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Changes in precipitation patterns can destabilize plant species coexistence via changes in plant–soil feedback

Jan-Hendrik Dudenhöffer ✉, Noah C. Luecke and Kerri M. Crawford

Climate change can alter species coexistence through changes in biotic interactions. By describing reciprocal interactions between plants and soil microbes, plant–soil feedback (PSF) has emerged as a powerful framework for predicting plant species coexistence and community dynamics, but little is known about how PSF will respond to changing climate conditions. Hence, the context dependency of PSF has recently gained attention. Water availability is a major driver of all biotic interactions, and it is expected that precipitation patterns will change with ongoing climate change. We tested how soil water content affects PSF by conducting a full factorial pairwise PSF experiment using eight plant species common to southeastern United States coastal prairies under three watering treatments. We found coexistence-stabilizing negative PSF at drier-than-average conditions shifted to coexistence-destabilizing positive PSF under wetter-than-average conditions. A simulation model parameterized with the experimental results supports the prediction that more positive PSF accelerates the erosion of diversity within communities while decreasing the predictability in plant community composition. Our results underline the importance of considering environmental context dependency of PSF in light of a rapidly changing climate.

The anthropogenically driven climate crisis impacts biodiversity and ecosystems worldwide[1,2]. With ongoing alterations in species distributions[3–5] and increasing novelty in ecosystems[6], our ability to predict the structure of future plant communities has become a key research challenge of the twenty-first century. In addition to the direct climatic impact on habitat suitability, climate-mediated biotic interactions can greatly affect plant community structure[7–9], making changes in plant communities even more difficult to predict[10]. The reciprocal interaction between plants shaping their associated soil communities and the impact of these communities on subsequently growing plants is an especially important mechanism for the maintenance and trajectory of plant community diversity and composition[11–14].

Since its inception more than 20 years ago[15,16] the concept of plant–soil feedback (PSF) has become foundational in plant ecology. The conceptualization and the derivative metric (I_s) of net pairwise PSF[17] provides a defined experimental and theoretical framework to measure and quantify the contribution of PSF to plant species coexistence. PSF is generally measured in experiments encompassing two phases. In a conditioning phase, soil communities are structured via species-specific interactions with the conditioning plant. In the response phase, performance is measured for plants growing with soil communities conditioned by conspecifics and heterospecifics. For a given species pair, negative pairwise PSF occurs if the plants exhibit a lower relative performance in conspecific soil compared with heterospecific soil whereas positive pairwise PSF occurs if the plants perform relatively better in conspecific soil. The original theory predicts that negative PSF, acting as a density- or frequency-dependent mechanism, stabilizes diversity in plant communities by decreasing the relative performance of a species when it becomes more abundant while allowing rare species to recover from low abundances. In contrast, positive PSF destabilizes plant diversity by fostering the dominance of abundant species[18,19]. However, alternative outcomes are possible; for example, when negative PSF creates intransitive feedback loops that lead to oscillations with temporarily low species abundances and potential extinction[20] or when positive PSF allows for coexistence at the landscape scale[21]. In conjunction with the potential of plant–soil interactions affecting plant niche differences, PSF has become a key component in modern coexistence theory as a fitness equalizing mechanism[22]. The utilization of the PSF framework allows predictions of plant community dynamics using experimentally derived pairwise PSF values via simulation approaches[13,23–25], which have been used to predict species abundances in the field[26].

The underlying interactions between plants and their associated soil communities that form the basis of PSF do not act in isolation but are subject to environmental context. Biotic mediators such as competition[27–29] or herbivory[30,31] and abiotic constraints such as atmospheric and edaphic conditions can shape these interactions[32,33]. The context dependency of PSF has recently gained great attention[34–37] especially in the light of anthropogenically driven environmental change[38,39]. A major aspect of the climate crisis is the anticipated change in precipitation patterns[40,41] and thus the soil water content under which plant–soil biota interactions occur. Soil water content is an important driver of soil biota community structure and functioning[42–44] with varying effects on different community members across a broad range of taxonomic scales[45–47] and on the susceptibility and responsiveness of plants to soil biota[48–50]. Previous PSF studies have manipulated soil water during the conditioning phase or used field-collected soils with different precipitation legacies[51] focusing on the context dependency of the plants' influence on soil communities. Others have imposed watering treatments at the response phase, thereby focusing on the context dependency of the soil communities' impact on the plants[52,53]. To better predict how climate change will influence plant community dynamics, it is important to consider that often both phases of the feedback loop, the conditioning of soil biota communities by the

Department of Biology and Biochemistry, University of Houston, Houston, TX, USA. ✉e-mail: jhdudenhoeffer@gmail.com

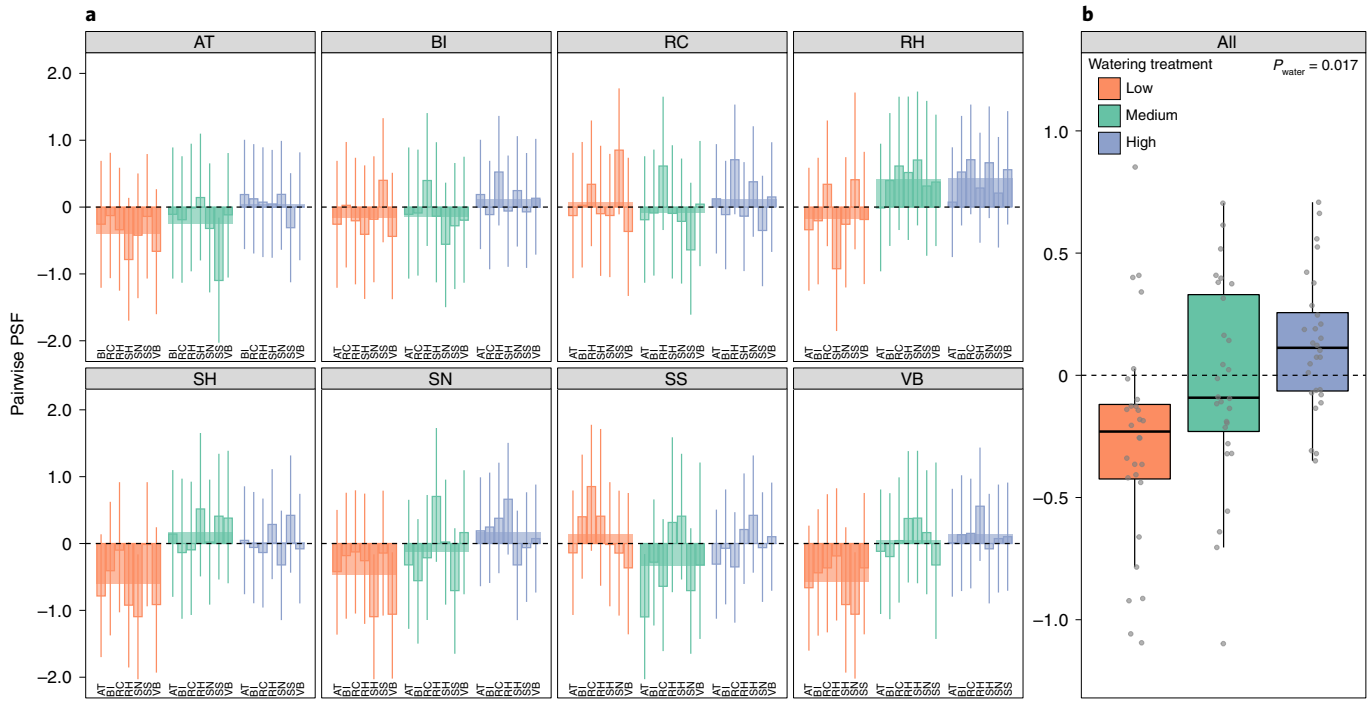

Fig. 1 | Net pairwise PSFs for all plant species combinations under different watering treatments. a, The small bars show all single pairwise feedbacks, and the large transparent bars show the average pairwise feedback for the focal species as indicated in the panel headers. Error bars indicate 95% bootstrap confidence intervals of the single pairwise feedbacks based on 10,000 iterations. **b**, All pairwise PSFs grouped by watering treatment; box and whisker plots indicate the median, 25th/75th percentile and 1.5 × interquartile range (IQR). Significance of the watering treatment (P_{water}) was evaluated using a linear mixed-effect model (Methods and Supplementary Table 1). Species codes: AT is *Asclepias tuberosa*, BI is *Bothriochloa ischaemum*, RC is *Ratibida columnifera*, RH is *Rudbeckia hirta*, SH is *Sorghum halepense*, SN is *Sorghastrum nutans*, SS is *Schizachyrium scoparium* and VB is *Verbena brasiliensis*. $n = 28$ pairwise PSFs per watering treatment.

plant and the impact of those communities on the subsequently growing plant, will be subject to a common environmental context.

Here we address this challenge by conducting a full factorial pairwise PSF experiment growing eight prairie plant species with soil communities that were either conditioned by conspecifics or by each of the heterospecific species in all pairwise combinations. We tested for the effect of different soil water regimes on PSF and subjected both phases, the conditioning phase and the response phase, to one of three different watering treatments. The treatments represented average and extremely high and low precipitation levels for the local area (Supplementary Fig. 1). We set up a total of nine replicate blocks and three additional blocks using sterilized soil. We estimated plant performance as a compound of survival and biomass production and determined net pairwise PSF for all species pairs. We further assessed if differences in soil fungal community composition at the end of the conditioning phase can be linked to shifts in PSF and if the similarity in fungal community composition between plant species can be linked to their pairwise PSF. To extrapolate how changes in pairwise PSF may translate to plant community dynamics under the different soil water regimes, we used a simulation model parameterized with the results of the PSF experiment.

Results and discussion

We found that wetter-than-average conditions produced coexistence-destabilizing positive PSF (relatively greater performance in conspecific vs. heterospecific soil) while drier-than-average conditions produced coexistence-stabilizing negative PSF (relatively lower performance in conspecifc vs. heterospecific soil; Fig. 1a,b and Supplementary Table 1). While the majority of reported PSF values are negative (coexistence stabilizing)[35,54], our results show that differences in soil water content can shift PSF in magnitude and even direction within the same plant community. Given our results, changing precipitation patterns might have dramatic consequences for plant community dynamics by causing shifts in the intensity or, more importantly, the direction of PSF. Consequently, the influence of PSF acting as a coexistence-stabilizing or destabilizing mechanism can change over time with shifting precipitation patterns, especially with increasing variability and more extreme patterns in precipitation as expected due to climate change[40,41].

The general trend towards more negative PSF in drier conditions was largely consistent across all species pairs, suggesting that this increased PSF-mediated coexistence may be general across plant species. However, we did uncover trends that may aid or hinder the use of PSF in predicting plant community structure. For example, negative PSF in dry conditions was especially visible for plant pairs including a non-native species (*Bothriochloa*, *Sorghum* and *Verbena*), while the effect of the watering treatment on PSF of exclusively native plant pairs seemed less pronounced (Extended Data Fig. 1). This is in contrast to the the general pattern of non-native species weakening coexistence-stabilizing negative PSF, possibly due to escape from species-specific pathogens[35]. Stronger negative PSF for pairs including non-native species could stabilize coexistence with native species and limit the spread of non-natives if conditions become drier in the future, while wetter conditions might destabilize coexistence. To compare how the different soil-conditioning species affected subsequent plant performance under different watering treatments, we calculated *z*-scores to standardize plant performance for each species within a watering treatment. Aside from more negative PSFs in drier conditions, there were idiosyncrasies in plant performance in species-trained soil by watering treatment combinations (Fig. 2a,b). There was no consistent effect of

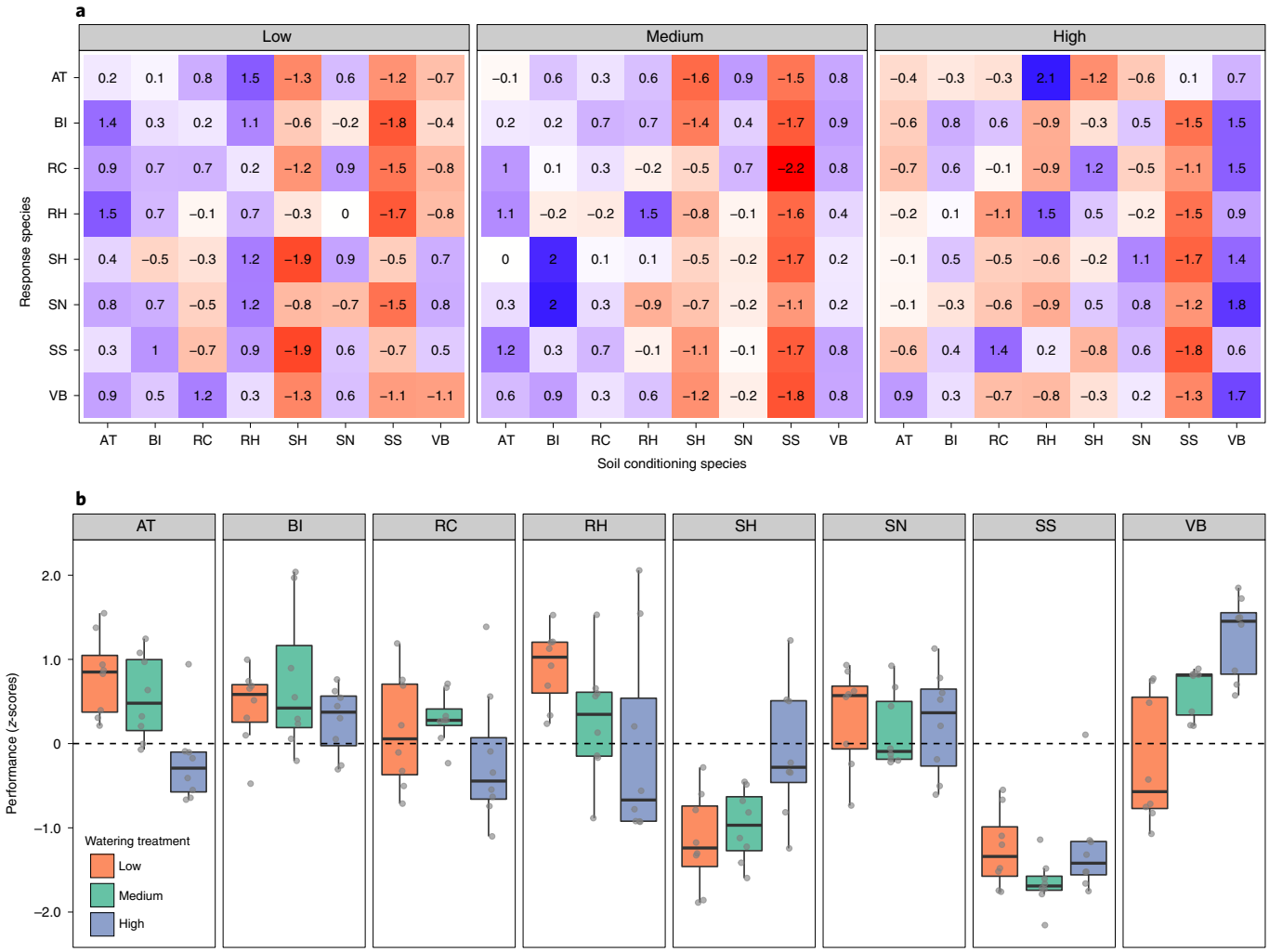

Fig. 2 | Standardized plant performance in conditioned soils under different watering treatments. a, Individual standardized performance of all response species by conditioning species combinations (watering treatments as indicated in the panel headers; negative values are indicated in red and positive values are indicated in blue). **b**, Standardized plant performance grouped by soil-conditioning species; box and whisker plots indicate the median, 25th/75th percentile and 1.5 × IQR. Species codes: AT is *Asclepias tuberosa*, BI is *Bothriochloa ischaemum*, RC is *Ratibida columnifera*, RH is *Rudbeckia hirta*, SH is *Sorghum halepense*, SN is *Sorghastrum nutans*, SS is *Schizachyrium scoparium* and VB is *Verbena brasiliensis*. $n = 64$ combinations of conditioning and response species per watering treatment; *z*-scores of plant performance were calculated separately for each response species within a watering treatment.

the watering treatments across the different species-specific conditioned soils on the performance of the subsequently growing plants. For example, while some plants conditioned the soil in a way that benefited the succeeding plants in dry conditions (*Asclepias* and *Rudbeckia*), others created soil that negatively affected subsequent plant performance (*Sorghum* and *Verbena*; Fig. 2b). Therefore, without further work relating these patterns to possible plant traits (for example, functional groups), changing environmental context can change the impact of a plant species on others within a community, contributing to the difficulty of predicting PSF-driven community dynamics[36].

Our observed changes in PSF were driven by interactions with soil biota. While the identity of the soil-conditioning species and the watering treatment affected soil nutrient composition and the concentrations of single nutrients in the inoculum soils (Supplementary Tables 2 and 3), we accounted for possible abiotic effects by adding only a small volume (5% by volume) of conditioned soil to a common sterile background soil[55]. In addition, we repeated the analysis for the three sterile blocks (Methods) and found no significant effect of the watering treatment on PSF (Supplementary Table 1). However, the statistical power of this analysis is low as it was only based on three replicate blocks. Overall, plants performed better in soils with living, compared with sterile, inocula across all species (Extended Data Figs. 2 and 3), implying that soil mutualists are an important component of the soil microbial community in this system.

Despite the apparent importance of mutualists as indicated by greater plant performance in living soils, the net outcome of PSF is caused by the combined effects of plant mutualists and antagonists[38]. While mutualists such as arbuscular mycorrhizal fungi may contribute to both negative[56,57] and positive PSF[58], pathogens are generally expected to cause negative PSF[59] because of the phylogenetic conservatism in pathogen–host associations causing species-specific negative conspecific effects[60]. The proliferation of pathogens and thus intensity of plant–pathogen interactions is assumed to increase with wetter conditions[61], creating more negative PSF. However, here we detected more negative PSF in drier conditions, consistent with other studies that found that dry soil conditions fostered negative PSF between species[62] and within species[51]. To better understand how changes in soil biota influenced PSF, we tested how soil water

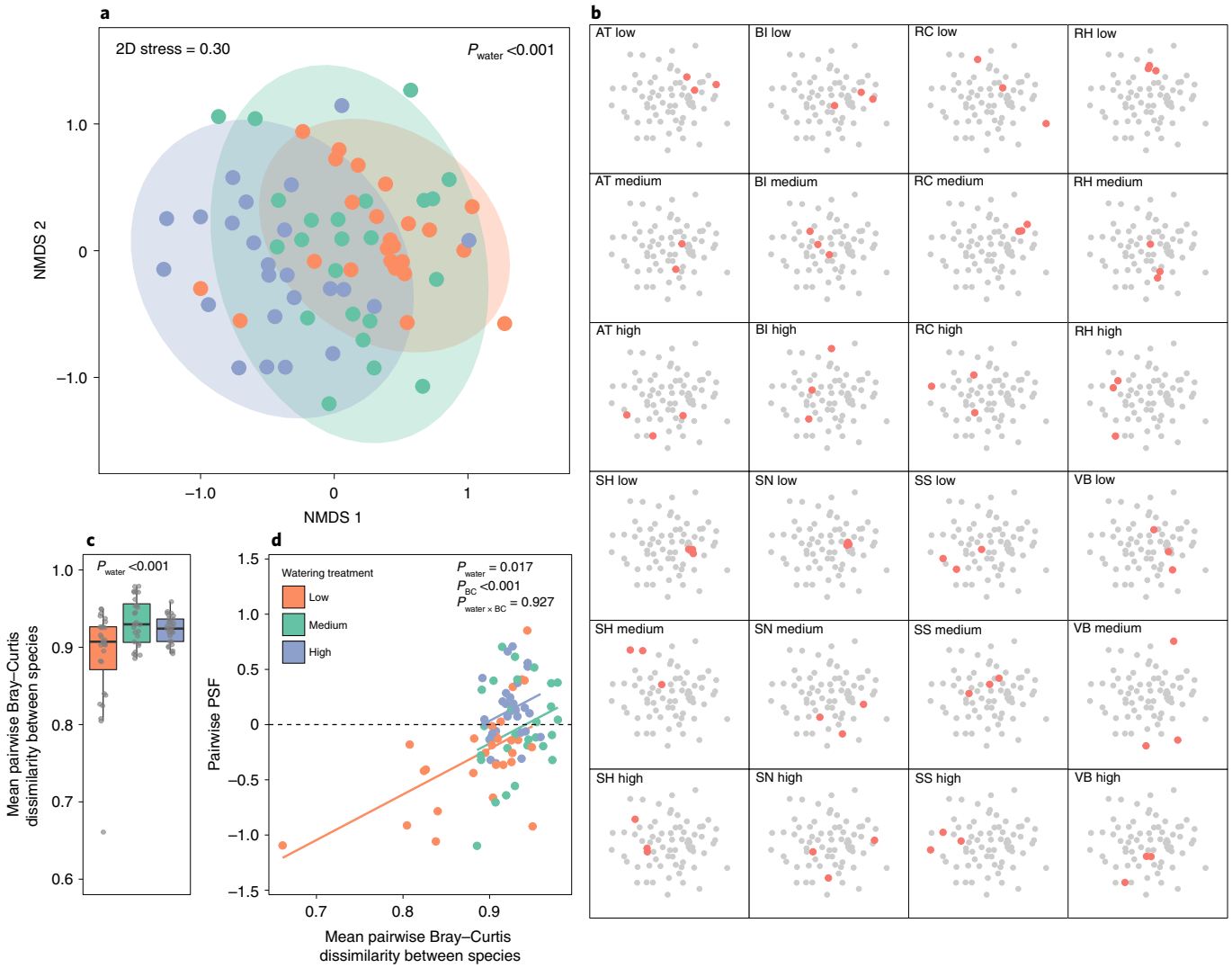

Fig. 3 | Non-metric multi-dimensional scaling (NMDS) of the fungal communities at the end of the conditioning phase and dissimilarities between the plant species. a, Each point represents one sample, and ellipses represent the 95% confidence limits of the multivariate *t*-distribution in the two-dimensional representation (NMDS1 and NMDS2). Significance of the watering treatment (P_{water}) was evaluated using permutational analysis of variance (Methods and Supplementary Table 5). **b**, All species by watering treatment combinations are highlighted in the small panels in red. **c**, Average pairwise Bray–Curtis dissimilarities of fungal communities between plant pairs in each watering treatment ($n = 28$ average pairwise Bray–Curtis dissimilarities per watering treatment). Box and whisker plots indicate the median, 25th/75th percentile and 1.5 × IQR. Significance of the watering treatment was evaluated using a linear mixed-effect model (Methods and Supplementary Table 1). **d**, Lines represent the fit of the linear regression between average pairwise Bray–Curtis dissimilarities of fungal communities and pairwise PSFs. Significance of the watering treatment (P_{water}), Bray–Curtis dissimilarity (P_{BC}) and their interaction ($P_{water \times BC}$) was evaluated using a linear mixed-effect model (Methods and Supplementary Table 1). Species codes: AT is *Asclepias tuberosa*, BI is *Bothriochloa ischaemum*, RC is *Ratibida columnifera*, RH is *Rudbeckia hirta*, SH is *Sorghum halepense*, SN is *Sorghastrum nutans*, SS is *Schizachyrium scoparium* and VB is *Verbena brasiliensis*. $n = 71$ soil samples; note that for *Asclepias tuberosa* in the medium watering treatment, only two samples were available.

content affected soil fungal communities at the end of the conditioning phase. We found no effects of the watering treatment on alpha diversity of the fungal communities, and only Simpson's diversity was significantly affected by the conditioning species identity (Supplementary Table 4 and Extended Data Fig. 4a,b). However, the composition of fungal communities was significantly affected by the interactive effect of the watering treatment and conditioning plant species identity (Fig. 3a,b and Supplementary Table 5).

Due to limitations in the fungal sequence data available for only three replicate blocks (Methods and Supplementary Table 6), we could not identify specific groups that might explain the differences in plant performance during the response phase. While the proportion of probable and putative pathogens seemed to increase in the low watering treatment for some conditioning plant species (for example, *Schizachyrium*), for other species it increased in the high watering treatment (for example, *Verbena*; Extended Data Fig. 4c,d). This partly contrasts with the observed pattern of plant performance in the respective conditioned soils; for instance, soils conditioned by *Verbena* in the high watering treatment exhibited a high proportion of probable and putative pathogens but largely benefited the subsequently growing plants relative to other soils (Fig. 2a,b).

While the role of specific fungal taxa remains unclear in our study, we tested the general expectation that more similar microbial

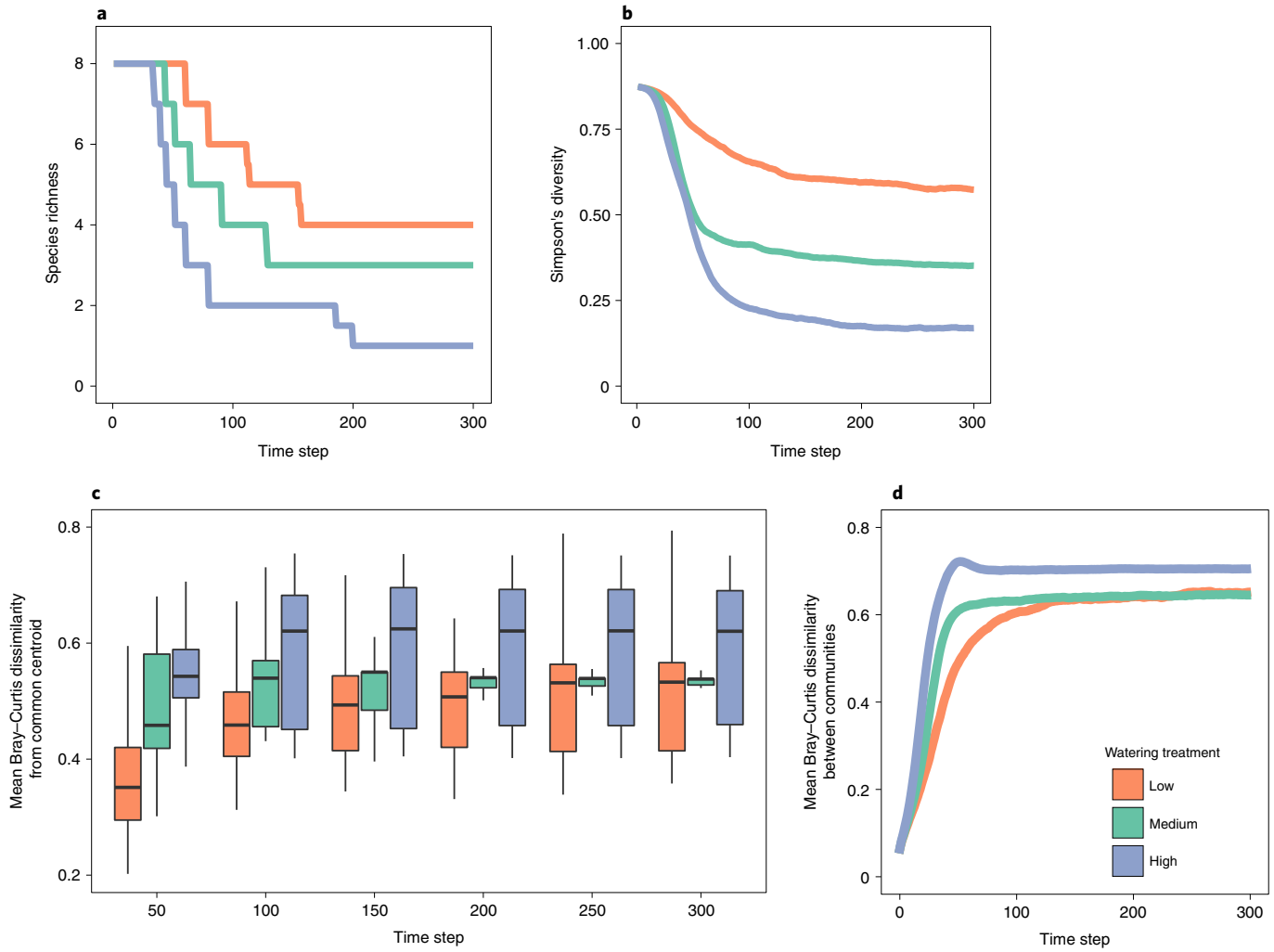

Fig. 4 | Dynamics of alpha and beta diversity of simulated plant communities under different watering treatments. a, Median species richness of the simulated communities. **b**, Average Simpson's diversity of the simulated communities. **c**, Dispersion of simulated communities around their common centroid based on Bray–Curtis dissimilarities after 50 generations; box and whisker plots indicate the median, 25th/75th percentile and 1.5 × IQR. **d**, Average Bray–Curtis dissimilarity between the simulated communities along 300 generations. $n = 200$ simulated plant communities per watering treatment.

community compositions between plants should lead to more neutral pairwise PSF regardless of whether mutualistic or antagonistic interactions dominate. Therefore, we calculated the average Bray–Curtis dissimilarity in fungal ASV composition for each plant pair based on three replicate blocks (Methods). Generally, we observed lower average dissimilarities in fungal community composition between the plant species in the low watering treatment compared with the medium and high watering treatments (Fig. 3c and Supplementary Table 1). The lower beta diversity might be a result of abiotic filtering towards more drought-tolerant taxa, whereas the high dissimilarities of the fungal communities between the plants in the medium and high watering treatments reflect a stronger plant-driven structuring of fungal communities during the conditioning phase. Lower pairwise dissimilarity in fungal community composition between plant species was linked to more negative pairwise PSF, which was especially noticeable in the in low watering treatment (Fig. 3d and Supplementary Table 1). This contrasts with the expectation that more similar microbial community compositions between plant species should lead to more neutral pairwise PSF, irrespective of weather mutualists or pathogens prevail in driving PSF.

According to the optimal allocation of resources, it is expected that plants invest photosynthates into soil biota, helping to access the most limiting resource[63]. With greater water availability, plants can invest more photosynthates into soil biota, subsequently increasing plant-driven selection via preferential allocation of resources towards the most beneficial mutualists[64]. Increased plant-driven selection during the conditioning phase might further explain the more distinct fungal communities between the plant species in the medium and high watering treatments. Assuming the eminence of mutualistic interactions, as indicated by the generally increased plant performance in the live soil blocks compared with the sterile blocks (Extended Data Figs. 2 and 3), this might create more positive PSF.

However, explaining the more negative PSF with increasing similarity in fungal community compositions between the plant species, especially in the low watering treatment, remains difficult and suggests further mechanisms in action not uncovered in our study. Attributing the net effect of the watering treatments to specific mechanisms of plant–soil biota interactions is challenging. Soil water differentially affects different groups of soil biota across a broad range of taxonomic levels[45–47] that may influence

PSF[65,66]. Further, the outcome of specific plant–microbe interactions can shift from mutualistic to antagonistic depending on the environmental context[67], so the same soil community could have differential impacts on plant performance under different soil water conditions during the response phase. For example, the stronger negative effects of conspecific conditioned soil at drier conditions may result from a higher susceptibility to host-specific pathogens of drought-stressed plants[48,49]. Conversely, plants in the high watering treatment may be better defended against soil pathogens, mitigating their potential to create negative PSF and may benefit more from host-specific mutualistic interactions that can generate positive PSF.

Theory implies that a change from negative to positive PSF in wetter conditions would destabilize species coexistence within plant communities[18,19]. To test this assumption, we conducted a spatially explicit simulation to model a hypothetical plant community. The simulation was parameterized with the relative performance of the plant species in the differentially conditioned soils as derived from the PSF experiment (Fig. 2a). We found that negative pairwise PSF at drier conditions created a more stable pattern of plant community diversity in contrast to the coexistence-destabilizing effect of positive PSF in wetter soil conditions. Species richness and Simpson's diversity of the simulated plant communities declined at accelerated rates over time in wetter conditions (Fig. 4a,b). The model assumed no dispersal limitation and annual life cycles (adult mortality = 1) for the simulated plants. This simplification was chosen to avoid arbitrary assumptions as our data do not reflect net differences in species-specific fitness or life history but only relative within species differences depending on the soil type. The more stable pattern at dry conditions was largely consistent across alternative parameterizations of plant mortality and the spatial scale of plant recruitment (Methods and Extended Data Fig. 5a). However, the decay of diversity in the medium watering treatment was as fast or even faster compared with the high watering treatment, especially at local scales of plant recruitment. When offspring recruitment is concentrated in close vicinity around conspecifics, strong intraspecific microbial effects in conspecific conditioned soil might get leveraged[23]. For instance, in the medium watering treatment, *Rudbeckia* experiences a particularly positive intraspecific microbial effect relative to the other species and often outperforms them in the simulation runs under the assumption of local recruitment. In the high watering treatment, two species, *Rudbeckia* and *Verbena*, experience relative strong positive intraspecific microbial effects and often stably coexist at the landscape scale in the simulations despite a positive pairwise feedback (Extended Data Fig. 5b).

In addition to decreasing alpha diversity, the dynamics of community assembly were also more unpredictable in wet conditions as indicated by a higher dispersion in community composition among the simulated plant communities (Fig. 4c) and a faster increase in average community dissimilarity (Fig. 4d). Small random differences in species abundances in the initial communities (analogous to priority effects; for example, due to stochastic dispersal events) are amplified by positive PSF benefiting initially more abundant species over less abundant species. Thus, more positive PSF in wetter conditions not only accelerates the erosion of diversity within plant communities but also renders plant community dynamics less predictable. This implies that the impact of priority effects[68,69] on community assembly might increase if environmental change leads to more positive PSF.

Our study imposed the watering treatments consistently onto both phases of the PSF loop and thus helps to indicate a general direction of what to expect from future baseline shifts in average precipitation. Given the results, we would expect less stable patterns of diversity within plant communities and less predictable dynamics of community assembly under wetter conditions. However, climate change is expected to also increase the temporal variability of precipitation patterns. Periods of more extreme dry and wet conditions might alternate and so would the effect of PSF as a diversity stabilizing or destabilizing mechanism within a given plant community. Especially for short-lived plants with a high generational turnover, high frequency in precipitation alterations could subject the phase of soil conditioning by one generation and the response phase of the succeeding generation to contrasting soil water conditions as targeted in studies focusing on differences in soil water during one of the two phases[51–53].

Predicting the consequences of environmental change for ecological communities is a challenge that must be met to manage and mitigate the effects of climate change. Our study highlights that plant–soil biota interactions measured as pairwise PSF may be used to predict how plant communities will change in response to differences in climate. The range of temporal scales at which climate change-driven alterations in precipitation patterns manifest, from increased short-term variability to long-term baseline shifts in average precipitation, calls for further studies that focus on the various temporal windows. In addition, future work should examine how the roles of root-associated fungal assemblages and saprotrophs (that is, via litter-mediated feedbacks) might change with precipitation change and how other coexistence mechanisms such as storage effects might act in conjunction with PSF. Integrating the results to better understand the context dependency of PSF will be an important step forward to better predict the impact of future climate change on ecosystems as PSF has successfully been used to predict patterns of plant community composition and dynamics in many systems.

Methods

Conditioning phase. We conducted a full factorial pairwise PSF experiment where we subjected eight common prairie plant species (*Asclepias tuberosa* L., *Bothriochloa ischaemum* (L.) Keng, *Ratibida columnifera* (Nutt.) Wooton & Standl., *Rudbeckia hirta* L., *Schizachyrium scoparium* (Michx.) Nash, *Sorghum halepense* (L.) Pers., *Sorghastrum nutans* (L.) Nash and *Verbena brasiliensis* Vell.) to soil microbial communities that were conditioned by their conspecifics or heterospecifics in all pairwise combinations. To assess the effect of different precipitation regimes, we conducted both phases, the conditioning phase and the response phase, under three different watering treatments. The treatments relate to average and extremely high and low precipitation levels of the local area (Supplementary Fig. 1a).

Prior to planting, the seeds (Native American Seeds) were surface sterilized in a 0.45% NaOCI solution for 5 min, thoroughly rinsed with deionized water and germinated on sterilized sand. We transferred single seedlings to 1 l deepots (D60L, Stuewe & Sons Inc.) filled with common non-sterile background soil. The pots were vertically suspended in racks to minimize cross-contamination. The background soil consisted of a sand/field soil mixture in a 2:1 ratio by volume. Field soil was obtained from a coastal prairie at the University of Houston Coastal Center (La Marque, TX, USA). Additionally, we added 10 ml from a suspension of fresh field soil (3.5 g soil dry equivalent) and thoroughly mixed it into the upper 5 cm of each pot to provide a common baseline microbial community. All pots were saturated to water holding capacity (day 0) prior to planting (day 3). Initial soil water after saturating the pots was sufficient for the tiny plants to establish before we started the different watering treatments (day 28). From then on, the plants were watered three times a week with fixed amounts of water corresponding to the watering treatments (low: 10 ml, medium: 25 ml, high: 50 ml). We monitored the gravimetric soil water content during the conditioning phase in weekly to biweekly intervals (Supplementary Fig. 1b).

The experiment was set up in nine replicate blocks, each holding all combinations of plant species and watering treatments, resulting in a total of 216 pots (8 species × 3 watering treatments × 9 replicates). All of the following experimental procedures and measurements were done in correspondence to the replicate block order. The plants were grown for a total of 140 days (115 days under the different watering treatments) in a climate-controlled greenhouse kept at 26.7 °C at the University of Houston after which we harvested aboveground and belowground biomass (Extended Data Fig. 6). We clipped the plant shoots at the base of the plant and rinsed the roots from adhering soil. The plant material was dried at 60 °C for 72 h before weighing. The conditioned soil of each pot was collected and individually stored. The soil was kept at 4 °C for two months prior to use as inocula for the response phase. The conditioning phase took place from July 2019 to November 2019.

Response phase. For the response phase, we grew the same eight species in 0.3 l deepots (D16H, Stuewe & Sons Inc.) filled with sterile, common background soil

that was inoculated with the live soils collected from the conditioning phase. We used the same sand/soil mixture as for the conditioning phase, sterilized by double autoclaving at 121 °C for 60 min with a 24 h rest period between sterilization cycles. We mixed 15 ml live inoculum soil into the upper 2 cm of the background substrate, which corresponds to 5% live inoculum by volume to focus on biotic mediated PSFs and minimizing potential abiotic effects[55]. We transferred single seedlings that were propagated from surface sterilized seeds as described above into the pots.

We replicated each combination of conditioned soil and plant species for the three watering treatments nine times in correspondence to the replicate block order of the conditioning phase[70]. Additionally, we set up sterile versions of three full replicate blocks (3rd, 6th and 9th blocks). These sterile blocks were set up in the same way as the live soil blocks but with the respective soil inocula sterilized by double autoclaving as described above. Thus, the response phase consisted of a total of 2,304 pots (8 conditioned soils × 8 plant species × 3 watering treatments × (9 + 3) replicate blocks). We started the watering treatments immediately to ensure treatment constancy across both phases of the experiment. The plants were watered three times a week in correspondence to the watering treatments during the conditioning phase yet with modified fixed amounts to account for the smaller pot volume and a gradual decline of the soil water content over time as observed in the conditioning phase (Supplementary Fig. 1b; low: 10 ml, medium: 20 ml, high: 30 ml). The plants were grown for a total of 105 days (105 days under different watering treatments) in a climate-controlled greenhouse at 26.7 °C after which we harvested aboveground and belowground biomass as described above (Extended Data Fig. 2). The response phase took place from January 2020 to June 2020.

Soil nutrient analyses. At the end of the conditioning phase, soil samples from five replicate blocks of each plant species and watering treatment (approximately 1,000 mg) were collected. Each pot of soil was homogenized and a subsample (approximately 50 ml) was sent to Texas A&M AgriLife Extension Service Soil, Water and Forage Testing Laboratory (College Station, TX, USA) for nutrient analysis. Soils were dried at 65 °C for 16 h and pulverized through a 2 mm open-mesh sieve. Nutrients including P, K, Ca, Mg, S and Na were extracted using Mehlich III extractant and determined by inductively coupled plasma spectroscopy[71]. Soil pH and electrical conductivity were calculated using a 1:2 soil water extract using deionized water and a hydrogen selective electrode and conductivity probe[72,73]. Nitrate–nitrogen (NO_3–N) was extracted from soils using a 1 M KCl solution. Nitrate was determined by reduction of nitrate (NO_3–N) to nitrite (NO_2–N) using a cadmium column followed by spectrophotometric measurement[74] (Supplementary Table 3).

DNA extraction and sequencing. We used next-generation sequencing to capture the fungal community structure for post-conditioned soils. Originally, we used the first five replicate blocks of each species by watering treatment combination (120 samples) plus 30 additional samples (5 samples of the common background soil, 10 samples of the initial soil suspension used for the conditioning phase and 15 samples from empty pots containing only the background soil plus the initial soil suspension). DNA was extracted from a 0.25 g subsample of lyophilized soil by using DNeasy PowerSoil Pro Kit (catalogue number 47016, Qiagen). Quality and concentration of DNA were checked for each sample using a Qbit fluorometer (Thermo Fisher Scientific) and samples were diluted to 1 ng μl^{-1} as per instructions in the library preparation kit. Libraries of the fungal internal transcribed spacer (ITS) region were prepared using the QIAGEN QIAseq ITS region panels using phased primers according to the kit's protocol (catalogue number 333845, Qiagen). The polymerase chain reaction products of all samples (150 total) were normalized to equimolar amounts and sequenced for 500 cycles on the Illumina MiSeq PE300 platform. However, due to an error during library preparation, we obtained valid samples from only the first three replicate blocks resulting in a total of 71 samples (3 samples per conditioning plant species in each watering treatment; note that for *Asclepias tuberosa* in the medium watering treatment, only 2 samples were available after filtering), which the results reported here are based on.

Bioinformatics. We obtained 1,293,067 single-end forward-read sequences across all samples (72 of the 150 samples in the MiSeq run) for an average of 16,163 reads per sample. Two samples had reads well below the other samples (8 and 764 read sequences) and were removed from the dataset. We analysed the single-end forward-read sequences with DADA2 (ref. [75]) in QIIME2 version 2020.8 (ref. [76]) to identify amplicon sequence variants (ASVs)[77]. Reads with more than two errors were discarded and reads were truncated at the first instance of a quality score less than or equal to 2. We assigned taxonomy to representative ASV sequences using a QIIME2 classifier trained on the UNITE ITS reference sequences[78]. After filtering, samples were represented by an average of 15,980 reads (86,057 maximum; 2,275 minimum), and 13,782 reads (66,447 maximum; 1,984 minimum) with an average read length of 275 base pairs after removing chimeric sequences. This resulted in 11,342 total ASVs. ASVs that occurred in less than 2 samples[79] were excluded from analyses, resulting in a total of 851 ASVs.

We first used FUNGuild to assign fungal guilds to the ASVs[80]. Due to the low resolution of the data (Supplementary Table 6), we limited the assignment to putative and probable pathogens. For taxa that were 'highly probable' or 'probable', we used the FUNGuild assignments and classified them as probable pathogens. In cases where FUNGuild returned multiple probable guilds, we conducted a literature search to determine whether the guild was more likely pathogenic or saprotrophic. For ASVs that were identified to genus or species, we supplemented FUNGuild designations with a search of the primary literature to characterize additional plant pathogens (*Fusarium spp*., *Alternaria spp*. and *Periconia macrospinosa*)[79]. Following the same strategy, we additionally classified putative pathogens including taxa with a 'possible' confidence ranking.

Calculating pairwise PSF. We applied a model fitting approach to estimate average plant performance measures (compound of survival rates and biomass production) in the nine blocks with live inocula by using zero-inflated Gamma mixed-effect models (R package glmmTMB version 1.0.2; ref. [81]). Plant mortality (biomass = 0; the zero-inflated component) was fitted to a binomial distribution using a logit link function. Total biomass production of the surviving plants (non-zero continuous variable; the conditional component) was fitted to a Gamma distribution using a log link function. We accounted for the experimental block as random intercept. We fitted separate models for each watering treatment including only the plant species × soil type interaction term and no intercept. Thus, the fixed effect coefficients represent the average mortality and the average biomass production of the surviving plants for each plant–soil combination at the respective link scale. To get a single measure, we calculated plant performance from the model coefficients at the response scale as $\mu \times (1-p)$, where μ is the average biomass of the surviving plants (fit of the conditional Gamma component) and p is the occurrence probability of zero biomass values (fit from the zero-inflated binomial component). From there, pairwise PSF was calculated as following[17]:

$$I_s = \ln(\alpha_A) - \ln(\alpha_B) - \ln(\beta_A) + \ln(\beta_B)$$

where α_A is the performance of species A in its own soil, α_B is the performance of species A in the soil of species B, β_A is the performance of species B in the soil of plant species A and β_B is the performance of species B in its own soil. Thus, each value of I_s represents the average pairwise PSF of a given species pair in the respective watering treatment. To get estimates of uncertainty for pairwise I_s values, we applied parametric bootstrap (R package lme4 version 1.1–26; ref. [82]) to the zero-inflated Gamma models using 10,000 iterations. We performed the downstream calculation of I_s for each iteration and calculated 95% confidence intervals based on the bootstrap replicates.

We calculated ASV richness and Simpson's diversity as indicators of fungal alpha diversity. We tested for the effects of conditioning species identity, watering treatment and their interaction using a linear model. Simpson's diversity was transformed to effective species numbers prior to statistical testing[83]. As ASV data were available for only three replicate blocks, we accounted for the replicate block as an additional fixed effect in the linear model. We used Bray–Curtis dissimilarities based on Hellinger transformed ASV counts to test for differences in fungal community composition among the plant species at the end of the conditioning phase using permutational analyses of variance (R package vegan version 2.5–7; ref. [84]) based on 1,000 permutations. We fitted the replicate block as a fixed effect before conditioning species identity, watering treatment and their interaction.

We further calculated the average pairwise Bray–Curtis dissimilarities (based on three replicates per species pair) between all plant species within the watering treatments and tested for the effect of the watering treatment on the average dissimilarities using a linear mixed model (LMM) accounting for the specific species pair as random intercept. We tested for the effect of the soil watering treatment and the average Bray–Curtis dissimilarities between the plant species and their interaction on average pairwise PSF using a LMM accounting for the specific species pair as random intercept. To test if the effect of the watering treatment was driven by soil biota interactions, we tested for its effect on pairwise PSF calculated as described above but based on the three sterile blocks. Significance of fixed effects for the LMMs was assessed using single-term deletions followed by *F*-tests of the nested models using the Kenward–Roger method for computing the denominator degrees of freedom (R package lmerTest version 3.1–3; ref. [85]).

Simulation. We ran a simulation model to estimate how changes in pairwise PSF driven by the watering treatments would translate into plant community dynamics. We simulated a hypothetical community of eight plant species using Netlogo version 6.1.1 (ref. [86]). The simulated area is defined as a rectangular grid of 40 by 40 cells. Each cell can be occupied by a single plant individual at a time. The cells hold a soil history corresponding to the identity of the previous plant occupying the given cell. Each individual plant has a fitness value depending on the soil history of the cells it is occupying. The fitness values for each plant by soil history combination are drawn from the relative performance values of the respective watering treatments. The basic model assumed no dispersal limitation and annual life cycles (adult mortality = 1) for the simulated plants. This simplification was chosen to avoid arbitrary assumptions as our data do not reflect net differences in species-specific fitness or life history but only relative within species differences depending on the soil type. Therefore, we calculated the relative performance as *z*-scores for each species within a watering treatment (Fig. 2a). These values were

mapped equidistantly to an interval from 1 to 100 to yield strictly positive values to be used as weights in the recruitment procedure. This entails that all species have an equal average fitness and only their relative fitness changes, depending on the soil history. Initially each cell gets populated with a single plant. The plant's species identity is randomly selected from the pool of the eight species with equal probabilities. All plants of this initial generation have an equal fitness of one. At each time step (generation), the following procedure occurs:

The global fitness of a species is calculated by summing up the fitness across all individuals of the respective species in the entire simulated area. This follows the assumption that a species' contribution to the pool of recruits scales with its abundance and the fitness of the plant individuals. The soil history of the cells is set to the species identity of the currently occupying plant. All plants die, and the empty cells get populated with a new plant. The species identity is randomly selected from the pool of all species with weights equal to the species' global fitness. The individual fitness of the new recruits is set according to the relative performance value of the given species in the given soil. To estimate model sensitivity to this assumption, we ran additional simulations with varying fixed mortality rates for adult plants (0.75, 0.5 and 0.25) and limiting the spatial scale at which recruitment occurs. For the local recruitment procedure, we calculated the local fitness of the species in a given cell by summing up the fitness of all conspecific individuals of only the neighbouring cells up to first degree or up to fifth degree. The species identity of the newly recruited plant in the respective cell was then randomly selected from the species pool with weights equal to the species' local fitness at the given location (Extended Data Fig. 5a).

We ran a total of 200 simulations across 300 time steps for each watering treatment and parameterization using different random seeds for each run (R package nlrx version 0.4.2; ref. [87]). The numbers of individuals for all species were recorded at each time step, and species richness and Simpson's diversity were calculated to assess how changes in pairwise PSF affects the maintenance or erosion of alpha diversity within the simulated plant communities[84]. We further assessed if the stochasticity of community dynamics (that is, predictability) is affected by the watering treatments. We calculated the Bray–Curtis dissimilarities between the 200 simulated communities for each watering treatment and parameterization at each generation and the distance of the single communities to their common centroid every 50 generations[84].

For data acquisition we used Microsoft Excel version 16, and data preparation and visualization was done using the functionalities of the R package tidyverse version 1.3.0 (ref. [88]). All analyses were performed in R version 4.0.2 (ref. [89]).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data associated with this study is available in the Open Science Framework repository: https://doi.org/10.17605/osf.io/x2wds. The sequences generated for this study can be found in GenBank BioProject PRJNA804565.

Code availability

The code for the simulation model is available in the Open Science Framework repository: https://doi.org/10.17605/osf.io/x2wds.

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Author contributions

K.M.C. acquired funding and initiated the study. J.-H.D., N.C.L. and K.M.C. participated in the study design. J.-H.D. and N.C.L. performed the greenhouse experiment and data collection. N.C.L. and K.M.C. performed the bioinformatics for fungal community sequencing. N.C.L. performed the nutrient analysis. J.-H.D. performed the data analyses and wrote the simulation model. J.-H.D. wrote the initial manuscript with significant edits from K.M.C. and N.C.L. All authors contributed to revisions.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Jan-Hendrik Dudenhöffer.

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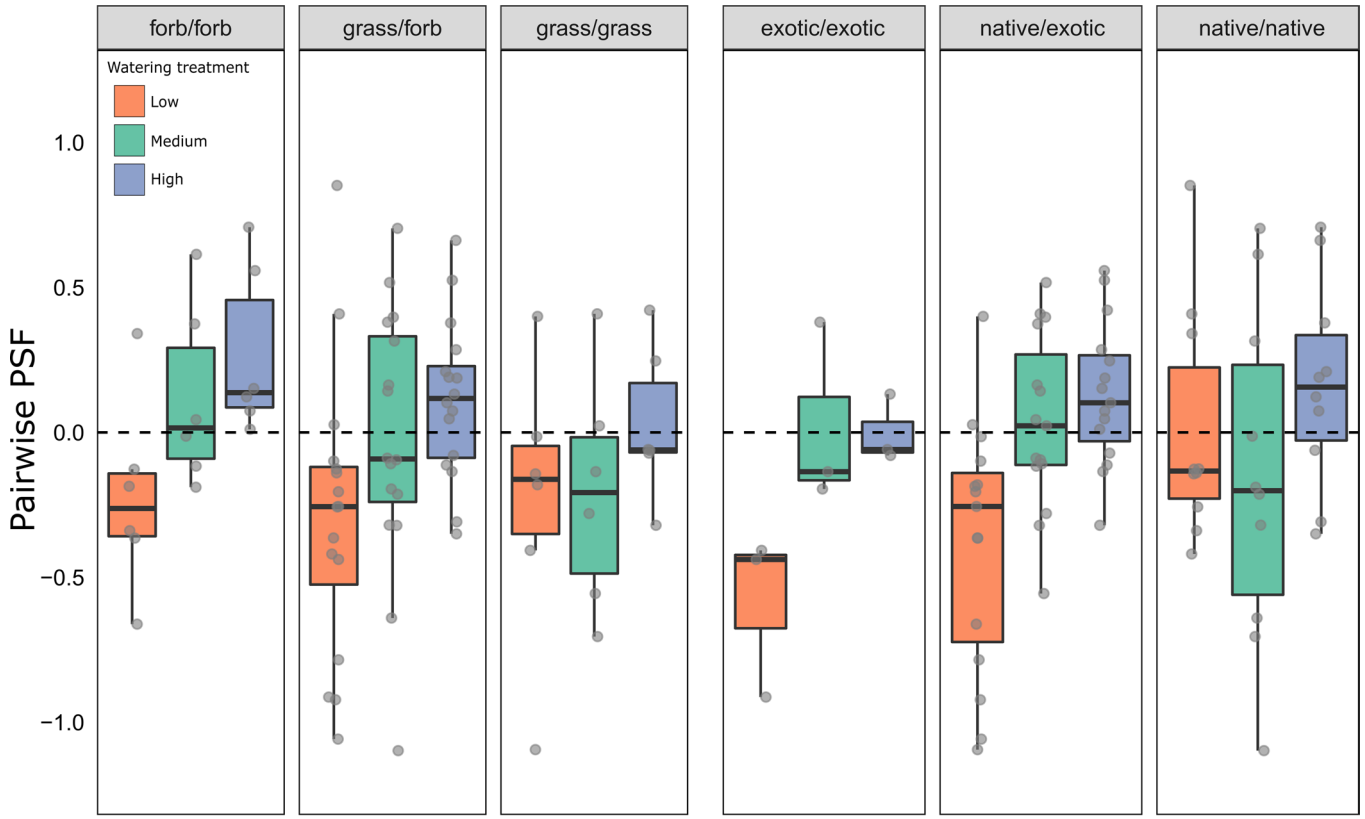
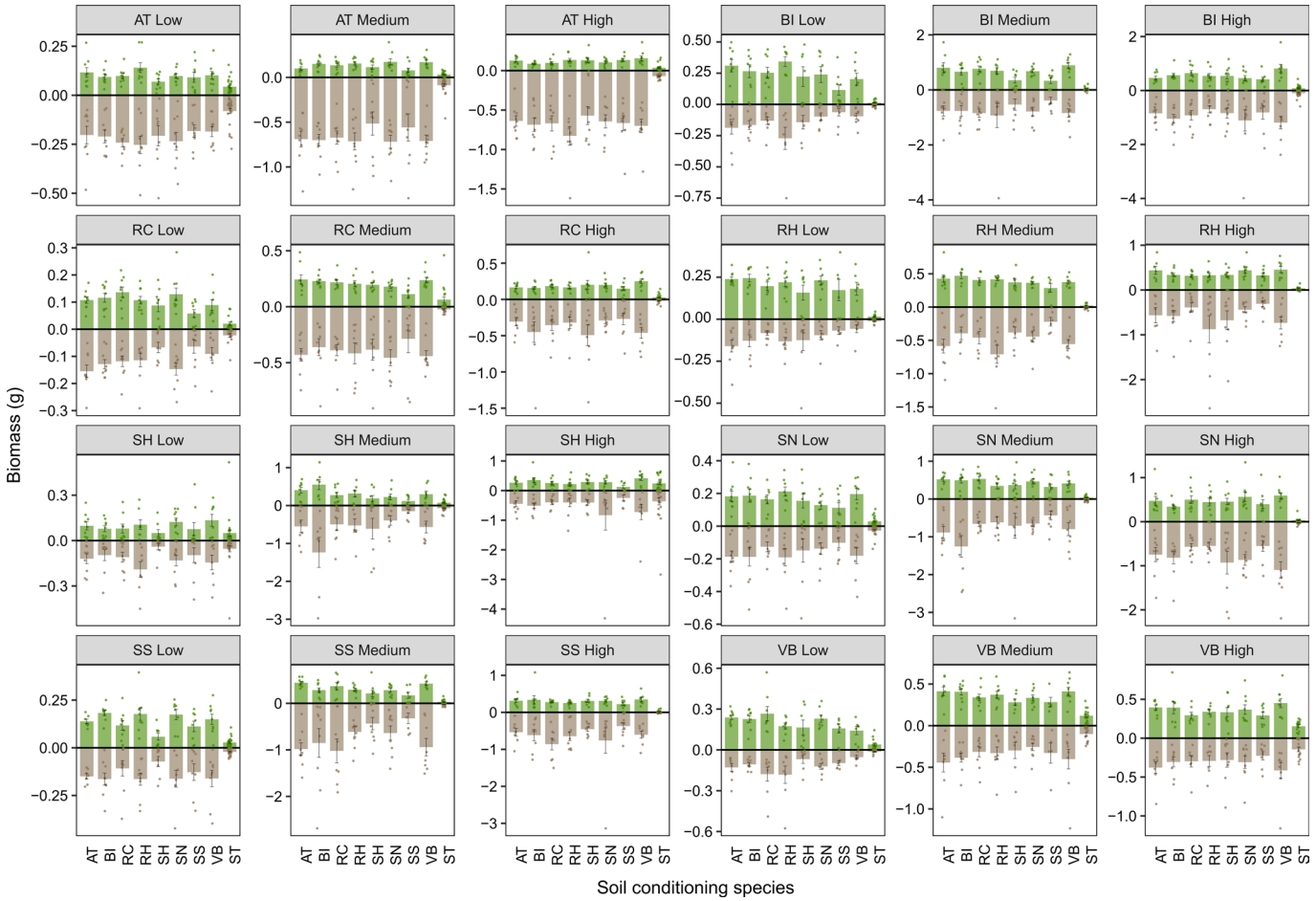
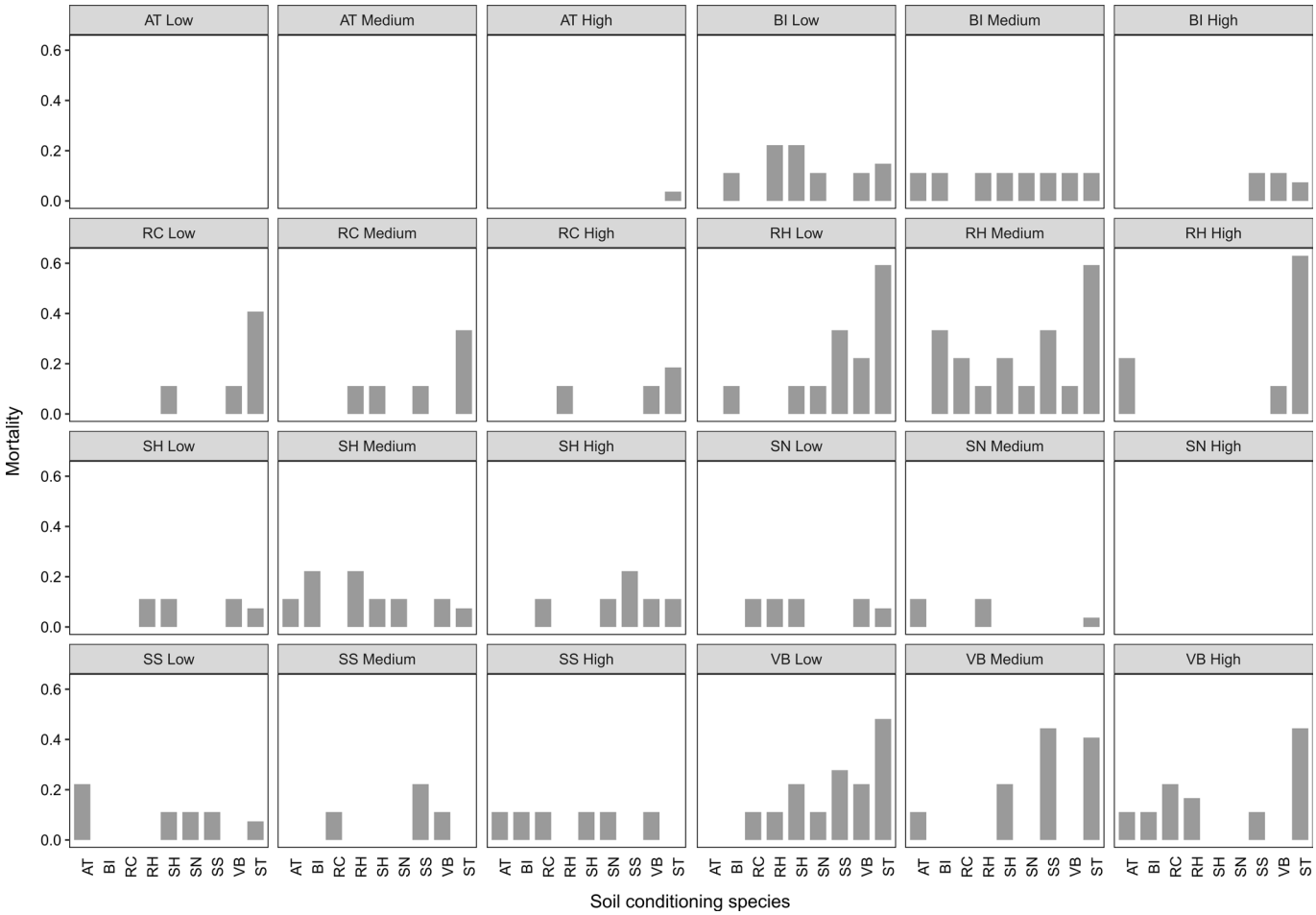


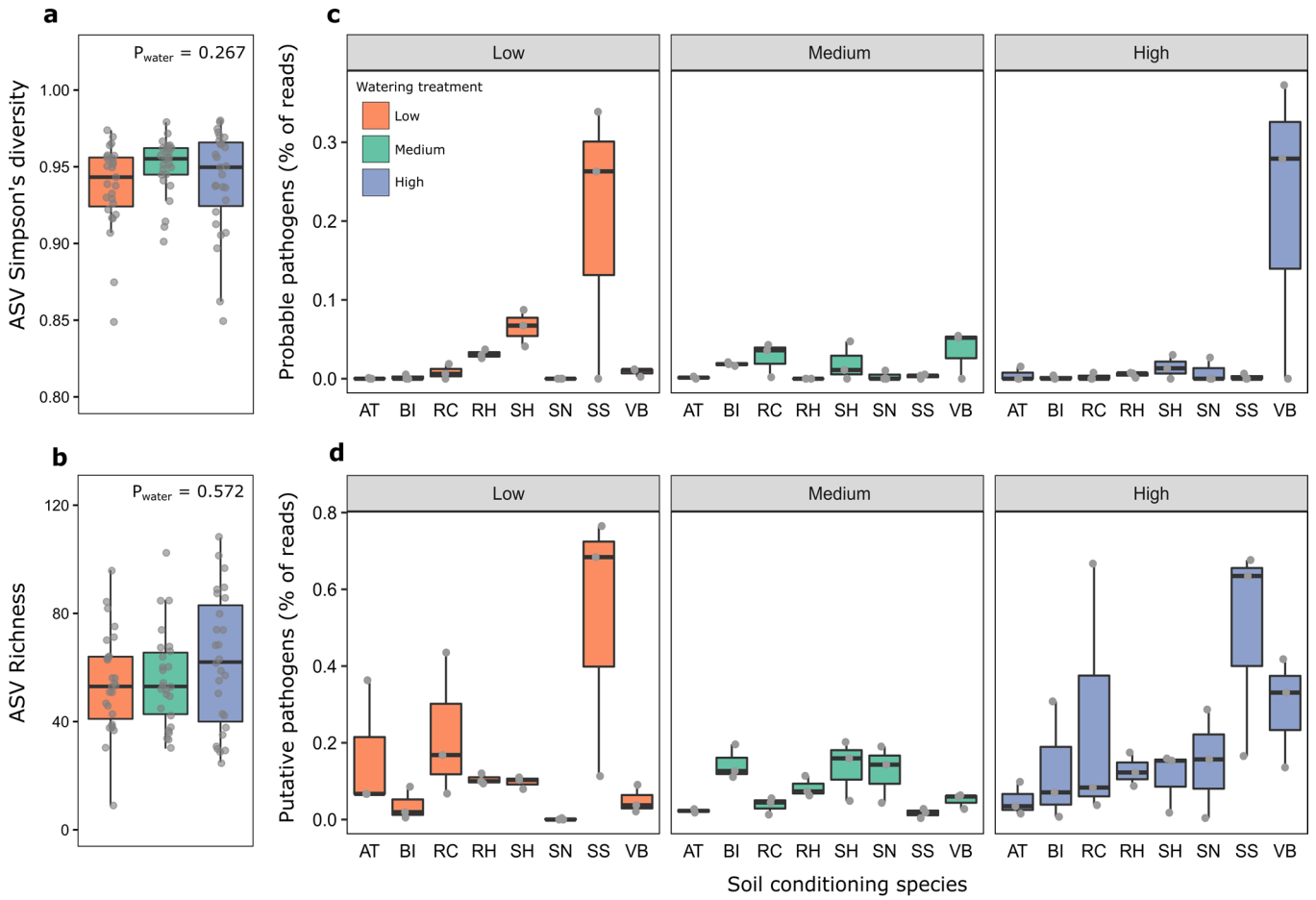
Extended Data Fig. 1 | Pairwise plant–soil feedbacks by growth form and naturalization status. Pairings of growth form (grass vs. forb) and naturalization status (native vs. exotic) are indicated in the panel headers (*n* forb/forb = 6, *n* grass/forb = 16, *n* grass/grass = 6, *n* exotic/exotic = 3, *n* native/exotic = 15, *n* native/native = 10). Box-whisker plots indicate the median, 25th/75th percentile and 1.5 x IQR.



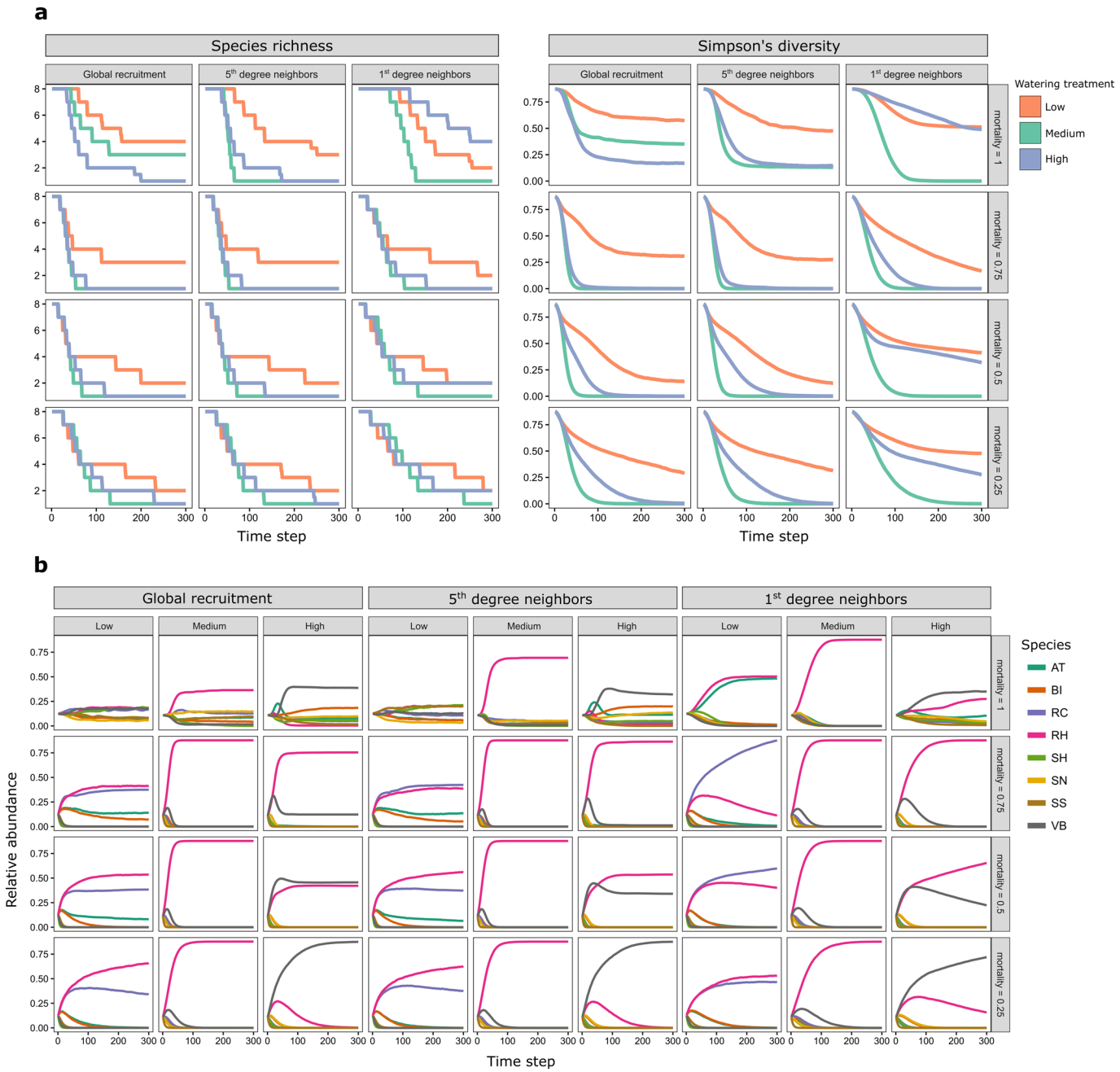
Extended Data Fig. 2 | Plant biomass of the response phase. Bars above and below the zero intercept represent aboveground biomass and belowground biomass of the surviving plants respectively (Mean ± SE). Focal species and watering treatment are indicated in the panel headers and soil conditioning species at the x-axes. Species codes: AT = *Asclepias tuberosa*, BI = *Bothriochloa ischaemum*, RC = *Ratibida columnifera*, RH = *Rudbeckia hirta*, SH = *Sorghum halepense*, SN = *Sorghastrum nutans*, SS = *Schizachyrium scoparium*, VB = *Verbena brasiliensis*, ST = sterilized inocculum. *n* = initially 9 plants per conditioned soil in each watering treatment; note that only surviving plants are represented here.



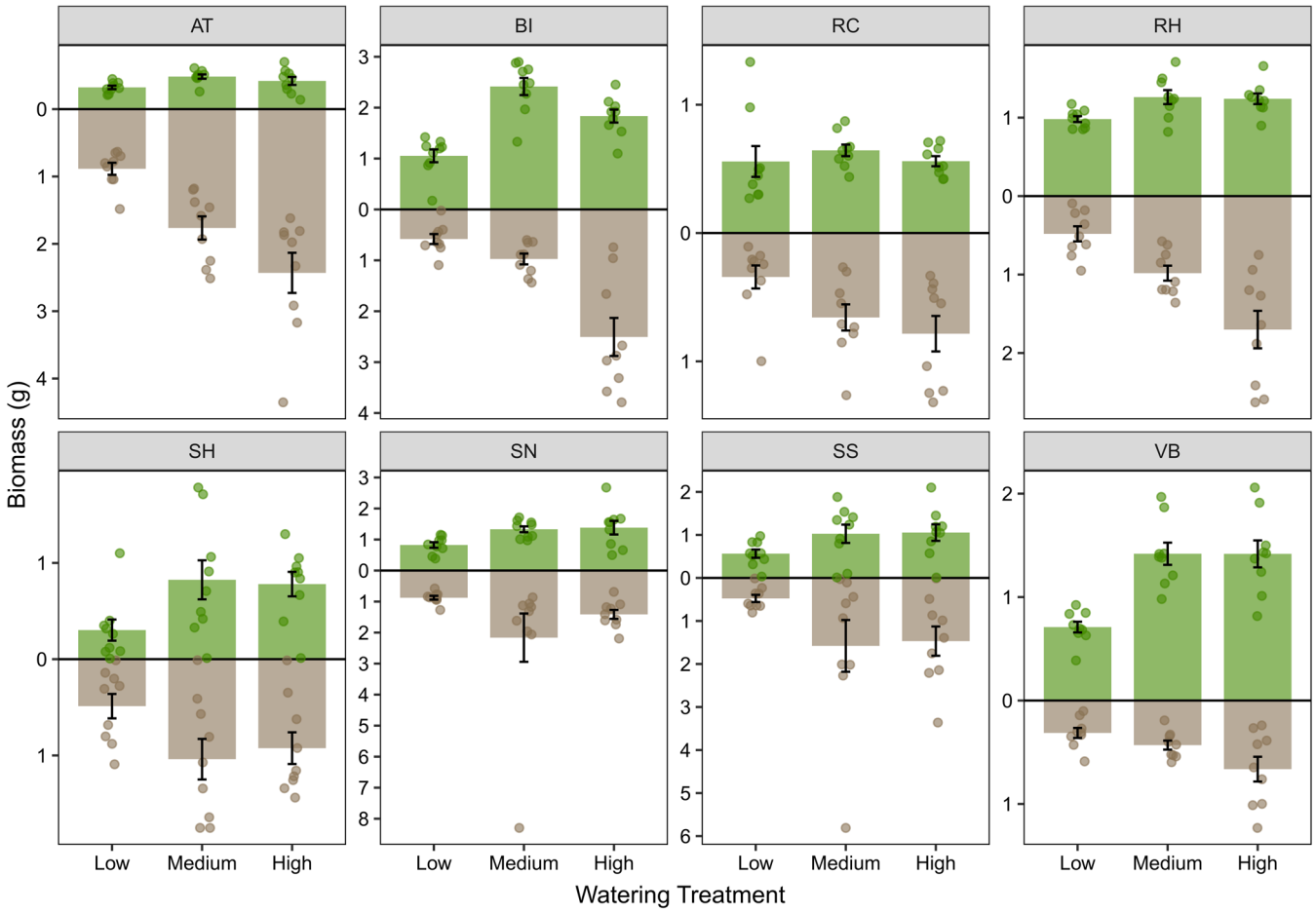
Extended Data Fig. 3 | Plant mortality of the response phase. Bars represent plant mortality rates. Focal species and watering treatment are indicated in the panel headers and soil conditioning species at the x-axes. Species codes: AT = *Asclepias tuberosa*, BI = *Bothriochloa ischaemum*, RC = *Ratibida columnifera*, RH = *Rudbeckia hirta*, SH = *Sorghum halepense*, SN = *Sorghastrum nutans*, SS = *Schizachyrium scoparium*, VB = *Verbena brasiliensis*, ST = sterilized inocculum. $n = 9$ plants per conditioned soil in each water treatment.



Extended Data Fig. 4 | Alpha diversity and relative pathogen abundance of fungal communities at the end of the conditioning phase. (a) Simpson's diversity of fungal ASVs, and **(b)** richness of fungal ASVs. Significance of the watering treatment (P_{water}) was evaluated using linear models (Methods and Supplementary Table 4). **(c)** Relative abundance of probable pathogens, and **(d)** relative abundance of putative pathogens. Box-whisker plots indicate the median, 25th/75th percentile and 1.5 x IQR. Species codes: AT = *Asclepias tuberosa*, BI = *Bothriochloa ischaemum*, RC = *Ratibida columnifera*, RH = *Rudbeckia hirta*, SH = *Sorghum halepense*, SN = *Sorghastrum nutans*, SS = *Schizachyrium scoparium*, VB = *Verbena brasiliensis*. *n* = 71 soil samples; note that for *Asclepias tuberosa* in the medium watering treatment only two samples were available.



Extended Data Fig. 5 | Simulation results under alternative parameterizations of plant mortality and the spatial extent of recruitment under different watering treatments of simulated plant communities. (a) Alpha diversity (median species richness and average Simpson's diversity). **(b)** Average relative abundance of the single species. Species codes: AT = *Asclepias tuberosa*, BI = *Bothriochloa ischaemum*, RC = *Ratibida columnifera*, RH = *Rudbeckia hirta*, SH = *Sorghum halepense*, SN = *Sorghastrum nutans*, SS = *Schizachyrium scoparium*, VB = *Verbena brasiliensis*. *n* = 200 simulated plant communities per watering treatment and parameterization.



Extended Data Fig. 6 | Plant biomass of the conditioning phase. Bars above and below the zero intercept represent aboveground biomass and belowground biomass of the surviving plants respectively (Mean ± SE). The focal plant species is indicated in the panel headers; note the different y-axis scaling. Species codes: AT = *Asclepias tuberosa*, BI = *Bothriochloa ischaemum*, RC = *Ratibida columnifera*, RH = *Rudbeckia hirta*, SH = *Sorghum halepense*, SN = *Sorghastrum nutans*, SS = *Schizachyrium scoparium*, VB = *Verbena brasiliensis*. $n = 9$ plants per species in each watering treatment.

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Corresponding author(s): Jan Hendrik Dudenhoeffer

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Reporting Summary

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Data acquisition was done using Microsoft Excel version 16.0. The simulation model was performed using Netlogo version 6.1.1 and the r-package nrlx version 0.4.2. Data preparation and visualization was done using the functionality of the r-package tidyverse version 1.3.0. All analyses and data operations were performed in R version 4.0.2. The code of the simulation model is available in the Open Science Framework repository: https://doi.org/10.17605/osf.io/x2wds
Data analysis	Amplicon sequence variants were identified using DADA2 in QIIME2 version 2020.8. Statistical models were fitted using the r-packages glmmTMB version 1.0.2 and lme4 version 1.1-26 with additional functionality from the r-package lmerTest version 3.1-3. Multivariate analyses were performed using the r-package vegan version 2.5-7.All analyses were performed in R version 4.0.2.

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Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Data associated with this study is publicly available in the Open Science Framework repository: https://doi.org/10.17605/osf.io/x2wds

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We conducted a full factorial, pairwise plant-soil-feedback experiment where we subjected eight common prairie plant species to soil microbial communities that were conditioned by their conspecifics or heterospecifics in all pairwise combinations. To assess the effect of different precipitation regimes we conducted both phases, the conditioning phase and the response phase, under three different water treatments. The experiment was conducted in a greenhouse at the University of Houston.
Research sample	The plant species used in this study were: Asclepias tuberosa L., Bothriochloa ischaemum (L.) Keng, Ratibida columnifera (Nutt.) Wooton & Standl., Rudbeckia hirta L., Schizachyrium scoparium (Michx.) Nash, Sorghum halepense (L.) Pers., Sorghastrum nutans (L.) Nash, and Verbena brasiliensis Vell., representing species common to Southeastern United States coastal prairies. The seeds were obtained from a local supplier (Native American Seeds, Junction, TX, USA).
Sampling strategy	Each unit of measurement (i.e. the specific combination of plant species x conditioned soil x watering treatment) was replicated 9 times. This level of replication is in the common range of published plant-soil feedback studies. The soils from the conditioning phase ware kept individually and used as inoculum avoiding soils to be mixed across experimental units.
Data collection	At the end of the conditioning phase plant biomass was harvested (below- and aboveground). Data collection was performed by the authors with the help of Shoaib Y. Aziz, Kwame Boakye, Shileen Durand-Luecke, Jeremy Nicholas, Olubunmi Oladapo & Anja Soelter (as stated in the acknowledgements). At the end of the conditioning phase, soil samples from five replicate blocks of each plant species and watering treatment (approximately 1000 mg) were collected. Each pot of soil was homogenized and a subsample (approximately 50 mL) was sent to Texas A&M Agrilife Extension Soil, Water and Forage Testing Laboratory (College Station, TX, USA) for nutrient analysis. We used next generation sequencing to capture fungal community structure for post-conditioned soils. We used the first 3 replicate blocks of each species by watering treatment combination. DNA was extracted from a 0.25g subsample of lyophilized soil by using DNeasy PowerSoil Pro Kit (Qiagen, Hilden, Germany). Quality and concentration of DNA was checked for each sample using a Qbit fluorometer (Thermo Fisher Scientific, Waltham, MA, USA) and samples were diluted to 1ng/µl as per instructions in library preparation kit. Libraries were prepared using the QIAGEN QIAseq ITS region panels using phased primers according to the kit's protocol. The PCR products of all samples were normalized to equimolar amounts and sequenced for 500 cycles on the Illumina MiSeq PE300 platform.
Timing and spatial scale	The conditioning phase of the experiment was conducted from July 2019 to November 2019 and the response phase was conducted from January 2020 to June 2020.
Data exclusions	Originally, we used the first 5 replicate blocks of each species by watering treatment combination (120 samples), plus an 30 additiona samples (5 samples of the common background soil, 10 samples of the initial soil suspension used for the conditioning phase, and 15 samples from empty pots containing only the background soil plus the initial soil suspension) for sequencing. However, due to an error during library preparation we obtained valid samples from only the first three replicate blocks.
Reproducibility	Not applicable. The entire experiment was performed once.
Randomization	The treatment combinations (plant species x conditioned soil x watering treatment) were arranged randomly within 9 replicate blocks. The replicate blocks were used to account for potential uncontrolled variation e.g. the exact position in the greenhouse.
Blinding	Blinding was not intentionally applied to our study. However, the pots had anonymous identifiers (numbers) containing no information about the treatment combination during data acquisition or entry. Blinding was not applicable during data analyses.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging