

Species abundance fluctuations over 31 years are associated with plant–soil feedback in a species-rich mountain meadow

Dina in 't Zandt¹  | Tomáš Herben^{2,3}  | Annelien van den Brink¹ | Eric J. W. Visser¹  | Hans de Kroon¹ 

¹Department of Experimental Plant Ecology, Institute for Water and Wetland Research, Radboud University, Nijmegen, the Netherlands

²Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic

³Department of Botany, Faculty of Science, Charles University, Praha 2, Czech Republic

Correspondence

Dina in 't Zandt
Email: d.intzandt@science.ru.nl

Present address

Dina in 't Zandt, Institute of Botany, Czech Academy of Sciences, CZ-252 43, Průhonice, Czech Republic and Institute of Ecology, University of Innsbruck, Sternwartestraße 15, A-6020, Innsbruck, Austria

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Abstract

1. Increasing evidence suggest that plant–soil interactions play an essential role in plant community assembly processes. Empirical investigations show that plant species abundance in the field is often related to plant–soil biota interactions; however, the direction of these relations have yielded inconsistent results.
2. We combined unique 31-year long field data on species abundances from a species-rich mountain meadow with single time point plant–soil feedback greenhouse experiments of 24 co-occurring plant species. We tested whether these relations were dynamic in time, whether coupled increases and decreases in abundance between years were related to plant–soil feedback and whether these changes were underlain by years in which manuring was applied.
3. The prevailing negative relationship between plant–soil feedback and plant relative abundance in the field was significantly time-dependent, which may reconcile the contrasting results in literature. Furthermore, significantly coupled oscillations appeared between species relative abundance changes and plant–soil feedback, which were likely moderated by years in which manuring was applied. Our results are consistent with the notion that the more abundant species are stabilised by negative plant–soil feedback, and the less abundant species co-vary with the fluctuations of these more competitive species.
4. *Synthesis.* Our results project plant–soil feedback as an important regulatory mechanism in plant communities, operating in conjunction with species' competitive ability and soil nutrient availability. We suggest that negative feedback is particularly prominent in more abundant plant species that profit from more readily available soil nutrients than less abundant species with positive feedback. Negative plant–soil feedback may thus prevent more abundant plant species from out-competing less abundant plant species, facilitating stable species co-existence.

KEYWORDS

abundance fluctuations, grassland, manuring, nutrient availability, oscillations, plant–soil feedback, soil biota, species co-existence

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1 | INTRODUCTION

Natural grasslands are highly biodiverse systems with up to 89 species/m² (Cantero et al., 1999; Wilson et al., 2012). The mechanisms of how this diversity is maintained remain a topic of research and debate. Increasing evidence suggests that interactions between plants and their associated soil biota play a major role in species co-existence (Bardgett & van der Putten, 2014; Bever et al., 2010, 2012; van der Putten et al., 2013). Specifically, co-existence is suggested to result from the accumulation of species-specific pathogens in the rhizosphere over time (Bever et al., 2015; Chung & Rudgers, 2016; Prober et al., 2015; Wagg et al., 2014), decreasing the species' growth, competitive ability and survival (Bonanomi et al., 2005; Dudenhöffer et al., 2018; Laliberté et al., 2015; Lekberg et al., 2018). These so-called negative plant-soil feedback effects are hypothesised to limit the relative abundance of the plant species in the community (Anacker et al., 2014; Crawford et al., 2019; Diez et al., 2010; Klironomos, 2002; Mangan et al., 2010; McCarthy-Neumann & Ibáñez, 2013). Indeed, in temperate grasslands, a shrub-steppe, savanna, and tropical and temperate forests, a positive relation between plant-soil feedback and abundance was found. However, in several grasslands, no such relationship occurred (Bauer et al., 2015; Kempel et al., 2018; Klinerová & Dostál, 2020; Reinhart, 2012), and in a montane grassland (Maron et al., 2016), a savanna grassland (MacDougall et al., 2011) and a montane forest (Corrales et al., 2016), the opposite was found: negative plant-soil feedback was associated with the most abundant species.

These discrepancies may be reconciled if the relation between abundance and plant-soil feedback is dynamic in time. There are reasons to assume that this is the case. Soil-borne pathogen effects are namely expected to affect a species' abundance in a density-dependent manner, that is, negative effects are strongest when the plant species is in high abundance (Bever, 2003; Bonanomi et al., 2005; Revilla et al., 2013; Vincenot et al., 2017). At high abundance, plant species accumulate more soil-borne pathogens (Maron et al., 2016) hampering their growth and reducing their density. Conversely, when declined to low abundance, species will be released from these negative effects and growth will be stimulated. Such relative abundance changes around a mean are expected from plant-soil feedback as a stabilising agent in plant species co-existence (Adler et al., 2018; Broekman et al., 2019). If true, the relation between plant-soil feedback and species abundance will depend on when in these temporal cycles it is tested (Kardol et al., 2013; Maron et al., 2016), and as a result, this relation may occur, fade and re-occur over time and change in direction.

To test whether plant-soil feedback is related to species relative abundance fluctuations over time, we combined unique, 31-year long, plant species abundance data from a species-rich mountain meadow with single time point plant-soil feedback greenhouse experiments of 24 co-occurring plant species. The mountain meadow is located in the Krkonoše Mountains, Czech Republic, and was established 300–400 years ago. The meadow has been maintained according to its traditional regime with a manuring event

every 4 years ever since. On the large scale, the meadow is stable in species numbers, but on the local scale (3.3 × 3.3 cm²), species abundances are highly dynamic in time (Herben et al., 1993, 2017, 2019). Such local fluctuations in species abundances are not uncommon in natural ecosystems (Crone et al., 2013; Firbank, 1993; Herben et al., 1993) and are driven in part by weather events, management such as manuring and grazing events, and competitive and facilitative interactions between plant species as well as plant-soil interactions (Herben et al., 2017; Ingrisch et al., 2018; Manning et al., 2008; Medina-Roldán et al., 2012). Here, we investigated (a) if species relative abundance fluctuations over time resulted in fluctuations in the relation between abundance and single time point plant-soil feedback, (b) whether coupled species' increases and decreases in abundance in time were related to plant-soil feedback and (c) whether these abundance changes were moderated by manuring events. Apart from its direct effects on species relative abundances, nutrient enrichment has also been shown to modify or even overrule plant-soil feedback and its effect on plant species community composition (Castle et al., 2016; in 't Zandt, Hoekstra, et al., 2020; in 't Zandt et al., 2019; Manning et al., 2008). Based on our results, we discuss the long-term role of plant-soil feedback in shaping plant communities and the potential underlying mechanisms driving these processes.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is located in a species-rich mountain hay meadow in the Krkonoše Mountains, North Bohemia, Czech Republic (vicinity of Pec pod Sněžkou, 50°41'28"N, 15°47'35"E, 880 m a.s.l.). The growing season lasts from mid-April to mid-November and species richness is about 32–36 spp./m². The grassland is 300–400 years old and is maintained by mowing in late June and early September. In 1985, four 0.5 × 0.5 m plots were established at spots representative of the study site (Herben et al., 1995; Herben, Krahulec, Hadincová, & Kovářova, 1993). Two plots received manure in late autumn (following traditional regimes; Herben, Krahulec, Hadincová, & Skálová, 1993) in 1985, 1989, 1993, 1997, 2001 and 2005 (six manuring events) and the other two only in 1997, 2001 and 2005 (three manuring events).

2.2 | Field data collection

Every year in mid-June from 1985 to 2015, the plant community composition of the permanent plots was recorded in a grid with 15 × 15 cells of 3.3 × 3.3 cm. For each cell, the number of tillers (grasses and graminoids), number of rosettes (small dicots) and number of leaves (larger dicots) per rooted species were counted and are here referred to as number of modules. Flowering stems were counted as one module and small seedlings with only young leaves were not considered, since these differ in their dynamics from

established plants. Mowing was simulated by cutting at 3 cm above the soil, collecting the cut biomass and separating this per species per plot. Cutting took place when the whole meadow was mown according to the traditional regime. Cut biomass was dried at 60°C for at least 72 hr and weighed. In 1985, no biomass was collected. The number of modules is a non-destructive measure to determine shifts in species abundance over time.

2.3 | Plant-soil feedback experiment

We selected 24 plant species from the study site that had a frequency of >20 modules in a plot in at least two recordings, since reliable temporal patterns could only be calculated for these more frequent species (Table S1). A typical plant-soil feedback pot experiment was performed consisting of a conditioning and a feedback phase (e.g. Brinkman et al., 2010). In the conditioning phase, species were grown on a mixture of 5% inoculum soil from the field and 95% sterile soil comparable in texture and nutrient availability to the field ($n = 9$). Field inoculum soil was collected from the rooting zone in two 30-m transects, 5 m below the field plots in April 2015 and sieved on a 1.8-mm sieve to remove roots and debris. The area where field soil was collected had similar plant species composition and land-use history as the field plots. Sterile soil was obtained from an excavation site on a former natural forest area (excavated at 1- to 6-m depth near Spaubeek, the Netherlands; comparable to study site soil in terms of nutrient levels and silt-loam texture), 1 cm sieved and subsequently γ -irradiated at 25 kGy (Synergy Health). The experimental inoculation approach is comparable to numerous other studies (e.g. Bauer et al., 2017; Gundale et al., 2014; Wilschut et al., 2019) and soil inoculation of <5% of the total soil has been shown to significantly affect microbial species richness and network complexity (Wagg et al., 2019). Following convention in testing effects of plant-soil feedback, we tested the difference in growth between own conditioned soil and soil consisting of a mixture of conditioned soil of all plant species in the feedback phase ($n = 4$; Figure S1; e.g. Cortois et al., 2016; Kardol et al., 2007; Wubs & Bezemer, 2018). In the mixed soil in the feedback phase, soil of the focal species was included as well to avoid overestimation of plant-soil feedback and mimic field conditions more closely. In the field, plant species grow in high densities and, especially below-ground, closely intermingled with little clustering of roots (Herben et al., 2018; Pecháčková et al., 1999). Plant species are therefore not likely to avoid their own species-specific antagonists completely.

2.4 | Conditioning phase

Eight seedlings per species were transferred into disinfected (3 days in 1% MENNO clean, KaRo BV), free draining 1.5-L pots (top diameter 13 cm, bottom diameter 11.5 cm, height 15 cm) lined with root cloth at the bottom and a plastic cover with holes for the plants to grow through on top of the soil ($n = 9$). Pots were filled with a

mixture of 95% sterile soil and 5% (based on dry soil weight; w/w) dry, thoroughly mixed, inoculum soil from the study site. Seedlings were thinned to four evenly distributed individuals per pot within the first 10 days, with exception of *Nardus stricta* for which 16 seedlings were planted and thinned to eight individuals per pot because of its small root system. Plants were grown for 6 weeks in the greenhouse between 20 and 24°C during the 16-hr light period (MASTER GreenPower Plus 1000W EL/5X6CT lights, Phillips Lighting B.V.) at minimally 250 $\mu\text{mol PAR m}^{-2} \text{s}^{-2}$ at pot level and 17–20°C during the 8-hr dark period and were watered three to five times per week with deionised water. After 6 weeks, the shoot was cut-off below the growing point and soil with roots was cut into pieces of 2–3 cm. All cut soils of each species were thoroughly mixed, and the mixture of all species-specific soils was made by thoroughly mixing equal parts of every species-specific soil (w/w). For each conditioned soil, plant available nitrogen (N) and potassium (K; mg/kg dry soil) was determined by adding 50 ml of 0.2 mol/L NaCl to 10 g of fresh soil, shaking for 2 hr at 120 rpm and filtering the soil out. NO_3^- , NH_4^+ and K^+ concentrations were measured on an AutoAnalyzer 3 (Bran + Luebbe GmbH, Norderstedt, Germany; $n = 3$). Plant available phosphorous (P; mg/kg dry soil) was determined according to Olsen et al. (1954) and measured on an ICP-OES iCAP 6000 (Thermo Fisher Scientific Inc.; $n = 3$).

2.5 | Feedback phase

From a second batch of seedlings, eight seedlings per species were transferred into the same size pots as in the conditioning phase and thinned to four individuals per pot within the first 10 days. Each species was grown on its own conditioned soil and on a mixture of all species-specific conditioned soils as a control ($n = 4$; Figure S1). The soil mixture of all species-specific conditioned soils contained conditioned soil from the selected 24 species and additionally also from *Alchemilla monticola*, *Briza media*, *Campanula patula* and *Veronica officinalis*. Due to low germination rates in the second phase, these species were excluded from the feedback phase. Plants were placed in pairs (own and mixed soil per species) in a block design and grown for 6 weeks under comparable conditions as in the conditioning phase. After 6 weeks, the shoots were cut-off at soil level, dried at 70°C for at least 72 hr and weighed. Roots were washed out of the soil on a sieve with tap water during which dead roots from the previous phase were removed. This was done based on size (dead roots were typically 2–3 cm long due to cutting of the conditioned soil), discoloration, especially at the cut edges, floatation, rigour and absence of lateral roots. Root biomass was dried at 70°C for at least 72 hr and weighed.

2.6 | plant-soil feedback calculation

All calculations were done in R 3.2.5 (R Core Team, 2016). Responses between shoot and root biomass were comparable for the species and

plant-soil feedback was, therefore, calculated based on total plant biomass as $(\text{total dry weight}_{\text{own soil}} - \text{total dry weight}_{\text{mixed soil}}) / \text{total dry weight}_{\text{mixed soil}}$. The purpose of the plant-soil feedback experiment was to calculate the degree of negative and positive feedback resulting largely from the accumulation of species-specific soil microbiota. Plant-soil feedback should therefore not be affected by large soil nutrient differences. However, such nutrient effects can easily arise due to differences in soil nutrient depletion between the plant species in the conditioning phase (Bezemer et al., 2006; Kaisermann et al., 2017; Münzbergová & Šurinová, 2015). We therefore quantified the relationships between plant-soil feedback and nutrient availability, and corrected for these to obtain an unbiased plant-soil feedback estimate for further analysis. We tested the relations between plant-soil feedback and soil nutrient availability at the start of the feedback phase by linear models using `lm` from the `stats` package (R Core Team, 2017) and beta regression models using `betareg` (Cribari-Neto & Zeileis, 2010). Plant-soil feedback values showed significant correlations with soil NO_3^- , NH_4^+ and K^+ concentrations, whereas Olsen-P was not significantly related. Fast-growing, acquisitive plant species that had depleted NO_3^- , NH_4^+ and K^+ to a large extent in the conditioning phase showed negative plant-soil feedback in the feedback phase, whereas slow-growing, conservative species only took up a small fraction of the available nutrients in the conditioning phase and showed positive feedback in the following phase (Figure S2). Differences in soil nutrient availability after the conditioning phase were large due to high NO_3^- , NH_4^+ and K^+ availability at the start of the conditioning phase, which resulted from the soil sterilisation treatment (data not shown). As a result, plant-soil feedback for a large part reflected soil nutrient availability effects and not more subtle effects resulting from soil microbiota accumulation. This is not the intention of the experiment and, moreover, unrealistic compared to natural grassland field conditions where such large differences in soil nutrient availability are not a likely driver of plant abundance fluctuations. At the field site, nutrient availability is generally low and spatial variation in nutrient availability is largely absent, and if present, short-lived in time (Březina et al., 2019). To avoid plant-soil feedback values to mainly represent differences in plant available NO_3^- , NH_4^+ and K^+ concentrations, overestimating feedback effects due to differences in soil nutrient depletion by the different plant species in the conditioning phase and, with that, having plant-soil feedback to largely reflect plant growth rates (Forero et al., 2019; Kulmatiski et al., 2008; Münzbergová & Šurinová, 2015), we corrected observed plant-soil feedback values for differences in nutrient availability at the beginning of the feedback phase. Standardised NO_3^- , NH_4^+ and K^+ values were captured in a PCA score explaining 84% of the variation. The relation between plant-soil feedback and soil nutrient availability was best described by a simple Michaelis-Menten saturation curve (see Supporting Information). This relation showed that with increasing NO_3^- , NH_4^+ and K^+ availability in the soil, plant-soil feedback became less negative and that this relation levelled off at high NO_3^- , NH_4^+ and K^+ availability. Plant-soil feedback values were corrected for the differences in nutrients by taking the residuals of the Michaelis-Menten regression (Figure S3a,b). These nutrient-corrected plant-soil

feedback values were used in all further analyses without incorporation of phylogeny as no significant phylogenetic signal was found (see Supporting Information). The correction did not affect the overall direction of the correlation between plant-soil feedback and relative abundance (Figure S4).

2.7 | Plant abundance relations

We analysed all relations between plant abundance and plant-soil feedback in R 3.4.3 (R Core Team, 2017). Total module count and biomass differed per year (Figure S5), which corresponded to differences in monthly precipitation and average temperature (data not shown). Differences in total counts and biomass were accounted for by calculating relative counts and biomass by dividing module counts and biomass per species per plot per year by the total number of counts or biomass for all species in the plot and year. Relative abundance data contained 18% and 20% zeros for counts and biomass, respectively, which resulted in excessive variation and over-dispersion in our statistical models. We, therefore, used a zero-altered model approach according to Zuur and Ieno (2016), which involves splitting the relative abundance data into a binary occurrence (presence/absence) part and a continuous, presence-only part (relative abundances without zeros; see full approach in Supporting Information). Models for relative abundance based on both module counts and biomass contained corrected 'plant-soil feedback', scaled 'year' and the factor 'manuring' and all their interactions as fixed effects. Species crossed with plot was included as random effect to address the temporal correlation between years and model validation followed recommendations of Zuur et al. (2010).

Plant-soil feedback was only significantly related the continuous part of the model (Table 1; Table S2; Figure S6). The relations from the continuous part of the model were visualised by fitting a linear model between \ln -transformed relative abundance and plant-soil feedback for each plot in each year and taking the standardised beta slope using `lm.beta` from the `QUANTPSYC` package (Fletcher, 2012; Figure S7). In each year, the relation between relative abundance and plant-soil feedback in plots with three and six manuring events was tested using a beta regression model with a logit-link using `betareg` (Cribari-Neto & Zeileis, 2010).

2.8 | Plant abundance increase/decrease relations

Species increase/decrease over time was calculated as relative abundance in year $t + 1$ minus relative abundance in year t for both counts and biomass. Relations between species increase/decrease ($\sqrt{\text{transformed absolute value times sign}}$) and 'plant-soil feedback', the factors 'manuring' and 'year' (scaled), and their interactions were tested using linear mixed models (LMMs) with species

TABLE 1 Results of zero-altered models and linear mixed models testing the effect of plant–soil feedback (PSF), year and manuring on species relative abundance and relative abundance increase/decrease between subsequent years respectively. Species relative abundances were based on module counts and biomass

	Relative abundance				Increase/decrease			
	Counts		Biomass		Counts		Biomass	
	z-value	p-value	z-value	p-value	χ^2	p-value	χ^2	p-value
PSF	-0.753	0.451	-0.007	0.994	0.243	0.622	3.724	0.054
Year	0.134	0.893	-4.952	<0.001	7.320	1.000	2.080	1.000
Manuring	1.403	0.161	0.404	0.686	0.280	0.596	0.054	0.816
PSF × year	-5.606	<0.001	-5.245	<0.001	49.246	0.011	42.518	0.038
PSF × manuring	-2.491	0.013	-2.192	0.028	0.022	0.882	1.112	0.292
Year × manuring	-0.696	0.487	0.684	0.494	6.791	1.000	1.820	1.000
PSF × year × manuring	2.755	0.006	2.862	0.004	23.013	0.776	37.216	0.114

Note: Significant *p*-values ($p < 0.05$) presented in bold. For relative abundance, zero-altered models with gamma distribution (ZAG) and species crossed with plot as random effect were performed. For relative abundance increase/decrease, linear mixed models with species crossed with plot as random effect were performed.

crossed with plot as a random effect to address temporal correlations (Zuur et al., 2009). LMM was performed using lme from the nlme package (Pinheiro et al., 2017). Again, these relations were visualised in time by taking the standardised beta slope of the linear relation between square root-transformed increase/decrease in relative abundance and plant–soil feedback between each subsequent year (Figure S8). Significance of this relation between each subsequent year was tested with linear models (R Core Team, 2017). Importantly, the degree of increase/decrease was not significantly related to the species' relative abundance for both species increase/decrease based on counts and on biomass (data not shown). Species increase/decrease in relative abundance was thus robust against regression towards the mean, that is, a common bias in temporal data that plant species in either high or low abundance cannot increase or decrease even more the following year was absent. Abundant species were thus not that abundant that these could not further increase; likewise, the least abundant species could still decrease even further.

As presented below, the relation between species increase/decrease in relative abundance and plant–soil feedback showed cyclical patterns in time. We, therefore, asked (I) whether these patterns were significant in time, and (II) whether these patterns were significantly affected by the plant–soil feedback of the species. We answered these questions using temporal autocorrelation analyses on the cyclical patterns followed by a data randomisation approach comparable to Yenni et al. (2017). In short, we calculated the occurrence of cyclic patterns when (I) relative abundance data were randomised in time and (II) when plant–soil feedback was randomised between the plant species. Five thousand iterations created a frequency distribution of cyclic patterns that may have occurred by chance with which we compared the strength of the actual observed cyclic patterns to calculate whether these were (I) significant in time and (II) significantly related to plant–soil feedback. For more details, see Supporting Information.

3 | RESULTS

3.1 | Species differ in plant–soil feedback

Plant–soil feedback of the 24 co-occurring grassland species ranged from strongly negative to slightly positive (Figure 1a). Plant–soil feedback was correlated with nutrient availability at the start of the feedback phase and more negative at low NO_3^- , NH_4^+ and K^+ concentrations (Figure S2). As spatial variation in nutrient availability in the field is limited (Březina et al., 2019) and therefore likely plays a limited role in plant–soil feedback effects, we corrected our plant–soil feedback values for differences in nutrient availability between soils in our experiment. This correction resulted mainly in less strong, negative plant–soil feedback with most species showing a negative to neutral feedback (Figure 1b). The corrected plant–soil feedback measure represents the species' potential to accumulate negative and/or positive own soil effects relative to the average potential of other species, but with exclusion of nutrient depletion effects that may overestimate feedback effects and largely reflect differences in nutrient availability that are not likely to drive differences between soil legacies in the field.

3.2 | The feedback–abundance relation fluctuates over time

Plant species abundances in the field fluctuated over 31 years' time (Figure S9). The magnitude of these fluctuations over the full 31 years was not related to plant–soil feedback (Figure S10), nor was plant–soil feedback significantly associated with overall species relative abundance in the field (Table 1). However, a significant interaction between plant–soil feedback and year occurred, indicating that the relation between plant–soil feedback and relative abundance changed over time (Table 1; Figure S6). To visualise these patterns over time, the slope of the linear relation between relative abundance (ln-transformed) and plant–soil

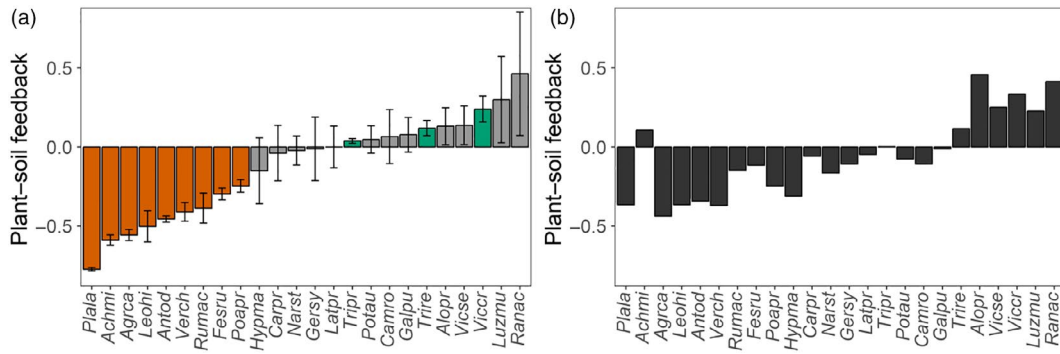


FIGURE 1 Plant-soil feedback of 24 co-occurring plant species. (a) Initial plant-soil feedback and (b) plant-soil feedback after correction for differences in NO_3^- , NH_4^+ and K^+ concentrations at the start of the feedback phase. Plant-soil feedback was calculated as $(\text{DW}_{\text{own soil}} - \text{DW}_{\text{mixed soil}}) / \text{DW}_{\text{mixed soil}}$ and indicates the percentage change in total biomass on own compared to mixed soil. Plant-soil feedback was corrected for nutrient differences based on a Michaelis-Menten curve fitted between the initial plant-soil feedback values and PCA axis score 1 that summarised NO_3^- , NH_4^+ and K effects (Figure S3). The residuals of this curved were taken as the nutrients-corrected plant-soil feedback. In a, bars in dark orange indicate species with a significant negative plant-soil feedback, in light grey species with a neutral plant-soil feedback and in green species with a significant positive plant-soil feedback (based on 95% confidence intervals). Values are $M \pm SE$; $n = 4$. For species abbreviations, see Table S1

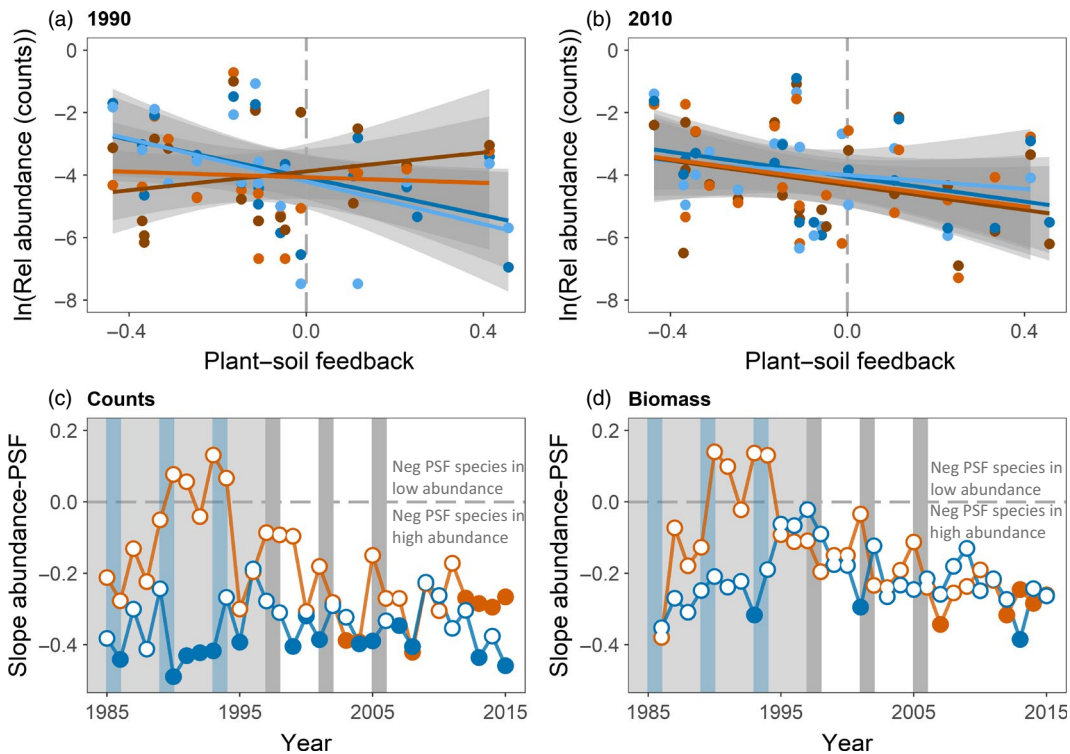


FIGURE 2 Relations between field relative abundance and plant-soil feedback (PSF) for 24 co-occurring species over 31 consecutive years. Linear fit between \ln -transformed relative abundance based on counts and plant-soil feedback for two plots manured six times (light and dark blue) and two plots manured three times (light and dark orange) as an example in (a) 1990 and (b) 2010. Grey shading indicates the 95% confidence interval. Average slope (standardised beta) of the linear fit between \ln -transformed relative abundance based on (c) counts and (d) biomass in each year. A negative slope indicates that negative plant-soil feedback species were in high relative abundance, for example, the plots manured six times in a. A positive slope indicates that negative plant-soil feedback species were in low abundance (see also text in c and d). Two plots received manure three times during this time period (orange line; grey vertical bars represent manuring events) and two plots received manure six times (blue line; grey and blue vertical bars represent manuring events). Closed dots represent significant relations ($p < 0.05$; $n = 2$), open dots non-significant relations. Grey shading indicates the time period in which only plots with six manuring events received manure. The years selected in a and b illustrate both neutral and negative relations in an early and late year, that is, the neutral and negative slopes presented in c and d for all years. In addition, these years also represent years in which plots receiving different manuring frequencies differed in their relation between relative abundance and plant-soil feedback. See Figure S7 for feedback-abundance relations in all years separately and Table 1 for statistics

feedback was calculated for each year and plotted over time (Figure 2; Figure S7). In most years, a negative relation occurred: species experiencing strong, negative feedback in the greenhouse had a higher relative abundance in the field than species experiencing positive feedback (such as in Figure 2a, blue lines). This relation was, however, in many years not significant (such as in Figure 2b), and in some years this relation tended to be positive rather than negative (such as in Figure 2a, dark red line).

Manuring frequency significantly interacted with the occurrence of the relation between field relative abundance and greenhouse plant–soil feedback (Table 1). From 1985 until 1997, when only two of four plots received manure, a consistent negative relation between feedback and relative abundance occurred in plots that were manured. In plots without manuring, this relation varied from slightly negative to slightly positive (Figure 2a,c,d). In years where all plots were manured, that is, 1997 to 2005, the feedback–relative abundance relations were comparable between the plots and overall negative. After 2005 when manuring was ceased, this pattern did not change (Figure 2b–d). Temporal patterns in the relation between relative abundance and plant–soil feedback were comparable between relative abundances based on counts and on biomass (Figure 2c–d).

3.3 | Species abundance increase/decrease and plant–soil feedback form coupled oscillations over time

To test whether local abundance fluctuations in the field may be explained by plant–soil feedback, we calculated plant species increase or decrease in relative abundance between subsequent years. No overall plant–soil feedback, year and manuring effects on species increase/

decrease between years occurred. However, a significant interaction between plant–soil feedback and year on species increase/decrease indicated a time dependency (Table 1). This effect was visualised by plotting the slope of the linear relation between species increase/decrease and plant–soil feedback in each year over time (Figure 3; Figures S8 and S11). Overall, the relation between species increase/decrease and plant–soil feedback fluctuated over time without an overall trend to it. In some years, the relation was positive, that is, negative plant–soil feedback species decreased in relative abundance (such as in Figure 3a, orange lines), and in other years the relation was negative, that is, negative plant–soil feedback species increased in relative abundance (such as in Figure 3a, blue lines; Figure 3b). After 1997 when all plots received manure, this fluctuation occurred in a remarkable cyclic fashion with intervals of 4 years coinciding with the manuring regime. Between years with manuring, negative plant–soil feedback species increased in relative abundance, whereas between years without manuring no or a positive relation occurred, that is, negative plant–soil feedback species decreased in relative abundance. After 2005 when manuring was ceased, the oscillation frequency increased to 5–6 years (Figure 3b). Temporal patterns in the relation between increase/decrease in relative abundance and plant–soil feedback were comparable between relative abundances based on counts and on biomass (Figure S11).

3.4 | The observed coupled oscillations are significant in time

We tested whether the cyclical nature of the relation between the increase/decrease in plant species relative abundance in the field and

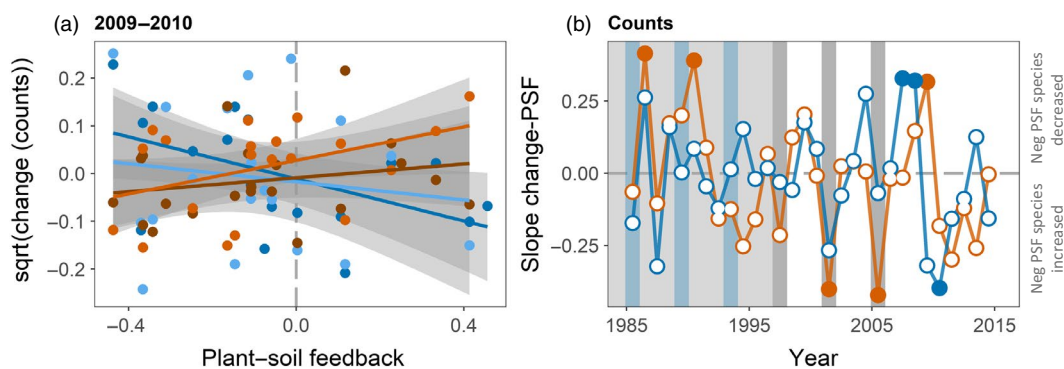


FIGURE 3 Relations between field increase/decrease (change) in relative abundance and plant–soil feedback (PSF) for 24 co-occurring species over 31 consecutive years. (a) Linear fit between sqrt-transformed (absolute value times sign) increase/decrease in relative abundance based on counts between 2009 and 2010 and plant–soil feedback in four permanent plots, as an example. Two plots were manured six times (light and dark blue) and two plots three times (light and dark orange) over 31 consecutive years. Grey shading indicates the 95% confidence interval. (b) Average slope (standardised beta) of this linear fit between each subsequent year from 1985 to 2015 plotted over time. A negative slope indicates that negative plant–soil feedback species decreased in relative abundance between two subsequent years, for example, the plots manured six times in a. A positive slope indicates that negative plant–soil feedback species increased in relative abundance between two subsequent years, for example, the plots manured three times in a (see also text on right y-axis in b). Two plots received manure six times (blue line; blue and grey vertical bars represent manuring events) and two plots received manure three times during this time period (orange line; grey vertical bars represent manuring events). Closed dots represent significant relations ($p < 0.05$; $n = 2$), open dots non-significant relations. Grey shading indicates the time period in which only plots with six manuring events received manure. The years 2009–2010 in a were selected as these illustrate both directions of the change–PSF relationship, that is, negative and positive slopes of which all years are presented in b. See Figure S8 for change–feedback relations in all years separately, Figure S11 for figures based on biomass and Table 1 for statistics

greenhouse plant–soil feedback were (I) significant in time and (II) significantly linked to plant–soil feedback. We first examined whether a predictable pattern underlay the observed relations by using a common approach in time-series analysis: temporal autocorrelation. We found sinusoid patterns, which occurred significantly more in the observed dataset than (I) when these sinusoid patterns were calculated based on relations where relative abundances were randomised between years (Figures S12 and S13). Significant oscillations with a specific time-lag are thus evident, and cannot be explained by random fluctuations in relative abundance over time. Using a similar approach, we (II) found that in plots with six manuring events, the cyclic pattern was significantly related to plant–soil feedback and, therefore, did not only occur due to fluctuations in relative abundances through time (Figures S12 and S13). In certain conditions, plant–soil feedback was thus significantly related to the observed coupled oscillations in time and thus played an important part in shaping these cycles.

4 | DISCUSSION

The importance of plant–soil feedback effects in plant community assembly has been demonstrated in several studies by correlating species relative abundance in the field with experimentally obtained plant–soil feedback. However, contrasting relations have been found, if a relation was present at all (e.g. Klironomos, 2002; Maron et al., 2016; Reinhart, 2012). In a species-rich mountain meadow, we found that the relation between the species' potential

to accumulate plant–soil feedback effects and relative abundance was highly time-dependent. Over the course of 31 years, the relation between feedback and relative abundance occurred, faded and re-occurred. Our results suggest that this time dependency may explain the varying results reported in literature (MacDougall et al., 2011; Maron et al., 2016; Reinhart, 2012) assuming that species abundances also fluctuate in the other systems investigated. Consequently, these previous seemingly contrasting results may not be contrasting at all, but part of a temporal pattern in species abundances of which a snapshot in time was taken by earlier studies. Given the highly dynamic nature of most plant communities, time is an indispensable factor that needs consideration in species co-existence studies.

The prevailing direction of the relative abundance–feedback relation was negative, indicating that, most of the time, a high relative abundance was related to a high potential to accumulate negative plant–soil feedback. Casper and Castelli (2007) showed that plant–soil feedback interacts with species competition and, in a meta-analysis across 150 plant species, Lekberg et al. (2018) showed that strong competitors generally have stronger, negative plant–soil feedback than weak competitors. The strongest competitors in our grassland system were likely the most fast-growing, nutrient acquisitive species, since manuring events generally promote species with such traits (Robson et al., 2007). Previous studies have also shown that nutrient acquisitive species are more strongly hampered by their pathogenic soil community than nutrient conservative species (Laliberté et al., 2015; Semchenko

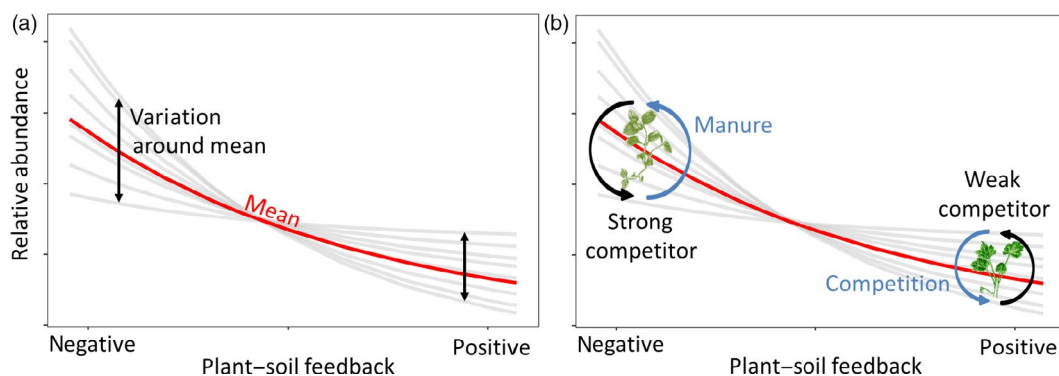


FIGURE 4 Conceptual framework of plant relative abundance in relation to plant–soil feedback over time. (a) Illustration of the coupled oscillations suggested by our study indicating the mean relation between relative abundance and plant–soil feedback independent of time (red) and relations in single years (grey) creating variation around the mean relation. Negative plant–soil feedback species were, on average, in a higher relative abundance than positive plant–soil feedback species, resulting in a mean negative relation between relative abundance and plant–soil feedback. The relation, however, fluctuates between years and single year relations cross the mean line creating coupled oscillations: when negative plant–soil feedback species increase in relative abundance, positive plant–soil feedback species tend to decrease. (b) Proposed regulatory mechanisms of oscillations: an interplay between plant species' competitive ability, plant–soil feedback and manuring events. Limiting factors result in strong competitors attaining, on average, relative high abundance, whereas weak competitors remain in, on average, relative low abundance, which coincides with plant–soil feedback resulting in an overall negative relative abundance–feedback relation. The variation in time around this mean relation is regulated by plant–soil feedback and driven by manuring events. Negative plant–soil feedback species increase in relative abundance in years with manuring, resulting in a decrease in relative abundance of positive plant–soil feedback species via competitive effects (blue arrows). The years after a manuring event, strong competitors are decreased by negative plant–soil feedback, allowing for positive plant–soil feedback species to increase in relative abundance via competitive effects and positive feedback (black arrows). Plant–soil feedback may thus only indirectly determine a species' mean abundance, but mainly act as an important regulatory mechanism in plant communities averting already successful species from increasing even further in abundance and averting monodominance of such successful species in the community. Presented relations are conceptual and not data-derived

et al., 2018; Teste et al., 2017), which is in line with the often found negative relation between plant–soil feedback and root diameter (Cortois et al., 2016; Semchenko et al., 2018). The observed prevalently negative relation between relative abundance and feedback may thus result from a higher abundance of plant species that were strong competitors in the particular conditions presented in the mountain meadow compared to a lower abundance of weaker competitors in the particular conditions in our study system (Figure 4a). Competitive effects are generally larger than plant–soil feedback effects (Klinerová & Dostál, 2020; Lekberg et al., 2018), which suggests that the average relative abundance of plant species is not a result of plant–soil feedback itself, but depends on limiting factors such as resource availability and suitable spots for seedling establishment in relation to plant species traits. Besides the moment in time, the relation between plant species abundance and plant–soil feedback may thus depend on the limiting factors of the system, which determine the species' competitive ability and its overall mean abundance (Figure 4a).

Our results further showed that species increase/decrease in relative abundance between subsequent years showed significantly coupled oscillations in time, in which negative and positive feedback species alternate in relative abundance changes over time with similar frequencies. How may these cyclic patterns with positive feedback species arise? Due to their generally higher abundance, negative feedback species are expected to have a large influence on plant community processes (Grigulis et al., 2013; Herben et al., 2013, 2019) and, therewith, determine performance of the generally less abundant, positive feedback species. Positive feedback species may thus follow the trends in the negative feedback species leading to the observed coupled oscillations (Figure 4b). In our study system, plant–soil feedback may thus mainly moderate performance of the abundant plant species and keep these in check via negative feedback, avoiding monodominance in the community (Maron et al., 2016). Where limiting factors may determine the species' mean abundance, negative plant–soil feedback may be one critical regulating factor stabilising species populations around their mean on either side of the plant–soil feedback spectrum (Adler et al., 2018; Broekman et al., 2019; Figure 4b).

The observed synchronisation between negative and positive plant–soil feedback species corroborated with the effects of manuring. Years with manuring were a common force that affected all species at the same points in time and often resulted in an increase in relative abundance of negative feedback species followed by a decrease in relative abundance of these species the years after (Figure 4b). Manuring may increase the plant species' ability to cope with negative feedback effects (in 't Zandt et al., 2019; Klinerová & Dostál, 2020), by changing microbial soil communities (Fierer et al., 2009; Leff et al., 2015; Ramirez et al., 2012) and the input of a foreign microbial community affecting plant–microbe interactions. As a result, manuring events may have alleviated a species' negative feedback effects and allowed these species to increase in relative abundance, driving a decrease in relative abundance of species with positive feedback potential. Conversely, the years after a

manuring event, negative feedback effects may have become stronger, decreasing these negative feedback species again with opportunity for expansion of positive feedback species (Figure 4b). Indeed, cyclic patterns were stronger in plots that received manuring in 6 out of 31 years of study than plots that received manure in only 3 years. Moreover, plots receiving no manure the first 13 years of the experiment showed a non-significant tendency towards a positive feedback–abundance relation again indicating positive effects of manuring on especially the negative feedback species.

Abundance-related plant community dynamics may thus result from an interplay of nutrient and plant–soil feedback cycles in time. Not only plant abundance fluctuations in time are therefore critical elements in species co-existence, but also fluctuations in plant–soil feedback strength (Figure 4b). In this study we determined plant–soil feedback at a single point in time and therewith assumed plant–soil feedback to be a constant in time. We thus found fluctuations in the relation between relative abundance and soil feedback resulting from changes in relative abundance, but not tested the dynamics in the abundance–feedback relation. Where negative feedback is generally assumed to increase in strength over time, it is most likely affected by an array of environmental parameters, such as manuring, resulting in nonlinear temporal fluctuations in soil feedback effects (Bonanomi, Giannino, et al., 2005; Fry et al., 2018; in 't Zandt et al., 2019; Vincenot et al., 2017). Similarly, feedback effects are expected to be density-dependent with negative effects being most strong in high intraspecific competition. Future challenges lie in uncovering the dynamic nature of feedback effects in time as well as in density-dependent competitive settings. Long-term density-dependent plant–soil feedback experiments will be vital assets in linking soil feedback fluctuations to plant community processes (Broekman et al., 2019).

Is it likely that the plant–soil feedback patterns elucidated in this mountain grassland occur more generally? If limiting factors largely determine plant species abundance, ecosystems with different limiting factors may then find plant species with other traits dominating, which is expected to shift the relation between plant–soil feedback and species abundance. This notion is consistent with some of the deviating (positive) relative abundance–feedback relationships observed in other ecosystems, such as temperate and tropical forests (Mangan et al., 2010; McCarthy-Neumann & Ibáñez, 2013). In addition, grasslands where other processes played a prominent role, such as species invasion and establishment time, showed deviating relationships (Anacker et al., 2014; Diez et al., 2010; Klironomos, 2002), whereas in a mountain grassland where environmental stressors were likely similar to our study site, a comparable negative relationship between abundance and feedback was found (Maron et al., 2016). In our grassland system, plant–soil feedback seemed to regulate the abundance of mature plants (seedlings were not taken into account), but this may not be the case in other ecosystems such as forests. Here, evidence has accumulated for direct negative effects of soil biota on seedling establishment (Liu et al., 2015; Mangan et al., 2010; McCarthy-Neumann & Ibáñez, 2013), rather than on mature trees,

affecting community dynamics in a different way. Additionally, mutualistic interactions with ectomycorrhizal fungi have been found to aid seedling survival in both forest and shrubland ecosystems, explaining local plant community dynamics much better than is the case for arbuscular mycorrhizal fungi in grassland systems (Corrales et al., 2016; Hiiesalu et al., 2014; Semchenko et al., 2018; Teste et al., 2017). The specific role of plant–soil feedback in plant communities may thus consistently differ between ecosystems that differ in their dominant life-form, mutualistic relationships and limiting factors.

5 | CONCLUSIONS

In a species-rich mountain meadow, we were able to link experimentally obtained plant–soil feedback of 24 co-occurring plant species to 31 years of plant relative abundance measurements. We show that this relation was highly time-dependent, suggesting that species abundance fluctuations may underlie the contrasting results in literature. Our results add to an increasing number of theoretical (Broekman et al., 2019; Kandlikar et al., 2019) and empirical studies (in 't Zandt, Hoekstra, et al., 2020; in 't Zandt et al., 2019; Kulmatiski et al., 2017; Lekberg et al., 2018; Teste et al., 2017) emphasising that plant traits, competitive ability and soil nutrient availability must be taken into account in interpreting community effects of plant–soil feedback. Indeed, our cyclic patterns can only be understood if negative feedback is particularly prominent in more abundant species that profit more from readily available soil nutrients than less abundant species with positive feedback. Our results corroborate the notion that plant–soil feedback is an important regulatory mechanism in plant species co-existence, preventing the more abundant species from out-competing less abundant plant species.

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AUTHORS' CONTRIBUTIONS

T.H. designed the permanent mountain meadow plots and collected data; All the authors contributed to the design of the plant–soil feedback experiment; D.i.t.Z. and A.v.d.B. performed the experiment, collected and analysed samples; D.i.t.Z. analysed the data and performed the statistics; H.d.K., E.J.W.V. and T.H. were involved in analysis and statistics discussions; D.i.t.Z. and H.d.K. wrote the manuscript, all the others were involved in discussions and commented. All the authors contributed critically to the manuscript and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13574>.

DATA AVAILABILITY STATEMENT

Field data on plant species abundances are available from the LOng Term Vegetation Sampling (LOTVS) database of Valencia et al., (2020). Experimental plant–soil feedback data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.k0P2n-gf76> (in 't Zandt et al., 2020).

ORCID

Dina in 't Zandt  <https://orcid.org/0000-0001-6487-0273>

Tomáš Herben  <https://orcid.org/0000-0002-6636-0012>

Eric J. W. Visser  <https://orcid.org/0000-0002-4763-3775>

Hans de Kroon  <https://orcid.org/0000-0001-6151-3561>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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