Universiteit Leiden
The Netherlands

Current and legacy effects of neighborhood communities on plant growth and aboveground herbivory

Liu, X.; Bezemer, T. M.

Citation

Liu, X., & Bezemer, T. M. (2023). Current and legacy effects of neighborhood communities on plant growth and aboveground herbivory. *Basic And Applied Ecology*, *66*, 63-75. doi:10.1016/j.baae.2022.12.007

Version:	Publisher's Version
License:	Creative Commons CC BY 4.0 license
Downloaded from:	https://hdl.handle.net/1887/3677552

Note: To cite this publication please use the final published version (if applicable).

GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 66 (2023) 63–75
Basic and Applied Ecology
www.elsevier.com/locate/baae

RESEARCH PAPER

Current and legacy effects of neighborhood communities on plant growth and aboveground herbivory

Xiangyu Liu[a], T. Martijn Bezemer[a,b,*]

[a]*Institute of Biology, Section Plant Ecology and Phytochemistry, Leiden University, P.O. Box 9505, 2300 RA, Leiden, the Netherlands*
[b]*Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB, Wageningen, the Netherlands*

Received 9 September 2022; accepted 21 December 2022
Available online 22 December 2022

Abstract

Current and legacy effects can greatly affect the growth of a focal plant and its interactions with herbivores and such effects can be mediated by above- and belowground effects. However, determining the relative importance of current and legacy above- and belowground effects in natural conditions is a major challenge. In a long-term grassland experiment, we examined the relative importance of the current and legacy above- and belowground effects of plant communities on the growth and aboveground herbivore damage on a focal plant, *Leucanthemum vulgare*. Focal plants were planted into tubes with soil collected from different plant communities and placed back into the plant communities. Weekly, plant growth and damage were recorded and after 12 weeks plant biomass was measured. We analyzed how well aboveground and belowground characteristics of the current and legacy plots explained plant growth and herbivory. We found both current plant communities and legacy plant communities significantly affected plant growth (shoot biomass and the number of leaves) and herbivory. Root biomass of the focal plants was influenced by current plant communities only. Current and legacy above- and belowground characteristics explained 12% and 11% of the variation in shoot biomass. Root biomass was mainly explained by current above- and belowground characteristics with a total explained variation of 10%, while legacy effects explained 3%. Legacy effects explained most variation in the number of leaves during the first two weeks of measurements, and the effect remained present during the growth season. In contrast, characteristics of the current community explained most of the variation in herbivory throughout the growth period, with on average 6% explained variance aboveground vs. 5% belowground. Our grassland field study highlights that both current and legacy effects influence plant growth, but herbivory on focal plants is caused by current neighborhood effects only and not by legacy effects.

© 2022 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/)

Keywords: Aboveground herbivory; Legacy effects; *Leucanthemum vulgare*; Plant performance; Soil

Introduction

Plants compete for light, space, water and nutrients with neighboring plants and are exposed to a community of antagonists such as herbivores and pathogens. These factors

*Corresponding author.
E-mail address: t.m.bezemer@biology.leidenuniv.nl (T.M. Bezemer).

https://doi.org/10.1016/j.baae.2022.12.007
1439-1791/© 2022 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/)

are important for the performance of the plant. Competing plants are also exposed to antagonists, plant-plant and plant-herbivore interactions (Barbosa et al., 2009; Hambäck et al., 2014; Underwood et al., 2014). An important question in community ecology is therefore how surrounding plants, and their above- and below-ground associated communities, affect the performance (e.g. growth, survival or herbivory) of a focal plant (Otway et al., 2005; Kostenko et al., 2012b, 2017; Kim et al., 2015; Kostenko & Bezemer, 2020). Importantly, an increasing body of literature is highlighting that these community effects on the performance of a plant are not limited to those caused by the community that is currently present, but can also be imposed by legacy effects of the community that was previously present at this location (van der Putten et al., 2013; Kulmatiski et al., 2017; Heinen et al., 2020). For example, plant species-specific effects on abiotic or biotic characteristics of the soil can remain present in the soil when the plants that induced these changes are not present anymore. Such soil legacy effects can influence the performance of a focal plant that grows later in the soil and influence the interactions between this plant and e.g. aboveground insect herbivores (Kostenko et al., 2012a). A prime question is how important these current and legacy effects are for a focal plant. However, testing the relative importance of the current and legacy community effects on plant performance and plant-herbivore interactions in an empirical setting is challenging and, as far as we are aware, this has rarely been investigated (but see Peltzer, 2001; Kulmatiski et al., 2006).

It is well established that the identity and diversity of neighboring plants that surround a focal plant can greatly influence the growth of this focal plant and influence the interactions between this plant and insect herbivores (White & Whitham, 2000; Kostenko et al., 2012b, 2017; Pashalidou et al., 2020). These effects can be caused by aboveground and by belowground neighboring effects (Kos et al., 2015). Surrounding plant communities can directly affect the amount of herbivory a focal plant endures, both above- and belowground, e.g. via creating heterogeneity in physical and chemical properties (Agrawal et al., 2006), or via changes in e.g. the microclimate or in the abundance of alternative hosts for herbivores (Otway et al., 2005; Stokes & Stiling 2013; Castagneyrol et al., 2018). Moreover, neighboring plants can also influence the quality or performance of the focal plant itself which then can influence the amount of herbivory it experiences (Agrawal & Van Zandt, 2003). For example, emission of volatiles by neighboring plants either above- or belowground can influence the resistance of a focal plant to herbivores (Huang et al., 2019; Pashalidou et al., 2020). However, the relative importance of these above- and belowground effects of the surrounding plant community on the growth of and herbivory on focal plants are poorly understood.

Apart from the effects of the current neighborhood in which a focal plant grows, soil legacies left by plants growing previously in the soil can also influence the growth of a focal plant and the interactions between this plant and herbivores (Kos et al., 2015; Ristok et al., 2019; Kostenko & Bezemer, 2020; Heinen et al., 2020). These legacies can be of abiotic or biotic nature. For example, previous agricultural land use can greatly influence soil abiotic characteristics that, in turn, can affect the growth and nutritional quality of later growing plants, and the susceptibility of these plants to aboveground herbivores (de la Peña et al., 2016). Interestingly, these soil legacies can also arise from aboveground effects. For example, aboveground herbivory on a plant can create soil legacies that affect the performance and the interactions with aboveground insects of later growing plants (Kostenko et al., 2012a; Friman et al., 2021). Variation in the composition of plant species in a community or variation in the relative abundance of those plant species can also create soil legacy effects (Heinen et al., 2018, 2020). However, whether and to what extent soil legacy effects affect the growth and herbivory of a focal plant in natural conditions, and whether these legacies are related to aboveground (e.g. vegetation composition) or belowground (e.g. soil biota or nutrient availability) properties of the community that created the legacy is an open question.

Aboveground herbivory on plants varies seasonally (Barton & Koricheva, 2010) and both plant biomass and the level of herbivory generally increase during the growth season, as the build-up of insect herbivore populations generally follows the development of the host plant (Lowman, 1982; Fei et al., 2014). Therefore, we may expect that the association between the level of herbivory a focal plant experiences and characteristics of the neighboring plant community will increase during the growth season. The effect of soil legacies on the growth of a focal plant may also vary over time. First, because several studies have shown that young plants are more responsive to soil legacies than older, larger plants (Dudenhöffer et al., 2018; Bezemer et al., 2018). Moreover, the longer a plant grows in a soil, the longer the time it can influence and shape this soil and, as a consequence, the less will remain of the soil legacy that was present originally (Hannula et al., 2021). This suggests that soil legacy effects on the growth and herbivory of a focal plant will diminish over time.

In this study, we used a long-term grassland experiment with 15 plots of 100 m^2 each to investigate the relative importance of current and legacy effects of the neighborhood community on the growth of focal plants and the amount of herbivory these focal plants endure. We used a reciprocal soil transplant approach and examined growth and herbivory of focal *Leucanthemum vulgare* plants grown in tubes with soil collected from 15 plots, that were placed back in the same and in different plots. *Leucanthemum vulgare* is a native perennial species that is a common species in the semi-natural grassland we used for the study. The impact of the current neighborhood community and the soil legacy of the previous community on plant growth and the amount of herbivory was then assessed during an entire

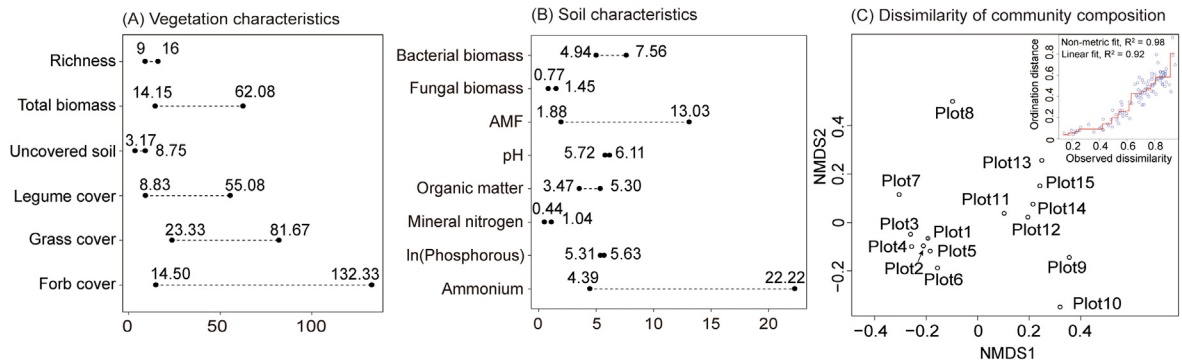

Fig. 1. Vegetation (A) and soil (B) characteristics, and dissimilarities in community composition of plant species (C) for 15 plant communities. (A) The variation in vegetation characteristics present in the 15 plant communities. (B) The variation in soil characteristics present in the 15 plant communities (Phosphorous was ln-transformed before plotting and the original range was 203-280 mg/kg). (C) Dissimilarities in community composition of plant species for 15 plant communities in a Nonmetric multidimensional scaling analysis (NMDS; the stress value was 0.13).

growth season. We tested the following hypotheses for the focal plants:

(i) Plant growth and herbivory are influenced both by the current community and by the soil legacy of the previous community.
(ii) The effect size of the current neighborhood on plant growth will increase over the season when the community develops. However, as plants over time shape the abiotic and biotic characteristics of the soil in which they grow, the legacy that is initially present in the soil will diminish over time, and the effect size of the soil legacy on plant growth will decline over time.

(iii) Herbivory will be influenced more by the current neighboring plant and herbivore community than by soil legacies as the local neighborhood determines herbivore density to a large extent. This difference will increase over time as the neighborhood plant and herbivore community develop over the season.

Materials and methods

Field site

This study was carried out in an existing field experiment at Planken Wambuis, Ede, The Netherlands (52.04 N, 5.45 E). The experiment is located at a former arable field in an area where species-rich grasslands are restored. In spring 1996, after the last crop was harvested, plots of 10 × 10 m were sown with four (low diversity, LD) or fifteen (high diversity, HD) later-succession plant species or not sown (natural colonization, NC) to examine the effects of sowing and seed diversity on plant succession and nature restoration. *Leucanthemum vulgare* was not one of the sown species. The initial design focused on the effects of sown plant species diversity in a randomized block design with five blocks. A detailed description of the field experiment is presented elsewhere (van der Putten et al., 2000; Bezemer et al., 2006; Veen et al., 2018). After sowing, the plots were not weeded, and plants could colonize from the surroundings and the seedbank. Hence, the plant communities that established are the result of self-assemblage following initial sowing. The current study was carried out in 2003 when the individual plots differed in vegetation and soil characteristics (Fig. 1; see Appendix A: Table A.1). Here we focus on characteristics of the communities and on the legacy effects of these communities and therefore consider each plot as a unique community. Hence, for this study, we focus on 15 communities each confined to a 10 × 10 m plot. Current and legacy effects of the initial sowing treatment (HD/LD/NC) on the growth and herbivore damage on *L. vulgare* are presented in the Appendix B.

Vegetation characteristics of the plots

To characterize the vegetation in each plot, in mid July 2003, plant species cover and vegetation height in each experimental plot of 100 m^2 was recorded in 12 permanent quadrats of 1 m^2 each. The cover of each species was assessed individually, total cover within a quadrat often exceeds 100%, because plants overlap at different heights. The cover of the bare soil without plants was also assessed. For each plot, the cover of different functional groups (forbs, grasses and legumes) was calculated as the cumulative cover of all species belonging to the respective functional group, and the number of plant species per m^2 (richness) was calculated. In September, the aboveground biomass in each plot was clipped at 2 cm above the soil surface in 12 0.25 × 0.25 m^2 subplots adjacent to the permanent quadrats. Plant biomass was oven-dried at 70 °C and weighed and average aboveground biomass per m^2 was then calculated.

Soil abiotic and biotic characteristics of the plots

In mid-September 2003, we took a soil sample from each of the 0.25 × 0.25 m^2 subplots for each plot after plants were clipped (12 per plot, 3 cm diameter, and 15 cm deep). Per plot, the samples were pooled and homogenized. From each pooled sample, a subsample was freeze-dried and

another subsample was dried at 40 °C and sieved (4 mm) to remove roots and stones. Three grams of dried soil were mixed with 30 ml of 0.01 M $CaCl_2$ and shaken for 2 h on a mechanical shaker. The filtrate was then used to measure phosphorous (P) and mineral nitrogen (N_{min}, NH_4^+ and NO_3^-) using a Traacs 800 auto-analyzer (TechniCon Systems Inc., Oakland, CA, United States). Ammonium (NH_4^+−N) was extracted with 2 M KCI for 1 h on a mechanical shaker. The filtrate was used to measure ammonium by a colorimetric technique according to Fawcett and Scott (1960). Soil pH was measured in 2:5 dry soil: water suspensions. To determine soil organic matter content, 5 g soil was dried at 105 °C for 16 h in the oven and weighed. The sample was then burned at 550 °C for 5 h and weighed again. Soil organic matter was calculated as the percentage weight loss between the oven-dried and burned samples. The frozen subsamples were used to determine biomass of soil bacteria and fungi and arbuscular mycorrhizal fungi (hereafter, AMF) by analyzing phospholipid fatty acids (PLFA) and neutral lipid fatty acids (NLFA). PLFAs and NLFAs were extracted from the freeze-dried soil according to Boschker and concentrations were measured on a Thermo Trace Ultra gas chromatograph coupled to a Thermo Scientific Combustion Interface III and a Thermo Scientific Delta V IRMS. The internal standard methyl nonadecanoate fatty acid (19:0) was used to calculate concentrations. Identification of the compounds was based on a BAME mix (Supelco 47080-u) and a FAME mix (Supelco 18919-1AMP). The following fatty acids were used as biomarkers for bacterial biomass: i14:0, i15:0, a15:0, i16:0, 16:1ω7t, 17:1ω7, a17:1ω7, i17:0, cy17:0, 18:1ω7c and cy19:0. The PLFA marker 18:2ω6.9 was considered as an indicator for fungal biomass (Frostegard et al., 1993) and the NLFA marker 16:1ω5 was used as an indicator of AMF (Olsson et al., 1995).

Focal plants

For the current study we selected *L. vulgare* as the focal species. It is a perennial species that is native and widespread in Europe (Clements et al., 2004) and occurs abundantly at the field site. This species was not sown in the experiment but was present in all plots (Bezemer & van der Putten, 2007; Veen et al., 2018). To examine the current and legacy effects of the 15 communities on the focal plants, *L. vulgare* plants were grown in each community in tubes filled with soil collected from different plots. Seeds of *L. vulgare* were collected locally in the grassland area, "De Mossel", Planken Wambuis, Ede, The Netherlands. Seeds of *L. vulgare* were sterilized and germinated in containers (10 × 10 × 4 cm) filled with sterilized glass beads submerged in water in a climate chamber at 16/8 h light-dark regime and a 20/15 °C temperature regime. At the end of April 2003, 12 soil cores were taken from the west side of each of the 15 plots. Each core was labeled. As cores we used pvc tubes (10 cm diameter, 20 cm deep). The cores were collected 1.5 m from the edge of the plot with a distance of 70 cm between each core (and 1.15 m distance from each side of the plot). Roots were removed from the soil and the soil was then put back into each tube. The bottom of each tube was sealed with fine meshed cloth. The tubes were watered and one seedling of *L. vulgare* was planted in each tube. The tubes were then kept in a climate-controlled greenhouse for two weeks so that the seedlings could establish in the soil and were then placed back into holes that were still present after removing the soil cores in the field plots in the second week of May 2003. One of the tubes collected from a single plot was placed back into the same plot while the other 11 tubes were placed into different plots based on a randomized design (Fig. 2).

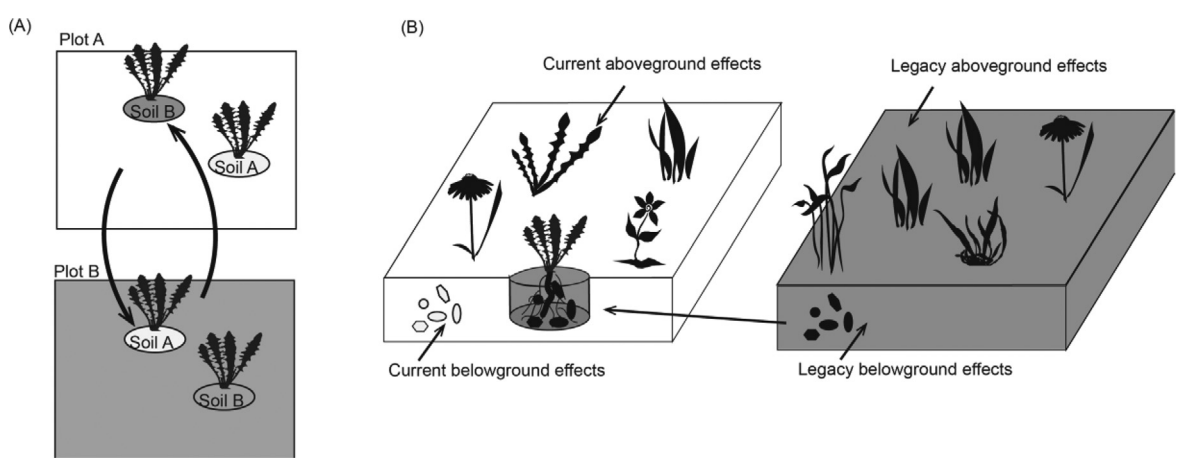

Fig. 2. Experimental design to test for current and legacy neighborhood effects on plant growth and aboveground herbivore damage on *L. vulgare*. (A) Focal plants were established in different plant communities and grew in tubes filled with soil collected from different plots (different legacies). (B) The growth and herbivory of a focal plant can be affected by current above- and belowground effects, and by above- and belowground legacy effects of the previous community.

Growth and aboveground herbivory

To determine the relative importance of the current and legacy effects on plant growth and aboveground herbivory on *L. vulgare*, weekly, starting 19th of May 2003, the number of leaves, the number of damaged leaves and the percentage of total plant damage (hereafter, percent plant damage) by herbivores were estimated until August 1st 2003 (11 weeks in total). For each plant, the percentage of damaged leaves per week was also calculated. In the second week of August 2003, the tubes were collected. In the laboratory, for each tube all leaves were clipped at soil level, the soil was removed from the tube and roots were washed. All plant material was then dried at 70 °C and the shoot and root dry weight of each plant was determined.

Data analysis

To examine the effect of current and legacy treatments on the growth of *L. vulgare*, final shoot and root dry mass per plant and the number of leaves per week were analyzed. The shoot and root dry mass of *L. vulgare* were analyzed using two-way ANOVA with current (15 levels) and legacy (15 levels) effects as main factors with the "aov" function in R. In all analyses, residuals were checked for homogeneity of variance based on a Levene's test and normality by a Shapiro Wilk test using the "levene_test" and "shapiro_test" functions from the "rstatix" package (Kassambara, 2020). Shoot and root dry weight were square-root transformed to fulfil requirements of normality. Generalized linear mixed effect models, with a Poisson distribution and the factor plant ID nested into week as a random effect, were used to test the current and legacy effects on the number of leaves of *L. vulgare*. Generalized linear mixed effect models were performed using the "glmer" function with the "lme4" package (Bates et al., 2015). Significance of factors was assessed by comparing models with and without the factor using a Wald Chi-squared test on the residual deviance. Marginal R^2 (proportion of the variation explained by fixed effects) and conditional R^2 (proportion of the variation explained by both fixed and random effects) were derived using the function "r.squaredGLMM" from the package "MuMIn" (Bartoń, 2022). Contribution of current and legacy were partitioned using the "partR2" function from the package "partR2" (Stoffel et al., 2021).

Herbivore damage on *L. vulgare*: Generalized linear mixed effect models were used to test for current and legacy effects on the number of damaged leaves and percent plant damage. As percent plant damage was proportion data, generalized linear mixed effect models with a binomial error structure were used first. Then we applied model diagnosis and checked whether generalized linear mixed effect models were over-dispersed using the function "check_overdispersion" from the package "performance" (Lüdecke et al., 2021). If there was an over-dispersion in the model, we instead used generalized linear mixed effect models with a beta error structure (Douma & Weedon, 2019). Because herbivory was measured 11 weeks on each individual plant repeatedly, we first included the factor plant ID nested into week as a random effect. The variance of random factors was extracted by "VarCorr" from "lme4" package (Bates et al., 2015), if the variance component of plant ID was close to zero, we re-specified the random structure with only week as a random effect. The significance of the factors was determined by Wald Chi-squared tests. Marginal R^2 and conditional R^2 were derived using the function "r.squaredGLMM" from the package "MuMIn". The contribution of each fixed effect was partitioned using the "partR2" function from the package "partR2".

To determine to what extent the current and legacy above- and below-ground characteristics contributed to the growth and herbivore damage on *L. vulgare*, variation partitioning was used to examine how well characteristics of the current neighborhood and of the previous community explain variation in final plant biomass, number of leaves, percent plant damage and the number of damaged leaves respectively. Aboveground characteristics of the current neighboring community were richness, non-covered (bare) soil, cover of legumes, cover of grasses, cover of forbs, total biomass and sample scores for the first and second axes derived from a nonmetric multidimensional scaling (NMDS) analysis of plant species composition. NMDS was conducted using the "metaMDS" function from the package "vegan" (Oksanen et al., 2019) with Bray-Curtis dissimilarity. Belowground characteristics of the current neighboring community were bacterial biomass, fungal biomass, arbuscular mycorrhizal biomass, soil pH, organic matter content, nitrogen mineralization, phosphorus content and ammonium content.

Legacy aboveground and belowground characteristics were the same as described above but then those of the community where the soil originated from. Characteristics with a Pearson correlation r larger than 0.65 to another characteristic were removed to reduce the collinearity of explanatory variables (see Appendix A: Fig. A.1). As all characteristics had different units and ranges, they were standardized with the "scale" function before the variation partitioning analyses were carried out. Variation partitioning was carried out with the "varpart" function and the significance of each main effect was assessed with the "rda" function from the package "vegan" (Oksanen et al., 2019). Linear regression was used to examine the relationship between time and the explained variance in weekly number of leaves of *L. vulgare* of current and of legacy effects. We also used linear regressions to examine relationships between time and the difference in the explained variance of current and legacy effects in percent plant damage and in number of damage leaves. A paired t-test was performed to examine the difference between the explained variance of current and legacy effects in aboveground herbivory over time.

All analyses were performed using the R statistical language, version 4.0.4 (R Core Team, 2022).

Table 1. Results of a two-way ANOVA testing current and legacy effects (plot identity) on the shoot and root dry mass of *L. vulgare*. Presented are degrees of freedom (df; treatment, error) and F values. The interaction effect between the current and legacy effect cannot be tested due to the incomplete design. * and ** indicate significant difference between current or legacy communities at $P < 0.05$ and $P < 0.01$, respectively.

	Shoot biomass of *L. vulgare*		Root biomass of *L. vulgare*	
	df	F	df	F
Current	14, 151	2.18*	14, 151	2.43**
Legacy	14, 151	2.48**	14, 151	1.29

Results

Current and legacy effects on plant growth

Shoot biomass of *L. vulgare* was significantly influenced by both the current and legacy neighborhood effects, while root biomass was only significantly affected by current effects (Table 1; Fig. 3). The current effect accounted for 8% and 11% of the total variation in shoot and in root biomass, respectively (Fig. 3C and F). The legacy effect accounted for 10% of the total variation in shoot biomass, while it was only 2% for root biomass (Fig. 3C and F). Both the current and legacy effects significantly affected the weekly number of leaves of *L. vulgare* and explained 8% and 10% of the variance, respectively (Table 2; see Appendix A: Fig. A.2).

Current and legacy effects on herbivory

Percent plant damage and the number of damaged leaves per plant increased during the growth season (see Appendix A: Figs. A.3, A.4). Average damage per plant was 6% (SE = 0.2) and the average number of damaged leaves per plant was 15 (SE = 0.4) at the last measurement. The current and legacy treatments both significantly affected percent plant damage and number of damaged leaves (Table 3). The current neighborhood explained 2% of the variation in both percent plant damage and the number of damaged leaves, and it explained 5% of the variation in the percentage of

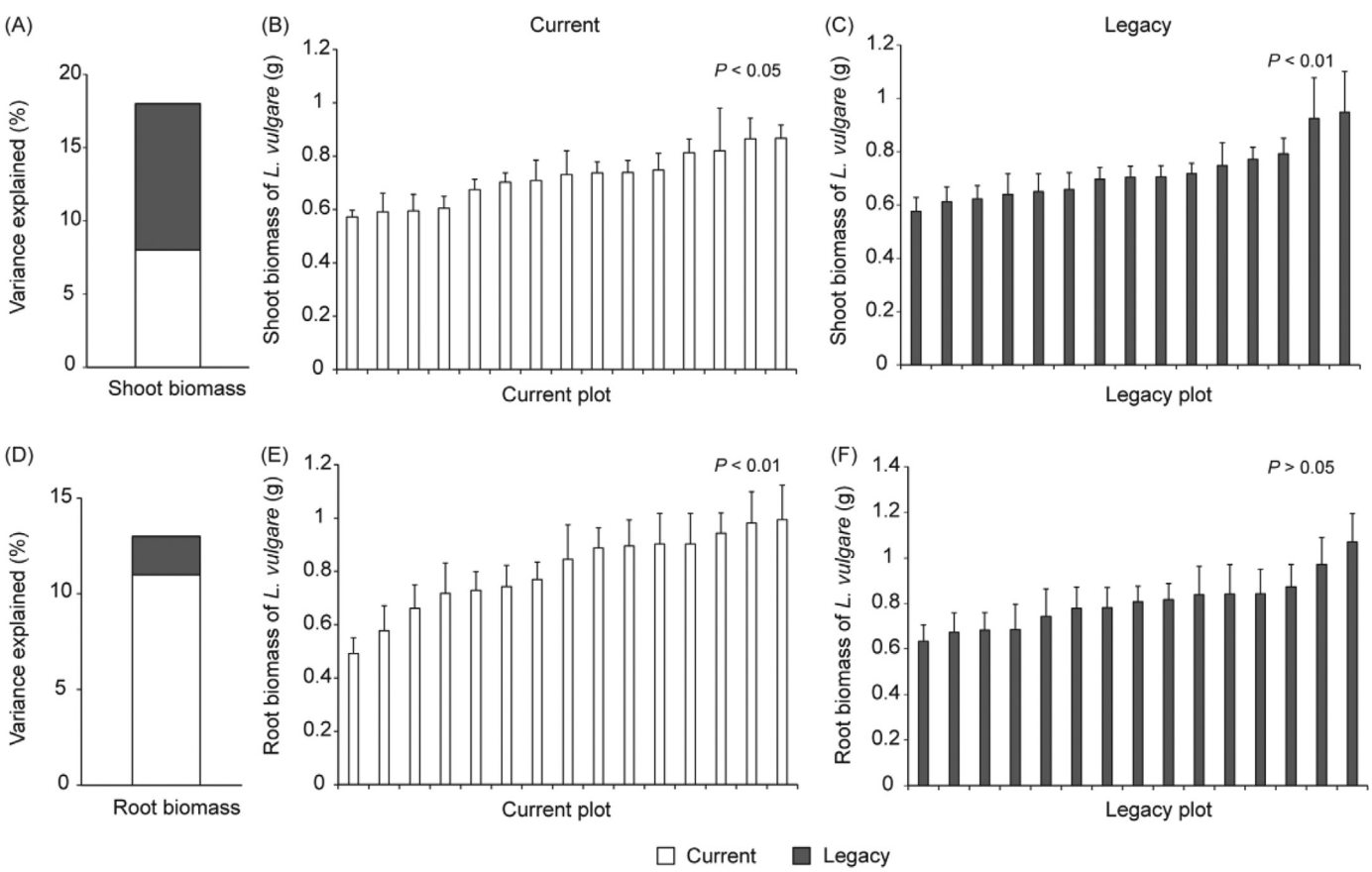

Fig. 3. Explained variance of the current and legacy effects (plot identity) for shoot (A) and root biomass (D), and mean (± SE) individual shoot and root biomass of *L. vulgare* separated for current plots (B, E) and for legacy plots (C, F). In (B, E, C, F) error bars are calculated for all plants in the same plot (current plot) or in the same soil (legacy plot). P values of the current and legacy treatments are also presented.

Table 2. Results of a generalized linear mixed effect model testing current and legacy effects (plot identity) on the number of leaves of *L. vulgare*. Presented are degrees of freedom (df), Wald Chi-squared values, R^2 values for each fixed effect, and marginal R^2 and conditional R^2 obtained from a generalized linear mixed effect model. The interaction effect between current and legacy effects cannot be tested due to the incomplete design. *** indicates significant difference between current or legacy communities at $P < 0.001$.

	Number of leaves			
	df	χ^2	R^2	R^2m (R^2c)
Current	14	241.47***	0.08	0.18 (0. 43)
Legacy	14	255.57***	0.10	

Table 3. Results of generalized linear mixed effect models testing current and legacy effects (plot identity) on percent plant damage and on the number of damaged leaves of *L. vulgare*. Presented are degrees of freedom (df), Wald Chi-squared values, R^2 values for each fixed effect, and marginal R^2 and conditional R^2 obtained from a generalized linear mixed effect model. *** indicates significant difference between current or legacy communities at $P < 0.001$.

	Percent plant damage			
	df	χ^2	R^2	R^2m (R^2c)
Current	14	105.67***	0.02	0.04 (0.57)
Legacy	14	79.95***	0.01	
	Number of damaged leaves			
Current	14	135.41***	0.02	0.04 (0.71)
Legacy	14	114.91***	0.02	

damaged leaves (Table 3; see Appendix A: Table A.2). The legacy treatment explained 1% in both percent plant damage and the percentage of damaged leaves, and it explained 2% in the number of damaged leaves (Table 3; see Appendix A: Table A.2).

Effects of current and legacy characteristics

Shoot biomass of *L. vulgare* plants significantly correlated with above- and belowground characteristics of the legacy plots with in total 11% explained variation (Fig. 4). Legacy above- and belowground characteristics accounted for 1% and 3%, and the shared effect accounted for 7% (Fig. 4). Characteristics of the current neighborhoods explained 12%, with soil accounting for 10% and vegetation accounting for 2% (Fig. 4). For root biomass of *L. vulgare* plants, current characteristics accounted for 10% with current above- and belowground characteristics explaining 5% and 2%, respectively, and the shared effect explaining 3%. Legacy characteristics accounted for 3% of the variation in root biomass with legacy aboveground characteristics explaining 1% and the shared effect explaining 2% (Fig. 4). For the number of leaves of *L. vulgare*, the percentage of variation explained by current characteristics increased over time with the highest total explained variation (30%) in week eight (second week of July) (Fig. 4; see Appendix A: Table A.3, Fig. A.5). On average, total variation in the number of leaves that was explained by legacy characteristics was 7% and this remained relatively constant during the season (Fig. 5; see Appendix A: Table A.3, Fig. A.5).

Total variation in aboveground herbivory on *L. vulgare* explained by current characteristics was significantly higher than that explained by legacy characteristics (see Appendix A: Table A.4). On average, current and legacy characteristics accounted for 14% and 3%, respectively, of the total variation in percent plant damage (Fig. 6A; see Appendix A: Table A.5). Specifically, current above- and belowground characteristics explained 6% and 5%, respectively, and the shared effect was 3%, while legacy above- and belowground characteristics only explained 2% and 1%, respectively (Fig. 6A; see Appendix A: Table A.5). On average, current characteristics explained 16% of the total variation in the number of damaged leaves of which vegetation, soil characteristics and the shared effect all explained 5% (Fig. 6B; see Appendix A: Table A.5). On average, the total variation in

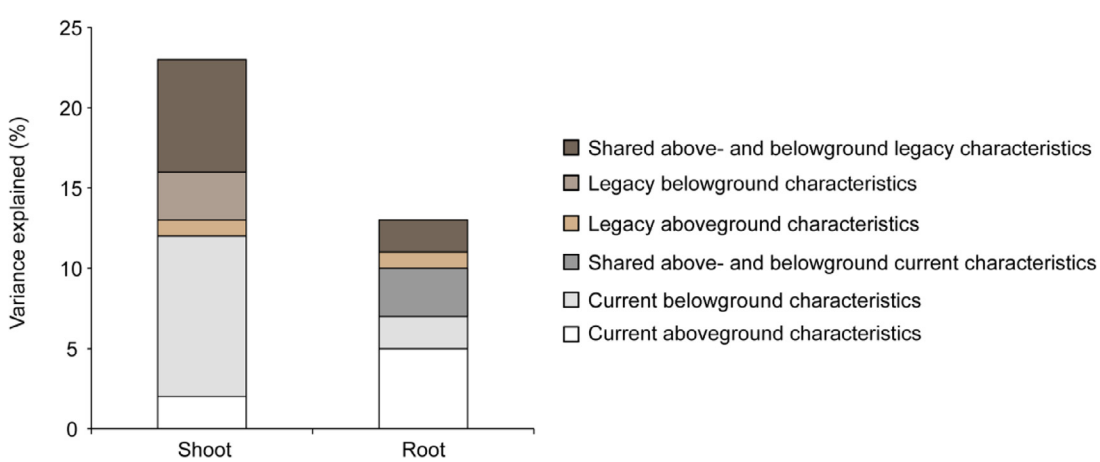

Fig. 4. Explained variance of current and legacy above- and belowground characteristics for shoot and root biomass of *L. vulgare*.

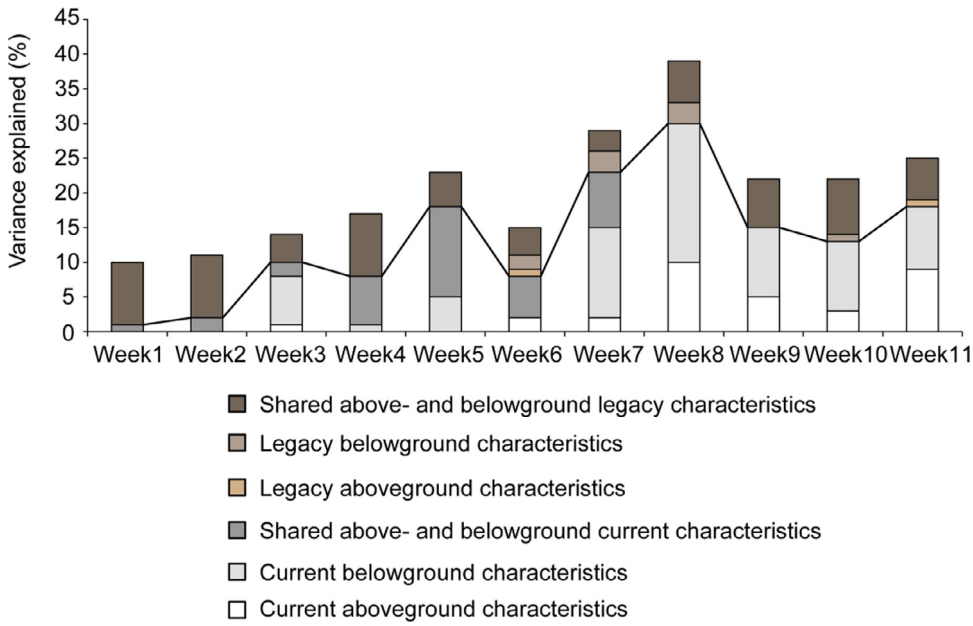

Fig. 5. Explained variance of current and legacy above- and belowground characteristics for the number of leaves of *L. vulgare* over a period of 11 weeks.

the number of damaged leaves that was explained by characteristics of legacy effects was 5%. Specifically, legacy above- and belowground characteristics accounted for 0.5% and 1%, and the shared effect was 3% on average (Fig. 6B; see Appendix A: Table A.5). On average, current and legacy characteristics accounted for 15% and 2%, respectively, of the total variation in the percentage of damage leaves (see Appendix A: Table A.6, Fig. A.6). The difference between the explained variance of current and legacy characteristics in percent plant damage and in number of damage leaves did not increase over time (see Appendix A: Fig. A.7).

Discussion

Our study demonstrates that both current and legacy effects were key factors influencing the growth of the focal *L. vulgare* plants, with legacy effects being the most important in the early stages and current effects later during the season. Interestingly, the impact of legacy effects on plant growth did not fade away during the season, but current neighborhood effects overruled legacy effects on herbivore damage on the focal plant during the growth season. Hence, our study provides evidence that legacy effects created by previously growing plants can continue to influence the growth of later growing plants throughout the season. However, the herbivore damage these later growing plants endure is mainly determined by the characteristics of the current neighborhood.

Our first hypothesis predicted that plant growth and herbivory would be influenced by both the current community and by the soil legacy of the previous community. This is confirmed by our results. Characteristics of the current community explained most of the variation in root biomass, while both current and legacy characteristics explained a similar part of the variation in shoot biomass. Based on the optimal partitioning theory, plants are predicted to allocate relatively more energy to aboveground parts e.g. stem elongation and larger specific leaf area, when they are exposed to a crowded neighborhood (Wilson, 1988; Aerts et al., 1991; Casper et al., 1998). In the design of the experiment, focal plants were only exposed to aboveground competition with neighboring plants and not to belowground competition as they were growing individually in tubes. *Leucanthemum vulgare* is a species that develops a rosette aboveground, and it may develop larger and thinner leaves in response to shading of neighboring plants but for growth resources from the local soil are needed (Forster et al., 2011; Poorter et al., 2012; Liu et al., 2016). This can explain why both current and legacy effects explained variation in shoot biomass of the focal plants. We speculate that because belowground competition was absent in our experimental setting, roots of the focal plants grew and filled the available space in all tubes irrespective of the legacy of the soil. Alternatively, recent evidence has shown that interactions among plants can reduce plastic responses of *L. vulgare* (e.g. allocation to root biomass) to the abiotic environment (Wang & Callaway, 2021). As root biomass was mainly explained by current effects this suggests that root growth in our study was mainly limited by photosynthesis or light availability. In our field study herbivory was explained by the current neighborhood. Other studies have shown that soil legacy effects influence herbivore damage on focal plants (Wurst & Ohgushi, 2015; Kim, 2017; Heinen et al., 2018). More

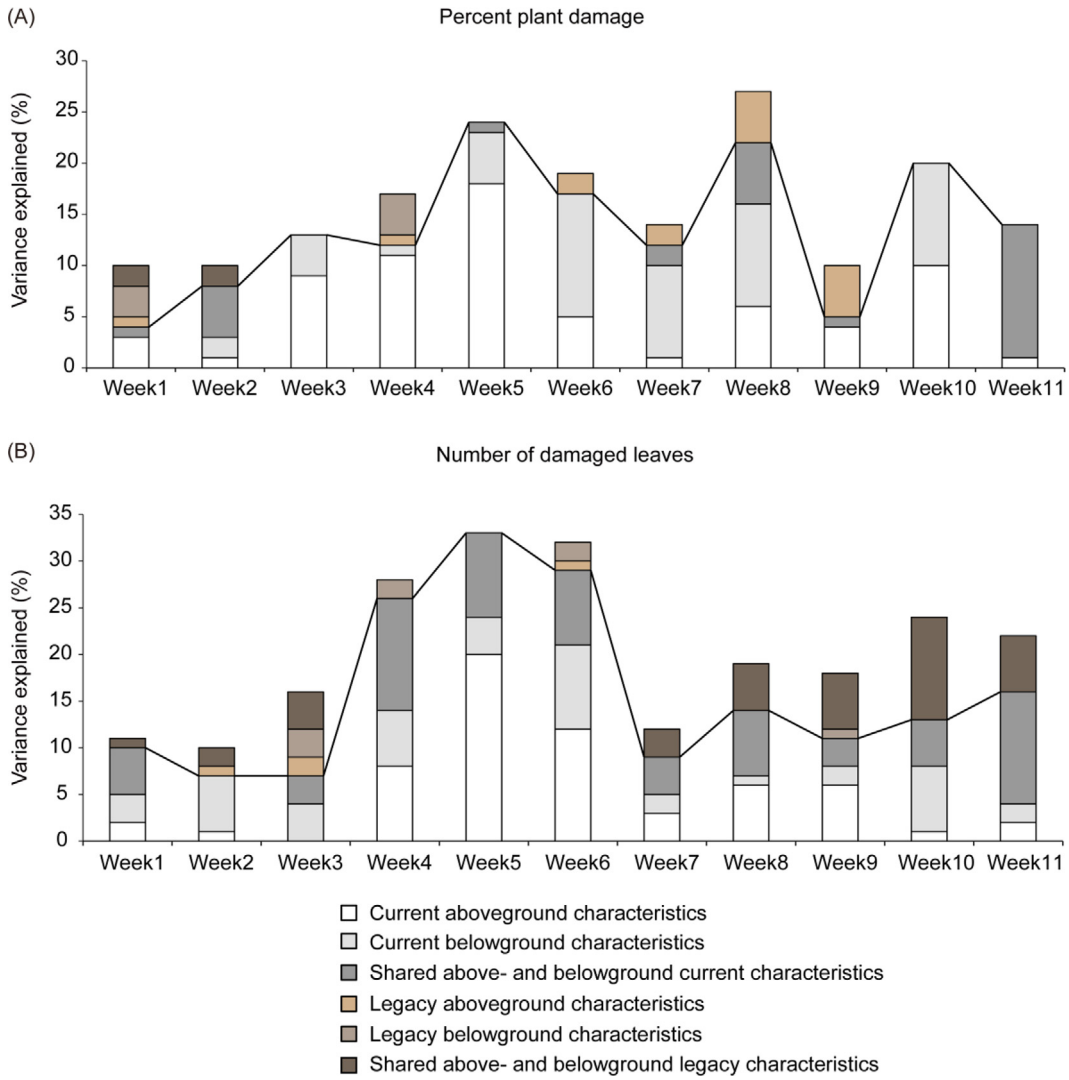

Fig. 6. Explained variance of current and legacy above- and belowground characteristics for percent plant damage (A) and number of damaged leaves (B) of *L. vulgare* over a period of 11 weeks.

studies are needed in different systems to quantify the importance of soil legacy effects for interactions between plants and aboveground herbivores.

In line with our second hypothesis, the effect size of the current neighborhood on plant growth increased over time and reached a peak in the second week of July. The focal plants were placed in the current communities in the second week of May when the neighboring plant community had just started to grow and develop. Along with the development of the current vegetation, plant-plant interactions e.g. competition for light and/or space likely increasingly influenced the growth of the focal plants that were embedded in these communities. This may explain the initial increase in the effect size of the current neighborhood during the growth season. Closer to the end of the growth season when the growth of the neighboring plants started to decline, also due to a drought that occurred during this field season. The impact of the neighboring community on the focal plants declined again, resulting in a temporal hump-shaped pattern in the percentage explained variation by the current neighborhood. Interestingly, the contribution of legacy effects to variation in plant growth persisted throughout the season and did not diminish over time. This is different with a previous transplant experiment in a prairie-forest ecosystem, where soil origin did not influence plant performance (Peltzer, 2001). This highlights that the identity of the focal species and the study system can be important factors influencing legacy effects on plant performance. The influence of a plant on the soil it grows in increases over time, and hence the effect of the current plant on the soil increases over time, and the legacy effect of plants that grew previously in the soil diminishes (Bezemer et al., 2018; Hannula et al., 2021). Therefore we expected that the impact of legacy effects on plant growth would diminish over time. Unfortunately in the current study we did not measure how biotic and abiotic characteristics of the different soils in the

tubes changed over time, and hence we cannot draw conclusions about this. Further studies are needed that examine the temporal changes in biotic and abiotic characteristics of the soil in presence and absence of plant growth and neighboring plants.

The plant community surrounding a focal plant can greatly influence the amount of damage this plant experiences (Agrawal et al., 2006; Kostenko et al., 2012b, 2017; Kos et al., 2015; Kim, 2017). Our results confirm this as characteristics of the current neighborhood explained most of the herbivore damage on the focal plants. Interestingly, in our study both aboveground and belowground neighborhood characteristics were important. Aboveground, neighboring plants can influence the herbivore damage on a focal plant via associational effects and/or indirectly affect the herbivory a focal plant endures via influencing the quality of the focal plant (Agrawal et al., 2006; Barbosa et al., 2009). This has been well documented in previous studies and may explain why in our study there was a high percentage of variance explained by current aboveground characteristics. Furthermore, in our study, belowground neighborhood characteristics and shared above- and belowground characteristics were as important as aboveground characteristics. It is well known that the above- and belowground compartments in terrestrial ecosystems are tightly linked (Bardgett & Wardle, 2010) and disentangling the effects of the two compartments remains a major challenge. However, there is also ample evidence that belowground changes can have important consequences for aboveground multi-trophic effects (Hu et al., 2018; Zhu et al., 2018; Friman et al., 2021). For example, inoculation with soil conditioned by a plant species that is different from the current one, can result in a greatly altered leaf metabolome of the current plant, resulting in altered interactions between the plant and aboveground herbivores (Badri et al., 2013; Huberty et al., 2020). In our study, we focused on plant damage, and did not look at specific herbivore responses and this may explain why we detected little evidence for soil legacy effects on aboveground herbivory. Moreover, it is important to note that in our design, both current and legacy effects operated in tandem, and that we did not have treatments with only soil legacy effects without current neighborhood effects (i.e. tubes placed in plots where the vegetation was regularly clipped at soil level or in bare plots). The effects of soil legacies on an individual plant may have been overruled by the effects of the current aboveground neighboring community in natural conditions. This is in line with a previous study, where the surrounding plants greatly influenced insect communities associated with a focal plant (Heinze & Joshi, 2018). It is also important to note that our choice for the focal plant species may overestimate current effects. In the first year, *L. vulgare* develops a rosette and in the experiment these rosettes were surrounded by taller plants. Hence the focal plants may be hidden from herbivores.

In conclusion, our study shows that both above- and belowground effects of the current and of the legacy community matter for the growth of a focal plant but that the herbivory these focal plants experience is mainly driven by current neighborhood effects.

Author contributions

T.M.B designed and carried out the study. X.Y.L. and T.M.B developed and discussed analysis and presentation of the data, and X.Y.L analyzed all data. X.Y.L. and T.M.B. wrote the manuscript and improved subsequent versions of the manuscript.

Declaration of Competing Interest

We declare that this work is original. We also declare that we have no conflict of interest and that our work complies with the current laws of the Netherlands.

Acknowledgements

We thank Wim H. van de Putten who designed and set up the field experiment and the TLinks project members for plot background data. X.Y.L. was funded by a Chinese Scholarship Council (CSC) grant (No.201906140116).

Supplementary materials

Supplementary material associated with this article can be found, in the online version at doi:10.1016/j.baae.2022.12.007.

References

Aerts, R., Boot, R. G. A., & van der Aart, P. J. M. (1991). The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia*, *87*(4), 551–559. doi:10.1007/BF00320419.

Agrawal, A. A., & Van Zandt, P. A. (2003). Ecological play in the coevolutionary theatre: Genetic and environmental determinants of attack by a specialist weevil on milkweed. *Journal of Ecology*, *91*(6), 1049–1059. doi:10.1046/j.1365-2745.2003.00831.x.

Agrawal, A. A., Lau, J. A., & Hambäck, P. A. (2006). Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology*, *81*(4), 349–376. doi:10.1086/511529.

Badri, D. V., Zolla, G., Bakker, M. G., Manter, D. K., & Vivanco, J. M. (2013). Potential impact of soil microbiomes on the leaf metabolome and on herbivore feeding behavior. *New Phytologist*, *198*(1), 264–273. doi:10.1111/nph.12124.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational resistance and

associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 1–20. doi:10.1146/annurev.ecolsys.110308.120242.

Bardgett, R. D., & Wardle, D. A. (2010). *Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change*. Oxford University Press.

Bartoń, K. (2022). *MuMIn: Multi-Model Inference. R package version 1.46.0.* . https://CRAN.R-project.org/package=MuMIn.

Barton, K. E., & Koricheva, J. (2010). The ontogeny of plant defense and herbivory: Characterizing general patterns using meta-analysis. *American Naturalist*, *175*(4), 481–493. doi:10.1086/650722.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi:10.18637/jss.v067.i01.

Bezemer, T. M., & van der Putten, W. H. (2007). Ecology: Diversity and stability in plant communities. *Nature*, *446*(7135), 2006–2008. doi:10.1038/nature05749.

Bezemer, T. M., Harvey, J. A., Kowalchuk, G. A., Korpershoek, H., & van Der Putten, W. H. (2006). Interplay between *Senecio jacobaea* and plant, soil, and aboveground insect community composition. *Ecology*, *87*(8), 2002–2013. doi:10.1890/0012-9658(2006)87[2002:IBSJAP]2.0.CO;2.

Bezemer, T. M., Jing, J., Bakx-Schotman, J. M. T., & Bijleveld, E. J. (2018). Plant competition alters the temporal dynamics of plant-soil feedbacks. *Journal of Ecology*, *106*(6), 2287–2300. doi:10.1111/1365-2745.12999.

Casper, B. B., Cahill, J. F., & Hyatt, L. A. (1998). Above-ground competition does not alter biomass allocated to roots in *Abutilon theophrasti*. *New Phytologist*, *140*(2), 231–238. doi:10.1046/j.1469-8137.1998.00271.x.

Castagneyrol, B., Jactel, H., & Moreira, X. (2018). Anti-herbivore defences and insect herbivory: Interactive effects of drought and tree neighbours. *Journal of Ecology*, *106*(5), 2043–2057. doi:10.1111/1365-2745.12956.

Clements, D. R., Cole, D. E., Darbyshire, S., King, J., & McClay, A. (2004). The biology of Canadian weeds. 128. *Leucanthemum vulgare* Lam. *Canadian Journal of Plant Science*, *84*(1), 343–363. doi:10.4141/P02-112.

de la Peña, E., Baeten, L., Steel, H., Viaene, N., De Sutter, N., De Schrijver, A., & Verheyen, K. (2016). Beyond plant−soil feedbacks: mechanisms driving plant community shifts due to land-use legacies in post-agricultural forests. *Functional Ecology*, *30*(7), 1073–1085. doi:10.1111/1365-2435.12672.

Douma, J. C., & Weedon, J. T. (2019). Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution*, *10*(9), 1412–1430. doi:10.1111/2041-210X.13234.

Dudenhöffer, J. H., Ebeling, A., Klein, A. M., & Wagg, C. (2018). Beyond biomass: Soil feedbacks are transient over plant life stages and alter fitness. *Journal of Ecology*, *106*(1), 230–241. doi:10.1111/1365-2745.12870.

Fawcett, J. K., & Scott, J. E. (1960). A rapid and precise method for the determination of urea. *Journal of Clinical Pathology*, *13*, 156–159. doi:10.1136/jcp.13.2.156.

Fei, M., Gols, R., & Harvey, J. A. (2014). Seasonal phenology of interactions involving short-lived annual plants, a multivoltine herbivore and its endoparasitoid wasp. *Journal of Animal Ecology*, *83*(1), 234–244. doi:10.1111/1365-2656.12122.

Forster, M. A., Ladd, B., & Bonser, S. P. (2011). Optimal allocation of resources in response to shading and neighbours in the heteroblastic species, *Acacia implexa*. *Annals of Botany*, *107*(2), 219–228. doi:10.1093/aob/mcq228.

Friman, J., Karssemeijer, P. N., Haller, J., Kreek, K., Loon, J. J. A., & Dicke, M. (2021). Shoot and root insect herbivory change the plant rhizosphere microbiome and affects cabbage−insect interactions through plant−soil feedback. *New Phytologist*, *232*(6), 2475–2490. doi:10.1111/NPH.17746.

Frostegard, A., Tunlid, A., & Baath, E. (1993). Phospholipid fatty acid composition, biomass, and activity of microbial communities from two soil types experimentally exposed to different heavy metals. *Applied and Environmental Microbiology*, *59*(11), 3605–3617. doi:10.1128/aem.59.11.3605-3617.1993.

Hambäck, P. A., Inouye, B. D., Andersson, P., & Underwood, N. (2014). Effects of plant neighborhoods on plant-herbivore interactions: Resource dilution and associational effects. *Ecology*, *95*(5), 1370–1383. doi:10.1890/13-0793.1.

Hannula, S. E., Heinen, R., Huberty, M., Steinauer, K., De Long, J. R., Jongen, R., & Bezemer, T. M. (2021). Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. *Nature Communications*, *12*(1), 1–13. doi:10.1038/s41467-021-25971-z.

Heinen, R., Hannula, S. E., De Long, J., Huberty, M., Jongen, R., Kielak, A., Steinauer, K., Zhu, F., & Bezemer, T. M. (2020). Plant community composition steers grassland vegetation via soil legacy effects. *Ecology Letters*, *23*, 973–982. doi:10.1111/ele.13497.

Heinen, R., van der Sluijs, M., Biere, A., Harvey, J. A., & Bezemer, T. M. (2018). Plant community composition but not plant traits determine the outcome of soil legacy effects on plants and insects. *Journal of Ecology*, *106*(3), 1217–1229. doi:10.1111/1365-2745.12907.

Heinze, J., & Joshi, J. (2018). Plant−soil feedback effects can be masked by aboveground herbivory under natural field conditions. *Oecologia*, *186*(1), 235–246. doi:10.1007/s00442-017-3997-y.

Heinze, J., Wacker, A., & Kulmatiski, A. (2020). Plant−soil feedback effects altered by aboveground herbivory explain plant species abundance in the landscape. *Ecology*, *101*(6), e03023. doi:10.1002/ecy.3023.

Hu, L., Robert, C. A. M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., van Der Heijden, M. G. A., Schlaeppi, K., & Erb, M. (2018). Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nature Communications*, *9*(1), 1–13. doi:10.1038/s41467-018-05122-7.

Huang, W., Gfeller, V., & Erb, M. (2019). Root volatiles in plant−plant interactions II: Root volatiles alter root chemistry and plant−herbivore interactions of neighbouring plants. *Plant Cell and Environment*, *42*(6), 1964–1973. doi:10.1111/pce.13534.

Huberty, M., Choi, Y. H., Heinen, R., & Bezemer, T. M. (2020). Above-ground plant metabolomic responses to plant−soil feedbacks and herbivory. *Journal of Ecology*, *108*(4), 1703–1712. doi:10.1111/1365-2745.13394.

Kassambara, A. (2020). *rstatix: Pipe-Friendly framework for basic statistics tests. R package version 0.6.0.999*. . https://rpkgs.datanovia.com/rstatix/.

Kim, T. N. (2017). How plant neighborhood composition influences herbivory: Testing four mechanisms of associational resistance and susceptibility. *PLoS ONE*, *12*,(5) e0176499. doi:10.1371/journal.pone.0176499.

Kim, T. N., Underwood, N., & Cronin, J. T. (2015). Plant neighborhood effects on herbivory: Damage is both density and frequency dependent. *Ecology*, *96*(5), 1431–1437. doi:10.1890/14-1097.1.

Kos, M., Bukovinszky, T., Mulder, P. P. J., & Bezemer, T. M. (2015). Disentangling above- and belowground neighbor effects on the growth, chemistry, and arthropod community on a focal plant. *Ecology*, *96*(1), 164–175. doi:10.1890/14-0563.1.

Kostenko, O., & Bezemer, T. M. (2020). Abiotic and biotic soil legacy effects of plant diversity on plant performance. *Frontiers in Ecology and Evolution*, *8*, 87. doi:10.3389/fevo.2020.00087.

Kostenko, O., Grootemaat, S., van der Putten, W. H., & Bezemer, T. M. (2012). Effects of diversity and identity of the neighbouring plant community on the abundance of arthropods on individual ragwort (*Jacobaea vulgaris*) plants. *Entomologia Experimentalis et Applicata*, *144*(1), 27–36. doi:10.1111/j.1570-7458.2012.01251.x.

Kostenko, O., Mulder, P. P. J., Courbois, M., & Bezemer, T. M. (2017). Effects of plant diversity on the concentration of secondary plant metabolites and the density of arthropods on focal plants in the field. *Journal of Ecology*, *105*(3), 647–660. doi:10.1111/1365-2745.12700.

Kostenko, O., van de Voorde, T. F. J., Mulder, P. P. J., van der Putten, W. H., & Martijn Bezemer, T. (2012). Legacy effects of aboveground-belowground interactions. *Ecology Letters*, *15*(8), 813–821. doi:10.1111/j.1461-0248.2012.01801.x.

Kulmatiski, A., Beard, K. H., Norton, J. M., Heavilin, J. E., Forero, L. E., & Grenzer, J. (2017). Live long and prosper: plant−soil feedback, lifespan, and landscape abundance covary. *Ecology*, *98*(12), 3063–3073. doi:10.1002/ecy.2011.

Kulmatiski, A., Beard, K. H., & Stark, J. M. (2006). Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology*, *43*(5), 868–876. doi:10.1111/j.1365-2664.2006.01192.x.

Liu, Y., Dawson, W., Prati, D., Haeuser, E., Feng, Y., & Van Kleunen, M. (2016). Does greater specific leaf area plasticity help plants to maintain a high performance when shaded? *Annals of Botany*, *118*(7), 1329–1336. doi:10.1093/aob/mcw180.

Lowman, M. D. (1982). Seasonal variation in insect abundance among three Australian rain forests, with particular reference to phytophagous types. *Australian Journal of Ecology*, *7*(4), 353–361. doi:10.1111/j.1442-9993.1982.tb01310.x.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of statistical models. *The Journal of Open Source Software*, *6*, 3139. doi:10.21105/joss.03139 dOI.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Maintainer, H. W. (2019). vegan: Community Ecology Package. R package version 2.5-5. *Community Ecology Package*, *2*(9). https://CRAN.R-project.org/package=vegan.

Olsson, P. A., Bååth, E., Jakobsen, I., & Söderström, B. (1995). The use of phospholipid and neutral lipid fatty acids to estimate biomass of arbuscular mycorrhizal fungi in soil. *Mycological Research*, *99*(5), 623–629. doi:10.1016/S0953-7562(09)80723-5.

Otway, S. J., Hector, A., & Lawton, J. H. (2005). Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology*, *74*(2), 234–240. doi:10.1111/J.1365-2656.2005.00913.X.

Pashalidou, F. G., Eyman, L., Sims, J., Buckley, J., Fatouros, N. E., De Moraes, C. M., & Mescher, M. C. (2020). Plant volatiles induced by herbivore eggs prime defences and mediate shifts in the reproductive strategy of receiving plants. *Ecology Letters*, *23*(7), 1097–1106. doi:10.1111/ele.13509.

Peltzer, D. A. (2001). Plant responses to competition and soil origin across a prairie−forest boundary. *Journal of Ecology*, *89*(2), 176–185. doi:10.1046/j.1365-2745.2001.00544.x.

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist*, *193*(1), 30–50. doi:10.1111/j.1469-8137.2011.03952.x.

Core Team, R. (2022). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Ristok, C., Poeschl, Y., Dudenhöffer, J. H., Ebeling, A., Eisenhauer, N., Vergara, F., Wagg, C., van Dam, N. M., & Weinhold, A. (2019). Plant species richness elicits changes in the metabolome of grassland species via soil biotic legacy. *Journal of Ecology*, *107*(5), 2240–2254. doi:10.1111/1365-2745.13185.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2021). partR2: partitioning R^2 in generalized linear mixed models. *PeerJ*, *9*, e11414. doi:10.7717/peerj.11414.

Stokes, K., & Stiling, P. (2013). Effects of relative host plant abundance, density and inter-patch distance on associational resistance to a coastal gall-making midge, *Asphondylia borrichiae* (Diptera: Cecidomyiidae). *Florida Entomologist*, *96*(3), 1143–1148. doi:10.1653/024.096.0355.

Underwood, N., Inouye, B. D., & Hambäck, P. A. (2014). A conceptual framework for associational effects: When do neighbors matter and how would we know? *The Quarterly Review of Biology*, *89*(1), 1–19. doi:10.1086/674991.

van der Putten, W. H., Mortimer, S. R., Hedlund, K., Van Dijk, C., Brown, V. K., Lepš, J., Rodriguez-Barrueco, C., Roy, J., Diaz Len, T. A., Gormsen, D., Korthals, G. W., Lavorel, S., Santa Regina, I., & Smilauer, P. (2000). Plant species diversity as a driver of early succession in abandoned fields: A multi-site approach. *Oecologia*, *124*(1), 91–99. doi:10.1007/s004420050028.

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F. J., & Wardle, D. A. (2013). Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*(2), 265–276. doi:10.1111/1365-2745.12054.

Veen, G. F., van der Putten, W. H., & Bezemer, T. M. (2018). Biodiversity-ecosystem functioning relationships in a long-term non-weeded field experiment. *Ecology*, *99*(8), 1836–1846. doi:10.1002/ecy.2400.

Wang, S., & Callaway, R. M. (2021). Plasticity in response to plant−plant interactions and water availability. *Ecology*, *102* (6), 1–11. doi:10.1002/ecy.3361.

White, J. A., & Whitham, T. G. (2000). Associational susceptibility of cottonwood to a box elder herbivore. *Ecology*, *81*(7), 1795–1803. doi:10.1890/0012-9658(2000)081[1795:ASOCTA]2.0.CO;2.

Wilson, J. B. (1988). Shoot competition and root competition. *The Journal of Applied Ecology*, *25*, 279–296. doi:10.2307/2403626.

Wurst, S., & Ohgushi, T. (2015). Do plant- and soil-mediated legacy effects impact future biotic interactions? *Functional Ecology*, *29*(11), 1373–1382. doi:10.1111/1365-2435.12456.

Zhu, F., Heinen, R., van der Sluijs, M., Raaijmakers, C., Biere, A., & Bezemer, T. M. (2018). Species-specific plant−soil feedbacks alter herbivore-induced gene expression and defense chemistry in *Plantago lanceolata*. *Oecologia*, *188*(3), 801–811. doi:10.1007/s00442-018-4245-9.

Available online at www.sciencedirect.com

ScienceDirect