Cover crops influence aboveground and belowground invertebrates in farmlands

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Abstract

1. Maintaining vegetation diversity through cover crops could counteract the decreasing soil carbon and biodiversity in intensive monoculture farming, but its impacts on fauna have rarely been quantified.
2. To investigate how cover crops influence the abundance and trophic structure of invertebrates, or inorganic N (proxy of soil functioning), barley (*Hordeum vulgare*) was grown with up to eight undersown cover crops. Soil fauna (nematodes, enchytraeids and earthworms), slugs, and arthropods living on soil surface, vegetation, and barley were sampled, and soil inorganic N availability measured.
3. Cover crops increased the abundance of aboveground and belowground invertebrates compared to barley monoculture. The proportion of predatory arthropods increased, suggesting that cover crops improved the potential for biological control.
4. Cover crop functional traits (N_2-fixation and deep roots) had selective effects. For example, legumes increased soil inorganic N availability and the abundance of aboveground herbivores, while deep-rooted species benefited earthworms. The species richness of cover crops did not affect invertebrates or soil N.
5. *Synthesis and applications*: Our results suggest that cover crops can improve agroecosystem diversity and functioning, and that significant effects on invertebrate-mediated ecosystem functions such as biological control can already be achieved at low levels of added vegetation diversity.

Key words: agroecosystem, biological control, cover crop, invertebrate, monoculture, soil fauna, soil N, vegetation diversity

Introduction

Invertebrates provide many ecosystem services in agriculture. In soils, detritivores feed on dead organic matter and micro-organisms, thereby enhancing decomposition, nutrient mineralization and plant production (McCary & Schmitz, 2021; Mikola et al., 2002). Soil nitrogen (N) availability, essential for crop production, is improved by decomposer fauna ranging from large ecosystem engineers such as earthworms (Eriksen-Hamel & Whalen, 2007) to microscopic microbial-feeding nematodes (Mikola & Setälä, 1998). Aboveground invertebrates are irreplaceable in plant pollination (Dainese et al., 2019), and predators and parasites contribute to biological pest control (Altieri, 1999). Simultaneously, intensive land management degrades soils (Geisen et al., 2019) and monoculture farming deteriorates biodiversity and associated ecosystem functions (Altieri, 1999; Le Provost et al., 2022). Maintaining invertebrate abundance and diversity in agroecosystems could address this sustainability crisis.

Adding functionally complementary species in crop rotations and avoiding bare soil periods can improve plant productivity and reduce the need for chemical inputs and fertilizers (Cooledge et al., 2022; Scavo et al., 2022). Diverse vegetation can positively impact aboveground arthropods (Billeter et al., 2008; Blaise et al., 2022; Cozim-Melges et al., 2024) but diversity impacts have been mostly quantified from natural systems. While some studies report effects mainly on herbivores (Balvanera et al., 2006; Ebeling et al., 2018; Scherber et al., 2010), others found increasing predatory abundance (Blaise et al., 2022; Ebeling et al., 2018; Haddad et al., 2001; Unsicker et al., 2006) which could improve biological control (Iverson et al., 2014). Increasing plant diversity can enhance ecosystem functioning (plant productivity, organic matter decomposition and nutrient cycling), through increased or more efficiently used resources, or beneficial species-species interactions (Barry et al., 2019; Wright et al., 2017).

Carbon (C) farming, through applying cover crops or rotations with ley mixtures, aims at increasing soil C but can also influence biodiversity (Cappelli et al., 2022; Jansson et al., 2021). For example, introducing legumes can benefit earthworms (Eisenhauer et al., 2009), attract pollinators (Boetzl et al., 2023) and modify plant canopy properties affecting invertebrates (Lipowsky et al., 2015; Meyer et al., 2017; Zaret et al., 2023). Root architecture including depth can modify soil functioning by affecting porosity (Cooledge et al., 2022), C content (Jansson et al., 2021) or transfer water to shallow soil layers (Culman et al., 2013; Sekiya & Yano, 2004) with implications for nutrient and microbial distributions (Emerman & Dawson, 1996). Rooting depth affects soil microbes (Steinauer et al., 2017) but few experiments have investigated its effects on invertebrates (Beugnon et al., 2019; Lees et al., 2016). Overall, despite substantial research efforts on the effects of plant diversity on invertebrates, the results remain mixed indicating high context-dependency (Borer et al., 2012; Koricheva et al., 2000; Loranger et al., 2014; Scherber et al., 2006; Siemann et al., 1998).

Here, we examine the effects of cover crops (including legumes, non-legumes and shallow- and deep-rooted species) on invertebrates in agriculture. Similarly to previous experiments (Cappelli et al., 2024; Domeignoz-Horta et al., 2024; Shrestha et al., 2025), we grew barley (*Hordeum vulgare* L. var. Harbringer) as a monoculture or intercropped with either a single cover crop or a combination of 2–8 cover crops. We describe the effects of vegetation, barley monoculture, cover crops, and the cover crop traits and richness on the abundance of aboveground and belowground invertebrates. Further, we investigate the associations between soil invertebrates and soil inorganic N availability (proxy for soil functioning). To assess the different effects of vegetation, we ask:

1. how the presence of vegetation or barley monoculture affects invertebrate abundances and soil N availability compared to bare soil,
2. how cover crops influence invertebrates and soil N availability compared to the barley monoculture; and
3. whether species richness and functional traits (N_2-fixation, root architecture) influence the general cover crop effect.

We hypothesize that barley monoculture increases invertebrates and decreases soil inorganic N availability compared to bare soil. The presence of cover crops and increasing their species richness and the relative legume and deep-rooted cover, should produce more variable (Srivastava & Lawton, 1998) and abundant (Borer et al., 2012; Eisenhauer, 2012) resources for invertebrates than barley monoculture, thus increasing invertebrate abundances both above- and belowground. Higher faunal abundances should better support higher trophic levels, thus increasing the proportion of predators and parasites (Oksanen et al., 1981; Welti et al., 2020). Finally, in addition to the positive legume effects, the increased belowground fauna should facilitate nutrient mineralization and increase plant-available inorganic N in the soil.

Materials and methods

Experimental setup

Polyculture farming with cover crops (also called service, nursery or catch crops, or living mulches) was studied on an experiment established on 60 plots (4m × 10m) at the agricultural field of the University of Helsinki, Finland (60.224799°N, 25.020295°E) in 2019. The mean temperatures were 6.5°C (annual) and 15.1°C (growing season, May-August), and the yearly precipitation was 653mm in 1991-2020 (Jokinen et al., 2021). The soil has a pH 6.3, 3% C and 0.24% N.

The treatments randomized within 4 blocks included barley monoculture (8 plots), barley with cover crops (44 plots) and bare soil control (4 plots) without herbicides. To study the influence of a typical weed control, herbicide (Berner Ally 50WG, 35g/260L water/ha) was added on four additional barley monoculture plots. Eight cover crops (*Lolium multiflorum*, *Phleum pratense*, *Trifolium hybridum, T. repens, T. pratense*, *Medicago sativa*, *Festuca arundinacea, Cichorium intybus*) with variable functional traits were sown few days after barley (22nd–25th May) as substitutive intercrops (Balvanera et al., 2006) either singly (3 plots per species) or in combinations of two, four or eight species (10, 6 or 4 plots, respectively; Table S1). Plots were fertilized with 80kg N ha^{-1}. Vegetated plots were weeded after five weeks, and bare soil plots every 2–3 weeks. After barley harvest (11th–14th September), the remaining cover crops were left to recover and grow until the next spring, when their residues were tilled into the topsoil and new barley and cover crops were sown.

Invertebrate fauna

Aboveground arthropods were sampled from vegetation, barley shoots, and soil surface (Table 1). Within-vegetation arthropods were collected from **suction-sampled transects** (estimated area 2.5m^2; Halbritter et al., 2020). **Barley arthropods** were counted from barley shoots, and **soil surface arthropods** and the abundance and biomass of slugs (Supplement S1) were quantified from pitfall traps (Halbritter et al., 2020). Arthropods were classified into herbivorous (causing significant plant damages), neutral (with mixed diet or presumably neutral relationship to plants), or predatory or parasitic (hereafter predatory; Table S2).

Belowground micro- and mesofauna were quantified from topsoil (Table 1). Nematodes and enchytraeids were wet-extracted (Supplement S2) from 20g and 80g fresh weight soil (corresponding to ca. 17g and 67g dry weight), respectively, and counted alive. Fifty nematodes per sample, preserved in 4–5 v-% formaldehyde, were classified to feeding groups: bacterivores, fungivores, herbivores, omnivores, and predators (Yeates et al., 1993). Enchytraeid biomass was calculated based on their size distribution (length 0–2, 2.1–4, 4.1–6, 6.1–8, 8.1–10, 10.1–12, or >12mm; (Abrahamsen, 1973). No enchytraeids were detected in most summer samples (Supplement S2). Soil water content was measured by drying (105°C, 24h) and weighting ca. 30g of soil samples. Earthworms, representing **belowground macrofauna,** were hand-sorted and chemically extracted (0.1mL/L allyl-isothiocyanate, 2mL/L isopropanol; Nuutinen, 2018) from soil monoliths (Table 1). Earthworms preserved in 4 v-% formaldehyde were counted and weighted to measure the total fresh biomass.

Soil nutrients and plants

Plant available inorganic N (NO_3^- and NH_4^+) was quantified using PST-1 ion exchange resin capsules (Unibest; Table 1; Pampolino & and Hatano, 2000), extracted in 50mL of hydrochloric acid at Unibest laboratories (WA, USA). The **cover of barley and cover crops** (%) was visually assessed (Table 1). Mean covers per species were calculated, and the relative covers defined as the proportion of the sum of all covers. **Aboveground biomass** of barley and other vegetation (cover crops and weeds) was quantified (Table 1) as dry weight after 48h at 60°C.

Statistical analyses

The responses of invertebrates and soil mineral N to the addition of vegetation (compared to bare soil), the cover crops (compared to barley monoculture) or the herbicide addition on barley monoculture was studied within all plots (Table S3) or plots without cover crops (Table S4), as well as the effects of cover crop species richness and the relative cover of legumes and deep-rooted species within cover crop plots (Table S5). Appropriate contrasts were fit on three different sets of univariate mixed models based on lmerTest (Kuznetsova et al., 2017), lme4 (Bates et al., 2015) and glmmTMB (Supplement S3; Brooks et al., 2017).

To investigate the relationship between soil fauna and N availability in autumn 2021 (when the earthworm and enchytraeid data was available; Table 1), linear mixed effect models for NO_3^--N and NH_4^+-N were fit to investigate the effects of most abundant soil fauna. Least correlated faunal variables (transformed for normality; Table S6) were fit as fixed variables, and blocks as random intercepts (Table S7). The relationship between microbivorous (bacterivorous and fungivorous) nematodes and N availability in summer 2021 was checked with corresponding models accounting for microfauna.

The linear relationships between invertebrates or N availability with the aboveground biomass of non-barley or all vegetation was examined with pairwise Pearson or Spearman correlations.

Results

Vegetation and herbicide effects

In the vegetated plots, the average arthropod abundance in suction samples was 10-fold compared to bare soil (316 vs. 32 individuals/m^2, respectively) and the proportion of herbivores increased from 8% to 33% (Fig. 1a, Table S3). The abundance of pitfall-trapped arthropods was 69% higher and the average slug size 35% lower (Fig. 1c, Fig. S1i, Table S3) in vegetated compared to bare soil plots. The within-vegetation arthropods in barley monoculture were mostly neutral (Diptera, Collembola) and herbivorous (Thysanoptera), while 61% of arthropods on barley stalks were herbivorous aphids (Fig. 1a), and 59% of arthropods in pitfall traps were Carabidae.

In soil, the enchytraeid biomass was 35-fold, the earthworm numbers 6.4-fold and their biomass 15.6-fold in vegetated compared to bare soil plots (Fig. 1e,f, Table S3). Vegetated plots had more bacterivorous (3.3-fold), fungivorous (2.2-fold), omnivorous (10.2-fold) and predatory (8.7-fold) nematodes than bare soil (Fig. 1d,

Table S3). Most nematodes under barley monocultures were bacterivores (41–44%) and fungivores (29–41%; Fig. 1d). Enchytraeids and all except fungivorous nematodes were more abundant in autumn than summer (Table S8). The resin concentration of NO_3^--N was on average 58% lower in vegetated compared to bare soil plots (Fig. S2a, Table S3) and lower in autumn than in summer (Table S8), while the concentration of NH_4^+-N did not differ between bare soil and vegetated treatments or between seasons (Fig. S2b, Table S3).

Treating barley monoculture with herbicide decreased earthworm abundance by 60% (Fig. 1f) but did not influence N availability or the aboveground arthropods (Table S3). Analysing the effects of monoculture vegetation compared to bare soil from the 16 plots without cover crops (Table S4) revealed largely similar monoculture effects as the contrast between bare soil and vegetation for all 60 plots (Table S3).

General cover crop effects

In comparison to barley monoculture, adding cover crops increased within-vegetation arthropods by 22% (from 280 to 330 individuals/m^2; Fig. 1a, Table S2) and bacterivorous and fungivorous nematodes in soil by 61% and 40%, respectively (Fig. 1d, Table S2). Cover crops decreased soil surface arthropods by 17% (Fig. 1c, Table S2) but did not affect resin concentrations of NO_3^--N and NH_4^+-N (Fig. S2; Table S2). The NO_3^--N concentrations associated negatively with microbivorous nematodes in autumn but not in summer (Fig. 4c, Table S5, Table S8).

The arthropods in vegetation of cover crop plots were mostly neutral and herbivorous (Fig. 1a), but the proportion of predators/parasites increased by 24% (Fig. 2b) compared to monocultures. With cover crops, 31% of arthropods on barley stalks were thrips and 58% aphids or their exoskeletons (herbivorous Thysanoptera and Aphidoidea), 57% of pitfall-trapped arthropods were Carabidae, and the nematodes in soil were mostly bacterivores (44–52%) and fungivores (28–49%) in both seasons (Fig. 1d), similarly to monocultures.

The total aboveground biomass of cover crops and weeds correlated positively with earthworm and within-vegetation arthropod abundances, the proportion of predatory within-vegetation arthropods, the number and biomass of slugs, the autumn abundances of total, bacterivorous and omnivorous nematodes and the autumn resin concentrations of NO_3^--N and NH_4^+-N (Fig. S3). Only the abundance of pitfall-trapped arthropods correlated negatively with total and non-barley biomass (Fig. S3).

Cover crop functional trait and species richness effects

In plots with cover crops, the relative legume cover associated positively with within-vegetation arthropods and slugs (Fig. 3a, Table S5) and the average resin concentrations of NO_3^--N (Fig. 4a, Table S5). The relative deep-rooted cover associated positively with within-vegetation arthropods, bacterivorous nematodes, and earthworm abundance and biomass (Fig. 3b, Table S5). Legume cover increased NH_4^+-N when deep-rooted cover crops were abundant (Fig. 4d,e, Table S5). Among within-vegetation arthropods, the proportions of predatory and herbivorous taxa increased, and neutral taxa decreased with increasing legume cover (Fig. 3a, Table S5), while increasing the deep-rooted cover increased neutral taxa at the expense of herbivores (Fig. 3b, Table S5). Cover crop species richness did not affect the invertebrate abundances or resin N concentrations (Fig. 3c, Fig. S3s,t, Table S5).

Discussion

We show that while grain crop monocultures already significantly support invertebrates, adding cover crops further increased their abundances in soil and aboveground, particularly of predatory arthropods in vegetation. Cover crop functional traits but not their species richness affected the invertebrates. Thus, the significance of cover crops for agricultural systems likely arises from shifting the invertebrate community structure towards higher trophic levels, and the desired effects may be reached at low species richness with proper functional traits. We found no evidence that increasing soil invertebrates would directly increase inorganic N availability, suggesting that manipulating N availability through soil fauna is not straightforward and the N cycling processes related to soil food webs are complex.

Monoculture vegetation supports many invertebrates, but herbicides may partially counteract the effects

The huge positive effect of barley monoculture on most invertebrate groups highlights the pivotal role of plants for agroecosystem fauna (Osler, 2007; Sylvain & Wall, 2011). Invertebrate abundances on bare soil were very low only two years after last cultivation. Periods with uncultivated bare soil can cause nutrient leaching and erosion (Scavo et al., 2022). The strong link between the simple monoculture vegetation and fauna found here (see also Mamabolo et al., 2024; Siemann et al., 1998; Silva et al., 2010) indicates that avoiding bare soil is crucial for pest control, pollination and soil animal activity. However, weed control by herbicides may partially counteract the positive effects on soil, as earthworms were strongly reduced after herbicide application (see also García-Pérez et al., 2016; Gaupp-Berghausen et al., 2015).

Efficient nutrient uptake by vegetation (Hooper & Vitousek, 1998; Niklaus et al., 2006) shown also in our study supports avoiding bare soil to reduce N leaching. Seasonal increase in plant biomass likely explains the decreased NO_3^--N availability from summer to autumn, while the fast nitrification could explain the lacking responses in NH_4^+-N.

Cover crops sustain invertebrates and enhance the herbivore control potential

The positive effect of cover crops on within-vegetation arthropods aligns with earlier studies on vegetation diversity (Billeter et al., 2008; Blaise et al., 2022; Cozim-Melges et al., 2024). The positive cover crop effect on microbivorous nematodes in our study, and on microbial biomass carbon in a corresponding study (Shrestha et al., 2025) highlights the fast responses of soil communities to diversified vegetation. Contrasting earlier studies (Abalos et al., 2021; Hooper & Vitousek, 1998; Niklaus et al., 2006; Tilman et al., 1996), neither cover crop presence nor their richness reduced inorganic N availability in soil, suggesting that complementary resource use by diverse vegetation may not always decrease nutrient availability (Tilman et al., 1997). This could partly relate to fauna-mediated effects on inorganic N, since microbial-feeding soil invertebrates are known to release NH_4^+-N and enhance N mineralization (Gebremikael et al., 2016; Mikola et al., 2002; Mikola

& Setälä, 1998). However, disentangling the different mechanisms remains difficult when the inorganic N released by animals is instantly assimilated by plants and microbes.

Higher vegetation diversity affects the entire food web (Buzhdygan et al., 2020) but contrasting effects may be detected at different trophic levels. Often, the strongest effects of vegetation diversity are detected on herbivores (Balvanera et al., 2006; Ebeling et al., 2018; Scherber et al., 2010). In our study, cover crops increased the proportion of predatory arthropods in vegetation, supporting earlier findings of decreased herbivore abundance (Letourneau et al., 2011) and increased biological control (Beaumelle et al., 2021; Iverson et al., 2014; Scherber et al., 2010) in diverse communities, especially in productive systems where predators can reach high abundances (Koricheva et al., 2000; Oksanen et al., 1981; Srivastava & Lawton, 1998; Welti et al., 2020). Supporting this, we found that despite more arthropods with cover crops, neither the leaf-sucking herbivores counted from barley, nor the herbivore damage measured from barley leaves (unpublished data) increased. This could indicate biological control by abundant predators and parasites, or herbivore preference of cover crops since the within-vegetation arthropods were positively correlated with cover crop biomass.

We show that higher vegetation diversity does not necessarily increase the herbivore proportion in the arthropod community (Andow, 1991), implying a potential for biological pest control through agroecosystem diversification. Moreover, as the aboveground invertebrate predators may increase at lower plant species richness than herbivores (Scherber et al., 2010), the biological control effect could be achieved by modest increase in vegetation diversity.

Functional traits, but not species richness of cover crops matter for invertebrates

While the cover crop presence influenced invertebrates, their species richness (with 1–8 added species) did not affect invertebrate abundances. Instead, following the earlier studies that stress the importance of plant community composition (Haddad et al., 2009; Sylvain & Wall, 2011), our study shows that cover crop composition and traits matter.

In our study, increasing the legume cover increased the proportion of within-vegetation predatory and herbivorous arthropods and slugs. Legumes can attract herbivores (Buzhdygan et al., 2025; Haddad et al., 2009; Loranger et al., 2014; Neff et al., 2023; Scherber et al., 2006; Unsicker et al., 2006) to crop mixtures, reducing their positive influence on yield (Iverson et al., 2014; Scherber et al., 2006). However, simultaneously increasing predatory arthropods, as found in our study, and herbivores preferring legumes over the main crop can alleviate the problem. Intercropping with legumes increases the probability of win-win yield- and biocontrol scenarios in dense vegetation (Iverson et al., 2014). In a corresponding experiment, (Cappelli et al., 2024) and (Shrestha et al., 2025) showed the efficacy legumes in suppressing disease in barley and among soil fungi. Contrasting the earlier results (Abalos et al., 2021; Eisenhauer, 2012), legume cover did not increase earthworms, but still increased NO_3^--N availability, reinforcing their potential in reducing the need for inorganic fertilizers (Li et al., 2020). Clearly, selecting functional plant species for agricultural diversification can influence nutrient availability (Abalos et al., 2014) although the intricacies of plant-fauna-soil interactions remain to be studied.

Scarce earlier research found no effects of rooting depth on grassland soil arthropods (Beugnon et al., 2019). In our study, the deep-rooted cover increased faunal abundances above- and belowground (Fig. 3b), supporting our hypothesis of enhanced consumer resources and habitats. Looser soil structure or the quality of plant residues (Cooledge et al., 2022) could explain the association of earthworms with deep-rooted plants (Katsvairo et al., 2007). Larger soil volume affected by root exudates may also increase soil microbial activity (Jansson et al., 2021), and accordingly, deep-rooted plants increased both bacterivorous nematodes (this study) and the most abundant soil bacteria (*in prep*.). The surprising effect of plant root architecture on the aboveground trophic composition could be mediated by springtails moving between above- and belowground habitats or the aboveground traits of deep-rooted species.

Overall, we found trait-specific effects of cover crop functional traits on invertebrates in different habitats, suggesting distinct effects on ecosystem services. This suggests that carefully selecting the species for crop field diversification is crucial for optimizing agroecosystem services such as biological control, pollination

(Boetzl et al., 2023), pathogen suppression (Cappelli et al., 2024) and microbial carbon use efficiency (Domeignoz-Horta et al., 2024).

To conclude, we showed that continuous plant cover is crucially important for invertebrate fauna in agroecosystems. Cover crops, in addition to potentially reducing soil C loss, increase the invertebrate abundances above levels maintained by crop monocultures, as well as the potential of biological pest control. Cover crops affect soil invertebrates, but this does not lead to predictable effects on soil inorganic N. Leguminous cover crops increase inorganic N availability, whereas the deep-rooted cover crops seem to benefit soil invertebrates without increasing herbivores. Taken together, our findings suggest that cover crops can maintain aboveground and belowground invertebrates and support their role in pest control and soil functioning. Notably, when appropriate functional traits are included, high species richness is not needed to achieve these effects.

Author's contributions J.H., A-L.L., J.M. and M.T. conceived the ideas and designed methodology; P.T., J.M., M.T., M.H., S.C. and S.G. collected and P.T. analyzed the data; P.T. and J.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Figures and tables

Table 1: Variables measured from different habitats on each plot (n=60) over growing seasons 2–3 of the experiment.

habitat	variable	method	time of sampling/measurement
within-vegetation	arthropod abundance and proportions of trophic groups[1]	suction sample from a 10-m transect per plot	30th June 2021 8th August 2021 7th September 2021
barley	arthropod abundance	arthropods[2] manually searched from 10 randomly chosen barley shoots per plot	18th August 2020 27th–28th August 2021
soil surface	arthropod abundance	2 pitfall traps per plot for 8 days	18th–26th August 2020 23rd–31st August 2021
soil surface	slug abundance, biomass and mean size per plot	2 pitfall traps (4 dL) per plot for 8 days, see Supplement S1	23rd–31st August 2021
aboveground	relative cover of barley and individual cover crops[3]	survey of 4-5 randomly selected $1 m^2$ subplots per plot	29th June–2nd July 2020 27th–31st July 2020 25th–26th August 2020 30th June–2nd July 2021 6th–8th August 2021 24th–27th August 2021
aboveground	biomass of barley and cover crops/weeds	aboveground vegetation cut from representable 50 cm x 50 cm per plot, and sorted to barley and non-barley	24–27th August 2020 23rd August 2021
topsoil	nematode abundance (total and trophic groups) and enchytraeid biomass	wet funnel extraction from 2 soil samples (diameter 5.3 cm, depth 4 cm) per plot, see Supplement S2	29th June 2020 2nd October 2020 5th July 2021 4th October 2021
soil	earthworm abundance and biomass	hand-sorting a soil monolith (25 cm x 25 cm x 20 cm) and 30-min chemical extraction from each plot	18th–29th October 2021
topsoil	NO_3^--N and NH_4^+-N availability	2 resin capsules per plot, buried at 6 cm depth for ca. 4 weeks	20th July–18th August 2021 20th September–19th October 2021

[1] mean of 3 samplings over the growing season 2021 was analyzed
[2] arthropods collected from barley shoots included shed exoskeletons of aphids
[3] plant cover measured on date closest to invertebrate sampling dates were used for analysis

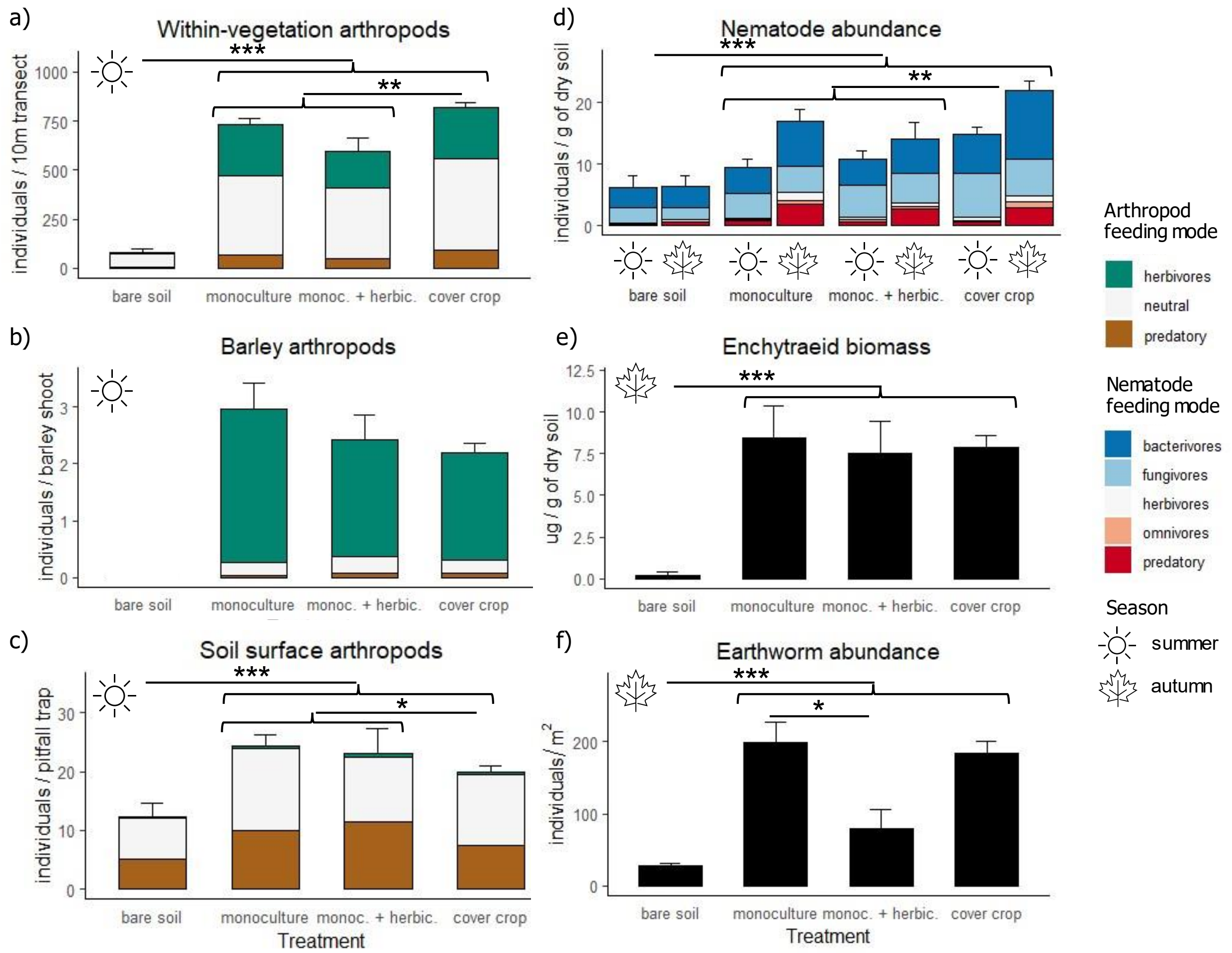

Figure 1. Invertebrates from a) suction samples, b) barley shoots, c) pitfall traps, and d-f) soil, from bare soil (n=4), monoculture (without and with herbicide; n=8 and n=4, respectively) and cover crop plots (n=44), with means and standard errors from one (a and f) or two years (b-e), and significant contrasts at 0.01<p<0.05 (*), 0.001<p<0.01 (**) or p<0.001 (***).

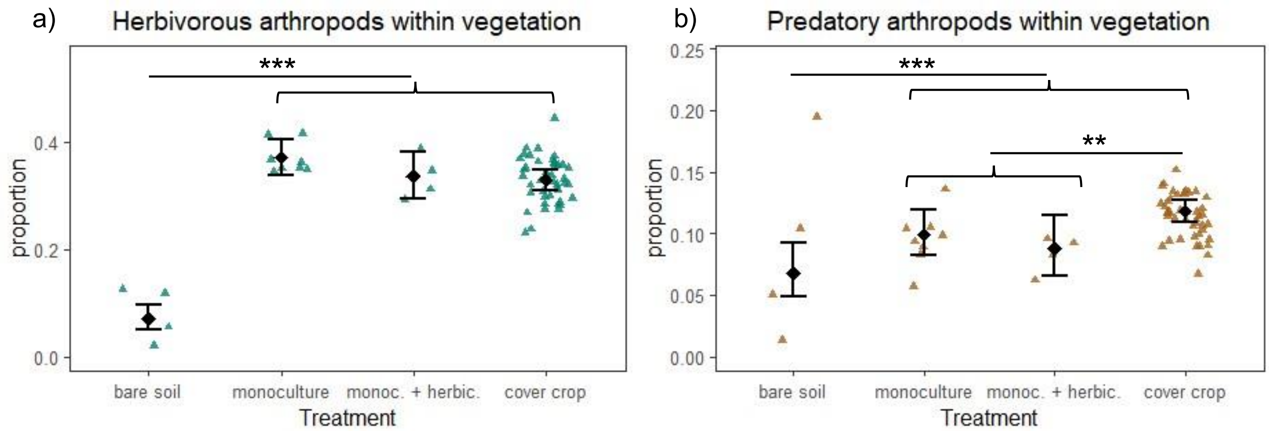

Figure 2. Proportion of a) herbivores and b) predators in suction-sampled arthropods from bare soil (n=4), monoculture (without and with herbicide; n=8 and n=4, respectively) and cover crop plots (n=44). Averages over three samplings per plot (points), modelled estimates (diamonds), 95% confidence intervals (error bars), and significant contrasts (0.01<p<0.05 *, 0.001<p<0.01 ** or p<0.001 ***) are shown. Note the different y-axis scales.

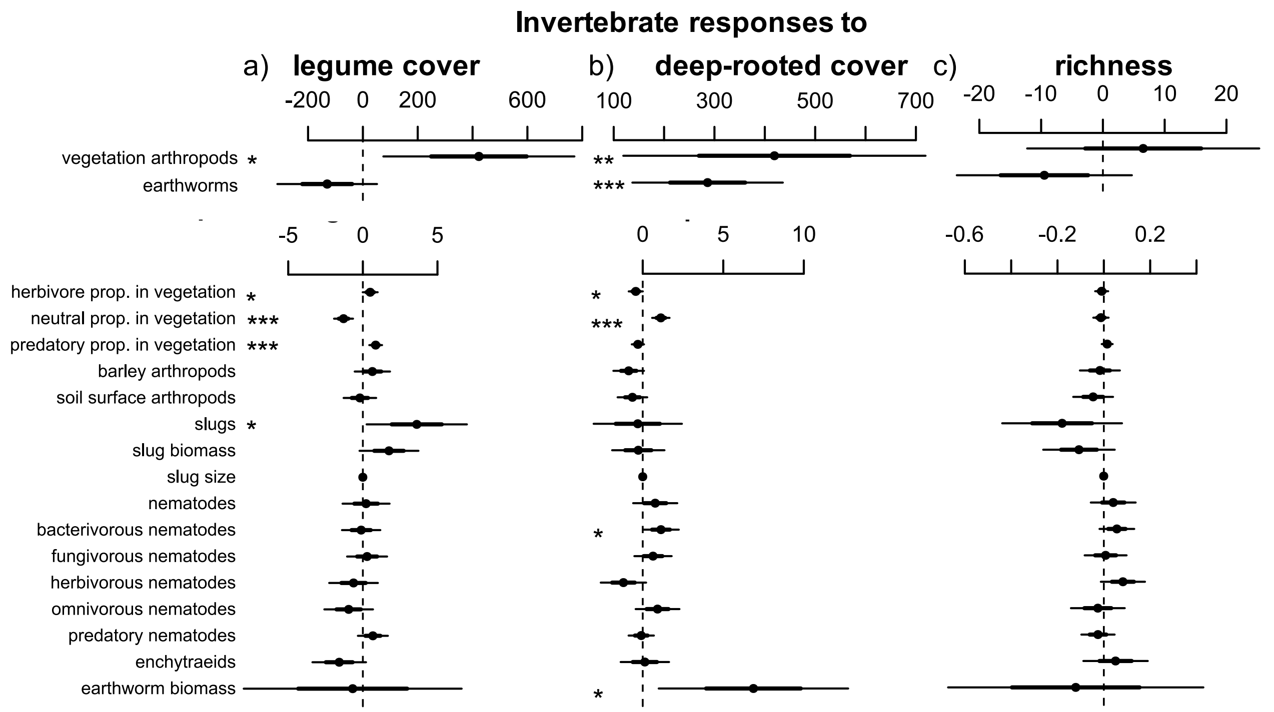

Figure 3. Effects of relative a) legume cover, b) deep-rooted cover and c) cover crop richness on invertebrates from cover crop plots (n=44; responses are abundance when not otherwise mentioned; prop. equals proportion). Standard error (wide whiskers) and 95% confidence interval (narrow whiskers) of estimates (dots), and statistically significant effects are shown at 0.01<p<0.05 (*), 0.001<p<0.01 (**) or p<0.001 (***).

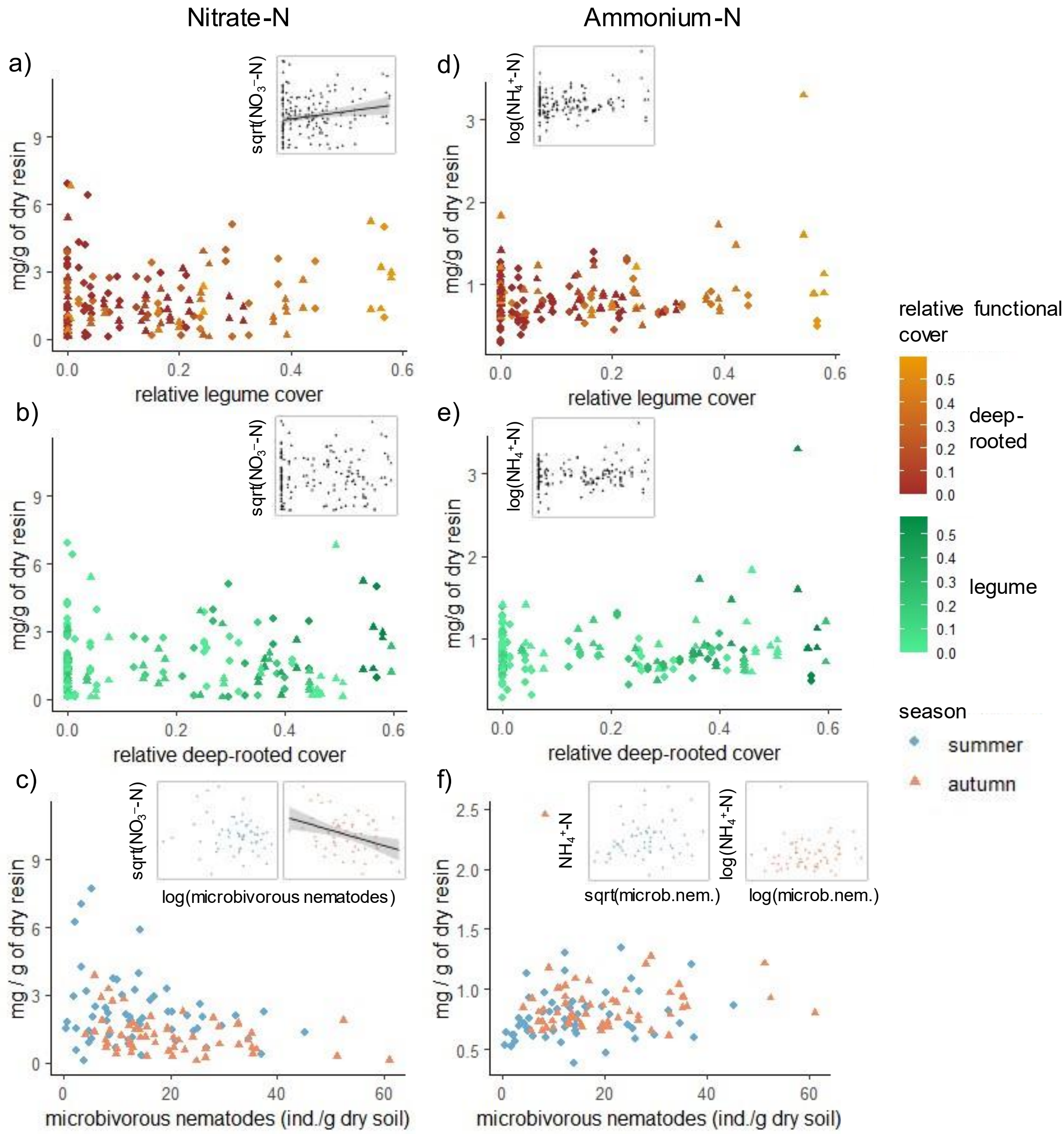

Figure 4. Effect of cover crop functional traits on nitrate and ammonium availability in topsoil from 44 cover crop plots (a-b, d-e), and the relationship between microbivorous nematodes and N-forms from 60 plots. Insets with trendlines indicate statistically significant (0.001<*P*<0.01) linear effects.