

RESEARCH ARTICLE

Plant community composition but not plant traits determine the outcome of soil legacy effects on plants and insects

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Abstract

1. Plants leave species-specific legacies in the soil they grow in that can represent changes in abiotic or biotic soil properties. It has been shown that such legacies can affect future plants that grow in the same soil (plant–soil feedback, PSF). Such processes have been studied in detail, but mostly on individual plants. Here, we study PSF effects at the community level and use a trait-based approach both in the conditioning phase and in the feedback phase to study how 12 individual soil legacies influence six plant communities that differ in root size.
2. We tested if (1) grassland perennial species with large root systems would leave a stronger legacy than those with small root systems, (2) grass species would leave a more positive soil legacy than forbs, and (3) communities with large root systems would be more responsive than small-rooted communities. We also tested (4) whether a leaf-chewing herbivore and a phloem feeder were affected by soil legacy effects in a community framework.
3. Our study shows that the six different plant communities that we used respond differently to soil legacies of 12 different plant species and their functional groups. Species with large root systems did not leave stronger legacies than species with small root systems, nor were communities with large root systems more responsive than communities with root systems.
4. Moreover, we show that when communities are affected by soil legacies, these effects carry over to the chewing herbivore *Mamestra brassicae* (Lepidoptera: Noctuidae) through induced behavioural changes resulting in better performance of a chewing herbivore on forb-conditioned soils than on grass-conditioned soils, whereas performance of the phloem feeder *Rhopalosiphum padi* (Hemiptera: Aphididae) remained unaffected.
5. **Synthesis.** The results of this study shed light on the variability of soil effects found in previous work on feedbacks in communities. Our study suggests that the composition of plant communities determines to a large part the response to soil legacies. Furthermore, the responses to soil legacies of herbivores feeding on the plant communities that we observed, suggests that in natural ecosystems, the vegetation history may also have an influence on contemporary herbivore assemblages. This

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opens up exciting new areas in plant–insect research and can have important implications for insect pest management.

KEYWORDS

herbivore, *Mamestra*, plant community, plant–herbivore interactions, plant–soil (below-ground) interactions, plant–soil feedback, root size, soil conditioning, soil legacy effects, trophic levels

1 | INTRODUCTION

Soil biota critically depend on plants, because they provide the primary resources for the soil food web (Bardgett & Wardle, 2010; Wardle et al., 2004). Plant growth, in turn, also depends on the composition of the soil biotic community, as soil biota recycle and provide nutrients to the plant or influence plant health (Berendsen, Pieterse, & Bakker, 2012; Van Der Heijden, Bardgett, & Van Straalen, 2008). Plant species can differ greatly in how they influence soil biota as well as soil abiotic conditions such as pH, or the concentration of allelochemicals in the soil (Bais, Vepachedu, Gilroy, Callaway, & Vivanco, 2003; Bais, Weir, Perry, Gilroy, & Vivanco, 2006). Furthermore, via their effect on the soil, plants can also influence other plants that grow later in the soil, a process known as plant–soil feedback (PSF; Bever, 1994).

Plants differ in how they influence the soil, but species also vary greatly in how they respond to differences in soil conditions. An important question is whether these effects on soils and responses to soils can be predicted by plant traits, such as those related to defence (Bardgett, Mommer, & de Vries, 2014; Kulmatiski, Beard, Stevens, & Cobbold, 2008; Van der Putten et al., 2013). Several studies have shown that the strength and direction of the PSF effect induced by a species differs between plant functional groups, and that grasses induce overall more positive effects than forbs (Kos, Tuijl, de Roo, Mulder, & Bezemer, 2015; Van de Voorde, van der Putten, & Bezemer, 2011; Wubs & Bezemer, 2016). Plant roots directly interact with the soil and soil biota and hence plants with large root systems may have a larger zone of influence per unit soil, or a larger contact area for interacting with soil organisms than plants with small roots. It is well known for many plant species that there is a positive relationship between the root size and root growth rate of a plant and the amount of exudates that the roots deposit in the soil (De Deyn, Cornelissen, & Bardgett, 2008; Dennis, Miller, & Hirsch, 2010; der Krift, Kuikman, Möller, & Berendse, 2001). Larger root systems also provide more habitat for root-associated (micro)-organisms such as bacteria or nematodes, for example, by having a larger surface area (Latz, Eisenhauer, Scheu, & Jousset, 2015). The surface area of the roots could also affect the response to soil. Roots with a larger size and surface area may, by chance, encounter more soil organisms. The size of a root system at any particular point in time will be influenced by growth rate, since a plant that grows fast, will accumulate more biomass in a fixed time frame than a plant that grows more slowly. Another determinant of root size could be the relative investment of plant species in their root biomass. Several studies have shown that fast growing, early successional plant species typically create negative PSF effects, while slow growing, later-successional plants tend to leave

a more positive legacy (Cortois, Schröder-Georgi, Weigelt, van der Putten, & De Deyn, 2016; Heinze, Bergmann, Rillig, & Joshi, 2015; Jing, Bezemer, & van der Putten, 2015; Kardol, Martijn Bezemer, & van der Putten, 2006). Previous studies suggest that fast growers may accumulate more pathogens in their rhizosphere than slow growers (Bever, Westover, & Antonovics, 1997; Van der Putten, Van Dijk, & Peters, 1993; Van der Putten et al., 2013). Fast growing plants may invest less in plant defence such as allelochemicals than slow growing ones (Coley, Bryant, & Chapin, 1985; Herms & Mattson, 1992). Hence, root traits related to growth and defence may also play a vital role in a plant's response to soil legacy effects.

Most PSF studies focus on plant growth effects, but several recent studies have shown that PSF effects can also influence above-ground herbivorous insects and their natural enemies (Kos et al., 2015; Kostenko, van de Voorde, Mulder, van der Putten, & Martijn Bezemer, 2012; Wurst, 2013). Soil biota can influence above-ground insect herbivores via influencing the size and ontogeny of the host plant, or via changing the nutritional quality of above-ground plant parts (Wardle et al., 2004). How different feeding guilds of above-ground insect herbivores respond to PSF is poorly understood. Insects of different feeding guilds vary greatly in how they respond to qualitative or quantitative changes in their host plants (Awmack & Leather, 2002; Bezemer & Jones, 1998). Furthermore, many studies have shown that the magnitude and even direction of effects of soil biota such as root herbivores, mycorrhizal fungi or even non-pathogenic bacteria on above-ground insects can differ between feeding guilds (Biere & Goverse, 2016; Johnson et al., 2012; Pangesti, Pineda, Pieterse, Dicke, & Van Loon, 2013; Soler et al., 2012). Root damage, for example, often increases the performance of above-ground sap suckers while it reduces the performance of leaf chewers (Bezemer & Jones, 1998; Johnson, Mitchell, McNicol, Thompson, & Karley, 2013; Johnson et al., 2012).

Plant–insect interactions are likely to differ between individual plants, monocultures and mixed communities. Moving from single species to mixed cultures increases biological diversity, chemical diversity and phylogenetic diversity of the study system (Andow, 1991; Salazar, Jaramillo, & Marquis, 2016). Studies show that performance of generalists increases in more diverse systems, as a result of higher productivity in diverse plant communities (Loranger et al., 2014; Marquard et al., 2009; Roscher et al., 2005; Scherber et al., 2006). Most likely, the increased performance of generalists in such systems can be explained by increased plant diversity, as they can digest a wider range of host plants (Andow, 1991; Root, 1973). It should be noted that herbivores differ in their tolerance to different chemical compounds (Ali & Agrawal, 2012; Lankau, 2007), which may play an important role in

the performance of different generalists on a range of different communities. In mixed plant communities, PSF effects may also influence above-ground insect herbivores by altering the relative abundance of host plants within the community (Jing et al., 2015; Kardol et al., 2006). However, how PSF influences above-ground insects in mixed plant communities remains largely unknown (Wurst & Ohgushi, 2015).

In this study, we examine the effects of soil legacies on a selection of large- and small-rooted grasses and forbs (based on their accumulation of root biomass over 7 weeks) and in turn how this affects the performance of two generalist herbivores from different feeding guilds. The cabbage moth (*Mamestra brassicae* L., Lepidoptera: Noctuidae) is a polyphagous chewing herbivore with a wide range of host plants and occurs all over the Palearctic (Metspalu, Jõgar, Hiisaar, & Grishakova, 2004; Turnock & Carl, 1995). The bird cherry-oat aphid (*Rhopalosiphum padi* L., Hemiptera: Aphididae) is a phloem feeder that has a world-wide distribution and feeds on a wide range of grasses during its vegetative (summer) cycle (Dixon, 1971). We conditioned the soil by growing monocultures of each species for 10 weeks. We then planted mixed plant communities consisting of either large- or small-rooted plants on the conditioned soils and introduced *M. brassicae* and *R. padi* to each plant community. We predicted that (1) large-rooted plants will create more negative soil legacies than small-rooted plants, and this will, in turn, affect above-ground herbivores; (2) legacies left by grasses will be more positive than legacies left by forbs; (3) large-rooted plant communities will be more responsive to soil legacies than small-rooted communities. (4) Lastly, we expected that the two insect species will be differentially affected by soil legacies.

2 | MATERIALS AND METHODS

2.1 | Field soil and soil sterilization

Field soil used in this experiment was collected from a restoration grassland field site, "De Mossel" (Natuurmonumenten, Ede, The Netherlands) that has been abandoned from agriculture in 1996. This site has sandy loam soils (83% sand, 10% silt, 4% clay, 3% organic matter, for chemistry see Table S1); the area is known to be poor in nutrients, except for phosphorus (a legacy of decades of heavy fertilization with manure). The live field soil originated from the top 5–10 cm of soil. For sterile soils, the soil layer of 10–30 cm depth was sterilized by γ -irradiation (Synergy Health, Ede, The Netherlands). Soil was sieved to remove roots, stones and most macro-invertebrates (sieve mesh Ø1.0 cm).

2.2 | Plants

Growth of roots and shoots of 24 common grassland species was followed under standard greenhouse conditions over the course of 6 weeks, simultaneous with the conditioning phase of present study. A selection of 12 species was made based on root biomass; large root (R+) or small root (R-) and functional group; grass (G) or forb (F) (see Table S2).

Seeds were surface-sterilized using 2.5% bleach solution and then rinsed with water. For germination, seeds were placed on sterile glass

beads in a climate cabinet (light regime 16:8, L:D, day temperature 21°C, night temperature 16°C). Because plants differ in their germination time, as soon as a species had germinated, the seedlings were stored at 4°C under the same light regime, until all species had sufficiently germinated. Seeds were obtained from Cruydt-Hoeck (Nijberkoop, The Netherlands).

2.3 | Insects

Eggs of the Cabbage moth, *M. brassicae* were provided by the Department of Entomology at Wageningen University. The colony has been in production for many years on Brussel's Sprout, *Brassica oleracea* var. *gemmifera* cv. Cyrus. The larvae were originally collected from cabbage fields near Wageningen University.

A starter colony of the bird cherry-oat aphid, *R. padi*, was provided by Plant Research International at Wageningen University. The colony has been in rearing for more than 25 years. The original specimens were caught in Wageningen and have since been reared on Oat, *Avena sativa*, in a climate chamber with long day light (16:8, L:D) at 19°C.

2.4 | Soil conditioning phase

To condition the soils by each of the 12 conditioning plant species, six round 2-L pots per plant species were filled with 1,800 g of homogenized live field soil. In each of the pots, five seedlings were grown to condition the soil. In addition, 10 smaller square pots (11 × 11 cm) were filled with 1,050 g homogenized live field soil in which only one seedling was planted, resulting in a total of 2,850 g of conditioned soil per plant species. The smaller pots were planted for an experiment that was performed simultaneously with the same live soils and seed batches in the same greenhouse compartment. These pots were also used to determine the root and shoot productivity for the 12 species used in this experiment. The soils were carefully homogenized per replicate. After planting, the seedlings were covered with shade cloth for 4 days to acclimatize. Pots were topped off with a 1 cm layer of fine sand against weeds and fungus gnats. Weeds that emerged from the soil were removed daily. The used plant species differed in their water use and soil moisture was kept at 17%. After a conditioning phase of 10 weeks, soils were harvested by removing all root pieces. For each of the conditioning species, soils of the individual and community conditionings were mixed by volume in a 1:1 ratio and divided over five independent replicates (each consisting of soil from one of the large and two of the smaller pots) to avoid pseudo-replication in the feedback phase. Soil from the sixth large pot per conditioning species was equally divided over the five replicates. The resulting conditioned soils were mixed with sterilized (by γ -irradiation) field soil (1:1 v:v). A subsample of each replicate soil was frozen at -80°C and the composition of soil bacteria and fungi was determined using Illumina Miseq sequencing. Results and details about the methods and analysis are presented in the Supporting Information.

Six different plant communities were composed before the start of the feedback phase of the experiment. Three communities contained plants that invest in quick root biomass addition (large-rooted communities; C+) and the other three communities contained plants that

remain small rooted (small-rooted communities; C-). Each community consisted of four individuals: two forbs and two grasses (see also Table S3a). The experiment had a fractional factorial design (see Table S3b). Each of the six communities was grown on eight of the 12 conditioned soils (two R+ grasses; two R+ forbs, two R- grasses; two R- forbs) and thus, on every soil, four out of six communities were grown (see Table S3b for experimental combinations). Every combination was replicated five times, using soil from one of the independent pools from the conditioning phase.

2.5 | Feedback phase

Four round 2-L pots were filled per independent replicate pool. Each round pot was filled with a fixed volume (1.3 L) of conditioned soil. Soils were then topped off with a 1–2 cm layer of fine filter sand. All pots were watered and left to acclimatize for 2 days. Four germinated seedlings were planted in a square shape with roughly 5 cm distance between individuals to form the distinct communities. Plants were watered as needed three times per week. On day 41, the plants were placed in Bugdorm rearing bags (66 × 100 cm, MegaView Science, Taiwan) that were modified into hanging cylindrical cages for the insect assays (33 cm wide × 90 cm high). After the insect assay ended, on day 66 of the experiment, all above-ground parts were harvested for each plant species individually. Roots were harvested per community, as they could not be separated by species. Root parts were washed on a sieve to remove sand, stones and foreign organic material. Plant material was weighed after oven-drying for at least 72 hr at 70°C.

2.6 | Caterpillar assay

On day 43 of the feedback phase, two *M. brassicae* were placed in each cage. Caterpillar damage was scored for each individual plant in each community on days 9, 16 and 23 of the insect assay. The larger of the two caterpillars was left on the plant after the first weighing for continuation of the assay. On days 10, 17 and 24, caterpillars were weighed and damage was measured as the estimated number of 25 mm² squares that were eaten per plant. After the third measurement, the caterpillars were taken off the plants.

2.7 | Aphid assay

On day 15 of the caterpillar assay, five *R. padi* individuals of nymphal instar 4 were placed in each cage. The aphids were left to reproduce asexually for 19 days, after which the above-ground biomass of the plants was harvested and the number of aphids was counted on each plant species.

2.8 | Statistical analyses

2.8.1 | Multivariate analyses of individual plant biomass and individual consumption

Unconstrained, principal component analyses were performed separately for each community for the response variables “individual plant

biomass” and “consumed leaf area per individual plant” in each pot. Furthermore, constrained, redundancy analyses (RDA) were performed separately for each community for the same response variables, with root size (R+/R-) of the conditioning species, functional group (G/F) of the conditioning species and identity of the species (eight soil species per community) that conditioned the soils, as explanatory variables. All multivariate analyses were conducted in Canoco 5.03 (Microcomputer Power, Ithaca NY, USA).

2.8.2 | Across-community effects

General linear mixed-effect models were used to analyse community root and shoot biomass, as well as caterpillar consumption, caterpillar biomass and aphid colony size. The raw data were z-transformed (as follows: $z = (x - \mu)/\sigma$, in which x = the observed value, μ = the community mean and σ = the community standard deviation) in order to allow assessing effects of soil conditioning on plant community types (C+/C-) while taking into account the differences in community composition. We analysed the main effects and interactions between root size of the conditioning plant species (R+/R-), functional group of the conditioning plant species (G/F) and community type (C+/C-) as fixed effects, with soil identity (conditioning plant species) nested in community identity (composition 1–6) as random effect. Analyses were performed in R version 3.0.3 (R Development Core Team, 2008) using the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017).

2.8.3 | Within community effects on plant and insect biomass

We analysed (1) the main effects and interaction between root size (R+/R-) and functional group (G/F) as factors as well as (2) the effect of soil identity (conditioning plant species) as factor on total shoot biomass, total root biomass, caterpillar biomass, caterpillar consumption and aphid colony size by ANOVAs. Analyses were performed for each community separately, using the raw data (log-transformed for root and shoot biomass, and square root-transformed for caterpillar biomass and aphid colony size) because we wanted to compare communities of the same composition on different soils, not different communities, as was the case in the z-score analyses. Analyses were performed in R version 3.0.3 (R Development Core Team, 2008).

2.8.4 | Growth of individual plants and leaf consumption of individual plants across six communities

The biomasses of individual species within each community are not independent samples and therefore should not be treated as such. Hence, the main body of this paper contains only the multivariate analyses of these data. However, because how the plant species grow and compete in different communities on different soils contains valuable information, these results are presented in the Supporting Information, accompanied by the respective ANOVAs (see Figure S1, Table S2).

Likewise, the data of the individual consumption gives valuable insights into the behaviour and preferences of the caterpillars in different communities and therefore are also supplied along with the accompanying ANOVAs (see Figure S2, Table S4).

3 | RESULTS

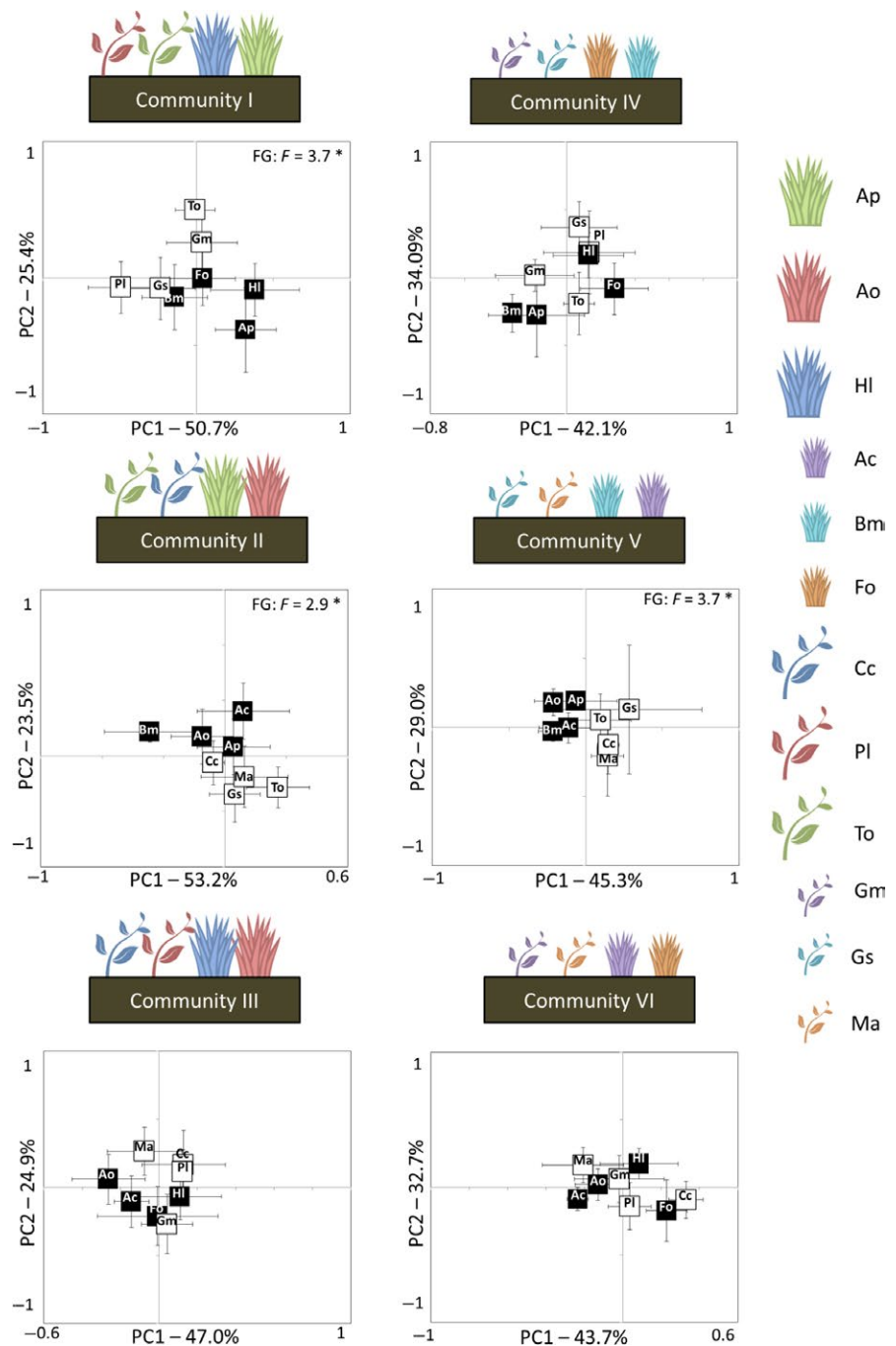
3.1 | Multivariate analyses

The relative distribution of above-ground biomass across plant species within a community was affected by the soils the communities were grown on. There was a significant effect of the

identity of the species that conditioned the soils on the composition of the biomass in communities II, IV and VI (RDA: community II: $F = 2.1$, $p < .001$; IV: $F = 1.8$, $p = .05$; VI: $F = 2.1$, $p = .01$, respectively, see Figure 1). In community I, II and V there was a significant effect of the functional group of the conditioning species (I: $F = 6.1$, $p < .01$; II: $F = 6.7$, $p < .01$; V: $F = 3.1$, $p = .02$, resp., see Figure 1). Only in community VI, was there an effect of root size of the species that conditioned the soil ($F = 4.2$, $p = .01$, see Figure 1).

The relative consumption of the different plant species by *M. brassicae*, was significantly affected only by functional group of the species that conditioned the soils. This effect was found in communities I, II

FIGURE 1 Principal component analysis (unconstrained PCA) plots showing effects of soil conditioning by 12 plant species on the distribution of shoot biomass over the four individual plant species in six different plant communities (I–VI). Each plant community was grown on 8 of 12 soils (fractional factorial design). Squares represent mean sample scores for the different conditioned soils ($n = 5$ for each square). Error bars represent SEs of the mean PCA scores for both axes. White squares represent forb soils and black squares represent grass soils. The composition of each of the six communities is also presented above each panel. Ac = *Agrostis capillaris*, Ao = *Anthoxanthum odoratum*, Ap = *Alopecurus pratensis*, Bm = *Briza media*, Cc = *Crepis capillaris*, Fo = *Festuca ovina*, Gm = *Geranium molle*, Gs = *Gnaphalium sylvaticum*, Hl = *Holcus lanatus*, Ma = *Myosotis arvensis*, Pl = *Plantago lanceolata*, To = *Taraxacum officinale*. Statistics shown in the panels are the F -statistic of constrained redundancy analysis (RDA) on functional group (FG), root size (R) and soil identity (Soil). Asterisks represent significance: * $p < .05$; ** $p < .01$; *** $p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]



and V (I: $F = 3.7$, $p = .01$; II: $F = 2.9$, $p = .05$; V: $F = 3.7$, $p = .01$, resp., see Figure 2).

3.2 | Across-community effects

Total above-ground biomass was not affected by main effects of root type (R+/R-) or functional group (G/F) of the conditioned soils, or the type of community (C+/C-). However, a marginally significant interaction was found between community type and functional group of the species that conditioned the soil. As shown in Figure 3a, on forb-conditioned soils large-rooted communities tended to have a higher

above-ground biomass than small-rooted communities, whereas on grass-conditioned soils, the small-rooted communities tended to have a higher biomass than the large-rooted communities (non-significant: $F_{1,36} = 3.95$, $p = .055$, see Figure 3a).

The identity of the functional group of the species that conditioned the soil had a significant effect on caterpillar biomass after 3 weeks of feeding. Caterpillars were significantly larger on food plants grown on forb-conditioned soils than on grass-conditioned soils ($F_{1,36} = 9.56$, $p < .01$, see Figure 3b). Neither root size of the conditioning species nor community type significantly affected caterpillar biomass.

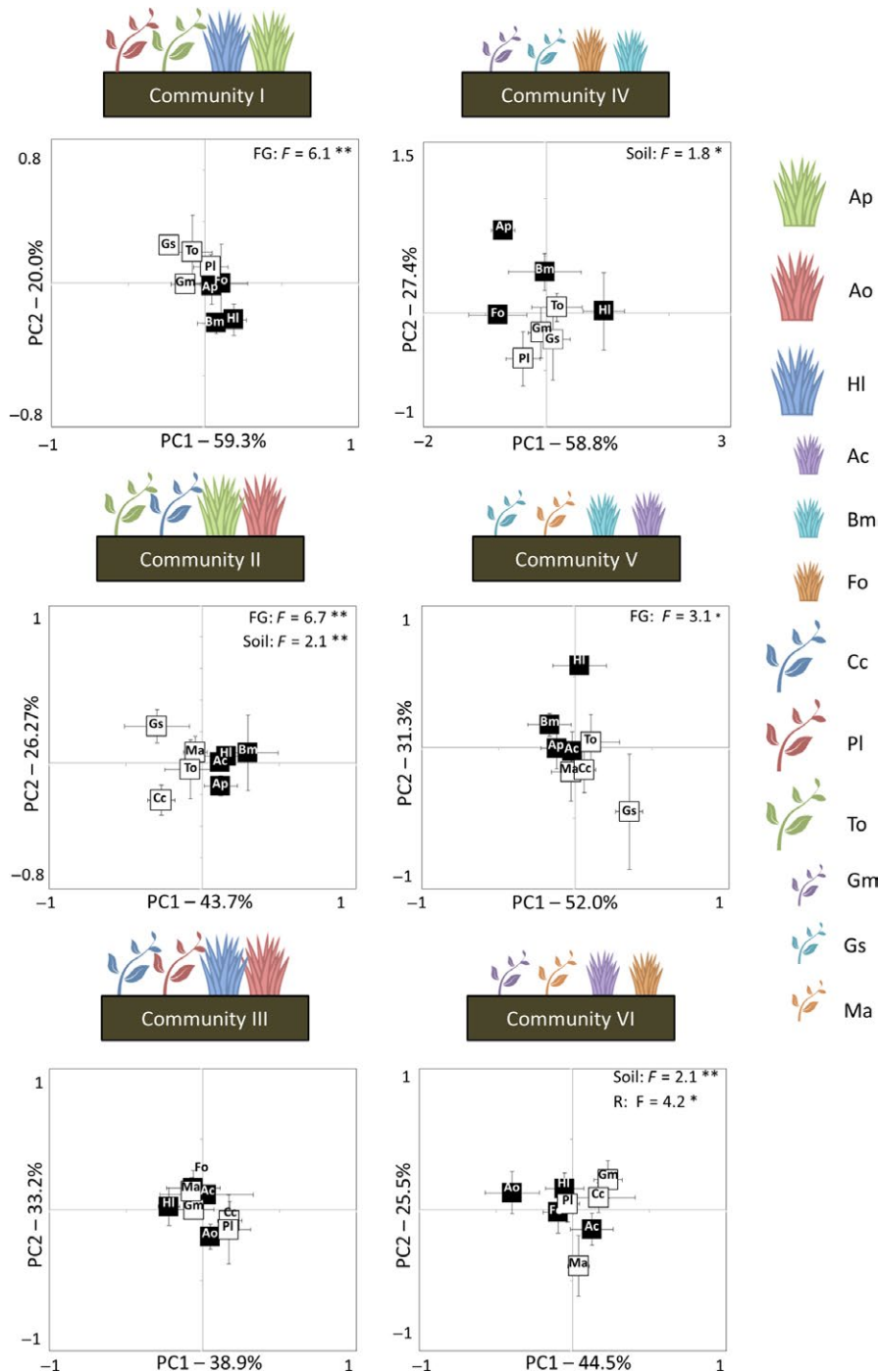


FIGURE 2 Principal component analysis (unconstrained PCA) plots showing effects of soil conditioning by 12 plant species on the distribution of herbivory (measured as consumed area) over the four individual plant species in six different plant communities (I–VI). Each plant community was grown on 8 of 12 soils (fractional factorial design). Squares represent mean sample scores for the different conditioned soils ($n = 5$ for each square). Error bars represent SEs of the mean PCA scores for both axes. White squares represent forb soils and black squares represent grass soils. The composition of each of the six communities is also presented above each panel. Ac = *Agrostis capillaris*, Ao = *Anthoxanthum odoratum*, Ap = *Alopecurus pratensis*, Bm = *Briza media*, Cc = *Crepis capillaris*, Fo = *Festuca ovina*, Gm = *Geranium molle*, Gs = *Gnaphalium sylvaticum*, HI = *Holcus lanatus*, Ma = *Myosotis arvensis*, PI = *Plantago lanceolata*, To = *Taraxacum officinale*. Statistics shown in the panels are the F -statistic of constrained redundancy analysis (RDA) on functional group (FG) and soil identity (Soil). Asterisks represent significance: $*p < .05$; $**p < .01$; $***p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

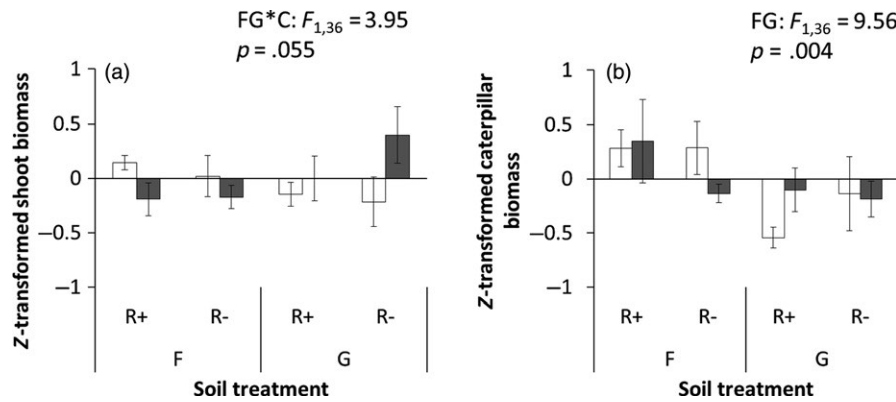


FIGURE 3 Effects of soil conditioning by large-rooted (R+) or small-rooted (R-) grasses (G) and forbs (F) on (a) community shoot biomass and (b) caterpillar biomass after 24 days of feeding. As different plant communities inherently differ in their community shoot biomass, as well as the suitability as food source for herbivores, data for shoot biomass and caterpillar biomass were z-transformed ($M = 0$ and $SE = 1$, See methods) for each of the six (different) plant communities. In this way, the mean and SDs were centralized, which makes it possible to compare the effects of soil conditioning between communities and test for general treatment effects across the data. Error bars represent SEs. White bars represent large-rooted communities (C+) and grey bars represent small-rooted communities (C-). Statistics shown are main effects and interactions of community type (C), functional group (FG) and root size (R) derived from mixed models

No effects of functional group or root type of the conditioning species were found on aphid numbers (data not shown). Since only one plant species (*Alopecurus pratensis*) supported formation of aphid colonies and this species only occurred in two of six communities, no further analyses were performed.

3.3 | Within community effects on plant and insect biomass

Conditioning species identity had a significant effect on total above-ground biomass in three of six communities (I: $F_{7,31} = 7.95$, $p < .001$; V: $F_{7,26} = 4.38$, $p < .001$; VI: $F_{7,30} = 3.08$, $p = .01$ resp., see Figure 4). Community I accumulated most biomass on *Gnaphalium* soil, whereas biomass was approximately one-third lower on *Briza* and *Holcus* soils. Community V had highest biomass on *Taraxacum*, *Alopecurus* and *Agrostis* soils and lowest biomass on *Crepis* soils. Similarly, community VI grew best on *Agrostis* soil and worst on *Crepis* and *Festuca* soils.

The functional group identity of the conditioning species only affected total above-ground biomass in community I ($F_{1,35} = 13.1$; $p < .001$). Communities grown on forb soils (*Plantago*, *Taraxacum*, *Geranium*, *Gnaphalium*) on average accumulated more biomass than those grown on grass-conditioned soils (*Alopecurus*, *Holcus*, *Briza*, *Festuca*). Root size of the conditioning plant species did not affect total above-ground biomass of any of the communities.

Functional group or identity of the conditioning species did not have any effects on total root biomass in any community. However, in community I we observed a significant effect of root size on the total root biomass of that community ($F_{1,35} = 6.8$; $p < .001$, see Figure S4). This community had significantly larger root systems when grown on soils that were conditioned by large-rooted grass or forb species, than when they were grown on those of small-rooted species.

Functional group of conditioning species had an effect on caterpillar biomass, but only in those feeding on community I and II (I: $F_{1,33} = 6.7$, $p = .01$; II: $F_{1,22} = 12.1$, $p < .01$, resp. see Figure 5). In both

communities, the caterpillars grew larger on plants grown on soils conditioned by forbs.

Conditioning led to significant differences in the composition of bacteria and fungi. These effects were significant when all species were compared and when comparing grasses and forbs. However, the latter effect was much stronger for fungi than for bacteria (Figure S4a,b).

4 | DISCUSSION

Plant species differ in the way they influence the soil and via these changes they can affect plants that grow later in the same soil, as well as the insects that develop on them. In this study, we tested if such effects are still apparent if whole plant communities are grown on the soils in a feedback phase and whether insects would be affected by soil legacies in plant communities with several host plant species. Furthermore, we tested whether grassland plants that differ in root traits and functional group create different legacy effects.

We show here that 12 test plant species left specific soil legacies that differed in soil microbial composition, and that these legacies affected the relative performance of plant species in plant communities that grew later on the conditioned soils. In turn, this led to altered performance in an associated chewing herbivore, whereas a phloem feeder was not affected. Remarkably, while we found a clear effect of functional group on composition of soil communities and on plant community performance, root size of the conditioning plant species had very little influence on composition of soil communities and on plant community performance. The rooting type (large or small rooted; C+/C-) of the response community also did not affect the response to legacy effects.

The functional group the conditioning plant species belonged to, grass or forb, significantly explained the distribution of plant biomass over the plant species during the feedback phase in three out of six

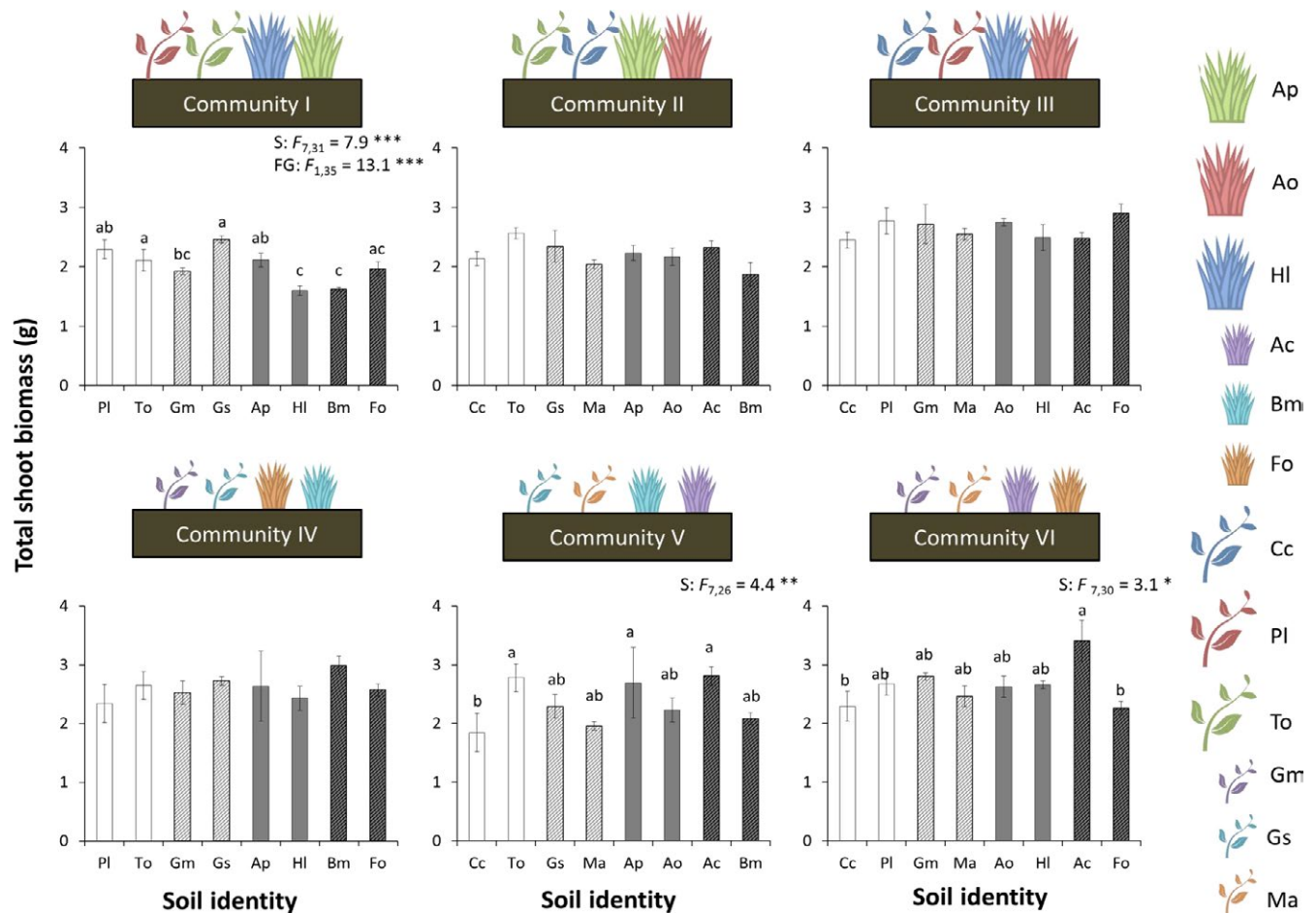


FIGURE 4 Effects of soil conditioning of species of grasses and forbs on community shoot biomass. White bars represent large-rooted forbs, striated white bars represent small-rooted forbs; grey bars represent large-rooted grasses, striated grey bars represent small-rooted grasses. Error bars represent SEs. The composition of each of the six communities is also presented above each panel. Ac = *Agrostis capillaris*, Ao = *Anthoxanthum odoratum*, Ap = *Alopecurus pratensis*, Bm = *Briza media*, Cc = *Crepis capillaris*, Fo = *Festuca ovina*, Gm = *Geranium molle*, Gs = *Gnaphalium sylvaticum*, HI = *Holcus lanatus*, Ma = *Myosotis arvensis*, PI = *Plantago lanceolata*, To = *Taraxacum officinale*. Statistics in the panels represent main effects of soil identity (S), root size (R) and soil functional group (FG) derived from one-way ANOVAs. Asterisks represent significance: * $p < .05$; ** $p < .01$; *** $p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

communities. This in itself is an interesting finding, as many studies incorporate just one focal plant or one focal community in the feedback phase and show the effects of different soils on this single plant species or plant community (e.g. Kardol, Cornips, van Kempen, Bakx-Schotman, & van der Putten, 2007). We did find plant species-specific (as well as functional group-specific) microbial profiles in the soil. This is in line with other studies using the same study system that show that plants leave species-specific microbial profiles in the soils, and that changes in soil biota differ significantly between the species and functional group the conditioning plants belong to (Kos et al., 2015). Our findings suggest that biotic legacies indeed are generally present in the soils, but that it is very much dependent on the composition of the community that grows later on these soils whether and how a community responds to these changes in soils. In our experiment we used 50% of conditioned soil and mixed this with 50% sterilized soil. Hence, potential differences in soil nutrients among the conditioned soils were diluted, but we cannot exclude that they may have played a role in the observed effects on plants and herbivores, in

addition to the effects incurred by plant-induced changes in microbial communities.

Several studies have shown that grasses leave different biotic profiles in the soil than forbs (e.g. Kos et al., 2015; Latz et al., 2012, 2015). Grass-conditioned soils have been shown in previous studies to be rich in plant growth-promoting rhizobacteria (Latz et al., 2012), which may prime plant defences in some plant species (Pangesti et al., 2015; Van Oosten et al., 2008). It has been proposed that these rhizobacteria may aid the grasses in fighting off (fungal) pathogens (Hol, Bezemer, & Biere, 2013; Latz et al., 2012, 2015). Alternatively, conditioning by different functional groups (as well as species) may lead to different endophyte communities in the plants of the feedback community, which in turn may also affect herbivores (Cripps, Edwards, & McKenzie, 2013; Zhang, Li, Nan, & Matthew, 2012). A lowered level of pathogens in grass soils as opposed to forb soils could result in different defence patterns in future plants growing on their soils, thus explaining our findings in this study. Unfortunately, interactions between the plant species used in this study and soil pathogens are

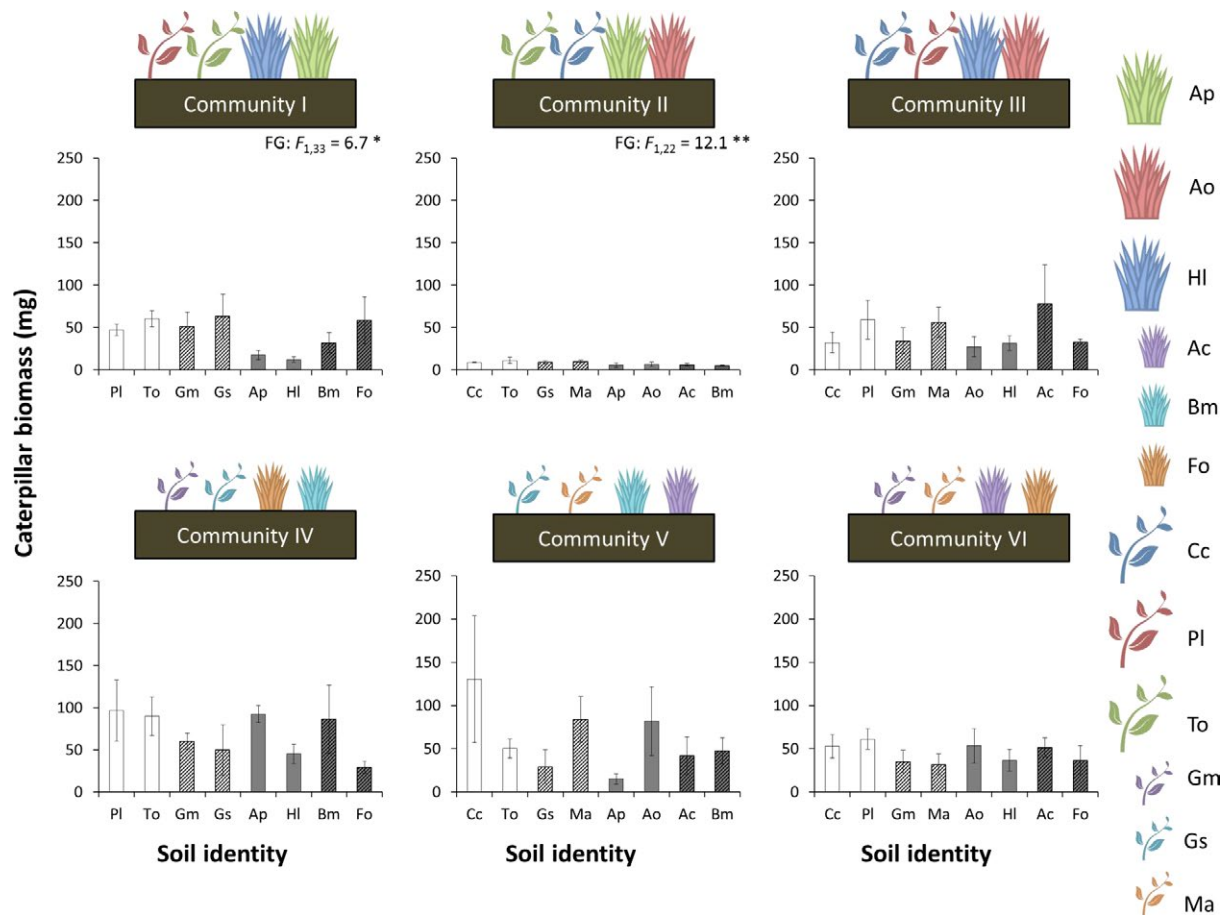


FIGURE 5 Effects of soil conditioning of species of grasses and forbs on *Mamestra brassicae* biomass after 24 days. White bars represent large-rooted forbs, striated white bars represent small-rooted forbs; grey bars represent large-rooted grasses, striated grey bars represent small-rooted grasses. Error bars represent SEs. The composition of each of the six communities is also presented above each panel. Ac = *Agrostis capillaris*, Ao = *Anthoxanthum odoratum*, Ap = *Alopecurus pratensis*, Bm = *Briza media*, Cc = *Crepis capillaris*, Fo = *Festuca ovina*, Gm = *Geranium molle*, Gs = *Gnaphalium sylvaticum*, Hl = *Holcus lanatus*, Ma = *Myosotis arvensis*, Pl = *Plantago lanceolata*, To = *Taraxacum officinale*. Statistics in the panels represent main effects of soil identity (S), root size (R) and soil functional group (FG) derived from one-way ANOVAs. Asterisks represent significance: * $p < .05$; ** $p < .01$; *** $p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

poorly understood, making it difficult to test such hypotheses and draw definite conclusions.

We found significant effects of functional group of the conditioning species on productivity (total above-ground biomass) in only one community. Furthermore, we found significant effects of soil conditioning species on productivity in three of six communities. The other three communities were remarkably stable in their efficiency to convert the available resources into biomass, regardless of the soil legacy they grew on. As we observed effects of soil conditioning on individual species in all communities, this exemplifies that in plant communities where a species is negatively affected by a soil legacy, other species may exploit the resources that this species would otherwise have utilized. It is difficult to pinpoint what exactly caused three communities to respond to soil legacies, whereas three others remained unchanged. Communities without a significant overall response to soil conditioning could have consisted of species that all did not respond to the changes in the soil. However, in this study, we find that in all communities, at least one plant species in the communities responded differently

to the different conditioned soils (see also Figure S1), regardless of whether the community as a whole was responsive. Furthermore, several studies have shown that conspecific PSF is generally negative and often is stronger when plants are grown in competition with other plants than when they are alone in a pot (Jing et al., 2015; Petermann, Fergus, Turnbull, & Schmid, 2008).

Because our design allowed us to test for differences in response to soils by communities differing in root productivity, we can thus conclude that the root productivity (C+/C-) of a community does not influence its response to soil legacies. Interestingly, the species composition of communities that were responsive to soils conditioned by different functional groups partly overlapped with the species composition of communities that were non-responsive. This suggests that there is not just one species that explains the observed functional group effect, as each species always occurred in two of three communities of that type. More likely, it is the competitive interplay between the four species in each community that determines the outcome of its response to soil legacies. How balances between different

plant species may influence the interactions between soil organisms and plants in a community, is a largely unexplored area that requires further study.

In the three communities where biomass distribution was affected by functional group of the conditioning species, we also found that herbivore behaviour was affected by the functional group to which the conditioning plant belonged. Studies have shown effects of functional group of conditioning species on insect performance (e.g. Kos et al., 2015), but, to our knowledge, this study is the first one to show altered feeding preferences in plant communities due to soil legacies and suggests that *M. brassicae* is able to detect soil legacy-mediated changes in host plant quality. Perhaps the herbivore switched between host plants in an attempt to escape host plants in which soil legacies had affected nutritional quality too negatively. Alternatively, herbivores may forage for those plants that are poorly defended above-ground, but these hypotheses require further study. This is especially relevant in the context of soil legacy studies, since legacy effects are often attributed to either pathogens (negative feedback) or growth promoters (positive feedback) (Van der Putten et al., 2013). If allocation of defences to local attack by root pathogens is traded off with defence against attack by above-ground herbivores, then interactions with soil pathogens, that is, negative soil legacies, may render above-ground plant parts less defended and more prone to attack by herbivores (Bezemer & van Dam, 2005).

Not only did the functional group of the conditioning plant species affect behavioural aspects of plant–herbivore interactions (as discussed above) but we also found a strong overall effect of functional group of the soil conditioning plant species on the performance (biomass) of the herbivore. That is, herbivores grew bigger on plant communities growing on soils that were conditioned by forbs than on soils that were conditioned by grasses. Conditioning by plants of different functional groups may result in differences in resource uptake and use, leading to a nutritional legacy effect, which may not always be evident in the biomass of a community. However, such effects could be reflected in individual plant nutritional values and in turn affect herbivore performance. However, biomass (both of the community as a whole and individual plants) was not limiting to the herbivore, we cannot exclude that a difference in nutritional value may have played a role, as this was not measured.

Although we found a strong effect of functional group of the conditioning species on the generalist chewing herbivore, we found no effect of soil identity or functional group on performance of a generalist grass-feeding aphid (*R. padi*). Recent work has demonstrated that performance of the specialist aphid *Aphis jacobaeae* on *Jacobaea vulgaris* was affected by the functional group of the plant species that conditioned the soil. Grass-conditioning showed positive effects on aphid colony size, whereas performance of the generalist *Brachycaudus cardui* was not affected by functional group (Kos et al., 2015). The aphid used in our study has a broad host range of monocots (Dixon, 1971). Likely, the degree of specialism plays an important role in an herbivore's capability to cope with variation in host plant quality (Ali & Agrawal, 2012; Lankau, 2007). It is important to note that different feeding guilds often show different responses to changes in plant

quality, due to differences in feeding strategies, as well as in the defence pathways invoked by plants (Awmack & Leather, 2002; Pangesti et al., 2013; Pineda, Zheng, van Loon, Pieterse, & Dicke, 2010). In plant cells, secondary (defence) chemicals and the hydrolytic enzymes that activate them are often stored in different intracellular compartments. Phloem feeders, using their stylets to penetrate individual cells during feeding, often leave these compartments largely intact. Leaf chewers damage cells and intracellular compartments and bring defence chemicals and hydrolytic enzymes into contact, leading to stronger defence responses (Gehring & Bennett, 2009; Koricheva, Gange, & Jones, 2009; Pangesti et al., 2013; Pineda et al., 2010). Therefore, possible changes in defence chemistry in response to soil legacy effects may affect different feeding guilds in different ways. However, to test this would require additional studies using multiple species from each feeding guild.

5 | CONCLUSIONS

Our study shows that 12 common grassland species created species-specific soil legacies, which, in the feedback phase, influenced the composition of the plant communities. There was no effect of root size of the conditioning plants on the response of plants or insects. Instead, the soil effects were partly explained by the functional group the plant species that conditioned the soil belonged to. Soil legacies also affected the feeding behaviour of a chewing herbivore. The chewing herbivore performed significantly better on communities growing on forb-conditioned soils than on grass-conditioned soils. To our knowledge, this is the first time that this has been shown in a community context. This finding may have implications in natural communities and it may explain why insects are often found on certain individuals of a host species in a particular area, but not on other individuals of the same species in the same area (or other areas). Future studies should focus on unravelling mechanisms that underlie these soil legacy effects, first of all, through more thorough analysis of the soil communities and interactions and directional changes therein under different conditioning scenarios. Secondly, there is a need for better understanding of processes (such as defence chemistry and gene expression) that may occur in response to shifts in microbial communities, within a wider range of plants. Other studies are needed that examine the broader generalities of these plant–soil insect interactions also in real communities in the field. Such soil legacy effects could then potentially be used to improve the abundance of beneficial or “target” insects in natural communities, or instead repel or deter those that are unwanted or causing problems, such as pests, for example, in agricultural systems (Pineda, Kaplan, & Bezemer, 2017).

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AUTHORS' CONTRIBUTIONS

R.H., A.B., J.A.H. and T.M.B. conceived the ideas and designed methodology; R.H. and M.S. collected the data; R.H. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.39f10> (Heinen, van der Sluijs, Biere, Harvey, & Martijn Bezemer, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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