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RESEARCH ARTICLE*

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Legacy effects of diversity in space and time driven by winter cover crop biomass and nitrogen concentration

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Abstract

1. Plant diversity can increase nitrogen cycling and decrease soil-borne pests, which are feedback mechanisms influencing subsequent plant growth. The relative strength of these mechanisms is unclear, as is the influence of preceding plant quantity and quality. Here, we studied how plant diversity in space and time influences subsequent crop growth.
2. During 2 years, we rotated two main crops (*Avena sativa*, *Cichorium endivia*) with four winter cover crop (WCC) species in monocultures and mixtures. We hypothesized that, relative to monocultures, WCC mixtures promote WCC biomass (quantity) and nitrogen concentration (quality), soil mineral nitrogen, soil organic matter, and reduce plant-feeding nematode abundance. Additionally, we predicted that preceding crops modified WCC legacies. By structural equation modelling (SEM), we tested the relative importance of WCC shoot biomass and nitrogen concentration on succeeding crop productivity directly and indirectly via nitrogen cycling and root-feeding nematode abundance.
3. WCC shoot biomass, soil properties and succeeding *Avena* productivity were affected by first-season cropping, whereas subsequent *Cichorium* only responded to the WCC treatments. WCC mixtures' productivity and nitrogen concentration showed over- and under-yielding, depending on mixture composition. Soil nitrogen and nematode abundance did not display WCC mixture effects. Soil organic matter was lower than expected after *Raphanus sativus* + *Vicia sativa* mixture. Subsequent *Avena* productivity depended upon mixture composition, whereas final *Cichorium* productivity was unresponsive to WCC mixtures. SEM indicated that WCC legacy effects on subsequent *Avena* (R^2 = 0.52) and *Cichorium* (R^2 = 0.59) productivity were driven by WCC biomass and nitrogen concentration, although not by the quantified soil properties.
4. *Synthesis and applications.* Through understanding plant–soil feedback, legacy effects of plant species and species mixtures can be employed for sustainable management of agro-ecosystems. Biomass and nitrogen concentration of plants returned to the soil stimulate subsequent plant productivity. Winter cover crop quantity and quality are both manipulable with mixtures. The specificity of spatial

and temporal diversity effects warrants consideration of plant species choice in mixtures and rotations for optimal employment of beneficial legacy effects.

KEYWORDS
agriculture, agroecology, crop rotation, plant diversity, plant productivity, plant-feeding nematodes, plant–soil feedback, soil mineral nitrogen, soil organic matter, winter cover crops

1 | INTRODUCTION

Studies on plant diversity in space (diversity experiments) and time (plant–soil feedback, PSF) are mostly executed in natural ecosystems. Agro-ecology could greatly benefit from this knowledge as an ecological basis for sustainable management (Dias, Dukes, & Antunes, 2014; Wood et al., 2015). Although soil-mediated influences of preceding on succeeding plants is an established phenomenon (Tilman, 2001; Van der Putten, Bradford, Pernilla Brinkman, van de Voorde, & Veen, 2016), how and to what extent legacy effects of diversity influence subsequent-plant growth is unresolved. Biodiversity experiments showed that niche differentiation allows mixtures to be more productive than the average of their component monocultures (Loreau & Hector, 2001; Tilman, 2001). Additionally, mixtures promote the build-up of soil C- and N-stocks (Cong et al., 2014; De Deyn et al., 2009), and reduce pest pressure (Iverson et al., 2014; Schnitzer et al., 2011), forming potential feed-backs to subsequent-plant growth.

Plant–soil feedback is the phenomenon in which preceding-plant conditioning of the soil forms a legacy influencing subsequent-plant growth (Bever, 1994; Ehrenfeld, Ravit, & Elgersma, 2005). Legacies can be understood mechanistically through specific feedback pathways between plants and soil properties such as nutrient cycling, plant mutualists and enemies (Van der Putten et al., 2016; Wardle et al., 2004). Soil legacies are not restricted to the next generation of plants, but can persist for over a year (Bartelt-Ryser, Joshi, Schmid, Brandl, & Balser, 2005; Campiglia, Mancinelli, Di Felice, & Radicetti, 2014). Indirect PSF between plant species separated in time finds its application in agriculture (Bever, Westover, & Antonovics, 1997), forming the cornerstone of crop rotation. Indeed, crop rotation is recommended because it disrupts the build-up of specialist herbivores and pathogens (Dias et al., 2014; Snapp et al., 2005). However, to what extent previous plant growth affects the feedback between current and subsequent crops has not been quantified. Yet, such tests are needed to design optimal crop sequences.

Crop rotation increases diversity in time. Through increased quantity and quality of plant residues (Dias et al., 2014; Tiemann, Grandy, Atkinson, Marin-Spiotta, & McDaniel, 2015), farmers can employ positive PSFs without losing the summer season by growing winter cover crops (WCCs; Snapp et al., 2005). Deep or dense-rooting and productive cover crops can improve nutrient retention (Thorup-Kristensen, Magid, & Jensen, 2003), whereas leguminous cover crops can fix atmospheric nitrogen. Although growing plants stimulate plant-feeding nematodes, careful selection of cover crop species can reduce specific nematode species (Fourie, Ahuja, Lammers, & Daneel, 2016; Thoden, Korthals, & Termorshuizen, 2011), and reduce yield losses in subsequent crops (Singh, Hodda, & Ash, 2013). Traditionally both nutrient cycling and pathogen suppression feedback pathways have been studied in isolation. Mechanistic underpinning of how these PSF pathways act in concert can improve crop rotation guidelines.

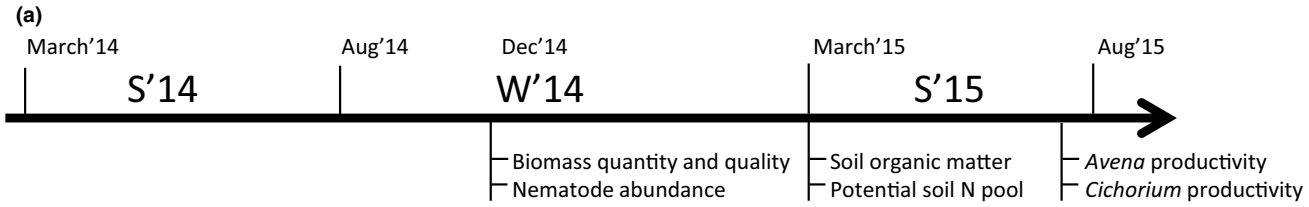
Including cover crop mixtures into rotations combines beneficial spatial and temporal diversity effects. Finney and Kaye (2017) confirmed the diversity-ecosystem functioning relationship in agriculture. Next-crop productivity is positively correlated with cover crop biomass and nitrogen concentration (Finney, White, & Kaye, 2016). Plant-feeding nematode densities decreased with increasing plant diversity in natural grasslands (Cortois et al., in press). Moreover, mixing cover crops could suppress nematode numbers as host plants are harder to find (Iverson et al., 2014; Mitchell, Tilman, & Groth, 2002). How cover crop mixture legacies act on nitrogen cycling and pest management simultaneously, however, remains unaddressed.

Understanding legacies of plant diversity in space and time is essential for successful application of WCC mixtures. We, therefore, studied soil-mediated legacies of WCC mixtures compared to monocultures on succeeding-crop productivity. We tested (1) if WCC mixtures increase WCC productivity and nitrogen concentration, soil organic matter (SOM) content, soil mineral nitrogen and subsequent-plant productivity, and if plant-feeding nematode abundance differentially increases under WCC monoculture and mixtures in comparison to winter fallow. For the latter, we predicted neutral to negative mixture effects on plant-feeding nematode abundance. Additionally, we tested (2) for differential influence of two previous main crops (*Avena sativa* and *Cichorium endivia*) on these WCC legacies. Lastly, through structural equation modelling (SEM) we quantified (3) the relative importance of WCC quantity and quality on next-crop productivity through mediation of soil properties. In this 2-year field study, we demonstrate that WCC biomass and shoot nitrogen concentration increase subsequent-crop productivity and that these properties can be promoted by mixing functionally complementary plant species, without trading-off with increased root-feeding nematode abundance. This makes WCC mixtures, a promising avenue for sustainable agro-ecosystem management.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

Legacy effects of WCC mixtures and monocultures and the previous main-crop history on the productivity of *A. sativa* L. and *C. endivia* L.



(b)

S'13	S'14	W'14		S'15
Phacelia	Avsa	Fallow		Cien
				Avsa
		Lope		Cien
				Avsa
		Trre		Cien
				Avsa
		Rasa		Cien
				Avsa
		Visa		Cien
				Avsa
		R+V*	L+T*	Cien
				Avsa
	Cien	Fallow		Cien
				Avsa
		Lope		Cien
				Avsa
		Trre		Cien
				Avsa
		Rasa		Cien
				Avsa
		Visa		Cien
				Avsa
		R+V*	L+T*	Cien
				Avsa

(c)

FIGURE 1 Experimental set-up. (a) Timeline field experiment in three phases: summer 2014 (S′14), winter 2014/2015 (W′14), summer 2015 (S′15), indicating when measurements were taken. (b) Rotation design (n = 5): *Phacelia* was grown in summer 2013 (S′13) prior to cultivating main crops *Avena sativa* (Avsa) and *Cichorium endivia* (Cien), followed by winter cover crop monocultures *Lolium perenne* (Lope), *Trifolium repens* (Trre), *Raphanus sativus* (Rasa), *Vicia sativa* (Visa) and mixtures *Lolium+Trifolium* (L+T) and *Raphanus+Vicia* (R+V), with fallow as control. Subsequently, *Avena* and *Cichorium* were grown. (c) Aerial photograph during S′15, showing 60 *Avena* (dark) and 60 *Cichorium* (light) plots of two experimental units (1.5 × 3 m) in five randomised blocks (by J. Suomalainen). *Mixtures grown on one experimental unit [Colour figure can be viewed at wileyonlinelibrary.com]

(henceforth generic names are used) were tested in a factorial rotation experiment consisting of three phases (Figure 1). The experiment was carried out on sandy soil (91% sand, pH 5.8, 1.31 g total N/kg, 284 mg total P/kg of which 7.2 mg plant-available P/kg, and 93.8 mg K/kg; Nergena, Wageningen, The Netherlands, 51°59′41.9″N, 5°39′17.5″E).

In summer 2014, *Avena* and *Cichorium* were grown as preceding main crops (S′14) followed by autumn cultivation of WCCs (W′14): four monocultures (*Lolium perenne* L., *Trifolium repens* L., *Raphanus sativus* L., and *Vicia sativa* L.), two mixtures [*Lolium+Trifolium* (henceforth L+T); *Raphanus+Vicia* (R+V)] and fallow as control. Lastly, *Avena* and *Cichorium* were cultivated as subsequent main crops (S′15). The rotation treatments were replicated five times following a randomized block design of 120 plots of 3 × 3 m (Figure 1c). Each plot consisted of two experimental units (1.5 × 3 m). Monocultures and fallow were applied on full 3 × 3 m plots (one of two experimental units was randomly selected for sampling). Mixtures were grown on one of the experimental units (1.5 × 3 m) per plot. Plots were separated by grass strips (*Phleum pratense* L., 1.5 m width).

2.2 | Plant and soil treatments

All plant material was obtained from commercial suppliers in The Netherlands and chemically untreated. *Avena* (var. Dominik), *Phleum* (var. Grindstad), *Lolium* (var. Mathilda) and *Vicia* (var. Ebena) seeds

were purchased from Agrifirm (Apeldoorn, NL). Organically reared *Cichorium* seedlings were obtained from Jongerius (Houten, NL). *Trifolium* (var. Alice) was provided by Barenbrug (Nijmegen, NL), and *Raphanus* (var. Terranova) by Joorden's Zaadhandel (Kessel, NL).

To homogenize the field cultivation history prior to the experiment, *Phacelia tanacetifolia* Benth. (var. Angelia) (June–August 2013) was grown, mown and residues left on the field (Figure 1b). In March 2014, the field was ploughed (25 cm depth). All plots were fertilized in both spring 2014 and 2015, following general practice. At the end of March 2014 all plots received: 82 kg N/ha, 249 kg K/ha, 168 kg S/ha, 84 kg Ca/ha. In early May another 28 kg N/ha and 4.2 kg Ca/ha was given. In March 2015, 41 kg N/ha, 203 kg K/ha, 137 kg S/ha, 6.4 kg Ca/ha were applied, and additionally 14 kg N/ha and 3 kg Ca/ha in May. In 2015, the N fertilization was halved compared to 2014 to facilitate observation of WCC effects on nitrogen cycling without potential overruling effects of high levels of fertilizer application. No P was added to the soil as this was amply available.

2.2.1 | Main crop cultivation (S'14 and S'15)

Avena and *Cichorium* cultivation was similar in 2014 and 2015. In end March, *Avena* was sown (193.5 kg/ha; 12.5 cm row spacing, 3–5 cm depth). In early May, all plots were treated with herbicide to suppress dicot weeds (Damine 500 2 L/ha, mcpa 500 1 L/ha, Starane 200 1 L/ha), and 4-week-old *Cichorium* seedlings were planted (interplant distance 30 × 30 cm). Thereafter, all *Cichorium* plots were manually weeded. All plots were irrigated according to general agricultural practice. *Cichorium* was grown until mid-July and *Avena* was harvested in late-July. Shoots were harvested and stubble left on the field.

2.2.2 | Winter cover crop cultivation (W'14)

All plots were hoed prior to WCCs sowing on 25 August (12.5 cm row spacing, 2–3 cm depth, *Lolium* 25 kg/ha, *Trifolium* 10 kg/ha, *Raphanus* 30 kg/ha, *Vicia* 125 kg/ha). Mixtures were composed of 50/50 proportions of the monoculture seeding densities. Mid-September, plots were manually weeded and additionally 10 kg/ha *Trifolium* was hand-sown to ensure establishment (5 kg/ha for L+T). Weeding was repeated early October. WCCs were mown mid-February and the residue incorporated into the soil by milling (10 cm depth), twice with a 1-week interval.

2.3 | Measurements

2.3.1 | Winter cover crop biomass and nitrogen concentration

Winter cover crop shoot and root biomass were determined mid-December 2014, at time of first frost. Shoots were cut (25 × 25 cm) in the centre of each experimental unit. Root biomass was determined from soil cores (8 cm diameter, 0–30 cm depth) taken from the centre of each sampling square. Roots were gently rinsed with tap water. Samples were dried at 70°C for 72 hr and weighed. Shoots were ground with a Retsch MM 2000 ball grinder (Retsch Benelux VERDER NV, Aartselaar, Belgium). N concentration of shoots from blocks 1, 3 and 5 was measured with a CHN analyser (LECO Corporation, St Joseph, MI, USA).

2.3.2 | Plant-feeding nematodes

Nematode samples were taken mid-December 2014. Per plot, 12 cores (6 per experimental unit) were taken with an auger (2.5 cm diameter, 20 cm depth) and mixed. Samples were stored at 4°C until processing within 2 weeks. Nematodes were extracted from 100 g fresh soil following Oostenbrink (1960). The elutriator suspension was washed over four stacked sieves (mesh 45 μm), then poured over double cotton filters on a coarse sieve on a shallow tray with 90 ml tap water. After 24 hr, the filtrate was collected and filled up to 100 ml. Total number of nematodes was counted in a 9 ml subsample from the 100 ml suspension. Next, nematode suspensions were concentrated into 2 ml and subsequently fixed by adding 4-ml hot and 4-ml cold formalin (concentration of 4%). Nematodes were identified microscopically by applying 0.15 ml formalin suspension on microscope slides. In each sample, 150 individuals were assigned to feeding groups (Yeates, Bongers, De Goede, Freckman, & Georgieva, 1993).

2.3.3 | Soil organic matter and mineral nitrogen

Soil abiotic properties were quantified on 7 April 2015. Mixed soil samples were collected per experimental unit, by taking three cores (diameter 2.5 cm, depth 0–30 cm). Samples were stored 1 week at 4°C and sieved over 2 mm. SOM content was determined as loss-on-ignition (550°C for 4 hr). Potential soil nitrogen pool was defined as total mineral N (NO_3^- and NH_4^+) after incubation (3 weeks, 20°C, 60% water holding capacity) (see Appendix S1). Mineral N was measured on dried soil (40°C), using KCl extraction (Keeney & Nelson, 1982).

2.3.4 | Productivity of main crops in 2015

Cichorium was harvested on 6 July. Average dry weight per plant was determined by harvesting three plants per experimental unit. Samples were taken equally spaced, omitting the outer rows. Plants were cut at soil surface and stored at 4°C until processing within 4 days. *Avena* was harvested on 24 July, by cutting 25 × 25 cm area (containing two rows) 6 cm above soil surface in the centre of the experimental unit. Samples were dried at 70°C.

2.4 | Data analysis

Statistical analyses were performed with R statistical software version 3.2.1 (R Core Team 2015) using the below-mentioned packages.

2.4.1 | Winter cover crop performance

Differences between WCC treatments effects on crop biomass (quantity) and nitrogen concentration (quality) were tested using linear mixed effects models (nlme package; Pinheiro, Bates, DebRoy, & Sarkar, 2016), with cropping history as a covariate. For model selection and optimization we followed the protocol outlined in Zuur, Ieno, Walker, Saveliev, and Smith (2010). In brief, full models included WCC treatments (W′14), previous cropping history (S′14) and their interaction (W′14 × S′14) with block as a random factor. To account for heteroscedasticity, we selected variance structures best capturing the difference in variance between the strata. Models were further optimized by backwards removal of non-significant interactions and main effects. The goodness-of-fit of the simplified model and the original model were compared through the likelihood-ratio test. Parameters of the final models were estimated with restricted maximum likelihood. Normality and homogeneity of residual variances of each model were verified with resp. Kolmogorov–Smirnov and Levene's test. Differences between treatments were evaluated post-hoc with Tukey's test.

2.4.2 | Soil properties

We tested whether soil properties of the WCC treatments differed from fallow by a linear mixed model with fallow as baseline and block as random factor.

We quantified the WCC effect on soil properties by expressing the response of the soil parameters (*Y*) per treatment (*i*) relative to the fallow (*f*) according to Equation 1 (Brinkman, Van der Putten, Bakker, & Verhoeven, 2010). Treatment-control comparisons were made pairwise, within the same previous cropping history (*j*) and block (*b*).

$$\text{relative WCC}_{i,j,b} = \left(\frac{\ln Y_{i,j,b}}{Y_{f,j,b}} \right) \quad (1)$$

Next, the relative WCC effect on soil parameters and previous cropping effect thereupon were tested with a linear mixed effects model as described above.

2.4.3 | PSF effects

Subsequent *Avena* and *Cichorium* productivity on former WCC plots was compared to the productivity on former fallow plots. In addition, the feedback-effects of WCC on the productivity of both main crops and the influence of previous cropping thereupon was quantified with Equation 1 and tested with a linear mixed effects model.

2.4.4 | Mixture effects

WCC mixtures effects were tested separately for WCC biomass and nitrogen concentration, as well as for soil properties (SOM, potential N pool, nematode abundance) and productivity of subsequent *Avena* and *Cichorium*. Per response variable, the expected value (Y_E) was calculated as the average of the observed component monocultures values. The mixture effect was quantified as the natural logarithm of the ratio of the observed response to the mixture treatment (Y_O) and the expected value (Y_E) (Equation 2) within block (*b*).

$$\text{mixture effect}_b = \ln \left(\frac{Y_{O,b}}{Y_{E,b}} \right) \quad (2)$$

Mixture effects were considered significant if they deviate from zero based on a two-sided Student's *t*-test ($\alpha = 0.05$). Positive mixture effects on productivity were considered as overyielding. Mixtures would overyield transgressively when productivity exceeded the most productive component monoculture (Schmid, Hector, Saha, & Loreau, 2008).

2.4.5 | Testing relative importance of PSF pathways

The extent to which the legacies of WCC mixtures were mediated by soil properties and affect biomass production of subsequent plants was evaluated by SEM, using packages Lavaan (Rosseel, 2012) and MVN (Korkmaz, Goksuluk, & Zararsiz, 2014).

The degree of model fit given the data was tested in a multigroup model grouped per subsequent main crop (*Avena* or *Cichorium*), in which we constrained the paths between WCC shoot biomass and nitrogen concentration, and soil properties SOM, potential soil nitrogen pool and plant-feeding nematode abundance, as well as the pathway between SOM and potential N pool to be equal across both groups (see Appendix S2). Data on fallow were excluded. The degree of fit was measured with maximum likelihood chi-square statistics (multivariate normal distribution of endogenous variables was verified). We verified the model outcome with methods for small sample size by Bollen–Stine bootstrapping and Monte Carlo χ^2 simulations (Shipley, 2016).

3 | RESULTS

3.1 | Winter cover crop performance

Winter cover crop shoot biomass varied by WCC treatment (W′14: $F_{5,104} = 82.78$, $p < .001$), previous main crop (S′14: $F_{1,104} = 10.37$, $p = .0017$) and displayed an interaction effect (S′14 × W′14: $F_{5,104} = 2.35$, $p = .0457$). The WCC treatments that included *Raphanus* were threefold more productive than *Lolium* and *Trifolium* monocultures and mixture (Figure 2a). *Lolium* was more productive on former *Cichorium* plots than on former *Avena* plots. Other WCC species were unaffected by previous cropping. The *Lolium+Trifolium* (L+T) mixture was as productive as expected based on monoculture biomass (Figure 2a), whereas the *Raphanus+Vicia* (R+V) mixture overyielded on both former *Avena* ($t_9 = 3.18$, $p = .011$) and *Cichorium* soil ($t_9 = 5.29$, $p < .001$).

Standing root biomass differed significantly between WCC treatments (W′14: $F_{5,110} = 57.35$, $p < .001$, Figure 2b), while previous main crop effect on root biomass was non-significant. Treatments with *Lolium* and *Raphanus* had the highest root biomass, whereas the legume treatments, specifically *Vicia* monoculture, had low root biomass. The L+T mixture had a significantly larger root biomass than

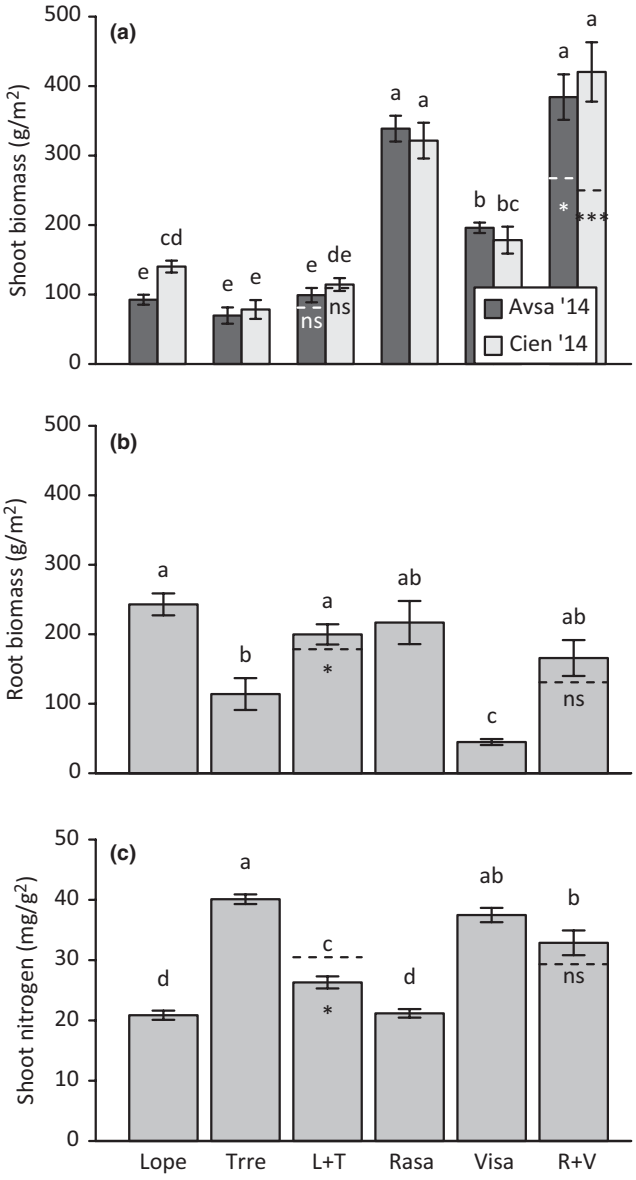


FIGURE 2 Winter cover crop (WCC) biomass of shoot (a), root (b) and shoot nitrogen concentration (c). For abbreviations see Figure 1. Shoot biomass (a) is specified per previous main crop *Avena* (Avsa ′14) or *Cichorium* (Cien ′14). Dashed lines specify expected mixture response based on component monoculture performance. *Specifies a significant deviation from expected response based on a two-sided *t*-test ($p < .05$), ***$p < .001$, ns ($p > .05$). For (a) $n = 10$, (b) $n = 20$, (c) $n = 12$ except Lope ($n = 11$). Error bars ± 1 *SE*, letters indicate significant differences based on Tukey post hoc test. Note: Shoot biomass (a) of *Lolium* differed per preceding main crop, as indicated by different letters

expected ($t_{19} = 2.30$, $p = .033$), whereas R+V mixture root biomass did not significantly deviate from the expectation (Figure 2b).

Shoot nitrogen concentration differed between WCC treatments ($F_{5,63} = 95.98$, $p < .0001$, Figure 2c) and was unaffected by previous main crop. Nitrogen concentration in legume shoots was twice as high as in *Lolium* and *Raphanus*. The L+T mixture showed a lower shoot nitrogen concentration than expected ($t_{10} = -3.58$, $p = .005$, Figure 2c), whereas the nitrogen concentration of R+V mixture did not differ from expectation.

3.2 | Legacy effects on soil properties

Most WCC treatments left SOM content unaltered compared to fallow, except for a reduction by former *Lolium* monocultures ($t_{129} = -3.38$, $p = .0009$, Table 1). Mixtures effects varied with composition; SOM levels in former L+T plots were as expected, but SOM in R+V plots was lower than expected ($t_{19} = -2.50$, $p = .022$, Table 1). The relative effect sizes of WCCs on SOM were small but significantly different between WCC treatments ($F_{5,109} = 2.83$, $p = .019$, Figure 3a) and lower on plots with legacies of *Avena* than of *Cichorium* ($F_{1,109} = 6.95$, $p = .01$, Figure 3b).

The potential soil nitrogen pool was increased by all WCC treatments except *Lolium* monoculture (Table 1), with highest values in *Raphanus* and R+V plots. WCC mixture effects were non-significant. Relative WCC effects on the potential N pool were different between WCC treatments (W′14: $F_{5,109} = 3.33$, $p = .008$, Figure 3c), and more positive on former *Cichorium* plots than on *Avena* plots (S′14: $F_{1,109} = 6.38$, $p = .013$, Figure 3d).

The abundance of plant-feeding nematodes showed large differences between WCC treatments ($F_{5,109} = 9.03$, $p < .0001$, Figure 3e). Compared to fallow, plant-feeding nematode abundances were almost doubled in plots with *Vicia* and R+V. *Raphanus* also significantly increased nematode abundances. No mixture effects were observed (Table 1, Figure 3e). Previous cropping history influenced the relative WCC effect significantly ($F_{1,109} = 6.38$, $P = .013$), with nematode abundance being higher on former *Cichorium* plots than *Avena* plots (Figure 3f).

3.3 | Legacy effects on subsequent-crop growth

Relative to fallow, WCC treatments resulted in contrasting feedback effects on both *Avena* ($F_{5,49} = 15.68$, $p < .001$, Figure 4a) and *Cichorium* biomass ($F_{5,50} = 3.90$, $p = .005$, Figure 4c). Mixtures of WCCs influenced *Avena* productivity differently than *Cichorium* (Table 1). *Avena* productivity on former L+T plots was lower than expected ($t_9 = -2.63$, $p = .027$), while R+V mixtures led to higher *Avena* biomass than expected ($t_9 = 2.59$, $p = .029$). WCC mixtures effects on *Cichorium* productivity were non-significant. More specifically, *Avena* grown on former *Trifolium* ($t_{59} = 4.04$, $p < .001$, Table 1), *Vicia* ($t_{59} = 4.15$, $p < .001$) and R+V ($t_{59} = 4.20$, $p < .001$) plots resulted in higher *Avena* biomass compared to the fallow treatment, whereas *Lolium* reduced it ($t_{59} = -2.37$, $p = .02$). Overall, *Cichorium* biomass increased by most WCC treatments (except *Lolium*) compared to fallow.

Previous main crops influenced the WCC legacy effects on *Avena* ($F_{1,49} = 43.58$, $p < .001$, Figure 4b), with more positive feedback on former *Cichorium* than on former *Avena* plots, whereas the identity of the preceding main crop did not influence the WCC feedback effects on succeeding *Cichorium*.

3.4 | Relative strength of PSF pathways

Our SEM model including both indirect and direct effects of WCC above-ground biomass (quantity) and nitrogen concentration (quality) on subsequent-plant productivity was consistent with our data

TABLE 1 Means and standard error of soil properties and productivity of succeeding plants per winter cover crop treatment (W′14) and previous cropping history (S′14): soil organic matter (SOM), potential soil nitrogen pool and plant-feeding nematodes abundance per soil dry weight (dw), and dry biomass (Bm) of *Avena* (Avsa ′15) and *Cichorium* (Cien ′15). For abbreviation see Fig 1. Significant differences (two-sided *t*-test $p < .05$) between expected and observed mixture responses are underlined and the direction indicated [(+) positive, (−) negative]. Bold values indicate a significant difference ($p < .05$) of W′14 treatments relative to fallow in a linear mixed model

	SOM (%)	Potential N pool (mg/kg dw)	Nematodes (#100 per g dw)	Bm Avsa′15 (g/m^2)	Bm Cien′15 (g per plant)
W′14					
Fallow	4.75 (0.06)	20.58 (0.93)	707 (63)	999.66 (26.59)	34.37 (1.23)
Lope	**4.53 (0.06)**	21.54 (1.00)	822 (69)	**836.53 (43.29)**	33.86 (0.90)
Trre	4.79 (0.06)	**26.79 (1.46)**	620 (72)	**1,295.74 (44.17)**	**41.03 (0.90)**
L+T	4.65 (0.05)	**25.04 (1.50)**	788 (47)	836.42 (53.98) (−)	**38.99 (1.01)**
Rasa	4.82 (0.06)	**29.77 (1.19)**	**992 (91)**	941.94 (85.32)	**43.22 (0.91)**
Visa	4.75 (0.07)	**24.69 (1.24)**	**1,385 (132)**	**1,292.18 (44.83)**	**40.55 (0.68)**
R+V	4.65 (0.06) (−)	**28.69 (1.22)**	**1,295 (123)**	**1,477.39 (75.94)** (+)	**41.32 (1.13)**
S′14					
Avsa14	4.73 (0.03)	25.34 (0.73)	1,059 (63)	1,016.89 (42.98)	39.53 (0.62)
Cien14	4.68 (0.04)	25.26 (0.77)	830 (47)	1,177.35 (36.20)	38.57 (0.66)

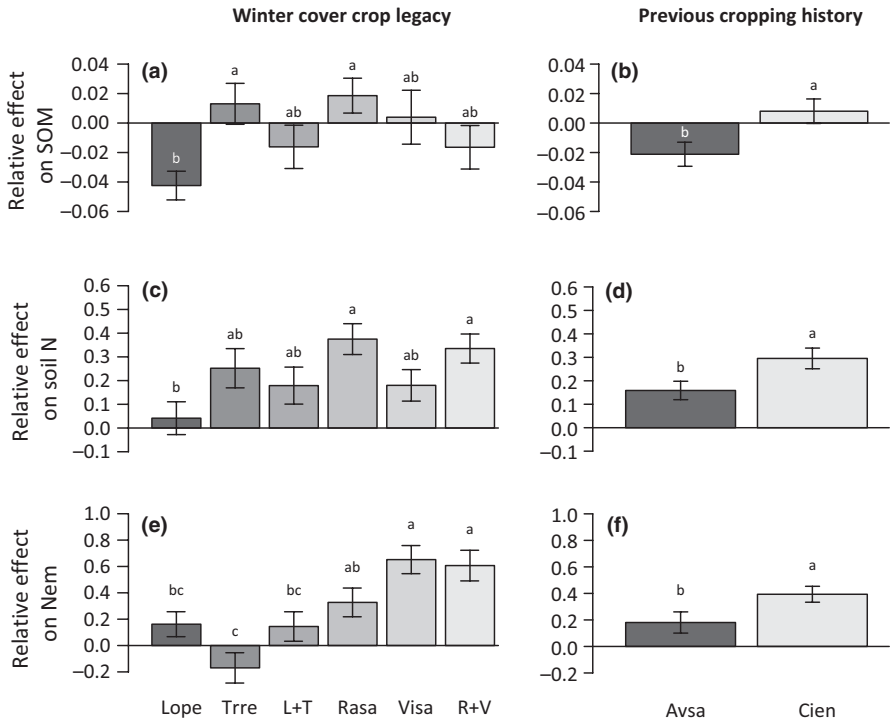


FIGURE 3 The effect of winter cover crops (WCCs) relative to fallow on four soil properties: soil organic matter content (SOM, a and b), potential mineral nitrogen (soil N, c and d), abundance of plant-feeding nematodes (Nem, e and f) specified per WCC treatment (left panels) and aggregated per previous cropping history (right panels). Positive effects indicate values in WCC treatments are higher than in fallow. For (a), (c) and (e) $n = 20$, for (b), (d) and (f) $n = 60$. For abbreviations see legend Fig 1. Error bars ± 1 *SE*. Letters indicate significant differences ($p < .05$), based on Tukey post hoc test. *y*-axes are scaled differently

($\chi^2 = 13.01$, $df = 14$, $p = .526$, Figure 5). Biomass of succeeding *Avena* and *Cichorium* was positively related to WCC quantity and quality. *Avena* biomass was more strongly influenced by quality than quantity, while for *Cichorium* productivity quantity was a stronger driver than quality (Figure 5). Moreover, *Cichorium* biomass was most influenced by SOM, whereas this was not a significant factor for *Avena*.

Winter cover crop biomass positively affected the potential N pool and plant-feeding nematode abundance. However, biomass did not influence SOM content. Neither did WCC shoot nitrogen concentration influence the potential N pool, nor nematode abundance. SOM did positively influence the potential N pool. Although there was a strong positive effect of WCC biomass and N concentration on the biomass of both main crops, these effects did not operate via the quantified soil parameters.

4 | DISCUSSION

Significance of temporal and spatial diversity in agro-ecological management is increasingly recognized by scientists and policy makers (FAO

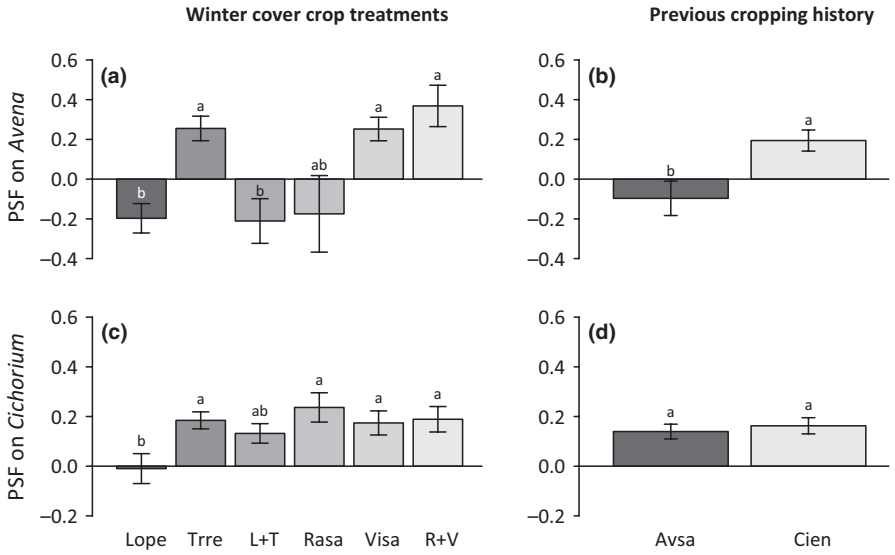


FIGURE 4 Plant-soil feedback effects on subsequent *Avena* (a and b) and *Cichorium* (c and d) per winter cover crop treatment (left panels) and previous cropping history (right panels). Positive values indicate subsequent-crop biomass on former winter cover crop plots is higher than on former fallow plots. For species abbreviations see legend Fig 1. Error bars ± 1 *SE*. For (a and c) $n = 10$; (b and d) $n = 30$. Letters indicate significant differences ($p < .05$), based on Tukey post hoc test

2017; Finney & Kaye, 2017). Including cover crops and their mixtures in rotation is promoted (Dijksma, 2014; FAO 2017), although the scientific basis to decide which crops to include is lagging behind (Dias et al., 2014). We discuss our results in the light of biodiversity-ecosystem functioning (BEF) theory to assess WCC diversity effects in space, and place the role of crop diversity in time in the context of indirect PSF.

4.1 | Winter cover crop performance

We hypothesized our WCC mixtures to overyield. Indeed, we found positive mixture effects for shoot biomass of *Raphanus+Vicia* (R+V) and root biomass of *Lolium+Trifolium* (L+T). Legumes fix nitrogen, improving nitrogen availability to neighbouring plants (Thorup-Kristensen et al., 2003). Nyfeler et al. (2009) demonstrated above-ground overyielding in grass-clover mixtures. However, we did not observe above-ground overyielding of our L+T mixture. Interspecific competition is a possible explanation as *Trifolium* is cold sensitive (Brandsæter, Heggen, Riley, Stubhaug, & Henriksen, 2008) leading to reduced competitive ability when grown with *Lolium* in late summer/autumn (Nesheim & Boller, 1991). *Lolium* domination is reflected in the overyielding of L+T root biomass, which was similar to *Lolium* root biomass. In contrast, R+V mixture showed above-ground overyielding as was also observed by Möller and Reents (2009), indicating decreased competition for N in the mixture.

We expected increased levels of mixture shoot N due to complementarity by legumes. The neutral mixture effect on R+V shoot N suggests improved nitrogen-use efficiency rather than a quality increase. In contrast, the nitrogen concentration in L+T shoots showed a negative mixture effect, probably because the species with the lowest nitrogen concentration was most abundant (own observations).

Ideally, WCC mixtures increase nitrogen input into the soil through increased biomass and/or plant nitrogen content. Positive mixture effects (overyielding) are desirable mixture properties (Schmid et al., 2008). Since the choice of species in a mixture is key to its performance, studying the behaviour of species in mixtures under winter growing conditions is needed to validate BEF principles in utilizing WCC mixtures.

4.2 | Winter cover crop legacy effects on soil properties

As predicted, most WCCs increased the potential soil N pool relative to winter fallow. However, the hypothesized mixture effects were not observed. Previous field experiments showed that WCC species differ in productivity and N concentration and consequently in their nitrogen supply to following crops (Campiglia et al., 2014; Finney et al., 2016). The potential N pool in our SEM was, indeed, driven by WCC shoot biomass. However, the proposed causal pathway between WCC shoot N concentration and potential N pool was non-significant, indicating that the N pools are steered by plant productivity rather than plant quality. Orwin et al. (2010) found that highly productive plants often produce easily decomposable litter compared to less productive plants, making it likely that highly productive WCCs promote soil nitrogen through high inputs of easily mineralizable plant residues.

Increased plant diversity in both time and space increases SOM (i.e. Dias et al., 2014; Tiemann et al., 2015). Here, the observed relative effects of WCC treatments were small and, except for a reduction by *Lolium*, did not differ from fallow. Moreover, the causal pathway between WCC shoot biomass and SOM in our SEM was non-significant. The L+T mixture did not influence SOM differently than its monocultures, whereas the R+V treatment displayed a negative mixture effect. Build-up of SOM requires carbon inputs exceeding its turnover. The incorporation of residues into the SOM pool takes time, whereas there is a continuous break-down of old SOM. The presence of growing plants and the addition of fresh organic matter could prime the break-down of old SOM (Kuzyakov, 2010), and the effect-size can depend on the residing organic matter quality (Saar, Semchenko, Barel, & De Deyn, 2016). Understanding carbon and nutrient dynamics of WCC residues in rotation through decomposition studies would be crucial for available N synchronization with crop requirements.

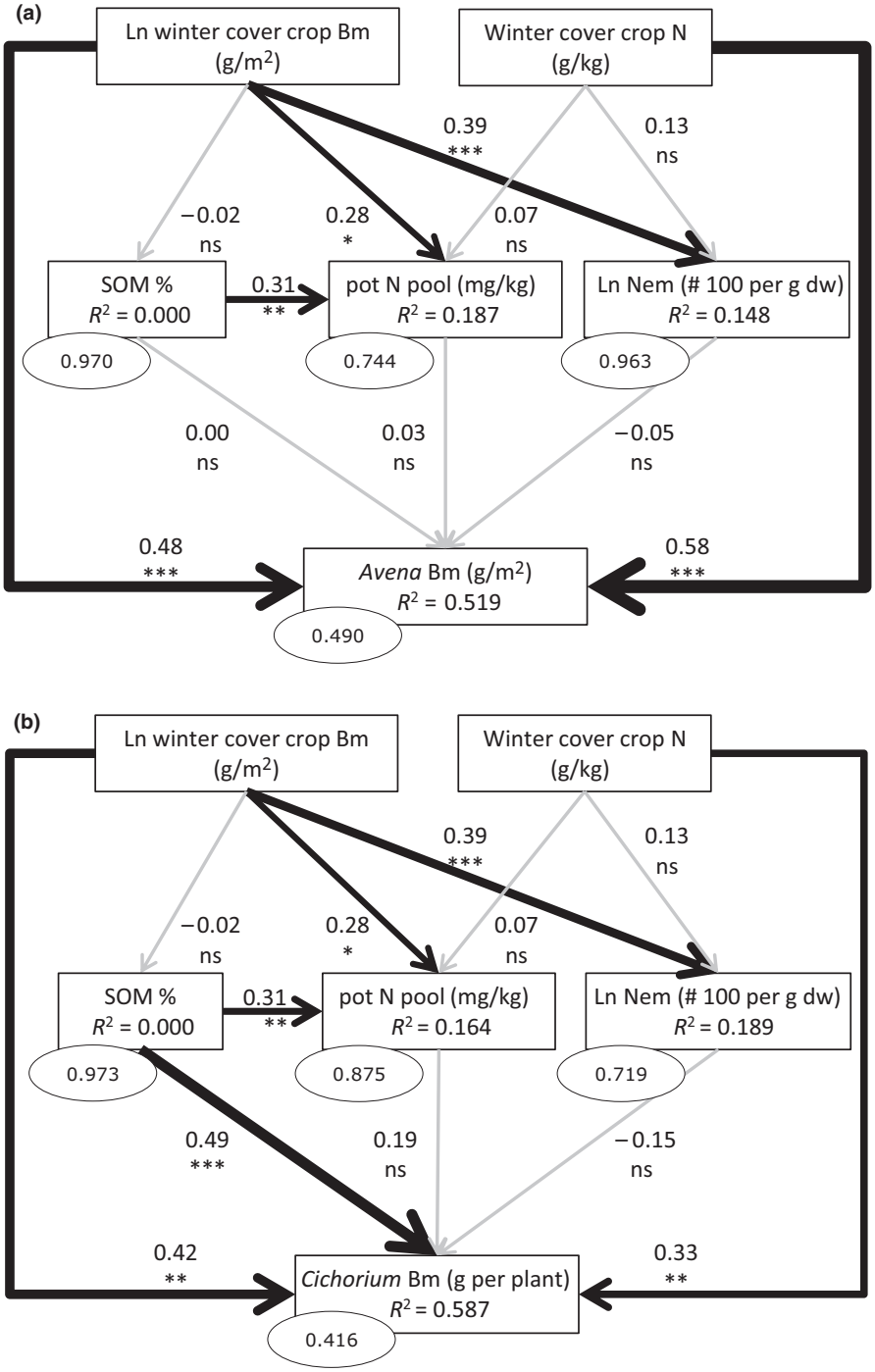


FIGURE 5 Multigroup structural equation model explaining soil-mediated effects of winter cover crops on productivity of *Avena* (a, $n = 36$) and *Cichorium* (b, $n = 35$) (ML) $\chi^2 = 13.01$, $df = 14$, $p = .526$. Biomass quantity (Ln winter cover crop Bm) and quality (winter cover crop N) were tested to influence subsequent-plant productivity (*Avena* or *Cichorium* Bm) directly or indirectly via soil organic matter (SOM), potential nitrogen availability (pot N pool) and plant-feeding nematode abundance (Nem). Black lines are significant: $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$, grey lines are non-significant. Numbers near arrows are standardised path coefficients. Encircled numbers are standardized residual variances. R^2 is given for each endogenous variable

Plant-feeding nematode abundances were expected to increase in WCC plots compared to fallow. *Raphanus*, *Vicia* and R+V mixture increased nematode abundances in comparison to fallow. Our SEM estimated that WCC shoot biomass stimulated nematode abundances, whereas WCC shoot N did not. Increased plant productivity could lead to increased feeding area for herbivorous nematodes (Thoden et al., 2011). Also, increase in bottom-up resource quantity (Chen et al., 2016) or quality (Cortois et al., in press) can stimulate nematode herbivory.

Additionally, mixtures were expected to dilute the abundance of nematode host plants, resulting in neutral to negative mixture effects. Our increased root productivity of L+T mixtures had neutral effects on nematode abundances. These results are in line with Cortois et al. (in press) who show a decrease in plant-feeding nematode density per unit of root biomass in plant species rich communities. Although, plant productivity generally stimulates nematode abundance, diversifying the biomass composition is a potential bio-control for nematode increases.

4.3 | WCC legacy effect on *Avena* and *Cichorium*

The legacy effects of WCCs on subsequent *Avena* and *Cichorium* represent indirect (or interspecific) feedback effects (Bever et al., 1997). All WCC treatments except *Lolium* monoculture promoted *Cichorium*

productivity, while *Avena* productivity increased only after legume treatments (*Trifolium*, *Vicia* and R+V). Preceding *Lolium* reduced *Avena* productivity. We expected that WCC mixtures generate non-additive effects on *Avena* and *Cichorium* productivity via changes in mineral N availability and plant-feeding nematode abundances. We found significant mixture effects on *Avena* biomass in that L+T suppressed, and R+V promoted *Avena* biomass beyond the expectation. *Cichorium* biomass did not show WCC mixture effects.

Avena and *Cichorium* display differential feedback responses because of species identity and associated management. Plants exhibit different feedback effects depending on their functional traits (Cortois, Schröder-Georgi, Weigelt, van der Putten, & de Deyn, 2016; Kulmatiski, Beard, Stevens, & Cobbold, 2008). Our crops likely profited differently from WCCs, since *Avena* and *Cichorium* have different growing seasons. The differential responses are exemplified in our SEM by varying relative pathway strengths. *Avena* biomass was most influenced by WCC shoot N, whereas *Cichorium* biomass was principally driven by SOM, representing the importance of soil structure related processes (Carter, 2002). These results emphasize the specificity of plants responding to their environment and the need to tailor crop management.

Our SEM supports the findings of Finney et al. (2016) that both WCC biomass quantity and quality promote subsequent-crop productivity, indicating the relevance of nutrient-cycling for positive PSF effects. Despite the significant pathways from WCC biomass to soil nitrogen and plant-feeding nematode abundance, those soil properties did not capture the hypothesized PSF mechanisms. To build a sound scientific foundation of crop rotation principles, the components of soil-mediated WCC legacies that promote subsequent growth of specific crops are yet to be identified. Taking the growth requirements of subsequent crops as starting point, future studies should make efforts to disentangle nutrient cycling processes from direct biotic influences (pathogens, mutualists, decomposers) that underlie the WCC biomass quantity and quality pathways.

4.4 | Legacy effects of previous main cropping

Despite the increasing PSF literature, most studies are limited to legacy effects of preceding plants to directly succeeding plants wherein persistence of plant legacies remains unclear (Kardol, De Deyn, Laliberté, Mariotte, & Hawkes, 2013). The positive indirect feedback effects on subsequent *Avena* growing on former *Cichorium* plots illustrate that preceding-crop legacies can persist for at least 1 year, which agrees with other studies (Bartelt-Ryser et al., 2005; Campiglia et al., 2014). Previous studies show reduced plant-productivity on soils previously occupied by closely related species (Kulmatiski et al., 2008). Particularly grasses show strong negative feedback effects on soil conditioned by (near-)congeneric species (Cortois et al., 2016; Kulmatiski et al., 2008). Indeed, *Lolium* shoot biomass was lower on previous *Avena* than *Cichorium* plots. *Lolium* significantly reduced subsequent *Avena* productivity. These observations strengthen the general rotation recommendations of avoiding successive cultivation of closely related crops. Therefore, persistence of legacies should be considered when employing legacy effects for sustainable management.

4.5 | Synthesis

Disentangling the relative strength of PSF mechanisms is vital for management of (agro-) ecosystems (Dias et al., 2014; Kardol et al., 2013; Van der Putten et al., 2016). Here, we showed that plant diversity effects can influence subsequent-plant growth in agro-ecosystems. The effects of plant–soil interactions are species combination specific and warrant consideration of previous plant growth. Both biomass quantity and quality are key drivers of soil legacies on subsequent-plant productivity, and research should undertake efforts to disentangle nutrient cycling processes from direct biotic influences. Understanding these underlying pathways is essential to sustainably manage ecosystem functioning through spatial and temporal dynamics of plant mixture effects. Well-chosen WCC species mixtures are a promising agricultural practice to promote biological and chemical soil quality.

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AUTHORS' CONTRIBUTIONS

J.M.B., T.W.K., W.B. and G.B.D.D. conceived the ideas and designed the experiment. J.M.B. and G.B.D.D. executed the experiment and collected the data, which was analysed by J.M.B., and B.D. J.M.B. and G.B.D.D. led the writing of the manuscript. All authors contributed critically to drafts and approved the final manuscript for publication.

DATA ACCESSIBILITY

Data supporting the results of this manuscript are archived in Dryad Digital Repository: https://doi.org/10.5061/dryad.sp21b (Barel Kuyper, de Boer, Douma, & De Deyn, 2017).

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