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Johannes Heinze  
*University of Potsdam*

Alexander Wacker  
*University of Greifswald*

Andrew Kulmatiski  
*Utah State University*

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# Plant–soil feedback effects altered by aboveground herbivory explain plant species abundance in the landscape

JOHANNES HEINZE <sup>1,2,5</sup> ALEXANDER WACKER <sup>3</sup> AND ANDREW KULMATISKI<sup>4</sup>

<sup>1</sup>*Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 1, D-14469 Potsdam, Germany*

<sup>2</sup>*Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstrasse 6, 14195 Berlin, Germany*

<sup>3</sup>*Zoological Institute and Museum, University of Greifswald, Loitzer Strasse 26, 17489 Greifswald, Germany*

<sup>4</sup>*Department of Wildland Resources and the Ecology Center, Utah State University, 84322-5230 Logan, Utah, USA*

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**Abstract.** Relatively little is known about how plant–soil feedbacks (PSFs) may affect plant growth in field conditions where factors such as herbivory may be important. Using a potted experiment in a grassland, we measured PSFs with and without aboveground insect herbivory for 20 plant species. We then compared PSF values to plant landscape abundance. Aboveground herbivory had a large negative effect on PSF values. For 15 of 20 species, PSFs were more negative with herbivory than without. This occurred because plant biomass on “home” soils was smaller with herbivory than without. PSF values with herbivory were correlated with plant landscape abundance, whereas PSF values without herbivory were not. Shoot nitrogen concentrations suggested that plants create soils that increase nitrogen uptake, but that greater shoot nitrogen values increase herbivory and that the net effect of positive PSF and greater aboveground herbivory is less aboveground biomass. Results provided clear evidence that PSFs alone have limited power in explaining species abundances and that herbivory has stronger effects on plant biomass and growth on the landscape. Our results provide a potential explanation for observed differences between greenhouse and field PSF experiments and suggest that PSF experiments need to consider important biotic interactions, like aboveground herbivory, particularly when the goal of PSF research is to understand plant growth in field conditions.

**Key words:** *aboveground herbivory; biotic interactions; field experiment; grassland; landscape abundance; plant–soil feedback; shoot nitrogen content; soil legacy effects.*

## INTRODUCTION

Plant–soil feedbacks (PSFs) have become an important concept in explaining plant growth and coexistence (van der Putten et al. 2013, Smith-Ramesh and Reynolds 2017). The concept of PSFs is based on the idea that plants, via litter production, exudation, and uptake processes, induce changes in abiotic and biotic soil properties that, in turn, influence subsequent plant growth (Bever et al. 1997, Ehrenfeld et al. 2005). To measure PSF effects, experiments typically compare measurements of plant growth on “home” soils (i.e., self-cultivated or conspecific soils) to plant growth on “away” soils (i.e., non-self-cultivated or heterospecific soils; Bever et al. 1997, Brinkman et al. 2010, van der Putten et al. 2013). PSFs are positive when plant growth is greater on home than away soils and negative when plant growth is greater on away than home soils (Bever 1994). Because PSFs impact a plant’s biomass production, they are expected to alter plant species’ abundances

in communities and the landscape (e.g., Klironomos 2002, Mangan et al. 2010, Bennett et al. 2017). Mathematical models of PSFs suggest that, as a form of negative frequency dependence, negative PSFs encourage species coexistence through species replacements over time (Bever et al. 1997). In contrast, these models predict that positive PSFs encourage the development of plant dominance (see e.g., Bever 2003, Bonanomi et al. 2005, Revilla et al. 2013). However, because PSFs are one of many factors that may affect plant growth, there are likely to be many situations where PSFs do not determine plant coexistence and abundance (Reinhart 2012, Bauer et al. 2015, Heinze et al. 2015a; Kulmatiski 2016). For instance, there are many abiotic (e.g., temperature, light, moisture, nutrients) and biotic (e.g., above- and belowground herbivores) environmental drivers that directly and indirectly influence PSFs (Smith-Ramesh and Reynolds 2017, Bennett and Klironomos 2019, DeLong et al. 2019). Hence, as PSFs are one of many factors that may affect plant growth on the landscape studies are needed that can link observed PSF effects to plant abundance on the landscape.

PSFs not only impact plant biomass production but also influence the nutritional quality of plants (Kos et al.

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<sup>5</sup> E-mail: jheinze@uni-potsdam.de

2015, White et al. 2015) as well as the composition of secondary metabolites involved in herbivory defense (Bezemer et al. 2005, Kostenko et al. 2012, Zhu et al. 2018). These chemical plant traits (i.e., nutritional quality and palatability) have been found to influence the amount of biomass reduction by insect herbivores (e.g., Mattson 1980, Massey et al. 2007). Hence, the outcome of PSFs can be influenced by herbivory (Heinze and Joshi 2018, Heinze et al. 2019). These recent findings are, however, based on studies with a small set of plant species; therefore tests on a broader species set are needed.

Most PSF experiments have been performed in greenhouse conditions that fail to place PSFs in the context of environmental conditions that are likely to affect the role of plant growth in communities (Heinze et al. 2016). Relative to PSFs measured in field conditions, greenhouse-based PSF experiments have been found to produce different PSFs, mainly because of the diverse abiotic and biotic interactions that plants and soils receive under natural field conditions (Casper et al. 2008, Heinze et al. 2016). Under field conditions, PSFs are, however, only one of many environmental factors that influence plant biomass production and thus local abundance (Wardle et al. 2004).

Among these abiotic and biotic environmental factors, herbivory by aboveground insects is viewed as a prominent factor affecting plant biomass production and thus local abundance (Crawley 1989, Branson and Sword 2009). By selectively damaging particular plant species, insect herbivores alter competitive relationships and thus codetermine species local abundances (Borgström et al. 2016, Engelkes et al. 2016). Though it has rarely been examined (Smith-Ramesh and Reynolds 2017), herbivores can also differently influence individuals within a single species (Bezemer et al. 2005, Heinze and Joshi 2018, Heinze et al. 2019, Kirchhoff et al. 2019). These studies suggest a potentially strong interaction between PSF and aboveground herbivory, though they have generally been performed in greenhouse and not in field conditions (e.g., Bezemer et al. 2005, Engelkes et al. 2008, Kos et al. 2015; but see, e.g., Heinze and Joshi 2018, Hannula et al. 2019). Therefore, several publications have highlighted the need for field-based PSF experiments (Kulmatiski and Kardol 2008, van der Putten et al. 2013, Heinze et al. 2016).

The overarching goal of this research was to test the effect of aboveground herbivory on the ability of PSF data to explain plant abundance on the landscape. To accomplish this goal, we used a potted field experiment to measure PSFs with and without herbivory for 20 co-occurring plant species. PSF values with and without herbivory were correlated with plant abundance on the landscape. We expected that PSFs measured with aboveground herbivory would explain more of the observed species abundance, compared to PSFs without herbivory, because under natural conditions both factors influence landscape abundance of plant species. To identify a potential mechanism through which PSF may

affect herbivory, we additionally measured nitrogen (N) content in plant shoots on home and away soils.

## MATERIAL AND METHODS

### *Study site and species*

The experiment was conducted in a meadow at a field site of the University of Potsdam (52°24′29.76″ N, 13°1′13.74″ E, Brandenburg, Germany) that has been described elsewhere (Heinze et al. 2016, Heinze and Joshi 2018). Briefly, over the last 10 yr, average annual precipitation (550 mm) and temperature (11.5°C) at this site varied from highest mean values in July (79 mm; 18.4°C) to lowest mean values in January/February (35 mm; −1.2°C). The meadow is located on nutrient-poor slightly sandy loam, was less intensively managed for the last 20 yr with no fertilization, and comprises a high plant species diversity.

To test the PSF vs. abundance relationship, we selected 20 plant species according to their abundance determined in previous vegetation surveys (Table 1; Heinze et al. 2016, Heinze and Joshi 2018). Seeds for each species were collected by hand on site. Species abundance in the season of experiment was assessed in 30 (2 × 2 m) plots using visual estimation in July 2017 (Table 1). Plots were subdivided into 100 (20 × 20 cm) cells and percent cover by species was determined to 1%.

### *Plant–soil feedback experiment*

A natural-experiment approach was used to measure PSFs (Kulmatiski and Kardol, 2008). In the meadow of the field site of the University of Potsdam following Brandt et al. (2014), 2 L of species-specific rhizosphere soil was collected from up to 60 individuals per species and composited into one bulk sample. One half of the composited sample was used as home soil (i.e., conspecific soil), and the remaining half was used to create away soils (i.e., soils of the remaining heterospecific species). In total there were 40 soils: For each of the 20 species, there was one home soil and one away soil that was created by mixing equal portions of each of the other 19 species studied. This mixing procedure is suggested to decrease variance in plant responses among individual soil samples and therefore to increase the likelihood of falsely detecting PSFs (Reinhart and Rinella 2016). However, because soil handling methods depend on specific research questions and feasibility (Cahill et al. 2017, Gundale et al. 2019) and our research goal was to test the effect of herbivory at the research site and not to provide inference to all sites with these species, this approach was appropriate (see also, e.g., Kulmatiski 2016, Teste et al. 2019). To avoid potential differences in soil nutrient availability among the 40 soils, the soils were inoculated (10%) into an autoclaved soil:sand mixture (five times within 24 h; 20 min, 121°C; see also Brinkman et al. 2010). The soil:sand mixture consisted

TABLE 1. Information on plant species used in the plant–soil feedback experiment.

Family	Art	Code	Abundance (%)	Frequency
Cyperaceae	<i>Luzula campestris</i>	Lc	1.63 ± 1.17	13
Poaceae	<i>Anthoxanthum odoratum</i>	Ao	2.47 ± 2.45	22
Poaceae	<i>Arrhenatherum elatius</i>	Ae	52.17 ± 11.27	30
Poaceae	<i>Bromus hordeaceus</i>	Bh	0.3 ± 0.48	11
Poaceae	<i>Bromus sterilis</i>	Bs	1.08 ± 1.88	10
Poaceae	<i>Dactylis glomerata</i>	Dg	1.03 ± 1.43	21
Poaceae	<i>Festuca brevipila</i>	Fb	2.18 ± 4.48	8
Poaceae	<i>Helictotrichon pubescens</i>	Hp	12.17 ± 8.17	25
Poaceae	<i>Holcus lanatus</i>	Hl	2.83 ± 4.38	15
Poaceae	<i>Poa pratensis</i>	Pp	10.77 ± 8.57	22
Ranunculaceae	<i>Ranunculus acris</i>	Ra	0.53 ± 1.26	10
Polygonaceae	<i>Rumex acetosella</i>	Rac	3.18 ± 3.56	22
Polygonaceae	<i>Rumex thyrsiflorus</i>	Rt	4.3 ± 3.9	22
Plantaginaceae	<i>Plantago lanceolata</i>	Pl	4.13 ± 3.08	26
Fabaceae	<i>Lotus corniculatus</i>	Lco	0.22 ± 0.55	5
Fabaceae	<i>Trifolium dubium</i>	Td	0.13 ± 0.43	3
Fabaceae	<i>Trifolium pratense</i>	Tp	1.7 ± 2.31	20
Asteraceae	<i>Achillea millefolium</i>	Am	8.33 ± 11.05	19
Asteraceae	<i>Hypochaeris radicata</i>	Hr	1.25 ± 1.72	15
Asteraceae	<i>Taraxacum officinale</i>	To	1.18 ± 1.63	19

Note: Abundance represents the mean (±SD) percent cover of each species in 30 plots in July 2017.

of a 50:50 mixture of sieved (mesh size: 5 mm) field soil collected from the same meadow at the field site of the University of Potsdam and purchased sand (grain size: 2 mm; Brun & Böhm, Potsdam, Germany).

Pots (Deepots D25L: volume 0.41 L; height 25 cm; diameter 5 cm; Stuewe & Sons, Tangent, Oregon, USA) were filled with the inoculated soils. To prevent cross-contamination, each pot was placed in an individual sterile plastic saucer and received an additional layer (1 cm) of sterilized sand on top. In June 2017, seeds were surface sterilized (3 min in 7% sodium hypochlorite solution) to prevent microbial contamination. Afterwards, seedlings were germinated on autoclaved sand in sterile plastic chambers (32 × 50 × 14 cm; Meyer, Rellingen, Germany) in a greenhouse (min/max: temperature 15°C/25°C; relative humidity 33%/90%; additional light: 140 μmol·s<sup>-1</sup>·m<sup>-2</sup>; 12/12 h light/dark) at the University of Potsdam. In early July 2017, 2-week-old, similar-sized seedlings were planted in the prepared pots, one individual seedling per pot. Immediately after planting, pots were moved from the greenhouse to the meadow at the field site. There, to ensure the survival of the young seedlings under field conditions, seedlings were shaded for 1 week. Seedlings that died during this week were replaced.

#### Herbivory treatment

All pots were buried (25-cm depth) to match the soil surface. Pots were located in 10 replicate blocks that paired herbivory treatments. Paired plots were equipped with cages (length 80 cm × width: 80 cm × height 90 cm) that were either completely covered with fly mesh (mesh size: 1.3 mm; Meyer) or only shaded with the fly

mesh at the upper 50 cm; this allows access for herbivores but ensures the same light conditions in both treatments (see Appendix S1: Fig. S1). The fully covered plots are referred to as “–herbivory”, whereas the partially covered plots are referred to as “+herbivory” treatment throughout the manuscript. To reduce potential differences in microclimate, pots were shifted among blocks weekly. To prevent direct competition, plants adjacent to the experiment were mowed monthly (see Appendix S1: Fig. S1).

Each species × soil combination was replicated 10 times within each herbivory treatment (i.e., + or –herbivory), resulting in 800 pots (20 species × 2 soils × 2 herbivory treatments × 10 replicates). Pots were arranged in a randomized block design. All plants were watered with tap water once a week.

#### Measurements

After 12 weeks, herbivory effects were assessed by visual assessment. Damage by chewing herbivores was assessed without any further discrimination of feeding guilds. In accordance with Heinze et al. (2019), we visually estimated biomass removal (in percent; severity) at 10 randomly chosen leaves per individual plant (see also, e.g., Johnson et al. 2016). We furthermore determined the proportion of damaged leaves by counting the number of damaged as well as total leaves (incidence) for each single experimental plant (see Russell et al. 2010). Severity and incidence were used to assess the shoot biomass removal by aboveground insect herbivores for whole experimental plants according to Smith et al. (2005). After visual assessments of herbivory, shoots of

the experimental plants were harvested and the roots were washed. Shoot and root biomass was dried (shoot 48 h, 80°C; root 72 h, 70°C) and weighed. To place herbivory observed in the experiment in context, herbivory was also assessed using the same visual estimates of herbivory for 10 randomly selected individuals of each species in the meadow.

Nutrient differences among soil types were tested using chemical digestion and photometric methods as in Heinze et al. (2017). To test whether the different home and away soils affected the nutritional quality in plant shoots, we analyzed N concentrations according to Cornelissen et al. (2003) for a subsample of plants. Complete shoots of three replicates per species, soil, and herbivory treatment ( $n = 240$ ) were dried at 80°C (48 h), ground (Retsch MM200; Germany), and subsequently analyzed for N concentrations using an elemental analyzer (HEKAtech GmbH, Wegberg, Germany; Euro EA 3000).

To test for potential differences in abiotic and biotic conditions between the +herbivory and –herbivory plots as well as at control plots that were located adjacent to the herbivory plots (see Appendix S1: Fig. S1) we performed several measurements as previously described in Heinze and Joshi (2018). Briefly, HOBO Pro v2 data loggers (Onset Computer, Bourne, Massachusetts, USA) were used to measure air temperature and relative air humidity continuously at 20-cm height, and a rod thermometer (Roth, Germany) was used to determine soil temperature (15-cm depth) biweekly in randomly chosen pots in each treatment plot per site and in the soil of the respective control plots. Light conditions (light intensity; klx; Testo 545 Luxmeter, Testo SE & Co., Lenzkirch, Germany and photosynthetically active radiation;  $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$  PhAR; Quantum sensor, Li-1400; Li-Cor, Lincoln, Nebraska, USA) were measured (30 cm height) on two cloudless days in the treatment and control plots. Precipitation was measured by placing plastic cups (diameter: 7 cm, height: 10 cm, volume: 200 mL) for 14 d at the treatment and control plots.

Pitfall (plastic cups filled with 100 mL water-based solution containing detergent and covered with plastic roof at 10 cm height) and sticky traps (8 × 12 cm; NexaLotte, Mainz, Germany; at 15 cm height) were installed in all treatment and control plots, to check whether and which herbivorous insects were excluded by our –herbivory treatment and to compare natural conditions in the meadow with experimental conditions. We recorded the number of insects per trap after 14 d.

Overall, abiotic conditions did not differ between the herbivory and control plots (Appendix S1: Table S1). The number of insects was similar in the +herbivory plots and controls, whereas the –herbivory treatment excluded most insects (see Appendix S1: Tables S1 and S2).

### *Statistical analyses*

All analyses were performed in R version 3.1.2 (R Development Core Team 2014). Prior to analyses

residuals were checked for homogeneity of variance and tested for normality.

We used one-way analyses of variance (ANOVA) with subsequent Tukey's honestly significant difference (HSD) post hoc tests to test for differences in abiotic and biotic environmental conditions between the three plots (+herbivory, –herbivory, and control) and to determine differences in damage caused by aboveground insect herbivores between the 20 species.

PSFs were calculated as  $\log(\text{home}_A/\text{away}_A)$ ; where  $\text{home}_A$  is the biomass of species A with its own soil biota and  $\text{away}_A$  is the biomass of species A with soil biota of the 19 remaining heterospecific species (see Brinkman et al. 2010). PSFs were calculated pairwise per block (i.e., replicate) for total biomass separately for the + and –herbivory plots.

Therewith we compared plant growth on home and away soils with herbivory vs. plant growth on home and away soils without herbivory. Because we were interested in understanding the role of PSF and herbivory in natural plant communities, we have not compensated PSF values for biomass lost to herbivory, as this would have changed the result of PSFs and would not have reflected natural conditions. To test whether PSFs of the 20 plant species differed between the + and –herbivory plots we performed ANOVA with linear mixed effects models using the “nlme” package (Pinheiro et al. 2017). The model included the predictors “species” and “herbivory treatment” as fixed factors, as well as their interactions, and tested their effects on PSFs. We used “blocks” (10) as a random factor. To test differences in PSFs between the + and –herbivory plots for each species we performed two-sample *t* tests. Within + and –herbivory plots, we used one-sample *t* tests to assess the effect of home soils on plant biomass in comparison with away soils for each species. Furthermore, we used ANOVA and two-sample *t* tests to test whether total biomass differed between soils in the herbivory plots and whether damages by herbivores (i.e., shoot biomass removal) differed between home and away soils for plants in the +herbivory plots (plants in the –herbivory plots showed no noteworthy damages by herbivores; see Appendix S1: Table S3). Similar to the model for PSFs, this ANOVA tested effects and interactions between the predictor variables “species” and “soil treatment” as fixed factors on herbivory, as response variables, whereas “replicates” were used as random factors.

To test the relative importance of soil vs. species effects we calculated average differences in final biomass between home vs. away soils and between all species-pair combinations on home soils in the –herbivory plots, where final biomass was not affected by herbivory.

In addition, to test whether home and away soils differentially affect plant nutritional quality, we performed ANOVA for N concentrations in shoots. The ANOVA included species, soil treatment (home and away), and herbivory-exclusion treatment (+herbivory and –herbivory), as well as their interactions as predictor variables. We used

replicate as random factor. Afterwards, differences in N concentrations between home and away soils were tested with two-sample *t*-tests for every species.

To determine whether or not PSF with or without herbivory can predict plant abundance on the landscape, the relationship between landscape abundance and PSFs of the 20 species in the two herbivore-exclusion levels were analyzed using linear regressions. As *Arrhenatherum elatius* is an outlier in regard to abundance compared to the other species (see Table 1) and as this species showed almost no damages by aboveground herbivores (see Appendix S1: Table S3), we performed regressions with and without this species.

## RESULTS

### Soil effects on plant nutritional quality and herbivory

The soils used in this experiment did not differ in plant-available nutrients among species or between home and away soil within species (Appendix S1: Table S4).

However, plant shoot N concentration for the 20 species was differently affected by the different home and away soils (species  $\times$  soil interaction:  $F_{19, 158} = 4.74$ ;  $P < 0.001$ ; Fig. 1a), but not by herbivory (soil  $\times$  herbivory interaction:  $F_{19, 158} = 1.23$ ;  $P = 0.24$ ). Shoot N concentration was highest on home soils for 15 species, on away soil for one species (*Anthoxanthum odoratum*), and similar on both soils for four species (Fig. 1a). Similarly, shoot biomass removal by aboveground insects differed on home vs. away soils ( $F_{19, 338} = 2.84$ ,  $P < 0.001$ ; Fig. 1). For 12 species shoot biomass removal was greater when grown on home soils; for *A. odoratum* it was greater on away soil and remaining species demonstrated no differences in damages between home and away soils (Fig. 1b). Across species herbivory decreased total plant biomass 36% on home soils ( $F_{1, 386} = 38.02$ ;  $P < 0.001$ ;  $R^2 = 0.10$ ) but had no effect on away soils ( $F_{1, 390} = 0.74$ ;  $P > 0.1$ ;  $R^2 = 0.01$ ; Appendix S1: Fig. S2). Overall, levels of herbivory in the +herbivory experimental plots were similar to levels of herbivory on the landscape (see Appendix S1: Table S3).

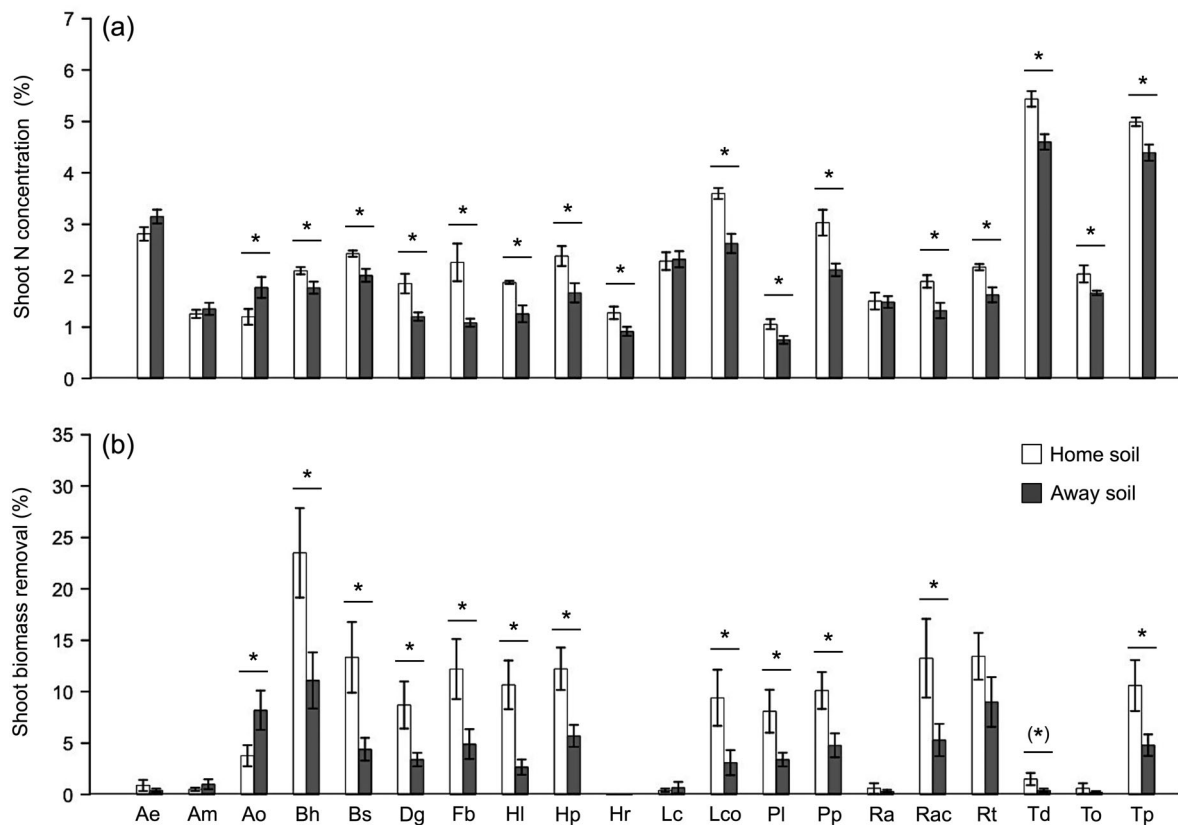


FIG. 1. Shoot nitrogen (N) concentration (a) and shoot biomass removal by aboveground insect herbivores (b) for 20 plant species grown on their home (blank) and away (gray) soils. See Table 1 for species codes. Data represent mean  $\pm$  SE; with  $n = 6$  for a and  $n = 10$  for b. Asterisks above bars represent significance after *t*-test analysis: \* $P < 0.05$ ; (\*)  $P < 0.1$ . Ae, *Arrhenatherum elatius*; Am, *Achillea millefolium*; Ao, *Anthoxanthum odoratum*; Bh, *Bromus hordeaceus*; Bs, *Bromus sterilis*; Dg, *Dactylis glomerata*; Fb, *Festuca brevipila*; Hl, *Holcus lanatus*; Hp, *Helictotrichon pubescens*; Hr, *Hypochaeris radicata*; Lc, *Luzula campestris*; Lco, *Lotus corniculatus*; Pl, *Plantago lanceolata*; Pp, *Poa pratensis*; Ra, *Ranunculus acris*; Rac, *Rumex acetosella*; Rt, *Rumex thyrsiflorus*; Td, *Trifolium dubium*; To, *Taraxacum officinale*; Tp, *Trifolium pratense*.

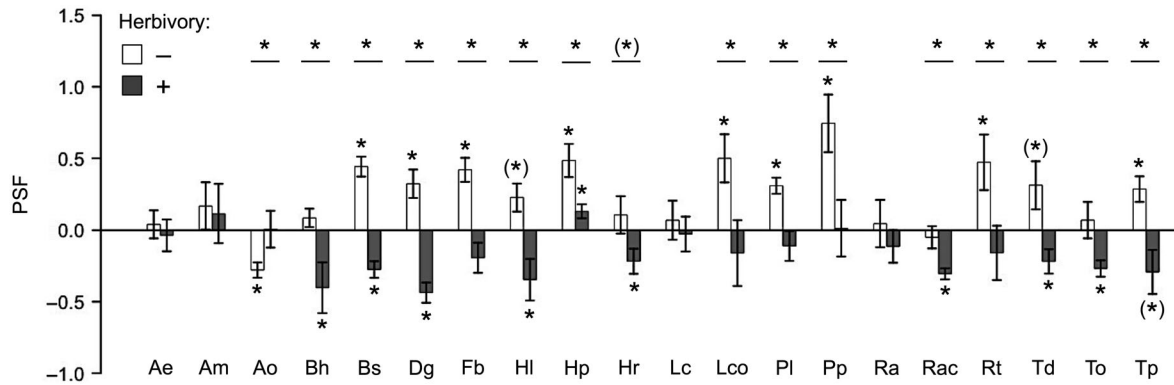


FIG. 2. Plant–soil feedbacks (PSFs) for 20 plant species grown without (blank) and with (gray) aboveground insect herbivores. See Table 1 for species codes. Data represent mean  $\pm$  SE ( $n = 10$ ). Asterisks above/below bars represent significant differences in plant growth when grown in home vs. away soils after one-sample  $t$  tests. Asterisks above bar pairs represent significant differences between PSFs measured in the presence vs. absence of aboveground herbivores for each species: \* $P < 0.05$ ; (\*)  $P < 0.1$ . Ae, *Arrhenatherum elatius*; Am, *Achillea millefolium*; Ao, *Anthoxanthum odoratum*; Bh, *Bromus hordeaceus*; Bs, *Bromus sterilis*; Dg, *Dactylis glomerata*; Fb, *Festuca brevipila*; Hl, *Holcus lanatus*; Hp, *Helictotrichon pubescens*; Hr, *Hypochaeris radicata*; Lc, *Luzula campestris*; Lco, *Lotus corniculatus*; Pl, *Plantago lanceolata*; Pp, *Poa pratensis*; Ra, *Ranunculus acris*; Rac, *Rumex acetosella*; Rt, *Rumex thyrsoiflorus*; Td, *Trifolium dubium*; To, *Taraxacum officinale*; Tp, *Trifolium pratense*.

#### PSF and herbivory experiment

The presence of aboveground insect herbivores influenced the outcome of PSFs for total plants (shoots and roots), but these effects differed among the 20 species ( $F_{19, 333} = 2.39$ ;  $P = 0.001$ ; Fig. 2). Without herbivores 11 species (*Bromus sterilis*, *Dactylis glomerata*, *Festuca brevipila*, *Holcus lanatus*, *Helictotrichon pubescens*, *Lotus corniculatus*, *Plantago lanceolata*, *Poa pratensis*, *Rumex thyrsoiflorus*, *Trifolium dubium*, and *Trifolium pratense*) showed positive PSFs, 8 species (*Arrhenatherum elatius*, *Achillea millefolium*, *Bromus hordeaceus*, *Hypochaeris radicata*, *Luzula campestris*, *Ranunculus acris*, *Rumex acetosella*, and *Taraxacum officinale*) neutral PSFs, and 1 species (*A. odoratum*) negative PSFs (Fig. 2). However, when grown with herbivores final biomass of *A. odoratum* was greater on home soils relative to away soils (i.e., PSFs were positive). Because herbivory was greater on home relative to away soils final biomass of 15 species was greater on away soils or similar on home and away soils; that is, PSF values for these species decreased to neutral or negative (Fig. 2). PSFs of four species (*A. elatius*, *A. millefolium*, *L. campestris*, and *R. acris*) that in general showed low levels of damage and no difference in biomass removal between home and away soils, were not affected by herbivory (Fig. 2). Across all species, PSFs were positive in the presence ( $0.235 \pm 0.031$ ) and negative in the absence ( $-0.167 \pm 0.03$ ) of herbivores (Fig. 2).

The average difference in final biomass between species pairs on home soils was 41% (e.g., species A produced 100 g biomass and species B produced 141 g biomass), whereas, in contrast, the average difference in biomass between soil types (i.e., the PSF effect) was 20%.

#### Correlations with landscape abundance

With herbivory, PSF values were weakly positively correlated with plant landscape abundance ( $F_{1,18} = 3.12$ ;  $P = 0.092$ ;  $R^2 = 0.10$ ; Fig. 3), but there was no correlation without herbivory ( $F_{1,18} = 0.078$ ;  $P = 0.784$ ;  $R^2 = 0$ ; Fig. 3). When biomass data were removed from the outlier species, *A. elatius* improved correlations. Without this species both the – and +herbivory PSFs were positively correlated with species landscape abundances (–herbivory:  $F_{1,17} = 3.65$ ,  $P = 0.073$ ,  $R^2 = 0.18$ ; +herbivory:  $F_{1,17} = 16.64$ ,  $P < 0.001$ ,  $R^2 = 0.49$ ; see Fig. 3).

#### DISCUSSION

In this study, we tested plant biomass production in response to home and away soils (i.e., PSF effects) in the presence and absence of aboveground insect herbivores for 20 grassland species. We found PSF values with herbivory were correlated with plant abundance on the landscape, whereas PSF values without herbivory showed no or only weak correlations. Without herbivores, PSF effects were positive for most species because plant growth was greater on home than away soils. Further, shoot N concentrations were greater on home than away soils. Not surprisingly, herbivory was greater on plants with higher shoot N concentrations (i.e., mostly on plants on home soils). In fact, herbivory had a greater negative effect on plant biomass than effects of soils, so even though plants increased their own growth on self-cultivated soils, the net effect of both PSF and herbivory was that plants had less biomass on home vs. away soils. This net effect appeared to be biologically relevant because combined effects of growth responses to soils (i.e., PSFs) and herbivory were better correlated

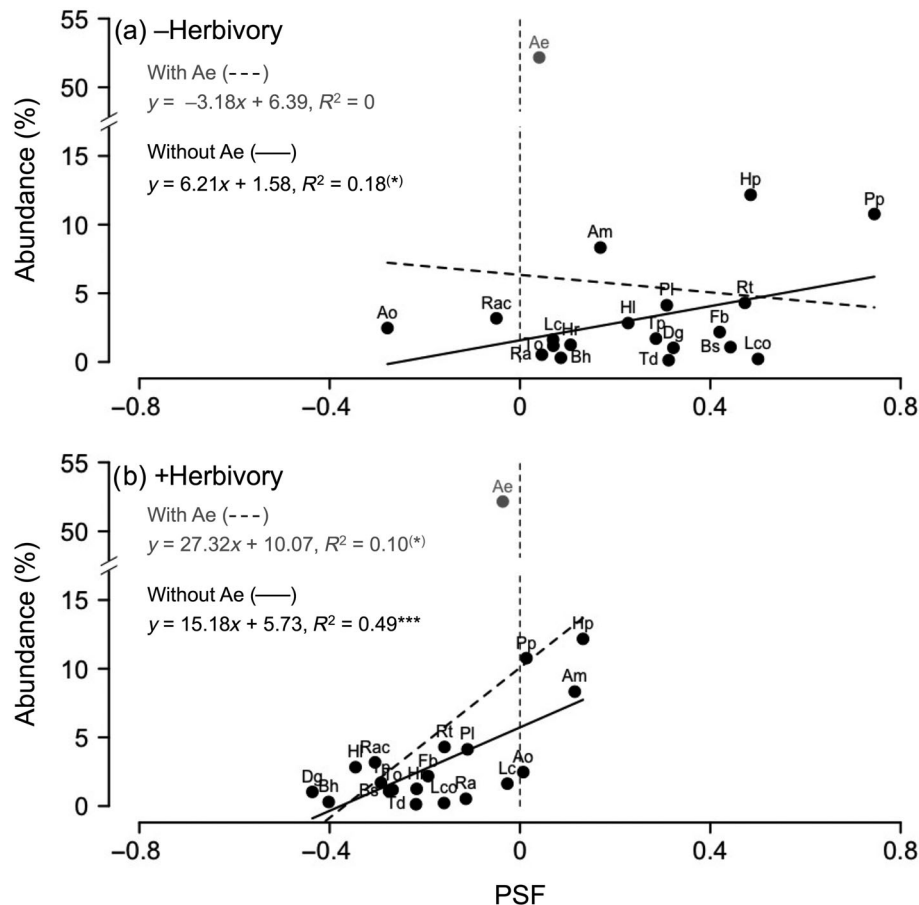


FIG. 3. Relationship between plant–soil feedback (PSF) and local abundance for 20 and 19 plant species, respectively (excluding the outlier species *Arrhenatherum elatius* [Ae]) when grown (a) without and (b) with aboveground insect herbivores. See Table 1 for species codes. Asterisks represent significance: (\*)  $P < 0.1$ ; \*\*\* $P < 0.001$ . Ae, *Arrhenatherum elatius*; Am, *Achillea millefolium*; Ao, *Anthoxanthum odoratum*; Bh, *Bromus hordeaceus*; Bs, *Bromus sterilis*; Dg, *Dactylis glomerata*; Fb, *Festuca brevipila*; Hl, *Holcus lanatus*; Hp, *Helictotrichon pubescens*; Hr, *Hypochaeris radicata*; Lc, *Luzula campestris*; Lco, *Lotus corniculatus*; Pl, *Plantago lanceolata*; Pp, *Poa pratensis*; Ra, *Ranunculus acris*; Rac, *Rumex acetosella*; Rt, *Rumex thyrsoiflorus*; Td, *Trifolium dubium*; To, *Taraxacum officinale*; Tp, *Trifolium pratense*.

with plant landscape abundance than PSF values without herbivory. Results suggest that herbivory can change and override PSF effects and is more important for landscape abundance than PSF effects alone, and furthermore provide an example of a likely mechanism that can explain why greenhouse and field PSF experiments may produce different results (Heinze et al. 2016, Forero et al. 2019).

#### Landscape abundance

The plant community in the investigated meadow can be assigned to the *Arrhenatherion* association (Dierschke 1997) in which *A. elatius* is by far the most dominant element (cover:  $52.17\% \pm 11.27\%$ ). Previous studies in the same system revealed that *A. elatius* shows almost no damage by aboveground herbivory and commonly neutral PSFs that are not changed by herbivore presence (Heinze et al. 2016, Heinze and Joshi 2018). Because it is an outlier

in several traits, we performed correlations with and without this species. These correlations revealed that without herbivores there were no or only weak correlations between PSFs and landscape abundance. With herbivores, PSF values were positively correlated with landscape abundance. In other words, plants with more positive PSF effects were more abundant on the landscape. That PSF values in the presence of herbivores were better correlated with landscape abundance of the species and not in the absence of herbivores makes sense, because the observed landscape abundance, and abundance in general, is influenced by the interactive effects of many factors, including PSF effects and aboveground herbivory (Wardle et al. 2004). Such combined effects of PSF and herbivory are neglected in PSF greenhouse experiments, and this might explain, besides the different growth conditions, why few studies have found correlations between PSF and landscape abundance (e.g., Klironomos 2002, Mangan et al. 2010) and



many have not (e.g., Reinhart 2012, Bauer et al. 2015, Heinze et al. 2015a, Kulmatiski 2016). We suggest that positive correlations are more likely to be found between field-based PSF measurements and plant landscape abundance because field-based PSF measurements inherently include herbivory effects (see Kulmatiski et al. 2017, Kulmatiski 2018). Taken together, results revealed that correlations of PSF values measured with herbivory better explained the species abundance on the landscape than PSF effects alone. This suggests that besides PSF effects, other species traits that impact plants' biomass and thus competitiveness, such as palatability, are more important for abundance of a plant species on the landscape than PSFs. Consequently, in future experiments, there is a need to incorporate further biotic interactions, such as herbivory.

It makes intuitive sense that plants that increase their own growth through changes in the soil would be more abundant on the landscape. This idea has been supported by mathematical PSF models (Bever et al. 1997, Chisholm and Muller-Landau 2011, Mack and Bever 2014). These models, however, often assume that plants are competitively equivalent (Bever et al. 1997, Bever 2003). Under this assumption, plants with the most positive PSF will out-compete others. Of course, plants are not competitively equivalent. As a result, PSF effects must be large relative to intrinsic differences in growth rates to affect relative abundance (Kulmatiski et al. 2016, 2017). In this study, the average difference in final biomass among species was 41%, whereas the average difference in growth among soil types (i.e., PSF effect) was 20%. As a result, it was unlikely that PSF effects would "overcome" intrinsic differences in growth among species. Hence, in addition to herbivory effects, an integration of competition effects into PSF experiments might further strengthen our understanding of the importance of PSFs in explaining plant local abundance, also because soil biota act differently when interacting with single plants compared to plants in mixture (Heinze et al. 2015b).

#### *Effects of herbivory on plant growth and PSFs*

Without herbivory, most plant species experienced positive PSF effects, that is, plants grew larger on home than away soils. The use of a sand growth medium that showed lower plant-available phosphorus concentration compared to the meadow soil (see Appendix S1: Table S1; Heinze et al. 2016, Heinze and Joshi 2018) may have stressed plants and possibly encouraged symbiotic relationships between plants and soil organisms, resulting in positive PSF effects. Because PSF effects without herbivory were positive, our results are not consistent with the commonly assumed role of PSFs as a mechanism of negative frequency dependence (i.e., Janzen–Connell effects; Petermann et al. 2008) and that dominant species in this system are suppressed by soil biota (de Deyn et al. 2003). Instead, our results suggest that landscape abundance is determined more by plant size and competitive ability (Aarssen 2015, Heinze et al. 2015a), than on species replacement caused by negative PSFs.

Herbivory changed the outcome of PSFs for most species in our experiment because damages by insect herbivores were soil-specific (i.e., differed between home vs. away soils). Generally, herbivory had little effect on plant growth on away soils, but decreased final biomass on home soils by 36%. This is in line with findings of a recent study, which showed that soil legacy effects impact the plant biomass consumption of aboveground insect herbivores (Heinen et al. 2019). However, as PSF calculations are mostly based on biomass ratios (home vs. away; see Brinkman et al. 2010) it is clear that any disproportional plant biomass removal by insect herbivores in home relative to away soils will change the outcome of PSFs (see also Heinze et al. 2019).

It is known that insect herbivores, because of their high protein content and poor N use efficiency, need to ingest relatively large amounts of N (Mattson 1980, Bernays and Chapman 1994) and thus prefer to feed on plants with high N content (Bernier et al. 2005, Behmer 2009). In our experiment, herbivores may have been attracted to plants in which soil effects encouraged highly productive and nutrient-rich plants (White et al. 2015, Stajković-Srbinić et al. 2016, Heinze et al. 2019). This is supported by the shoot N concentrations measured in this experiment. Most species that showed highest shoot N concentrations on home soil compared to away soils also experienced highest biomass removal on home soils. For these species, PSFs decreased (i.e., PSFs became more negative) under herbivory. In contrast, *A. odoratum* showed the highest shoot N concentration and damages by herbivores in away soils, resulting in positive PSFs. Species whose shoot N concentration did not differ between home and away soil also did not differ in damages by herbivores between soils or PSF effects.

Furthermore, PSF effects may have changed plant secondary compounds in ways that affected palatability (e.g., Massey et al. 2007, Kostenko et al. 2012, Kos et al. 2015). It is also possible that generalist pathogens on away soils induced secondary defense plant responses that inhibited herbivory (Zhu et al. 2018) and thus generated positive PSFs for most species. In any case, it was clear that for most species the negative effect of herbivory on the outcome of PSF was caused by herbivore response to plant growth (i.e., high shoot N concentration) on home soils and not to plants on away soils. Hence, by testing a relatively large set of plant species, this study confirms that aboveground herbivory has the potential to influence the outcome of PSFs (Heinze and Joshi 2018) and indicate that herbivory, depending on its intensity, is more important for plant species performance than PSF effects (Heinze et al. 2019).

#### CONCLUSIONS

Taken together, herbivory by aboveground insects affected the outcome of PSFs for most species, and combined effects of herbivory and PSFs better explained the landscape abundance of the plant species than PSF effects alone. Overall, these results suggest that effects of herbivory are stronger than PSF effects for final biomass

and that PSFs, when measured with herbivory, are important to plant landscape abundance, though the mechanism through which PSFs affect landscape abundance remains unclear. Hence, our results highlight that PSF research needs to consider important (above-ground) biotic interactions between plants and their consumers, in order to gain a more comprehensive understanding of their roles in shaping PSFs.

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