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ORIGINAL RESEARCH

Impact of native community diversity and plant-soil feedbacks on invasiveness in experimental temperate grasslands varies among invasive species

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Abstract

Plant-soil feedbacks (PSFs) are a key mechanism regulating species dynamics in plant communities, typically negative due to the buildup of species-specific pathogens. Species-rich communities experience less negative PSFs than species-poor ones due to pathogen dilution, making PSFs a proposed mechanism behind the positive biodiversity-productivity relationship. PSFs may also benefit invasive species through the loss of their pathogens enhancing competitiveness according to the enemy release hypothesis (ERH). We hypothesized that invasive species would benefit from enemy release in species-poor communities, but less in species-rich ones where the advantage of enemy release disappears due to pathogen dilution. Accordingly, we expected that in sterilized soils, community diversity would not affect invasion success. We conducted a greenhouse experiment measuring the invasion success of three invasive forbs (*Solidago gigantea*, *Avena sterilis*, and *Lupinus polyphyllus*) in plant communities of varying richness (1, 2, 4, 8, and 12 species) in both unsterilized and sterilized soils. In unsterilized soils species diversity had a significant positive impact on native community biomass, while *S. gigantea* showed a clear negative effect from this increased competition at higher species diversities, as predicted. In sterilized soils these effects were strongly reduced. Growth of the two other invasive species was not affected by species diversity of the native community, showing that this mechanism may be species-specific. These findings support the ERH but only when exotic plants invade species-poor communities. Furthermore, our results suggest that the greater resistance of diverse plant communities to invasion may be at least partly be ascribed to increased competitive strength of the native community due to pathogen dilution.

Keywords Enemy release hypothesis · Species richness · Competition · Pathogen dilution · Solidago gigantea · Avena sterilis · Lupinus polyphyllus · Greenhouse experiment

Introduction

Plant-soil feedbacks (PSF) are considered a key mechanism regulating plant species dynamics within plant communities (Bever et al. 2015; Lekberg et al. 2018). Positive PSFs arise when mutualistic microbes accumulate in the rhizosphere, benefiting conspecific plants (Bever et al. 2012). Conversely, soil-borne pathogens can create negative PSFs by impairing the growth of plants or their offspring (Connell 1971; Janzen 1970; Jia et al. 2020; Liu et al. 2012).

PSFs are highly species-specific, with some species exhibiting more positive feedbacks while others experience predominantly negative ones (Klironomos 2002; Thakur et al. 2021). The strength and nature of PSFs can vary significantly depending on the community context (Abbott et

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al. 2015; Casper and Castelli 2007), as PSFs can be altered by plant-plant competition, environmental stresses and by disturbances (Beals et al. 2020; Ke and Wan 2020). For non-legume forbs and grasses, PSFs are generally negative (Kulmatiski et al. 2008; Wang et al. 2023), particularly in monocultures or species-poor plant communities. In species-rich communities, PSFs tend to be less negative or even positive, especially for rare or less dominant species due to pathogen dilution (Bever 2003; Goossens et al. 2023). This pattern of negative density dependence, where dominant species are suppressed by negative PSFs while rarer species benefit from positive feedbacks, is thought to promote species coexistence, although most evidence supporting this idea is theoretical (Bever 2003; Bonanomi et al. 2005; Chesson 2000; Kulmatiski et al. 2011; Revilla et al. 2013). Empirical evidence for negative density dependence is limited (van Ruijven et al. 2020), but some recent greenhouse studies (Goossens et al. 2023; Wang et al. 2023) and meta-analyses (Crawford et al. 2019; Lekberg et al. 2018) provided support for it. For instance, Goossens et al. (2023) showed that subordinate species receive positive PSFs due to pathogen dilution when grown in species mixtures, even when those species received negative PSFs when grown in monocultures.

The pronounced negative PSFs in monocultures or species-poor communities may contribute to the positive relationship between biodiversity and productivity (van Ruijven et al. 2020). Traditionally, the benefits of biodiversity on productivity (Grace et al. 2016) have been attributed to enhanced use of limiting resources by niche partitioning, interspecific complementarity, and/or facilitation (Mahaut et al. 2020; Tilman et al. 2014; van Ruijven et al. 2020; Weisser et al. 2017). Although substantial evidence supports these mechanisms, they typically can explain only part of the observed variation in productivity, hence leaving a considerable proportion unexplained (Cardinale et al. 2007; Hector et al. 2002). Negative density dependence introduces an additional mechanism: the negative impact of pathogens. Specifically, the dilution of species-specific pathogens in species-rich communities appears to be a key mechanism driving increased productivity in more biodiverse systems (Forero et al. 2022; Maron et al. 2011; Schnitzer et al. 2011). Indeed, experimental evidence suggests that due to pathogen dilution in more biodiverse systems, PSFs can be less negative (Goossens et al. 2023; Kulmatiski et al. 2008) or even positive (Heinze et al. 2016) in diverse communities, resulting in higher biomass production.

For native plants, PSFs are often negative (Kulmatiski et al. 2008). Invasive alien species may evade these negative effects through mechanisms such as the loss of natural enemies or pathogens, resulting in neutral or even positive feedbacks—an idea encapsulated in the enemy release hypothesis (ERH) (Keane 2002; Maron and Vilà 2001). According to the ERH, invasive plants thrive because species-specific pathogens are absent in their introduced range (Vilà et al. 2005; Wolfe 2002). While some studies support this hypothesis, showing more positive or less negative PSFs for invasives compared to natives (Callaway et al. 2004; Klironomos 2002; Kulmatiski et al. 2008), others yield contradictory or inconclusive results (Colautti et al. 2004; Fahey and Flory 2022; Jeschke et al. 2012; Shannon et al. 2012).

Given the variability in PSFs across different species and community contexts, it is challenging to draw conclusions about the ERH based on comparisons between natives and invasives in monoculture or species-poor setups. There is thus a notable knowledge gap in PSF research conducted within diverse plant communities (Heinze et al. 2016; Kulmatiski et al. 2008; van der Putten et al. 2013), and how the ERH is affected by the diversity of the invaded community. Biodiverse ecosystems often show greater resistance to invasion (Beaury et al. 2020; Case 1990; Elton 1958; Kennedy et al. 2002; Levine 2000) -the biotic resistance hypothesis- a phenomenon primarily attributed to complementarity effects due to niche partitioning (Eisenhauer et al. 2013). In these systems, different plant species from similar functional guilds or niches are present and preoccupy available resource niches, limiting opportunities for invaders (Fargione et al. 2003; Symstad 2000). Additionally, resource scarcity in diverse communities (Tilman 2004) may further impede invasion. However, it remained so far uninvestigated whether reduced negative PSFs for native plants in diverse ecosystems due to pathogen dilution contribute to this resistance by diminishing the advantages invasive species derive from their neutral or positive PSFs due to enemy release (Li et al. 2024). When native plants can receive neutral or positive PSFs in more biodiverse communities, invasive species could possibly lose their competitive edge. This mechanism, if confirmed, could challenge the relevance of the enemy release hypothesis in more biodiverse ecosystems, as it suggests that increasing native community diversity may reduce rather than enhance the advantages typically predicted for invasive species under the ERH.

The aim of this study was to determine whether invasion success of three invasive forb species is influenced by the diversity of the invaded community and whether this relationship differs between sterilized and unsterilized soil conditions. In contrast to previous studies, this study will thus not only assess whether invasion is facilitated due to loss of pathogens, but will clarify if this facilitation only occurs when invading species-poor plant communities. Invasion success was measured by biomass production under both unsterilized (with pathogens and mutualists) and sterilized (without pathogens and mutualists) soils. Furthermore, plant–soil feedbacks (PSFs) -measured as the ratio of biomass production in unsterilized and sterilized soils- for both native communities and invasives were assessed. We used experimental setups with one invasive and 1, 2, 4, 8, or 12 native species. We hypothesized that:

1. PSFs for native species will be negative in species-poor communities due to high species-specific pathogen loads, but they become more neutral in species-richer communities due to pathogen dilution (Bever 2003).
2. Due to this pathogen dilution at higher species richness, the positive biodiversity-productivity relationship for native species will be found for unsterilized soil, but not for sterilized soil where biodiversity effects on productivity will be absent (cf. (Maron et al. 2011; Schnitzer et al. 2011).
3. In unsterilized soil invasive species will perform worse in species-richer communities due to increased competition, whereas in sterilized soil the diversity of native communities will not influence invasive success (cf. Goossens et al. 2023).

Materials & methods

We conducted a two-phase PSF experiment in the greenhouse of the Vrije Universiteit Brussel (VUB main campus, Brussels, Belgium) to assess how species diversity in plant communities affects biomass production of both native and invasive species, and whether this impact changes after soil sterilization. During the first phase, the conditioning phase, native plant communities with varying species richness (1, 2, 4, 8, or 12 species) were grown in pots for eight weeks, allowing soil microbiota, including mutualists and species-specific pathogens, to accumulate. These communities were assembled from 12 native plant species typical of moist mesotrophic European grasslands (see EUNIS habitat classification; habitat types R211-214, R2211-2212, R351-354, R361; Chytrý et al. 2020), comprising four grasses (Poaceae: *Holcus lanatus* L., *Anthoxanthum odoratum* L., *Agrostis capillaris* L., *Alopecurus pratensis* L.), four legumes (Fabaceae: *Lotus corniculatus* L., *Medicago lupulina* L., *Trifolium pratense* L., *Anthyllis vulneraria* L.), and four non-legume forbs (Plantaginaceae: *Plantago lanceolata* L., Polygonaceae: *Rumex acetosa* L., Asteraceae: *Centaurea jacea* L., and Ranunculaceae: *Ranunculus repens* L.). Seeds of all native species were obtained from Cruydt-Hoeck (The Netherlands).

Prior to the experiment, seeds were germinated (January 2024) on universal potting soil (Viano, Belgium, pH = 6): i.e., 14 up to 28 days prior to transplanting, depending on germination rates. A total of 186 mesocosms with plant communities were set up, each consisting of 12 native plant individuals (2232 plants in total) by transplanting seedlings into 5 L pots (23 cm diameter, Göttinger, Germany). In total, 31 different community compositions were created: 12 monocultures (1 species), six community types with two, four and eight species each, and one with all 12 species. Each community type was replicated six times (see Ext. Data Fig. 1 & Ext. Data Table 1 for species compositions). Planting locations were randomized within each pot, by using a grid consisting of an inner and outer circle, where six individual plants were randomly allocated within each circle. Plants were spaced evenly within each circle.

Conditioning phase

Before transplanting the seedlings into the 5 L pots, these were filled with a 97.5–2.5 vol% sand-inoculum mixture and placed in a randomized setup in the VUB greenhouse. We planted the seedlings in January 2024, and plants were subsequently grown for eight weeks (February & March 2024). The sand fraction consisted of dried white quartz sand (Sibelco, Type M31, nitrogen and phosphorus concentrations below detection limits). Soil inoculum was collected from a moist, mesotrophic meadow (Doode Bemde, Belgium, 50.815538°N, 4.644776°E), by sampling the upper 10 cm of soil (0.15 L per sample) at 200 randomly selected locations within this meadow, air-drying the samples for 2 days after which they were mixed. Roots were manually removed. Pots received a half-strength Hoagland solution, supplying a total of 30.0 mg N, 2.00 mg P, 86.2 mg K, 28.6 mg Ca, 6.9 mg Mg, 4.9 mg Fe, 0.034 mg Cu, 0.40 mg B, 0.24 mg Mn, 0.12 mg Zn, and 0.070 mg Mo per plant individual over eight weeks (Hoagland and Arnon 1950; Minden et al. 2021). Nutrients were added weekly in increasing amounts: 10 ml per pot for the first two weeks, 20 ml per week in the next four weeks, and 30 ml per week in the last two weeks, accounting for rising nutrient demands during growth of the plants (Olde Venterink and Güsewell 2010). Pots were watered three times a week with deionized water into a saucer to avoid leaching of nutrients or microbiota.

After eight weeks, plants were harvested and cut at the root-stem transition. Aboveground biomass was dried for 72 h at 70 °C and weighed. Belowground biomass of the individual species was not measured due to strong root interweaving. The conditioned soil, with roots removed, was used for the response phase.

Response phase

In the response phase, two soil treatments were applied: (1) *unsterilized soil* - conditioned soil from the conditioning

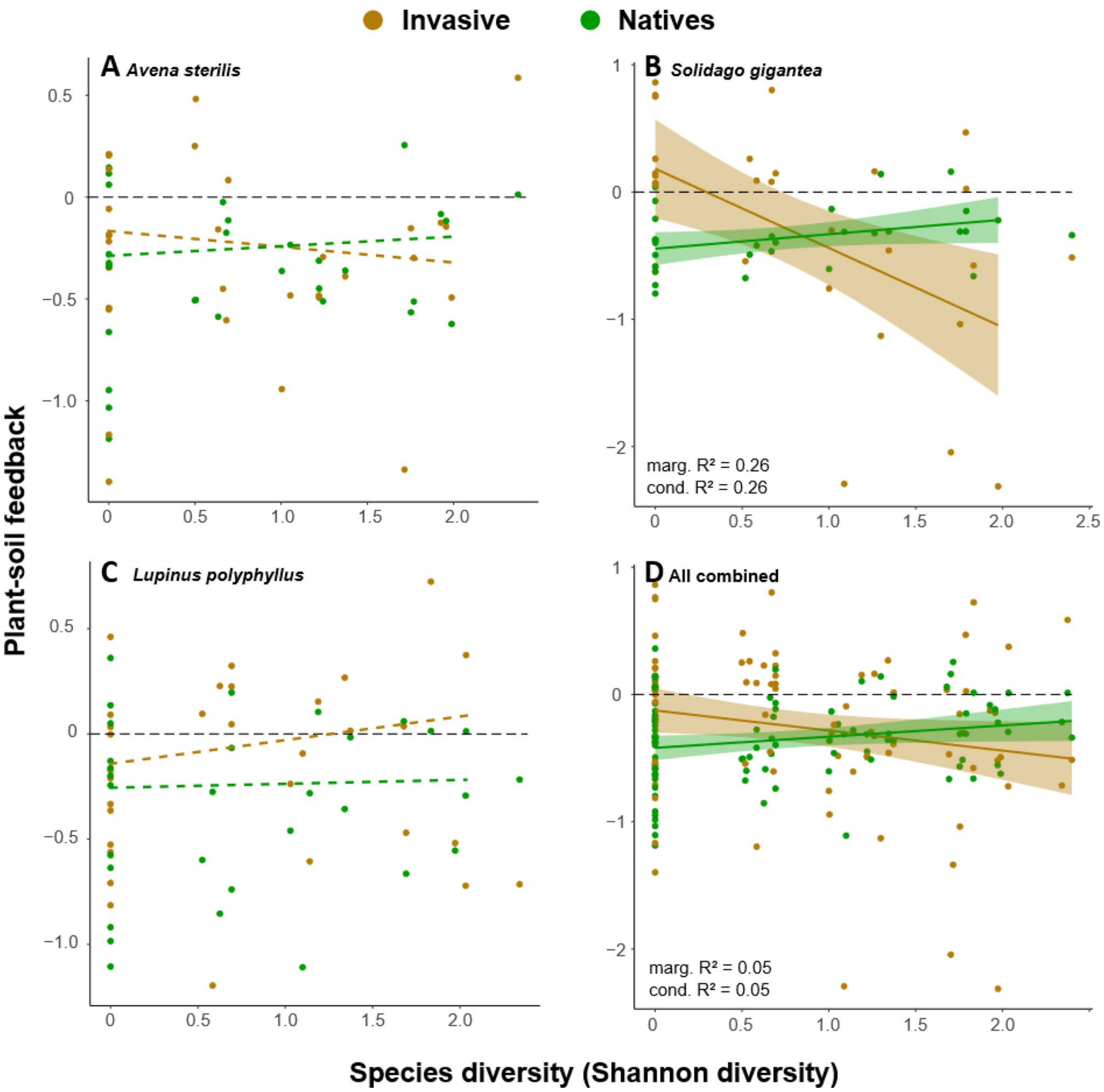

Fig. 1 PSF for native and invasive species in function of species diversity of the community. PSF was calculated as the natural logarithm of the ratio of the dry shoot biomass in unsterilized and sterilized soil, for (**a**) native community with *Avena sterilis*, (**b**) native community with *Solidago gigantea*, (**c**) native community with *Lupinus polyphyllus*, and (**d**) all pots combined. Native communities consist of different combinations of following species: *Lotus corniculatus*, *Medicago lupulina*, *Trifolium pratense*, *Anthyllis vulneraria*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *Alopecurus pratensis*, *Plantago lanceolata*, *Rumex acetosa*, *Centaurea jacea*, *Ranunculus repens*. Significant relationships are indicated with solid lines. Dashed lines indicate non-significant relationships

phase used without further treatment, or (2) *Sterilized soil* - conditioned soil from the conditioning phase treated with steam sterilization at 121 °C for one hour in an autoclave (VAPOUR-line, VWR). Nutrient release due to soil sterilization was considered negligible, as the soil inoculum (mostly organic) made up only 2.5% of the mixture, with the remainder being mineral soil (Brinkman et al. 2010).

During the response phase, the same native plant communities as used in the conditioning phase were grown in their respective conditioned soils for eight weeks also (April & May 2024, Ext. Data Fig. 1). We therefore used new seedlings, which were grown in the conditioned soils reused from the conditioning phase. Additionally, one of three invasive species, *Lupinus polyphyllus* Lindl. (legume,

Table 1 Effects of species diversity, plant type (invasive or native) and their interaction on PSF

Community	Fixed factors								
	Species diversity			Plant type (native vs. Invasive)			Sp. div. x Plant type		
	Estimate	t-value	*P*	Estimate	t-value	*P*	Estimate	t-value	*P*
Overall	**–0.16**	**–2.4**	**0.016**	**–0.29**	**–2.9**	**0.004**	**0.25**	**2.7**	**0.008**
S. gigantea	**–0.62**	**–4.4**	**< 0.001**	**-0.63**	**–3.1**	**0.003**	**0.74**	**3.7**	**< 0.001**
L. polyphyllus		1.0	0.35		–1.1	0.27		–0.2	0.85
A. sterilis		–0.7	0.47		–0.9	0.37		1.0	0.32

Results are presented for all communities combined (overall) and separately for communities invaded by *A. sterilis*, *S. gigantea*, and *L. polyphyllus*. A negative value for plant type implicates an overall more negative PSF for the native community than for the invasive species. A positive value for the interaction term means species diversity has a more positive effect on PSF for the native community. Significant *P*-values are indicated in bold. Estimates not given when not significant

Fabaceae), *Avena sterilis* L. (grass, Poaceae), or *Solidago gigantea* Aiton (forb, Asteraceae), was introduced at the center of each community. Germination procedures for the seedlings of these invasives were as for the natives, after which one individual of an invasive species was added to the native community at the onset of the response phase. These species, all invasive in European mesotrophic grasslands, were chosen to match the functional groups of the native plants. Seeds of *L. polyphyllus* were purchased from Cruydt-Hoeck (The Netherlands), *A. sterilis* from B&T World Seeds (France), and *S. gigantea* seeds were collected from the wild in the region of Brussels, Belgium, during the winter of 2023–2024.

Two soil treatments were used -sterilized and unsterilized soil- resulting in 186 treatments (31 community types x 3 invasive species x 2 soil treatments, each with 13 plant individuals per pot, for a total of 2418 plants). Growth conditions, watering, and nutrient supply were identical to the conditioning phase. After eight weeks, aboveground biomass of each individual species was harvested per mesocosm, dried for 72 h at 70 °C, and weighed.

Additionally, a smaller experiment was performed to determine relative growth rates of each plant species when grown individually. For each species, 20 plants were grown separately in a 0.75 L pot (12 cm diameter, Soparco) without soil inoculum. These plants were grown for 3, 7, 14, 28 or 56 days, after which the plants were clipped at soil surface and aboveground dry biomass was determined. At every time step 4 replicate pots per species were harvested. Hence, we used in total 300 pots (15 species x 5 moments in time x 4 replicates per plant species). Growth conditions, watering, and nutrient supply (per plant individual) were identical to the other experiment. Additionally, biomass was also measured of four seedlings per species at day 0 (seedlings from the germination trays).

Statistics

To assess whether native species were positively affected by a higher species diversity in unsterilized soils a mixed linear model (lmer function from the lme4 package; (Bates et al. 2015) was performed. Aboveground dry biomass of each native community as a whole was inserted as response variable and species diversity (continuous) and soil treatment (2 levels, unsterilized or sterilized) as fixed factors with interaction. Community type and which species of invasive species were both inserted as random factors, the former nested in the latter. Similarly, to asses if invasive species were negatively affected by an increase in species diversity through increased competition from those native species in unsterilized soils, three more mixed linear models were made, one for each invasive species. Here, aboveground dry biomass of the invasive species was inserted as response variable, fixed factors remained the same as above. As random factor community type was inserted.

The species diversity used in these mixed models was calculated as the Shannon Wiener diversity (SWD) index H' (Shannon and Weaver 1949) where the relative frequency p_i of each species in a community was calculated from their biomass:

$$H' = -\sum_{i=1}^{S} p_i.\ln(p_i) \qquad with \quad p_i = \frac{biomass_i}{total\ biomass\ community}$$

where S = the number of species in a community. Biomasses used were those from the conditioning phase, as we were mostly interested in the effect of the microbiota linked to the plant communities and these were build up during this first phase.

In the mixed models for the invasives, as there was only one replication of the plant community containing all 12 species for each invasive species, this pot was excluded from the analysis to account for heteroscedasticity. We note however that results remained the same when it was included. The same applies to the species diversity as a fixed factor: results remained the same when this was exchanged by species richness. Model assumptions were checked visually with the help of residual histograms and a qqplot. Multicollinearity between fixed factors was analysed with VIF values with a cut-off at < 3.

Furthermore, PSFs representing how plant species were affected by the presence of pathogens and mutualists were calculated for each pair of plant communities, using following equation (Brinkman et al. 2010; Petermann et al. 2008):

$$PSF = \ln\left(\frac{Biomass_{unsterilized}}{Biomass_{sterilized}}\right)$$

where biomass is the aboveground dry biomass of the single invasive species within the community when calculating PSF for invasive species, or of the entire native community when calculating PSF for native communities. For each pair of plant communities in the experiment two PSF values were calculated, one for the invasive species and one for the native community. Positive PSFs were obtained when plants grew better in unsterilized soils than in its paired sterilized pot, and vice versa for negative PSFs. It is important to note that PSFs calculated here reflect both direct plant-soil interactions and indirect changes in competition influenced by those interactions.

A mixed linear model was made to investigate whether PSF would increase for native and decrease for invasive species with increasing species richness of the community. Species richness and plant origin (native or invasive), together with their interaction, were inserted as fixed factors and PSF as response variable. PSF for invasives was calculated with the biomass of each single invasive individual within each community, while PSF for natives was calculated with the biomass of the entire native community. Community type, nested in which invasive species was added, was inserted as random factor. Afterwards, three separate mixed models were made with the same response variable and fixed factors, one for each invasive species and their invaded communities. Community type was inserted as random factor. Assumptions were checked as above.

Data analyses were all performed in R version 4.2.1 (R Core Team, 2022). All figures were made with ggplot (Wickham 2016).

Results

PSFs were generally negative for both native and invasive species (Fig. 1), but significantly more so for natives (Table 1, negative estimates for plant type). For native species, PSF slightly increased (i.e., becomes less negative) with increasing community species diversity, whereas for invasive species it decreased (Fig. 1d; Table 1). However, the PSF models for the individual invasive species revealed that the latter was only observed in communities invaded by *S. gigantea* (Fig. 1a-c; Table 1).

In mesocosms with unsterilized soil, native aboveground biomass (shoot biomass of all native species) increased significantly with plant community diversity, whereas this effect was weaker in mesocosms with sterilized soil (Fig. 2a-d; Table 2). Although the same trend is visible in all four plots, this was only significant when all species were combined (Fig. 2d). Biomass of the invasive species *S. gigantea* decreased significantly with increasing plant community diversity in mesocosms with unsterilized soil (Fig. 2f; Table 2). This effect was markedly weaker in sterilized soils, although still significant and negative (Fig. 2f; Table 2). For the other two invasive species, *A. sterilis* and *L. polyphyllus*, plant community diversity nor its interaction with soil sterilization had significant effects on aboveground biomass (Fig. 2e & g respectively, Table 2).

Lastly, both invasives *A. sterilis* and *L. polyphyllus* showed a rapid initial growth, outgrowing all native species immediately after germination (Fig. 3). *S. gigantea* in contrast, showed a slow initial growth compared to the native species used in our experiment (at least for the first 28 days), with a sudden growth burst in the following 28 days (Fig. 3).

Discussion

Overall, the results of this study support our first two hypotheses: firstly, that PSFs for native species would be negative in species-poor communities and become more neutral in species-richer communities, and secondly that a biodiversity-productivity relationship would only be found in unsterilized soils. The results concerning our third hypothesis, i.e. that diversity of native communities would negatively impact invasive success only in unsterilized soils, were twofold and highly dependent on the invasive species obtained in the plant community. The results of the mesocosms with native communities invaded by *S. gigantea* largely supported our third hypothesis, where *S. gigantea* grew worse in more diverse communities, and this effect was strongest in unsterilized soils. The communities invaded by the other two invasive species however, did not support our third hypothesis.

Overall, negative PSFs for native species became more neutral in species-rich communities (Fig. 1d), resulting in a positive biodiversity-productivity relationship for native species in unsterilized soils but not in sterilized ones (Fig. 2d), supporting our first two hypotheses. Although not significant for separate models (i.e. based on individual invasive species instead of all three combined), this trend was the same for all communities, regardless of invasive species (Fig. 2a-c). We suggest the reduction in negative PSFs with increasing plant diversity in unsterilized soils results from species-specific pathogen dilution, as PSFs

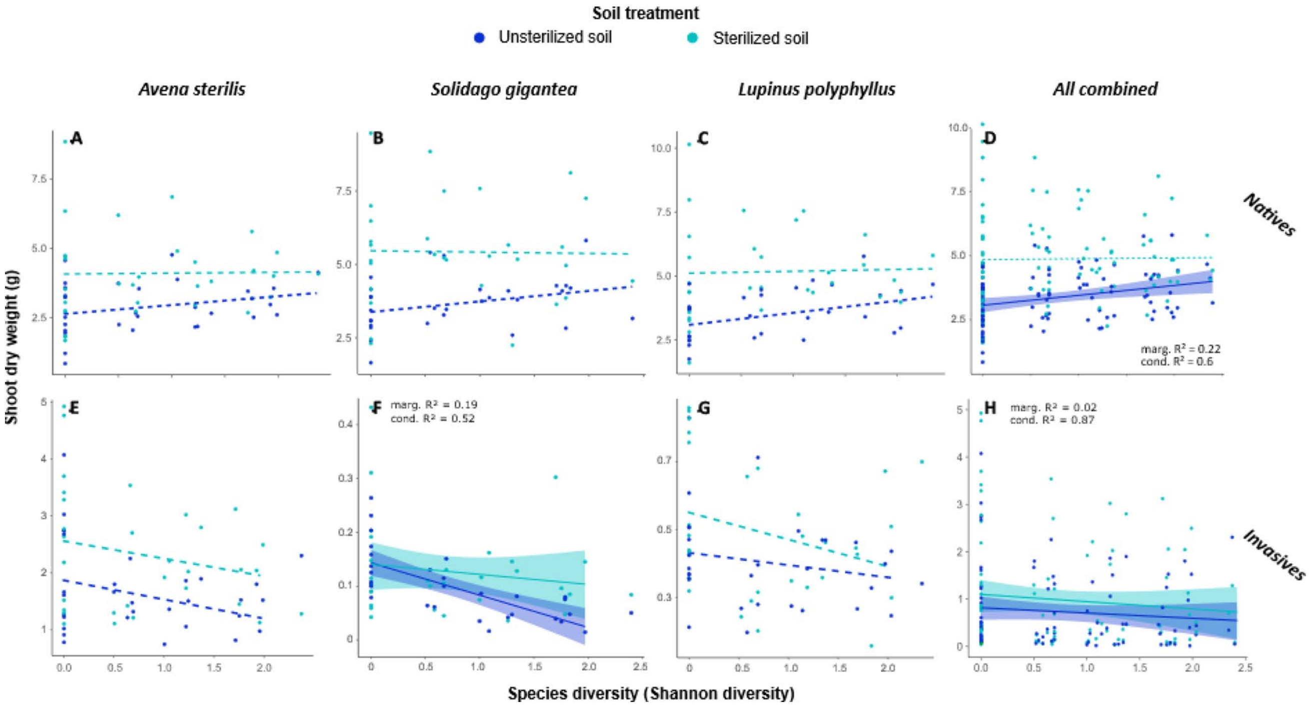

Fig. 2 Aboveground biomass for native species (a–d) and invasive species (e–h) as a function of the species diversity of the community they were grown in. **a–d**: Aboveground biomass of (a) all native species per mesocosm combined when invaded by *A. sterilis*; (b) as in (a), but when invaded by *S. gigantea*; (c) as in (a), but when invaded by *L. polyphyllus*; and (d) all natives combined, representing an assembly of panels a–c. Native communities consist of different combinations of the following species: *Lotus corniculatus*, *Medicago lupulina*, *Trifolium pratense*, *Anthyllis vulneraria*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *Alopecurus pratensis*, *Plantago lanceolata*, *Rumex acetosa*, *Centaurea jacea*, and *Ranunculus repens*. **e–h**: Aboveground biomass of (e) *A. sterilis* per mesocosm, (f) *S. gigantea*, (g) *L. polyphyllus*, and (h) all invasive species combined, representing an assembly of panels e–g. Significant relationships are indicated with solid lines, while dashed lines indicate marginally significant (0.05 < *P* < 0.1) and non-significant relationships. Blue dashed lines indicate non-significant relationships

Table 2 Effects of species diversity, soil treatment, and their interaction on the biomass of the native community (N.) and invasive species (I.)

Community		Fixed factors								
		Species diversity			Soil treatment			Sp. div. x Soil tr.		
		Estimate	t-value	*P*	Estimate	t-value	*P*	Estimate	t-value	*P*
Overall	N.	**0.38**	**2.1**	**0.04**	**1.79**	**8.1**	**<0.001**	***–0.35***	***–1.8***	***0.08***
	I.	**–0.12**	**–1.6**	**0.03**	**0.28**	**3.1**	**<0.001**		–0.5	0.65
A. sterilis	N.		0.7	0.47	**1.39**	**4.4**	**<0.001**		-0.6	0.57
	I.		–1.6	0.12	**0.66**	**2.9**	**0.007**		0.1	0.90
S. gigantea	N.		1.3	0.21	2.08	5.9	**<0.001**		–1.2	0.23
	I.	**–0.06**	**-3.3**	**0.002**		–0.1	0.89	**0.04**	**2.1**	**0.048**
L. polyphyllus	N.		1.2	0.23	**1.88**	**3.8**	**<0.001**		-0.87	0.39
	I.		–1.0	0.32	**0.12**	**2.5**	**0.02**		–1.1	0.28

Results are presented for all communities combined (overall) and separately for communities invaded by *A. sterilis*, *S. gigantea*, and *L. polyphyllus*. A positive estimate for soil treatment indicates higher biomass under sterilized compared to unsterilized soil conditions. A negative interaction estimate indicates that species diversity has a more positive effect on biomass under unsterilized conditions, whereas a positive interaction estimate indicates that species diversity has a more negative effect under unsterilized conditions. Significant values are indicated in bold; marginally significant effects (0.05 < P < 0.1) are indicated in italics. Estimates are omitted when non-significant

were generally negative for native species (Fig. 1a-d). The predominant negative PSFs were consistent with findings by Kulmatiski et al. (2008), and indicate that pathogen effects outweigh those of mutualists. Our results also align with earlier studies (Maron et al. 2011; Schnitzer et al. 2011) identifying pathogen dilution as a key driver of biodiversity-productivity relationships (but see Luo et al. 2017 for these effects disappearing at high soil fertility), potentially more influential than mechanisms such as facilitation, resource partitioning, or interspecific niche complementarity (Tilman et al. 2014; van Ruijven et al. 2020). For instance, Wang et al. (2023) provided strong evidence that

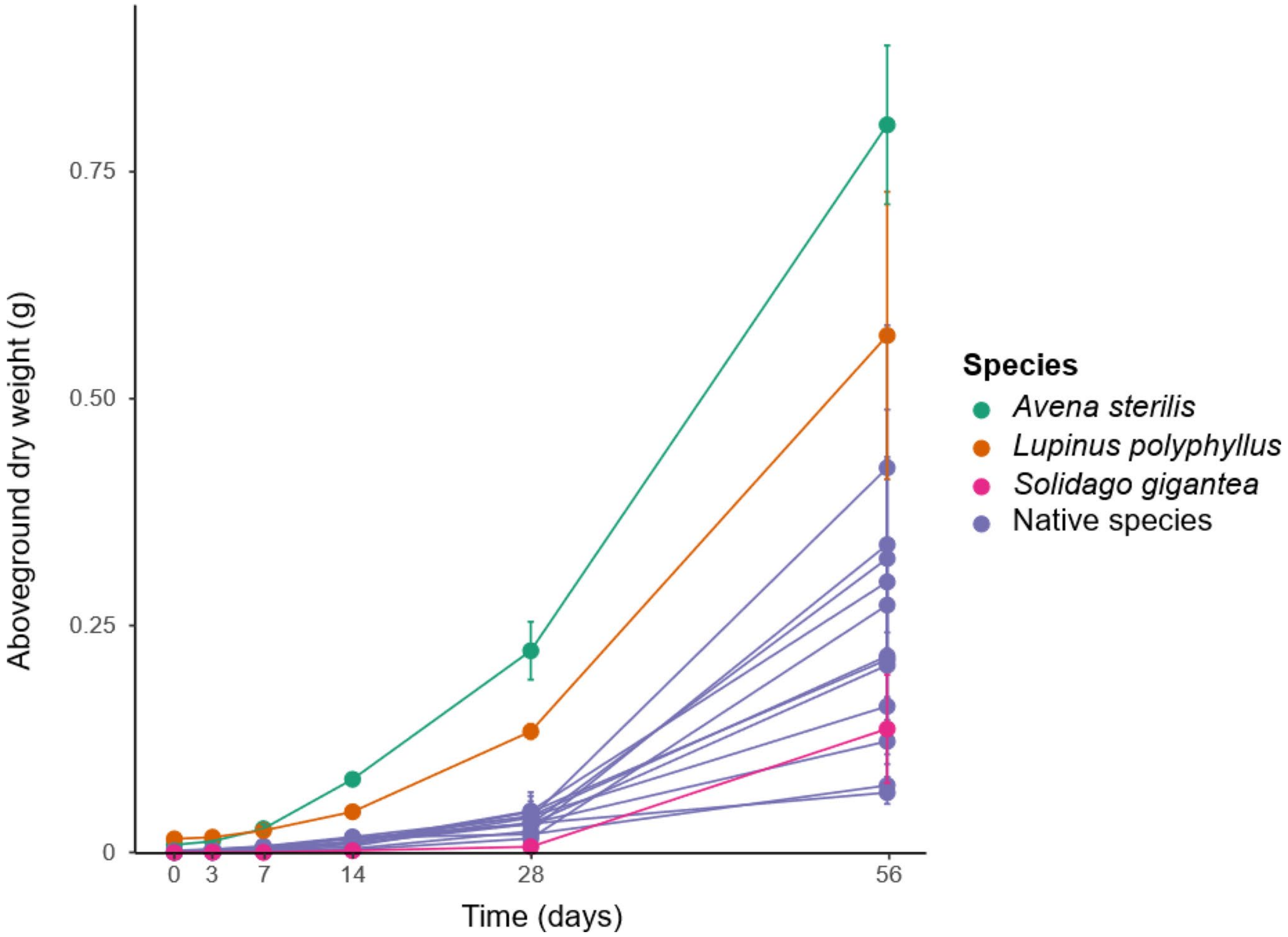

Fig. 3 Growth curves for all species. Growth curves were made for all species, grown separately ($n = 4$ for each growth stage per plant species) without soil inoculum. Growth curves are based on aboveground biomass. Standard errors are given

host-specific pathogens underpin biodiversity-productivity relations, while they did not find support for resource partitioning. In contrast, Meyer et al. (2016) argued that positive biodiversity effects, such as niche complementarity, are as important for increased productivity in species-rich communities as negative feedbacks are for reduced productivity in species-poor ones. While our findings point to negative PSFs as the primary mechanism reducing biomass at low diversity, we can not rule out that other processes might also have played a role. These include inefficient nutrient uptake leading to leaching losses (Leimer et al. 2015) and a limited capacity for temporal species turnover (Allan et al. 2011). It is likely that such mechanisms were not detected in our study, as their effects typically emerge over longer temporal scales (Meyer et al. 2016).

We also found some evidence that increasing native species diversity, particularly in unsterilized soils, significantly reduced the success of invasive species (Fig. 2h) through increasingly negative PSFs (Fig. 1d). However, this trend was only significant for *S. gigantea*, supporting our third hypothesis for this species (Fig. 2f). Although species diversity also negatively impacted *S. gigantea* biomass in sterilized soils, the effect was weaker. Since in unsterilized soils, the native community exhibited strongest growth in species-rich communities where it experienced lower pathogen loads (Fig. 2a-d), we attribute the reduced growth of *S. gigantea* here to increased competition of the native community (Michalet et al. 2023; Weigelt et al. 2002). Conversely, in sterilized soils, where the native community benefited less from pathogen dilution at higher species diversities, *S. gigantea* experienced only marginally increased competition in species-rich communities. This is in contrast to Ostfeld and Keesing (2012), who proposed that species-rich communities have a lower abundance of host plants for pathogens and therefore a reduced pathogen prevalence and lowered negative impact on invasive plants (Li et al. 2024; but we note that these studies did not work with sterilized soil as control). However, presuming that many plant pathogens are species-specific (Bever 2003; Mitchell et al. 2002), a reduced pathogen prevalence in species rich communities resulted in increased growth and competition of native species, and reduced growth of the invasive species *S. gigantea*. We remark that for the two other invasive species such a pattern was not observed (Fig. 2e & g), which does not support our third hypothesis for these species.

Our findings for both native plant species and for the invasive species *S. gigantea* have implications for invasion ecology and the enemy release hypothesis (ERH). We propose that the validity of the ERH, even within a single species, depends on the composition and species diversity of the invaded community. This was evident in *S. gigantea*, which exhibited positive PSFs at lower species diversity -opposite to the pattern observed in native species (Fig. 1b)- thereby supporting the ERH. However, this advantage disappeared at higher species diversity, where *S. gigantea* experienced mostly negative PSFs (Fig. 1b).

While some previous studies supported the ERH (Callaway et al. 2004; Klironomos 2002) and others did not (Colautti et al. 2004; Fahey and Flory 2022; Shannon et al. 2012), our results highlight its context dependency. Importantly, most studies supporting the ERH have been conducted in monoculture settings, where invasive plants were grown separately and only the direct effects of soil conditioning were assessed (see Klironomos 2002 and experiments 1 and 2 in Callaway et al. 2004). Other studies have included competition with native species, but typically under low-diversity conditions, such as one-to-one competition experiments (e.g. experiment 3 in Callaway et al. 2004). In contrast, studies that did not find support for the ERH for the invasive species examined were conducted in experiments with more diverse native communities (Fahey and Flory 2022; Shannon et al. 2012). The review by Colautti et al. (2004) also notes that many community-level studies fail to support the ERH. Taken together, the consistent support for the ERH in monoculture or species-poor setups, and the lack of support in more diverse community experiments, strengthens the interpretation of our results, that ERH becomes less valid when invading species-rich communities.

Furthermore, our findings suggest that the greater resistance of biodiverse systems to invasion (“the biotic resistance hypothesis”; Beaury et al. 2020; Maron and Marler 2007) is largely due to increased competition from the native community following pathogen dilution. We propose that rather than viewing biodiverse systems as more resistant to invasion, species-poor communities should be seen as more susceptible to plant invasions due to higher species-specific pathogen loads in their associated microbiome (Maron et al. 2011; Schnitzer et al. 2011; Wang et al. 2023). Mechanisms such as complementarity effects due to niche partitioning (Eisenhauer et al. 2013) and resource scarcity (Tilman 2004) seem to play a minor role in our setup, as *S. gigantea* showed only minimal growth reduction with increasing diversity in sterilized soils. Complementarity effects might have been absent due to niche partitioning not contributing to a diversity-productivity relation for the native communities in our study (Mahaut et al. 2020; Weisser et al. 2017). This does not necessarily imply that niche partitioning is unimportant in our study system. Rather it may have been absent due to the experimental setup, in which nutrients were supplied in fixed forms and plants were unable to develop differentiated rooting systems due to temporal and spatial constraints.

These mechanisms mentioned above do not seem universal however. For the two other invasive species investigated here, *Avena sterilis* and *Lupinus polyphyllus*, species diversity had no effect on invasion success in either unsterilized or sterilized soils (Fig. 2e & g). We attribute this to the rapid initial growth of these two species (Fig. 3, both *A. sterilis* and *L. polyphyllus* outgrow all native species immediately after germination), which allowed them to avoid direct competition for light with the native community (Hautier et al. 2009; Vojtech et al. 2007), regardless of its species diversity and of the soil sterilization treatment. In contrast, *S. gigantea* showed a slower initial growth rate in our setup (Fig. 3, see first four weeks). It should be noted that this is not always necessarily the case for this highly plastic species as it can adjust its growth pattern to changes in environmental conditions (Jakobs 2004). This initial slow growth made it more dependent on reduced competition in species-poor native communities, as both growth and vitality of *S. gigantea* are strongly reduced under shaded conditions (Voser-Huber 1983; Weber and Jakobs 2005). This latter scenario, as for *S. gigantea*, may better reflect real-world invasions, where newly introduced invasive species must compete as seedlings with the already established native flora (but see Dickson et al. (2012) and Hess et al. (2019) for priority effects favouring invasive over native seedlings).

To avoid the absence of light competition for invasive species, and to simulate real-world invasions better, future studies could use a larger, further developed native community in the response phase. This would ensure that invasive species need to compete for light, regardless of their initial growth rate. Possible considerations are how large the native community used in the response phase should be, as using fully grown, established plants could result in time constraints and less negative overall PSFs due to stronger plant defences. Secondly, it could be considered to not transplant invasive seedlings into the native communities, but to sow their seeds directly into them as this mimics field situations better.

Conclusion

Our findings reveal that invasion resistance emerges from how species diversity shapes interactions between plants and soil biota. By demonstrating that species-specific pathogens are diluted in diverse native communities, we show how negative plant–soil feedbacks among natives are weakened and invaders like *S. gigantea* face greater biotic resistance. We highlight a key ecological mechanism: invasion is facilitated not simply by low competition, but also by the disruption of soil microbial balance in species-poor communities, which allows pathogens of natives to accumulate and inadvertently benefit invasive species. This reframing of the enemy release hypothesis, as dependent on the diversity and soil composition of the invaded community, offers a more mechanistic understanding of when and where invasion success is likely. It suggests that protecting biodiversity does more than preserve ecosystem function: it maintains the complex biological interactions that limit opportunities for invasive species to establish. In a time of rapid global change, these insights stress the need to consider soil biota and community context in both invasion ecology and restoration strategies. Managing for biodiversity may be most powerful not in suppressing invaders directly, but in sustaining the invisible networks that make communities resilient to them.

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Author contributions E.P.G. and H.O.V. conceived the ideas and designed methodology; E.P.G. collected the data; E.P.G. analysed the data; E.P.G. led the writing of the manuscript; E.P.G., V.M., and H.O.V. contributed critically to the drafts and all authors gave final approval for publication.

Declarations

Competing interests The authors declare no competing interests.

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