Received: 7 December 2017 | Accepted: 11 April 2018

DOI: 10.1111/1365-2745.12999

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Plant competition alters the temporal dynamics of plant-soil feedbacks

T. Martijn Bezemer[1,2] | **Jingying Jing**[1] | **J. M. Tanja Bakx-Schotman**[1] | **Erik-Jan Bijleveld**[1]

[1]Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

[2]Institute of Biology, Section Plant Ecology and Phytochemistry, Leiden University, Leiden, The Netherlands

Correspondence
T. Martijn Bezemer, Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB, Wageningen, The Netherlands.
Email: m.bezemer@nioo.knaw.nl

Handling Editor: Paul Kardol

Abstract

1. Most studies on plant-soil feedback (PSF) and plant competition measure the feedback response at one moment only. However, PSFs and competition may both change over time, and how PSF and competition interact over time is unclear.
2. We tested the temporal dynamics of PSF and interspecific competition for the forb *Jacobaea vulgaris* and the grass *Holcus lanatus*. We grew both species individually and in interspecific competition in soil that was first conditioned in the greenhouse by *J. vulgaris*, *by H. lanatus* or without plant growth. For a period of 11 weeks, we harvested plants twice a week and analysed the fungal and chemical composition of the different soils at the end of the first and second growth phase.
3. During the second growth phase, when grown in isolation, both species produced more biomass in heterospecific conditioned soil than in conspecific conditioned soil. Young *J. vulgaris* exhibited a strong negative conspecific feedback, but this effect diminished over time and became neutral in older plants. In contrast, when grown in competition, the negative conspecific feedback of *J. vulgaris* exacerbated over time. Older *H. lanatus* plants benefited more from heterospecific conditioning when competing with *J. vulgaris*, then when grown isolated.
4. Fungal community composition and soil chemistry differed significantly between soils but this was mainly driven by differences between plant-conditioned and unconditioned soils. Remarkably, at the end of the second growth phase, fungal community composition was not explained by the legacy of the species that had been grown in the soil most recently, but still reflected the legacy of the first growth phase. We reexamined plant growth during a third growth phase. Biomass of *J. vulgaris* was still influenced by the treatments imposed during the first phase, while *H. lanatus* responded only to the plant growth treatments imposed during the second phase.
5. *Synthesis*. Our study shows that the direction and magnitude of PSF depends on plant age and competition, and also on soil legacy effects of earlier plant growth. These results highlight the need to incorporate dynamic PSFs in research on plant populations and communities.

KEYWORDS
interspecific competition, plant life stage, plant–soil (below-ground) interactions, plant–soil feedback, repeated harvesting, soil chemistry, soil legacy, T-RFLP

1 | INTRODUCTION

Plant-soil feedback (PSF) is the process in which a plant first alters the biotic and abiotic characteristics of the soil which then, in turn, influence the performance of another plant that grows later in the same soil (Bever, Westover, & Antonovics, 1997; Van der Putten et al., 2013). The vast majority of PSF studies have been carried out over short time periods, and measure the biomass response at one time point (But see Dudenhöffer, Ebeling, Klein, & Wagg, 2018; Hawkes, Kivlin, Du, & Eviner, 2013). However, as Kardol and coworkers (Kardol, De Deyn, Laliberte, Mariotte, & Hawkes, 2013) recently proposed, plant–soil interactions may not be constant over time and can vary greatly depending on the plant life stage. Plant seedlings are much more sensitive to soil pathogens than larger, mature plants (Hersh, Vilgalys & Clark, 2012; Packer & Clay, 2000) and generally respond stronger than older individuals of the same species to the same soil conditions (Kardol et al., 2013). PSF theory is based on the assumption that a plant alters the biotic and abiotic characteristics of the soil it grows in (Van der Putten et al., 2013). Clearly, this will not only happen during the conditioning phase but also during the response phase, something that is frequently overlooked in PSF research. An increase in the duration of the response phase therefore also increases duration of the influence of the plant itself on the soil it is growing in, and this may reduce the soil-mediated influence of the preceding plant (Dudenhöffer et al., 2018; Hawkes et al., 2013). Moreover, as plants generally produce more root biomass over time, the surface area where plant–soil interactions occur will increase with increasing growth periods and this in itself can also strengthen the influence of a plant on soil properties (Heinen, Van der Sluijs, Biere, Harvey, & Bezemer, 2018). Overall, these arguments suggest that the soil feedback effect of a preceding plant on a test plant will diminish with increasing time the test plant grows in the soil.

Our current understanding of PSF is based almost exclusively on experiments that use soils that are conditioned once by a single species. However, in the field where plants replace each other, plants belonging to different species can condition the soil sequentially. *Jacobaea vulgaris*, for example, is a species with a strong negative conspecific feedback and heterospecific feedback responses that differ greatly depending on the species that conditioned the soil (Jing, Bezemer, & Van der Putten, 2015; Kos, Tuijl, De Roo, Mulder, & Bezemer, 2015; Van de Voorde, Van der Putten, & Bezemer, 2011). However, the feedback of this species is not only determined by the identity of the plant species that has conditioned the soil during the most recent conditioning phase but also by which species had been grown in the soil previously (Wubs & Bezemer, 2018). How sequential conditioning by the same or by different plant species influences the composition of the soil microbial community is poorly understood. We postulate that conditioning twice by the same species will increase the influence of that plant species on the soil microbial community, similar to what can be expected by increasing the time of conditioning the soil. Growing a species in a soil that is previously conditioned by another species, may then diminish the effect of the first species on the soil community and steer it more towards the soil community affiliated to the later growing plant species (Wubs & Bezemer, 2018). Whether this assumption is true remains to be tested.

Most PSF studies focus on the response of an individual plant to changes in the soil. However, in nature, plants often compete with other plants for nutrients, water, light and space (Grime, 1973). Several studies have shown that the outcome of PSF can depend greatly on whether a plant competes with other plants or not and that PSF effects are generally stronger when plants compete with other plants (e.g. Casper & Castelli, 2007; Jing et al., 2015; Kardol, Cornips, Van Kempen, Bakx-Schotman, & Van der Putten, 2007; Petermann, Fergus, Turnbull, & Schmid, 2008; but see e.g. Crawford & Knight, 2017). As most conspecific PSFs are negative (Kulmatiski, Beard, Stevens, & Cobbold, 2008), the competitive strength of a plant may be reduced when it is grown in soil conditioned by conspecific individuals (Ke & Miki, 2015). However, heterospecific PSF, i.e. the effects of a plant, via the soil on the performance of a plant of another species, can be as important as conspecific feedbacks (Van de Voorde et al., 2011; Wubs & Bezemer, 2016). Hence, when two plants that belong to different species compete in a soil conditioned by one of the two plant species, both species may experience specific feedback effects of that soil and this may influence their competitiveness (Jing et al., 2015).

Plant growth and competition are both dynamic and competitive interactions can change over time (Paine et al., 2012; Trinder, Brooker, Davidson, & Robinson, 2012). Hence, competitive interactions during the later stages of the experiment can be completely different from early stages and the competitive balance between two species can even change directionally over time (Connolly, Wayne, & Murray, 1990; Menchaca & Connolly, 1990; Turkington & Jolliffe, 1996). To study competition, it is therefore important to measure the performance of the competing species repeatedly throughout an extended growth period. This may be particularly important when examining the effects of PSF on competition as the soil-mediated effects may also change over time. While an increasing number of studies has now examined how PSF influence plant–plant interactions, to the best of our knowledge no studies have examined how these interactions change over time.

In this study, we examine how conspecific and heterospecific PSF influence the dynamic growth pattern of two grassland species, the grass *Holcus lanatus* and the forb *J. vulgaris*, grown in isolation and in

competition. Both species have well-documented negative conspecific PSFs that are probably caused by soil pathogenic fungi and they both grow better in the heterospecific than in conspecific conditioned soil or in a mixture of heterospecific conditioned soils (Bezemer et al., 2006, 2013; Jing et al., 2015; Van de Voorde, Ruijten, Van der Putten, & Bezemer, 2012; Van de Voorde, Van der Putten, & Bezemer, 2012; Van de Voorde et al., 2012b). We grew plants in field soil conditioned in the greenhouse for 8 weeks by *J. vulgaris*, by *H. lanatus* or in field soil in which no plant had been grown for the past 8 weeks. We harvested plants twice a week for a period of 11 weeks and hypothesized that (a) the strength of the negative conspecific feedback of both species would diminish over time and that (b) the competitive ability of both species will decline when grown in conspecific conditioned soil, but that the soil-mediated effects of conditioning on competition would decline over time. We also analysed fungal community composition in the soils from the conditioning and feedback phase, and hypothesized that (c) repeated conspecific conditioning would increase the dissimilarity in soil fungal communities over time, while successive heterospecific conditioning would reduce dissimilarity. We then grew the two species again in the soils that were sequentially conditioned for two time periods, and hypothesized that in the third growth phase, (d) the species that most recently conditioned the soil would have the greatest influence on feedback effects, and that the differences in soil feedback effects would be strongest between the soils that had been conditioned twice by the same species. Growing different species sequentially would reduce the effects. We harvested 5-week-old and 9-week-old plants, and expected that, again, feedback effects would be most prominent in the younger plants.

2 | MATERIALS AND METHODS

2.1 | Plant species

Holcus lanatus L. (Poaceae) is a fast-growing perennial grass native to Europe and western Asia (Beddows, 1961). *Jacobaea vulgaris* Geartn. subs. *vulgaris* (syn. *Senecio Jacobaea* L.; Asteracaea) is a biennial that forms a rosette in its first year and a stem with flowers in the second year (Harper & Wood, 1957). Both species are very common in (semi)natural grasslands and along road sides in the Netherlands and the two species frequently co-occur. *J. vulgaris* seeds were collected from a population of wild plants growing in a natural grassland near the village Wolfheze, The Netherlands. Seeds of *Holcus lanatus* were purchased from Cruydt-Hoeck (Nijeberkoop, The Netherlands), a supplier of seeds obtained from wild plants.

2.2 | Greenhouse experiment

Soil was collected in September 2013 from a natural grassland area, "De Mossel" near Ede, The Netherlands (52.06N, 5.75E) at 0–20 cm depth. The soil was a sandy loam with particle size distribution: 3% <2 mm, 17% 2–63 mm, 80% >63 mm, with 4% organic matter. Both species co-occur at this site. Soil was sieved (0.5 cm mesh) to remove pebbles and large root fragments, homogenized and mixed 1:1 with sterilized soil collected from the same field. Soil was sterilized using gamma irradiation (>25 Kgray, Isotron, Ede, The Netherlands). Seeds from both species were sterilized (1 min in 2.5% sodium hypochlorite solution and rinsed with water afterwards) and germinated on sterile glass beads in a climate chamber at 16/8 h light–dark regime and a 20/15°C temperature regime. After germination (c. 1 week), seedlings were stored at 4°C until further use.

The experiment consisted of three phases (Figure 1). In the first phase, soil was conditioned by growing either *J. vulgaris* or *H. lanatus* in monocultures on the soil. Pots (10 × 10 × 11 cm) were filled with 1 kg homogenized soil and kept for 1 week in a climate-controlled greenhouse (60% relative humidity; 16 h light (21°C) and 8 h dark (16°C) photo regime) for the soil to settle. Natural daylight was supplemented by 400 W metal halide lamps (225 mmol m^{-2} s^{-1} PAR, 1 lamp per 1.5 m^2). Seedlings that emerged from the soil were removed. After 1 week, four seedlings of a single species were then transplanted into each pot. There were 288 pots for both species. A third set of 288 pots filled with 1 kg soil was not planted. All planted seedlings of a species were similar in size. Seedlings that died during the first week of the experiment were replaced. The 288 pots of each of the three treatments (*J. vulgaris* monocultures, *H. lanatus* monocultures or "unconditioned" soil) were allocated randomly to one of three replicates. To minimize the effects of local differences in microclimate in the greenhouse, pots were randomly placed on trolleys in the greenhouse and the trolleys were randomly redistributed within the greenhouse twice a week. All pots were watered once every 2 days with demineralized water (18% soil moisture). Eight weeks after transplantation, all above-ground biomass was harvested from each pot, and large root fragments were removed from the soil. The soils from the different pots that belonged to the same treatment-replicate were homogenized so that there were nine batches of soil (3 conditioning treatments × 3 replicates). Subsamples of each of the nine soils were collected to determine soil moisture levels, soil chemical characteristics and soil fungal communities (see below).

2.2.1 | Phase 2

In the second phase, *J. vulgaris* and *H. lanatus* were grown isolated and in interspecific competition, in the three types of soils. A total of 1,026 pots were filled with 930 g (dry weight) soil from the conditioning phase (38 replicate pots for each of the 27 planting/soil combinations). Pots were then planted with a single seedling (*J. vulgaris* or *H. lanatus*) or with one seedling of both species (competition). All planted seedlings of a species were similar in size. In 16 pots, a plant died. Mortality was not related to the treatments and these pots were excluded from the experiment. All pots were watered twice a week with 50 ml 1/8th Hoagland solution (Hoagland & Arnon, 1950) to avoid nutrient deficiency. The soil moisture level in each pot was reset once a week to 18% with demineralized water using a balance. The climatic conditions in the greenhouse were as described above.

At the beginning of the experiment, pots from all treatment combinations were allocated to different sets of 27 pots (3 plantings × 9

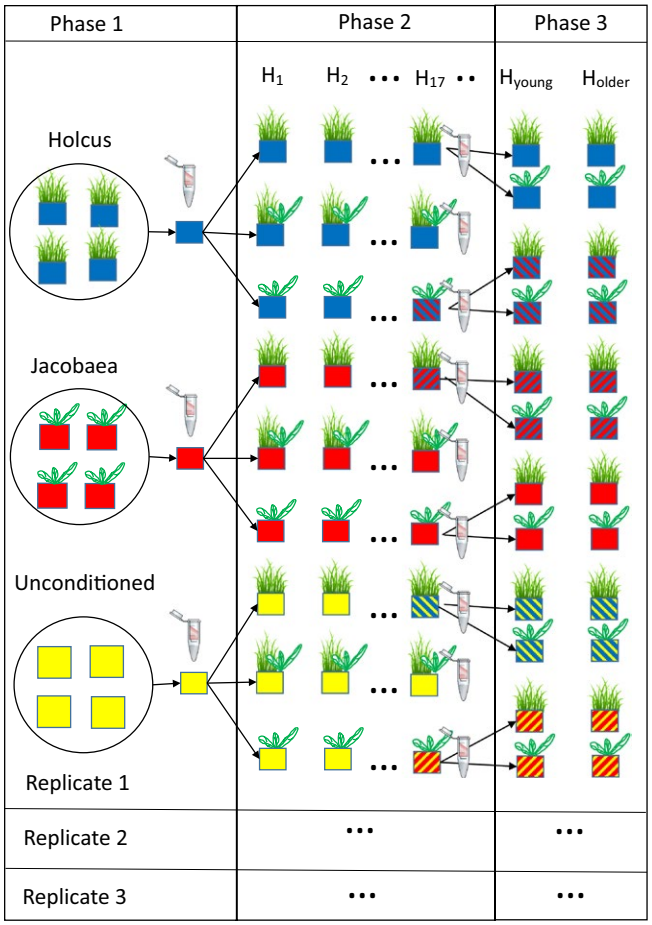

FIGURE 1 Schematic drawing of the experimental design. During the Phase 1, *Holcus lanatus* and *Jacobaea vulgaris* were grown in monocultures in different pots for 8 weeks. A third set of pots filled with soil was not planted (unconditioned). Pots were divided between three replicates, so that there were nine soils. For these nine soil samples, fungal composition and soil abiotic characteristics were determined. In Phase 2, *H. lanatus* and *J. vulgaris* were grown in the nine soils individually, or in interspecific competition (one plant of both species per pot). Twice a week plants were harvested (H) and root–shoot biomass was determined. This was done for 19 harvests. At harvest 17 soils were kept from all treatments and fungal composition and soil abiotic characteristics of these 27 soils were determined again. The soils of the pots with isolated plants were then used in Phase 3 to grow isolated *H. lanatus* or *J. vulgaris* plants for 5 weeks (young) or 9 weeks (older). Details for one of the three replicates are presented

soils). Twice a week one or two sets were randomly selected, and the plants were harvested. This was done for a period of 10 weeks (week 2–11 after transplanting). In total, there were 19 harvests. Harvests were always on Monday morning and Thursday afternoon, so that the time between two harvests was always 3.5 days. The experiment was initially aimed to last for 19 weeks but terminated after 11 weeks, because it became increasingly more difficult to disentangle the roots of the two plants in the pots where two plants were grown, and therefore during the second half of the experiment two sets or 27 plants were harvested. In the latter cases, the two data points from each plant/soil replicate combination were averaged before analysis. At each harvest, the soil was carefully rinsed and the roots cleaned manually by submerging in water. Hereafter, the plant was divided into root and shoot material. For pots that contained one individual of both species, the roots of both plants were carefully separated by hand disentangling them submerged in water. Root and shoot material of each plant was labelled, oven-dried at 70°C for at least 48 hr and weighed. Total biomass and root/shoot ratios were then calculated.

2.2.2 | Phase 3

In week 10 (27 January 2014; 1 week before the final harvest), three randomly selected pots from each of the 27 planting/soil replicate combinations were used to collect soil for a third phase of the experiment. The roots were removed from the soil of each pot, and the soil from the three pots belonging to the same treatment combination was homogenized. A subset of the soil was used for chemical and fungal analysis (See below). New pots (0.5 L) were then filled with 360 g of soil and a single *J. vulgaris* or *H. lanatus* seedling was transplanted into each pot. All planted seedlings of a species were similar in size. The pots were kept in the greenhouse under conditions described above. There were four replicate pots for each soil/plant combination (96 pots). Once a week 35 ml of 1/8th Hoagland solution was added to the pots and pots were watered regularly with demineralized water and kept at 18% soil moisture as described above. After 5 weeks, half of the pots were harvested and root and shoot biomass was measured. Total biomass and root/shoot ratios were then calculated. The other pots were harvested 9 weeks after transplantation.

2.3 | Soil properties

Soil samples collected at the end of the Phase 1 and Phase 2 (27 January 2014; 1 week before the final harvest) were analysed as described by Houba, Temminghoff, Gaikhorst, and Van Vark (2000). Soil samples were oven-dried at 40°C, sieved through a 0.5 mm mesh and 3 g of soil was shaken for 3 hr with 30 ml 0.01 M calcium chloride ($CaCl_2$) solution. pH was measured in the suspension and the filtrate was used to measure phosphate, potassium, nitrate and ammonium concentrations. Soil organic matter content was estimated by loss-on-ignition (LOI) analysis (Ball, 1964). Soil samples were dried at 105°C and 5 g of soil was heated at 430°C and reweighed again. Soil organic matter was calculated as the percentage weight loss.

2.4 | Molecular detection of soil fungal community

The composition of the fungal community in the soil samples collected at the end of the conditioning Phase and the end of Phase 2 was determined by terminal restriction fragment length polymorphism (T-RFLP) analysis as described in Bezemer et al. (2013). Details about the methods are presented in the Supporting Information.

Peaks were aligned to terminal restriction fragments (TRFs) among the soil samples by applying a clustering threshold of 0.5 base pairs. Peaks of each sample were normalized by dividing all peak areas by the total peak area, and true peaks were distinguished from background noise by iteratively removing peaks with larger values than three standard deviations as described in Abo et al. (2006). These analyses were done manually in MS Excel.

2.5 | Data analysis

All data are available in the Dryad Repository (Bezemer, Jing, Bakx-Schotman, & Bijleveld, 2018). The response of total biomass of the two species to the three soils over time was analysed using repeated measures ANOVA with soil identity (three levels) as fixed factor. The analysis tests for an overall effect of soil and for the interaction between soil and time. As plant biomass increases over time, the pure time effect will always be highly significant; these effects are not reported. Total biomass was log-transformed prior to the analyses to fulfil requirements of normality and homogeneity of variance. Data of isolated plants and plants exposed to competition were analysed separately. Individual comparisons between the three soils (independent of time) were based on a Tukey HSD test. The analyses were also carried out for root/shoot ratios.

The absolute growth rate (AGR), the amount of mass increase per day, was determined after fitting the Gompertz plant growth function (Paine et al., 2012) through the total plant biomass data: $Y_t = K(M_0/K)^{\exp^{-r*t}}$, where Y_t is the biomass at time t; K is the upper asymptote of the growth curve, M_0 is the initial biomass and r is the growth rate constant. The curve was fit in MS Excel through each replicate/treatment combination separately. We then used the predicted fit to determine AGR for each of the 19 sampling points for each replicate. Differences in AGRs between soils were analysed using repeated measure analysis as described above. The severity of competition was calculated as the log response ratio (ln[biomass of isolated plant/biomass of plant in competition]) and was calculated for each harvest and each replicate separately (n = 3).

Plant soil feedbacks in Phase 2 were calculated as: ln(conspecific soil) − ln(heterospecific soil), so that negative values indicate that plants grow better in heterospecific soil. In this calculation, only data from plants growing in conditioned soils were used. The feedback effect was calculated separately for each replicate (i.e. ln(conspecific soil replicate 1) − ln(heterospecific soil replicate 1), etc., so that there were three independent data points for each sampling time. This was done for plant species grown in isolation or in competition. Statistical significance was not determined based on these feedback values, but was based on a repeated measure analysis comparing log-transformed biomass data from plants grown in own and foreign soil over time. A significant effect of soil identity indicates that the feedback effect is significant. We tested for an overall feedback effect (overall significant difference between the two soil types) and whether the feedback effect changed over time (soil x time interaction).

Soil properties were analysed using one-way ANOVA (end of Phase 1) and two-way ANOVA (end of Phase 2). For the latter, the two main factors were conditioning treatments during Phase 1 (*J. vulgaris*, *H. lanatus*, Unconditioned), and conditioning treatments during Phase 2 (*J. vulgaris* isolated, *H. lanatus* isolated, both species in competition). Organic matter for Phase 1 and NO_3 for Phase 2 were log-transformed to improve normality.

Fungal community composition (based on the presence/absence of TRFs) was analysed using multivariate analyses in Canoco 5 (Ter Braak & Šmilauer, 2012). Unconstrained principle component analysis (PCA) was used to visualize the different treatments imposed during Phase 1 and Phase 2. This was done for the combined dataset of Phase 1 and Phase 2. Subsequently, we analysed the data collected during Phase 1 and Phase 2 separately with a distance-based redundancy analysis (DB-RDA) using constrained PCO scores (Jaccard similarity matrix), to determine to what extent the treatments influenced fungal composition. For Phase 1 data, the impact of the three conditioning treatments was analysed. For Phase 2 data, we analysed how the soil treatments imposed during (a) Phase 1 (three conditioning types) and (b) Phase 2 (three planting types) influenced fungal community composition. Significance was inferred from a permutation test with 999 permutations.

To examine whether repeated conspecific soil conditioning resulted in more distinct fungal communities than heterospecific conditioning, we analysed the number of unique TRFs in samples from soils with repeated conspecific (*Jacobaea–Jacobaea* or *Holcus–Holcus*) and with successive heterospecific conditioning (*Jacobaea–Holcus* or *Holcus–Jacobaea*). We predicted that the proportion of unique TRFs would be highest when the two repeated conspecific conditioned soils were compared (i.e. that the fungal communities in these samples would be most different). This was determined for each replicate pair, and pseudo-replicates (there are three comparisons possible for each replicate of one treatment with the replicates of the other treatment) were averaged. The dissimilarities among the different conditioning treatments were then analysed using ANOVA.

The relationship between fungal composition and plant growth in Phase 2 and Phase 3 was determined using constrained multivariate analyses (CCA). We determined the % explained variance for total biomass of young and older plants during both Phase 2 and Phase 3. For Phase 2, we used the mean total biomass of the first four harvests as data for young plants, and the mean total biomass of the final four harvests as data for older plants. The % explained variance for young and older plants was then determined using the initial fungal composition at Phase 2 (measured at the end of Phase 1) and the fungal composition measured at the end of Phase 2. The percentage explained variance for young and older plants grown in Phase 3 was determined using the initial fungal composition at Phase 3 (measured at the end of Phase 2). Similar analyses were carried out for soil abiotic characteristics. These data were continuous and were analysed using linear constrained multivariate analyses (RDA). Since the range in values varies greatly between the

chemical characteristics, the abiotic data were standardized prior to analysis. All multivariate analyses were carried out in Canoco 5 (Ter Braak & Šmilauer, 2012).

Biomass of young and older plants in Phase 3 was analysed using three-way ANOVA with the following factors: soil treatment during Phase 1 (*Jacobaea* soil, *Holcus* soil or unconditioned soil); soil treatment during Phase 2 (isolated *J. vulgaris* or isolated *H. lanatus*) and plant age (young or older). This was done for *J. vulgaris* and *H. lanatus* separately, data (total biomass) were log-transformed prior to analysis. Two-way ANOVAs were then used to determine the effects of (i) the Phase 1 and (ii) the Phase 2 treatments separately for young and older plants. All univariate analyses were carried out using Statistica 13.0 (Statsoft).

3 | RESULTS

3.1 | Biomass responses during Phase 2

Young isolated *J. vulgaris* plants produced more than twice as much biomass in *Holcus* soil than in *Jacobaea* soil and intermediate in unconditioned soil (Figure 2; Table 1). However, the soil effect diminished over time, and from week 6 onwards productivity was similar in all soils resulting in a significant soil x time interaction (Figure 2; Table 1). Isolated *H. lanatus* plants produced slightly (10%) more biomass in *Jacobaea* soil than in the other soils (p = .053; Table 1) but this did not change over time (Figure 2, Table 1). In competition, biomass of *J. vulgaris* was strongly reduced (42%) and that of *H. lanatus* increased (34%) in *Jacobaea* soil (Figure 2; Table 1).

The root:shoot ratio of isolated *J. vulgaris* plants increased over time from 0.5 to 2, but did not differ between soils. The root:shoot ratio of isolated *H. lanatus* varied between soils and was lowest in unconditioned soil. In competition, the root:shoot ratio of both species was highest when grown in conspecific soil; 21% higher for *J. vulgaris* plants in *Jacobaea* soil, and 17% higher for *H. lanatus* in *Holcus* soil (Figure S1; Table 1).

The predicted biomass productivity per day (AGR) of isolated *J. vulgaris* plants was lower in *Jacobaea* soil and unconditioned soil than in *Holcus* soil during the first weeks of growth but higher in the two other soils during the last weeks resulting in a significant soil × time interaction (Table 1; Figure 3). Overall, in competition, the AGR of *H. lanatus* was much higher than that of *J. vulgaris* in all soils. In competition, AGRs in *Jacobaea* soil were highest for *H. lanatus* and lowest for *J. vulgaris* plants. For isolated plants, initially the AGR of *H. lanatus* plants was higher than that of *J. vulgaris* in *Jacobaea* soil and unconditioned soil, but this pattern was reversed during the later stages of growth when the AGR of *J. vulgaris* was larger than *H. lanatus* in all soils, but particularly so in *Jacobaea* soil (Figure S2).

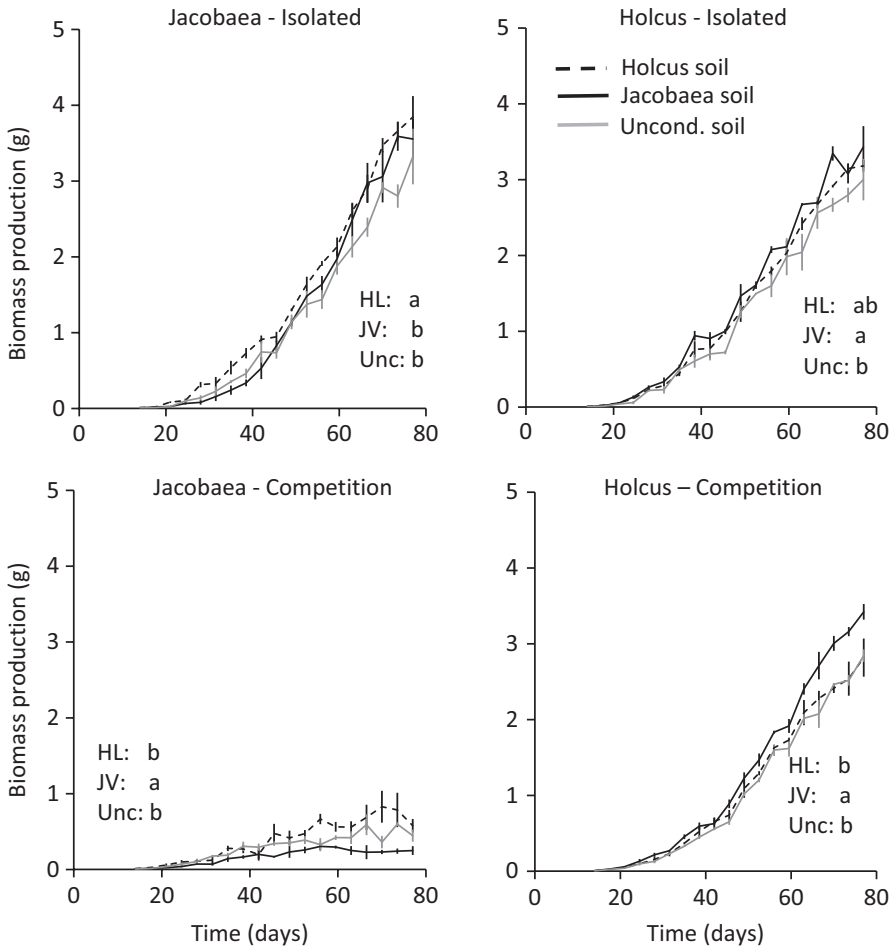

FIGURE 2 Temporal dynamics of biomass productivity of *Jacobaea vulgaris* and *Holcus lanatus* in Phase 2. Plants were grown isolated or in interspecific competition in soil conditioned by *J. vulgaris* (black line), *H. lanatus* (dashed line), or in unconditioned soil (grey line) and harvested twice a week for a period of 11 weeks. Mean total biomass is shown (±1 *SE*), n = 3 for each harvest. For each panel, the results of a Tukey HSD post hoc comparison for the overall treatment effect (independent of time) is also presented. Treatments with identical letters are not significantly different. Statistical results of the repeated measures ANOVA are presented in Table 1

Isolated *J. vulgaris* plants exhibited a strong negative conspecific feedback but the strength of the feedback effect diminished over time (Figure 4; Table 1). Isolated *H. lanatus* also had a negative conspecific feedback effect but this was only marginally significant (p = .053) and did not change over time (Table 1). In competition, both species had a negative conspecific feedback, but the negative feedback of *J. vulgaris* became more negative, while for *H. lanatus* there was no significant change over time (Figure 4; Table 1).

The severity of competition for *J. vulgaris* plants increased strongly over time and was higher in *Jacobaea* soil than in the other two soils particularly during the final weeks resulting in a significant soil effect and soil × time interaction (Table S1; Figure S3). The severity of competition for *H. lanatus* was much lower and did not differ between soils. Interestingly during the seedling stage, when grown in *Jacobaea* soil, *H. lanatus* performed better when competing with *J. vulgaris* than when grown alone (facilitation, i.e. negative competition severity; Figure S3).

3.2 | Abiotic and biotic soil characteristics

At the end of Phase 1, in pots with plant growth, independent of which species had been grown in the soil, K levels were 48% lower and organic matter 16% lower than in the unconditioned soil. NO_3 levels were 40% lower in soil in which *H. lanatus* had been grown than in the other two treatments (Table 2). At the end of Phase 2, differences in soil characteristics inferred in Phase 1 were still visible. K levels in Phase 2 were all lower than in Phase 1, but also in Phase 2, K levels were still more than twice as high in soil in which no plant had grown during Phase 1 than in the soils where plants had been grown during Phase 1. The pH was slightly lower in soil conditioned by *H. lanatus* during Phase 1 than in the other soils (Table 2).

Soil fungal composition at the end of Phase 1 differed from the composition at the end of Phase 2 (Figure 5). At the end of Phase 1, the three conditioning treatments explained 27.1% of the variation in TRFs, but due to low sample size, this was not significant (RDA, F = 1.1; p = .08). For Phase 2 soil, all treatments combined explained 21.1% of the fungal community composition (F = 1.4; p = .001) but this was mainly explained by the treatments imposed during Phase 1 (12.3%; F = 1.6; p = .001) and not significantly by the treatments imposed during Phase 2 (8.8%; F = 1.1; p = .14). In the PCA, the soils originating from the unconditioned treatment in Phase 2 were still separate from the two Phase 1 treatments with plants at the end of Phase 2 (Figure 5). At the end of Phase 2, there was no clear distinction between the fungal communities from soil where *H. lanatus* or *J. vulgaris* had been grown in Phase 1 or 2 (Figure S4).

Comparison of the number of unique TRFs among samples showed that the largest number of unique TRFs was detected when fungal communities from soil where *H. lanatus* had been grown twice

TABLE 1 Results of repeated measure analyses testing the effects of soil treatments (*Jacobaea* soil, *Holcus* soil, unconditioned soil) in Phase 1 on total biomass, root:shoot ratio, absolute growth rates (AGR) and conspecific plant soil feedback effects of *Jacobaea vulgaris* or *Holcus lanatus* grown in isolation or in competition during Phase 2. F-values and p-values are presented and degrees of freedom (df) for the overall effect of "soil" and the "soil × time" interaction. Significant p-values are presented in bold

	Soil		Soil × time	
	F	*p*	*F*	*p*
Total biomass	(*df* = 2,6)		(*df* = 36,108)	
Jacobaea isolated	20.24	**.002**	1.59	**.035**
Jacobaea competition	18.22	**.003**	2.29	**<.0001**
Holcus isolated	4.95	.053	1.45	.074
Holcus competition	57.24	**<.0001**	1.30	.15
Root:Shoot ratio	(*df* = 2,6)		(*df* = 36,108)	
Jacobaea isolated	1.83	.24	1.22	.22
Jacobaea competition	13.75	**.005**	0.60	.95
Holcus isolated	24.43	**.001**	1.58	**.038**
Holcus competition	11.98	**.008**	1.22	.22
AGR	(*df* = 2,6)		(*df* = 36,108)	
Jacobaea isolated	3.13	.12	10.37	**<.0001**
Jacobaea competition	12.99	**.007**	2.32	**.0004**
Holcus isolated	4.96	.053	1.32	.14
Holcus competition	10.21	**.011**	1.40	.094
Conspecific plant-soil feedback	(*df* = 1,4)		(*df* = 18,72)	
Jacobaea isolated	17.79	**.014**	2.10	**.014**
Jacobaea competition	37.00	**.004**	3.14	**.0003**
Holcus isolated	7.28	.054	1.05	.42
Holcus competition	63.60	**.001**	1.44	.13

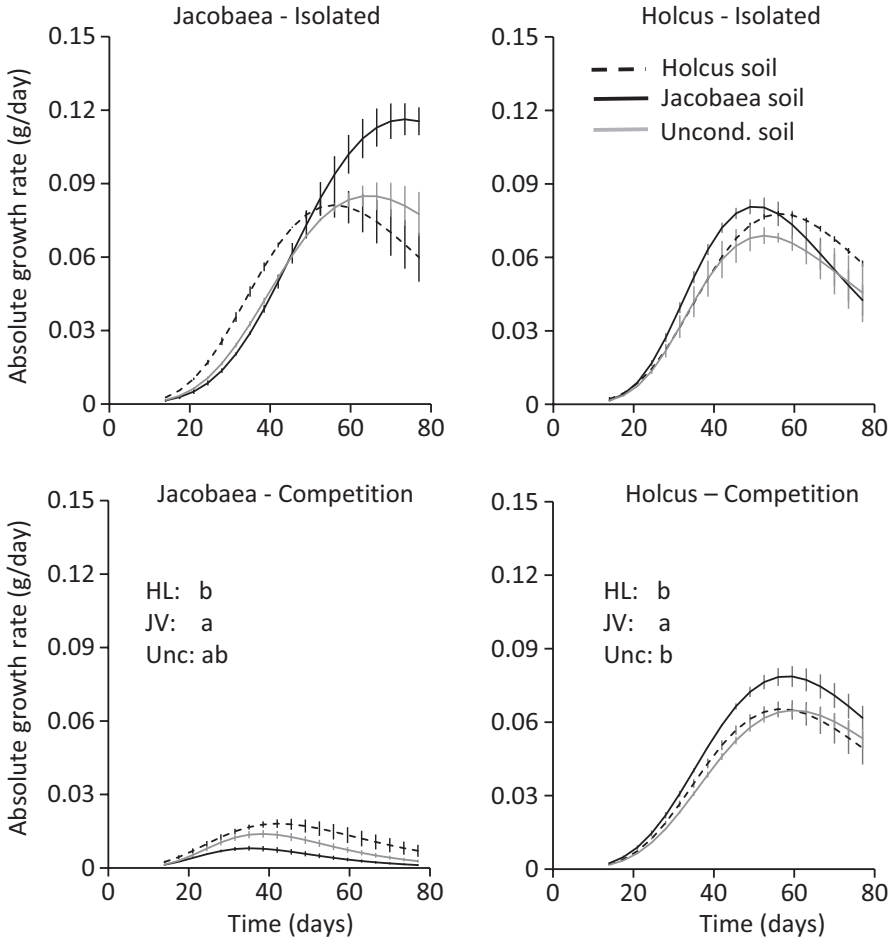

FIGURE 3 Temporal dynamics of the predicted absolute growth rates (AGR, mg biomass per day) for *Jacobaea vulgaris* and *Holcus lanatus* in Phase 2. Plants were grown isolated or in interspecific competition in soil conditioned by *J. vulgaris* (black line), *H. lanatus* (dashed line) or in unconditioned soil (grey line). The AGR was fitted through the 19 data points of each of the three replicate datasets for each treatment. The fitted relationships through each dataset are presented in the appendix Figure S6. Means are shown (±1 *SE*), $n = 3$. For the two panels where the overall treatment effect (independent of time) was significant, the results of the Tukey HSD post hoc comparison for the three treatments are also presented. Treatments with identical letters are not significantly different. Statistical results of the repeated measures ANOVA are presented in Table 1

were compared with communities where *J. vulgaris* had been grown twice. Heterospecific conditioned communities were less dissimilar. These results indicate that plant species create specific fungal communities, but that this is reversible by growing another species subsequently in the soil (Figure S5).

During Phase 2, biomass of young *J. vulgaris* plants grown in competition was related to the composition of fungi in the soil the plants were growing in (i.e. measured at the end of Phase 1). The biomass of older *J. vulgaris* plants grown in isolation was also related to the current fungal community composition (i.e. measured at the end of Phase 2; Table S2). Biomass of young and older *H. lanatus* plants was not related to fungal community composition. When grown in isolation, the biomass of both *H. lanatus* and *J. vulgaris* was related to soil abiotic characteristics (Table S2). During Phase 3, the biomass of older *J. vulgaris* plants was significantly explained by the abiotic starting conditions (i.e. measured at the end of Phase 2), but the fungal community also explained a marginally significant part of the variation for young *H. lanatus* and older *J. vulgaris* plants (Table S3).

3.3 | Biomass responses during Phase 3

In Phase 3, young *J. vulgaris* plants tended to produce less biomass in soil in which *J. vulgaris* had been grown in Phase 2, but this was not significant due to large variation among replicates ($F_{2,18} = 2.79$; $p = .088$; Figure 6). Independent of plant age, *J. vulgaris* produced most biomass in soil where *H. lanatus* had been grown in Phase 1, intermediate in soil that was unconditioned in Phase 1 and least in soil where *J. vulgaris* had been grown during the first phase, resulting in a significant Phase 1 effect (Table 3). *H. lanatus* produced least biomass in soil where *H. lanatus* plants had been grown during Phase 2 (Figure 6), and this was true for young and older plants (significant Phase 2 effect, Table 3).

4 | DISCUSSION

In this study, we examined the dynamic growth patterns of two plant species grown in insolation and in competition in soil conditioned by conspecifics, heterospecifics or in unconditioned soil. Furthermore, we tested the response of both plant species again in a third growth phase to examine whether the growth responses observed during the second phase were due to changes in the soil or due to changes in the responsiveness of younger and older plants. At the same time, we also determined how sequential conditioning influenced feedback responses. Our results highlight three important aspects of the temporal dynamics of PSFs that are often overlooked in this research field. First, the response to soil conditioning

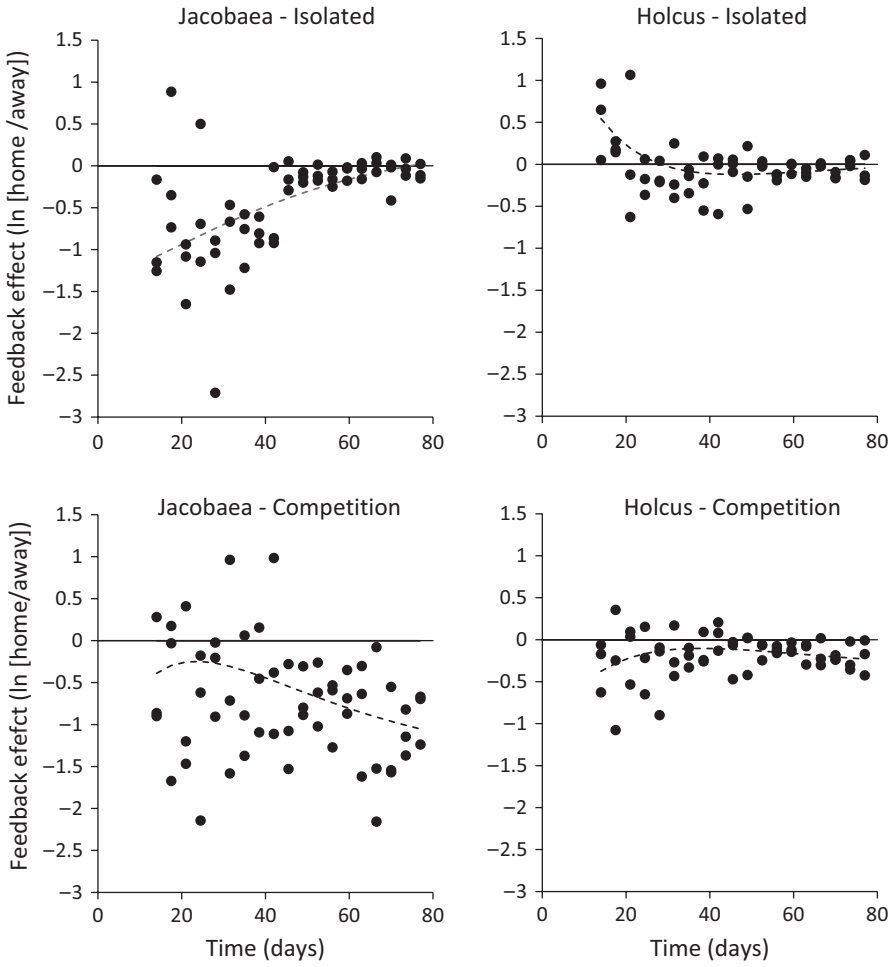

FIGURE 4 Temporal dynamics of the conspecific feedback effects for *Jacobaea vulgaris* and *Holcus lanatus* grown in isolation and in competition. The feedback effects were calculated for each harvest time as ln(performance in own soil) − ln(performance in other soil) and were calculated for each of the three replicates separately. The dotted line is the mean feedback effect derived from the fitted relationships between biomass and time (see methods). Statistical results comparing performance in own and other soil over time are presented in Table 1

depends greatly on the age of the response plant. Second, these temporal responses to soil conditioning vary, even directionally, depending on when the plant grows in isolation or competes with other plants. Third, PSFs depend on legacies of previously grown plants that remain in the soil. Below we will discuss these findings in more detail.

When grown in isolation, *J. vulgaris* produced less biomass in soil conditioned by conspecifics but this effect diminished over time. Older plants even produced more biomass per day in conspecific than in heterospecific conditioned soil. Although less strong, a similar trend was observed for *H. lanatus*. This means that depending on the growth period during the test phase, we would come to different conclusions about the strength and even direction of PSF effects. Hence, our results provide strong evidence that feedbacks can differ greatly between younger and older plants (Dudenhöffer et al., 2018; Kardol et al., 2013). Variability in feedback during plant growth stages could be due to, e.g. changes in vulnerability to soil pathogens or the relative benefits derived from arbuscular mycorrhizal fungi (Bardgett, Bowman, Kaufmann, & Schmidt, 2005; Hartnett, Samenus, Fischer, & Hetrick, 1994). Several studies have shown, for example, that seedling stages are particularly susceptible to soil pathogens (Hersh et al., 2012; Packer & Clay, 2000) and sometimes respond negatively to mycorrhizal fungi even though the adult plant benefits from those fungi (Hartnett et al., 1994; Koide, 1985). This could explain the positive effect in self-conditioned soil for individually grown *J. vulgaris* plants during later growth stages in our study. Alternatively, it is also possible that abiotic limitations such as pot size or nutrients hampered the later growth of the already larger *J. vulgaris* plants in pots with *Holcus* soil or with unconditioned soil. However, we did not see evidence for this in changes in the root–shoot ratios which increased similarly in all soil treatments for this plant species. Furthermore, all pots were fertilized weekly which we assume has limited nutrient deficiency effects on plant growth. In contrast, isolated *H. lanatus* plants had the lowest root–shoot ratios when grown in unconditioned soil. In this treatment, *H. lanatus* plants also produced least biomass. This could be due to differences in the microbial community but we did not find evidence for this. Instead the multivariate analyses show that changes in *H. lanatus* biomass were related to differences in nutrients of the different soils (Table S2). Interestingly, at the end of Phase 1, organic matter content in soils in which plants had been grown was lower than in soils where no plant had been grown for the previous months. It is possible that the microbial community in the soil was more active in the presence of plants, probably because plants via root exudates supply the soil food web with easily accessible carbon, providing energy which can be used by microbes

TABLE 2 Abiotic characteristics of soils collected at the end of Phase 1 and at the end of Phase 2 (week 10). Means are shown (±1 *SE*), and *F*-values obtained from a one-way ANOVA for Phase 1, and a two-way ANOVA for Phase 2. The two main factors for the analysis for Phase 2 are treatments during Phase 1 (*Jacobaea vulgaris*, JV; *Holcus lanatus*, HL; Unconditioned, Unc), and treatments during Phase 2 (JV isolated, HL isolated and the mix of both species). Degrees of freedom (*df*) are also presented. **p* < .05; ***p* < .01; ****p* < .001. Within columns, means followed by identical letters are not significantly different based on a Tukey HSD test. Significant *p*-values are presented in bold

	K (mg/kg)	PO_4 (mg/kg)	NH_4 (mg/kg)	NO_3 (mg/kg)	pH	OM (%)
End Phase 1						
JV conditioned (JV)	29.5 ± 0.1a	11.8 ± 0.4	2.4 ± 0.2	4.5 ± 0.6a	5.1 ± 0.03	2.9 ± 0.01a
HL conditioned (HL)	30.5 ± 0.4a	11.7 ± 0.7	3.9 ± 0.8	6.6 ± 0.5b	5.1 ± 0.01	3.1 ± 0.1ab
No plant (Unc)	58.0 ± 0.5b	11.8 ± 0.7	4.2 ± 1.9	3.4 ± 0.1a	5.1 ± 0.03	3.6 ± 0.2b
F (*df* = 2,6)	**1,726.3*****	0.03	0.64	**14.6***	0.1	**9.4***
End Phase 2						
JV-JV	7.5 ± 0.3a	11.3 ± 0.4	0	0.3 ± 0.26	5.1 ± 0.02bd	3.6 ± 0.1
JV-HL	7.1 ± 0.9a	12.0 ± 0.1	0	0.2 ± 0.10	5.0 ± 0.01ad	3.9 ± 0.1
JV-mix	8.2 ± 1.6a	12.1 ± 0.2	0	0.0 ± 0.00	5.1 ± 0.01bd	4.0 ± 0.1
HL-JV	6.6 ± 0.5a	10.2 ± 0.2	0	0.3 ± 0.03	5.0 ± 0.00ac	3.7 ± 0.4
HL-HL	7.6 ± 1.5a	10.6 ± 0.6	0	0.4 ± 0.00	4.9 ± 0.06a	3.8 ± 0.1
HL-mix	6.5 ± 0.2a	11.7 ± 0.8	0	0.2 ± 0.03	4.9 ± 0.02ac	4.1 ± 0.1
Unc-JV	18.1 ± 3.1b	11.0 ± 0.7	0	0.1 ± 0.03	5.1 ± 0.00b	4.3 ± 0.2
Unc-HL	17.4 ± 1.7b	10.4 ± 0.4	0	0.2 ± 0.19	5.1 ± 0.01b	3.8 ± 0.4
Unc-mix	17.1 ± 1.9b	11.5 ± 0.3	0	0.1 ± 0.06	5.0 ± 0.00bcd	3.9 ± 0.4
Phase 1: *F* (*df* = 2,18)	**43.4*****	**3.7***	n.a.	1.8	**62.9*****	0.2
Phase 2: *F* (*df* = 2,18)	0.01	3.2	n.a.	1.6	**4.9***	0.3
P1 × P2: *F* (*df* = 4,18)	0.2	0.9	n.a.	0.3	**6.8****	1.0

to break down organic matter (Dijkstra & Cheng, 2007; Kuzyakov, Friedel, & Stahr, 2000). It is also important to mention that plant growth can alter abiotic characteristics of the soil such as soil aggregation or density, which, in turn can also influence the rooting of plants growing later in that soil.

A large number of studies have shown that PSFs depend on whether the plant grows alone or in competition (e.g. Casper & Castelli, 2007; Crawford & Knight, 2017; Jing et al., 2015). Our study now shows that the temporal response to soil conditioning is also greatly influenced by whether the plant experienced competition or not. In competition, the negative conspecific feedback of *J. vulgaris* increased in strength over time, and this benefited the competitor *H. lanatus*. These effects could not be predicted from the results obtained from the individually potted plants. Our results therefore have important implications for plant soil feedback research. Not only does the PSF of an individually grown plant differ from that of a plant that experiences competition but the temporal dynamics of PSF also differ greatly depending on these conditions, and hence the time of harvest and the experimental design will greatly influence the outcome of the experiment. In a recent study, Maron, Laney Smith, Ortega, Pearson, and Callaway (2016) found no significant interaction effects between competition and PSF on plant growth. Maron et al. (2016) argued that when a plant competes with a heterospecific plant species in conspecific-cultured soil, this will dilute the negative feedback effects of species-specific soil pathogens. In contrast, by repeatedly measuring throughout the growth period, we found that *J. vulgaris*, a species that exhibits negative conspecific feedback, suffered increasingly form interspecific competition in its own soil over time. It appears that *H. lanatus*, the stronger competitor of the two, benefits from the additional soil-mediated negative effect on *J. vulgaris*. So both the negative conspecific feedback and the weak competitiveness of *J. vulgaris* resulted in the poor performance of *J. vulgaris* in conspecific soil. Interestingly, during the first 2 weeks of growth, when the two species were too small to compete for space, *H. lanatus* performed better in competition than when grown alone. This suggests that *J. vulgaris* seedlings in the conspecific soil may have increased the potential of this soil for *H. lanatus* growth or facilitated the growth of *H. lanatus* directly. The mechanisms for these positive effects are unknown but there are several plausible explanations. For example, plant-mediated changes in soil moisture levels, release of particular chemical compounds in the soil or indirectly via the effects of *J. vulgaris* on microbes that benefit *H. lanatus* (Bardgett & Wardle, 2010; Miki, Ushio, Fukui, & Kondoh, 2010). Taken together, our results demonstrate that interspecific competition can exacerbate negative conspecific PSF, but this does not necessarily change the hierarchy of competition.

During the third phase, young *J. vulgaris* plants again tended to be more susceptible to negative soil feedbacks than older plants, suggesting that the patterns that we observed during the second

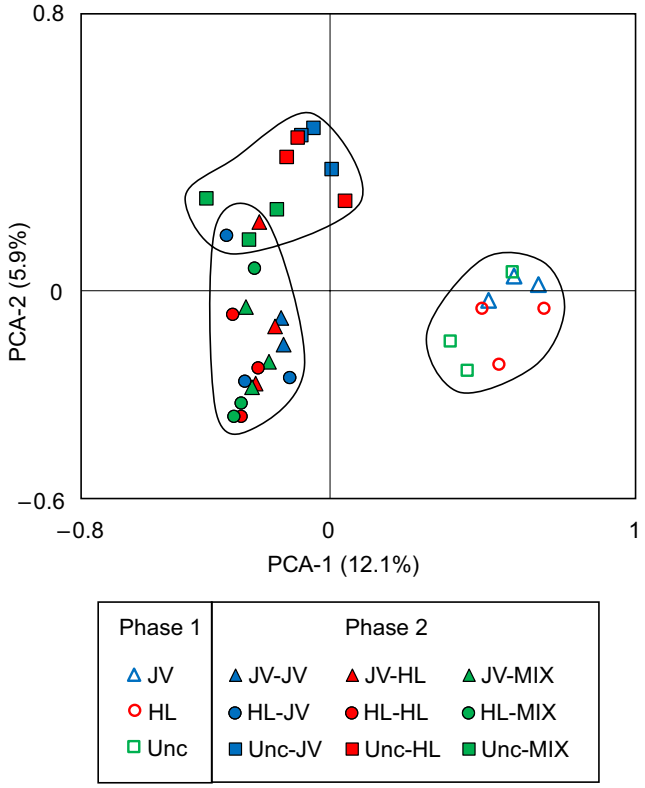

FIGURE 5 Composition of the fungal community at the end of Phase 1 and at the end of Phase 2. Sample scores for the first two axes of an unconstrained principle component analysis (PCA) are presented. Percentage variation explained by both axes is also shown. Open symbols represent samples from Phase 1, closed symbols those from Phase 2. In Phase 2, blue symbols represent soils in which *Jacobaea vulgaris* had been grown in Phase 2, red symbols soils from *Holcus lanatus* and green samples soils in which both species were grown in competition. Triangles (*J. vulgaris* soil), circles (*H. lanatus* soil) and squares (unconditioned soil) represent Phase 1 treatments

phase were not due to changes in the soil but rather due to temporal changes in the responsiveness of the plant. Remarkably, the growth of *J. vulgaris* was still influenced by the soil conditioning treatments of the first growth phase, and not by conditioning during the later growth phase, while an opposite response was observed for *H. lanatus*. This illustrates how legacies that are already present in the soil can influence PSF responses. The results have important implications for PSF research since it is evident from our study that the origin and conditions of the starting soil can greatly influence the outcome of the experiment. Standardizing among experiments in the starting conditions of the soil (community) is virtually impossible as microbial communities are highly variable over time and space and greatly depend on the plant species that are growing in the soil, but the implications of different starting conditions on the outcome of the experiments are rarely considered. Such sequential legacy effects on plant growth were recently shown in another study (Wubs & Bezemer, 2018) and our study now provides evidence that these legacy effects are also detectable in the composition of the soil fungal community. There were clear differences in the fungal community at the end of Phase 2, depending on whether during Phase 1 plants had grown in the soil or not. How long these legacies will remain in the soil is not known but our study shows that they can be more important than the conditioning effects created by the most recent plant species. Wubs and Bezemer (2018) showed that the sequence of species that condition the soil impacted the sign and magnitude of PSF for *J. vulgaris*. We now show that while this was true for *J. vulgaris*, this was not significantly so for *H. lanatus*. *J. vulgaris* is a plant that responds sensitively to biotic and abiotic changes in the soil (Joosten, Mulder, Klinkhamer, & Van Veen, 2009; Van de Voorde et al., 2011). Whether this explains why this species is more sensitive to previous soil legacies than *H. lanatus* and how general these legacy effects are among species remains to be tested. Interestingly, even though we found that repeated conspecific conditioning for both species had a tendency to lead to more negative PSFs which is consistent with previous studies (Mazzola, 1999; Packer & Clay, 2004), this was not evident from the fungal community patterns. We therefore did not find direct evidence supporting our hypothesis that repeated conditioning leads to more distinct plant species-specific soil fungal communities. However, we did find that repeated conspecific conditioning led to an increase in the number of unique TRFs providing some indirect evidence for our hypothesis. It is important to note that the soil that was used for the next phase was first removed from the pot so that we could remove the roots from the soil. This action undoubtedly has disturbed the soil and influenced soil communities, in particular soil inhabiting fungi. More studies are needed that examine at what time-scales plant growth changes the composition of soil communities, how the duration of plant growth influences these effects and how rapidly later growing plants of different species can change this.

In conclusion, we show that the direction and magnitude of conspecific feedback depends on plant life stage and competition, and also on previous legacy effects in the soil of earlier plant growth. The frequently reported negative conspecific PSF of *J. vulgaris* diminished over time when the plant grew alone but exacerbated over time when the plant was exposed to interspecific competition. Our study highlights the need to incorporate dynamic PSFs in research on plant population, community and ecosystem dynamics.

ACKNOWLEDGEMENTS

We thank Jan van Walsem at the Plant Ecology and Nature Conservation group of Wageningen University for support with the chemical analysis, and two anonymous reviewers and the Associate Editor Paul Kardol for very useful comments on an earlier version of the manuscript. The research was supported by the Netherlands Organisation for Scientific Research (NWO VICI grant 865.14.006 to T.M.B.). This is publication number 6511 of the Netherlands

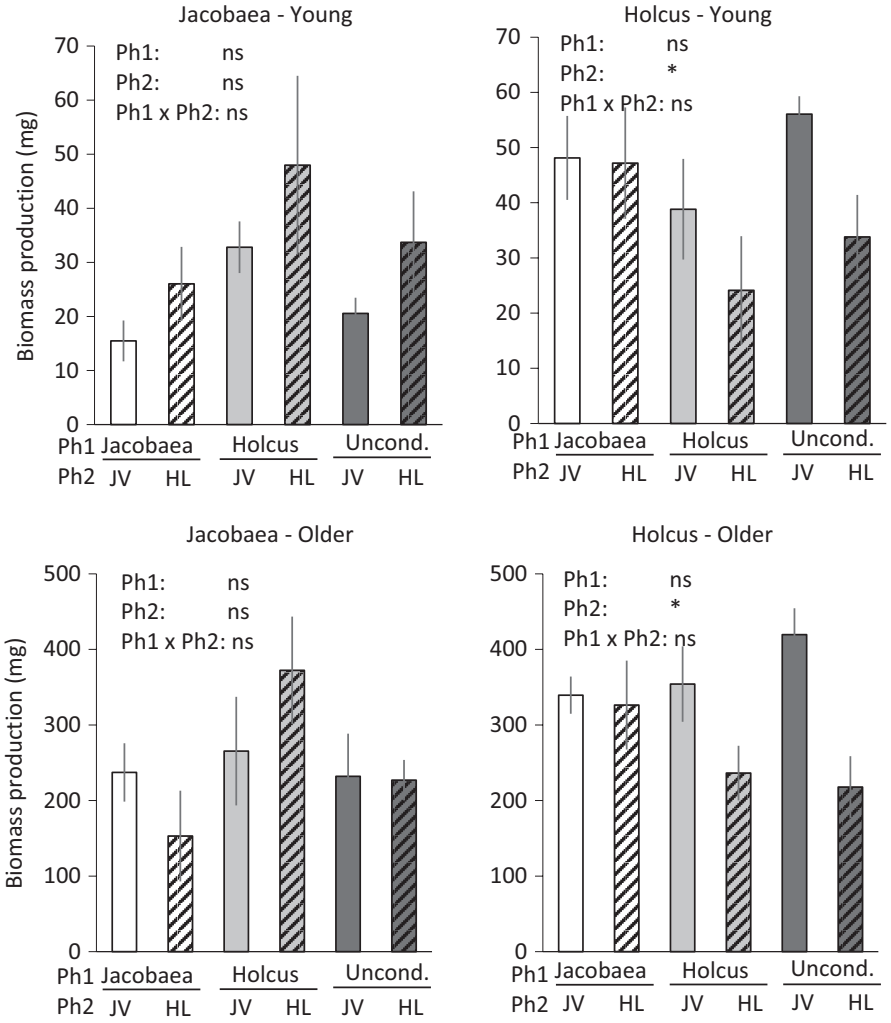

FIGURE 6 Biomass production of 5-week-old (young) and 9-week-old (older) *Jacobaea vulgaris* (JV) and *Holcus lanatus* (HL) plants grown in Phase 3. Plants were grown in isolation in soil conditioned during Phase 1 (Ph1) by JV, HL or in unconditioned soil (Uncond.), and in Phase 2 (Ph2) by isolated JV or HL plants. Means are shown (± *SE*), $n = 4$. Within each panel, the results of a two-way ANOVA testing the effects of Phase 1 and Phase 2 are also presented. *$p < .05$; ns indicates not significantly different

TABLE 3 Results of a three-way ANOVA testing the effects of Phase 1 treatments (*Jacobaea vulgaris* soil, *Holcus lanatus* soil, unconditioned soil), Phase 2 treatments (isolated *J. vulgaris*, isolated *H. lanatus*) and plant age (young and older plants) on total biomass of *J. vulgaris* and *H. lanatus* during Phase 3. *F*-values, *p*-values and degrees of freedom (*df*) are presented. Significant *p*-values are presented in bold

		J. vulgaris		*H. lanatus*	
	df	*F*	*p*	*F*	*p*
Phase 1	2,36	4.89	**.013**	2.70	.081
Phase 2	1,36	0.79	.38	11.38	**.002**
Plant age	1,36	182.1	**<.0001**	296.1	**<.0001**
Phase 1 × Phase 2	2,36	0.50	.61	1.96	.16
Phase 1 × age	2,36	0.02	.98	1.23	.31
Phase 2 × age	1,36	1.77	.19	0.00	.99
Phase 1 × Phase 2 × age	2,36	1.54	.23	0.15	.86

Institute of Ecology (NIOO-KNAW). The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

T.M.B., J.J. and E.-J.B. designed the experiment and collected the data. T.B.-S. performed the molecular analysis. T.M.B. analysed the data and wrote the first draft of the manuscript. J.J. and E.-J.B. contributed to later versions of the manuscript and all authors approved publication.

DATA ACCESSIBILITY

All data related to this publication are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c3648g4 (Bezemer et al., 2018).

ORCID

T. Martijn Bezemer http://orcid.org/0000-0002-2878-3479

REFERENCES

Abo, Z., Schuette, U. M. E., Bent, S. J., Williams, C. J., Forney, L. J., & Joyce, P. (2006). Statistical methods for characterizing diversity of microbial communities by analysis of terminal restriction fragment length polymorphisms of 16S rRNA genes. *Environmental Microbiology*, *8*, 929–938.

Ball, D. F. (1964). Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. *European Journal of Soil Science*, *15*, 84–92. https://doi.org/10.1111/j.1365-2389.1964.tb00247.x

Bardgett, R. D., Bowman, W. D., Kaufmann, R., & Schmidt, S. K. (2005). A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution*, *20*, 634–641. https://doi.org/10.1016/j.tree.2005.08.005

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

Beddows, A. R. (1961). Biological flora of the British isles: *Holcus lanatus* L. *Journal of Ecology*, *49*, 421–430. https://doi.org/10.2307/2257274

Bever, J. D., Westover, K. M., & Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology*, *85*, 561–573. https://doi.org/10.2307/2960528

Bezemer, T. M., Jing, J., Bakx-Schotman, J. M. T., & Bijleveld, E. J. (2018). Data from: Plant competition alters the temporal dynamics of plant-soil feedbacks. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.c3648g4

Bezemer, T. M., Lawson, C. S., Hedlund, K., Edwards, A. R., Brook, A. J., Igual, J. M., … Van der Putten, W. H. (2006). Plant species and functional group effects on abiotic and microbial soil properties and plant-soil feedback responses in two grasslands. *Journal of Ecology*, *94*, 893–904. https://doi.org/10.1111/j.1365-2745.2006.01158.x

Bezemer, T. M., Van der Putten, W. H., Martens, H., Van de Voorde, T. F. J., Mulder, P. P. J., & Kostenko, O. (2013). Above- and below-ground herbivory effects on below-ground plant–fungus interactions and plant–soil feedback responses. *Journal of Ecology*, *101*, 325–333. https://doi.org/10.1111/1365-2745.12045

Casper, B. B., & Castelli, J. P. (2007). Evaluating plant-soil feedback together with competition in a serpentine grassland. *Ecology Letters*, *10*, 394–400. https://doi.org/10.1111/j.1461-0248.2007.01030.x

Connolly, J., Wayne, P., & Murray, R. (1990). Time course of plant-plant interactions in experimental mixtures of annuals – Density, frequency, and nutrient effects. *Oecologia*, *82*, 513–526. https://doi.org/10.1007/BF00319795

Crawford, K. M., & Knight, T. M. (2017). Competition overwhelms the positive plant–soil feedback generated by an invasive plant. *Oecologia*, *183*, 211–220. https://doi.org/10.1007/s00442-016-3759-2

Dijkstra, F. A., & Cheng, W. (2007). Interactions between soil and tree roots accelerate long-term soil carbon decomposition. *Ecology Letters*, *10*, 1046–1053. https://doi.org/10.1111/j.1461-0248.2007.01095.x

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

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*, 344–347. https://doi.org/10.1038/242344a0

Harper, J. L., & Wood, W. A. (1957). *Senecio jacobaea* L. *Journal of Ecology*, *45*, 617–637. https://doi.org/10.2307/2256946

Hartnett, D. C., Samenus, R. J., Fischer, L. E., & Hetrick, B. (1994). Plant demographic responses to mycorrhizal symbiosis in tallgrass prairie. *Oecologia*, *99*, 21–26. https://doi.org/10.1007/BF00317079

Hawkes, C. V., Kivlin, S. N., Du, J., & Eviner, V. T. (2013). The temporal development and additivity of plant-soil feedback in perennial grasses. *Plant and Soil*, *369*, 141–150. https://doi.org/10.1007/s11104-012-1557-0

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

Hersh, M. H., Vilgalys, R., & Clark, J. S. (2012). Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology*, *93*, 511–520. https://doi.org/10.1890/11-0598.1

Hoagland, D. R., & Arnon, D. I. (1950). The water-culture method for growing plants without soil. Circular. California Agricultural Experiment Station, 347, 32 pp.

Houba, V. J. G., Temminghoff, E. J. M., Gaikhorst, G. A., & Van Vark, W. (2000). Soil analysis procedures using 0.01 M calcium chloride as extraction reagent. *Communication in Soil Science and Plant Analysis*, *31*, 1299–1396. https://doi.org/10.1080/00103620009370514

Jing, J., Bezemer, T. M., & Van der Putten, W. H. (2015). Interspecific competition of early successional plant species in ex-arable fields as influenced by plant–soil feedback. *Basic and Applied Ecology*, *16*, 112–119. https://doi.org/10.1016/j.baae.2015.01.001

Joosten, L., Mulder, P. P. J., Klinkhamer, P. G. L., & Van Veen, J. A. (2009). Soil-borne microorganisms and soil-type affect pyrrolizidine alkaloids in *Jacobaea vulgaris*. *Plant and Soil*, *325*, 133–143. https://doi.org/10.1007/s11104-009-9963-7

Kardol, P., Cornips, N. J., Van Kempen, M. M. L., Bakx-Schotman, J. M. T., & Van der Putten, W. H. (2007). Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs*, *77*, 147–162. https://doi.org/10.1890/06-0502

Kardol, P., De Deyn, G. B., Laliberte, E., Mariotte, P., & Hawkes, C. V. (2013). Biotic plant-soil feedbacks across temporal scales. *Journal of Ecology*, *101*, 309–315. https://doi.org/10.1111/1365-2745.12046

Ke, P.-J., & Miki, T. (2015). Incorporating the soil environment and microbial community into plant competition theory. *Frontiers in Microbiology*, *6*, 1066.

Koide, R. (1985). The nature of growth depressions in sunflower caused by vesicular arbuscular mycorrhizal infection. *New Phytologist*, *99*, 449–462. https://doi.org/10.1111/j.1469-8137.1985.tb03672.x

Kos, M., Tuijl, M. A. B., De Roo, J., Mulder, P. P. J., & Bezemer, T. M. (2015). Species-specific plant–soil feedback effects on above-ground plant–insect interactions. *Journal of Ecology*, *103*, 904–914. https://doi.org/10.1111/1365-2745.12402

Kulmatiski, A., Beard, K. H., Stevens, J. R., & Cobbold, S. M. (2008). Plant–soil feedbacks: A meta-analytical review. *Ecology Letters*, *11*, 980–992. https://doi.org/10.1111/j.1461-0248.2008.01209.x

Kuzyakov, Y., Friedel, J. K., & Stahr, K. (2000). Review of mechanisms and quantification of priming effects. *Soil Biology & Biochemistry*, *32*, 1485–1498. https://doi.org/10.1016/S0038-0717(00)00084-5

Maron, J. L., Laney Smith, A., Ortega, Y. K., Pearson, D. E., & Callaway, R. M. (2016). Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology*, *97*, 2055–2063. https://doi.org/10.1002/ecy.1431

Mazzola, M. (1999). Transformation of soil microbial community structure and Rhizoctonia-suppressive potential in response to apple roots. *Phytopathology*, *89*, 920–927. https://doi.org/10.1094/PHYTO.1999.89.10.920

Menchaca, L., & Connolly, J. (1990). Species interference in white clover-ryegrass mixtures. *Journal of Ecology*, *78*, 223–232. https://doi.org/10.2307/2261047

Miki, T., Ushio, M., Fukui, S., & Kondoh, M. (2010). Functional diversity of microbial decomposers facilitates plant coexistence in a plant-microbe-soil feedback model. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 14251–14256. https://doi.org/10.1073/pnas.0914281107

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, *404*, 278–281. https://doi.org/10.1038/35005072

Packer, A., & Clay, K. (2004). Development of negative feedback during successive growth cycles of black cherry. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 317–324. https://doi.org/10.1098/rspb.2003.2583

Paine, C. E. T., Marthews, T. R., Vogt, D. R., Purves, D., Rees, M., Hector, A., & Turnbull, L. A. (2012). How to fit nonlinear plant growth models and calculate growth rates: An update for ecologists. *Methods in Ecology and Evolution*, *3*, 245–256. https://doi.org/10.1111/j.2041-210X.2011.00155.x

Petermann, J. S., Fergus, A. J. F., Turnbull, L. A., & Schmid, B. (2008). Janzen-connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, *89*, 2399–2406. https://doi.org/10.1890/07-2056.1

Ter Braak, C. J. F., & Šmilauer, P. (2012). *Canoco reference manual and user's guide: Software for ordination (version 5.0)*. Ithaca, NY: Microsoft Power.

Trinder, C., Brooker, R., Davidson, H., & Robinson, D. (2012). Dynamic trajectories of growth and nitrogen capture by competing plants. *New Phytologist*, *193*, 948–958. https://doi.org/10.1111/j.1469-8137.2011.04020.x

Turkington, R., & Jolliffe, P. A. (1996). Interference in *Trifolium repens* – *Lolium perenne* mixtures: Short- and long-term relationships. *Journal of Ecology*, *84*, 563–571. https://doi.org/10.2307/2261478

Van de Voorde, T. F. J., Ruijten, M., Van der Putten, W. H., & Bezemer, T. M. (2012). Can the negative plant-soil feedback of *Jacobaea vulgaris* be explained by autotoxicity? *Basic and Applied Ecology*, *13*, 533–541. https://doi.org/10.1016/j.baae.2012.08.012

Van de Voorde, T. F. J., Van der Putten, W. H., & Bezemer, T. M. (2011). Intra- and interspecific plant-soil interactions, soil legacies and priority effects during old-field succession. *Journal of Ecology*, *99*, 945–953. https://doi.org/10.1111/j.1365-2745.2011.01815.x

Van de Voorde, T. F. J., Van der Putten, W. H., & Bezemer, T. M. (2012). The importance of plant-soil interactions, soil nutrients, and plant life history traits for the temporal dynamics of *Jacobaea vulgaris* in a chronosequence of old-fields. *Oikos*, *121*, 1251–1262. https://doi.org/10.1111/j.1600-0706.2011.19964.x

Van der Putten, W. H., Bardgett, R., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., … Wardle, D. A. (2013). Plant-soil feedback: The past, the present and future challenges. *Journal of Ecology*, *101*, 265–276. https://doi.org/10.1111/1365-2745.12054

Wubs, E. R. J., & Bezemer, T. M. (2016). Effects of spatial plant-soil feedback heterogeneity on plant performance in monocultures. *Journal of Ecology*, *104*, 364–376. https://doi.org/10.1111/1365-2745.12521

Wubs, E. R. J., & Bezemer, T. M. (2018). Temporal carry-over effects in sequential plant–soil feedbacks. *Oikos*, *127*, 220–229. https://doi.org/10.1111/oik.04526

SUPPORTING INFORMATION

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

How to cite this article: Bezemer TM, Jing J, Bakx-Schotman JMT, Bijleveld E-J. Plant competition alters the temporal dynamics of plant-soil feedbacks. *J Ecol*. 2018;00:1–14. https://doi.org/10.1111/1365-2745.12999