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Climate change-driven shifts in plant–soil feedbacks: a meta-analysis

Kamrul Hassan[1,2*], K. M. Golam Dastogeer[3], Yolima Carrillo[1] and Uffe N. Nielsen[1]

Abstract

Background: Climate change is expected to affect plant–soil feedbacks (PSFs, i.e., the effects of a plant on the growth of another plant or community grown in the same soil via changes in soil abiotic and biotic properties), influencing plant community dynamics and, through this, ecosystem functioning. However, our knowledge of the effects of climate changes on the magnitude and direction of PSFs remains limited, with considerable variability between studies. We quantified PSFs associated with common climate change factors, specifically drought and warming, and their corresponding ambient (control) conditions using a meta-analytical approach. We investigated whether drought and warming effects on PSFs were consistent across functional groups, life histories (annual versus perennial) and species origin (native versus non-native), planting (monoculture, mixed culture) and experimental (field, greenhouse/laboratory) conditions.

Results: PSFs were negative (a mechanism that encourage species co-existence) under drought and neutral under corresponding ambient conditions, whereas PSFs were negative under both ambient and elevated temperatures, with no apparent difference in effect size. The response to drought was largely driven by stronger negative PSFs in grasses, indicating that grasses are more likely to show stronger negative PSFs than other functional groups under drought. Moreover, non-native species showed negative drought-induced PSFs while native species showed neutral PSFs under drought. By contrast, we found the opposite in pattern in response to warming for native and non-native species. Perennial herbs displayed stronger drought-induced negative PSFs than annual herbs. Mixed species communities displayed more negative PSFs than monocultures, independent of climate treatment. Finally, warming and drought treatment PSF effect sizes were more negative in experiments performed in the field than under controlled conditions.

Conclusions: We provide evidence that drought and warming can induce context-specific shifts in PSFs, which are dependent on plant functional groups, life history traits and experimental conditions. These shifts would be expected to have implications for plant community dynamics under projected climate change scenarios.

Keywords: Climate change, Drought, Warming, Plant functional group, Life cycle, Species origin

Introduction

Plant–soil feedbacks (PSFs) refer to the ability of a given plant or community to alter soil abiotic or biotic conditions in ways that modify the growth of a plant or community subsequently growing in the same soil (Bever et al. 1997; van der Putten et al. 2016; Pugnaire et al. 2019). Over the last three decades, PSFs have been increasingly recognized as important drivers of plant community assembly and, through this, of ecosystem functioning (Bever 2003; van der Putten et al. 2016). There is now evidence that PSFs influence plant community structure and dynamics, plant succession and invasion processes (Bonanomi et al. 2005; Kardol et al. 2006; Klironomos 2002; Revilla et al. 2013). Moreover, there is also growing evidence that climatic and environmental

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*Correspondence: kamrul.hassan@westernsydney.edu.au

[1] Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia
Full list of author information is available at the end of the article

factors influence plant–soil biotic interactions causing shifts in PSFs with implications for the future of plant population dynamics (Bardgett 2018; Weidner et al. 2015; Wubs and Bezemer 2018). Accordingly, several recent studies have shown climate change induced shifts in PSFs related to both direct effects on the plant and indirect effects driven by changes in the composition and activity of soil biota (Crawford and Hawkes 2020; Snyder and Harmon-Threatt 2019; Xi et al. 2018). However, our knowledge about how climate changes alter PSFs, and the potential implications for plant community dynamics, remains limited (van der Putten et al. 2016; Pugnaire et al. 2019).

The term 'plant–soil feedback' has been used increasingly in the literature over the past two decades, and the definition varies somewhat among studies (see examples of PSF definitions in Table 1). Most PSF studies focus on the proportional change in biomass when a given species is grown in soil conditioned by the same species (i.e., 'home') compared to when the same species is grown in soil conditioned by another species (i.e., 'away'); hence, PSFs are generally presented as a relative measure rather than as biomass per se (i.e., PSF = 'biomass in the home soil'/'biomass in the away soil'). In this case, PSFs are considered positive and negative when plants modify soil biotic and abiotic conditions in ways that enhance or reduce the biomass production of an individual of the same species subsequently grown in the same soil, respectively (Bever et al. 1997). We follow this definition throughout this paper. Given that PSFs can occur via influences on edaphic and biotic properties, it is a composite measure that is driven by multiple processes. It is inherently difficult to disentangle the relative influence of each of these; hence, few studies report what causes the observed shifts in PSFs and it is beyond the scope of this meta-analysis to evaluate the potential drivers of such shifts.

Plant–soil feedbacks can be induced via both abiotic and biotic pathways that are likely to be impacted by projected climate change (Fig. 1). For instance, individual plants can increase their relative belowground carbon (C) allocation (Fig. 1, Pathway 1) which can enhance interactions with soil microbes, such as N-fixing bacteria and mycorrhizal fungi (Fig. 1, Pathway 4), resulting in a positive effect on plant biomass production through increased uptake of nitrogen (N) and phosphorus (P), respectively (van der Putten et al. 2016). Such beneficial associations promote positive feedbacks that may extend beyond the lifetime of an individual through a build-up of beneficial organisms (van der Putten et al. 2016; Revillini et al. 2016). Positive plant–soil biotic interactions may be particularly important in stressful environments, including under-nutrient or water-limited conditions (Lagueux et al. 2021; Rutten & Gómez-Aparicio 2018). Furthermore, climatic and environmental conditions influence plant physiological and morphological traits (Fig. 1, Pathway 2) in ways that can affect ecosystem functions, such as litter decomposition and nutrient cycling (Fig. 1, Pathway 3), resulting in subsequent changes in plant biomass production due to changes in nutrient availability. For example, both heatwaves and drought have been shown to result in the production of more recalcitrant litter (i.e., increased C:N ratios of leaf litter, higher lignin concentration; Almagro et al. 2015) which is likely to slow down decomposition and reduce nutrient availability resulting in negative PSFs. Moreover, plants are also exposed to pests and pathogens belowground that negatively affects plant growth (Fig. 1, Pathway 4). For example, the accumulation of root pathogens can reduce the growth of individual plants as well as individuals subsequently growing in the same soil if they are sensitive to those specific pathogens, causing negative PSFs (Bezemer et al. 2013; Domínguez-Begines et al. 2021). Similar effects are likely to occur aboveground in response to herbivory, but the broader effects of plant–herbivore interactions on PSFs are not well known and are difficult to predict given the greater mobility of herbivores (Heinze et al. 2020).

Several general patterns regarding the occurrence of PSFs have been revealed. PSFs are known to be species specific, but appear to differ consistently among plant functional groups (Hassan et al. 2021; Fry et al. 2018; Heinze et al. 2017; Kulmatiski et al. 2008). A growing body of literature has found that grasses and forbs generally show negative PSFs while woody species tend to show neutral PSFs (Chung and Rudgers 2016; Cortois et al. 2016). The first meta-analysis assessing PSFs showed that they are predominantly negative at the species level and positive, or at least less negative, at the community level (Kulmatiski et al. 2008). PSFs have similarly been shown to depend on plant life cycle characteristics (annual versus perennial) and species origin (native versus non-native). Species with annual life cycles tend to produce more negative PSFs relative to species with longer life cycles (i.e., perennial); however, the mechanisms underlying this pattern are still unknown (Kulmatiski et al. 2008). It is possible that long-lived perennial species, such as shrubs and trees, invest more in plant defences making them less sensitive to pest and pathogens than short-lived herbaceous species (Kulmatiski et al. 2008). Moreover, current literature suggests that native species may show negative PSFs due to increased pest and pathogen densities (Callaway et al. 2004; Meisner et al. 2013; van der Putten 2002). On the other hand, non-native species may escape from species-specific soil-borne pathogens in a foreign environment thus reducing negative plant–soil biotic interactions and promoting

Table 1 Summary of key definitions of plant–soil feedbacks (PSF) based on research objectives and nature of PSFs experimental system

Plant–soil feedbacks (PSFs)

Context	**Interpretation**	**Calculation**	**References**
One of the first experimental studies of PSFs and their role in population dynamics	Individual plants, or population of plants, affect the composition of the soil community in ways that affect the growth of the same plant or population Most studies follow this definition although experimental designs differ among studies and interpretations vary accordingly (see below)	PSF = Log (biomass of an individual or population of Species A when grown in soil conditioned by Species A/biomass of individual or population of Species A when grown in soil conditioned by another species)	Bever et al. (1997)
More recent definition often used to assess impacts of global changes (e.g., climate change, nutrient deposition)	Plant–soil feedback is a two-phase ecological concept focused on how plants modify their growing environment by altering biotic (e.g., soil biota) and abiotic (e.g., soil physicochemical properties, stoichiometry) factors which in turn influence the growth and development of individuals of the same species or other species subsequently growing in the same soil Such PSFs can be measured at the species or community level, with resulting differences in interpretation	PSF = Log (biomass of Species A or Community A when grown in soil conditioned by the same species or community/biomass of Species A or Community A when grown in soil conditioned by another species or community)	van der Putten et al. (2016)
PSF interpretation at the species level	Positive and negative PSFs occur when biomass production of a given species is higher or lower in soil conditioned by an individual of the same species, respectively. Positive PSFs will result in species becoming more dominant, whereas negative PSFs will result in species becoming less dominant	As above (1st calculation)	Hassan et al. (2021)
PSF interpretation at the community level	Positive and negative PSFs occur when biomass production of a community is higher or lower in soil conditioned by the same community, respectively. Positive PSFs will result in more stable communities, whereas negative PSFs will result in communities becoming less stable	As above (2nd calculation)	Hassan et al. (2021)
PSFs driven by the soil biotic community (also known as direct or absolute PSFs)	PSFs focussing on the effects of the soil biota can be quantified by comparing the performance of an individual plant species grown in soil conditioned by the same species with biomass produced when grown in a sterile soil	PSF = Log (biomass of Species A in soil conditioned by the same species/biomass of Species A in sterile soil)	Bever (2003), Bennett and Klironomos (2019)

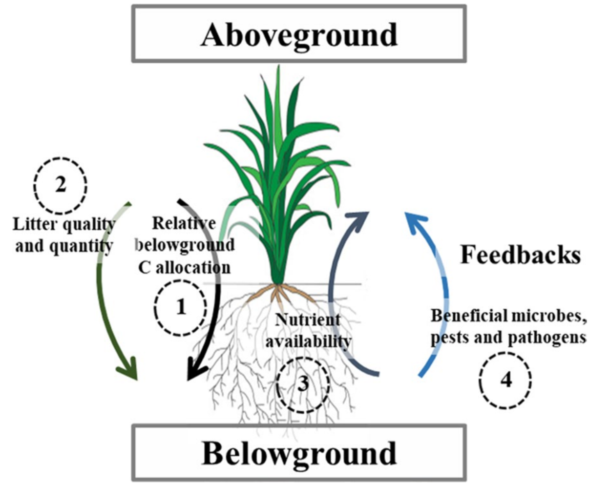

Fig. 1 The main pathways involved in plant–soil feedbacks. Plants predominantly influence belowground communities and soil chemistry through changes in belowground carbon allocation (1) and litter quality and quantity (2). Changes in plant inputs influence belowground communities and soil processes, which in turn influence the plant by changing nutrient availability (3) and by modifying plant interactions with beneficial microbes and pests and pathogens (4). Plant–soil feedbacks represent the net effect of the strength and direction of the combined feedbacks

positive PSFs (Callaway et al. 2004; Meisner et al. 2013; Perkins and Nowak 2013; van der Putten 2002; Zhang et al. 2019). How climate change influence these patterns is still unknown (Pugnaire et al. 2019).

The magnitude and direction of PSFs also change with how species are cultivated and the experimental environment (Kulmatiski and Kardol 2008; Brinkman et al. 2010; Forero et al. 2019). Previous studies have found that plants cultivated in mixtures or in a community (i.e., with multiple species grown together) show less negative-to-positive PSFs under drought conditions (Kaisermann et al. 2017; Hassan et al. 2021), whereas species grown in monocultures generally show stronger negative PSFs, likely due to increased densities of host-specific pathogens (Kaisermann et al. 2017; Hassan et al. 2021). Other studies have shown that drought can neutralize negative PSFs in studies undertaken in controlled environments (Fry et al. 2018; Snyder and Harmon-Threatt, 2019), whereas drought aggravates negative PSFs in field conditions, likely due to greater densities or activity of root herbivores, such as plant-parasitic nematodes (Franco et al. 2019; Hassan et al. 2022). Likewise, warming can aggravate negative PSFs due to rapid accumulation of pest and pathogens (Duell et al. 2019) or by a reduction of beneficial fungal associations in controlled experimental set-up (Rasmussen et al. 2020), but no data are available from field studies. In addition, the contrasting outcome of laboratory and field studies may be due to the use of smaller and less diverse biotic inoculum in laboratory conditions than experiments performed under field conditions (Brinkman et al. 2010; Forero et al. 2019). A comprehensive understanding of how climate changes moderate PSFs in relation to species growing and environmental condition is necessary.

Here, our aim was to assess the impact of elevated temperature (henceforth 'warming', ET) and reduced rainfall (henceforth 'drought', DT) on the magnitude and direction of PSFs. There were too few studies on other climate changes, such as elevated atmospheric CO_2 concentration, for these to be included in the meta-analysis. Synthesizing existing data will enhance our understanding of how warming and drought might modify PSFs and help predict the role of PSFs in shaping plant community dynamics in response to a changing climate. We specifically asked:

a. Do PSFs shift in response to warming and drought?
b. Do warming and drought effects on PSFs differ among plant functional types and species origin?
c. Do PSFs differ between species growing conditions (monoculture versus mixture)?
d. Are PSFs dependent on experimental conditions (greenhouse/laboratory versus field)?

Materials and methods

Literature search and study selection

Meta-analytical data were collected following the guidelines of Field and Gillett (2010). We collected literature using targeted search keywords in Web of Science, Scopus, PubMed, and Google Scholar. The terms included were 'plant soil feedback AND rainfall', 'plant soil feedback AND drought', 'plant soil feedback AND water availability', 'plant soil feedback AND temperature', 'plant soil feedback AND Carbon dioxide or CO_2' 'plant soil feedback AND global change AND experiments' and 'plant soil feedbacks AND climate change'. Based on search results (1990–2022) and the meta-analysis criteria, 52 papers were preliminary selected for the meta-analysis for full paper check after carefully looking into the title and abstract (Additional file 1: Fig. S1).

In this meta-analysis, we focused on studies that assessed PSFs under both ambient and manipulated climate conditions using a known PSF experimental design (Brinkman et al. 2010; Bever 2003). We extracted data from papers where authors measured effects of drought (ambient versus drought) or increased temperature (ambient versus elevated) on plant biomass production in a PSF experiment. We collected the following information about the experimental design for further analysis:

plant functional group, plant life history (annual or perennial), plant origin (native or non-native), plant growing conditions (monoculture or mixture), and experimental approach (greenhouse/laboratory or field). Papers where the authors did not provide PSF data were discarded. Species biomass was recorded as the performance in its own soils and other species soil using typical PSF experimental designs (Bukowski et al. 2018; Wubs and Bezemer 2018).

Data collection and extraction

The main meta-analytical data were plant biomass production in studies that manipulated temperature and/or rainfall using a PSF experimental approach where data for both ambient and manipulative conditions were provided. Due to the low number of studies, we combined studies that reported effects of reduced rainfall in any manner including experimental drought and drought legacies (legacies that had been established under long-term rainfall manipulation experiments). When a paper fulfilled the criteria (as discussed in the previous section), we recorded mean plant biomass, standard deviation ($\pm$SD) and sample sizes (N) for both ambient and manipulated climate. If standard deviation (SD) was not available, we calculated SD by multiplying standard error and square root of sample size ($\mathrm{SE} = \mathrm{SD}/\sqrt{\mathrm{N}}$). The X_E, SD_E and N_E represent the experimental group (E) mean, standard deviation and sample size and X_C, SD_C and N_C for the control group (C) mean, standard deviation and sample size (Blankinship et al. 2011; Hedges et al. 1999; Kulmatiski et al. 2008; Lekberg et al. 2018).

Data were gathered directly from tables, or from figures using *WebPlotDigitizer v. 4.1* (Rohatgi 2012), where possible or obtained from the corresponding author. Data were organized as plant biomass for a given species cultivated in its 'home' soil and the same species cultivated in 'away' soil under ambient and manipulated climate. Fourteen papers, including 2 unpublished datasets, were used for calculating effect sizes (Additional file 1: Table S1). These studies produced a total of 182 individual effect sizes representing ambient and manipulated climate across all species. A key summary of each study used in the meta-analysis is presented in Additional file 1: Table S2.

Meta-analysis

Choosing Hedges' d over Cohen's d

We calculated an unbiased mean PSF effect size as suggested by Hedges and Olkin (1985). The analyses of this meta-analysis were based on 14 independent studies (published and unpublished) that included 182 observations which is likely to cause a biased estimation of PSF effect size. Cohen's d (effect size that described the standardized difference between two means) in particular tend to overestimate the effect size in studies with few observations (Hedges 1981). For this reason, we calculated mean effect size as Hedges' d, which produces a very similar summary effect size but controls for this bias over Cohen's d by multiplying with a correction factor (J) using Eqs. 1 and 2, where n_1 represents the sample size of control group ('home') and n_2 for experimental group ('away'):

$$J = \left(1 - \frac{3}{4(n_1 + n_2) - 9}\right) \tag{1}$$

To estimate bias corrected Hedges' d, *metacont* function in the *metafor* R package were used (Viechtbauer 2010) using following Eq. 2:

$$d = \frac{\mu_1 - \mu_2}{S} \times J, \tag{2}$$

where d indicates Hedges' d, μ_1 is the mean biomass of a species in the control ('home' soil) population and μ_2 is the mean biomass of a species in the experimental ('away') population. S represents the pooled standard deviation. We estimated an unbiased pooled standard deviation by following equation:

$$S = \sqrt{\frac{(n_1 - 1)S_1^2 + (n_2 - 1)S_2^2}{n_1 + n_2 - 2}}, \tag{3}$$

where S_1 indicates standard deviation of control group ('home') and S_2 for experimental group ('away'), n_1 represents sample size of control group ('home') and n_2 for experimental group ('away') (Kulmatiski et al. 2008; Lekberg et al. 2018). Additionally, we calculated the ratio of mean (ROM) to validate the results of Hedges' d (Additional file 1: Table S3). The main patterns were consistent for ROM and Hedges' d; hence, we focus on Hedges' d in the main text.

Model fitting

Multiple observations were extracted from a single study contradicting the assumption of study independence in meta-analyses (Field and Gillett 2010). Therefore, we performed multilevel model (hierarchical model) analyses using *rma.mv* function in the *metafor* package (Viechtbauer 2010) of R version 4.0.3 (R Core Team 2020) to reduce potential study bias. The multilevel hierarchical model that considered individual observations within papers independently fit better in most cases, resulting in lower Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values (Additional file 1: Tables S4–S6). The multilevel model were fitted by using Hedges' d and sample variance (v) as response variable, and paper and study number as random effects (Cheung

2014). The Knapp–Hartung adjustment were used for confidence intervals (CI). The mean PSFs effect sizes were considered significantly different from zero when 95% CI for Hedges' *d* did not overlap zero.

Interpretation of effect size

The calculated effect size of PSF (Hedges' *d*) was described according to the explanation of plant performance between home and away conditioned soils (Kulmatiski et al. 2008). Positive values of Hedges' *d* indicate that species performed better in their own soils relative to soils cultivated by another species soil. Negative values of Hedges' *d* indicate that species performed worse in their own soil relative to another species soil. Values close to '0' indicate neutral PSFs when both positive and negative PSF cancel each other. Therefore, the size and sign of Hedges' *d* is related to magnitude and direction of PSF, respectively (Kulmatiski et al. 2008).

Locating publication bias

We tested for publication bias by producing a histogram of effect size to check the data depression around zero, including a funnel plot (Begg 1994; Kulmatiski et al. 2008). We found that the distribution of effect size does not indicate a publication bias towards significant results (Additional file 1: Fig. S2).

Moderator analysis

We specified five main moderators in this meta-analysis: plant functional group (grass, forb, legume, shrub, and tree), length of life cycle (annual and perennial), origin of species (native and non-native), growing condition (monoculture and mixture) and experimental condition (controlled environment and field). Therefore, we separately performed multilevel models to investigate the effects of each sub-moderator (e.g., grass) within individual moderators (e.g., plant functional group) on mean PSF effect size for each climate factor. We used Hedges' *d* and the corresponding sample variance (v) of each effect size as the response variable, and paper and study number as random effects including Knapp–Hartung adjustment for confidence intervals. The *rma.mv* function in *metafor* was used to fit each model (Cheung 2014).

Results

Overview of meta-data

Among 14 independent studies that met the criteria of this meta-analysis, we calculated 182 PSF effect sizes across two climate change factors (warming and drought; Additional file 1: Table S1). Most experiments focussed on herbaceous species (84%; grass, forbs, and legumes), with a large proportion of graminoids, and only 16% were on woody species (shrubs and trees). The majority of species were perennial species (69%) with fewer data for annual species, while there were about the same number of studies on native and non-native species. Most studies assessed PSFs in monocultures (70%) with the remainder being mixed communities (30%). Finally, the vast majority of the PSF experiments were conducted in growth chambers or greenhouses (83%), with only 17% completed under field conditions.

Overall effect of temperature and drought on PSFs

The mean PSF effect size was negative for all studies ($d = -0.408$; 95% CI -0.599 to -0.217; $Z = -4.183$, $p < 0.001$; Fig. 2), but significant variation was found across studies ($Q = 533.63$; $df = 181$; $p < 0.001$; Additional file 1: Table S3). The mean PSF effect size across all studies that imposed 'drought' was similarly negative (Fig. 2; Additional file 1: Table S3); however, PSFs were weakly negative and not significantly different from zero under 'ambient water' (Fig. 2; Additional file 1: Table S3). The mean PSF effect size for all studies that manipulated temperature was negative for both 'ambient' and 'elevated temperature' (Fig. 2; Additional file 1: Table S3).

Effects of temperature and drought on PSFs across functional groups

Although grasses displayed negative PSFs when grown under elevated temperature (Fig. 3a; Additional file 1: Table S4) and drought (Fig. 3a; Additional file 1: Table S5), mean PSF effect sizes were not different to

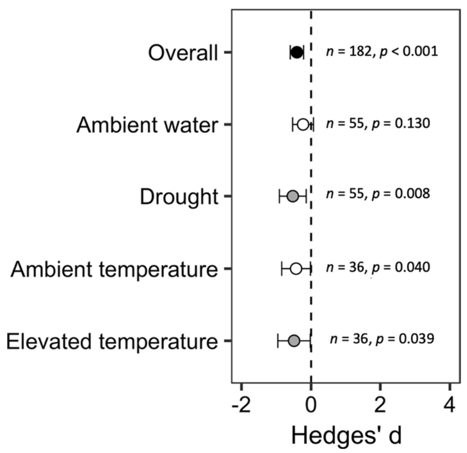

Fig. 2 Main effects of temperature and drought on PSFs. 'Overall' indicates the pooled effect size across all studies. Mean PSFs effect size is presented with 95% CIs. Mean PSFs effect size is significantly different from zero if the corresponding CIs do not overlap with zero (dashed line). *n* represents the total number of observations used during analysis and *p* indicated whether mean PSFs effect sizes were significantly different from zero. Hedges' *d*: 0 for no effect, − 0.2 for small (− 20%), − 0.5 for medium (− 50%), − 0.8 for large (-80%) and > − 1.0 (> 100%) for strong large negative effects, respectively

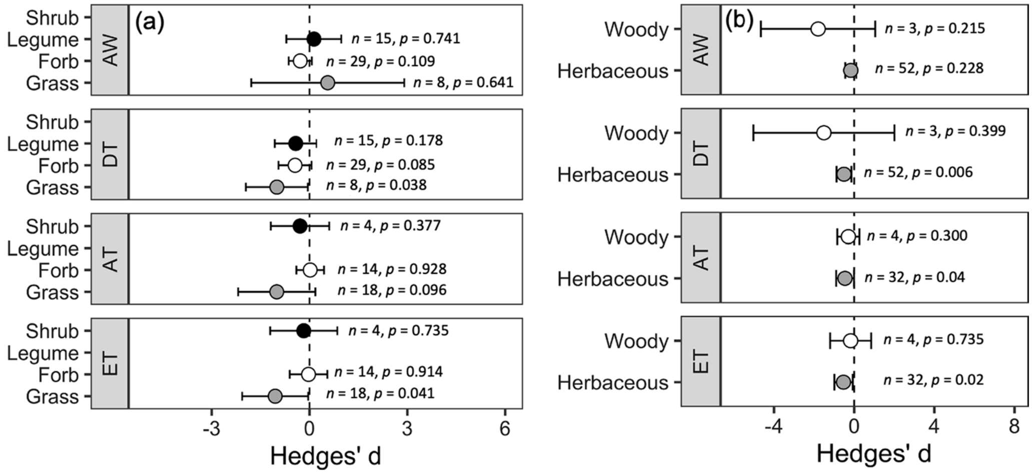

Fig. 3 Effects of temperature and rainfall on PSFs across plant functional groups (**a**, **b**). Mean PSFs effect size is presented with 95% CIs. Mean PSFs effect size is significantly different from zero if the corresponding CIs do not overlap with zero (dashed line). *n* represents the total number of observations used during analysis and *p* indicated whether mean PSFs effect sizes were significantly different from zero. Hedges' *d*: 0 for no effect, − 0.2 for small (− 20%), − 0.5 for medium (− 50%), − 0.8 for large (− 80%) and > − 1.0 (> 100%) for strong large negative effects, respectively. AW: ambient water; DT: drought; AT, ambient temperature; ET: elevated temperature

ambient water and temperature. All other functional groups showed less negative or neutral PSFs under both ambient and experimental climate conditions (Fig. 3a). We further pooled PSF effect sizes for ambient water and temperature as well as drought and elevated temperature considering two main functional groups, i.e., herbaceous (grass, forb, and legume) and woody plants (shrub). We found that drought induced significantly larger negative PSFs for herbaceous species compared with ambient water (Fig. 3b). Likewise, elevated temperature caused significantly larger negative PSFs for herbaceous species compared with ambient temperatures (Fig. 3b). Climate manipulation did not have significant effects on PSFs for woody species (Fig. 3b).

Effects of temperature and drought on PSFs depending on species origin and life cycle

Native species displayed negative PSFs irrespective of temperature manipulation while non-native species showed neutral PSFs (Fig. 4a). Interestingly, non-native species displayed negative PSFs under drought conditions while PSFs for native species were neutral (Fig. 4a).

Drought resulted in negative PSFs for perennial species but not for annual species (Fig. 4b). No differences in PSFs of species with different life cycles were observed under temperature manipulation (Fig. 4b).

Effects of temperature and drought on PSFs depending on growing and experimental condition

Species cultivated in mixed cultures showed negative PSFs while monocultures displayed neutral PSFs under both ambient and elevated temperature (Fig. 5a). Drought caused negative PSFs in mixed cultures with neutral PSFs observed under ambient conditions, whereas monocultures showed neutral PSFs under both drought and ambient water (Fig. 5a).

PSFs were negative under both ambient and elevated temperature under field condition, while less negative PSFs were observed in experiments conducted in controlled environments (Fig. 5b). PSFs were negative in experiments conducted in a laboratory environment both under ambient water and drought (Fig. 5b) conditions. By contrast, for experiments performed under field condition, PSFs were negative under drought and neutral under ambient conditions (Fig. 5b).

Discussion

We provide evidence that projected climate changes can modify plant–soil feedbacks in ways that will impact plant community dynamics (Pugnaire et al. 2019; Snyder and Harmon-Threatt 2019; van der Putten et al. 2016). Specifically, strong negative PSFs were observed in grasses under drought conditions while PSFs were less pronounced in the other functional groups, indicating that grasses may be disproportionately impacted by drought-induced shifts in PSF. Moreover, perennial species showed strong negative PSFs under drought while PSFs were less pronounced in annual species. Similarly, non-native species showed strong negative PSFs under drought while PSFs were less pronounced in native species. Strong negative PSFs were observed when species were grown in mixtures while PSFs were less pronounced

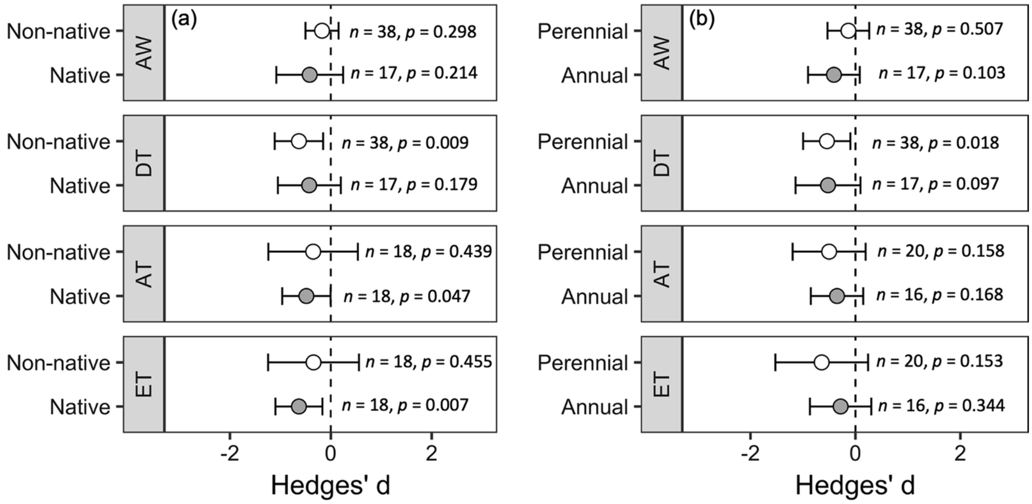

Fig. 4 Effects of temperature and rainfall on PSFs depending on origin of species (**a**) and life cycle (**b**). Mean PSFs effect size is presented with 95% CI. Mean PSFs effect size is significantly different from zero if the corresponding CIs do not overlap with zero (dashed line). *n* represents the total number of observations used during analysis and *p* indicated whether mean PSFs effect sizes were significantly different from zero. Hedges' *d*: 0 for no effect, − 0.2 for small (− 20%), − 0.5 for medium (− 50%), − 0.8 for large (− 80%) and > − 1.0 (> 100%) for strong large negative effects, respectively. AW: ambient water; DT: drought; AT: ambient temperature, ET: elevated temperature

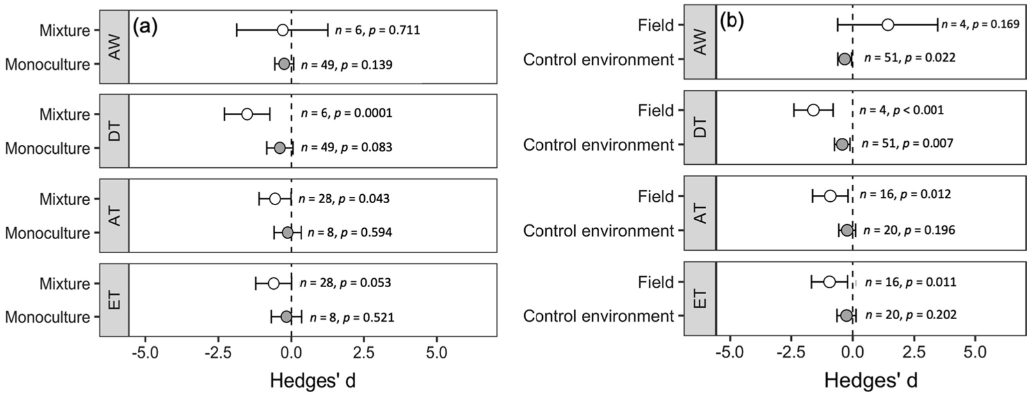

Fig. 5 Effects of temperature and rainfall on PSFs for growing condition (**a**) and experimental environment (**b**). Mean PSFs effect size is presented with 95% CIs. Mean PSFs effect size is significantly different from zero if the corresponding CIs do not overlap with zero (dashed line). *n* represents the total number of observations used during analysis and *p* indicated whether mean PSFs effect sizes were significantly different from zero. Hedges' *d*: 0 for no effect, − 0.2 for small (− 20%), − 0.5 for medium (− 50%), − 0.8 for large (− 80%) and > − 1.0 (> 100%) for strong large negative effects, respectively. AW: ambient water; DT: drought; AT, ambient temperature; ET: elevated temperature

in monocultures, likely driven by interspecific competition for resources, such as water limitations (Crawford and Knight 2017). Finally, the effects of drought and warming were more pronounced in PSF experiments conducted in the field than experiments in controlled conditions, possibly due to more realistic feedbacks between plants, soil biota and edaphic properties (Forero et al. 2019; Gundale and Kardol 2021; Kulmatiski & Kardol 2008). Our meta-analysis thus revealed that drought can cause negative PSFs, particularly in grasses, with some differences between functional groups, life history, origin, and species growing and experimental conditions, while warming appears to have less pronounced effects on PSFs.

The effects of drought on PSFs of plants from different functional groups and with contrasting life history traits, species growing and experimental conditions

Plants grown under drought conditions showed strong negative PSFs whereas neutral PSFs were observed under ambient water conditions. The apparent drought-induced shift in PSFs may be related to differences in soil nutrient availability and microbial associations (in't Zandt et al. 2019; Kaisermann et al. 2017; Fig. 2). For example, it has been shown that drought can reduce mycorrhizal associations thereby impeding uptake of essential mineral nutrients (Al-Karaki and Al-Raddad 1997). Drought was hypothesized to induce stronger negative PSFs but negative PSFs in grasses were also expected in the ambient treatments (Kulmatiski et al. 2008). Grasses displayed strong negative PSFs under drought conditions and weaker negative PSFs under ambient water, indicating a drought-induced shift in feedbacks. Previous studies have suggested that drought promotes positive PSFs for forbs due to increased nutrient availability (Fry et al. 2018) and greater reliance on beneficial microbes (Kaisermann et al. 2017). The strong negative PSFs observed in grasses and relatively weaker negative PSF for forbs in this study may be linked to their sensitivity to native pathogens (Lu et al. 2015). For example, grasses and forbs are susceptible to belowground enemies, such as plant-parasitic nematodes and pathogens, given their high root to shoot ratio, and large root systems with relatively poor investment in structural defences (Gleeson and Tilman 1994; Schenk and Jackson 2002; Wilsey and Polley 2006). The observed neutral PSFs for legumes are also consistent with the current literature (Cortois et al. 2016; Hassan et al., 2021). Currently, PSF experiments are largely dominated by grasses and forbs (Kulmatiski et al. 2008) with fewer studies investigating legumes (Teste et al. 2017) and woody species PSFs (Kulmatiski et al. 2008; Bennett et al. 2017). More studies are needed to assess whether PSFs in legumes and woody species are affected by climate change drivers.

Perennial species displayed strong negative PSFs under drought conditions while annual species showed less pronounced negative PSFs. Annual herbaceous species are more likely to be impacted by host-specific pathogens due to the rapid vegetative growth and lesser investment in defences (Kardol et al. 2006) relative to perennial species that invest more in defence and form stronger mutualistic relationships with soil microbes (Callaway et al. 2004; Suding et al. 2013; van der Putten et al. 2002). However, the contrasting outcome for perennial species may be related to fewer empirical studies (i.e., less data points) and methodological constraints, particularly a lack of studies assessing PSFs at time scales that suit perennial species (Brinkman et al. 2010). This meta-analysis also suggested that drought induced strong negative PSFs for non-natives but not for native species. A possible explanation is that drought disrupted the beneficial associations that non-native species rely on or that they are more susceptible to drought stress than native species (Hassan et al. 2021).

Strong negative PSFs were observed when species were grown in mixtures with less pronounced PSFs in monocultures. Generally, species cultivated in monoculture tend to accumulate more pathogens than mutualists thereby aggravating negative feedbacks (Klironomos 2002; Wang et al. 2021). In mixtures, positive feedbacks can occur due to an accumulation of beneficial microbes and dilution of negative effects of pathogenic microbes (Mommer et al. 2018). However, the strong negative PSFs in the mixtures observed here might be linked to competition for nutrients and water under field condition (Teste et al. 2017). Specifically, drought may exacerbate negative feedbacks by reducing nutrient availability resulting in increased competition or by disrupting plant–microbe beneficial associations (Kaisermann et al. 2017).

Our study also showed strong negative PSFs under drought conditions in studies conducted in the field with less pronounced PSFs in experiments in controlled environmental conditions. Conditions in the field likely represent more realistic effects of herbivory both aboveground and belowground, greater competition among plants and soil physicochemical properties as previously hypothesized (Beals et al. 2020; Ehrenfeld et al. 2005; Heinze et al. 2019, 2020; Snyder and Harmon-Threatt 2019). For example, aboveground herbivores have been shown to promote negative PSFs by reducing shoot biomass (Heinze et al. 2020) and indirectly via changing root morphological traits, such as increased production of thinner roots, that may change nutrient uptake (Heinze 2020). Likewise, belowground herbivores, such as root feeding nematodes, have been shown to promote negative PSFs in response to prolonged drought under field conditions (Hassan et al. 2022). Such effects are unlikely to be reflected in experiments conducted in growth chambers or glasshouses. Moreover, competition for nutrients may also reduce plant growth, thereby changing PSF effect sizes between laboratory and field (Beals et al. 2020; Lekberg et al. 2018). More field studies are required to generalize PSF response of plant communities to global changes under realistic environmental conditions.

The effects of warming on PSFs of plants from different functional groups and with contrasting life history traits, species growing and experimental conditions

Our meta-analysis indicates that warming have limited effects on PSFs, with weak negative PSFs of similar effect sizes observed under ambient and elevated temperatures. This pattern was consistent across all functional groups. It has been shown that warming can promote positive plant–soil biotic interactions in resource-limited systems where warming promotes beneficial microbes that help to access water and nutrients (Brookshire and Weaver 2015; Craine et al. 2012; Rasmussen et al. 2020). However, warming may induce negative PSFs by reducing beneficial associations due to increase soil nutrient availability via increasing mineralization or by promoting faster life cycles of pathogenic microbes (Bennett and Klironomos 2019; van der Putten et al. 2016; Pugnaire et al. 2019). For example, some studies found that warming reduce the colonization of mycorrhizae in grasses (Zhang et al. 2021) and flowering herbs (Wilson et al. 2016) as plants are less dependent on beneficial associations due to increased availability of nutrients. Therefore, warming effects on PSFs will depend on its influences on soil nutrient availability and microbial associations.

However, strong negative PSFs were observed in native species, with less pronounced PSFs in non-native species as predicted by a previous greenhouse experiment (van Grunsven et al. 2010). Warming can increase the density of pathogens rapidly which negatively impacts native species while non-native species may escape pathogens attack in new environments via the enemy release mechanism (Agrawal et al. 2005). Previous studies also indicate that native grasses and forbs are more sensitive to native soil pathogens than non-native species which can be exacerbated under warming (Hines et al. 2017; Kulmatiski et al. 2008; Meisner et al. 2014). Moreover, we found strong negative PSFs in a warmer environment when species were grown in mixtures, with less pronounced PSFs in monocultures. If plant communities are composed of closely related plant species, they may accumulate more pathogens under warming which likely result in negative PSFs (Mommer et al. 2018). On the other hand, plant communities composed of distantly related species representing a diversity of functional groups generally increase the diversity of beneficial microbes in communities and dilute the abundance of pathogenic microbes may reduce negative PSFs (Mommer et al. 2018). Hence, the effect of warming on PSFs at the community level will be highly context dependent.

We also found strong negative PSFs under warmer conditions when experiments were performed in the field, with less pronounced PSFs in studies conducted under controlled environmental conditions. This is likely due to differences in experimental conditions. Specifically, PSF experiments conducted in greenhouses or controlled environments tend to use a small portion of live inoculum collected from the field (Kulmatiski et al. 2008; Kulmatiski and Kadrol 2008 but see details in Chung et al. 2019; Kulmatiski 2019). This may exclude common root herbivores or pathogens, such as plant-parasitic nematodes, or symbionts that are important to plant growth under natural conditions and could more rapidly reproduce under warming conditions (Cortois and De Deyn 2012; Crawford et al. 2019; De Long et al. 2019). However, our findings stem from a limited pool of field studies, and more are required to quantify the contribution of PSFs on plant population dynamics in a warmer climate (Beals et al. 2020).

Conclusions

Our results indicate that drought enhances negative PSFs thus reducing plant growth. This effect is particularly clear in grasses but was observed across all herbaceous species. Moreover, drought appeared to induce negative PSFs in perennial species but not annual species, and in non-native species but not in native species. Warming by contrast had limited effects on PSFs across all studies but strong negative PSFs were observed in native species, with less pronounced PSFs in non-native species. Similarly, strong negative PSFs were observed under drought and warming when species were grown in mixtures and in experiments performed in the field whereas less pronounced PSFs were observed for species grown in monocultures and in studies conducted in controlled environments. We thus provide evidence that climate change can cause shifts in PSFs but that the effects differ among plant functional groups, life history strategy, and species origin as well as species growing and experimental condition. Future research should assess the effects of global change drivers including elevated CO_2 across environmental and climatic gradients to better quantify global change effects on PSFs.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-022-00410-z.

Additional file 1: Table S1. Studies included in the meta-analysis and the number of observations extracted from each paper. **Table S2.** Overview of main findings of papers used in the meta-analysis. **Table S3.** Summary of multi-variate meta-analysis model output for temperature and drought effects on mean PSF effect sizes based on Hedge's *d* and ratio of mean (ROM). **Table S4.** Summary of multilevel model output for temperature and drought effects on mean PSF effect sizes. **Table S5.** Summary of multilevel model output for ambient and elevated temperature PSF effect sizes. **Table S6.** Summary of multilevel model output for ambient water and drought on PSF effect sizes. **Fig. S1.** Flow diagram showing the information through the different phases of a systematic review. **Fig. S2.** Histogram (a) and Funnel plot (b) based on number of PSF experiments by effect size. Negative effect sizes suggest that plants grow better in soils cultivated by the same species than soils cultivated by another species ($n = 182$). The distribution of effect sizes does not suggest a publication bias toward significant results.

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Author contributions

KH and UNN conceived and designed the meta-analysis. KH collected the data directly from author and online data base. KH conducted all formal analysis with input from KMGD and UNN. KH written first draft with direct supervisions from UNN and YC. All authors reviewed the chapter critically. All authors read and approved the final manuscript.

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Availability of data and materials

Data made available on reasonable request to corresponding author.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors have consented to publish their work.

Competing interests

We have no conflicts of interest to disclose.

Author details

[1]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia. [2]Department of Entomology, Sylhet Agricultural University, Sylhet 3100, Bangladesh. [3]Department of Plant Pathology, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh.

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