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RESEARCH ARTICLE

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Does topsoil removal in grassland restoration benefit both soil nematode and plant communities?

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Abstract

1. Successful restoration of semi-natural grasslands on grasslands previously subject to intensive management needs to overcome manifold barriers. These include high soil fertility, the dominance of a few fast-growing plant species, degraded soil faunal communities and missing propagules of the targeted above- and below-ground flora and fauna. A combination of removing the topsoil and introducing propagules of target plants has become one of the major tools for nature conservation agencies and practitioners to reduce soil fertility and restore former species-rich grasslands in various European countries.
2. Using topsoil removal as a restoration measure has provoked an ongoing debate between supporting nature conservation and rejecting soil protection agencies. Although it favours species-rich plant communities, it strongly disturbs soil communities and affects physical and chemical soil properties and processes. Currently, there is a lack of long-term data to assess how restored grassland ecosystems develop and recover after topsoil removal. Here, we used two well-established bioindicators, soil nematodes and plants, to quantify restoration success of topsoil removal in comparison with alternative restoration measures and target communities 22 years after intervention.
3. The nematode community composition indicated reduced nutrient availability in the restored systems, as was aimed at by topsoil removal. Nevertheless, after this 22-year period following topsoil removal, nematode composition and structure revealed successful recovery.
4. Plant communities benefitted from the reduction of soil nutrients after topsoil removal as indicated by higher numbers of plant species and higher Shannon diversity. Furthermore, topsoil removal strongly promoted the re-establishment of plant species of the target plant community.
5. *Synthesis and applications*. Overall, our study demonstrates how a massive intervention by topsoil removal proved successful in converting intensively managed into species-rich grasslands. This contrasts with the mild intervention of repeated mowing and removing of the harvested plant material. We show that, in the long run, potential negative effects of topsoil removal on the soil fauna can be

successfully overcome and plant communities can develop into targeted species-rich grassland.

KEYWORDS
biodiversity, biological indicators, food web structure, long-term recovery, propagule availability, restoration success, semi-natural grasslands, topsoil removal

1 | INTRODUCTION

Species-rich, semi-natural oligo- to mesotrophic grasslands are among the most diverse ecosystems in Northern and Central Europe (Dengler, Janisová, Török, & Wellstein, 2014). Historically, they were only lightly fertilized with manure and harvested once or twice a year, which also helped preventing shrub and tree invasion (Poschlod & WallisDeVries, 2002). However, as many temperate grasslands worldwide, they suffer from degradation and biodiversity loss due to high-input farming, abandonment or urban sprawl (Török & Dengler, 2018). The remaining areas are often small, fragmented and isolated, and many plant and animal species specialized to inhabit these oligotrophic ecosystems went locally extinct (Fischer & Stöcklin, 1997). In Switzerland, 99% of the species-rich grasslands were lost by the late 19th century and further fragmentation and degradation of the few remnants became highly visible in the 1970s (Gimmi, Lachat, & Bürgi, 2011). Although conservation efforts increased, the loss of these grasslands did not stop (Gattlen, Klaus, & Litsios, 2017). As a counter measure, restoration of species-rich grasslands gained support in conservation management not only in Switzerland but also in many other European countries. Abandoned, previously intensively managed grassland became a major source to expand and reconnect the remnants of species-rich grasslands (Kardol & Wardle, 2010). However, these areas generally are highly enriched in soil nutrients due to excessive use of mineral fertilizer and manure, are dominated by a few fast-growing plant species and have degraded soil faunal communities. They contain soil communities that are dominated by bacteria, while fungi and larger soil biota are relatively scarce (De Deyn et al., 2003; Kardol & Wardle, 2010). In addition, propagules of the target vegetation are expected to be virtually missing in the soil seed bank due to the long and intense agricultural use (Bossuyt & Honnay, 2008; Stöcklin & Fischer, 1999). Together, these factors cause severe constraints that need to be overcome for successful conversion into semi-natural grasslands (Kiehl & Wagner, 2006).

Many studies have shown that a mild intervention, such as repeated mowing and removing of the harvested plant material, is rarely successful to overcome these constraints (e.g. Marss, Snow, & Evans, 1998). A combination of removing the topsoil—typically between 20 and 50 cm (e.g. Frouz et al., 2009)—and introducing propagules of target plant species proofed, in contrast, successful (e.g. Kiehl & Pfadenhauer, 2007) and became a promising tool for nature conservation agencies and practitioners in various European countries (Kiehl, Kirmer, Donath, Rasran, & Hölzel, 2010). However, in Switzerland, its implementation provoked an ongoing debate between nature conservation (pro) and soil protection (contra) agencies as topsoil removal—although favouring species-rich plant communities—strongly reduces soil communities and affects physical and chemical soil properties and the processes that emerge from them (Geissen et al., 2013). The opponents fear that systems are unable to overcome the negative effects of topsoil removal and therefore may not reach the targeted above- and below-ground community composition in the long term (Suding, 2011). However, there is a lack of data about the long-term recovery of restored grasslands. In the few cases where long-term data are available, the focus was primarily on above-ground properties such as plant communities (Kiehl et al., 2010). Soil communities were neglected despite their importance for decomposition processes and nutrient flows (Bardgett & van der Putten, 2014). Since recovery times of the above- and below-ground communities differ considerably (Kardol, Newton, Bezemer, Maraun, & van der Putten, 2009), it is essential to assess the composition of below-ground communities in addition to the vegetation. Only such comparisons will allow to validate the long-term success of restoration measures (Havlicek, 2012).

Here, we chose to use the soil nematode and plant community composition and structure to assess long-term success of different restoration methods including topsoil removal. Soil nematodes are excellent bioindicators for soil quality and ecosystem functioning as their community composition is very sensitive to nutrient enrichment and management changes (Bongers & Ferris, 1999; Yeates & Bongers, 1999). In addition, changes in nematode community compositions are known to take place considerably faster than the ones of plant communities, as soil nematodes are known to be fast colonizers (Bongers, 1990; Bongers & Ferris, 1999). Furthermore, nematodes operate at various trophic levels of the soil food web, so that quantifying structure and composition allows evaluating developments in food web complexity and ecosystem maturity after disturbances (Bongers & Ferris, 1999; Ferris, Bongers, & de Goede, 2001).

We chose three restoration methods representing increasing intervention levels for soil, flora and fauna, namely (a) ‘Harvest only’ to gradually reduce soil nutrients through multiple hay harvests per year, (b) ‘Topsoil’ removal to reduce soil nutrients and remove undesirable propagules from the soil seed bank and (c) ‘Topsoil + Propagules’ where topsoil removal was combined with the introduction of propagules of the target vegetation. Restoration success was compared to (a) intensively managed grasslands (‘Initial’) and (b) species-rich ancient grasslands (‘Target’). Evaluation took place 22 years after restoration measures were implemented.

According to the literature, we expected that the restoration success will considerably differ between our three restoration treatments as detailed in the following:

1. 'Harvest only': A minor reduction in soil nutrients and missing niches in the established above- and below-ground communities will hamper recolonization by targeted plant and animal species. In addition, ongoing disturbance due to multiple hay harvests each year will result in higher numbers of bacterivorous as well as stress-indicating soil nematodes.
2. 'Topsoil': Missing propagules of the target vegetation are expected to hamper the recolonization of targeted plant species. Thus, plant communities will differ from the ones of the target grassland ecosystem. For soil nematodes, we expect that 22 years will be sufficient to successfully re-establish food webs with a complexity comparable to the ones in targeted semi-natural grasslands. However, differences in the plant communities will lead to a different soil nematode community compared to the targeted species-rich grasslands.
3. 'Topsoil + Propagules': Reduced soil nutrients, suitable niches for the recolonization of oligotrophic grassland communities and the presence of target plant propagules will foster a successful re-establishment of a plant and animal community comparable to the target ecosystem. Similar to the 'Topsoil' treatment, we expect that 22 years are sufficient to re-establish complex soil nematode food webs with a composition that is most similar to the one of the target systems. At the same time, we expect to find the highest richness of targeted plant species in this treatment. Consequently, 'Topsoil + Propagules' is expected to be the restoration measure most successful in re-establishing a species-rich grassland system, both in terms of nematode and plant richness.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental settings

The study was conducted in a nature reserve (Eigental: 47°27′ to 47°29′N, 8°37′E, 461–507 m a.s.l.) that is located on the Swiss Central plateau close to Zurich airport (Canton Zurich, Switzerland). The mean annual temperature in this area ranges from 8.9 to 10.6°C, mean annual precipitation from 910 to 1,260 mm (10-year average [2007–2017]; MeteoSchweiz, 2018). The main soil types are calcaric to gleyic Cambisol and Gleysols (see Table S1). The reserve was established in 1967 to protect small remnants of oligotrophic semi-natural grasslands (roughly 12 ha). The plant community can be characterized as Molinion and Mesobromion (semi-wet to semi-dry), depending on the site-specific groundwater level and slope inclination (Table S1; Delarze, Gonseth, Eggenberg, & Vust, 2015). These remnants represent species-rich islands in an otherwise intensively managed agricultural landscape. Semi-natural grasslands covered an area of 60,000 ha in the Canton Zurich in 1939, however, by 2005 only roughly 600 ha remained (Baudirektion Kanton Zürich, 2007). In 1990, the government of Canton Zurich decided to enlarge the nature reserve Eigental. The goal was to incorporate 11 patches of 20 ha adjacent intensively farmed land and transform these patches into semi-natural grasslands. The patches had a different agricultural history, ranging from permanent (no tillage for >50 years) to temporary grassland (as part of crop rotation; last tillage <5 years, Table S1). On all freshly integrated patches, fertilization was stopped in 1992 and from then on biomass was harvested three times a year and removed. After 5 years without noticeable effects on vegetation composition, the Nature Conservation Agency of Canton Zurich decided to increase the restoration efforts. In 1995, a large-scale experiment was initialized to evaluate if certain treatments can facilitate restoration within a reasonable time frame of 5–10 years after treatment implementation.

The three restoration treatments used were:

1. 'Harvest only': Plots are being mowed two to three times a year and the biomass is removed.
2. 'Topsoil': Topsoil was removed to a depth of 10–20 cm, depending on the depth of the O and A horizon, in four randomly selected areas within each of the 11 patches in late autumn 1995. The size of each topsoil removal area depended on individual patch size and was between 2,700 and 7,000 m^2.
3. 'Topsoil + Propagules': Propagules from target vegetation were added on half of the area where topsoil was removed, using fresh, seed-containing hay originating from a mixture of semi-dry to semi-wet species-rich grasslands of local provenance (within a radius of 7 km). Hay applications were conducted twice in 1995 and 1996. Repeated applications were chosen to account for the low quantity of available plant material per transfer, since area ratio between receptor and donor sites was roughly 1:1. In addition, hand-collected propagules from 15 selected target species (Table S5) of regional provenance (within a radius of 30 km) were equally applied in 1996 and 1997.

'Topsoil' and 'Topsoil + Propagules' plots are mowed once a year, and the biomass is removed. Mowing on these plots started 5 years after the treatment was implemented.

Eleven permanent plots of 5 m × 5 m were randomly established in each treatment to monitor the vegetation development. The experiment was complemented with 11 control plots that represent the initial state of intensively managed grasslands, further referred to as 'Initial', and 11 control plots that represent the targeted state of donor sites for 'Topsoil + Propagules', further referred to as 'Target'. Consequently, the experiment consists of 55 plots (5 treatments × 11 replicates). The management of intensively used grasslands includes mowing and fertilizing (manure) between two to five times a year as well as different tillage regimes (no tillage for >50 years; last time of tillage <5 years; Table S1).

2.2 | Nematode and plant sampling

Soil nematodes were sampled in 2 m × 2 m plots, randomly established at least 2 m away from the vegetation plots. We collected eight soil cores with a 2.2 cm diameter soil core sampler (Giddings Machine Company, Windsor, CO) to a depth of 12 cm (representing the majority of the plant rooting system) in each plot at the beginning of July 2017. The eight cores within each replicate plot were combined, gently homogenized, placed in coolers and transported to the laboratory of NIOO in Wageningen, the Netherlands, within 1 week. Free-living nematodes were extracted from 200 g of fresh soil using Oostenbrink elutriator (Oostenbrink, 1960) and concentrated, resulting in 6 ml nematode solution. The nematode solution was subdivided into three subsamples, two for morphological identification and quantification and one for molecular work (not used in this study). For morphological identification and quantification, nematodes were heat-killed at 90°C and fixed in 4% formaldehyde solution (final volume 10 ml per subsample). All nematodes in 1 ml of formaldehyde solution were counted, and a minimum of 150 individuals per 1 ml sample (or all if less nematodes were present) were identified to family level using Bongers (1988). We then extrapolated the numbers of each nematode taxa identified to the entire sample and expressed them per 100 g dry soil for further analyses.

We calculated number of nematode taxa and Shannon diversity and assessed nematode community composition. In addition, we classified the nematode taxa into feeding types (herbivores, bacterivores, fungivores, omni-carnivores), structural and functional guilds (Table S4). Structural guilds assign nematode taxa according to life-history traits into five colonizer-persister (C-P) classes, ranging from one (early colonizers of new resources) to five (persisters in undisturbed habitats; Bongers, 1990). C-P classes can be categorized as indicators for nutrient-enriched (C-P1), stressed (C-P2) and structured (C-P3 + C-P4 + C-P5) soil conditions (Ferris et al., 2001). Functional guilds assign nematode taxa according to their C-P classification combined with their feeding habits (Ferris et al., 2001). Based on the structural and functional guild classification, we calculated five additional indices to assess soil nutrient status, disturbance and food web characteristics using NINJA (Sieriebriennikov, Ferris, & de Goede, 2014). (a) The Maturity index indicates the degree of different environmental perturbations (e.g. tillage, nutrient enrichment, pollution) and is used to monitor colonization and subsequent succession after disturbances (Bongers, 1990). (b) The Plant parasite (C-P of herbivorous nematodes only) to Maturity index ratio is used to monitor the recovery of disturbed habitats incorporating information of life-history traits for all feeding types (Bongers, van der Meulen, & Korthals, 1997). (c) The Enrichment index indicates nutrient-enriched soils and agricultural management practices (Ferris et al., 2001). (d) The Structure index provides information about the succession stage of the soil food web and therefore correlates with the degree of maturity of an ecosystem (Ferris et al., 2001). (e) The Channel index provides information about the predominant decomposition pathways, where higher values stand for a higher proportion of energy transformed through the slow fungal decomposition channel (Ferris et al., 2001). In addition, the Structure and Enrichment indices can be displayed in a biplot where nematode assemblages are plotted along a structure (*x*-axis) and enrichment (*y*-axis) trajectory (increasing index values). Each biplot quadrat reflects different levels of disturbance, soil nutrient pools and decomposition pathways (Ferris et al., 2001).

The plant surveys were conducted on the 25 m^2 permanent plots in June 2017. Plant species cover was visually assessed according to the semi-quantitative cover-abundance scale of Braun-Blanquet (1964; nomenclature: Lauber & Wagner, 1996). We calculated number of species and Shannon diversity and assessed plant community composition. We also counted the number of target species (all species recorded in the 11 target plots plus propagules of species applied by hand, resulting in a total of 143 species) and categorized plant species into species of concern based on their red list status in Switzerland as well as their protection status in Switzerland and the Canton Zurich (Moser, Gygax, Bäumler, Wyler, & Palese, 2002; Table S5). Furthermore, we calculated indicator values for soil moisture and soil nutrients for each species according to Landolt et al. (2010; Table S5).

2.3 | Statistical analyses

We assessed treatment differences in soil nematode and plant properties using generalized linear models for abundance-based data, zero-inflated negative binomial regression models for enrichment-indicating soil nematodes and beta regression models for proportional data. Nematode and plant properties were response variables; treatment was the explanatory variable (fixed factor). We plotted standardized residuals for number of nematode and plant taxa against plot coordinates to assess potential spatial autocorrelation among plots (Figure S1a,b). As there was no spatial autocorrelation, we did not need to correct our models. We used analyses of deviance (ANOVA type II test) to analyse the overall treatment effects on all univariate variables. Significant differences between treatments were identified using least square means for treatment levels. Post hoc pairwise comparisons were adjusted for multiple testing using the Tukey correction method. Normality and homogeneity of Pearson residuals were checked visually and with Shapiro–Wilk and Levene`s tests. Variables were transformed if necessary following suggestions explored via Tukey`s Ladder of Power transformation. In cases of heterogeneity of Pearson residuals (e.g. Shannon diversity index analyses), Generalized Least Squares models with weighted treatments effects were used, which allowed to account for different variances between the treatments (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

We assessed soil nematode and plant community composition using family data (nematodes) and individual species data (plants). Additionally, we used community structure based on feeding types and C-P classes to describe treatment-specific nematode assemblages and interpret food web complexity (Ferris et al., 2001). Plot-level differences in community composition and structure for nematodes and plants were calculated based on Bray–Curtis dissimilarity, followed by permutational multivariate analysis of variance with 10,000 iterations to assess overall treatment effects. Pairwise comparisons were adjusted with the Bonferroni correction method.

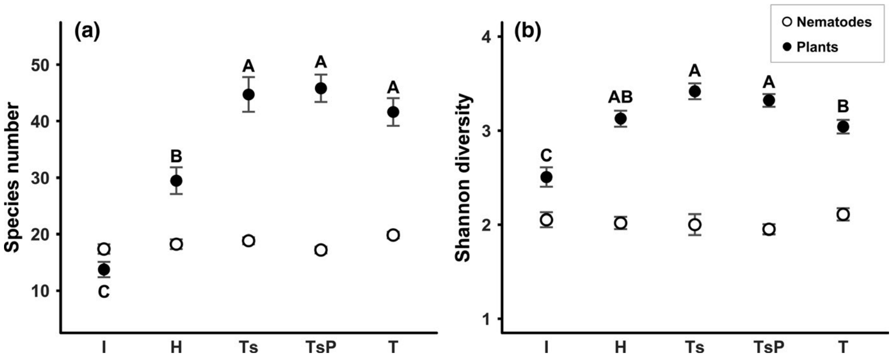

FIGURE 1 Treatment effects on species number (a) and Shannon diversity (b) of soil nematode and plant communities. Different capital letters indicate significant differences between treatments. 'I' = 'Initial'; 'H' = 'Harvest only'; 'Ts' = 'Topsoil'; 'TsP' = 'Topsoil + Propagules'; 'T' = 'Target'

A principle coordinate analyses was used to visualize nematode and plant community composition patterns. All statistical analysis and graphical outputs were performed in R version 3.4.0 (R Core Team, 2017). A full list of packages and functions can be found in Table S3.

3 | RESULTS

3.1 | Soil nematodes

Species number and Shannon diversity of soil nematodes did not significantly differ between our three restoration treatments or between these treatments and 'Target' (Figure 1a,b, Table 1). Yet, the nematode community composition in 'Topsoil', 'Topsoil + Propagules' and 'Target' significantly differed from 'Initial', while 'Harvest only' was not significantly different from any other treatment (Figure 2a, Table 2, Table S2). The intermediate position of 'Harvest only' can be attributed to abundances of Cephalobidae (bacterivores), Dolichodoridae (herbivores), Aphelenchidae (fungivores) and Aporcelaimidae (omnivores) similar to 'Initial', while Tripylidae (omnivores) and Nygolaimidae (carnivores) were missing from both 'Initial' and 'Harvest only' (Table S4). Overall, we identified 39 nematode families, of which 13 were herbivores, 13 bacterivores, nine omni-carnivores and four fungivores (Table S4).

Total nematode abundance was significantly lower in 'Topsoil' and 'Topsoil + Propagules' than in 'Initial' (Figure 3a, Table 1). Herbivorous nematode abundance did not show a strong response to our treatments and only differed between 'Initial' and 'Topsoil' (Figure 3b, Table 1, Figure S2). Bacterivorous nematodes were significantly more abundant in 'Initial' than in 'Topsoil', 'Topsoil + Propagules' and 'Target', but not in 'Harvest only', while fungivores abundance did not differ among the treatments (Figure 3c,d, Table 1). Omni-carnivores were significantly more abundant in 'Harvest only' and 'Target' than in 'Initial' and 'Topsoil + Propagules' (Figure 3e, Table 1). The overall composition of different feeding types did not significantly differ among treatments (Figure 3f, Table 2, Table S2). Herbivores and bacterivores were numerically dominant in all treatments, averaging 3,320 and 815 individuals per 100 g of dry soil respectively.

TABLE 1 Treatment effects on soil nematode and plant community characteristics. Degrees of freedom: numerator = 4, denominator = 50 (plants), 49 (nematodes). Abundance data of soil nematodes expressed as individuals per 100 g dry soil. Transformation: Omni-carnivores (log transformed), Enrichment indicators (square root transformed). Bold numbers indicate significance at 5% level

	Treatment overall	
Variable	*F*-value	*p*-values
Nematodes		
Species number	2.4282	0.060
Shannon diversity	0.5870	0.673
Total nematode abundance	3.5198	**0.013**
Herbivorous nematode abundance	2.5306	0.052
Bacterivorous nematode abundance	8.0608	**<0.001**
Fungivorous nematode abundance	0.4029	0.806
Omni-carnivorous nematode abundance	4.4063	**0.004**
Enrichment indicator abundance	9.7294	**<0.001**
Stress tolerance indicator abundance	9.0416	**<0.001**
Structure indicator abundance	5.4075	**0.001**
Maturity index	16.3470	**<0.001**
Plant parasite to Maturity index	16.9040	**<0.001**
Enrichment index	4.3307	**0.005**
Structure index	15.5620	**<0.001**
Channel index	2.8798	**0.032**
Plants		
Species number	37.8400	**<0.001**
Shannon diversity	14.4540	**<0.001**
Target species	48.1010	**<0.001**
Species of concern	19.0790	**<0.001**
Soil moisture indicator	4.0901	**0.006**
Soil nutrient indicator	71.6390	**<0.001**

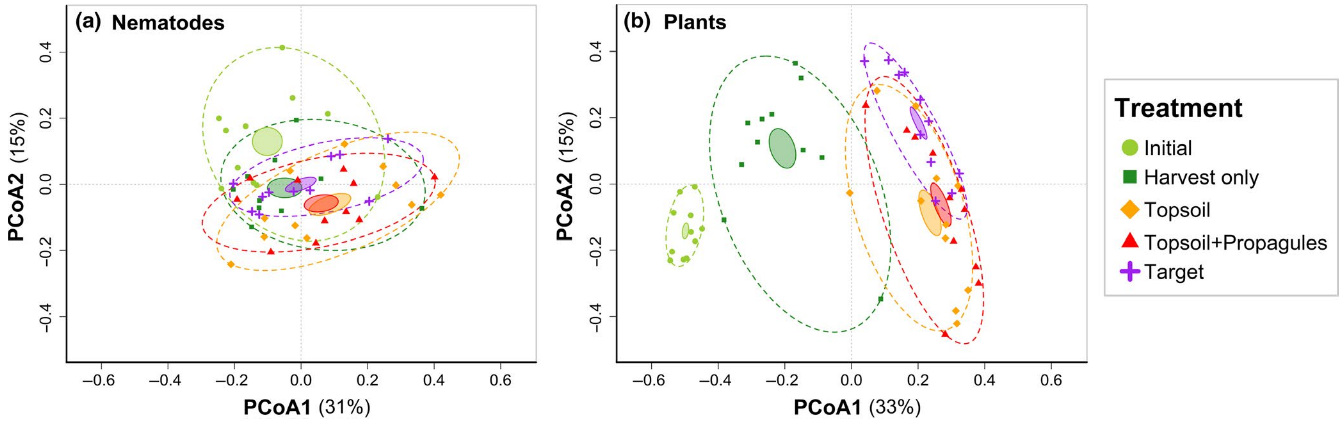

FIGURE 2 PCoA biplots of treatment effects on soil nematode (a) and plant community composition (b) Single plot coordinates = filled symbols; treatment ellipses = dashed; standard error ellipses = shaded. PCoA, principle coordinate analyses

Omni-carnivores (520 individuals) and particularly fungivores (480) were much less abundant.

The nematode communities also noticeably differed with regard to structural guilds. Enrichment and stress tolerators (C-P1, C-P2) were most abundant in ‘Initial’, while structure indicators (C-P3 to C-P5) were most abundant in all other treatments (Figure 4a–c, Table 1, Figure S2). The C-P structure of the nematode assemblages significantly differed between ‘Initial’ and all other treatments (Figure 4d, Table 2, Table S2). ‘Harvest only’ and ‘Target’ supported the most long-lived, stress-intolerant C-P5 nematodes, while ‘Topsoil’ and ‘Topsoil + Propagules’ showed higher numbers of C-P4 nematodes (intermediate succession; Figure 4d, Figure S2).

The five nematode indices calculated based on structural and functional guilds significantly differed between ‘Initial’ and all other treatments, except for the Channel index (Figure 5a–e, Table 1). The decreased Enrichment index and increased Structure index found in all restoration treatments compared to ‘Initial’ indicate reduced nutrient availability and increased stability of soil conditions (Figure 5c,d). Plotting the Structure against the Enrichment index (Ferris et al., 2001) revealed that the food webs in our ‘Initial’ plots were ‘maturing’ with moderate disturbance levels, nutrient-enriched soils and bacterial dominated decomposition channels (Figure 5f). All other treatments had ‘structured’ food webs, characterized by undisturbed, fertile soils with bacterial or fungal dominated decomposition channels (Figure 5f).

3.2 | Plants

Number of plant species, Shannon diversity and community composition significantly differed between our treatments (Figure 1a,b, Figure 2b, Table 1, Table S2). We found more plant species in ‘Topsoil’ (45 species) and ‘Topsoil + Propagules’ (46) than in ‘Initial’ (14) and ‘Harvest only’ (29), but a similar number compared to ‘Target’ (42; Figure 1a). Plant diversity was significantly lowest in ‘Initial’ (Figure 1b). ‘Topsoil’ and ‘Topsoil + Propagules’ were more diverse than ‘Target’ but similar to ‘Harvest only’ (Figure 1b). Plant communities in all restoration treatments significantly differed from ‘Initial’ and ‘Target’. However, the plant compositions of ‘Topsoil’ and ‘Topsoil + Propagules’ were not different, but differed from ‘Harvest only’, which took an intermediate position between the two topsoil removal treatments and ‘Initial’ (Figure 2b, Table 2, Table S2). The differences in plant community composition were driven by species richness (Figure 1a) as well as number of species of high

TABLE 2 Community composition and pairwise comparisons of treatment dissimilarities for soil nematodes and plants using Bray–Curtis dissimilarity matrices based on abundance data. ‘Overall’: overall treatments differences in community composition; ‘Treatment’: pairwise comparison of treatment dissimilarities; ‘C-P’—Colonizer-persisters. Bold numbers indicate significance at 5% level. Different capital letters indicate significant differences between treatments (for full statistical output, see Table S2)

	Overall		Treatment				
Variable	*F*-value	*p*-value	Initial	Harvest only	Topsoil	Topsoil + Propagules	Target
Nematodes							
Families	2.3520	**<0.001**	A	AB	B	B	B
Feeding types	2.3527	**0.010**	A	A	A	A	A
C-P classes	5.3779	**<0.001**	A	B	B	B	B
Plants							
Species	10.2020	**<0.001**	A	B	C	C	D

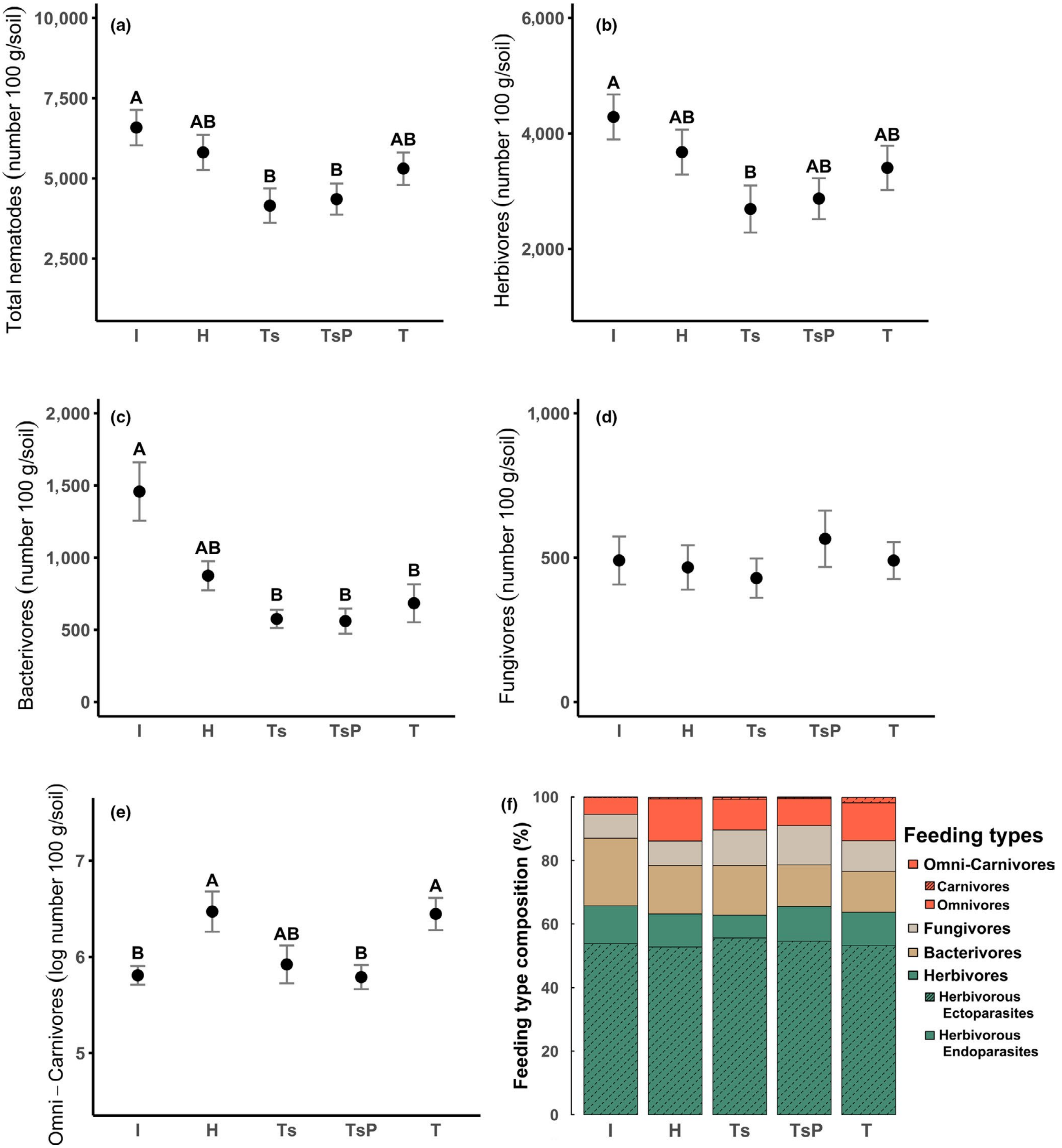

FIGURE 3 Treatment effects on individual nematode feeding type abundances (mean ± *SE*; a–e) and feeding type composition (%; f). Untransformed data used for all feeding types except for omni-carnivores (e; log transformed). Different capital letters indicate significant differences between treatments. 'I' = 'Initial'; 'H' = 'Harvest only'; 'Ts' = 'Topsoil'; 'TsP' = 'Topsoil + Propagules'; 'T' = 'Target'

conservation value (Figure 6b). A similar number of target species were found in 'Topsoil + Propagules' compared to 'Target'. All the other treatments had significantly less target species and their numbers dropped significantly from 'Topsoil' to 'Harvest only' to 'Initial' (Figure 6a). Surprisingly, a lot of species of concern were also found in 'Topsoil', suggesting that the introduction of target plant propagules may not necessarily be needed (Figure 6b, Table S5). Furthermore, eight of in total 32 species of concern were unique to 'Target' plots, while another eight species of concern were found in our topsoil removal treatments but not in 'Target' (Table S5). In addition, several non-target species established in the restoration plots, such as *Carex hirta*, *Juncus inflexus*, *Juncus subnodulosus*, *Poa pratensis*

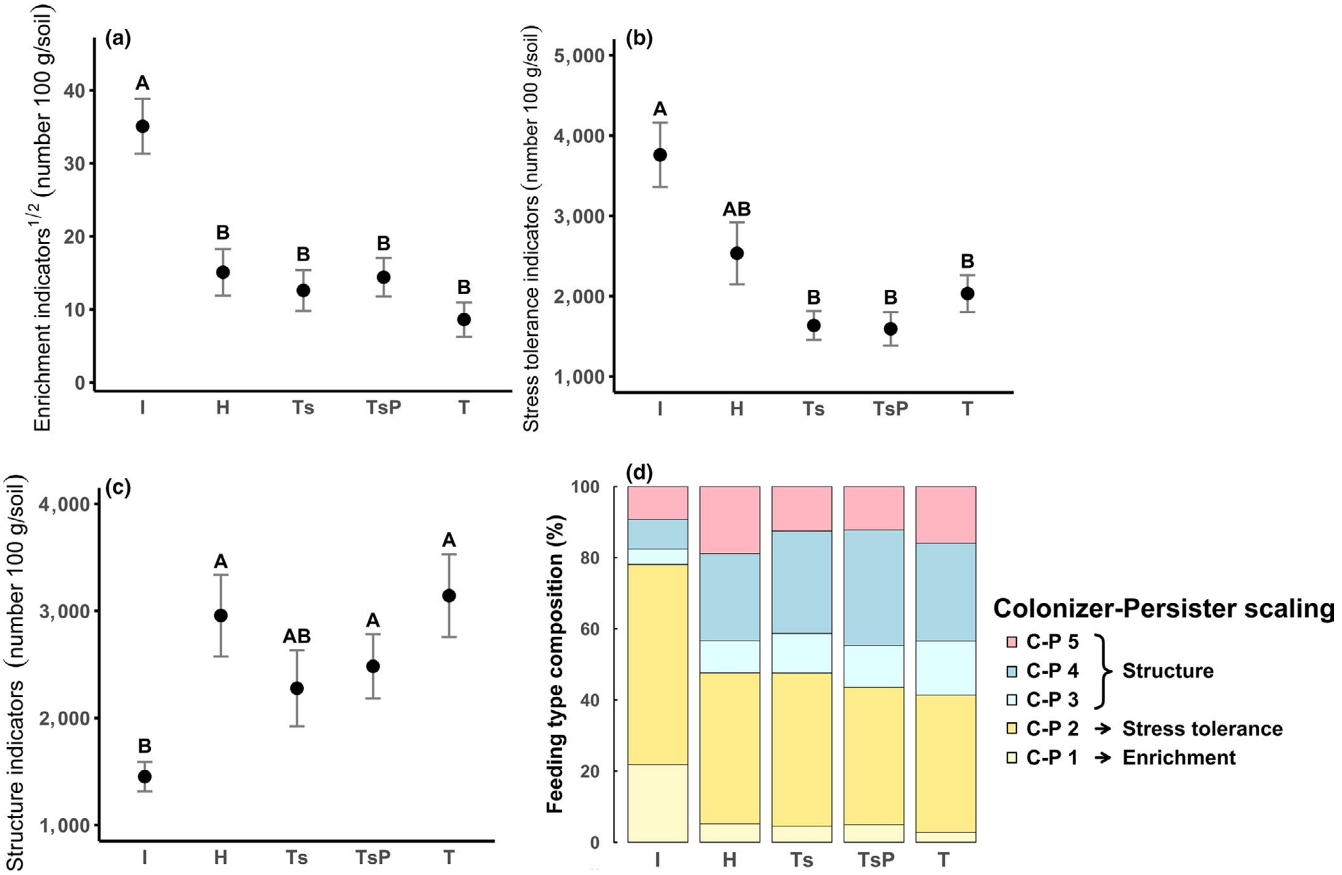

FIGURE 4 Treatment effects on individual nematode indicator abundances (mean ± *SE*; a–c) and structural guild composition (%; d). Untransformed data used for all indicators except for enrichment indicators (a; square root transformed). Different capital letters indicate significant differences between treatments. 'I' = 'Initial'; 'H' = 'Harvest only'; 'Ts' = 'Topsoil'; 'TsP' = 'Topsoil + Propagules'; 'T' = 'Target'

and *Poa trivialis* (Table S5), suggesting that recruitment from the soil seed bank might have happened. The analysis of the indicator value for soil moisture revealed that conditions were significantly wetter in the two topsoil removal treatments than in 'Target' (Figure 6c, Table 2). Furthermore, both topsoil removal treatments led to plant communities with lower nutrient demand according to the indicator values than 'Initial' and 'Harvest only'. The very low soil nutrient level indicated for 'Target' was, however, not reached by removing the topsoil (Figure 6d, Table 2).

4 | DISCUSSION

Numerous studies assessed the development of plant and animal communities after abandoning intensively managed grassland (e.g. Hanel, 2010; Morriën et al., 2017). However, comprehensive assessments of topsoil removal on ecosystem properties are scare (Kardol, Bezemer, & van der Putten, 2009; Kardol et al., 2008), especially considering the long-term development of below-ground fauna (Frouz et al., 2009; Wubs, van der Putten, Bosch, & Bezemer, 2016). In our experiment, we used soil nematodes and plants as biological indicators for assessing the long-term success of three restoration measures of increasing intervention level: (a) 'Harvest only', (b) removal of the topsoil ('Topsoil') and (c) removal of the topsoil and introduction of target plant propagules ('Topsoil + Propagules').

4.1 | Soil nematode communities recover fast after perturbation

As expected, 22 years after the massive intervention of removing the O and A horizon in our 'Topsoil' and 'Seeding' treatments, we no longer found differences in the structure of the soil nematode food webs compared to the one in 'Target' grassland systems. Surprisingly and contrary to our expectations, however, the soil nematode community compositions did not differ between our three restoration treatments and therefore changes in the abiotic conditions (e.g. decrease of soil nutrients) preponderated biotic constraints (e.g. differences in plant community composition).

All of our restored treatments were surrounded by intensively managed grasslands as well as species-rich grasslands. Consequently, these ecosystems may have served as sources for soil nematodes to recolonize the restored treatments as shown by Frouz et al. (2009). These authors did not find any differences in the nematode feeding type structure between intensively managed grasslands and natural heathland. Finding no differences in the community compositions of our restoration treatments could also be associated with a shift

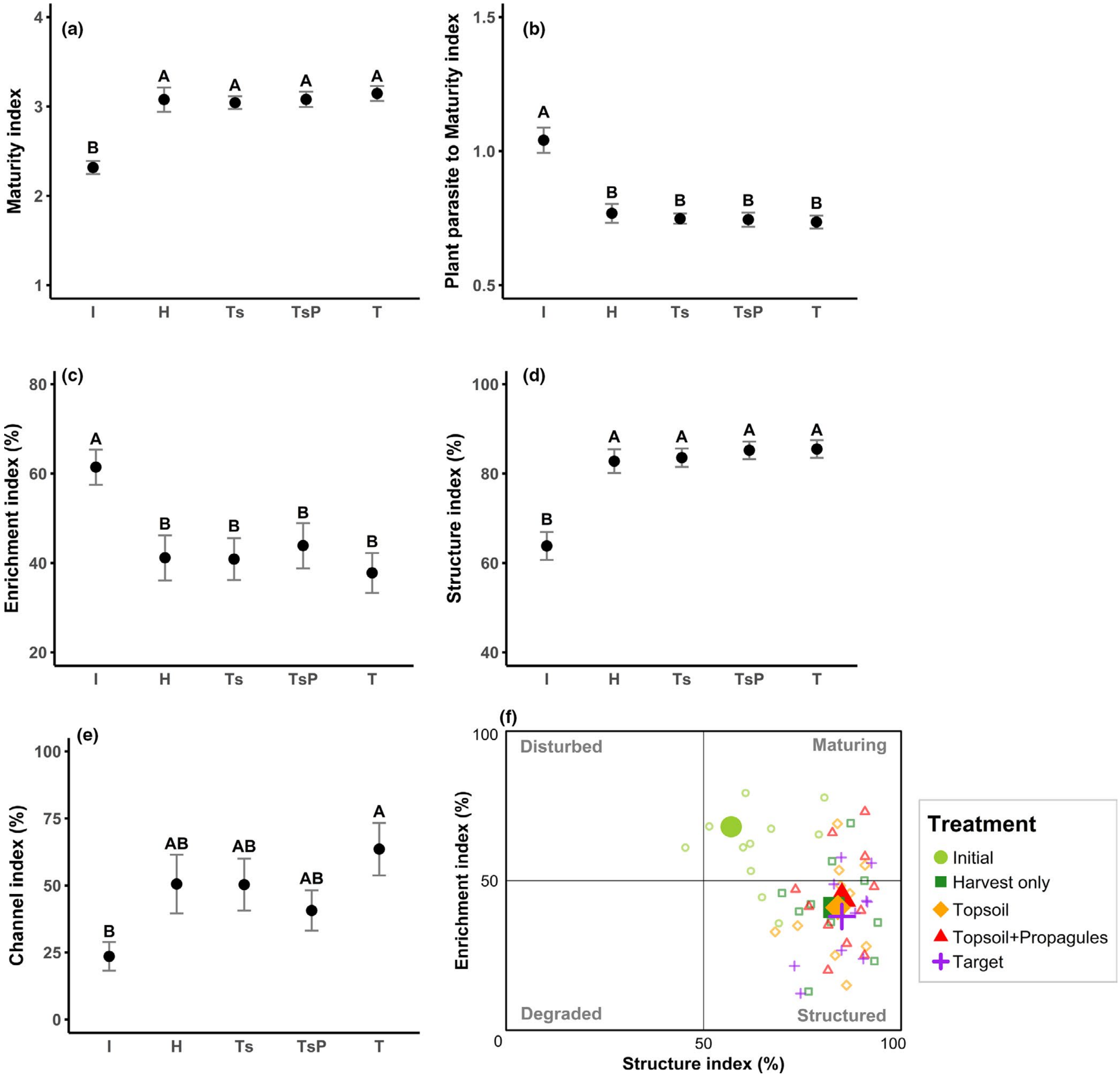

FIGURE 5 Treatment effects on individual nematode indices (mean ± *SE*; a–e) and the food web structure (f). Food web analyses show the relationship between Enrichment and Structure index (%; f). Each quadrat represents different stages of ecosystem maturity indicated by different levels of disturbance, nutrient availability and decomposition channels (Ferris, Bongers, & de Goede, 2001). Unfilled symbols represent single plot values (*n* = 54), filled symbols represent average values per treatment. Different capital letters indicate significant differences between treatments. 'I' = 'Initial'; 'H' = 'Harvest only'; 'Ts' = 'Topsoil'; 'TsP' = 'Topsoil + Propagules'; 'T' = 'Target'

of the dominance patterns in the established communities (Kardol, Newton, et al., 2009) rather than colonization of new taxa during secondary succession. Nevertheless, we need to acknowledge that similarities in soil nematode community compositions of our study might, at least in part, could be due to the chosen level of nematode identification (family). Differences in the community compositions between our treatments may be found at lower taxonomic levels.

Frouz et al. (2009) also showed that the depth of topsoil removal plays a crucial role in preserving local source populations of soil fauna: a removal of the upper 10–15 cm compared to 40–50 cm allowed survival of a local source population in deeper soil layers, which then can recolonize the newly created habitats. We removed the top 10–20 cm, which might have preserved the local source population allowing for vertical recolonization of our plots. In addition, our restored treatments featured characteristic groundwater fluctuations of semi-dry to semi-wet grasslands, which could have facilitated vertical recolonization of soil nematodes.

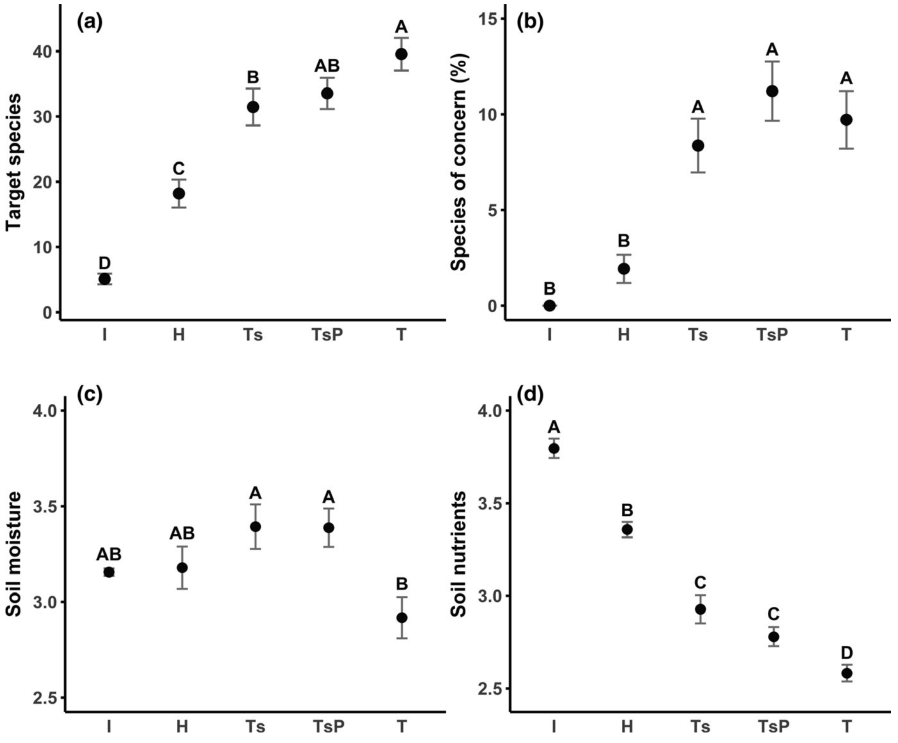

FIGURE 6 Treatment effects on number of target plant species (a), presence of species of concern proportional to the total number of plant species (b), as well as plant species indicator values for soil moisture (c) and soil nutrients (d) according to Landolt et al. (2010; mean ± *SE*). Different capital letters indicate significant differences between treatments. 'I' = 'Initial'; 'H' = 'Harvest only'; 'Ts' = 'Topsoil'; 'TsP' = 'Topsoil + Propagules'; 'T' = 'Target'

Colonization by soil nematodes mainly occurs passively though dispersal mechanisms such as windblown soil material from nearby surrounding, run-off, transport via farm machinery or introduction of plant material (Norton & Niblack, 1991; Yeates, 1978). Although active movement of soil nematodes is limited to a few centimetres per year (Norton & Niblack, 1991), over the course of 22 years recolonization from the surrounding is highly possible.

Generally, it has been shown that soil nematodes are sensitive indicators to distinguish between management practices. Different intensities of mowing and fertilization resulted in different soil nematode community compositions (Bongers & Ferris, 1999; Freckman & Ettema, 1993; Yeates & Bongers, 1999). In our study, we found no differences in nematode communities between treatments with intense mowing regimes 'Initial' (mowed two to five times per year) and 'Harvest only' (mowed two to three times per year), which contrasts the above-mentioned studies. However, a reduction in soil nutrients resulted in significantly different nematode community structure compared to 'Initial', similar to findings in other studies (Cesarz et al., 2015; Morriën et al., 2017). Therefore, differences in the nematode community compositions and structures found between intensively and less intensively managed grasslands seem to be driven by the excessive nutrient supply rather than by different sources of disturbance (e.g. mowing frequencies, tillage).

4.2 | Plant community recovery depends on nutrient reduction

Plant communities of all three restoration treatments significantly differed from the ones in intensively managed grasslands ('Initial') and successfully developed towards the 'Target' community. 'Harvest only', however, was much less successful than 'Topsoil' and 'Topsoil + Propagules', especially considering number of plant species in general, target species or species of concern. Twenty-two years after restoration, the composition of the vegetation in 'Harvest only' still resembled partly the one in 'Initial' (e.g. Kiehl & Wagner, 2006). These differences in long-term development of the plant communities among our treatments were similar to other findings (see review Kiehl et al., 2010). However, in our study, adding propagules ('Topsoil + Propagules') did not add much to re-establish a plant community similar to 'Target' vegetation compared to no propagule addition ('Topsoil'). Plant species number and even richness of species of concern did not differ between 'Topsoil' and 'Topsoil + Propagules'. This was surprising as numerous studies showed that missing propagules of target plants may critically hamper successful restoration (e.g. Pfadenhauer & Klötzli, 1996; Stöcklin & Fischer, 1999). Two different mechanisms might be responsible for the patterns observed. (a) The soil seed bank might play a more important role than expected, as suggested by the species of concern established in the topsoil removal plots but missing in 'Target', and by plant species that established and are known to build a persistent seed bank, for example, *Juncus* spp. (Bossuyt & Honnay, 2008). (b) As our restoration patches were closely interlocked with patches of the target vegetation, it is possible that re-establishment of species-rich communities in 'Topsoil' was more effective than in other studies where restoration sites were more strongly isolated from source areas (Bakker & Berendse, 1999).

Generally, the plant community in 'Topsoil' and 'Topsoil + Propagules' indicated successful reduction of the nutrient pool, but simultaneously resulted in an increase in soil moisture by lowering the soil surface in relation to the groundwater level, which is in accordance with previous studies (e.g. Patzelt, Wild, & Pfadenhauer, 2001). Since topsoil removal depended on the depth of the O and A horizons, the impact on groundwater level varied from restoration patch to restoration patch, which also led to higher heterogeneity in plant community composition in 'Topsoil' and 'Topsoil + Propagules' compared to 'Target'. As a consequence, plant communities found in 'Topsoil' and 'Topsoil + Propagules' still differed from the one in the 'Target' grasslands 22 years after starting the restoration.

Overall, our study demonstrated that in contrast to low levels of intervention ('Harvest only'), massive interventions such as topsoil removal are successful in converting intensively managed grasslands into species-rich grasslands, both above- and below-ground. However, our study also showed that restoration of 'Target' vegetation might be unfeasible even in the long term due to topsoil removal induced changes in groundwater level. Yet, topsoil removal did not have a long-term negative effect on the soil nematode community composition and structure.

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AUTHORS' CONTRIBUTIONS

M.C.R., M.S. and A.C.R. conceived the study and ideas for the paper; M.C.R. and U.G. collected the vegetation data; M.C.R. collected the nematode data; W.H.v.d.P. and R.W. led the lab work on soil nematodes; M.C.R, M.S. and A.C.R. designed the analyses and wrote the paper with substantial critical input from W.H.v.d.P. and the other authors. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via the EnviDat Repository https://doi.org/10.16904/envidat.65 (Resch, Schütz, & Risch, 2019).

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