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LETTER

Soil legacy effects of plants and drought on aboveground insects in native and range-expanding plant communities

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Abstract

Soils contain biotic and abiotic legacies of previous conditions that may influence plant community biomass and associated aboveground biodiversity. However, little is known about the relative strengths and interactions of the various belowground legacies on aboveground plant–insect interactions. We used an outdoor mesocosm experiment to investigate the belowground legacy effects of range-expanding versus native plants, extreme drought and their interactions on plants, aphids and pollinators. We show that plant biomass was influenced more strongly by the previous plant community than by the previous summer drought. Plant communities consisted of four congeneric pairs of natives and range expanders, and their responses were not unanimous. Legacy effects affected the abundance of aphids more strongly than pollinators. We conclude that legacies can be contained as soil ‘memories’ that influence aboveground plant community interactions in the next growing season. These soil-borne ‘memories’ can be altered by climate warming-induced plant range shifts and extreme drought.

KEYWORDS

aboveground–belowground interactions, climate change, drought, herbivores, plant–soil feedback, pollinators, range-expansion, soil legacy effect

INTRODUCTION

It is increasingly acknowledged that changes in soil microbial communities influence plants and aboveground biota using plants as resources (Hawkes & Keitt, 2015; Howard et al., 2020; Zhou et al., 2020). However, less is known about the consequences of these changes for belowground–aboveground interactions (Franco et al., 2019; van Moorsel et al., 2018). Changes in soil community composition and functioning induced by altered environmental conditions may remain for some time, even when the driver of change has disappeared (Hannula et al., 2021; Orwin & Wardle, 2004). This

altered state may be considered as the ‘legacy effect’ of a disturbance (Franklin et al., 2002; Griffin-Nolan et al., 2018). Legacy effects may influence the growth and development of plants, as well as interactions between plants and plant-associated biota, such as invertebrate fauna (Kostenko et al., 2012). Investigating legacy effects may help to further elucidate the factors that drive spatial and temporal dynamics in natural ecosystems and their responses to human-induced global changes.

Several factors have been identified that may cause legacy effects in soil, for example, plant–soil feedback (PSF) (Bever et al., 1997; van der Putten et al., 2013) and climate change-induced extreme weather events (de Vries

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et al., 2019; Kannenberg et al., 2020). Extreme drought can influence plants in the next growing season indirectly via biotic and abiotic legacies in the soil that are induced by altered rainfall and changes in root exudation patterns (Karlowsky et al., 2018; Manrubia et al., 2019; Williams & de Vries, 2019), thus altering soil community compositions (de Vries et al., 2019; Göransson et al., 2013; Meisner et al., 2013). While the existence of such legacy effects and impacts on plant performance and ecosystem functioning is increasingly recognised (Fahey & Flory, 2022; Kaisermann et al., 2017; Meisner et al., 2013), little is known about the relative strengths and interactions of the various types of legacy-causing factors (Hawkes & Keitt, 2015; Meisner et al., 2018; Preece et al., 2019). Here, we studied the legacies of soil conditioning within the context of climate change, by growing climate warming-induced range-expanding plant species and congeneric natives under extreme summer drought and ambient rainfall. We examined both their individual effects, and their interactive effects on plant biomass and flower production, as well as on the abundance of aboveground aphids and pollinators.

Climate change enables many plant species to expand their ranges to higher latitudes and altitudes where the new climate conditions more closely resemble their optimal thermal niches (Chen et al., 2011; Hagedorn et al., 2019; Parmesan & Yohe, 2003; Pecl et al., 2017). Plant species that migrate to higher latitudes may become disconnected from their co-evolved belowground enemies and symbiotic mutualists (Berg et al., 2010; van der Putten, 2012). As a result, in the new range, interactions between range-expanding plant species and their enemies and mutualists may differ from co-occurring plant species that are native in the expanded range (Engelkes et al., 2008). In addition, range-expanding plant species may have root exudates and provide litter inputs that are chemically novel to soil microbes in the new range (Kulkarni et al., 2018; Manrubia et al., 2019). These influences may all contribute to soil legacy effects that differ from those of native plant species (Berendsen et al., 2012; Koorem et al., 2020; Manrubia et al., 2020), with range expanders potentially having weaker effects on microbial community composition than congeneric natives (Ramirez et al., 2019). It is less well understood how differences in legacy effect strengths play out under increasingly occurring extreme weather conditions, such as summer drought.

Soil legacy effects may influence aboveground invertebrates (Heinen et al., 2020; Kos et al., 2015; Kostenko et al., 2012). Although range-expanding plants may encounter both antagonists (herbivores) and mutualists (pollinators) in the new range, little is known about how different soil legacy effects may influence their abundances on host plants (Hale et al., 2020; Lucas-Barbosa, 2016; Rusman et al., 2018; Sauve et al., 2016). The conditions of soil abiotic and biotic properties may influence host plant nutritional quality and defensive compounds (Bezemer & van Dam, 2005; Huberty

et al., 2020; Zhu et al., 2018). The magnitudes of such belowground effects on insect performance and abundance are expected to differ among functional types of insects, as well as among host plants. For example, pollinators, which are mostly generalists (Herrera, 1996, 2005; Olesen, 2000; Waser et al., 1996), might not discriminate well between range-expanding plants and native residents (Hegland et al., 2009; Tomiolo & Ward, 2018). Meanwhile, herbivorous insects, most of which are specialists (Loxdale & Harvey, 2016), might prefer natives, with which they have co-evolved, over range expanders (Engelkes et al., 2008, 2016; Keane & Crawley, 2002; Lakeman-Fraser & Ewers, 2013; Macel et al., 2017). The question is how soil legacies may influence insect herbivores and pollinators, and whether this depends on where the plants originate from.

In the present study, we conducted a common garden mesocosm experiment with range-expanding and congeneric native plants under three treatments. In the first treatment, we studied plant performances in northern soils, representing the novel range to range-expanding plants, and in southern soils, representing the native range to these plants. Then, both soil origins were exposed to two treatments that may cause a below-ground legacy effect. In one treatment, we examined the legacy effect of plant community origin (range-expanding vs. congeneric native plants, hereafter named 'plant legacy'). In the other treatment, we examined the effect of extreme drought versus water supplied as multi-year average rainfall amounts (hereafter named 'drought legacy'). All three treatments were carried out in a full-factorial outdoor mesocosm experiment. We used plant communities that were established with four pairs of co-occurring plant species, each consisting of a range expander and a congeneric native to avoid phylogenetic and habitat-related plant trait differences (Engelkes et al., 2008; Manrubia et al., 2019). Our general hypothesis was that legacy effects of plants and extreme drought may influence each other, and the outcome depends on soil origin. The following detailed hypotheses were tested: (i) soil legacies affect shoot biomass and flower production of natives more strongly than of range-expanding plant species, and these effects will be most pronounced in soils from the north, and (ii) soil legacies affect aboveground insect communities on natives more strongly than on range expanders. We also compared the effect strengths of legacies due to conditioning by plants with those resulting from extreme summer drought.

MATERIALS AND METHODS

Experiment set up and experiment design

In Fall of 2012, we placed 40 mesocosms of 1.1 m × 1.1 m × 0.9 m in the experimental garden of the Netherlands of Ecology (NIOO-KNAW, Wageningen,

the Netherlands) at a 0.5 m distance from each other. Each mesocosm was filled with 850 L (approximately 1300 kg) of soil. The lower parts of the mesocosms were filled with soil collected from a riparian area in Boven-Leeuwen as the background soil, the Netherlands (51°53'56.80", 5°33'45.49"), where range-expanding and native plants are co-occurring. We used subsurface soil, as this soil contains fewer local microbes, which enhances the possibility of the soil inocula to be established (Wubs et al., 2016). The top 20 cm of half the mesocosms were inoculated with 20% of field soil inoculum (Brinkman et al., 2010) originating from a riparian area in Millingerwaard (51°51'56.97", 5°59'33.60"), this area is part of the expansion range (hereafter named northern soil). The other half of the mesocosms were inoculated with topsoil collected from a riparian area near Solt in Hungary (46°47'58.95", 18°57'30.97"), which is part of the original range where the range-expanding plants were native (hereafter named southern soil) (Manrubia et al., 2019; Yang et al., 2022). Both northern and southern inoculum soils were collected from five independent locations that were minimally 60 m apart and these were kept separate throughout the inoculation process.

The soil inoculation was set up in 2013, the soil legacy of the plant community was set up in 2015–2017, and the extreme drought was set up in 2016–2018. Further details and the corresponding schematic for the mesocosm history are provided in the Supplementary Information (Figure S1). In 2019, the year of the current experiment, on April 30, we re-established plant communities using plant species that were the same as in 2018 (Yang et al., 2022): four range expanders and four congeneric natives (Table S1, seedlings culture details see Supplementary Information). We altered the position of individual plant species between 2018 and 2019 within the mesocosm, to avoid plant species-specific plant–soil feedback effects from the last year. Therefore, in 2019, we had the soil origin inoculations and soil legacies of plant communities and extreme drought from previous years. Plants grown in communities of range-expanding plants and congeneric natives (each mesocosm is considered a plant community).

All the historical treatments of soil origin, plant growth and drought resulted in a full-factorial design, with three factors and 40 experimental units: soil origin (southern vs. northern soil; established in 2012) × plant community legacy (range expanders vs. natives; years 2015, 2016, 2017) × extreme drought legacy (drought vs. control; years 2016, 2017, 2018) × 5 replicates (installed as blocks).

MEASUREMENTS

Biomass

At the end of the experiment, on September 18, 2019, the shoot biomass of each plant species was clipped off and oven-dried at 60°C until constant weight. In total, there

were around 1280 individuals harvested. Between June 17 to August 27, flower numbers were counted weekly for 11 weeks.

Aboveground insects

From the end of May until early September, aphids were counted once a week. There were possibly several aphid species on the plants, but only the total number of aphids associated with plant individuals was counted. When aphid densities were too high to count individuals, we counted the number of aphids on 1 cm of stem length and then multiplied this number by the length of stem (in cm) that was colonised by the aphids. Similarly, for aphids on leaves, we counted aphids on a 1 cm² leaf area and multiplied this by the total leaf area covered by aphids.

We recorded pollinator visitation abundance and richness by observation, 1 day a week over seven consecutive weeks. Every observation day, all mesocosms were observed in random order. The flowering stage and the fraction of ground covered by flowers of each plant species (named 'flower proportion') were also recorded. Consequently, the observation order, flowering stage and flower proportion were included as random effects factors in the statistical analyses.

DATA ANALYSIS

We analysed the data in R (R Core Team, 2021). In each mesocosm, we determined the total shoot biomass, the number of flowers, aphids and flower visitations per plant species. To test the impacts of legacy effects on shoot biomass, both the total biomass and the biomass per congeneric pair of native and range expander we performed a mixed-effect linear model using 'lme' in 'nlme' package (Pinheiro et al., 2022) with mesocosms ID (40 in total) nested in blocks as random effects and with the interactions of soil origin, plant legacy, drought legacy, species origin (native vs. range expander) as fixed effects, followed by *post hoc* (Tukey's honestly significant difference) tests.

To test the impacts of legacy effects on numbers of aphids, flowers and pollinators, we ran a 'glmmTMB' model in the 'glmmTMB' package (generalised linear mixed models using Template Model Builder) and included an extension for zero-inflation because our count data contained many zeros (Brooks et al., 2017). Interactions of time series, soil origin, plant legacy, drought legacy and species origin were taken as fixed effects. Mesocosm ID nested in blocks was used as the random effect. Additionally, for pollinator visitation, we took the recording order, congeneric pair's flowering stage, and flower proportion as random effects. To determine whether to use negative binomial 'one' or 'two'

in the zero-inflation models, we performed model selection comparing the AIC values using 'AICcTab' in 'bbmle' package (Bolker & R Development Core Team, 2022). This was done separately for each type of data (aphid, flower and pollinator number) and for each congeneric plant pair, because different pairs could have unique performances in the plant communities caused by soil legacy effects. The overall different types of data when comparing natives and range expanders in plant communities were also modelled. The residuals were checked using 'DHARMA' package (Hartig, 2020) for 'glmmTMB' models. To test whether pollinator abundance might have been driven by the number of flowers, pollinator richness by pollinator abundance, the number of flowers by plant shoot biomass, and the number of aphids by plant size, we used 'Spearman' correlations in the 'stats' package with 'cor.test' function (Figures S6 and S7 respectively), further details are described in the Supplementary Information.

RESULTS

Plant shoot biomass

In general, range-expanding plant species produced more shoot biomass than natives (Table 1, Figure 1). However, this effect depended on the soil legacy effects and the identity of the congeneric pairs (Figure S2 and Figure 1 respectively). Specifically, the two *Centaurea* species produced more shoot biomass than plants from

the other genera (Figure 1). There was one exception, as in the control with northern soil conditioned by range expanders the biomass of range expander *C. stoebe* was strongly reduced (Figure 1a).

In soils with a legacy of native plants, range expanders produced more shoot biomass than the congeneric natives, and several of these differences were significant (Table 1, Figure 1). However, the *Geranium* species pair was an exception, as the range expander of this genus produced more shoot biomass than the native species both in soils with a plant legacy of natives and of range expanders (Figure 1e,f).

The shoot biomass of both natives and range expanders was not affected by the interaction between soil origin and plant legacy (Table 1). However, the native *R. sylvestris* in northern soils produced the most shoot biomass when there was a legacy of range expanders (Figure 1c). In contrast, the range expander *T. dubius* in northern soils produced the least shoot biomass in soil with a legacy of range expanders (Figure 1g).

Drought legacies generally had weaker effects on shoot biomass than plant legacies (Table 1). Drought legacy enhanced shoot biomass only of the range-expanding plant *C. stoebe* in northern soil with a legacy of range-expanding plants (Figure 1a). In contrast, shoot biomass of the range expander *R. austriaca*, was lower in soil with drought legacy than in soil without drought legacy (Figure 1c). However, while these results led to significant interactions in the ANOVA, the significances were not present in the *post hoc* tests.

TABLE 1 The ANOVA results for plant shoot biomass in communities in response to soil legacy effects (each mesocosm data analysed per $m^2 n = 5$, using log-transformed data). Linear model with the mixed effects of soil origin (soils are from north-western and south-eastern Europe), plant legacy (soil conditioned by range-expanding plants and congeneric natives), drought legacy (soil conditioned by drought vs. control conditions) and species origin (range-expanding plants and congeneric natives)

Treatments	df	<i>Centaurea</i> (log)		<i>Rorippa</i> (log)		<i>Geranium</i> (log)		<i>Tragopogon</i> (log)	
		F	p	F	p	F	p	F	p
Soil origin (So)	28	0.475	0.496	0.000	0.991	2.989	0.095	0.007	0.932
Plant legacy (Pl)	28	4.754	0.038*	8.544	0.007**	0.650	0.427	5.804	0.023*
Drought legacy (D)	28	3.565	0.069	2.065	0.162	1.719	0.201	0.025	0.876
Species origin (Sp)	32	8.961	0.005**	42.877	0.000***	961.443	0.000***	12.908	0.001**
So × Pl	28	3.491	0.072	8.945	0.006**	0.006	0.939	2.156	0.153
So × D	28	1.576	0.220	0.847	0.365	1.055	0.313	0.044	0.836
Pl × D	28	0.538	0.469	0.496	0.487	0.226	0.638	0.209	0.651
So × Sp	32	0.981	0.329	0.686	0.414	3.227	0.082	0.076	0.784
Pl × Sp	32	1.205	0.281	6.283	0.017*	1.685	0.204	7.301	0.011*
D × Sp	32	6.478	0.016*	0.165	0.688	1.773	0.192	0.815	0.373
So × Pl × D	28	0.121	0.731	0.081	0.777	0.100	0.754	0.494	0.488
So × Pl × Sp	32	3.050	0.090	1.374	0.250	0.789	0.381	0.252	0.619
So × D × Sp	32	0.920	0.345	0.213	0.648	0.940	0.339	0.132	0.719
Pl × D × Sp	32	0.478	0.494	3.773	0.061	0.430	0.517	0.105	0.747
So × Pl × D × Sp	32	0.429	0.517	0.134	0.716	0.041	0.842	0.377	0.543

The values in bold indicate statistical significance (significance levels *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $p < 0.1$).

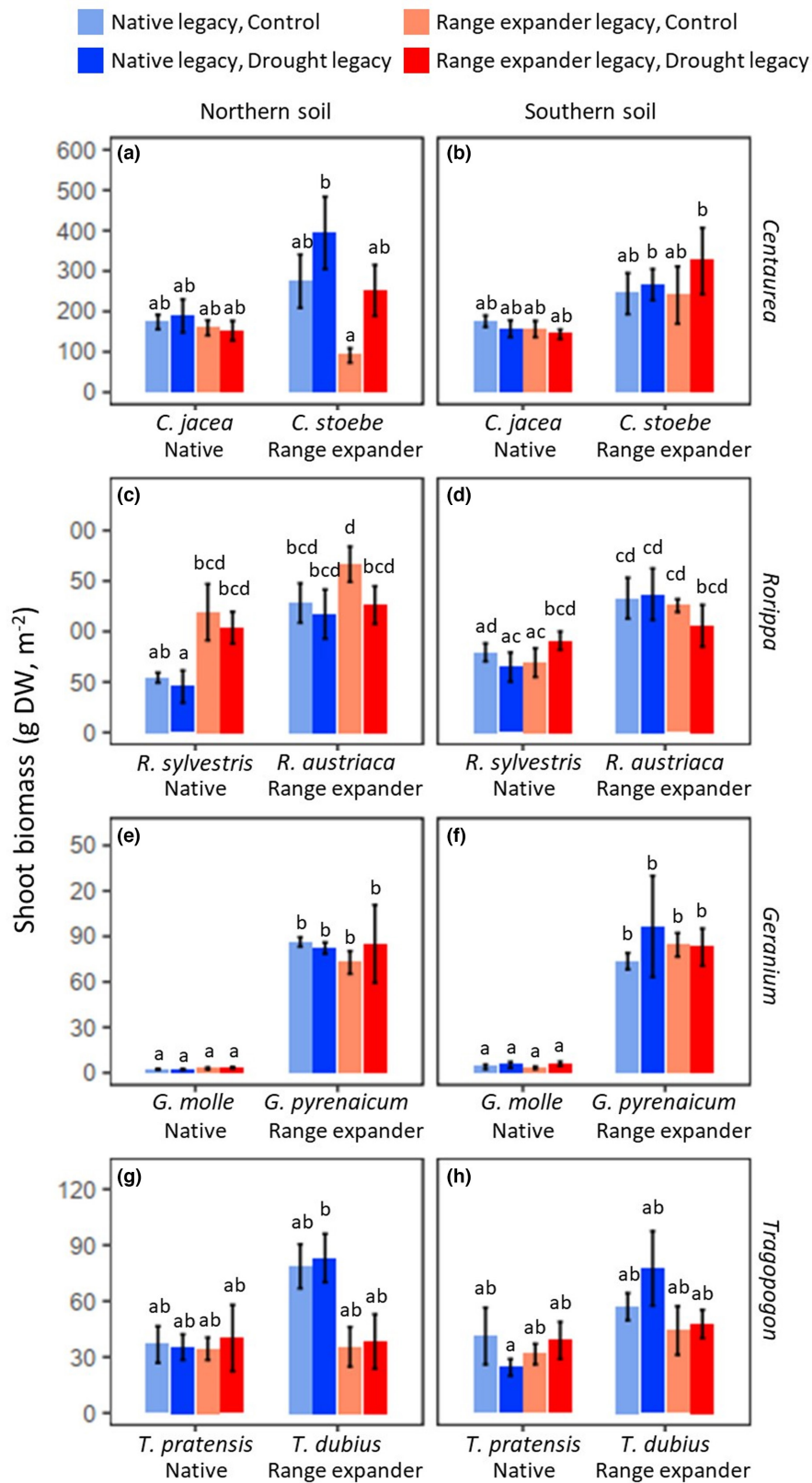


FIGURE 1 Shoot biomass (gram dry weight per m² mesocosm) for the congeneric pairs of range-expanding plant species and native congeners in response to soil origin (northern vs. southern region), plant community legacy (native vs. range expander) and drought legacy (control vs. drought). Bars indicate means with standard error ($n = 5$).

Aphid abundance

The number of aphids changed over time with the peak of aphid abundance being different, both between the plant genera, as well as between range expanders and congeneric natives within plant pairs (Table 2, Figure 2). For example, the native *R. sylvestris* had a second peak of aphid abundance towards the end of July, while this was not the case for the range-expanding *R. austriaca* (Figure 2e,f vs. g,h). Moreover, *Rorippa* species had more

aphids than species in the other plant genera (Figure 2e–h). During the peak period for most plant pairs in northern soils, aphids were most abundant on plants grown in soils with legacies of native plant species, except for the range expander *G. pyrenaicum* (Figure 2).

Overall, the total number of aphids was higher on both range expanders and natives in northern soils with a legacy of native plant species than in southern soils or soils with a legacy of range expanders (Figure S3a,c). However, this effect was largely driven by *Rorippa* species

TABLE 2 The *chi-square* and *p-values* are obtained from generalised linear mixed-effect models with negative binomial error terms output for week as the fixed effect, with the response variables of aphid number, the number of flowers, pollinators on range-expanding plant species and congeneric natives. Native *Geranium molle* died and therefore the *Geranium* pair had been removed from the number of flowers and pollinators analysis. *Rorippa* and *Trogopogon* pairs, either native or range-expanding plants had very few pollinators and therefore were removed from the analysis.

Treatments	Aphid number							
	<i>Centaurea</i>		<i>Rorippa</i>		<i>Geranium</i>		<i>Trogopogon</i>	
	<i>Chi-square</i>	<i>p</i>	<i>Chi-square</i>	<i>p</i>	<i>Chi-square</i>	<i>p</i>	<i>Chi-square</i>	<i>p</i>
Soil origin (So)	0.809	0.368	3.548	0.060	0.287	0.592	0.086	0.769
Plant legacy (Pl)	0.035	0.852	1.609	0.205	1.376	0.241	0.221	0.638
Drought legacy (D)	1.544	0.214	2.297	0.130	0.096	0.757	0.242	0.622
Species origin (Sp)	16.037	0.000***	5.723	0.017*	42.496	0.000***	7.825	0.005**
Week (W)	143.168	0.000***	20.406	0.000***	1194.756	0.000***	24.406	0.000***
So × Pl	7.808	0.005**	2.468	0.116	0.922	0.337	0.093	0.760
So × D	0.154	0.695	0.272	0.602	0.016	0.901	2.154	0.142
Pl × D	0.179	0.672	0.060	0.806	5.066	0.024*	0.978	0.323
So × Sp	0.036	0.850	2.263	0.133	1.432	0.232	2.606	0.106
Pl × Sp	0.004	0.949	4.573	0.032*	2.949	0.086	0.032	0.857
D × Sp	1.189	0.276	5.856	0.016*	0.003	0.960	0.047	0.828
So × W	0.291	0.589	0.224	0.636	0.708	0.400	0.110	0.741
Pl × W	0.254	0.615	2.307	0.129	1.565	0.211	0.000	0.990
D × W	1.193	0.275	0.164	0.686	0.000	0.988	0.461	0.497
Sp × W	0.798	0.372	108.800	0.000***	30.955	0.000***	28.977	0.000***
So × Pl × D	1.806	0.179	0.063	0.801	0.529	0.467	2.136	0.144
So × Pl × Sp	2.994	0.084	0.127	0.722	0.577	0.447	1.662	0.197
So × D × Sp	1.528	0.216	0.019	0.889	0.301	0.583	0.850	0.356
Pl × D × Sp	0.199	0.656	1.570	0.210	1.088	0.297	1.372	0.241
So × Pl × W	1.144	0.285	6.285	0.012*	0.197	0.657	0.003	0.956
So × D × W	0.012	0.911	0.679	0.410	0.025	0.874	2.629	0.105
Pl × D × W	0.170	0.680	0.751	0.386	1.298	0.255	1.215	0.270
So × Sp × W	0.045	0.833	1.767	0.184	0.133	0.715	1.723	0.189
Pl × Sp × W	0.193	0.660	0.943	0.332	0.854	0.356	0.006	0.939
D × Sp × W	1.357	0.244	1.234	0.267	0.376	0.540	0.083	0.773
So × Pl × D × Sp	2.968	0.085	2.598	0.107	0.000	0.999	4.117	0.042*
So × Pl × D × W	1.784	0.182	0.910	0.340	0.095	0.758	2.303	0.129
So × Pl × Sp × W	1.388	0.239	1.682	0.195	0.015	0.902	0.160	0.689
So × D × Sp × W	0.537	0.464	0.000	0.983	0.016	0.900	1.012	0.314
Pl × D × Sp × W	1.042	0.307	0.009	0.925	0.831	0.362	0.100	0.752
So × Pl × D × Sp × W	2.706	0.100	6.082	0.014*	0.164	0.685	0.471	0.492

The values in bold indicate statistical significance (significance levels *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $p < 0.1$).

(Figure 2). In addition, for native plants in northern soil with a legacy of native plant species, aphids were most abundant when the soils contained a legacy of drought (Figure S3a). In contrast, for native plants growing in soils with a range expander legacy, aphids were most abundant in soils without a legacy of drought (Figure S3a). Again, these patterns were different between plant species and pairs, with higher aphid abundance on plants growing in soils conditioned by native plants and with a legacy of drought, for example *G. molle* and *T. pratensis*,

whereas the opposite pattern was found, for example, the range-expander *C. stoebe*.

Number of flowers

Overall, range-expanding plant species had fewer flowers than congeneric natives, which was mainly driven by *Rorippa* species (Figure S4, Figure 3). The range expander *C. stoebe* produced most flowers towards the end

The number of flowers						Pollinators	
<i>Centaurea</i>		<i>Rorippa</i>		<i>Tragopogon</i>		<i>Centaurea</i>	
<i>Chi-square</i>	<i>p</i>	<i>Chi-square</i>	<i>p</i>	<i>Chi-square</i>	<i>p</i>	<i>Chi-square</i>	<i>p</i>
0.054	0.816	0.070	0.792	0.151	0.698	2.636	0.104
8.386	0.004**	4.792	0.029*	3.732	0.053	0.477	0.490
3.567	0.059	0.738	0.390	0.432	0.511	0.086	0.769
8.000	0.005**	494.784	0.000***	16.803	0.000***	0.045	0.832
269.177	0.000***	431.765	0.000***	8.339	0.004**	8.703	0.003**
1.354	0.245	1.703	0.192	0.007	0.932	0.046	0.831
0.001	0.969	0.099	0.753	1.739	0.187	0.351	0.554
2.693	0.101	0.155	0.694	0.649	0.420	0.068	0.794
0.504	0.478	3.436	0.064	1.312	0.252	0.510	0.475
0.851	0.356	2.868	0.090	0.920	0.337	0.123	0.726
1.785	0.181	0.407	0.523	0.917	0.338	3.379	0.066
0.151	0.698	0.072	0.789	0.881	0.348	0.108	0.742
0.530	0.467	0.079	0.779	3.008	0.083	0.337	0.562
0.016	0.900	0.001	0.971	5.296	0.021*	4.242	0.039*
181.102	0.000***	211.977	0.000***	2.218	0.136	1.251	0.263
1.027	0.311	0.575	0.448	0.238	0.626	0.640	0.424
1.434	0.231	3.687	0.055	0.004	0.952	1.321	0.250
0.926	0.336	1.475	0.225	5.664	0.017*	0.062	0.803
0.050	0.822	3.515	0.061	1.823	0.177	4.429	0.035*
0.128	0.721	4.310	0.038*	0.126	0.722	0.013	0.908
0.005	0.941	0.681	0.409	0.040	0.841	0.857	0.355
0.030	0.863	0.222	0.638	1.262	0.261	0.150	0.699
0.255	0.614	0.139	0.709	0.345	0.557	0.444	0.505
0.281	0.596	1.381	0.240	0.260	0.610	1.323	0.250
0.295	0.587	5.362	0.021*	0.012	0.912	2.089	0.148
2.967	0.085	5.247	0.022*	0.128	0.720	2.619	0.106
4.064	0.044*	1.518	0.218	0.005	0.945	2.254	0.133
0.234	0.628	10.497	0.001**	0.073	0.786	1.192	0.275
0.444	0.505	3.068	0.080	0.004	0.948	0.283	0.595
1.070	0.301	0.007	0.932	0.116	0.733	3.820	0.051
4.736	0.030*	1.450	0.228	0.050	0.823	0.671	0.413

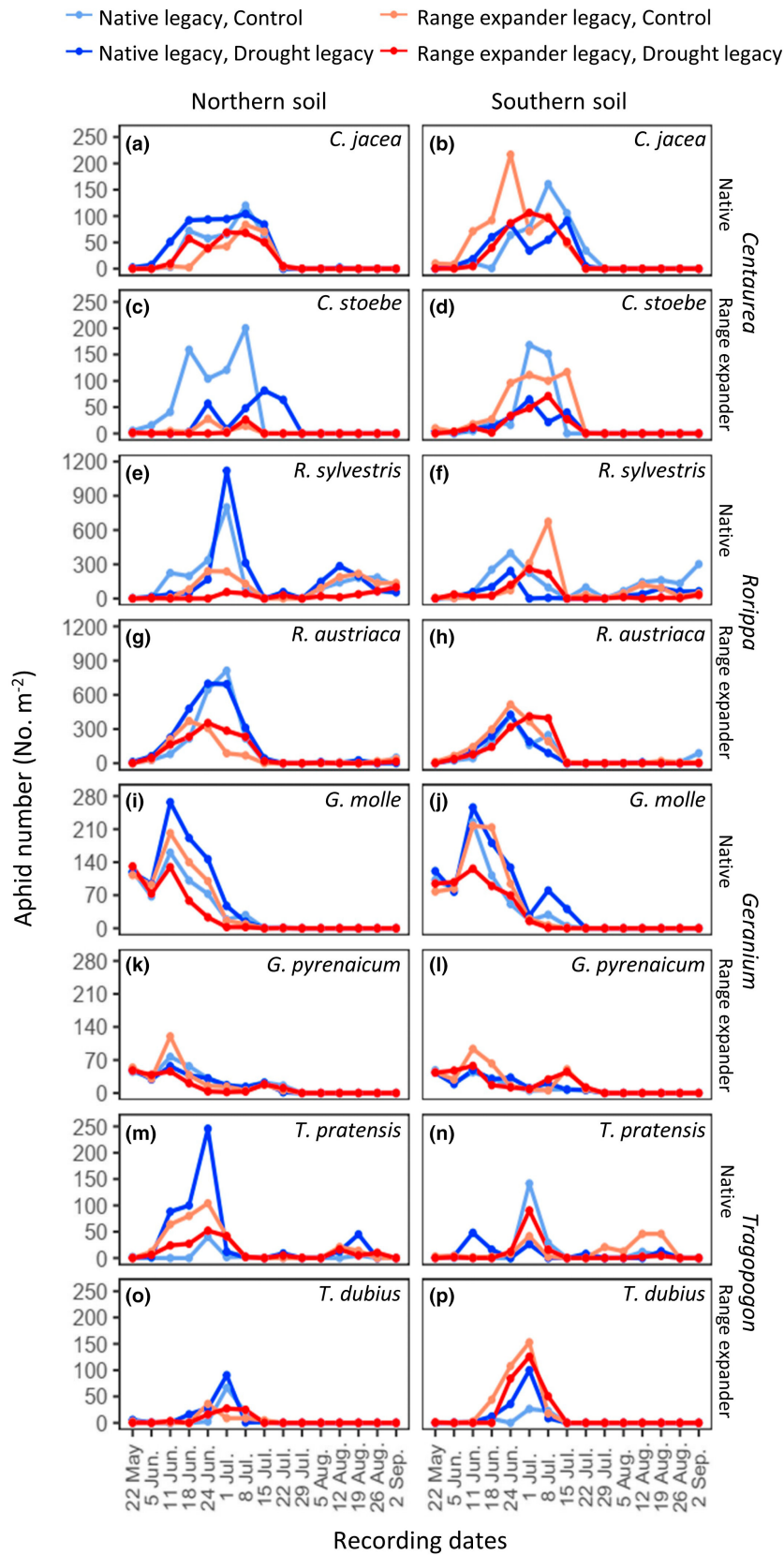


FIGURE 2 The total number of aphids during the various observation moments for each of the congeneric pairs of native and range-expanding plants in response to soil origin (northern vs. southern region), plant community legacy (native vs. range expander) and drought legacy (control vs. drought) in mesocosms ($n = 5$).

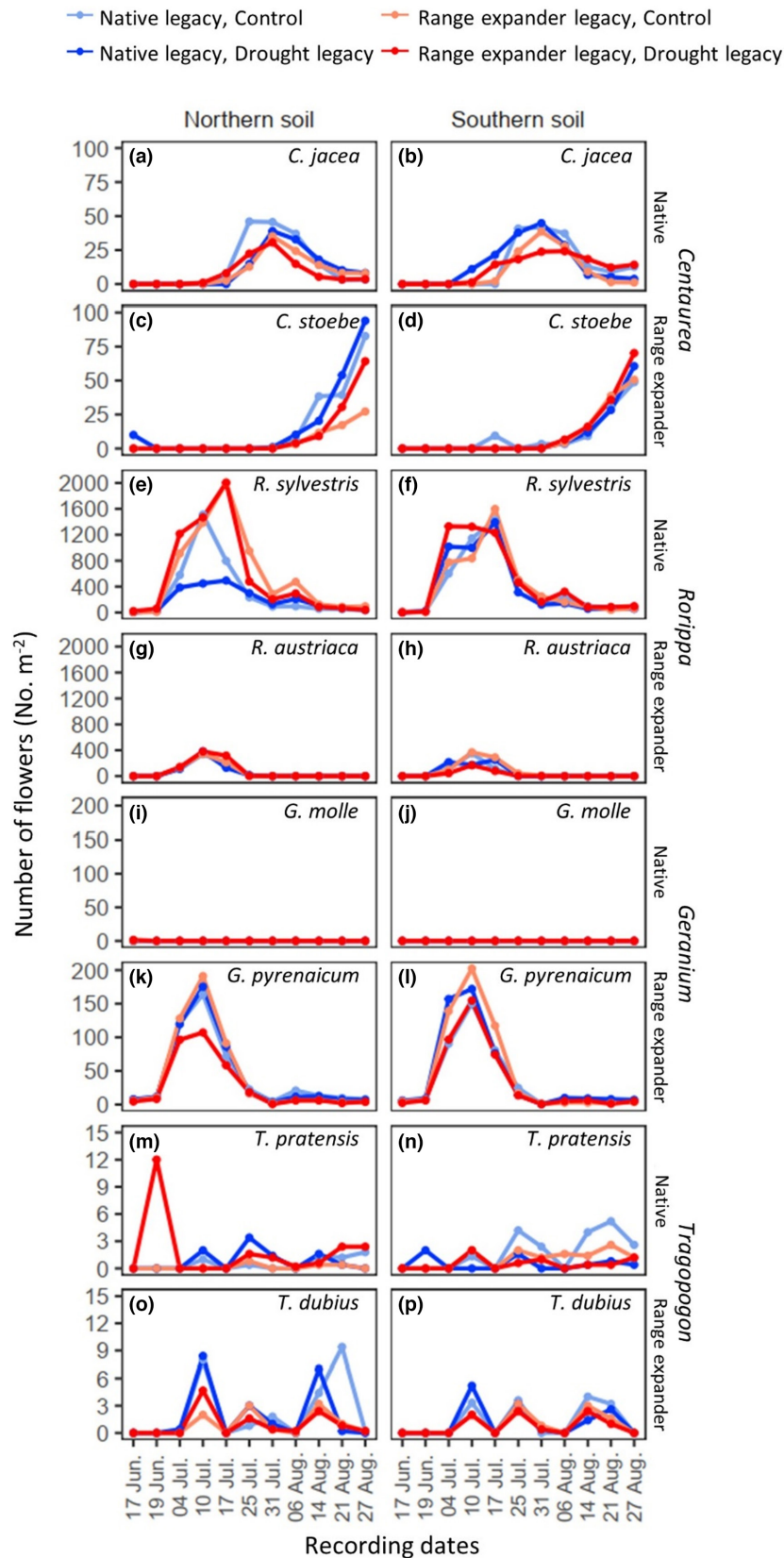


FIGURE 3 Total number of flowers during the growing season for each congeneric pair of native and range-expanding plant species in response to soil origin (northern vs. southern region), plant community legacy (native vs. range expander) and drought legacy (control vs. drought) in mesocosms ($n = 5$).

of the growing season (Figure 3c,d). The number of flowers was reduced only when native plants were growing in northern soil with a legacy of native plant species and a legacy of drought (Figure S4a). These patterns were again mostly driven by *Rorippa* species (Figure 3). The number of flowers on the range expanders was generally not affected by soil legacies.

The impact of the different soil legacies on the number of flowers differed among plant genera. For example, *Centaurea* species had the most and *Rorippa* species had the fewest flowers in soils with a legacy of natives (Figure 3c and e respectively). The range-expanding and native *Centaurea* were affected differently by the legacy effects. The range expander *C. stoebe* had most flowers in northern soils with a legacy of natives, while there was no effect of plant legacies for the native *C. jacea* (Figure 3c and e respectively). For *C. stoebe* in northern soils with a range expander legacy, the flower number was highest when the soils had a legacy of drought (Figure 3c). However, there was no effect of drought legacy in southern soils, or with the native *C. jacea* (Figure 3d).

In northern soils, the number of flowers was reduced by legacies of range expanders and drought, while in southern soils there were no legacy effects (N.B.: *G. molle* had no flowers as it died early). *Tragopogon* species were flowering early and the impact of the legacy effects seemed to vary over time (Figure 3m–p). In general, in northern soils with a legacy of drought, the native *T. pratensis* produced most flowers (Figure 3m). However, in northern soils with a legacy of natives, the range expander *T. dubius* produced more flowers than in soils with a legacy of range expanders (Figure 3o).

Pollinator abundance

The pollinator abundance appeared mostly correlated with the number of flowers (Figure S6). *Rorippa* species, which had the most flowers, also had the most pollinators (Figure 3, Figure S6). The number of pollinators was highest when plants were grown in northern soils with a legacy of range-expanding plants and no drought (Figure S5a). The same pattern was observed for *R. sylvestris* (Figure 4e). However, a different combination of plants and drought legacy appeared to change the pattern. For example, the number of pollinators was lowest when the native *R. sylvestris* grew in northern soil with a legacy of natives and without a legacy of drought (Figure 4e).

When comparing soil treatments, the pollinator visitation pattern was not always positively related to the number of flowers. For example, there was no significant legacy effect of drought on the number of flowers for *R. sylvestris* in northern soils with a legacy of range-expanding plants, whereas there was a significant difference in pollinator abundance (Figures 3e and 4e respectively). In another example, the range expander *C.*

stoebe in northern soil had the lowest number of pollinators when there was a legacy of range expanders and no legacy of drought (Figure 4c). Finally, the native *R. sylvestris* in northern soil had the highest numbers of pollinators in soil with a legacy of range expanders and without a legacy of drought (Figure 4e).

DISCUSSION

We used an outdoor mesocosm experiment to elucidate how plant range expansion and summer drought may influence plant biomass production and plant-associated aboveground biota under semi-natural conditions in inoculated soils from two origins. Our results reveal that both plants and drought legacy effects generated in the previous years (2015–2017 for plants and 2016–2018 for drought) affected newly established plants and their interactions with aboveground aphids and pollinators in the following year (2019). The legacy effects of soil conditioning by plants were generally stronger than of extreme summer drought, but the impact of both experimental factors depended on each other, as well as on the origin of the soil. This is in support of the general hypothesis.

Most legacy effects were strongest in northern soils and for native plants, which is in support of the first hypothesis. Aphids were more abundant on plants in northern soils with a legacy of conditioning by native plant species, which is in support of our second hypothesis. Thus far, the legacy effects of soil conditioning on plant–insect interactions have been demonstrated in short-term greenhouse experiments (Heinen et al., 2020; Kostenko et al., 2012). Evidence from experiments under field conditions generated only weak legacies (Heinze & Joshi, 2018; Schittko et al., 2016). Our results show that legacy effects contained by soils can be influenced by plants and drought, that these effects depend on soil origin, and that all factors have the potential to interact. This might make legacy effects so highly context-dependent, and difficult to be determined in the field. Our mesocosm approach enabled us to tease apart all individual factors.

Soil legacy effect on plant shoot biomass and flower number

Our results showed that plant biomass production differed between range-expanding and native plant species and depended on soil origin and on the legacy effect of plant conditioning. The legacy effects of drought had a relatively minor effect on shoot biomass. Careful inspection of the interaction effects revealed that the results are partly in line with our first hypothesis that soil legacies affect shoot biomass and flower production of natives more strongly than of range-expanding plant species. Range expanders might be less sensitive to legacy effects,

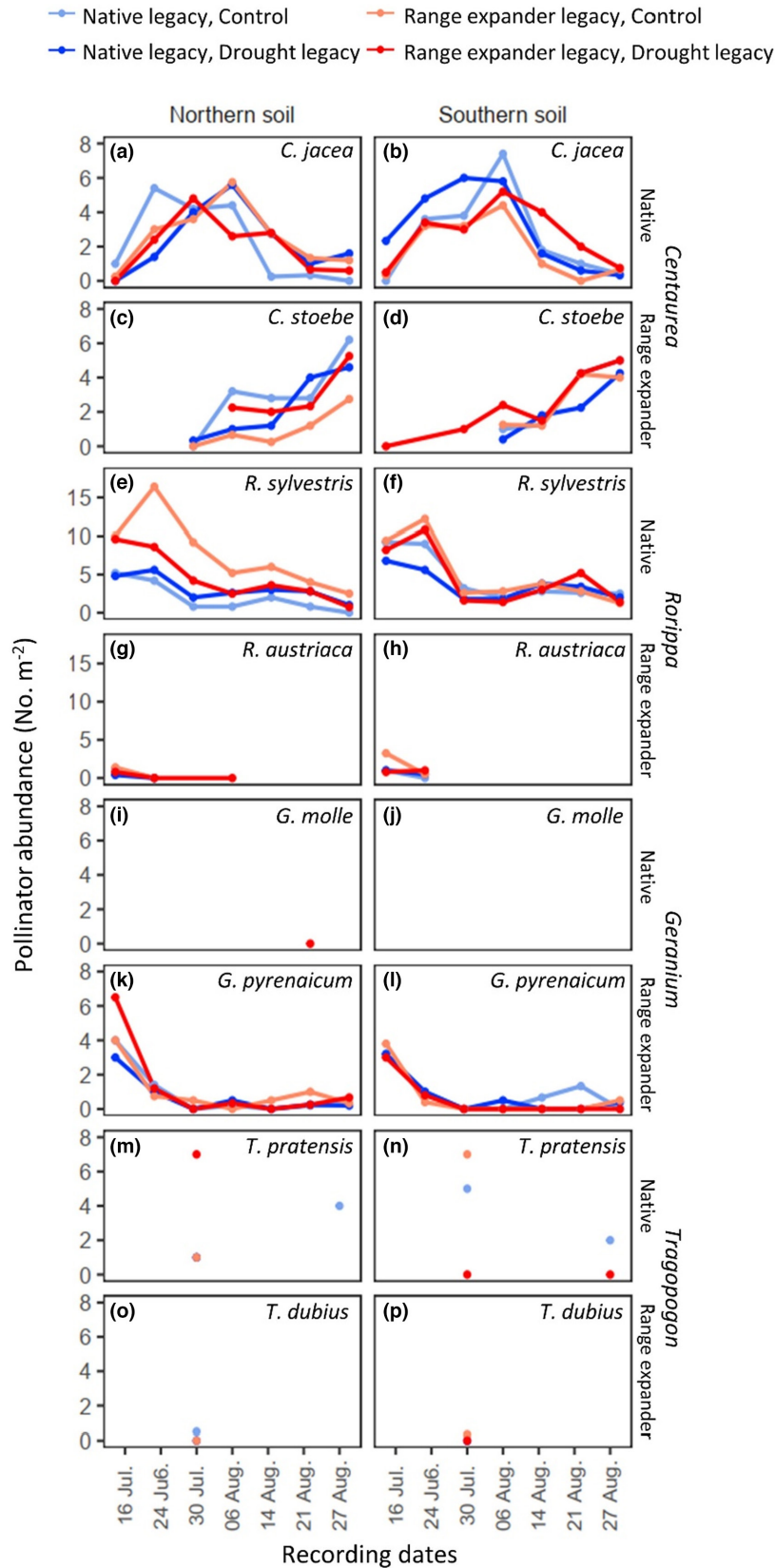


FIGURE 4 Total pollinator abundance over time for each congeneric pair of native and range-expanding plants in response to soil origin (northern vs. southern region), plant community legacy (native vs. range expander) and drought legacy (control vs. drought) in mesocosms ($n = 5$).

as they do not interact as much with soil fungi and nematodes as natives (Morriën & van der Putten, 2013; Wilschut, Geisen, et al., 2019). In field surveys along a latitudinal gradient from the original to the expanded range, both soil microbes (Ramirez et al., 2019) and nematodes (Wilschut, Geisen, et al., 2019) showed some variation in community composition. Variation in plant legacies between southern and northern soils, therefore, corresponds with differences in soil community composition in those two regions. However, few studies have examined the effects of soil origin between south and north on plant performance (De Frenne et al., 2014; van Grunsven et al., 2010). Further experimental studies are needed in order to determine which components of the soil community contribute the strongest to the legacy effects.

Complex interactions between soil legacies, origin and plant identity as observed in our study may have arisen as a result of range-expanding and native plants growing in mixed plant communities. Under such conditions, the greater biomass production of range expanders compared to natives in soils with a native plant legacy may result from several mechanisms. Range expanders may benefit from native plant legacies for example as a result of indirect plant–soil feedback (Bever et al., 1997; Zuppinger-Dingley et al., 2011), or from negative impacts of legacies on the native plant species themselves, for example, via specific growth-reducing soil biota (Van der Putten et al., 1993). In addition, we show that plant genera show very specific responses to legacies, which further enhances the complexity and context-dependency of plant responses to soil legacies. This variation among genera, and possibly among species within a genus (Wilschut, van der Putten, et al., 2019), may underline why we do not always observe general responses of range-expanding versus native plants (Koorem et al., 2018; van Grunsven et al., 2010). In contrast with shoot biomass, range expanders produced fewer flowers than natives. However, these patterns were strongly driven by a single plant species. Besides this exception, it appeared that flower production to some extent was under the control of soil conditions, as has been demonstrated before (Barber & Soper Gorden, 2015). Here, we show that these soil conditions may be influenced by legacies of previous plants, and that range expanders may influence legacy effects on flowers differently than congeneric natives.

Although legacy effects interacted to impact plant shoot biomass production, in general effects of plant legacies were stronger than those of extreme drought, even though plant community conditioning stopped half a year earlier than the summer drought treatment (Yang et al., 2022). This finding was unexpected, as previous studies found that extreme drought left strong soil legacies by altering soil community composition, which in turn influenced biomass production of subsequently grown plants (Kaisermann et al., 2017; Meisner

et al., 2013, 2018). In addition, both plant conditioning and drought may alter soil nutrient availability, which is known to have important feedback effects on plant biomass production (Buchenau et al., 2022; Van Nuland et al., 2017). In our study, the presence of plants might have affected soil communities that alleviate drought legacies (de Vries et al., 2012; Hicks et al., 2018). Alternatively, drought legacy effects may disappear quickly after rewetting (Rousk et al., 2013; Wu et al., 2018), most likely by re-arrangements in the soil community composition.

Range-expanding plant species generally produced more biomass than congeneric natives. This may be caused by a number of factors, including the evolution of increased competitive ability (Blossey & Notzold, 1995) in the new range, range expanders having more, or novel, defensive chemicals, may show reduced biomass loss to plant feeders compared to natives (Engelkes et al., 2008; Macel et al., 2017; Wilschut et al., 2017). Possibly, range expanders also may benefit from using mycorrhizal fungi in the new range while being released from natural enemies (van Grunsven et al., 2007). By growing plant communities in both northern and southern soils, we tried to mimic an original environment for range-expanding plants. However, as we only used seeds collected from plant populations in the north, we cannot compare the performance of range-expanders between their original and expansion range (Liu & Stiling, 2006). Therefore, we only compared the responses of closely related natives and range-expanding plants in our approach. This may result in a conservative comparison, as introduced exotics may be less invasive when they have congeneric natives (Agrawal et al., 2005).

Soil legacy effect on aphids and pollinators

We found that soil legacies affected aboveground insect communities and that these responses were often dependent on combinations of experimental treatments. For example, aphids were more strongly affected by legacies on natives than range expanders, and the legacy effects were more evident when host plants were growing in northern soils. This is in support of the second hypothesis. In contrast, the impacts of soil legacies on the number of pollinators were uncommon. They might have been mediated via legacy-induced changes in flower number, but that evidence was not unanimous. Previous studies have reported that weather-related phenomena, such as temperature and rainfall, can strongly affect the diversity and activity of pollinators (Corbet, 1990; Güler & Dikmen, 2017; Herrera, 1995). Other studies have shown that changes in the belowground community induced by soil legacy effects may also have important impacts on pollinator visitation (Barber & Soper Gorden, 2015; Poveda

et al., 2003). Our results show that soil legacy effects on pollinators are possible, but not as strong as legacy effects on aphids. Pollinators may mostly rely on flower numbers or flower traits, for example, flower colour, pollen qualities and olfactory cues to recognise host plants (Beyaert & Hilker, 2014; Dudenhöffer et al., 2018). Perhaps these factors are less strongly influenced by soil legacy effects than plant defences against aphids, which could vary from secondary metabolites to amino acids (Bezemer et al., 2005). Future work will benefit from integrating abiotic factors such as weather, soil legacy effects and plant–antagonist–mutualist interactions (Hale et al., 2020; Lucas-Barbosa, 2016), and studying their combined net effects on plant–pollinator interactions in both native and range-expanding plant species.

In addition to the legacy effects impacting aphid abundance, we also found that aphids were more abundant on native plants than on range expanders. This finding is in support of earlier work showing that range-expanding plant species were less colonised and consumed both by aboveground invertebrates than congeneric natives (Engelkes et al., 2016). These results may be due to native herbivore species having a longer co-evolutionary history with local plant species (Keane & Crawley, 2002), or range-expanding plants having more, or novel, defence compounds (Callaway & Ridenour, 2004; Hopkins et al., 2017; Wilschut et al., 2017). In contrast to aphids, pollinators were less affected by plant identity, indicating that they may benefit equally well from range-expanding plant species, as from native plant species (Morales & Aizen, 2002; Vilà et al., 2009). As a result, pollinators may even benefit from range-expanding plant species as these offer more feeding choices or plants that flower at different times in the growing season. Possibly, if pollinators visit range-expanding plant species, and aphids preferentially feed on natives, range expanders would have triple main benefits compared to natives: (1) increased biomass, (2) less herbivory and (3) more pollination (Charlebois & Sargent, 2017; Engelkes et al., 2008). Our study shows that these benefits may depend at least partially on the changing memory of the soil.

CONCLUSIONS

Our study has reported a range of complex and unpredictable community-level responses that are linked to different kinds of biotic and abiotic soil conditions and legacies. We found that legacies can remain in the soil for longer periods of time, for example, across seasons, and hence drive the dynamics of ecological communities across these time scales. Our experiment reveals that legacies of previous plants and drought influence community-wide responses depending on soil origin. Results differed between range-expanding and

congeneric native plant species, and these differences were plant genus-specific. Legacy effects of plants that conditioned the soil were stronger than the legacy of an extreme summer drought, even though plant conditioning ended half a year earlier than the drought. Soil origin effects were also weaker than plant conditioning effects. Our work clearly demonstrates complex multi-annual plant–soil and belowground–aboveground feedback effects under semi-natural outdoor conditions. Further studies of the role of such soil-contained legacy effects are needed to unravel community effects and identify possible mechanisms of altered trophic interactions in a changing world (van der Putten et al., 2004).

AUTHOR CONTRIBUTIONS

Keli Li, Wim H. van der Putten and Ciska (G. F.) Veen designed the experiment. Freddy C. ten Hooven installed and maintained the experiment across years. Jeffrey A. Harvey advised on aphid and pollinator analyses. Keli Li executed the data collection and wrote the initial manuscript with inputs from all co-authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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