of plants and soil biota would have any negative consequences on community structure via altered plant–soil biota interactions as observed in other systems (Cardinaux et al., 2018; Van Nuland et al., 2017). This may be due to the fact that the majority of the prokaryote and fungal taxa that were either unique or significantly more abundant at one of the study sites primarily play a role in nitrogen cycling and the degradation of organic matter rather than being plant pathogens or mutualists (manuscript in preparation). Soil mutualists and in particular soil pathogens are usually highly adapted to the local plants and vice versa (Crawford et al., 2019; Semchenko et al., 2022), commonly on species (e.g. Liu et al., 2012; Mangan et al., 2010) but even on genotype level (Eck et al., 2019). On the contrary, the degree of specialization of soil decomposers is generally much lower (Semchenko et al., 2022; Veen et al., 2019) and typically operates on a higher taxonomic or functional level (Austin et al., 2014; Ma et al., 2023; Veen et al., 2015).

Our experimental design followed the recommendations of Brinkman et al. (2010) how to perform PSF studies and it shows multiple strengths. First, we made sure that plant–soil interactions in our study system are well developed by using double conditioning, that is by using field-conditioned soil further conditioned under experimental conditions by *Festuca* versus community in a 10-month long conditioning phase. Second, we quantified PSF in two ways—as *Festuca* performance in live versus sterile soil and in *Festuca*- versus community-conditioned soil, as recommended by Brinkman et al. (2010). Last, we studied multiple measures of plant performance which provided us with a more complex view of plant responses to the studied treatments. The inconsistency in results shown by individual performance measures aligns with previous studies (e.g. Aldorfova et al., 2020; Dudenhoffer et al., 2018; Wilschut & van Kleunen, 2021) and highlights the importance of including multiple performance measures in PSF studies to reveal complex patterns not seen when using only a single measure like plant biomass.

However, it is important to also acknowledge the limitations of our study. First, we do not have data on soil chemistry and soil microbial communities from the feedback phase, lacking information on their response to individual treatments. We therefore do not fully understand the mechanisms behind different performance of *Festuca* in individual treatments. Second, our study was conducted using only two sites with differing climatic conditions, limiting our ability to differentiate between the effects of altered temperature and precipitation regimes. However, the inclusion of five factors in our fully factorial design—including plant origin, soil origin, cultivation climate, conditioning species, and soil sterilization—made it impractical to expand the study to additional sites.

Recent projections of future climatic conditions in our study area predict increase in temperature and increase in days with drought during the growing season (Hanssen-Bauer et al., 2017). The results of our study indicate that if the climate becomes warmer and drier as predicted, the soil biota's ability to regulate plant growth may diminish, leading to destabilization of plant communities. This is because soil biota are adapted to their native climate, and rapid climate changes can disrupt these adaptations. Practically, this could mean that certain plant species might become more dominant, potentially altering plant composition and function of ecosystems, as suggested previously (e.g. Bardgett & Wardle, 2010; Classen et al., 2015; van der Putten et al., 2016). In line with earlier research (e.g. Souriol & Henry, 2024; Stroud et al., 2022), our results also suggest that enhanced nutrient cycling under the warmer conditions might benefit plant growth initially, but these positive effects will likely be outweighed by the negative impacts of disrupted plant–soil interactions in the long term.

In conclusion, our study provides valuable insights into the interactive effects between plant origin, soil origin, and cultivation climate on PSF in *Festuca rubra*. The observed interactive effects underscore the complex nature of PSF and its responsiveness to changing environmental conditions. These findings contribute to the growing body of literature on PSF under climate change scenarios, highlighting the need for more comprehensive investigations to understand the mechanisms underlying these interactive effects. Future research should aim to elucidate the specific microbial mechanisms mediating these interactions and explore the generalizability of our findings across different plant species and ecosystems. Such knowledge is crucial for predicting and managing the ecological consequences of climate change on plant communities and ecosystem functioning.

AUTHOR CONTRIBUTIONS

Anna Florianová: Conceptualization, methodology, investigation, formal analysis, writing—original draft, writing—review and editing. Zuzana Münzbergová: Conceptualization, methodology, supervision, writing—review and editing, funding acquisition.

ACKNOWLEDGEMENTS

We are thankful to D. in't Zandt for providing data on soil biota communities at the two study sites, M. Brindzák for help with maintaining the experiments, student part-time workers for help with harvest,

and participants of the POPEKOL seminars for many useful comments on previous versions of the manuscript. During the preparation of this work the authors used ChatGPT 3.5 in order to improve language and readability. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication. This study was supported by Czech Science Foundation (project GAČR 22-00761S), and partly also by Institutional Funding (RVO 67985939 and Ministry of Education of the Czech Republic).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The datasets used and analysed in the current study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.37pvmcvvj (Florianová & Münzbergová, 2024).

ORCID

Anna Florianová https://orcid.org/0000-0002-8037-623X
Zuzana Münzbergová https://orcid.org/0000-0002-4026-6220

REFERENCES

Aares, K. H., Bockelie-Rosendahl, T., Priyadarshi, R., Pugnaire, F. I., Schöb, C., Alifriqui, M., Manrique, E., Jaakola, L. H., & Bråthen, K. A. (2023). One does not simply grow well: Performance of grassland plants in home and foreign soil and climate. *bioRxiv* preprint. https://doi.org/10.1101/2023.02.03.526963

Ainsworth, E. A., & Gillespie, K. M. (2007). Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin-Ciocalteu reagent. *Nature Protocols*, *2*, 875–877. https://doi.org/10.1038/nprot.2007.102

Aldorfova, A., Knobova, P., & Munzbergova, Z. (2020). Plant-soil feedback contributes to predicting plant invasiveness of 68 alien plant species differing in invasive status. *Oikos*, *129*, 1257–1270. https://doi.org/10.1111/oik.07186

Aldorfova, A., & Munzbergova, Z. (2019). Conditions of plant cultivation affect the differences in intraspecific plant-soil feedback between invasive and native dominants. *Flora*, *261*, 151492. https://doi.org/10.1016/j.flora.2019.151492

Ammerman, J. (2001). *Determination of nitrate/nitrite in 0.5 M K_2SO_4 soil extracts by flow injection analysis*. QuikChem Method 12-107-04-1-H. Lachat Instruments.

Anderson, J. T., & Song, B. H. (2020). Plant adaptation to climate change—Where are we? *Journal of Systematics and Evolution*, *58*, 533–545. https://doi.org/10.1111/jse.12649

Andresen, L. C., Michelsen, A., Jonasson, S., Schmidt, I. K., Mikkelsen, T. N., Ambus, P., & Beier, C. (2010). Plant nutrient mobilization in temperate heathland responds to elevated CO_2, temperature and drought. *Plant and Soil*, *328*, 381–396. https://doi.org/10.1007/s11104-009-0118-7

Austin, A. T., Vivanco, L., Gonzalez-Arzac, A., & Perez, L. I. (2014). There's no place like home? An exploration of the mechanisms behind plant litter- decomposer affinity in terrestrial ecosystems. *New Phytologist*, *204*, 307–314. https://doi.org/10.1111/nph.12959

Baker, N. R., & Rosenqvist, E. (2004). Applications of chlorophyll fluorescence can improve crop production strategies: An examination of future possibilities. *Journal of Experimental Botany*, *55*, 1607–1621. https://doi.org/10.1093/jxb/erh196

Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515*, 505–511. https://doi.org/10.1038/nature13855

Bardgett, R. D., & Wardle, D. A. (2010). *Aboveground-belowground linkages: Biotic interactions, ecosystem processes and global change*. Oxford Universtiy Press.

Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bergmann, J., Verbruggen, E., Heinze, J., Xiang, D., Chen, B., Joshi, J., & Rillig, M. C. (2016). The interplay between soil structure, roots, and microbiota as a determinant of plant-soil feedback. *Ecology and Evolution*, *6*, 7633–7644. https://doi.org/10.1002/ece3.2456

Bever, J. D., Westover, K. M., & Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology*, *85*, 561–573. https://doi.org/10.2307/2960528

Blankinship, J. C., Niklaus, P. A., & Hungate, B. A. (2011). A meta-analysis of responses of soil biota to global change. *Oecologia*, *165*, 553–565. https://doi.org/10.1007/s00442-011-1909-0

Blanquart, F., Kaltz, O., Nuismer, S. L., & Gandon, S. (2013). A practical guide to measuring local adaptation. *Ecology Letters*, *16*, 1195–1205. https://doi.org/10.1111/ele.12150

Brinkman, E. P., Van der Putten, W. H., Bakker, E. J., & Verhoeven, K. J. F. (2010). Plant-soil feedback: Experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology*, *98*, 1063–1073. https://doi.org/10.1111/j.1365-2745.2010.01695.x

Butler, S. M., Melillo, J. M., Johnson, J. E., Mohan, J., Steudler, P. A., Lux, H., Burrows, E., Smith, R. M., Vario, C. L., Scott, L., Hill, T. D., Aponte, N., & Bowles, F. (2012). Soil warming alters nitrogen cycling in a New England forest: Implications for ecosystem function and structure. *Oecologia*, *168*, 819–828. https://doi.org/10.1007/s00442-011-2133-7

Cardinaux, A., Hart, S. P., & Alexander, J. M. (2018). Do soil biota influence the outcome of novel interactions between plant competitors? *Journal of Ecology*, *106*, 1853–1863. https://doi.org/10.1111/1365-2745.13029

Chase, A. B., Weihe, C., & Martiny, J. B. H. (2021). Adaptive differentiation and rapid evolution of a soil bacterium along a climate gradient. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2101254118. https://doi.org/10.1073/pnas.2101254118

Chen, Y., Feng, J. G., Yuan, X., & Zhu, B. (2020). Effects of warming on carbon and nitrogen cycling in alpine grassland ecosystems on the Tibetan plateau: A meta-analysis. *Geoderma*, *370*, 114363. https://doi.org/10.1016/j.geoderma.2020.114363

Classen, A., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M. A., Moorhead, L. C., & Patterson, C. M. (2015). Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*, *6*, 1–21. https://doi.org/10.1890/ES15-00217.1

Cortois, R., Schroder-Georgi, T., Weigelt, A., van der Putten, W. H., & De Deyn, G. B. (2016). Plant-soil feedbacks: Role of plant functional group and plant traits. *Journal of Ecology*, *104*, 1608–1617. https://doi.org/10.1111/1365-2745.12643

Crawford, K. M., Bauer, J. T., Comita, L. S., Eppinga, M. B., Johnson, D. J., Mangan, S. A., Queenborough, S. A., Strand, A. E., Suding, K. N., Umbanhowar, J., & Bever, J. D. (2019). When and where plant-soil feedback may promote plant coexistence: A meta-analysis. *Ecology Letters*, *22*, 1274–1284. https://doi.org/10.1111/ele.13278

Crémieux, L., Bischoff, A., Šmilauerová, M., Lawson, C. S., Mortimer, S. R., Doležal, J., Lanta, V., Edwards, A. R., Brook, A. J., Tscheulin, T., Macel, M., Lepš, J., Müller-Schärer, H., & Steinger, T. (2008). Potential contribution of natural enemies to patterns of local

adaptation in plants. *New Phytologist*, *180*, 524–533. https://doi.org/10.1111/j.1469-8137.2008.02545.x

De Long, J. R., Fry, E. L., Veen, G. F., & Kardol, P. (2019). Why are plant-soil feedbacks so unpredictable, and what to do about it? *Functional Ecology*, *33*, 118–128. https://doi.org/10.1111/1365-2435.13232

Deveautour, C., Donn, S., Power, S. A., Bennett, A. E., & Powell, J. R. (2018). Experimentally altered rainfall regimes and host root traits affect grassland arbuscular mycorrhizal fungal communities. *Molecular Ecology*, *27*, 2152–2163. https://doi.org/10.1111/mec.14536

Dijkstra, F. A., Blumenthal, D., Morgan, J. A., Pendall, E., Carrillo, Y., & Follett, R. F. (2010). Contrasting effects of elevated CO_2 and warming on nitrogen cycling in a semiarid grassland. *New Phytologist*, *187*, 426–437. https://doi.org/10.1111/j.1469-8137.2010.03293.x

Dudenhoffer, J. H., Ebeling, A., Klein, A. M., & Wagg, C. (2018). Beyond biomass: Soil feedbacks are transient over plant life stages and alter fitness. *Journal of Ecology*, *106*, 230–241. https://doi.org/10.1111/1365-2745.12870

Duell, E. B., Zaiger, K., Bever, J. D., & Wilson, G. W. T. (2019). Climate affects plant-soil feedback of native and invasive grasses: Negative feedbacks in stable but not in variable environments. *Frontiers in Ecology and Evolution*, *7*. https://doi.org/10.3389/fevo.2019.00419

Eck, J. L., Stump, S. M., Delavaux, C. S., Mangan, S. A., & Comita, L. S. (2019). Evidence of within-species specialization by soil microbes and the implications for plant community diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 7371–7376. https://doi.org/10.1073/pnas.1810767116

Egan, L. (2001). *Determination of Amonia by flow injection analysis Colorimetry*. QuikChem Method 10-107-06-5-E. Lachat Instruments.

Ehrenberger, F., & Gorbach, S. (1973). *Methoden der organischen Elementar- und Spurenanalyse*. Verlag Chemie Weinheim.

Engelkes, T., Morriën, E., Verhoeven, K. J. F., Bezemer, T. M., Biere, A., Harvey, J. A., McIntyre, L. M., Tamis, W. L. M., & van der Putten, W. H. (2008). Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature*, *456*, 946–948. https://doi.org/10.1038/nature07474

Florianova, A., & Munzbergova, Z. (2018). The intensity of intraspecific plant-soil feedbacks in alien impatiens species depends on the environment. *Perspectives in Plant Ecology, Evolution and Systematics*, *32*, 56–64. https://doi.org/10.1016/j.ppees.2018.04.004

Florianová, A., & Münzbergová, Z. (2024). Data from: Climate-driven shifts in plant-soil feedback of a perennial grass species. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.37pvmcvvj

Fry, E. L., Johnson, G. N., Hall, A. L., Pritchard, W. J., Bullock, J. M., & Bardgett, R. D. (2018). Drought neutralises plant-soil feedback of two mesic grassland forbs. *Oecologia*, *186*, 1113–1125. https://doi.org/10.1007/s00442-018-4082-x

Hamann, E., Kesselring, H., Armbruster, G. F. J., Scheepens, J. F., & Stocklin, J. (2016). Evidence of local adaptation to fine- and coarse-grained environmental variability in Poa alpina in the Swiss Alps. *Journal of Ecology*, *104*, 1627–1637. https://doi.org/10.1111/1365-2745.12628

Hanssen-Bauer, I., Førland, E., Haddeland, I., Hisdal, H., Lawrence, D., Mayer, S., Nesje, A., Nilsen, J. E., Sandven, S., Sandø, A., Sorteberg, A., & Ådlandsvik, B. (2017). *Climate in Norway 2100—Knowledge base for climate adaptation, updated in 2017*. Norwegian Centre for Climate Services.

Hassan, K., Dastogeer, K. M. G., Carrillo, Y., & Nielsen, U. N. (2022). Climate change-driven shifts in plant-soil feedbacks: A meta-analysis. *Ecological Processes*, *11*. https://doi.org/10.1186/s13717-022-00410-z

Heinze, J., Gensch, S., Weber, E., & Joshi, J. (2017). Soil temperature modifies effects of soil biota on plant growth. *Journal of Plant Ecology*, *10*, 808–821. https://doi.org/10.1093/jpe/rtw097

Henneron, L., Kardol, P., Wardle, D. A., Cros, C., & Fontaine, S. (2020). Rhizosphere control of soil nitrogen cycling: A key component of plant economic strategies. *New Phytologist*, *228*, 1269–1282. https://doi.org/10.1111/nph.16760

Hoeksema, J. D., Bever, J. D., Chakraborty, S., Chaudhary, V. B., Gardes, M., Gehring, C. A., Hart, M. M., Housworth, E. A., Kaonongbua, W., Klironomos, J. N., Lajeunesse, M. J., Meadow, J., Milligan, B. G., Piculell, B. J., Pringle, A., Rúa, M. A., Umbanhowar, J., Viechtbauer, W., Wang, Y. W., … Zee, P. C. (2018). Evolutionary history of plant hosts and fungal symbionts predicts the strength of mycorrhizal mutualism. *Communications Biology*, *1*, 116. https://doi.org/10.1038/s42003-018-0120-9

Hoeksema, J. D., & Forde, S. E. (2008). A meta-analysis of factors affecting local adaptation between interacting species. *The American Naturalist*, *171*, 275–290. https://doi.org/10.1086/527496

IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Core Writing Team, R. K. Pachauri, & L. A. Meyer, Eds.). IPCC.

Jahns, P., & Holzwarth, A. R. (2012). The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. *Biochimica et Biophysica Acta-Bioenergetics*, *1817*, 182–193. https://doi.org/10.1016/j.bbabio.2011.04.012

Johnson, N. C., Wilson, G. W. T., Bowker, M. A., Wilson, J. A., & Miller, R. M. (2010). Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 2093–2098. https://doi.org/10.1073/pnas.0906710107

Kaisermann, A., de Vries, F. T., Griffiths, R. I., & Bardgett, R. D. (2017). Legacy effects of drought on plant-soil feedbacks and plant-plant interactions. *New Phytologist*, *215*, 1413–1424. https://doi.org/10.1111/nph.14661

Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS One*, *10*, e0130205. https://doi.org/10.1371/journal.pone.0130205

Koorem, K., Snoek, B. L., Bloem, J., Geisen, S., Kostenko, O., Manrubia, M., Ramirez, K. S., Weser, C., Wilschut, R. A., & van der Putten, W. H. (2020). Community-level interactions between plants and soil biota during range expansion. *Journal of Ecology*, *108*, 1860–1873. https://doi.org/10.1111/1365-2745.13409

Kosova, V., Hajek, T., Hadincova, V., & Munzbergova, Z. (2022). The importance of ecophysiological traits in response of Festuca rubra to changing climate. *Physiologia Plantarum*, *174*, e13608. https://doi.org/10.1111/ppl.13608

Kulmatiski, A., Beard, K. H., Stevens, J. R., & Cobbold, S. M. (2008). Plant-soil feedbacks: A meta-analytical review. *Ecology Letters*, *11*, 980–992. https://doi.org/10.1111/j.1461-0248.2008.01209.x

Kut'akova, E., Meszarosova, L., Baldrian, P., Munzbergova, Z., & Herben, T. (2023). Plant-soil feedbacks in a diverse grassland: Soil remembers, but not too much. *Journal of Ecology*, *111*, 1203–1217. https://doi.org/10.1111/1365-2745.14104

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26.

Liu, X. B., Liang, M. X., Etienne, R. S., Wang, Y. F., Staehelin, C., & Yu, S. X. (2012). Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. *Ecology Letters*, *15*, 111–118. https://doi.org/10.1111/j.1461-0248.2011.01715.x

Ma, A. R., Liu, H., Song, C., Tian, E. L., & Wang, X. Z. (2023). Home-field advantage in litter decomposition: A critical review from a microbial perspective. *Journal of Basic Microbiology*, *63*, 709–721. https://doi.org/10.1002/jobm.202200657

Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, *466*, 752–755. https://doi.org/10.1038/nature09273

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence—A practical guide. *Journal of Experimental Botany*, *51*, 659–668. https://doi.org/10.1093/jexbot/51.345.659

Meineri, E., Skarpaas, O., Spindelbock, J., Bargmann, T., & Vandvik, V. (2014). Direct and size-dependent effects of climate on flowering performance in alpine and lowland herbaceous species. *Journal of Vegetation Science*, *25*, 275–286. https://doi.org/10.1111/jvs.12062

Molina, R., & Horton, T. R. (2015). Mycorrhiza specificity: Its role in the development and function of common mycelial networks. In T. R. Horton (Ed.), *Mycorrhizal networks* (pp. 1–39). Springer.

Munzbergova, Z., & Hadincova, V. (2017). Transgenerational plasticity as an important mechanism affecting response of clonal species to changing climate. *Ecology and Evolution*, *7*, 5236–5247. https://doi.org/10.1002/ece3.3105

Munzbergova, Z., Hadincova, V., Skalova, H., & Vandvik, V. (2017). Genetic differentiation and plasticity interact along temperature and precipitation gradients to determine plant performance under climate change. *Journal of Ecology*, *105*, 1358–1373. https://doi.org/10.1111/1365-2745.12762

Munzbergova, Z., Latzel, V., Surinova, M., & Hadincova, V. (2019). DNA methylation as a possible mechanism affecting ability of natural populations to adapt to changing climate. *Oikos*, *128*, 124–134. https://doi.org/10.1111/oik.05591

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, *15*, 684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Nunez, M. A., Horton, T. R., & Simberloff, D. (2009). Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology*, *90*, 2352–2359. https://doi.org/10.1890/08-2139.1

Pankova, H., Munzbergova, Z., Rydlova, J., & Vosatka, M. (2011). The response of *Aster amellus* (Asteraceae) to mycorrhiza depends on the origins of both the soil and the fungi. *American Journal of Botany*, *98*, 850–858. https://doi.org/10.3732/ajb.0900350

Pánková, H., Munzbergová, Z., Rydlová, J., & Vosátka, M. (2014). Co-adaptation of plants and communities of arbuscular mycorrhizal fungi to their soil conditions. *Folia Geobotanica*, *49*, 521–540. https://doi.org/10.1007/s12224-013-9183-z

Pugnaire, F. I., Morillo, J. A., Peñuelas, J., Reich, P. B., Bardgett, R. D., Gaxiola, A., Wardle, D. A., & van der Putten, W. H. (2019). Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances*, *5*, eaaz1834. https://doi.org/10.1126/sciadv.aaz1834

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Remke, M. J., Hoang, T., Kolb, T., Gehring, C., Johnson, N. C., & Bowker, M. A. (2020). Familiar soil conditions help *Pinus ponderosa* seedlings cope with warming and drying climate. *Restoration Ecology*, *28*, S344–S354. https://doi.org/10.1111/rec.13144

Remke, M. J., Johnson, N. C., & Bowker, M. A. (2022). Sympatric soil biota mitigate a warmer-drier climate for *Bouteloua gracilis*. *Global Change Biology*, *28*, 6280–6292. https://doi.org/10.1111/gcb.16369

Remke, M. J., Johnson, N. C., Wright, J., Williamson, M., & Bowker, M. A. (2021). Sympatric pairings of dryland grass populations, mycorrhizal fungi and associated soil biota enhance mutualism and ameliorate drought stress. *Journal of Ecology*, *109*, 1210–1223. https://doi.org/10.1111/1365-2745.13546

Reynolds, H. L., Packer, A., Bever, J. D., & Clay, K. (2003). Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology*, *84*, 2281–2291. https://doi.org/10.1890/02-0298

Rubin, R. L., Koch, G. W., Martinez, A., Mau, R. L., Bowker, M. A., & Hungate, B. A. (2018). Developing climate-smart restoration: Can plant microbiomes be hardened against heat waves? *Ecological Applications*, *28*, 1594–1605. https://doi.org/10.1002/eap.1763

Rutten, G., & Gómez-Aparicio, L. (2018). Plant-soil feedbacks and root responses of two Mediterranean oaks along a precipitation gradient. *Plant and Soil*, *424*, 221–231. https://doi.org/10.1007/s11104-018-3567-z

Sammarco, I., Muenzbergova, Z., & Latzel, V. (2022). DNA methylation can mediate local adaptation and response to climate change in the clonal plant *Fragaria vesca*: Evidence from a European-scale reciprocal transplant experiment. *Frontiers in Plant Science*, *13*. https://doi.org/10.3389/fpls.2022.827166

Semchenko, M., Barry, K. E., de Vries, F. T., Mommer, L., Moora, M., & Macia-Vicente, J. G. (2022). Deciphering the role of specialist and generalist plant-microbial interactions as drivers of plant-soil feedback. *New Phytologist*, *234*, 1929–1944. https://doi.org/10.1111/nph.18118

Siebert, J., Sünnemann, M., Auge, H., Berger, S., Cesarz, S., Ciobanu, M., Guerrero-Ramírez, N. R., & Eisenhauer, N. (2019). The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. *Scientific Reports*, *9*, 639. https://doi.org/10.1038/s41598-018-36777-3

Smith, S. E., & Read, D. (2008). *Mycorrhizal symbiosis* (3rd ed.). Academic Press.

Souriol, B., & Henry, H. (2024). Short-versus long-term effects of nitrogen addition and warming on soil nitrogen mineralization and leaching in a grass-dominated old field. *Oecologia*, *205*, 59–68. https://doi.org/10.1007/s00442-024-05549-4

Stojanova, B., Kolarikova, V., Surinova, M., Klapste, J., Hadincova, V., & Munzbergova, Z. (2019). Evolutionary potential of a widespread clonal grass under changing climate. *Journal of Evolutionary Biology*, *32*, 1057–1068. https://doi.org/10.1111/jeb.13507

Stroud, E., Craig, B., & Henry, H. (2022). Short-term vs. long-term effects of warming and nitrogen addition on soil extracellular enzyme activity and litter decomposition in a grass-dominated system. *Plant and Soil*, *481*, 165–177. https://doi.org/10.1007/s11104-022-05625-9

Surinova, M., Hadincova, V., Vandvik, V., & Munzbergova, Z. (2019). Temperature and precipitation, but not geographic distance, explain genetic relatedness among populations in the perennial grass Festuca rubra. *Journal of Plant Ecology*, *12*, 730–741. https://doi.org/10.1093/jpe/rtz010

Tack, A. J. M., Thrall, P. H., Barrett, L. G., Burdon, J. J., & Laine, A. L. (2012). Variation in infectivity and aggressiveness in space and time in wild host-pathogen systems: Causes and consequences. *Journal of Evolutionary Biology*, *25*, 1918–1936. https://doi.org/10.1111/j.1420-9101.2012.02588.x

Tang, Y. L., Wen, X. G., Lu, Q. T., Yang, Z. P., Cheng, Z. K., & Lu, C. M. (2007). Heat stress induces an aggregation of the light-harvesting complex of photosystem II in spinach plants. *Plant Physiology*, *143*, 629–638. https://doi.org/10.1104/pp.106.090712

Thakur, D., Hadincová, V., Schnablová, R., Synková, H., Haisel, D., Wilhelmová, N., Dostálek, T., & Münzbergová, Z. (2023). Differential effect of climate of origin and cultivation climate on structural and biochemical plant traits. *Functional Ecology*, *37*, 1436–1448. https://doi.org/10.1111/1365-2435.14291

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., & Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, *17*, 1351–1364. https://doi.org/10.1111/ele.12348

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., van de Voorde, T. F. J., & Wardle, D. A. (2013). Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*, 265–276. https://doi.org/10.1111/1365-2745.12054

van der Putten, W. H., Bardgett, R. D., de Ruiter, P. C., Hol, W. H. G., Meyer, K. M., Bezemer, T. M., Bradford, M. A., Christensen, S.,

Eppinga, M. B., Fukami, T., Hemerik, L., Molofsky, J., Schädler, M., Scherber, C., Strauss, S. Y., Vos, M., & Wardle, D. A. (2009). Empirical and theoretical challenges in aboveground-belowground ecology. *Oecologia*, *161*, 1–14. https://doi.org/10.1007/s00442-009-1351-8

van der Putten, W. H., Bradford, M. A., Brinkman, E. P., van de Voorde, T. F. J., & Veen, G. F. (2016). Where, when and how plant-soil feedback matters in a changing world. *Functional Ecology*, *30*, 1109–1121. https://doi.org/10.1111/1365-2435.12657

van Grunsven, R. H. A., van der Putten, W. H., Bezemer, T. M., Tamis, W. L. M., Berendse, F., & Veenendaal, E. M. (2007). Reduced plant-soil feedback of plant species expanding their range as compared to natives. *Journal of Ecology*, *95*, 1050–1057. https://doi.org/10.1111/j.1365-2745.2007.01282.x

Van Nuland, M. E., Bailey, J. K., & Schweitzer, J. A. (2017). Divergent plant-soil feedbacks could alter future elevation ranges and ecosystem dynamics. *Nature Ecology & Evolution*, *1*. https://doi.org/10.1038/s41559-017-0150

Veen, G. F., Freschet, G. T., Ordonez, A., & Wardle, D. A. (2015). Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos*, *124*, 187–195. https://doi.org/10.1111/oik.01374

Veen, G. F., Fry, E. L., ten Hooven, F. C., Kardol, P., Morrien, E., & De Long, J. R. (2019). The role of plant litter in driving plant-soil feedbacks. *Frontiers in Environmental Science*, *7*. https://doi.org/10.3389/fenvs.2019.00168

von Holle, B., Weber, S. E., & Nickerson, D. M. (2020). The influence of warming and biotic interactions on the potential for range expansion of native and nonnative species. *AoB Plants*, *12*. https://doi.org/10.1093/aobpla/plaa040

Wilschut, R. A., & van Kleunen, M. (2021). Drought alters plant-soil feedback effects on biomass allocation but not on plant performance. *Plant and Soil*, *462*, 285–296. https://doi.org/10.1007/s11104-021-04861-9

Wubs, E. R. J., & Bezemer, T. M. (2018). Temporal carry-over effects in sequential plant-soil feedbacks. *Oikos*, *127*, 220–229. https://doi.org/10.1111/oik.04526

Zhou, Z. H., Wang, C. K., & Luo, Y. Q. (2020). Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nature Communications*, *11*. https://doi.org/10.1038/s41467-020-16881-7

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Soil substrate characteristics.

Appendix S2: Results of alternative analyses on raw plant performance data.

Appendix S3: Results of alternative analyses on biotic PSF index.

Appendix S4: Results of analyses on whole-soil PSF index.

Appendix S5: Soil available nitrogen after the conditioning phase.

How to cite this article: Florianová, A., & Münzbergová, Z. (2025). Climate-driven shifts in plant–soil feedback of a perennial grass species. *Journal of Ecology*, *113*, 126–139. https://doi.org/10.1111/1365-2745.14443