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LETTER

Single introductions of soil biota and plants generate long-term legacies in soil and plant community assembly

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Abstract

Recent demonstrations of the role of plant–soil biota interactions have challenged the conventional view that vegetation changes are mainly driven by changing abiotic conditions. However, while this concept has been validated under natural conditions, our understanding of the long-term consequences of plant–soil interactions for above-belowground community assembly is restricted to mathematical and conceptual model projections. Here, we demonstrate experimentally that one-time additions of soil biota and plant seeds alter soil-borne nematode and plant community composition in semi-natural grassland for 20 years. Over time, aboveground and belowground community composition became increasingly correlated, suggesting an increasing connectedness of soil biota and plants. We conclude that the initial composition of not only plant communities, but also soil communities has a long-lasting impact on the trajectory of community assembly.

Keywords

Community assembly, nature restoration, plant–soil biota interactions, soil legacy, whole-soil inoculation.

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INTRODUCTION

It is increasingly recognised that ecological dynamics are strongly determined by historical contingencies, which can generate long-term legacy effects (Jackson & Hobbs 2009; Fukami 2015). Centuries-old man-made legacies in the landscape still strongly influence present-day nutrient cycling, plant productivity and species composition in natural ecosystems. For instance, long-term human soil cultivation led to 'Dark Earths' (e.g. Terra preta de Índio) around the world, supporting fungal-dominated soil communities that still affect productivity and plant species composition centuries later (Glaser & Birk 2012; Wiedner *et al.* 2015; Palace *et al.* 2017; Camenzind *et al.* 2018). Likewise, Sami reindeer herd milking grounds can still be recognised by their distinct vegetation 100 years after abandonment. This is a result of self-reinforcing feedbacks between plant and soil communities and selective feeding by herbivores (Egelkraut *et al.* 2018). Together these examples from real ecosystems show that human-induced legacies in community assembly are widespread and can affect ecosystems over very long timescales (decades-centuries) through altered plant–soil community interactions. This, in turn, suggests that the targeted creation of community legacies, for example through altered soil biotic composition and plant seed banks, can improve long-term management of natural ecosystems. However, the previously documented legacies have all developed under long-term and repeated management. It remains unclear whether single interventions can create community legacies with knock-on effects for plant and soil community development over the long-term.

In natural ecosystems the importance of aboveground-belowground coupling for community development is becoming increasingly apparent (Bardgett & Wardle 2010; Risch *et al.* 2018). Plants are drivers of soil community composition, both as hosts and through inputs from root exudates and litter into the soil (Grayston *et al.* 1998; Eisenhauer *et al.* 2017; Zhalnina *et al.* 2018). These plant-induced changes in soil lead to specialised soil communities under individual plants in the field (Bezemer *et al.* 2010; Eisenhauer *et al.* 2010). Likewise, soil communities affect plant communities (Wardle *et al.* 2004; Bardgett & Wardle 2010), which is the driving force of plant–soil feedback (Kardol *et al.* 2006; Bauer *et al.* 2015; Bennett *et al.* 2017; Teste *et al.* 2017). Both greenhouse and field studies, including the use of belowground insecticides and fungicides, have shown that soil communities affect plant performance and community assembly (Brown & Gange 1992; Maron *et al.* 2011). Indeed, the composition of the soil community can determine which plant species become successful and thus steer plant community development (Wubs *et al.* 2016). However, the long-term consequences of above-belowground interventions on community assembly in nature have so far only been studied using model simulations (Kardol *et al.* 2013; Teste *et al.* 2017).

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Reciprocal feedbacks between plant and soil communities are expected to be strong enough to drive community dynamics over long timescales (Bever 1994; Fukami & Nakajima 2013; Lekberg *et al.* 2018), but so far experimental tests are lacking. Here, we address the question how long above-belowground interventions affect above-belowground community assembly in nature using a single experimental introduction of plant seeds and soil biota in just abandoned, early-successional, arable land. In a replicated field experiment, we introduced a novel soil community from mid-succession stage semi-natural grasslands. This belowground treatment was crossed with sowing of mid-succession plant seeds in a full factorial design. After the initial introductions, the communities were left to develop on their own and the setup was fully open to colonisation from the surroundings. We measured plant and soil nematode communities annually for 20 years to examine their temporal responses to the single soil biota and plant introductions. This setup allowed us to test for interactive effects of above-belowground interventions on above-belowground community development. For belowground biota, we studied nematodes which are important indicators of soil community composition. This is because they comprise a diverse set of species occurring at various positions in the soil food web (Coleman *et al.* 2018). In addition, nematodes are sensitive indicators of changes in both abiotic and biotic conditions (Neher 2010).

We tested the hypothesis that plant community composition would be more strongly influenced by seed addition than by soil inoculation. In contrast, we expected the soil community to respond most strongly to introduction of soil biota and less to seed addition. We further predicted that the combined introduction of new soil and plant communities would lead to the most persistent alteration of the nematode and plant community composition compared to the treatment where no biota introductions were made. Finally, we hypothesised that an increasingly tight association in the composition of the soil and plant community would develop over time, as plant–soil feedbacks are expected to lead to progressive species sorting in both communities. Here we show that single soil inoculation and seed addition events can reshape both belowground and aboveground community assembly leading to historical above-belowground legacies of at least 20 years.

METHODS

Site characteristics and experimental setup

The field experiment was established in spring 1996 on a former arable field in the Netherlands (“Mossel”, GPS: 52.07 °N 5.75 °E). The site is situated on a sandy loam soil and had been in agricultural production until autumn 1995 (last crop was maize, Van der Putten *et al.* 2000). A fence was erected around the experiment to keep large mammalian grazers out and the soil was mechanically and manually harrowed in April 1996. The experiment was implemented as a randomised block design with 20 plots (2 × 2 m) established in five replicate blocks and the seed addition and soil inoculation treatments were fully crossed in the design.

At the start of the experiment, half of the plots were treated with a soil inoculum collected from a nearby (< 1 km) mid-succession grassland (Mosschelseveld, GPS: 52.06 °N 5.75 °E) that had been undergoing natural secondary succession since 1985 (10 years at the start of the experiment) and was similar in abiotic conditions (Kardol *et al.* 2005; Van der Wal *et al.* 2006). Soil was collected from the top 15 cm of the donor site, gently mixed and was applied in a thin layer (2.5 L m^{-2}) and harrowed in at a depth of 5 cm in April 1996. Subsequently four turf monoliths (25 × 25 × 25 cm) of soil from the same donor site were introduced into the four corners of each plot in November 1996. The monoliths were used as a vehicle to introduce larger soil fauna that are typically sensitive to mechanical disturbance (Coleman *et al.* 2018).

Half the plots were sown with 15 mid-succession plant species, equally representing grasses, legumes and non-legume forbs (for selection criteria see Van der Putten *et al.* 2000). The species were *Agrostis capillaris* L., *Anthoxanthum odoratum* L., *Festuca rubra* L., *Phleum pratense* L., *Poa pratensis* L. (all Poaceae), *Hypericum perforatum* L. (Hypericaceae), *Hypochaeris radicata* L. (Asteraceae), *Linaria vulgaris* Mill., *Plantago lanceolata* L. (both Plantaginaceae), *Tanacetum vulgare* L. (Asteraceae), *Lotus corniculatus* L., *Trifolium arvense* L., *T. dubium* Sibth., *T. pratense* L., and *Vicia cracca* L. (all Fabaceae) and they were sown at a density of 500 seeds m^{-2} for each grass species and 100 seeds m^{-2} for legume and other forb species in April 1996. These rates are commensurate with seed addition rates in seed limitation experiments in grasslands (Turnbull *et al.* 2000). One species with heavy seeds (*Vicia cracca*) was reduced to 20 seeds m^{-2} to prevent it from becoming dominant. The seeds were hand-sown and mixed with sand to facilitate equal spreading. Subsequently, the plots were hand-harrowed to work the seeds into the soil surface layer. The experiment has been ongoing since 1996 until present. Towards the end of each growing season, in September, the aboveground vegetation of all plots and border rows was mown and removed.

Measurements

Annually the taxonomic composition of the plant and nematode community were recorded. Percent cover of all plant species was recorded each year in the central 1 × 1 m square of each plot in August 1997–2016 (nomenclature following der Van Meijden 2005). Twenty-four soil cores (0–15 cm depth, diameter 17 mm) were collected from each plot in August (1998–2016), homogenised, and nematodes were extracted from 100 ml fresh soil (Oostenbrink 1960), heat-killed at 90 °C, and fixed in 4% formaldehyde solution. Subsequently the total number of nematodes was counted and at least 150 were identified to genus or family level (following Bongers 1988). In cases where there were less than 150 nematodes, all nematodes were identified. To provide temporal continuity in the dataset and reduce observer bias, the nematode data were analysed at family level. At the start of the experiment, we sampled nematode community composition in both the experimental and the donor site (Table S1). In both fields, seven 10 × 10 m plots were haphazardly selected and 24 soil cores were taken and analysed as before for each of these plots.

Data analysis

Data analysis on communities was conducted on the relative abundances of each taxon. Analyses based on absolute abundance lead to the same conclusions (c.f. Fig. 1; S4). We used principal component analyses (PCA) to visualise differences in community composition, on log-transformed relative abundances. The strength of the (multivariate) association between the plant and the nematode community was quantified using co-inertia analysis using the RV-correlation coefficient (Legendre & Legendre 2012). The co-inertia analyses were calculated on log-transformed relative abundances of both plant and nematodes and we used all treatments in each year when we had data for both communities (i.e. 1998–2016). Analyses were conducted across all treatments to gain the most powerful test by incorporating the full spectrum of different plant and nematode communities present in the experiment (i.e. we tested over the longest available gradient).

To visualise the temporal effects of the experimental treatments we conducted partial redundancy analyses (partial RDA) for both communities separately (Alday & Marrs 2014), where the year effect was partialled out. We modelled the community responses as a linear function of the soil inoculation and sowing treatments, their interaction and interactions with time to allow the treatment effect size to vary over time. This is the same as a Principal Response Curve analysis (Van den Brink & Ter Braak 1999), except that the regression equations were not coded to take one treatment as a reference treatment (see Pierik *et al.* 2011). We tested for the significance of the experimental treatments, time and their interactions on community composition using multivariate permutation tests. Permutations were restricted within blocks and were further constrained to take into account the repeated observations within the plots (Legendre & Legendre 2012). To test for the influence of differences in taxonomic resolution among plants and nematodes, these analyses were repeated at two levels of taxonomic resolution: (1) at family level and (2) at the taxonomic resolution of the original identifications (species for plants, predominantly genus level for nematodes).

Differences in community composition were further analysed using Generalised Additive Mixed Models (GAMM), where temporal patterns in communities (the RDA axis 1 scores of the partial RDA analysis described above) over years were modelled using cubic regression splines (Wood 2006). Soil inoculation and seed addition and their interaction were included as fixed effects. Year was included as random effect to account for temporal sampling patterns. Interactions between the treatments and temporal patterns over years were tested by comparing two models, one with a regression spline per treatment and another where one common regression spline was used for all treatments. These models were compared using likelihood ratio tests (Wood 2006).

All analyses were conducted in R version 3.4.4 (R Core Team 2019). Multivariate analyses were done in the *vegan* v2.4-1 package (Oksanen *et al.* 2018), except for the co-inertia analyses done in *ade4* v1.7-8 package (Dray & Dufour 2007). GAMMs were implemented using the *mgcv* v1.8-12 package (Wood 2006). Model assumptions were checked graphically.

RESULTS

During the 20 years of study, both soil nematode and plant communities showed strong successional changes, which depended on the experimental treatments (Fig. S1; Table 1).

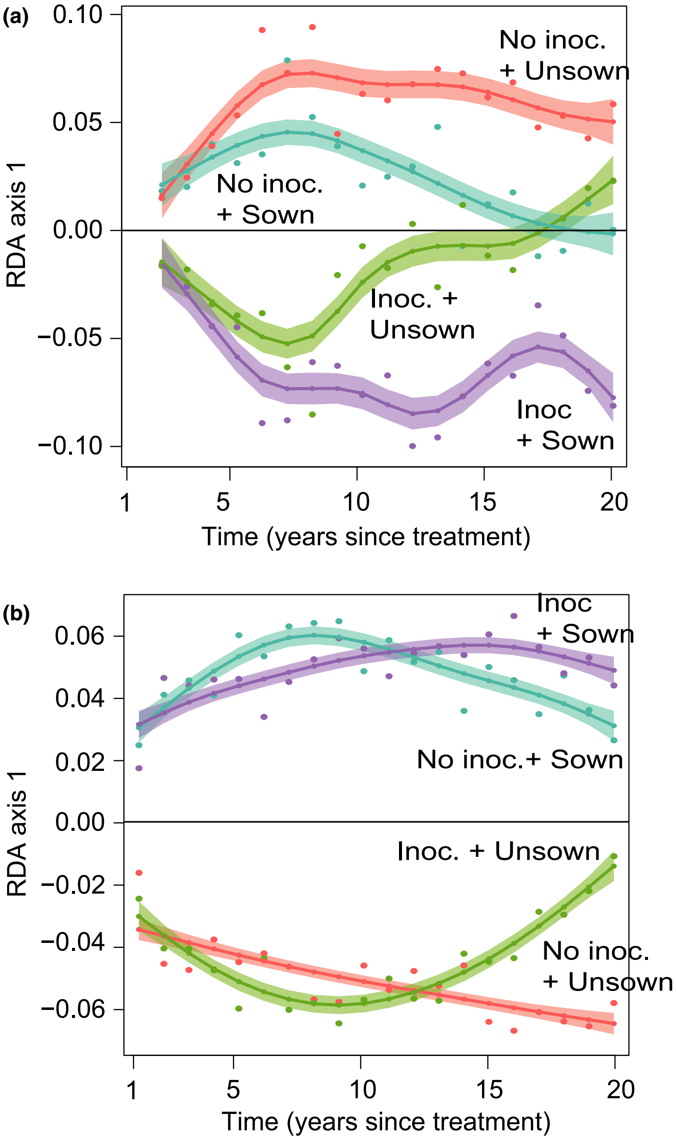

Figure 1 Soil-borne nematode (a) and plant (b) community composition over 20 years in response to a one-time soil inoculation and seed addition treatment. Shown are partial redundancy analyses (RDAs) on community composition that illustrate the direction of community changes as a result of the experimental treatments, after accounting for the difference across years (partialled out in RDA; see Fig S1 for unconstrained ordinations). The first RDA axes explain 4.1% (a) and 14.9% (b) of the variation for nematode and plant community composition, respectively, whereas the year effects accounted for 47.4% and 21.2%. Coloured lines show the mean trend and standard error for each treatment, based on Generalised Additive Mixed Models fitted using cubic regression splines (Table S2). The data points show the raw RDA scores for each treatment in each year. Taxa weights in the ordinations are shown in Fig. S2 on the same RDA axes. Inoc. indicates soil inoculation, no inoc. is the no inoculation control, sown indicates seed addition, whereas unsown is the sowing treatment control where no seeds were added.

Soil inoculation had a marked influence on soil nematode community composition (Fig. 1a; Table 1). The nematode communities in the inoculated and un-inoculated treatments progressively diverged during the first 7 years (Fig. 1a). Furthermore, the difference in nematode community composition due to soil inoculation persisted over the full 20-year study period (Fig. 1a). However, this was particularly so for the combined inoculation+sowing treatment. Plots that were inoculated but not sown, converged towards the two un-inoculated treatments during the later phase of the experiment (Fig. 1a). Seed addition influenced nematode community composition to a lesser extent than soil inoculation, but this became more pronounced over time (Fig. 1a, Table 1).

Plant community composition was strongly and immediately affected by sowing the mixture of mid-succession plant species (Fig. 1b; Table 1). In line with previous studies, this divergence persisted for the full 20 years of study (Fig. 1b). The effect of soil inoculation on the development of the plant community was less pronounced although still significant (Table 1). However, as for soil-borne nematodes, the combination of soil inoculation and sowing led the strongest differentiation in plant community composition between 15 and 20 years after the treatments were implemented (Fig. 1b). Over time, the association between the soil-borne nematode and plant community increased in strength (Fig. 2). Changes in the level of taxonomic resolution for both plants and nematodes did not alter the results (c.f. Fig. 1, S3).

DISCUSSION

We show that historical contingencies as a result of single introductions of soil biota and plants resulted in long-term alterations of above-belowground successional trajectories. It is well known that seed addition can have a long-term impact on plant community development (Egler 1954; Lepš *et al.* 2007; Fukami 2015) and that legacies in soil biota composition can be induced experimentally (Grman & Suding 2010; Wubs *et al.* 2016). However, our results now demonstrate that the legacy of such a historical contingency in soil can influence the dynamics of soil and plant communities on a two decade long timescale. The community developmental trajectories remained most distinct from the untreated controls when soil biota and seed introductions were combined, highlighting the important synergistic effects that plant–soil interactions have on ecosystem development.

Table 1 Statistical analysis of factors contributing to differences in community composition of soil-borne nematodes and plants over time. Significance (shown in bold face if p-value < 0.05) of each constrained partial RDA term was assessed using permutation tests (999 permutations), where the permutation scheme accounted for temporal and spatial dependence among observations

	Nematode community				Plant community			
Terms	d.f.	Pseudo-*F*	*P*-value	R^2 (%)	d.f.	Pseudo-F	*P*-value	R^2 (%)
Soil inoculation	1	24.28	**0.001**	8.01	1	7.35	**0.001**	2.30
Seed addition	1	19.93	**0.001**	6.58	1	99.38	**0.001**	31.15
Inoc. x seed add.	1	2.00	0.529	0.66	1	6.06	0.406	1.90
Yr. x inoc.	18	1.19	**0.011**	7.08	19	1.34	**0.001**	8.00
Yr. x seed add.	18	1.50	**0.001**	8.88	19	3.50	**0.001**	20.84
Yr. x inoc. x seed add.	18	0.83	0.680	4.95	19	0.99	0.059	5.89
Residuals	303				319			

The two-decade old legacies we report here were induced by a single seed and soil biota introduction event. This is in contrast to the long-term legacies of the previously studied Black Earth (Glaser & Birk 2012; Wiedner *et al.* 2015; Camenzind *et al.* 2018) and reindeer milking ground (Egelkraut *et al.* 2018) systems. Those legacies act over a much longer time scale than the twenty-year legacy we report here. However, importantly these examples were each induced by repeated and long-term application of human management practices. Our twenty-year legacy resulted from a single intervention, showing that long-lasting biotic legacies can be created with limited effort and time. In addition, if the legacies of the historical contingencies are indeed driven by feedbacks among

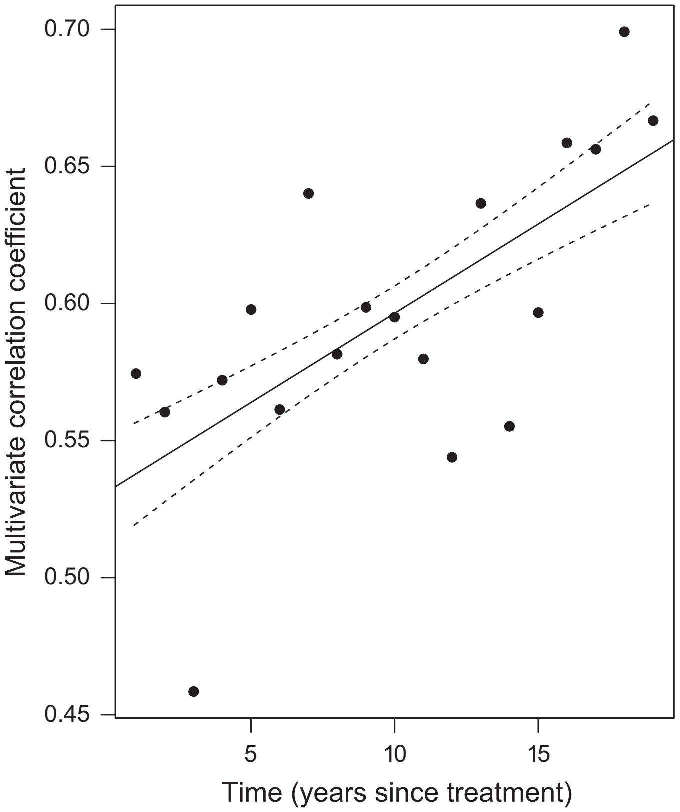

Figure 2 Association of soil-borne nematode and plant communities composition over time (t_0 = 1996). The association was quantified as the correlation between the plant and the nematode community composition (relative abundances of all taxa in the two communities) for each year, using a multivariate analogue of the Pearson correlation coefficient (the RV-coefficient from co-inertia analysis). Shown is the regression (±SE) of the multivariate RV-correlation coefficient over time ($F_{1,17}$ = 13.71, P = 0.0018).

plant and soil communities (Bever 1994; Fukami & Nakajima 2013; Wubs *et al.* 2016), they can be expected to persist well beyond the present twenty years of monitoring (Fukami & Nakajima 2013).

From within the same study system there is clear observational and experimental evidence that plants select for particular soil communities (Bezemer *et al.* 2010; Wubs & Bezemer 2018a) and that, in turn, soil community composition feeds back to affect plant performance (De Deyn *et al.* 2003; Kardol *et al.* 2006; Wubs *et al.* 2016). Based on this we expected that over time the plant and nematode community would become increasingly strongly associated as the plant–soil feedbacks would lead to progressive above-belowground species sorting. We indeed observed an increasingly strong association between plants and nematodes, which together with the prior experimental evidence, makes a strong albeit indirect case that the divergence in community composition was driven by reciprocal plant–soil biota interactions (Bever 1994; Kardol *et al.* 2006; Fukami & Nakajima 2013). It has been demonstrated that during succession soil communities become increasingly tightly associated (Morriën *et al.* 2017) and our study expands this by documenting increasingly tight plant–soil biota associations over successional time. Nevertheless, plant–soil feedback strengths can change over time (Hawkes *et al.* 2013; Kardol *et al.* 2013; Wubs & Bezemer 2018b) and further experimental work is required to establish how bidirectional plant–soil forcing may have operated over the full two decades that the experiment has been running.

Remarkably, it took 7 years for the divergence in soil community composition to become most pronounced, highlighting a substantial time lag in soil compared to plants, which responded immediately to seed addition. The same temporal dynamics were also observed when both plants and nematodes were analysed at the same, either fine or coarse, taxonomic resolution, showing that the coarser level of taxonomic resolution for nematodes (families) was not the cause of the observed time lag. Instead, the belowground time lag may be due to competition and predation by the resident soil community that was still in place (Wei *et al.* 2015). In contrast, the plants established on bare soil where arable practises had ceased just before installing the experiment. Our observation of an initial disconnect and subsequent progressive association between plants and nematodes is in line with previous, plant diversity, experiments. In these studies a clear association between plants and soil fauna was observed but only after a time lag of several (4-8) years (Viketoft *et al.* 2009, 2011; Eisenhauer *et al.* 2010). The consistency among these experimental results in the field suggests that time delays in belowground community development are a general phenomenon.

These results open up new opportunities for the effective management of above- and belowground community assembly in natural ecosystems. Our study was conducted in a fully open system, where both immigration and colonisation by plants and soil biota from the surroundings were not controlled. This suggests that the community developmental trajectories induced by the single experimental introductions are robust to external colonisations. Here the introduction of plants and soil biota followed the natural successional gradient, since mid-succession plants and soils were introduced into an early-successional recently abandoned arable soil. It is an open question whether introductions that go from earlier to later successional systems, and thus counter to the plant–soil interactions driven successional gradient (Kardol *et al.* 2006; Bauer *et al.* 2015), can be successful. Importantly, restoration results and plant–soil interactions depend strongly on the local abiotic and biotic conditions (Eviner & Hawkes 2008; Smith-Ramesh & Reynolds 2017), and we expect that our methods will need to be tailored to the local situation in order to attain place-specific restoration goals. Future studies need to address the potential to control and fine-tune community assembly processes using community-based approaches to plant–soil interactions to enhance ecosystem restoration and biodiversity conservation.

CONCLUSIONS

In a long-term field experiment we show that a single introduction of plant seeds and soil biota can create historical contingencies in community composition that affect plant–soil community development for over two decades. We found that the combination of both soil biota and seed addition jointly lead to the most persistent legacies in plant and soil community development. Over time, plant and soil-borne nematode communities became increasingly tightly associated, indirectly supporting the idea that reciprocal plant–soil feedbacks provide the momentum for the continued persistence of the legacy effects. Together these results show that plant–soil biota interactions play a central role in community assembly processes in terrestrial ecosystems. Finally, our results suggest that effective long-term ecosystem management may be elicited by targeted one-time introductions of plants and soil biota.

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COMPETING FINANCIAL INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

W.H.v.d.P., S.R.M. and G.W.K. designed and initiated the field experiment and T.M.B and W.H.v.d.P. maintained it. G.W.K., H.D. and R.W. annually sampled and analysed the nematode community composition. E.R.J.W. analysed the data and E.R.J.W., W.H.v.d.P. and T.M.B wrote the first draft. All authors contributed to the final version of the manuscript.

DATA ACCESSIBILITY STATEMENT

The data supporting the results are archived in Figshare: https://doi.org/10.6084/m9.figshare.7936724.v1.

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SUPPORTING INFORMATION

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

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