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Plant traits shape soil legacy effects on individual plant–insect interactions

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Plant-mediated soil legacy effects can be important determinants of the performance of plants and their aboveground insect herbivores, but, soil legacy effects on plant–insect interactions have been tested for only a limited number of host plant species and soils. Here, we tested the performance of a polyphagous aboveground herbivore, caterpillars of the cabbage moth *Mamestra brassicae,* on twelve host plant species that were grown on a set of soils conditioned by each of these twelve species. We tested how growth rate (fast- or slow-growing) and functional type (grass or forb) of the plant species that conditioned the soil and of the responding host plant species growing in those soils affect the response of insect herbivores to conditioned soils. Our results show that plants and insect herbivores had lower biomass in soils that were conditioned by fast-growing forbs than in soils conditioned by slow-growing forbs. In soils conditioned by grasses, growth rate of the conditioning plant had the opposite effect, i.e. plants and herbivores had higher biomass in soils conditioned by fast-growing grasses, than in soils conditioned by slow-growing grasses. We show that the response of aboveground insects to soil legacy effects is strongly positively correlated with the response of the host plant species, indicating that plant vigour may explain these relationships. We provide evidence that soil communities can play an important role in shaping plant–insect interactions aboveground. Our results further emphasize the important and interactive role of the conditioning and the response plant in mediating soil–plant–insect interactions.

Keywords: grassland, insect herbivore, *Mamestra brassicae*, plant–herbivore interactions, plant–soil feedback, soil legacy effects

Introduction

Understanding what drives the performance of insect herbivores on their host plants has been an important area in the field of ecology. Many mechanistic explanations for variation in herbivore performance on different plants have been put forward, including individual plant vigour (Price 1991), plant tissue nutrient content (Awmack and Leather 2002, Wetzel et al. 2016), levels of abiotic stress in plants (White 1969, 1974), or levels of constitutive and inducible plant defences (Kessler and Baldwin 2002). Plants that grow more vigorously, may present a higher-quality food source to herbivores than less vigorous plants (Price 1991). However, in most cases herbivore

performance is determined by a combination of these factors, which makes understanding plant–insect relationships challenging (Agrawal and Fishbein 2006). A recurring problem is that patterns observed in plant–insect ecology are often plant- or herbivore-specific, which adds another layer of complexity.

As primary producers, plants interact with a wide array of organisms, ranging from micro-organisms to grazing mammals. Plant roots, shoots and floral parts often simultaneously interact with different organisms. Roots, being embedded in the soil, encounter soil microorganisms and soil invertebrates, whereas aboveground structures, such as leaves or flowers, interact with insect herbivores or pollinators. It has been shown that interactions with the plant in one plant part can influence interactions in other plant parts (Soler et al. 2005, 2007, 2013, Erb et al. 2011, Wang et al. 2014), which is regulated by complex phytochemical signaling pathways (Bezemer and van Dam 2005, Biere and Goverse 2016, Erb and Reymond 2019). For example, a vast body of work has revealed how individual soil taxa can influence the performance of aboveground foliar feeding herbivores, mediated by the shared host plant (reviewed by Koricheva et al. 2009, Pineda et al. 2010, Johnson et al. 2012, Wondafrash et al. 2013). However, soils are inhabited by a vast amount of different (micro) organisms, and how entire soil communities and the interactions within them can influence aboveground herbivore performance on different plant species is not well understood (Kostenko et al. 2012, Pineda et al. 2017, Heinen et al. 2018a, b).

Soil communities and plants are intimately linked (Van der Putten et al. 2013, Bardgett and Van der Putten 2014). Plants can steer or passively alter the soil communities around their roots through exudation of metabolites into the soil (Phillipot et al. 2013), and as a consequence, different plant species leave very different microbial legacies in the soil (Bezemer et al. 2006, Kos et al. 2015, Heinen et al. 2018b). These specific soil communities, in turn, can have differential effects on the biomass of plants that grow in the same soil, a process known as plant–soil feedback (Van der Putten et al. 2013). Recent studies have shown that such soil legacy effects also influence the performance of aboveground herbivores that feed on plants that grow in soils with different legacies (Kostenko et al. 2012, Kos et al. 2015, Heinen et al. 2018b). For instance, on ragwort *Jacobaea vulgaris*, the colony development of aphids highly depends on the microbial communities in the different soils that the host plant is growing in (Kos et al. 2015). Moreover, the performance of a polyphagous chewing herbivore is also strongly influenced by microbial soil legacy effects when feeding on ragwort, and these effects are in part explained by soil-mediated variation in plant secondary defence metabolites (Kostenko et al. 2012, Bezemer et al. 2013, Wang et al. 2019). Although it is clear that soil legacies can alter herbivory in plant communities (Heinen et al. 2018b), how soil legacy effects alter individual plant–insect interactions across a broader range of host plant species has been rarely studied.

Soil legacy effects are strongly influenced by plant traits. For instance, plants that have a higher growth rate, generally create more negative soil legacy effects on plant growth (i.e. plant–soil feedbacks) than those that have a lower growth rate (Lemmermeyer et al. 2015, Bergmann et al. 2016, Cortois et al. 2016). The resource availability hypothesis posits that there are tradeoffs between plant growth and plant defense (Coley et al. 1985, Herms and Matson 1992). As a result, plants with higher growth rates are expected to have weaker defenses and to accumulate more pathogens in the soil than plants that have a low growth rate, which can result in negative soil legacy effects (Van der Putten et al. 2013). Soil legacy effects on plants also differ between plant functional types (Kulmatiski et al. 2008). Grasses, for example, generally create more positive soil conditions for the growth of future plant species than forbs (Van de Voorde et al. 2011, Wubs et al. 2016, Ma et al. 2017). Moreover, several studies have shown that forb soils and grass soils leave legacy effects that have contrasting effects on feeding preference and performance of aboveground herbivores on plants that grow in these soils (Kos et al. 2015, Heinen et al. 2018b). For instance, *Mamestra brassicae* caterpillars that were reared on plant communities growing in soils that were previously conditioned by grass species, had a lower biomass than caterpillars reared on plant communities growing on forb soils, which is likely mediated by changes in plant chemistry (Kos et al. 2015, Heinen et al. 2018b, Zhu et al. 2018). Alternatively, microbial soil legacy effects may directly or indirectly alter caterpillar performance via effects on the herbivore microbiome (Hannula et al. 2019).

In a full-factorial greenhouse experiment we reared the polyphagous chewing caterpillars of the cabbage moth *Mamestra brassicae* (Lepidoptera: Noctuidae), on twelve common grassland host plant species that differed in growth rate (fast or slow) and plant functional type (grass or forb). Each host plant species was grown in soils that were previously conditioned by the same twelve plant species (conditioning plants) individually. We measured individual plant biomass, herbivore biomass as well as consumption of the host plants, to test the consistency of soil legacy effects on plant–herbivore interactions across a range of plant species.

We hypothesize that 1) plant species will cause different soil legacy effects on plants and insects, and these can be explained by the functional type and growth rate of the conditioning plant. Specifically, we expect fast-growing plant species to have a negative soil-mediated effect on other plants growing in the conditioned soil, and slow-growing plants to have a positive soil legacy effect on plant growth and we test whether the effects of growth rate are similar across conditioning grasses and forbs. We further hypothesize 2) that host plants of different functional types and with contrasting growth rates will respond differently to soil legacy effects. Lastly, we hypothesize that 3) species-specific soil legacies will affect plant performance and vigour and 4) that this affects insect performance. Specifically, we hypothesize that soils with negative legacy effects on plant vigour also exert negative effects on growth and consumption of herbivorous insects, as these plants may be of lower quality and show stronger induced cross-resistance caused by potential accumulation of negative microbes in the soil.

Material and methods

Plants

Twelve plant species were selected based on functional type (six grasses and six forbs). Within each functional group, three of the species had high growth rates while the other three were slow growers (Table 1). Briefly, to characterize the growth rate of a broad selection of plant species and select the 12 species used in our study, we grew thirty replicates of 24 common grassland plant species (12 grasses, 12 forbs) in pots with field soil for ten weeks. Each week, three replicates of each species were harvested (above- and belowground biomass), dried and weighed. Based on these data, growth curves were fitted through the root and shoot biomass data according to Paine et al. (2012). Cumulative root and total biomass were derived from these models. Cumulative biomass reflects the sum of the biomass gained by a plant on each day, across all days of the growth period, which is a proxy for growth rate. The three highest and lowest ranking species within each functional type were selected (Table 1). Supplementary material Appendix 1 Fig. A2a–b shows root and shoot data from the current study and confirms that the fast and slow growing plants differed consistently (indicated by significant main effects of growth rate on shoot and root biomass; Supplementary material Appendix 1 Fig. A2a–b, Table A1).

Seeds of all species were surface-sterilized using 2% 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). After germination, the seedlings were stored at 4°C under the same light regime, for later use in experiments.

Insects

Eggs of the cabbage moth *Mamestra brassicae* (Lepidoptera: Noctuidae) were obtained from the Dept of Entomology at Wageningen Univ. The cabbage moth had been reared for many years on Brussels sprout *Brassica oleracea* var. *gemmifera* cv. Cyrus. The larvae were originally collected from cabbage fields near the university. Caterpillars of the cabbage moth are highly polyphagous (Rojas et al. 2000) and have been shown to feed readily on the host plant species used in this study (Heinen et al. 2018a).

Soil

Field soil was collected from a restoration grassland area 'De Mossel'. To minimize damage to the natural area, live soil was taken from the top 10 cm, which is the well-rooted layer containing most of the rhizosphere biota. Soil for the sterilization treatment, was collected from the 5–20 cm layer just below the dense root layer and sterilized by γ-irradiation. The soil texture of both layers was identical. Each pot received equal mixtures of live:sterilized soil. Both soil types were first sieved to remove roots, stones and most macro-invertebrates (sieve mesh Ø 1.0 cm).

Soil conditioning phase

Sixty square 1-l pots (11 × 11 cm) were filled with 1050 g live field soil, for each plant species (12 × 60 = 720 pots total). One individual seedling was grown for 10 weeks in each pot in a glasshouse. The first four days seedlings were covered with shade cloth to aid in their establishment. Egg deposition by fungus gnats was prevented by adding a layer of coarse sand to the surface of the pots. Germinating seeds originating from the seedbank were weeded daily. Plants were watered three times per week. After 10 weeks, the plants and their roots were removed from the soil and the soil was used in the feedback phase.

Feedback phase

Soil from the sixty individually conditioned pots per conditioning plant species was divided over five separate soil replicates. Each soil replicate contained all soil from twelve independently conditioned pots. The soil from these twelve

Table 1. Overview of the species used in the experiment and their functional type (grass or forb) and growth rate (fast or slow-growing). Selection of species was based on cumulative total biomass and cumulative root biomass which was measured over ten weeks. Plant growth was measured in soil from the same area, in the same greenhouse conditions as the current study. Cumulative growth parameters presented here were derived from growth curve models that were fit through the growth data.

Plant species	Label	Functional type	Growth rate	Cumulative total biomass (g)	Cumulative root biomass (g)
Crepis capillaris	CC	forb	fFast	125.53	71.26
Plantago lanceolata	PL	forb	fast	120.75	60.89
Taraxacum officinale	TO	forb	fast	115.62	84.26
Geranium molle	GM	forb	slow	101.57	39.59
Gnaphalium sylvaticum	GS	forb	slow	58.58	19.76
Myosotis arvensis	MA	forb	slow	82.60	35.53
Anthoxanthum odoratum	AO	grass	fast	96.54	49.78
Alopecurus pratensis	AP	grass	fast	139.84	71.43
Holcus lanatus	HL	grass	fast	122.96	71.67
Agrostis capillaris	AC	grass	slow	62.55	29.87
Briza media	BM	grass	slow	57.59	29.26
Festuca ovina	FO	grass	slow	60.64	27.18

pots was homogenized, and then mixed with sterilized field soil (one volume conditioned soil to two volumes sterilized soil) to obtain a sufficient amount of soil and to minimize abiotic differences among the conditioned soils. This resulted in 60 mixed conditioned soils (5 replicates × 12 conditioning species). Soils were then divided into two identical sets for the herbivory treatment (one herbivore treatment and one no-herbivore control). Thus, each of the 60 mixed conditioned soils was divided over two sets of twelve pots (9 × 9 cm, 650 g soil). Each pot within each set received an individual seedling from one of the twelve host plant species (12 conditioning species × 12 host plant species × 2 herbivore treatments × 5 replicates = 1440 pots, Supplementary material Appendix 1 Fig. A1). Plants were divided over four greenhouse tables. All host plants of the same species were placed in blocks together. Within these 'host plant blocks', pots with the different soil treatments and herbivore treatments were randomly allocated at the start of the feedback phase. Egg deposition by fungus gnats was prevented by adding a layer of coarse sand to the surface of the pots. Germinating seeds originating from the seedbank were weeded daily. Plants were watered three times per week.

After four weeks of growth, all 1440 pots were caged with a plastic tube made of transparent plastic with insect mesh fitted on top (9 cm diameter, 30 cm height). In each herbivore treatment cage, a freshly hatched cabbage moth caterpillar was introduced. After seven days of feeding, the caterpillars were collected and weighed to measure their performance. Moreover, for each plant the total area of leaf consumption by caterpillars was assessed using a reference area of 5 × 5 mm. For each plant we counted the number of times the reference area fitted within the consumed area on the plant (as in Heinen et al. 2018b). All plants were then clipped and fresh shoot biomass was recorded as shoot parts were used for metabolomic studies that are beyond the scope of this study. Roots from each pot were washed and belowground biomass was oven-dried at 70°C and weighed.

Data analysis

In this experiment, we measured herbivore and plant responses to soils by four response variables; responding host plant shoot biomass and root biomass, and caterpillar biomass and leaf consumption by caterpillars. Plant and insect responses were analysed in two separate ways: via overall analyses across plant species and by host species species-specific analyses.

Standardization of responses to soil conditioning of plants and insects

Within each responding host plant species, we determined standardized responses to soil (i.e. the soil legacy effect) for each individual sample per host plant species.

Standardization was performed separately for herbivore and no-herbivore (control) treatments and allowed us to compare the soil-induced variance across responding host plant species. As an example, using shoot biomass, we calculated standardized soil legacy effects for each species, by subtracting each observed value for shoot biomass of an individual of a species by the mean shoot biomass for that species and divided by the standard deviation of the shoot biomass for that species. This calculated standardized response tells us whether the shoot biomass of an individual plant of a species responds positively or negatively to a soil, relative to the overall mean across all soils of that species in units of standard deviation, effectively reflecting the soil legacy effect. We calculated this effect for leaf consumption by caterpillars, caterpillar biomass, and for shoot and root biomass.

Standardization more clearly visualizes the effects of conditioning plant functional type and growth rate on the response variables across responding host plant species (as standardization takes out the responding host plant main effects). Although standardization per responding host plant species is a good way to visualize the effects of conditioning plants, the effects of responding host plants cannot be visualized using standardized data. Therefore, we also used unstandardized data for the full analysis. We chose this approach for two main reasons. The first one is transparency. Showing both analyses confirms the similarity in statistical output between unstandardized and standardized data, except for the responding host plant main effects, which have been standardized in the latter analyses and hence have zero variance. Furthermore, the unstandardized data give important insights into the main effects of responding host plants. For plant data, this confirmed that our selection based on growth rate was valid in our study. For the herbivore data, this provides insights in caterpillar behaviour on different responding host plants (Supplementary material Appendix 1 Fig. A2, Table A1).

Effects of growth rate and functional type of conditioning and responding host plant species on plant–insect interactions

In the overall analysis, we tested whether functional type and growth rate of the conditioning plant species (hypothesis 1) and responding host plant species (hypothesis 2) affect standardized shoot and root biomass and standardized caterpillar biomass and leaf consumption. For these analyses we used shoot and root biomass of the control plants, so that soil legacy effects could be tested independent of herbivory. For the analyses of standardized caterpillar biomass and standardized leaf consumption, we used the herbivore data from the herbivore-treated plants. We tested the effects on all parameters using linear mixed models with 'Conditioning plant functional type' (C_f, grass/forb), 'Conditioning plant growth rate' (C_g, fast/slow), 'Responding host plant functional type' (H_f, grass/forb), 'Responding host plant growth rate' (H_g, fast/slow) and all interactions as fixed effects. 'Conditioning plant species' and 'Responding host plant species' were included as random intercepts. This way the model considers the species as the real replicates within the levels of the fixed factors.

The same model as discussed above for standardized data was also performed on all response variables on unstandardized data, which are presented as background information in the Supplementary material Appendix 1 Table A1, Fig. A2).

Soil legacy effects on plant–insect interactions across responding host plant species

The conditioning plant species-specific soil legacy effects (averaged across all responding host plant species; hypothesis 3) were tested on standardized shoot and root biomass as well as for standardized caterpillar biomass and leaf consumption. For plant data, this was done separately for both the control and herbivore treated plants. Averaged soil legacy effects were tested using a one way-ANOVA with 'Conditioning plant species' as factor with twelve conditioning species as factor levels.

Relationships between soil legacy effects on plants and insect performance

We also tested whether soil legacy effects on plant vigour can explain soil legacy effects on insect herbivores (hypothesis 4). We used the averaged soil legacy effects described above to test relationships between averaged soil legacy effects on plant shoot biomass, and leaf consumption by the associated caterpillar, or caterpillar biomass, using linear regressions. Soil legacy effects were calculated per individual sample by subtracting each observed value for the parameter of an individual of a species by the mean value of the parameter for that species and divided by the standard deviation of the parameter for that species. The averaged soil legacy effects were obtained as the average soil legacy effect across all responding host plant species and replicates.

All analyses were performed in R Studio ver. 1.1.419 (RStudio, Inc.) using R ver. 3.3.1 (<www.r-project.org>). General linear mixed models were performed using the R package 'nlme' (Pinheiro et al. 2018). Post hoc Tukey tests were performed using the R package 'emmeans' (Lenth et al. 2019).

Results

Effects of growth rate and functional type of conditioning species and responding host plant species on plant–insect interactions

Standardized shoot and root biomass of the responding host plants was affected by conditioning plant functional type and growth rate. On average, standardized shoot and root biomass was higher in soils conditioned by grasses and slow-growing plants, than in soils conditioned by forbs or fast-growing plants, respectively (significant C_f and C_g main effects, Table 2). However, various interactions were observed. Firstly, standardized shoot and root biomass, on average, was higher when plants were grown in soils conditioned by slow-growing forbs, than when they were grown in soils conditioned by fast-growing forbs, whereas in soils conditioned by grasses, the effect of growth rate was weaker, but opposite (Fig. 1a (shoot) and 1b (root) significant $C_f \times C_g$ interactions, Table 2). The interactive effects of conditioning plant functional type and growth rate on standardized shoot biomass differed between forbs and grasses (significant $H_f \times C_g \times C_f$ interaction, Table 2). Specifically, the $C_f \times C_g$ interaction pattern was only present in responding forb hosts. Grasses, generally showed weaker responses to soil, but had a higher standardized shoot biomass in soils of slow-growing plants than in soils of fast-growing plants (Fig. 1a). Lastly, we observed that standardized root biomass showed a very similar response pattern to that of standardized shoot biomass (Fig. 1b). However, for standardized root biomass only the two-way interaction between conditioning plant and responding host plant functional types was significant (Table 2).

Standardized caterpillar biomass was higher on plants that were grown in soils conditioned by slow-growing forbs, than on plants grown in soils conditioned by fast-growing forbs, whereas for soils conditioned by grasses, the effect of growth rate was opposite, i.e. leaf consumption tended to be lower on plants growing in soils conditioned by fast-growing than in soils conditioned by slow-growing grasses (significant $C_f \times C_g$ interaction, Table 2, Fig. 2a).

Standardized leaf consumption responded to the conditioning plant treatments in a pattern that was similar to the one observed for standardized caterpillar biomass (significant $C_f \times C_g$ interaction, Table 2, Fig. 2b).

Responding host plant growth rate and functional type also affected caterpillar biomass. This was analysed on unstandardized data (as standardization takes out the responding host plant main effects). Unstandardized levels of caterpillar biomass differed between responding host plant functional types, with caterpillar biomass, on average, being slightly higher on responding grass hosts than on responding forb hosts (Supplementary material Appendix 1 Fig. A2c, Table A1). Unstandardized levels of caterpillar biomass also depended on responding host plant growth rate, and biomass was higher on slow-growing responding host plants than on fast-growing responding host plants (Supplementary material Appendix 1 Fig. A2c, Table A1). Unstandardized levels of leaf consumption across responding host plant species did not differ significantly between responding host plant categories (Supplementary material Appendix 1 Fig. A2d, Table A1).

Conditioning plant-specific soil legacy effects on plant–insect interactions

Conditioning plants significantly differed in their soil legacy effects on the shoot biomass across twelve responding host plant species, both in the herbivore treatment and in the control plants (control: $F_{11,701} = 9.69$, $p < 0.001$, Fig. 3a; herbivore: $F_{11,690} = 9.1$; $p < 0.001$, Supplementary material Appendix 1 Fig. A3a). The control plants showed very similar responses as the herbivore treated plants, the main differences being that *Gnaphalium sylvaticum* soils had a less negative effect and *Holcus lanatus* soils had a less positive effect in control than in herbivore-treated plants (Fig. 3a, Supplementary material Appendix 1 Fig. A3a). In the herbivore treatment plants, soils conditioned by *Plantago lanceolata*, *G. sylvaticum* and *Taraxacum officinale* caused plants to have a lower than average shoot biomass than other conditioning plants, whereas in soils conditioned by *H. lanatus* responding host plants tended to have a higher than average shoot biomass (Supplementary material Appendix 1 Fig. A3a). Root biomass in both treatments showed a very similar response to

Table 2. Statistical output. A general linear mixed model testing the effects of 'Conditioning plant functional type' (grass or forb), 'Conditioning plant growth rate' (fast or slow growth), 'Host plant functional type' (grass or forb), 'Host plant growth rate' (fast or slow growth) and all interactions on standardized values of shoot and root biomass, caterpillar biomass, and leaf consumption by caterpillars. Values were standardized by subtracting each observed value for the response variable of an individual of a species by the mean of the response variable for that species and divided by the standard deviation of the response variable for that species. Linear mixed models were performed on the full dataset, including all plant species (and conditioning and host plant species included as random effects). Presented are degrees of freedom, F-statistics and p-values. Significant effects ($p < 0.05$) are highlighted in bold. For transparency, the analyses were also performed on unstandardized values. This is presented in Supplementary material Appendix 1 Table A1.

	Shoot biomass (control)			Root biomass (control)			Shoot biomass (herbivore)			Root biomass (herbivore)			Caterpillar biomass			Leaf consumption		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Host plant functional type (Hf)	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0
Host plant growth rate (Hg)	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0	1,8	0.0	1.0
Conditioning plant functional type (Cf)	1,689	15.24	<0.001	1,690	11.0	0.001	1,689	30.32	<0.001	**1,688**	**22.12**	**<0.001**	1,619	0.24	0.624	1,630	0.12	0.729
Conditioning plant growth rate (Cg)	**1,689**	**17.0**	**<0.001**	1,690	2.07	0.151	**1,689**	**9.82**	**0.001**	**1,688**	**4.45**	**0.035**	**1,619**	**4.25**	**0.040**	1,630	1.58	0.209
Hf×Hg	1,8	0.00	0.991	1,8	0.0	1.0	1,8	0.00	0.997	1,8	0.00	0.995	1,8	0.0	1.0	1,8	0.00	0.990
Cf×Hf	**1,689**	**6.51**	**0.011**	**1,690**	**11.70**	**<0.001**	**1,689**	**14.55**	**<0.001**	**1,688**	**10.73**	**0.001**	1,619	0.24	0.624	1,630	1.02	0.312
Cf×Hg	1,689	0.03	0.852	1,690	0.00	0.948	1,689	0.40	0.526	1,688	0.03	0.871	1,619	0.03	0.866	1,630	0.01	0.905
Cg×Hf	1,689	2.18	0.140	1,690	1.19	0.276	**1,689**	**4.28**	**0.039**	**1,688**	**8.40**	**0.004**	1,619	0.49	0.486	1,630	0.62	0.430
Cg×Hg	1,689	1.13	0.288	1,690	0.02	0.902	1,689	1.78	0.182	1,688	0.00	0.976	1,619	0.33	0.568	1,630	0.17	0.678
Cf×Cg	**1,689**	**19.43**	**<0.001**	**1,690**	**23.26**	**<0.001**	**1,689**	**21.71**	**<0.001**	**1,688**	**24.60**	**<0.001**	**1,619**	**6.70**	**0.010**	**1,630**	**5.22**	**0.023**
Cf×Hf×Hg	1,689	0.01	0.908	1,690	2.09	0.149	1,689	3.04	0.082	1,688	0.84	0.360	1,619	1.33	0.249	1,630	0.02	0.888
Cg×Hf×Hg	1,689	2.02	0.155	1,690	0.00	0.980	1,689	1.85	0.174	1,688	2.87	0.091	1,619	1.63	0.202	1,630	2.77	0.097
Cf×Cg×Hf	**1,689**	**8.61**	**0.004**	1,690	2.09	0.149	1,689	0.14	0.709	1,688	0.38	0.537	1,619	2.72	0.100	1,630	0.06	0.804
Cf×Cg×Hg	1,689	0.02	0.895	1,690	0.33	0.567	1,689	0.01	0.916	1,688	0.06	0.805	1,619	0.27	0.602	1,630	0.04	0.852
Cf×Cg×Hf×Hg	1,689	0.18	0.671	1,690	0.06	0.812	1,689	0.06	0.808	**1,688**	**4.25**	**0.040**	1,619	0.03	0.862	1,630	0.66	0.416

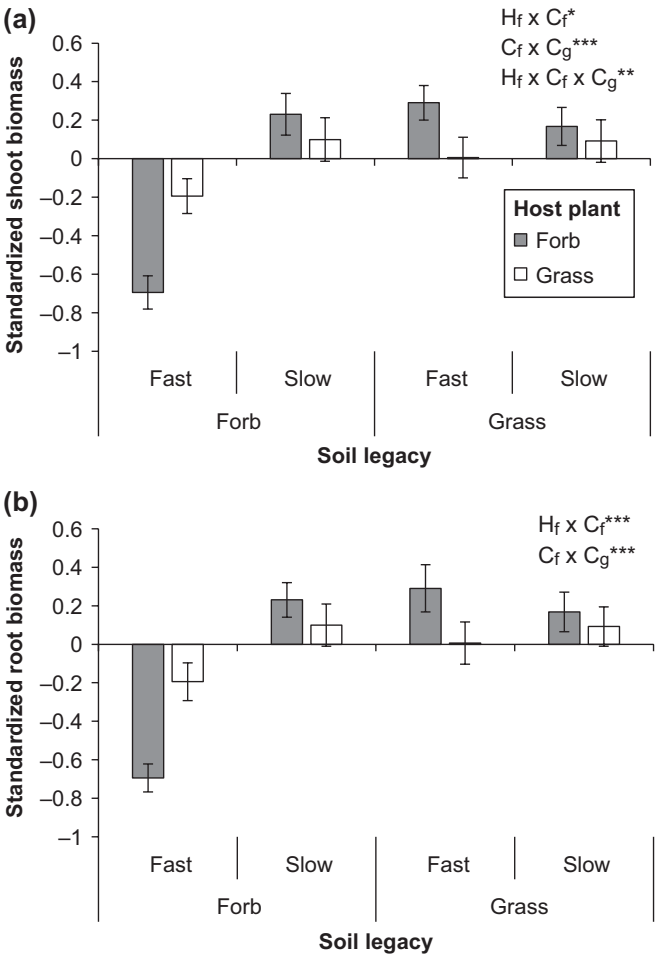

Figure 1. The effects of growth rate (C_g) and functional type (C_f) of the conditioning plants and growth rate (H_g) and functional type (H_f) of the host plants on standardized host plant (a) shoot and (b) root biomass of control plants (without herbivores). Only significant effects were plotted for clarity. The full model is presented in Supplementary material Appendix 1 Fig. A2a (shoot) and A2b (root). Error bars represent standard errors, which were calculated on values that were averaged across five replicates (12 × 12 species = 144 combinations), leading to n = 36 per bar. Asterisks represent significant results. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Statistical output of the full linear mixed model is presented in Table 2.

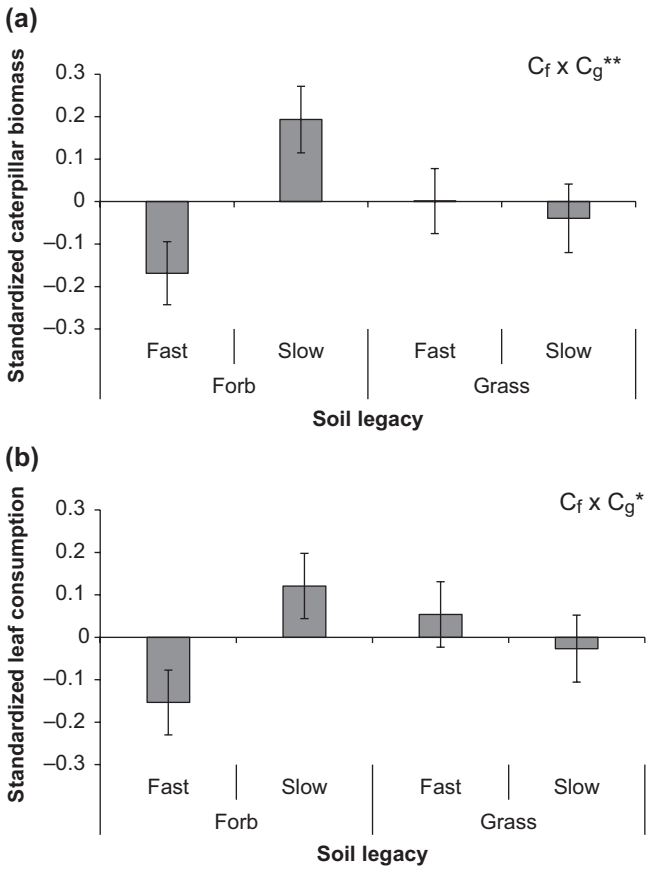

Figure 2. The effects of growth rate (C_g) and functional type (C_f) of the conditioning plants and growth rate (H_g) and functional type (H_f) of the host plants on (a) standardized caterpillar biomass, and (b) standardized leaf consumption by caterpillars. The four categories on the x-axis represent soil legacy effects of the four conditioning plant categories, consisting of combinations of fast- and slow-growing forbs and grasses. Error bars represent standard errors, which were calculated on values that were averaged across five replicates (12 × 12 species = 144 combinations), leading to n = 36 per bar. Asterisks represent significant results. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Statistical output of the full linear mixed model is presented in Table 2.

shoot biomass (Fig. 3b, Supplementary material Appendix 1 Fig. A3b).

Conditioning plants significantly differed in their soil legacy effects on the biomass of caterpillars feeding on the twelve different responding host plant species ($F_{11,631} = 2.03$; $p = 0.023$, Fig. 4a). Soils of *P. lanceolata*, *T. officinale* and *Festuca ovina* tended to reduce caterpillar biomass more than average across responding host plant species, whereas soils of *Alopecurus pratensis*, *Geranium molle* and *Myosotis arvensis* tended to reduce caterpillar biomass less than average across responding host plant species, although none of the comparisons between individual conditioning plant species in their effect on caterpillar biomass was significant in post hoc tests (Fig. 4a).

Conditioning plant species did not significantly differ in their soil legacy effects on leaf consumption by caterpillars on the twelve responding host plant species ($F_{11,642} = 1.42$; $p = 0.158$, Fig. 4b).

Relationships between soil legacy effects on plants and insect performance

There was a strong positive correlation between the average effect of a conditioning plant species, via the soil, on the average standardized shoot biomass of all responding plants and the average effect of that same conditioning plant species, via the soil, on the average standardized biomass of caterpillars and standardized leaf consumption on all responding host plants (caterpillar biomass: $R^2 = 0.63$; $F_{1,10} = 16.73$; $p = 0.002$; Fig. 5a, leaf consumption: $R^2 = 0.38$; $F_{1,10} = 6.14$; $p = 0.033$; Fig. 5b). Finally, the average soil-mediated effects

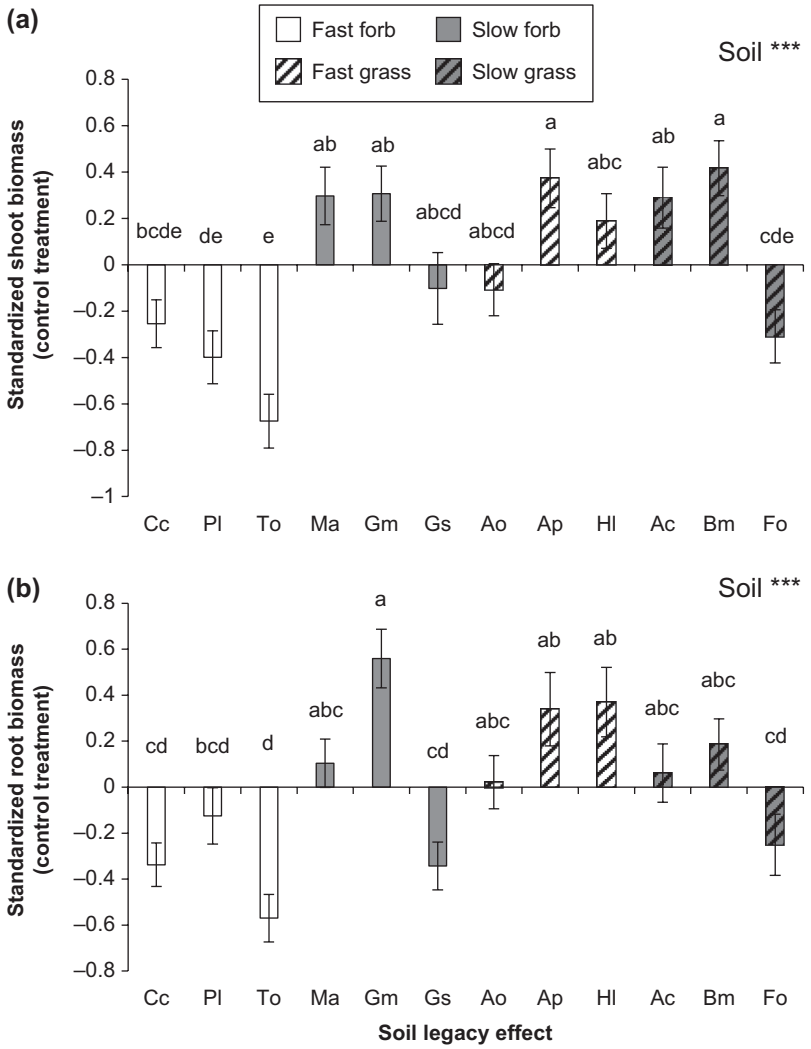

Figure 3. Averaged soil legacy effects of conditioning plants on (a) standardized shoot biomass of control plants, and (b) standardized root biomass of the control plants. Soil legacy effects were calculated by subtracting each observed value for the parameter of an individual of a species by the mean value of the parameter for that species and divided by the standard deviation of the parameter for that species. The averaged soil legacy effects were obtained as the average soil legacy effect across all responding host plant species. Positive values represent positive soil effects and negative values represent negative effects, standardized per host plant species. Presented are the averaged soil effects of a conditioning plant species on twelve plant species or their associated herbivore. Open bars represent forbs, striated bars represent grasses. White bars represent fast-growing species and grey bars represent slow-growing species. Error bars represent standard errors (calculated across 12 host plant species with five replicates, n = 60 per bar). Asterisks represent significant results. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Different letters above the bars indicate significantly different means, as tested with post hoc Tukey tests. Abbreviations are as follows for fast-growing forbs Cc = *Crepis capillaris*, Pl = *Plantago lanceolata*, To = *Taraxacum officinale*, for slow-growing forbs Gm = *Geranium molle*, Gs = *Gnaphalium sylvaticum*, Ma = *Myosotis arvensis*, for fast-growing grasses Ao = *Anthoxanthum odoratum*, Ap = *Alopecurus pratensis*, Hl = *Holcus lanatus*, and for slow-growing grasses Ac = *Agrostis capillaris*, Bm = *Briza media* and Fo = *Festuca ovina*.

of a conditioning plant species on standardized caterpillar biomass and on standardized leaf consumption by caterpillars were strongly positively correlated ($R^2 = 0.70$; $F_{1,10} = 23.25$; $p < 0.001$, Fig. 5c).

Discussion

The importance of soil legacy effects on plants for associated aboveground herbivores has recently received increasing attention (Wurst and Ohgushi 2015, De la Peña et al. 2016, Hu et al. 2018, Kaplan et al. 2018, Lu et al. 2018). In this study, we tested plant-mediated soil legacy effects on insect and plant performance across a range of plant species. Our study with twelve responding host plant species growing in twelve conditioned soils, with or without herbivores, shows that there are strong patterns in how plant-mediated soil legacies affect responding host plants growing later in that soil, as well as consumption by and biomass of a polyphagous insect herbivore feeding on these responding host plants. We show

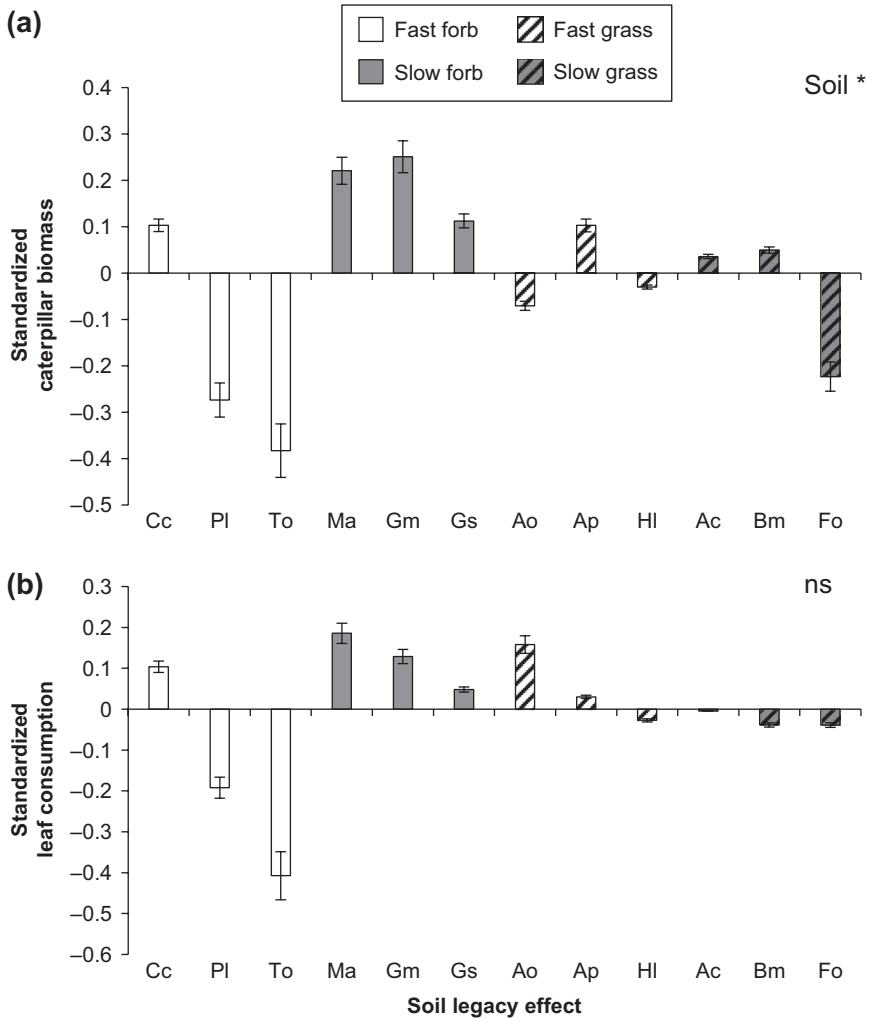

Figure 4. Averaged soil legacy effects of conditioning plants on (a) standardized caterpillar biomass, and (b) standardized leaf consumption. Individual soil legacy effects were calculated for each sample. Soil legacy effects were calculated by subtracting each observed value for the parameter of an individual of a species by the mean value of the parameter for that species and divided by the standard deviation of the parameter for that species. The averaged soil legacy effects were obtained as the average soil legacy effect across all responding host plant species. Positive values represent positive soil effects and negative values represent negative effects, standardized per host plant species. Presented are the averaged soil effects of a conditioning plant species on twelve plant species or their associated herbivore. Open bars represent forbs, striated bars represent grasses. White bars represent fast-growing species and grey bars represent slow-growing species. Asterisks represent significant results. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Differences in means were tested with post hoc Tukey tests, but were not significant. Abbreviations are as follows for fast-growing forbs Cc = *Crepis capillaris*, Pl = *Plantago lanceolata*, To = *Taraxacum officinale*, for slow-growing forbs Gm = *Geranium molle*, Gs = *Gnaphalium sylvaticum*, Ma = *Myosotis arvensis*, for fast-growing grasses Ao = *Anthoxanthum odoratum*, Ap = *Alopecurus pratensis*, Hl = *Holcus lanatus*, and for slow-growing grasses Ac = *Agrostis capillaris*, Bm = *Briza media* and Fo = *Festuca ovina*.

that soil legacy effects are to a large extent determined by an interaction between the functional group and growth rate of the conditioning plant species, as well as the responding host plant species. In addition, we find that there is a positive correlation between plants and insects in their overall response to conditioned soils.

In soils conditioned by forbs, we observed that fast-growing plants created soil legacies that negatively affected later growing plants, whereas slow-growing plants created soils that had a more positive effect. This finding is in line with previous studies that observed that fast-growing plants create more negative soil legacy effects than slow-growing plants (Lemmermeyer et al. 2015, Bergmann et al. 2016, Cortois et al. 2016) possibly due to the accumulation of pathogens in the soil. However, this finding is in contrast with our previous study on the same plant species, where we observed no effects of growth rate of conditioning plant species on responding plants in mixed communities, or in soil bacterial and fungal community composition (Heinen et al. 2018a). Surprisingly, we found that the effects of growth

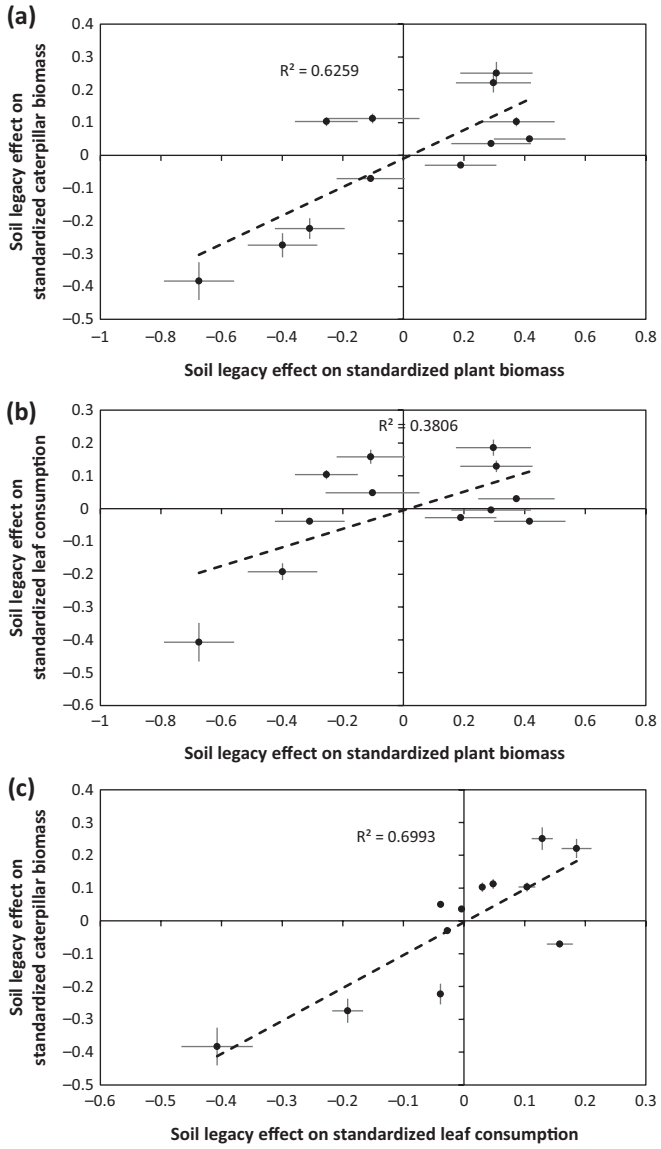

Figure 5. Relationships between (a) the average soil legacy effect on standardized shoot biomass of all host plants and the average soil legacy effect on standardized caterpillar biomass, (b) the average soil legacy effect on standardized shoot biomass of all host plants and the average soil legacy effect on standardized leaf consumption, and (c) the average soil legacy effect on standardized caterpillar biomass and the average soil legacy effect on standardized leaf consumption by caterpillars on host plants. Soil legacy effects were calculated by subtracting each observed value for the parameter of an individual of a species by the mean value of the parameter for that species and divided by the standard deviation of the parameter for that species. The averaged soil legacy effects were obtained as the average soil legacy effect across all responding host plant species.

rate of conditioning species were different in soils that were conditioned by grasses. On grass soils, overall, plants tend to accumulate higher than average biomass, and biomass accumulation was higher on fast grass soils than on slow grass soils. Grasses have been shown to have positive effects on other plant species (Petermann et al. 2008, De Kroon et al. 2012, Wubs et al. 2016), although they generally have very negative effects on their own species (Kulmatiski et al. 2008). Why growth rates have opposite soil legacy effects in grasses than in forbs is hard to explain. Grasses have been shown to accumulate bacteria that produce antifungal compounds (Latz et al. 2012, 2015) and we speculate that fast growing grasses, with larger root systems, may accumulate more bacteria and that this leads to more positive effects for the next plant.

Importantly, in our study the effects observed in the responding host plants were mostly driven by those that are forbs, which responded quite strongly to both growth rate and functional types of conditioning plants, whereas responding host plants that are grasses generally showed a much weaker response. This is also consistent with earlier observations in our group using the same model species and soils (Heinen et al. 2018a, Zhu et al. 2018). It indicates that plant traits, such as growth rate, can be important drivers of soil legacy effects, but that we should be careful with extrapolating soil effects observed for one functional type of responding plants to responding plants from another functional type.

For insect biomass and leaf consumption, we also find that responses to conditioned soils are dependent on functional type and growth rate of the conditioning plant species. Specifically, on plants growing in soils conditioned by fast-growing forbs insect biomass and leaf consumption are lower than on plants growing in soils conditioned by slow-growing forbs. In soils conditioned by grasses, insect growth rates showed a weaker, but opposite response. Interestingly, the effects of soil conditioning on insect biomass do not depend on the responding host plant, as is indicated by the absence of any interactive effects between responding host and conditioning plants on insect biomass. This is an important finding, as it suggests that soil legacy effects on insects are rather consistent across responding host plant categories. Some previous studies have also shown that the functional group to which the conditioning plant belongs can be important for insect performance (Kos et al. 2015, Heinen et al. 2018b). However, in a previous study with mixed communities of response plants rather than individual plants but with the same set of plant species and the same insect herbivore, interactions between conditioning plant functional type and growth rate were not observed (Heinen et al. 2018b), suggesting that soil legacy effects may affect insects on individually grown plants differently than those that feed on plant communities (e.g. due to selective feeding from different plant species).

Generally, plants and associated insects followed similar patterns in their response to soils, and soil effects on plant–insect interactions could thus be predicted by the soil effects on responding host plants (i.e. plant–soil feedback). Indeed, we did find a positive relationship between the soil effect on individual plants and the effect on their associated herbivore in this study. If plants grew more vigorously in a specific soil, the insects feeding on plants growing in that specific soil also

showed a positive growth response. These findings are in line with the vigour hypothesis (Price 1991). Obviously, there may be other aspects than plant vigour alone that may explain our findings. Negative soil legacy effects are often hypothesized to be due to accumulation of pathogens. Pathogens can negatively affect plant biomass (Berendsen et al. 2012), but may also cause cross-resistance, by interfering with phytohormonal defence pathways (Heil and Bostock 2002, Zhu et al. 2018). Soil pathogens can activate plant defences belowground, which can lead to elevated plant defences aboveground (Bezemer and Van Dam 2005, Biere and Goverse 2016). It has also been shown that soil microbiomes can alter plant secondary chemistry (Kostenko et al. 2012, Badri et al. 2013, Zhu et al. 2018, Ristok et al. 2019, Wang et al. 2019). Moreover, various plant-associated organisms are known to invoke resistance to aboveground herbivores, via priming of defences or inducing systemic resistance (Pieterse et al. 1998, Pozo and Azcon-Aguilar 2007). Hence, a likely explanation for the observed soil legacy effects on insect herbivores is that soils affected plant chemistry and that these changes may have affected insect feeding behaviour and performance (Zhu et al. 2018). The shoot parts of the plants harvested within current study have been used for metabolomic analysis. Briefly, these analyses suggest that soils strongly influence the plant metabolome and that secondary metabolism, but also many primary metabolites involved in plant structural processes including defence, can be altered by soil legacies (Huberty et al. unpubl.).

It remains difficult to explain mechanistically in what ways drivers (i.e. soil conditioning by plants that differ in traits) differ in how they condition the soil. Soil legacy effects reflect the effects of previous plant growth in soil biota and abiotic soil parameters. Each plant species interacts with different organisms in the soil, exuding different metabolites and thus creating different conditions (Phillipot et al. 2013). As such, each species leaves a distinct biotic pattern in the soil. We have previously reported that the composition of soil bacteria and fungi was strongly affected by conditioning plant species, as well as the functional type that they belong to, for the same set of plant species as used here, grown under very similar conditions and in similar soils (Heinen et al. 2018b). Thus, we have a broad idea of what microorganisms are present in the soil. However, for a large part, we do not have species names or the functional roles for many of the operational taxonomic units. Understanding the role of thousands of individual species of soil microorganisms that collectively shape plant–insect interactions is an immense challenge and requires further attention in ecology. As our understanding of functions of belowground organisms is rapidly expanding with advancement of high throughput sequencing technologies, the 'black box' of soil will gradually open.

There is an abundance of ecological theories on the role of individual soil biota in mediating various aboveground plant–insect interactions (reviewed by Bezemer and Van Dam 2005, Koricheva et al. 2009, Pineda et al. 2010, 2017, Johnson et al. 2012, Wondafrash et al. 2013, Heinen et al. 2018a). However, a common theme in these reviews is the difficulty of testing the role of individual soil organisms in natural (soil) communities in shaping plant–insect interactions. Future studies should take selective approaches to create different soil communities with different functions, for instance through sieving approaches (Johnson et al. 2001, 2002, Wagg et al. 2011, 2014, Wang et al. 2019), or via assembly of simplified artificial communities (Bai et al. 2015). When the presence of mutualists, pathogens or decomposers (Van der Putten et al. 2016), as well as their relative abundance, can be experimentally manipulated, this will allow us to empirically test standing hypotheses in more natural communities on a range of plant and insect species.

Lastly, in our study, insect biomass was not only affected by the functional group and growth rate of the plant species that conditioned the soils on which their host plants were growing, but it was also strongly affected by the functional group and growth rate of the responding host plants themselves. This is hardly surprising, as plant traits usually have a large impact on caterpillar growth and feeding. However, despite the fact that the biomass strongly differed between caterpillars feeding on different host plant species, the amount of leaf area that they consumed from these different host species was quite similar, indicating that these host plants were of different quality. What is even more surprising is that insect biomass was twice as high on slow-growing plant species than on fast-growing plant species, and this pattern was true in grasses and forbs. This is not what ecological theory predicts, as fast-growing plants are assumed to be less well-defended hosts than slow-growing plants that adopt a more conservative nutrient use strategy coinciding with better protection of produced plant tissue (Coley et al. 1985, Herms and Mattson 1992). Perhaps slow-growing host plant species invest in higher quality tissues that for instance have higher concentrations of leaf nitrogen, which could have driven this effect. Alternatively, fast-growing plants may induce defences faster or more often than slow-growing plants (Hahn and Maron 2016), which can break the growth–defence tradeoff, as has been shown in several intra- and interspecific plant–insect studies (Burghardt 2016, Hahn and Orrock 2016). Moreover, we observed that insect biomass was 23% higher on grass host plants than on forb hosts. *Mamestra brassicae*, as the name implies, is mostly studied on brassicaceous host plants, but has also been recorded on a range of other forb species (Rojas et al. 2000). We show here that they may alternatively accept grasses as hosts and perform well on them.

In conclusion, our study shows that plant-mediated soil legacies can play an important role in shaping plant–insect interactions. Soil legacy effects are mediated by growth rate of the conditioning plants, but also strongly depend on plant functional type of the conditioning plants. Our results also show that the effects of soils on plant growth and insect performance are positively linked. When studying insect performance, especially in natural soils, soil communities should not be overlooked. The evolutionary implications of soils for insects in the longer term are currently unknown

and it would be timely to study the effects of other potential soil legacy effects (e.g. legacy effects of anthropogenic disturbance, climatic disturbance) on insect performance and implement this knowledge in insect conservation.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.zs7h44j4q> (Heinen et al. 2019).

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Conflict of interest – The authors declare no conflict of interest.

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Supplementary material (available online as Appendix oik-06812 at <www.oikosjournal.org/appendix/oik-06812>). Appendix 1.