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RESEARCH ARTICLE

Artificial particles and soil communities interactively change heterospecific plant-soil feedbacks

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Abstract

Background and aims Microplastics affect plant growth and change abiotic and biotic soil properties, such as soil structure and soil-community composition. However, how microplastics affect plant-soil interactions, such as plant-soil feedbacks (PSFs), is still poorly understood. Here, we tested how artificial particles affect heterospecific PSFs, depending on an intact or depleted soil community.

Methods We conducted a two-phase-greenhouse experiment using *Centaurea jacea* to condition soil containing an intact or initially depleted (by sterilization) soil community in the first phase. Subsequently, we grew individuals of *Crepis biennis* and *Eragrostis minor* in all combinations of soil conditioning (presence or absence of *C. jacea* in the first phase), soil-community status, and different material treatments including no added particles, glass particles, or three microplastics individually and mixed. Effects of soil community, material treatment and their interaction on PSFs were assessed based on plant biomass and root-morphology traits.

Results Particles in general, microplastics and glass, strengthened PSFs based on plant biomass. PSFs tended to be negative with the intact but positive with the initially depleted soil community. Overall, particle-addition effects on PSFs were stronger in the initially depleted community, indicating interactive effects of artificial particles in the soil and soil biota. Interactive particle and soil-community effects generally depended on material type and concentration.

Conclusion Our findings indicate that artificial particles can affect heterospecific PSFs and that these effects are likely to be partly mediated by the initial soil community. Further, they highlight the need for studies assessing potential ecological implications of microplastics on plant-soil interactions.

Keywords Microplastic · Plant-soil feedback · Plastic pollution · Plant-soil interactions

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Abbreviations

AMF	Arbuscular mycorrhizal fungi
EPDM	Ethylene propylene diene monomer
LL	Average link length
PE	Polyethylene
PHA	Polyhydroxyalkanoate
PSF(s)	Plant-soil feedback(s)
RD	Average root diameter
RTD	Root-tissue density
RWR	Root-weight ratio
SRL	Specific root length

Introduction

Plastic pollution is a global issue receiving increasing social, political, and scientific attention (Bank et al. 2021; MacLeod et al. 2021; Rochman et al. 2013). The scale of this problem is obvious when considering that in 2021 almost 400 million tons of new plastics were produced in Europe alone (Plastics Europe 2022). Insufficient recycling strategies and improper disposal lead to ever increasing quantities of plastic waste accumulating in the environment (Geyer et al. 2017; Jambeck et al. 2015). Due to characteristics associated with their small size, such as easy distribution or large relative surface area, microplastics (particles < 5 mm; Thompson et al. 2009) might be particularly problematic for the environment, and humans (MacLeod et al. 2021; Vethaak and Legler 2021). Although research on microplastics was initially limited to marine environments (Andrady 2011; Cole et al. 2011), research on terrestrial ecosystems is increasing (Baho et al. 2021; Rillig 2012; Rochman 2018). Soils are the major sink for microplastics, making the plant-soil system especially prone to microplastic effects (Chia et al. 2021; Helmberger et al. 2020; Rillig and Lehmann 2020; Zhou et al. 2021). Microplastics can affect plant functioning and soil communities (Speißer and van Kleunen 2023; Sun et al. 2022), but impacts on plant-soil interactions are still poorly understood.

Plants change abiotic and biotic soil components while growing, in turn affecting neighboring and subsequent plants, a process known as plant-soil feedback (PSF) (Bever 1994; Ehrenfeld et al. 2005; Wardle 2002). PSFs can either be conspecific, if conditioning and affected plants belong to the same species, or heterospecific, for plants of different species (van der Putten et al. 2013). PSFs are driven by plants changing abiotic conditions, including nutrient availability and other soil properties, and biotic soil conditions, including the abundance of mutualists and antagonists (Bennett and Klironomos 2019). As effects range from positive (improved plant performance) to negative (reduced plant performance), PSFs play important roles in ecological processes such as community assembly and succession, and plant invasion (Bennett et al. 2017; Chapin et al. 1994; Chen and van Kleunen 2022; Klironomos 2002; van der Putten et al. 1993). However, human-driven global change is likely to affect PSFs (van der Putten et al. 2016), and microplastics in particular, due to their effects on plant functioning, physical soil properties and soil communities are likely to interact with PSFs.

By now, it has become clear that microplastics can affect both plant and soil properties. Microplastics change the soil structure, which can result in reduced water availability and increased nutrient leaching (Ingraffia et al. 2022a, 2022b; Kim et al. 2021b; Speißer and van Kleunen 2023; Wan et al. 2019). Regarding possible PSF modifications, microplastic effects on soil communities might be particularly important. Plastic particles can create a new type of habitat for microorganisms called the plastisphere, i.e. the environment and microbial community directly influenced by microplastics (Rillig et al. 2023). Microbial communities associated with microplastics have been found to contain more pathogenic bacteria and fungi (Gkoutselis et al. 2021; Zhu et al. 2021), which could lead to more negative PSFs. On the other hand, Lehmann et al. (2020) found positive effects of microplastics on mutualistic arbuscular mycorrhizal fungi (AMF), which could reduce negative PSF. Overall, experimental evidence for microplastic effects on AMF is very limited and effects are likely to be highly context dependent (Wang et al. 2020). While the exact mechanisms driving microplastic effects on plant-associated microbes are still unclear, they may be relevant for plant performance. However, although pathogenic bacteria and fungi and mutualistic AMF are main biotic drivers of PSF and have been shown to be affected by microplastics, there have been hardly any studies that tested microplastic effects on PSFs (but see Lozano and Rillig 2022; Xue et al. 2024).

Microplastics can affect plants both directly, due to phytotoxic effects (Maity and Pramanick 2020; Pignattelli et al. 2020) and indirectly, by

changing soil characteristics, including biogeochemical cycling and nutrient availability (Ingraffia et al. 2022b; Leifheit et al. 2021a). Most likely, both direct and indirect mechanisms are responsible for observed microplastic effects on plant performance and root growth (Lozano et al. 2021; Speißer and van Kleunen 2023; Speißer et al. 2022; van Kleunen et al. 2020). Moreover, microplastic effects on plants could feed back to plant-soil interactions. For example, microplastics can change plant secondary metabolites, in turn affecting soil nematodes (Kim et al. 2021a). A first study looking at effects of microplastics on PSFs found that soils previously exposed to microplastics exhibited more positive or negative PSFs compared to soils without microplastic ancestry, depending on microplastic characteristics (Lozano and Rillig 2022). However, whether such effects are common remains unknown.

As conspecific and heterospecific PSFs generally share the same mechanisms, both might be affected by microplastics. However, as heterospecific PSFs often receive less attention, we only focus on heterospecific PSFs in our study. To gain a better understanding of how microplastics affect heterospecific PSFs, we tested the hypothesis that microplastics affect PSFs depending on the plastic type and particle concentrations, by assessing how different microplastics affected soil-conditioning effects of *Centaurea jacea* on the growth of the forb *Crepis biennis* and the grass *Eragrostis minor*. Next to a control treatment without added particles and a chemically inert control using glass particles, we included three plastic types, low-density polyethylene (PE), ethylene propylene diene monomer (EPDM), and polyhydroxyalkanoate (PHA). We applied the different plastics individually and mixed in a low (0.5% vol) and a high (5% vol) concentration. We expected the effects of microplastics on PSFs to be mediated by both abiotic (e.g. soil structure, nutrient availability) and biotic (soil community) factors. Therefore, to disentangle biotic from abiotic effects, we grew *C. jacea* in substrate containing either an intact or depleted (by sterilization) soil community. In the feedback phase, we grew individuals of *C. biennis* and *E. minor* in all possible combinations of conditioning, soil community, material type, and material concentration. Finally, due to the closer relatedness to *C. jacea*, we expected PSF effects and microplastic-induced changes to be stronger for *C. biennis*, especially with the intact soil community.

Methods

Study species and precultivation

We used the perennial forb *Centaurea jacea* L. (Asteraceae) to condition the substrate in the first phase of the experiment (conditioning phase; Fig. 1). *Centaurea jacea* is native to Europe and is naturalized in other parts of the world, including North America and Australia (POWO 2024). We chose this species because it has been shown to induce detectable PSF effects on conspecifics and heterospecifics (Xue et al. 2018a, b). To examine heterospecific PSFs of *C. jacea*, and assess whether these are modified by microplastics, we used the distantly related *Eragrostis minor* Host (Poaceae) and the more closely related *Crepis biennis* L. (Asteraceae) as test species in the second phase of the experiment (feedback phase). *Eragrostis minor* is an annual grass that is native to large parts of Asia, the Mediterranean and parts of Africa, and is naturalized in Central Europe, Australia, and parts of North and South America (POWO 2024). *Crepis biennis* is a biennial forb native to large parts of Europe and occurs in parts of North America as naturalized species (POWO 2024). Seeds were sown separately by species into plastic trays (13.4 cm × 12.2 cm × 4.9 cm; TEKU® TK 1214, Pöppelmann GmbH & Co. KG, Lohne, Germany) filled with unsterilized potting soil (Einheitserde® CL P, Einheitserdewerke Werkverband e.V., Sinntal-Altengronau, Germany) and placed in a climatized greenhouse for germination two weeks before the beginning of the respective phase. That is, seeds of *C. jacea* were sown on 15 August 2022, and seeds of *E. minor* and *C. biennis* were sown on 10 October 2022. Seeds of *C. jacea* and *C. biennis* were obtained from a commercial seed company (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany), and *E. minor* seeds were obtained from the botanical garden of the University of Konstanz.

Microplastics

To test how different plastic types affect PSFs, we selected three plastic types differing in major

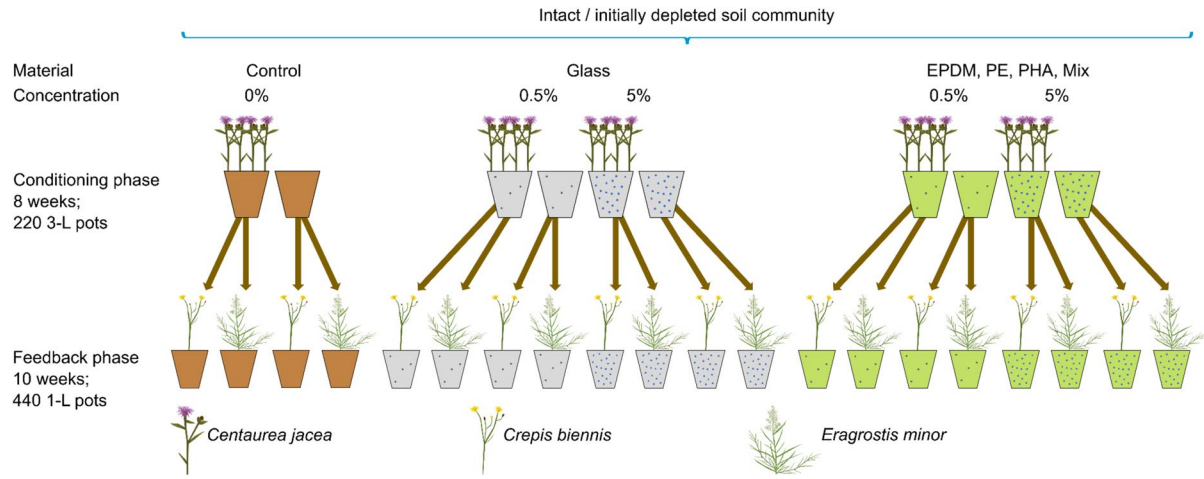


Fig. 1 Schematic overview of the experimental set-up. We used four individuals of *Centaurea jacea* to condition one half of the pots (120 pots) used in the conditioning phase. The other half remained as unconditioned control. We established different treatment combinations including an intact or initially depleted soil community (live or sterilized field soil) and different material treatments including a control without added material, a chemically inert glass control, accounting for physical effects of particles added to the soil, and different microplastics (EPDM, PE, PHA, mix of all microplastics). In addition, each material was applied in a low (0.5% vol) and high concentration (5% vol). For the feedback phase, the substrate of each conditioning-phase pot was split into two new pots, into one of which one seedling of *Crepis biennis*, and in the other one seedling of *Eragrostis minor* was planted. Each treatment combination was replicated five times for each species

characteristics, such as polymer type, surface structure and degradability. Polyethylene (PE) is the most commonly used plastic type (Geyer et al. 2017), and is characterized by a smooth surface and high resistance to biotic and abiotic degradation. In our experiment, we used granules (2.5 – 4 mm) of a non-additivated low-density PE (Lupolen 3020H, LyondellBasell Industries, Rotterdam, Netherlands), which is used to produce, amongst others, plastic bags, and food packaging. As the second conventional plastic type, we selected ethylene propylene diene monomer (EPDM). EPDM is an elastomer that is often used for outdoor applications, due to its high resistance against UV-degradation and abrasion. For example, EPDM granules are frequently used in artificial turfs (e.g. soccer pitches), from which they can easily spread into the surroundings (van Kleunen et al. 2020). These EPDM granules are a good example of primary microplastics. Here, we used such EPDM granules (0.5 – 2.5 mm; Resedagrün RAL 6011, GranuElastic Höfer & Stankowska GbR, Frankfurt (Oder), Germany). As the usage of biodegradable plastics is increasing continuously (Kumar et al. 2023), we also included the biodegradable polymer polyhydroxyalkanoate (PHA) in our experiment (PHI 002, NaturePlast, Mondeville, France). The PHA granules (2 – 4 mm) were similar to the PE granules in terms of their appearance. However, PHA is considered to degrade relatively quickly (Dilkes-Hoffman et al. 2019), and hence stronger short-term effects can be expected compared to conventional plastics (Qi et al. 2018). In addition to the different microplastics, to account for purely physical effects of adding particles to the substrate, we included glass granules (2 – 4 mm, Glasgranulat klar, Deco Stones, Vechelde, Germany) as a chemically inert control. To remove glass dust and other impurities, the glass granules were thoroughly washed prior to usage.

Conditioning phase

For the conditioning phase, we created a substrate consisting of sand-vermiculite (1:1, v:v) mixed with field soil in a 1:1 volume-ratio, to include a natural soil community. The field soil was collected from the topsoil layer of a grassland community close to the botanical garden of the University of Konstanz (N: 47°69′19.56″, E: 9°17′78.42″) and was sieved (mesh size 15 mm × 15 mm) to remove stones and break up large soil aggregates. To be able to investigate the

interactive effects of the soil community and our other treatments (soil conditioning, microplastics), we sterilized half of the substrate twice using a steam sterilizer, heating the substrate to 80 °C for approximately three hours (Erddämpfer Sterilo, Harter Elektrotechnik, Schenkenzell, Germany). Subsequently, we filled 3-L square pots with the respective substrates, i.e. either with pure sterilized or non-sterilized substrate for the control pots or with sterilized or non-sterilized substrate containing a low (0.5%, v:v) or high (5%, v:v) concentration of PE, EPDM, PHA, a mix of all three plastics (equal volumetric proportions), or glass. To ensure accurate concentrations of the microplastic and glass particles, we prepared the substrate for each pot individually. As soils are recolonized after sterilization (Baweja 1939; Li et al. 2019; Marschner and Rumberger 2004), we refer to an initially depleted vs intact soil community, rather than sterilized vs intact.

On 29 August 2022, to condition the substrate, we planted four similar-sized seedlings of *C. jacea* per pot into half of the pots, keeping the other half of the pots as unconditioned control. We used four seedlings per pot to strengthen the conditioning effects. We placed the 220 pots (2 conditioning × 2 soil communities × (((4 plastics + glass) × 2 concentrations) + 1 control) × 5 replicates) in the same greenhouse compartment described above in a randomized block design. Within the five blocks, the pots were randomly assigned to fixed positions. On 24 October 2022, after a growth period of eight weeks, we harvested the plants by first cutting the shoots and subsequently carefully removing the roots from the substrate. We collected the shoots and roots from each pot individually, dried them at 70 °C for at least 72 h and weighed them using a digital scale. We report the effects of microplastics and the soil community (depleted vs. intact) on *C. jacea* in the supplement (Supplementary Table 1; Supplementary Fig. 1).

Feedback phase

We thoroughly homogenized the substrate of each individual conditioning-phase 3-L pot, and subsequently redistributed it into two new 1-L pots. Into one of these two pots, we planted one seedling of *C. biennis*, and, into the other one, we planted one seedling of *E. minor*. This resulted in a total of 440 pots for the feedback phase (i.e., 220 pots per test species; Fig. 1), which again were arranged in the same greenhouse into five randomized replicate blocks. To be able to account for differences in initial size of the seedlings in the statistical analysis, for each seedling, we measured the length and width of the largest leaf, counted the number of leaves, and calculated a proxy of initial leaf area by multiplying the leaf length by the width of the largest leaf and by the number of leaves. After a growth period of ten weeks, we harvested both the aboveground and belowground parts of the plants, individually. The shoots of both species, as well as the roots of *E. minor* were directly dried at 70 °C for at least 72 h and subsequently weighed using a digital scale. For *C. biennis*, we stored the fresh roots in water-filled tubes at 8 °C for a maximum of 72 h prior to root-morphology analysis. For the root-morphology analysis of *C. biennis*, we scanned the individual root systems using a root scanner (modified Epson Expression 1100 XL and Epson Expression 1200 XL flatbed scanners) and analyzed the total root length, average root diameter, average link length (as a proxy for root ramification) and root volume (to calculate root-tissue density), using the WinRhizo™ Pro imaging software (Regent Instruments Inc., Canada). After scanning, the roots were dried and weighed as described above. As the root systems of *E. minor* were very dense and convoluted, we analyzed root-morphology traits only for *C. biennis*.

Statistical analysis

All statistical analyses were performed in R 4.2.2 (R Core Team 2022).

PSFs

To test how the three different types of microplastics in different concentrations affect heterospecific PSFs, and how potential effects might be influenced by soil-community depletion, we first calculated PSF values as log-response ratios:

$$PSF_X = \ln\left(\frac{X_{conditioned}}{X_{unconditioned}}\right)$$

That is, the PSF value for a given trait (X) was calculated as the natural logarithm of the quotient of the individual sample trait value from the conditioned soil and the mean of the control samples from

the unconditioned soil (grouped by material treatment and soil community). We used the mean of the control samples to reduce strong effect of sampling variance on the PSF metric and because some of the plants in the controls had died. The latter would otherwise have resulted in missing PSF values. For both response species, *C. biennis* and *E. minor*, we calculated PSFs for total biomass ($PSF_{biomass}$) and the proportion of root biomass to total biomass, i.e. root-weight ratio (PSF_{RWR}). For *C. biennis*, we also calculated PSFs for the root-morphology traits average root diameter (PSF_{RD}), specific root length (PSF_{SRL}), average link length (PSF_{LL}), and root-tissue density (PSF_{RTD}). We then fitted linear mixed-effects models using the *lme* function of the "nlme" package (Pinheiro et al. 2021), including PSF as response variable. We included material treatment (the one control and 10 combinations of material type and concentration), soil community (intact vs. initially depleted) and their interaction as fixed effects, and block as random effect. To improve homoscedasticity, we added variance structures for soil community for the $PSF_{biomass}$ model of *E. minor* and for all *C. biennis* models except for the PSF_{LL} and PSF_{RTD} models, using the *varIdent* fuction in the "nlme" package. For the PSF_{RWR} model of *E. minor*, adding variance structures for material treatment resulted in the best model fit (based on AIC). Significance of fixed effects was assessed using log-likelihood-ratio tests (Zuur et al. 2009).

Contrast models

To obtain more detailed information about differences in effects of the different material types and concentrations, we reran all models after creating ten orthogonal contrasts comparing specific combinations of the 11 material-treatments (Supplementary Table 2). The first contrast tested the effect of particle addition by comparing the average of the grouped material treatments (low and high concentrations of glass and microplastics) to the control (no added material). The second contrast tested the overall effects of plastics by comparing the average of the grouped microplastics to the average of low and high glass. The third contrast tested the effect of mixing the plastic types by comparing the average of the low and high microplastic mix to the average of the grouped individual microplastics. The fourth contrast tested the effect of the biodegradable plastic by comparing the average of the low and high biodegradable PHA to the average of the grouped conventional plastics (EPDM and PE). The fifth contrast tested whether the two conventional plastics had different effects by comparing the average of the low and high EPDM to the average of the low and high PE. The sixth to tenth contrasts compared the high vs. low concentration of each individual material type. We then replaced the material treatment with the ten a priori chosen contrasts as explanatory variables in the linear mixed-effects models, together with soil community and the specific two-way interactions between soil community and each contrast. We used orthogonal contrasts because they are statistically more powerful than comparing each material treatment to all others.

Results

Given the long-standing discussion about strictly binary decisions based on arbitrary *p*-value thresholds, we followed the recommendations of Muff et al. (2021), and wrote the results in a gradual evidence language. All results refer to effects on the calculated plant-soil feedback (PSF) values for the respective traits.

Heterospecific PSF effects on *Crepis biennis*

Biomass responses

$PSF_{biomass}$ and PSF_{RWR} of *C. biennis* ranged from negative to positive, and there was very strong evidence that both were interactively affected by the material treatment (combinations of different material types and concentrations) and the soil-community treatment (intact vs. initially depleted) ($p < 0.001$, respectively; Table 1, Fig. 2). Overall, $PSF_{biomass}$ tended to be positive for the initially depleted soil community, but negative for the intact soil community, and the material treatment further modified this pattern (Fig. 2A). Based on the a priori chosen contrasts, we identified different combinations driving these interactions (Table 1). For the initially depleted soil community, there was very strong evidence that particle addition generally shifted $PSF_{biomass}$ from negative to positive (C1 × soil community: $p < 0.001$; particles absent: -0.67 ± 0.6, particles present: 1.14 ± 0.18). In

Table 1 Results of linear mixed-effects models testing effects of material treatment, soil community and their interaction on PSFs on *Crepis biennis*, including orthogonal contrasts

		$PSF_{biomass}$		PSF_{RWR}		PSF_{SRL}		PSF_{LL}	
Fixed effects	df	LLR	*p*	LLR	*p*	LLR	*p*	LLR	*p*
Initial leaf area	1	0.87	0.35	6.05	**0.014**	1.41	0.23	0.23	0.64
Material treatment (M)	10	12.81	0.23	14.16	0.166	13.79	0.18	18.43	**0.048**
C1 (particles vs no particles)	1	0.12	0.73	0.40	0.53	1.10	0.29	0.10	0.75
C2 (glass vs plastics)	1	0.43	0.51	0.13	0.72	0.00	0.95	0.24	0.62
C3 (individual vs mixed plastics)	1	0.87	0.35	0.53	0.46	1.24	0.27	0.07	0.79
C4 (degradable vs conventional)	1	0.76	0.38	0.18	0.67	7.51	**0.006**	0.73	0.39
C5 (PE vs EPDM)	1	0.14	0.71	0.78	0.38	0.48	0.49	6.94	**0.008**
C6 (low vs high glass)	1	0.02	0.88	9.19	**0.002**	3.02	*0.08*	1.90	0.17
C7 (low vs high EPDM)	1	2.86	*0.091*	0.00	0.98	0.11	0.74	0.25	0.61
C8 (low vs high PE)	1	0.04	0.85	2.54	0.11	0.35	0.56	1.16	0.28
C9 (low vs high PHA)	1	0.68	0.41	1.66	0.20	0.00	0.98	2.17	0.14
C10 (low vs high mix)	1	8.26	**0.004**	0.09	0.77	0.70	0.40	6.17	**0.013**
Soil community (S)	1	37.60	**< 0.001**	6.25	**0.012**	48.43	**< 0.001**	47.73	**< 0.001**
M × S	10	45.69	**< 0.001**	34.58	**< 0.001**	48.61	**< 0.001**	13.89	0.18
C1 × S	1	16.94	**< 0.001**	16.67	**< 0.001**	3.62	*0.057*	0.16	0.69
C2 × S	1	0.01	0.91	11.14	**< 0.001**	15.33	**< 0.001**	2.12	0.15
C3 × S	1	1.99	0.16	0.04	0.84	1.36	0.24	1.73	0.19
C4 × S	1	13.65	**< 0.001**	3.00	*0.08*	0.47	0.49	1.92	0.17
C5 × S	1	3.27	*0.071*	0.04	0.85	0.00	0.98	2.50	0.11
C6 × S	1	9.20	**0.002**	0.14	0.70	0.78	0.38	0.19	0.66
C7 × S	1	13.64	**< 0.001**	4.61	**0.031**	28.17	**< 0.001**	1.39	0.24
C8 × S	1	0.46	0.50	3.22	*0.073*	0.11	0.74	2.05	0.15
C9 × S	1	0.00	0.98	0.83	0.36	6.22	**0.013**	2.09	0.15
C10 × S	1	1.49	0.22	1.34	0.25	1.80	0.18	0.10	0.76
Random effects		SD		SD		SD		SD	
Block		0.0024		0.0772		0.0024		0.0286	
Residual		0.3219		0.1567		0.2826		0.1936	

Orthogonal contrasts define individual material-treatment combinations (material type and low vs. high concentration; Supplementary Table 2) and were used to obtain detailed information about specific drivers of main effects of material treatment or interactions with soil community (intact vs. initially depleted). Effects were assessed for the calculated PSF values based on total plant biomass ($PSF_{biomass}$), root-weight ratio (PSF_{RWR}), specific root length (PSF_{SRL}), and average link length (PSF_{LL}). Fixed effects were assessed using log-likelihood ratio tests (Zuur et al. 2009). Log-likelihood ratios (LLR) are approximately χ^2-distributed. *P* values < 0.05 are indicated in bold, *p* values < 0.1 are indicated in italics

contrast, for the intact soil community, $PSF_{biomass}$ was generally negative, but more so if particles were added (particles absent: -0.30 ± 0.13, particles present: -0.49 ± 0.05; Fig. 2A). Further, there was very strong evidence that the biodegradable microplastics led to a weaker positive $PSF_{biomass}$ for the initially depleted community (C4 × soil community: $p < 0.001$; conventional: 1.44 ± 0.28, degradable: 0.16 ± 0.19), and a weaker negative $PSF_{biomass}$ for the intact community (conventional: -0.52 ± 0.08, degradable: -0.37 ± 0.08). There was also strong evidence for concentration effects for glass and EPDM. For the initially depleted community, $PSF_{biomass}$ was generally positive but less so for the high concentrations (C6 × soil community: $p < 0.001$; glass low: 2.1 ± 0.18, glass high: 0.29 ± 0.76; C7 × soil community: $p = 0.002$; EPDM low: 2.75 ± 0.16, EPDM high: 0.89 ± 0.68). For the intact community, $PSF_{biomass}$ was generally negative but weaker for the high concentration (glass

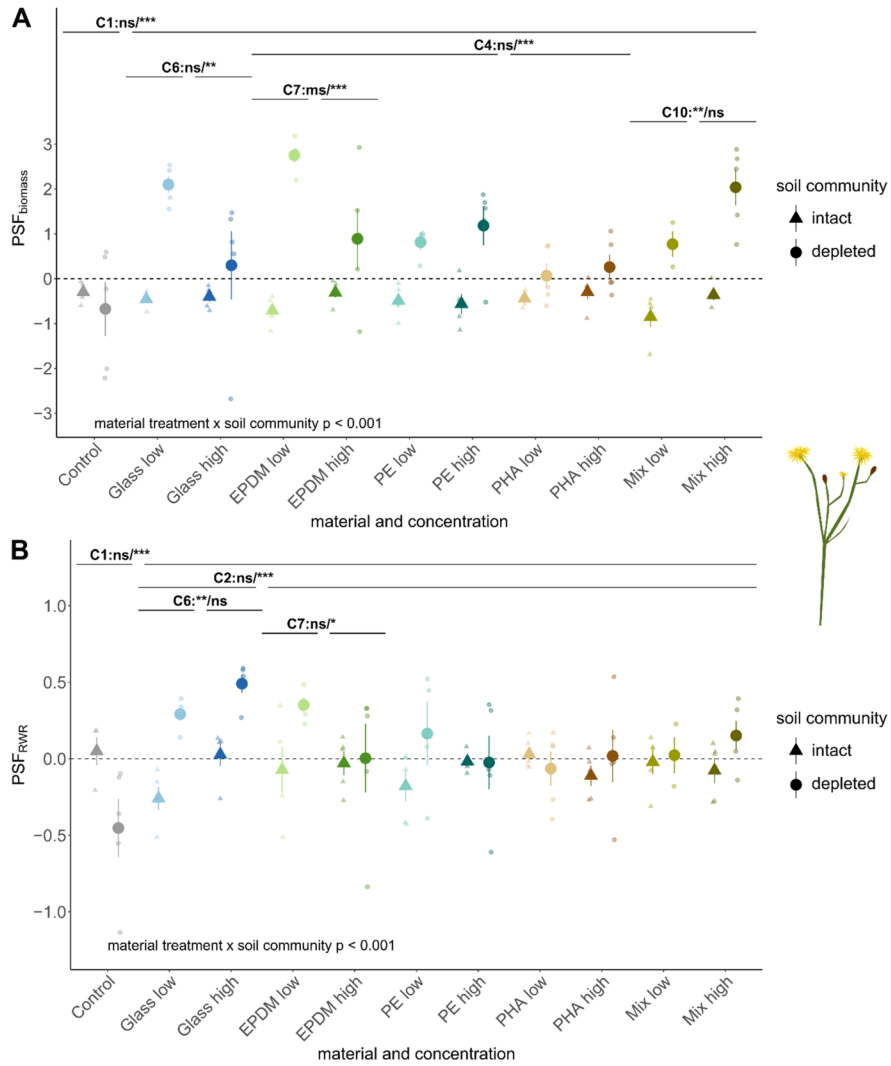


Fig. 2 PSF biomass responses of *Crepis biennis*. Effects of different materials (indicated by different colors) in low (light colors) or high (dark colors) concentrations and of intact (triangles) or initially depleted (circles) soil communities on plant-soil feedbacks based on total plant biomass ($PSF_{biomass}$; **A**) and root-weight ratio (PSF_{RWR}; **B**). Large symbols represent mean values of the specific treatment group, error bars show the respective standard error. Small symbols represent individual replicates. *P* values refer to basic models. Horizontal lines indicate significant results based on the contrast models (specific contrast: significance main contrast/significance contrast-soil-community interaction) and asterisks indicate which groups differ significantly from each other (Table 1; *** $p<0.001$, ** $p<0.01$, * $p<0.05$, ms (marginally significant) $p<0.1$, ns (not significant) $p>0.1$). Contrasts compare individual material-treatment combinations (material type, i.e. glass and different microplastics, and low vs. high concentrations; Supplementary Table 2) and were used to obtain detailed information about specific drivers of main effects of material treatment or interactions of the material treatment with soil community

low: -0.46 ± 0.08, glass high: -0.4 ± 0.11; EPDM low: -0.71 ± 0.14, EPDM high: -0.31 ± 0.11). In addition, there was strong evidence for a concentration dependency in the plastic mix, with a negative $PSF_{biomass}$ for the low concentration, but a positive $PSF_{biomass}$ for the high concentration (C10: $p<0.01$; low: -0.24 ± 0.34, high: 0.84 ± 0.45), irrespective of the soil community.

Similar to the results for $PSF_{biomass}$, there was very strong evidence that particle addition led to a shift

from negative to positive PSF_{RWR} (i.e. from a negative to a positive conditioning effect on biomass allocation to roots) for the initially depleted community (C1 × soil community: $p < 0.001$; particles absent: -0.45 ± 0.19, particles present: 0.15 ± 0.05). For the intact community, PSF_{RWR} was generally weak, but tended to be slightly positive without added particles (particles absent: 0.05 ± 0.09) and slightly negative with added particles (particles present: -0.07 ± 0.03; Fig. 2B). In addition, there was very strong evidence that microplastics, compared to glass, led to a weaker positive PSF_{RWR} for the initially depleted community (C2 × soil community: $p < 0.001$; glass: 0.39 ± 0.05, microplastics: 0.08 ± 0.05), and a weaker negative PSF_{RWR} for the intact community (glass: -0.12 ± 0.07, microplastics: -0.06 ± 0.03). Further, there was moderate evidence that the high EPDM concentration reduced PSF_{RWR} strength (from positive to neutral) for the initially depleted community (C7 × soil community: $p = 0.03$; low: 0.35 ± 0.04, high: 0.004 ± 0.22), and for the intact community (low: -0.07 ± 0.15, high: -0.03 ± 0.08). There was also moderate evidence that the high glass concentration led to a more positive PSF_{RWR} compared to the low concentration (C6: $p = 0.02$; low: 0.02 ± 0.10, high: 0.26 ± 0.09), irrespective of the soil community.

Root-morphology responses

For all root traits of *C. biennis*, except for average link length, we found very strong evidence that material and soil-community treatments interactively affected PSF responses (Table 1, Supplementary Table 3). PSF_{SRL} tended to be negative for the initially depleted soil community, but neutral or positive for the intact soil community, although there were some exceptions (Fig. 3A). Based on the material-treatment contrasts, we found different specific combinations driving those interactions (Table 1). For the initially depleted community, we found very strong evidence that microplastic particles, compared to glass, led to a less negative PSF_{SRL} (C2 × soil community: $p < 0.001$; glass: -1.04 ± 0.14, microplastics: -0.54 ± 0.08). For the intact community, PSF_{SRL} tended to be positive in general, but less so in the presence of microplastics (glass: 0.19 ± 0.09; microplastics: 0.08 ± 0.05). Further, we found very strong, and moderate evidence for concentration dependencies for EPDM (C7 × soil community: $p < 0.001$) and PHA (C9 × soil community: $p = 0.01$). For the combination of EPDM and the initially depleted community, PSF_{SRL} was negative for the low concentration (-0.97 ± 0.11) but turned positive for the high concentration (0.18 ± 0.25). In contrast, with the intact community, PSF_{SRL} was positive for the low EPDM concentration (0.41 ± 0.17) but rather neutral for the high concentration (0.03 ± 0.07). For PHA, the pattern was the other way around. Although PSF_{SRL} tended to be generally negative, for the initially depleted community, the high PHA concentration resulted in a more negative PSF_{SRL} (low: -0.32 ± 0.09, high: -0.90 ± 0.25). For the intact community, PSF_{SRL} tended to be negative for the low but rather neutral for the high concentration (low: -0.17 ± 0.06, high: -0.02 ± 0.15). In addition, we found strong evidence that, irrespective of the soil community, the biodegradable PHA led to a stronger negative PSF_{SRL} compared to the conventional plastics (C4: $p < 0.01$; conventional: -0.11 ± 0.09, degradable: -0.35 ± 0.10). As effects on SRL were generally inversely related to root thickness and root-tissue density, detailed results for PSF_{RD} and PSF_{RTD} are provided in the supplement (Supplementary Results, Supplementary Table 3, Supplementary Fig. 2).

We found moderate evidence that material treatment ($p < 0.05$), and very strong evidence that soil community ($p < 0.001$) independently affected PSF_{LL} (Table 1). Overall, PSF_{LL} was slightly positive for the intact soil community (0.07 ± 0.03) but negative for the initially depleted community (-2.1 ± 0.03). Regarding the material effects, we found strong evidence that PSF_{LL} was negative for EPDM (-0.16 ± 0.07) but neutral for PE (0.001 ± 0.05; C5: $p < 0.01$). In addition, there was moderate evidence that the high concentration of the mixed microplastics shifted PSF_{LL} from slightly positive to negative (C10: $p < 0.05$; low: 0.09 ± 0.08, high: -0.17 ± 0.06; Fig. 3B).

Heterospecific PSF-effects on *Eragrostis minor*

Biomass responses

We found strong evidence that the material treatment affected $PSF_{biomass}$ of *E. minor* ($p < 0.01$), but no evidence for soil-community effects ($p = 0.4$; Table 2). Based on the a priori chosen contrasts, we found strong evidence that particles in general led to

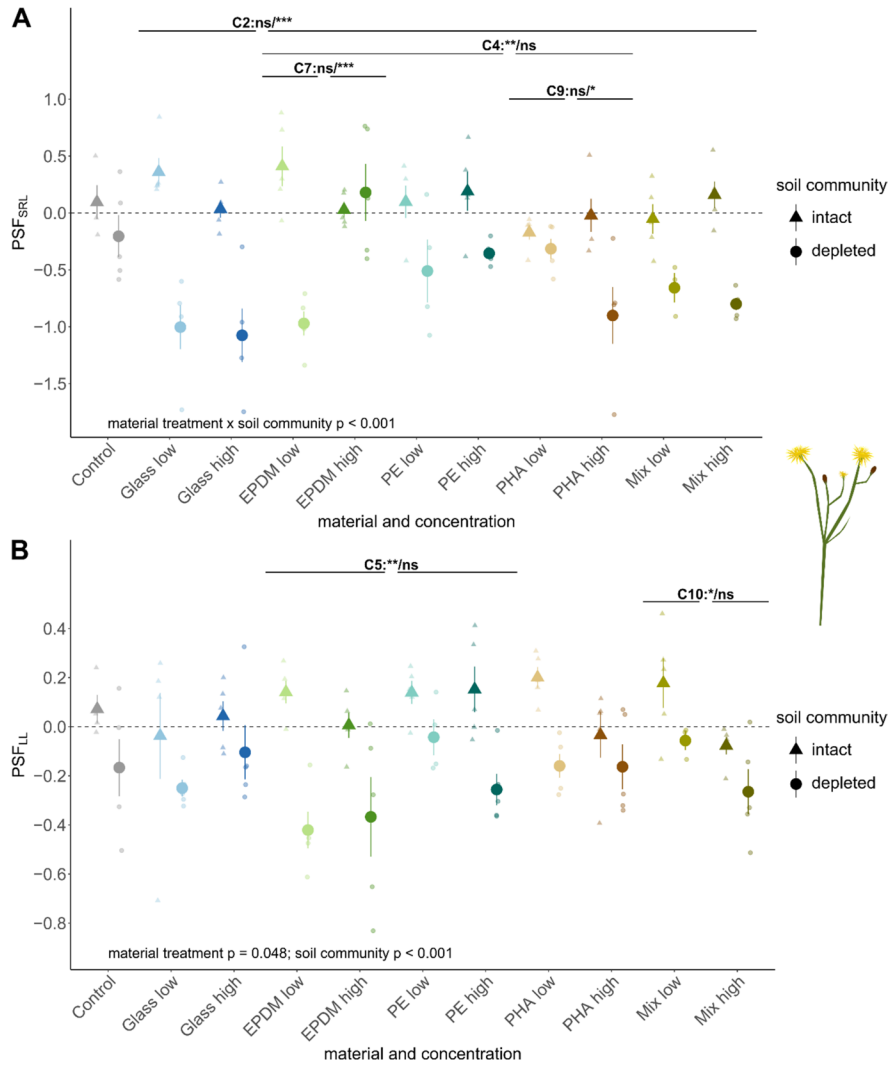


Fig. 3 PSF root-morphology responses of *Crepis biennis*. Effects of different materials (different colors) in low (light colors) or high (dark colors) concentrations and of intact (triangles) or initially depleted (circles) soil communities on plant-soil feedbacks based on specific root length (PSF_{SRL}; **A**) and average link length (PSF_{LL}; **B**). Large symbols represent mean values of the specific treatment group, error bars show the respective standard error. Small symbols represent individual replicates. *P* values refer to basic models. Horizontal lines indicate significant results based on the contrast models (specific contrast: significance main contrast/significance contrast-soil-community interaction) and asterisks indicate which groups differ significantly from each other (Table 1; *** $p<0.001$, ** $p<0.01$, * $p<0.05$). Contrasts compare individual material-treatment combinations (material type, i.e. glass and different microplastics, and low vs. high concentrations; Supplementary Table 2) and were used to obtain detailed information about specific drivers of main effects of material treatment or interactions of the material treatment with soil community

a more negative $PSF_{biomass}$ (C1: $p<0.01$; particles absent: -0.1 ± 0.1, particles present: -0.42 ± 0.04), and that the high PHA concentration led to a less negative $PSF_{biomass}$ than the low PHA concentration (C9: $p<0.001$; low: -0.71 ± 0.18, high: -0.17 ± 0.06; Fig. 4A).

We found strong evidence that the material treatment and the soil community interactively affected PSF_{RWR} of *E. minor* ($p=0.01$; Table 2). Overall, PSF_{RWR} tended to be weaker for the intact community treatment compared to the depleted one, but this was not true for all material-treatment combinations

Table 2 Results of linear mixed-effects models testing effects of material treatment, soil community and their interaction on PSFs on *Eragrostis minor,* including orthogonal contrasts

		$PSF_{biomass}$		PSF_{RWR}	
Fixed effects	df	LLR	*p*	LLR	*p*
Initial leaf area	1	0.15	0.70	6.92	**0.009**
Material treatment (M)	10	24.83	**0.006**	33.78	**< 0.001**
C1 (particles vs no particles)	1	7.78	**0.005**	3.95	**0.047**
C2 (glass vs plastics)	1	0.01	0.92	0.32	0.57
C3 (individual vs mixed plastics)	1	0.62	0.43	0.59	0.44
C4 (degradable vs conventional)	1	0.33	0.57	0.54	0.46
C5 (PE vs EPDM)	1	1.24	0.27	8.20	**0.004**
C6 (low vs high glass)	1	1.37	0.24	6.42	**0.011**
C7 (low vs high EPDM)	1	0.56	0.46	0.36	0.55
C8 (low vs high PE)	1	1.08	0.30	0.21	0.64
C9 (low vs high PHA)	1	14.25	**< 0.001**	0.53	0.47
C10 (low vs high mix)	1	0.56	0.46	0.99	0.32
Soil community (S)	1	0.78	0.38	20.52	**< 0.001**
M × S	10	13.54	0.19	22.96	**0.01**
C1 × S	1	0.38	0.54	1.35	0.25
C2 × S	1	6.84	**0.008**	16.26	**< 0.001**
C3 × S	1	0.20	0.65	0.02	0.88
C4 × S	1	0.02	0.88	3.62	*0.057*
C5 × S	1	1.74	0.19	1.65	0.20
C6 × S	1	1.27	0.26	1.83	0.18
C7 × S	1	1.55	0.21	0.35	0.55
C8 × S	1	1.80	0.18	2.30	0.13
C9 × S	1	0.17	0.68	4.89	**0.027**
C10 × S	1	0.39	0.53	0.22	0.64
Random effects		SD		SD	
Block		0.0056		0.1077	
Residual		0.2673		0.1771	

Orthogonal contrasts define individual material-treatment combinations (material type and low vs. high concentration; Supplementary Table 2) and were used to obtain detailed information about specific drivers of main effects of material treatment. Effects were assessed for the calculated PSF values based on total plant biomass ($PSF_{biomass}$) and root-weight ratio (PSF_{RWR}). Fixed effects were assessed using log-likelihood ratio tests (Zuur et al. 2009). Log-likelihood ratios (LLR) are approximately χ^2-distributed. *P* values < 0.05 are indicated in bold, *p* values < 0.1 are indicated in italics

(Fig. 4B). Based on the material-treatment contrasts, we found very strong evidence that microplastics led to a less negative PSF_{RWR} with the initially depleted community (C2 × soil community: $p < 0.001$; glass: -0.26 ± 0.08, microplastic: -0.04 ± 0.05), and a weaker PSF_{RWR} with the intact community, compared to glass (glass: 0.12 ± 0.06, microplastic: -0.01 ± 0.05). In addition, there was moderate evidence that the high PHA concentration led to a weaker positive PSF_{RWR} with the initially depleted community (C9 × soil community: $p < 0.05$; low: 0.19 ± 0.16, high: 0.03 ± 0.09), and a shift from negative to positive PSF_{RWR} for the intact community (low: -0.18 ± 0.07, high: 0.16 ± 0.13; Fig. 4B), compared to the low concentration. Further, there was moderate to strong evidence that different material-treatment groups differed from each other, irrespective of the soil community. Particle addition in general tended to shift PSF_{RWR} from positive to slightly negative (C1: $p < 0.05$; particles absent: 0.09 ± 0.06, particles present: -0.04 ± 0.03). Also, PSF_{RWR} was negative with EPDM (-1.16 ± 0.06) but positive and overall weaker with PE (0.09 ± 0.07; C5: $p < 0.01$). In addition, PSF_{RWR} tended to be slightly positive with the low glass concentration (0.04 ± 0.08) but turned negative for the high concentration (-0.18 ± 0.09; C6: $p < 0.05$).

Discussion

We tested how different types of microplastics, in combination with an intact or initially depleted soil community, affect heterospecific plant-soil feedbacks

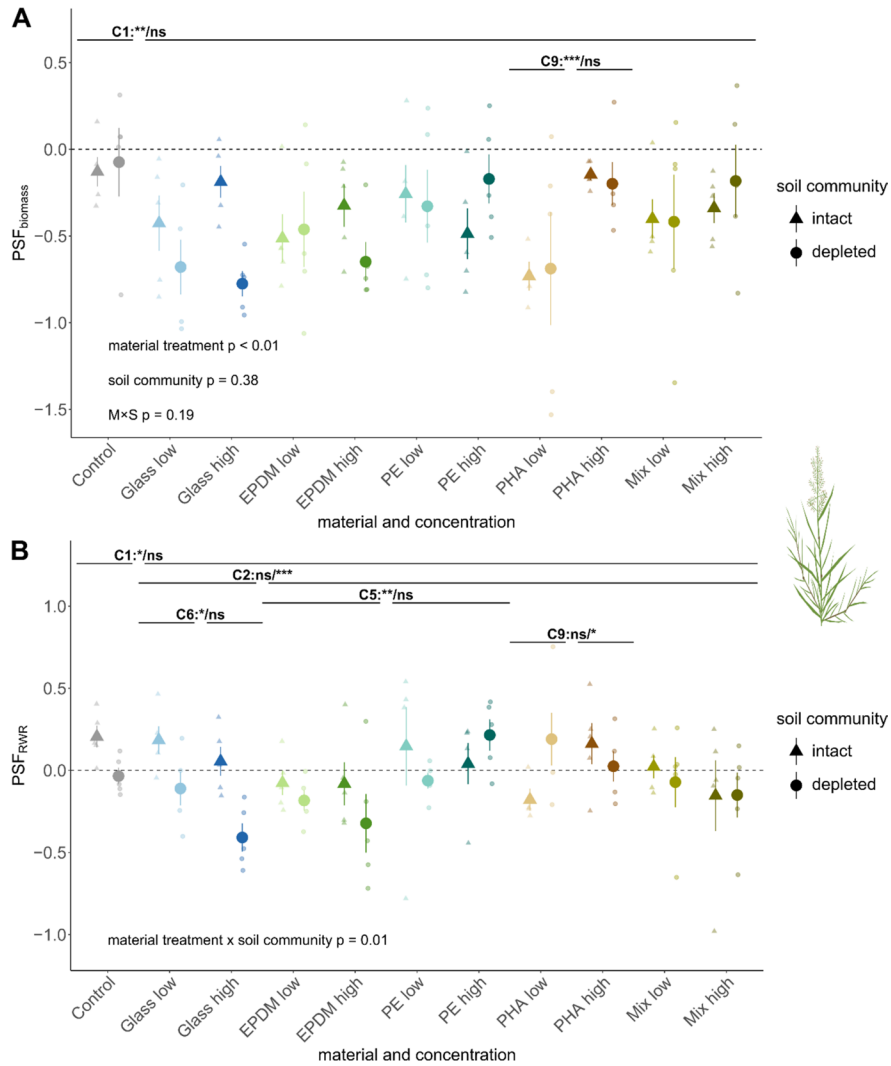


Fig. 4 PSF biomass responses of *Eragrostis minor*. Effects of different materials (different colors) in low (light colors) or high (dark colors) concentrations and of intact (triangles) or initially depleted (circles) soil communities on plant-soil feedbacks based on total plant biomass ($PSF_{biomass}$; A) and root-weight ratio (PSF_{RWR}; B). Large symbols represent mean values of the specific treatment group, error bars show the respective standard error. Small symbols represent individual replicates. *P* values refer to basic models. Horizontal lines indicate significant results based on the contrast models (specific contrast: significance main contrast/significance contrast-soil-community interaction) and asterisks indicate which groups differ significantly from each other (Table 2; *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Contrasts compare individual material-treatment combinations (material type, i.e. glass and different microplastics, and low vs. high concentrations; Supplementary Table 2) and were used to obtain detailed information about specific drivers of main effects of material treatment or interactions of the material treatment with soil community

(PSFs). For *Crepis biennis*, the direction of PSFs strongly depended on the initial state of the soil community. While PSFs were generally negative for the intact community, they were positive for the initially depleted community, indicating a positive effect of soil recolonization (Li et al. 2019). Soil-community status was less influential regarding PSFs on *Eragrostis minor*. Interestingly, artificial particles generally intensified $PSF_{biomass}$ for both species, although this effect depended on the soil community for *C. biennis* but not for *E. minor*. In most cases, microplastics, compared to glass particles, led to weaker PSFs based

on root-weight ratio (RWR) and root-morphological traits. Particle addition and soil-community effects largely depended on each other, suggesting that artificial particles in the soil are likely to change heterospecific PSFs interactively with the soil community.

Despite effects on PSFs, there was no evidence for overall particle-addition effects on plant productivity independent of soil conditioning or initial state of the soil community (Supplementary Fig. 3), indicating a strong context dependency of particle-addition effects (Krehl et al. 2022). In contrast, the very strong evidence for material-treatment effects, in addition to but independent of soil-community effects, on both productivity and RWR of the conditioning species *C. jacea* (Supplementary Table 1, Supplementary Fig. 1) suggests that particle addition could modify PSFs by changing the growth of conditioning plants. For the treatment combination most closely resembling natural conditions without pollution, i.e. no added particles and intact soil community, there was moderate evidence only for PSF effects on *C. biennis* biomass (-0.33 ± 0.16, $p = 0.049$) and on RWR of *E. minor* (0.19 ± 0.09, $p = 0.038$), indicating that PSF effects were rather weak, overall. However, PSF effects changed with particle addition and depended on whether soil communities were intact or initially depleted.

As expected, we found clear evidence for microplastic effects on PSFs, depending on plastic type and concentration. Moreover, this was true for particle presence in general. Glass and microplastic particles strengthened $PSF_{biomass}$ of both species, inducing positive feedbacks in *C. biennis* but negative ones in *E. minor*. A similar pattern for PSF_{RWR} (C1 in Figs. 2 and 4A) suggests that effects on $PSF_{biomass}$ might be strongly driven by changes in root biomass. That is, root biomass increased for *C. biennis* and decreased for *E. minor*, when grown in conditioned soil with artificial particles. The changed PSFs indicate that artificial particles in general, not just microplastics, can affect PSFs, which might be related to changes in physical soil properties that affect both plants and soil communities. For example, microplastics affect soil structure, bulk density, water flow and water holding capacity (de Souza Machado et al. 2018, 2019; Kim et al. 2021b), which can result in a higher water evaporation and reduced soil moisture (Speißer and van Kleunen 2023; Wan et al. 2019). Consequently, changed physical soil properties might affect plants and soil organisms directly (Krehl et al. 2022; Leifheit et al. 2021b), but also their interactions by, for example, changing root morphology or rhizosphere properties (de Souza Machado et al. 2019; Speißer and van Kleunen 2023). Both root morphology and rhizosphere properties are key determinants of PSFs (Kuzyakov and Blagodatskaya 2015; Kuzyakov and Razavi 2019; Wilschut et al. 2019), so changing those properties could be one way in which artificial particles alter PSFs.

The different effects of glass and microplastics (C2 in Figs. 2B, 3A, and 4B) indicate that chemical components are also likely to be involved in how artificial particles affect PSFs. Considering the high number and variety of additives in many plastics (Jones 2024; Wagner et al. 2024), this appears to be a plausible factor. In our study, EPDM was the only plastic type containing additives, and previous studies showed that its effects are dose-dependent and can affect root morphology (Speißer and van Kleunen 2023; van Kleunen et al. 2020). Also, EPDM was the plastic type showing the strongest concentration dependent effects for PSFs based on biomass and root traits (C7 in Figs. 2 and 3A, Supplementary Fig. 2), supporting the assumption that additives could be one factor of how microplastics change PSFs. As microplastics can differ in a wide array of characteristics next to additives, additional studies are needed to assess how specific properties (e.g. size, shape, chemical composition) contribute to effects of artificial particles on PSFs. Nevertheless, considering the clear differences in effects between glass and all grouped microplastics, it seems unlikely that EPDM was the only driver of these different effects. Differences between conventional and biodegradable microplastics on $PSF_{biomass}$ of *C. biennis* (C4 in Fig. 2A) and PSF_{RWR} for both species, and PHA-concentration effects on PSF_{SRL} of *C. biennis* and $PSF_{biomass}$ and PSF_{RWR} of *E. minor* (C9 in Figs. 3A and 4) point towards another potential component.

Plastics, mainly consisting of carbon chains, might serve as additional carbon source for microorganisms, potentially changing soil microbial composition and activity (Cao et al. 2023; Fei et al. 2020; Rong et al. 2021; Zheng et al. 2005). Altered microbial composition or activity could affect PSFs directly, but also indirectly by influencing plants, leading to follow-up effects on PSFs. Generally, the accessibility of carbon from plastics strongly depends on the plastic type

(Zheng et al. 2005). PHA, as biodegradable plastic, can be degraded relatively quickly, up to approximately 0.1 $mg \times day^{-1} \times cm^{-2}$ (Dilkes-Hoffman et al. 2019), and many bacteria and fungi are able to degrade PHA (Jendrossek and Handrick 2002). Additionally, despite the initial inertness of many plastics, aging due to environmental factors (e.g. UV, heat, mechanical abrasion) can induce physical and chemical changes making plastics more prone to further degradation (Shah et al. 2008). This means that more carbon (and other compounds) could be released from plastics, in the long term. Consequently, aging might lead to stronger microplastic effects in the environment (Lozano et al. 2023; Speißer 2023), which should also be considered in future investigations regarding PSFs.

Importantly, in line with our expectation, particle effects on PSFs largely depended on whether the soil communities were intact or initially depleted. Interactive effects of microplastics and soil organisms match previous findings that microplastics can affect soil microbial composition and activity (Fei et al. 2020; Rong et al. 2021). While artificial particles shifted $PSF_{biomass}$ of *C. biennis* from negative to positive with the initially depleted soil community, $PSF_{biomass}$ was generally negative with the intact community, but more so if particles were added (C1 in Fig. 2A). The positive $PSF_{biomass}$ for the combination of initially depleted community and particle addition is likely to be mainly driven by changes in root properties of *C. biennis*. The positive PSF_{RWR} (Fig. 2B) together with the positive PSF_{RTD} and negative PSF_{SRL} (Supplementary Fig. 2B, Fig. 3A) indicate that the plants did not just produce proportionally more roots, but also denser and heavier roots in conditioned soil with the initially depleted community and added particles (Supplementary Figs. 4 and 5). Moreover, compared to glass, microplastics led to weaker PSF_{RWR} (C2 in Fig. 2B), PSF_{SRL} and PSF_{RTD} (C2 in Fig. 3A and Supplementary Fig. 2B), especially with the depleted community. So, overall, plants invested more in roots in the conditioned soil with an initially depleted soil community, but less so when microplastics were present instead of glass (Supplementary Figs. 6 and 7). The differences between glass and microplastics could be explained by differing effects on soil communities due to distinct material properties. Indeed, microplastics can be associated with less diverse microbial communities of specific taxonomical and functional composition (Luo et al. 2022; Shi et al. 2022; Sun et al. 2022; Zhang et al. 2019; Zhu et al. 2021). A potential explanation for why these effects were stronger for the depleted soil community could be that the community structure in the intact community was more stable, so changes in composition and the resulting effects were less pronounced. However, as we did not analyze the community composition, future studies should clarify this.

In contrast to *C. biennis*, there was no evidence that the soil community affected $PSF_{biomass}$ of *E. minor* directly or via modifying microplastic effects (Table 2, Fig. 4 A), matching our expectation that interactive effects between particle addition and soil community are stronger for *C. biennis*. Although PSF responses of *C. biennis* tended to be stronger (larger absolute PSF values), potentially due to the closer relatedness to *C. jacea*, *E. minor* experienced more negative $PSF_{biomass}$ than *C. biennis* (-0.26 ± 0.16, -0.08 ± 0.41, respectively). This is in line with previous findings that short-lived species are more prone to negative PSFs (Kardol et al. 2006; Lemmermeyer et al. 2015; Xi et al. 2021). Accordingly, *C. biennis*, although just being biennial, had a clearly higher RWR than the annual *E. minor* (0.46 ± 0.01, 0.09 ± 0.002), matching previous findings that species with low relative root weight experience more negative PSFs (Wilschut et al. 2023). So, while the generally negative $PSF_{biomass}$ of *E. minor* could probably be explained by the low RWR and other root traits associated with fast-growing plants (Wilschut et al. 2023; Xi et al. 2021), the pattern for *C. biennis* was more complex, as $PSF_{biomass}$ also depended on the initial state of the soil community (Fig. 2A).

With the intact soil community, $PSF_{biomass}$ of *C. biennis* was overall negative but was positive for the initially depleted community (-0.39 ± 0.09 and 0.23 ± 0.91, respectively). This pattern could reflect that generalist pathogens drove the negative PSFs (Semchenko et al. 2022; Wilschut et al. 2019, 2023). Generalist pathogens might have dominated the intact community in general but were likely more abundant in the conditioned substrate. In contrast, the initially depleted community was probably less diverse with a lower total amount of pathogens. Further, conditioning by *C. jacea* could have led to a shift to relatively more specialist pathogens compared to the unconditioned substrate, resulting in a rather positive PSF. Why the PSF responses generally tended to be

stronger with the depleted community is not clear. However, soil sterilization itself can have positive effects on plant performance, when followed by recolonization of beneficial soil organisms (Li et al. 2019), although such effects might change over time (Marschner and Rumberger 2004). Our analysis showed that soil-community effects also depended on particle addition, suggesting that artificial particles in the soil might further modify effects of differing soil communities on PSFs. As we tried to simulate more realistic conditions and expected that the continuous presence of particles is an important factor for potential PSF modifications, we kept the particles in the substrate for the feedback phase. Although this design resembles a more realistic scenario, it makes it hard to fully disentangle legacy effects from current particle effects. Thus, future studies with different approaches, such as using inoculums to reduce the direct impact of particle presence in the feedback phase, and also testing effects on conspecific PSFs could help to better understand how artificial particles including microplastics affect PSFs in different stages.

In conclusion, our study shows that artificial particles in the soil can affect heterospecific PSFs, and that these effects are likely to be partly mediated by soil-community composition. As we did not analyze soil-community composition, further investigations are needed to gain a better understanding of the interplay of artificial particles and soil biota on PSFs. In the context of our results, suggesting that PSF changes are shaped by both physical and chemical mechanisms, future studies should also consider that effects of microplastics might change over time (Speißer 2023), with potential further implications for plant-soil systems. Our study adds evidence to first findings that microplastics could change PSFs, but also highlights the complexity of the mechanisms involved and the need for further studies assessing potential ecological implications of microplastics modifying plant-soil interactions.

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