Agriculture, Ecosystems and Environment 408 (2026) 110490

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Cover crops influence above- and belowground invertebrates in a northern grain field

Paula Thitz[a,*], Mikko Tiusanen[b], Seraina Lisa Cappelli[c], Stephanie Gerin[d], Rashmi Shrestha[e,f], Marleena Hagner[g], Jussi Heinonsalo[e,f], Anna-Liisa Laine[a], Juha Mikola[g]

[a] Faculty of Biological and Environmental Sciences, University of Helsinki, Finland
[b] IBZ, ETH Zürich, Switzerland
[c] Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, USA
[d] Finnish Meteorological Institute, Helsinki, Finland
[e] Faculty of Agriculture and Forestry, University of Helsinki, Finland
[f] Institute for Atmospheric and Earth System Research, University of Helsinki, Finland
[g] Natural Resources Institute Finland, Helsinki, Finland

ARTICLE INFO

Key words:
Agroecosystem
Biological control
Cover crop
Invertebrate
Monoculture
Soil N
Vegetation diversity

ABSTRACT

Maintaining vegetation diversity through cover crops could counteract the decreasing soil carbon and biodiversity in intensive monoculture farming. To investigate how cover crops influence the abundance and trophic structure of invertebrates and soil inorganic N availability (an example of an important soil function), barley (*Hordeum vulgare*) was grown with up to eight undersown cover crops (*Lolium multiflorum*, *Phleum pratense*, *Trifolium hybridum, T. repens, T. pratense*, *Medicago sativa*, *Festuca arundinacea, Cichorium intybus*) selected to include N_2-fixers, non-N_2-fixers and shallow- and deep-rooted species. Soil fauna (nematodes, enchytraeids and earthworms), slugs, and arthropods living on soil surface, vegetation, and barley were sampled, and soil inorganic N availability measured in summer and/or autumn in the second and third year of the experiment. 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. The cover crop functional traits that were missing in barley monoculture (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. Our results suggest that adding plant diversity to agroecosystems with cover crops supports invertebrate communities and their ecosystem functions. Additionally, significant effects on invertebrate-mediated ecosystem functions such as biological control may already be achieved at low levels of added vegetation diversity.

1. Introduction

Invertebrates provide many ecosystem services in agriculture. For instance, soil detritivores feed on dead organic matter and microorganisms, thereby enhancing decomposition, nutrient mineralization and plant production (McCary and Schmitz, 2021; Mikola et al., 2002). Soil nitrogen (N) availability, essential for crop production, is supported by decomposer fauna ranging from large ecosystem engineers such as earthworms (Eriksen-Hamel and Whalen, 2007) to microscopic microbial-feeding nematodes (Mikola and Setälä, 1998). Aboveground invertebrates, in turn, are irreplaceable in plant pollination (Dainese et al., 2019), and predators and parasites contribute to biological pest control (Altieri, 1999). These services are threatened by the deleterious effects of intensive land management on soils (Geisen et al., 2019) and of monoculture farming on biodiversity and associated ecosystem functions (Altieri, 1999; Le Provost et al., 2022).

Increasing vegetation diversity is a possible way to positively influence above- and belowground food webs and enhance the diversity-

---

* Correspondence to: Viikinkaari 1, Helsinki 00014, Finland.
E-mail address: paula.thitz@helsinki.fi (P. Thitz).

https://doi.org/10.1016/j.agee.2026.110490
Received 15 August 2025; Received in revised form 20 April 2026; Accepted 28 April 2026

related ecosystem functions in agricultural systems. Increasing species diversity in plant communities can enhance plant productivity through more efficient resource use and beneficial interspecific interactions (Barry et al., 2019; Wright et al., 2017), and thus reduce the need for chemical inputs and fertilizers (Cooledge et al., 2022). Diverse vegetation can also positively impact aboveground arthropods (Blaise et al., 2022; Cozim-Melges et al., 2024), and while these impacts have mostly been quantified from natural systems, Billeter et al. (2008) found a positive correlation between crop and arthropod diversity also across European agricultural landscapes. Some studies report effects mainly on herbivores (Balvanera et al., 2006; Ebeling et al., 2018; Scherber et al., 2010), but increasing abundance of predatory arthropods in suction and sweep-netted samples (Ebeling et al., 2018; Haddad et al., 2001), and increasing numbers of ground-dwelling and sweep-netted Arachnidae (Blaise et al., 2022; Unsicker et al., 2006) have also been observed, thus suggesting possibilities for improved biological control (Iverson et al., 2014).

Functional traits of vegetation can be important for both biodiversity and the soil carbon (C) content. Therefore, while carbon farming aims at increasing soil C through applying cover crops or rotations with ley mixtures, it 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 such as leaf N content, thus affecting invertebrates (Lipowsky et al., 2015; Meyer et al., 2017; Zaret et al., 2023). Root architecture, including root depth, may affect soil porosity (Cooledge et al., 2022) and C content (Jansson et al., 2021), as well as transfer water to shallow soil layers (Culman et al., 2013; Sekiya and Yano, 2004) with cascading effects on nutrient and microbial distributions (Emerman and Dawson, 1996). However, while the rooting depth is known to affect soil microbes (Steinauer et al., 2017), few experiments have investigated the 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, our main aim is to examine the effects of cover crops (including legumes, non-legumes and shallow- and deep-rooted species) on invertebrates and soil N availability in barley cropping system. We utilised an experimental set-up, where barley (*Hordeum vulgare* L. var. Harbringer) was grown as a monoculture or intercropped with either a single cover crop or a combination of 2–8 cover crops (Cappelli et al., 2024; Domeignoz-Horta et al., 2024; Gerin et al., 2026; Shrestha et al., 2025). 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, as an example of an important soil function. To assess the different effects of vegetation, we ask (i) how the presence of vegetation or barley monoculture affects invertebrate abundances and soil N availability compared to bare soil; (ii) how cover crops influence invertebrates and soil N availability compared to the barley monoculture; and (iii) whether species richness and functional traits (N_2-fixation, root architecture) influence the general cover crop effect.

We hypothesise that barley monoculture increases invertebrates and decreases soil inorganic N availability compared to bare soil. Adding cover crops and increasing their species richness and the relative legume and deep-rooted cover should produce more variable (Srivastava and 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.

Additionally, since herbicides can have non-target effects on other organisms than plants (Wan et al., 2025), we report the effects of the herbicide application within monoculture treatments on the examined variables.

2. Materials and methods

2.1. Experimental set-up

Polyculture farming with cover crops (also called service, nursery or catch crops, or living mulches) was studied on an experiment established on 60 plots (4 m × 10 m) at the agricultural field of the University of Helsinki, southern Finland (60.224799°N, 25.020295°E) in 2019. In the area, the mean annual temperature is 6.5°C, the mean growing season (May-August) temperature 15.1°C, and the yearly precipitation 653 mm (reference period 1991–2020; Jokinen et al., 2021). Soil at the experimental site consists mostly of loam (one block), clay loam and silty clay (three remaining blocks). The soil has a pH of 6.3, and 3% C and 0.24% N of dry mass.

The treatments randomised within 4 blocks included barley monoculture (8 plots), barley with cover crops (44 plots), bare soil control (4 plots) without herbicides and barley monoculture treated with herbicide (Berner Ally 50WG, 35 g/260 L water/ha; 4 plots; see detailed description in Cappelli et al., 2024). Monoculture with herbicides was included as an additional control treatment that corresponds to a typical grain cultivation, where herbicides are used to reduce weeds. Eight cover crops (*Lolium multiflorum*, *Phleum pratense*, *Trifolium hybridum, T. repens, T. pratense*, *Medicago sativa*, *Festuca arundinacea*, *Cichorium intybus*) that varied by their capacity to bind atmospheric N_2 and rooting depth 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). The cover crop species were chosen to enable studying the effect of N_2 fixation and rooting depth independently of plant species richness. Since these functional traits are typically missing from shallow-rooted grain monocultures, their inclusion should have substantial impact on the biological activity and C and N dynamics of the soils. The chosen species are currently used for cover cropping or ley mixtures in northern agricultural systems. Plots were fertilised with 80 kg N ha^{-1} (Belor premium N27 containing 27% N but no other nutrients) on the same date that barley was sown. Vegetated plots were weeded by hand after five weeks, removing weeds taller than barley (these were typically individuals from the previous growing season, that had survived the tilling), 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.

2.2. Invertebrate fauna

Aboveground arthropods were sampled from barley shoots and soil surface during the second and third summer, and from vegetation on the third summer of the experiment (Table 1). **Within-vegetation arthropods** were collected from suction-sampled transects (estimated area 2.5 m^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 on the second and third year of the experiment (Table 1). Nematodes and enchytraeids were extracted using wet funnels (Supplement S2) from 20 g and 80 g fresh weight soil (corresponding to ca. 17 g and 67 g dry weight) sampled in summer and autumn, respectively, and counted

Table 1
Variables measured from different habitats on each plot (n = 60) over growing seasons 2 (2020) or 3 (2021) of the experiment.

habitat	variable	method	time of sampling/ measurement
within-vegetation	arthropod abundance and proportions of trophic groups[a]	suction sample from a 10-m transect per plot	30th June 2021 8th August 2021 7th September 2021
barley	arthropod abundance	arthropods[b] 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 (Supplement S1)	23rd–31st August 2021
aboveground	relative cover of barley and individual cover crops[c]	survey of 4–5 randomly selected 1 m[b] 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× 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 (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×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

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

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 after sorting the animals into length classes (0–2, 2.1–4, 4.1–6, 6.1–8, 8.1–10, 10.1–12, and >12 mm; Abrahamsen, 1973). No enchytraeids were detected in most summer samples (Supplement S2). Soil water content was measured by drying (105 °C, 24 h) ca. 30 g of fresh soil samples. Earthworms, representing **belowground macrofauna,** were hand-sorted and chemically extracted (0.1 mL/L allyl-isothiocyanate, 2 mL/L isopropanol; Nuutinen, 2018) on the third autumn of the experiment from soil monoliths (Table 1). Earthworms preserved in 4 v-% formaldehyde were counted and weighed to measure the total fresh biomass.

2.3. *Soil nutrients and plants*

Plant available inorganic N (NO_3^- and NH_4^+) was quantified in the third summer and autumn of the experiment using PST-1 ion exchange resin capsules (Unibest; Table 1; Pampolino and and Hatano, 2000), extracted in 50 mL of hydrochloric acid and analysed with a FIA flow injection instrument combined with a spectrophotometer at Unibest laboratories (WA, USA). The **cover of barley and cover crops** (%) was visually assessed during each summer (Table 1). Species' mean covers were calculated, and the relative cover was defined as the proportion of the sum of all covers. **Aboveground biomass** of barley and other vegetation (cover crops and weeds) before each year's harvest was quantified (Table 1) as dry weight after 48 h at 60 °C.

2.4. *Statistical analyses*

All statistical analyses were conducted with R version 4.5.2 (R Core Team, 2025). The responses of invertebrates and soil mineral N to the addition of vegetation (compared to bare soil), cover crops (compared to barley monoculture) and herbicide (within barley monoculture treatments) were studied, using appropriate contrasts in univariate mixed models where treatment (bare soil, monoculture without herbicide, monoculture with herbicide, or polyculture with 1–8 cover crops) and season (summer or autumn, when appropriate) were treated as fixed variables (Table S3). Additionally, we compared bare soil plots to barley monocultures excluding the plots without cover crops. For these models, we initially coded treatments as bare soil, monoculture without herbicides, or monoculture with herbicides, pooling the two monoculture treatments only when no statistically significant differences between the two monoculture treatments were found (Table S4). Finally, to investigate the effects of cover crop species richness and the relative cover of legumes and deep-rooted species within cover crop plots, we fitted mixed models with season, cover crop richness and legume- or deep-rooted covers as fixed variables (Table S5). Non-significant interactions with season were removed from final models (Supplement S3). All mixed models included the necessary block-, plot- or year-specific random intercepts. We performed F-tests for type III hypotheses which in mixed models are robust to unbalanced number of observations in compared groups (Zuur et al., 2009, Kuznetsova et al., 2017) and assessed the model assumptions using residuals. The models were built with packages lmerTest (Kuznetsova et al., 2017), lme4 (Bates et al., 2015) and glmmTMB (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 were fit to investigate the effects of most abundant soil fauna on NO_3^--N and NH_4^+-N . Least correlated faunal variables (transformed for normality; Table S6) were fit as fixed variables, and blocks as random intercepts. The relationship between microbivorous (bacterivorous and fungivorous) nematodes and N availability in summer 2021 was checked with corresponding models accounting for microfauna.

Finally, 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.

3. Results

3.1. *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

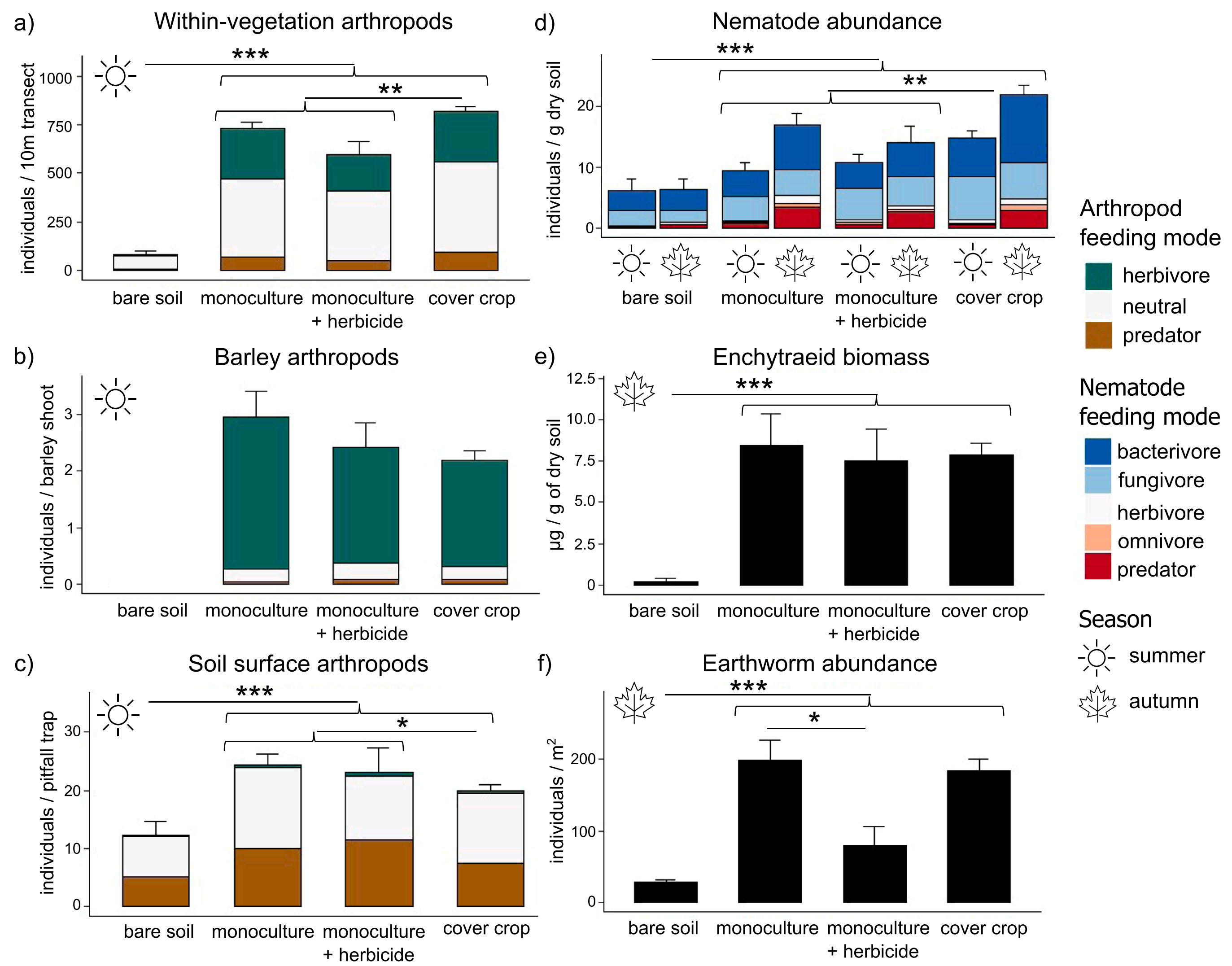

Fig. 1. Invertebrates from a) suction samples, b) barley shoots, c) pitfall traps, and d-f) soil of bare soil (n = 4), monoculture (without and with herbicide; n = 8 and n = 4, respectively) and cover crop plots (n = 44). Means and standard errors from one (a and f) or two years (b-e), and significant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

was 69% higher and the average slug size 35% lower in vegetated compared to bare soil plots (Fig. 1c, Fig. S1i, Table S3). 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. 1b), 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), 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 S7). 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 S7), 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 apart from the neutral within-vegetation arthropods, which were 11% more abundant when barley monoculture was treated with herbicide (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).

3.2. 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 S3) and bacterivorous and fungivorous nematodes in soil by 61% and 40%, respectively (Fig. 1d, Table S3). Cover crops decreased soil surface arthropods by 17% (Fig. 1c, Table S3) but did not affect resin concentrations of NO_3^--N and NH_4^+-N (Fig. S2; Table S3). The NO_3^--N concentrations associated negatively with the abundance of microbivorous nematodes in autumn but not in summer (Fig. 2c, Table S8, Table S9).

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. 3b) compared to monocultures. The predatory arthropods whose abundance increased due to cover cropping included Arachnidae and Hymenoptera, which may have led to lower abundances of adult herbivorous Thysanoptera in vegetation with cover crops compared to monoculture (data not shown). With cover crops, 31% of arthropods on barley stalks were thrips and 58% aphids or their

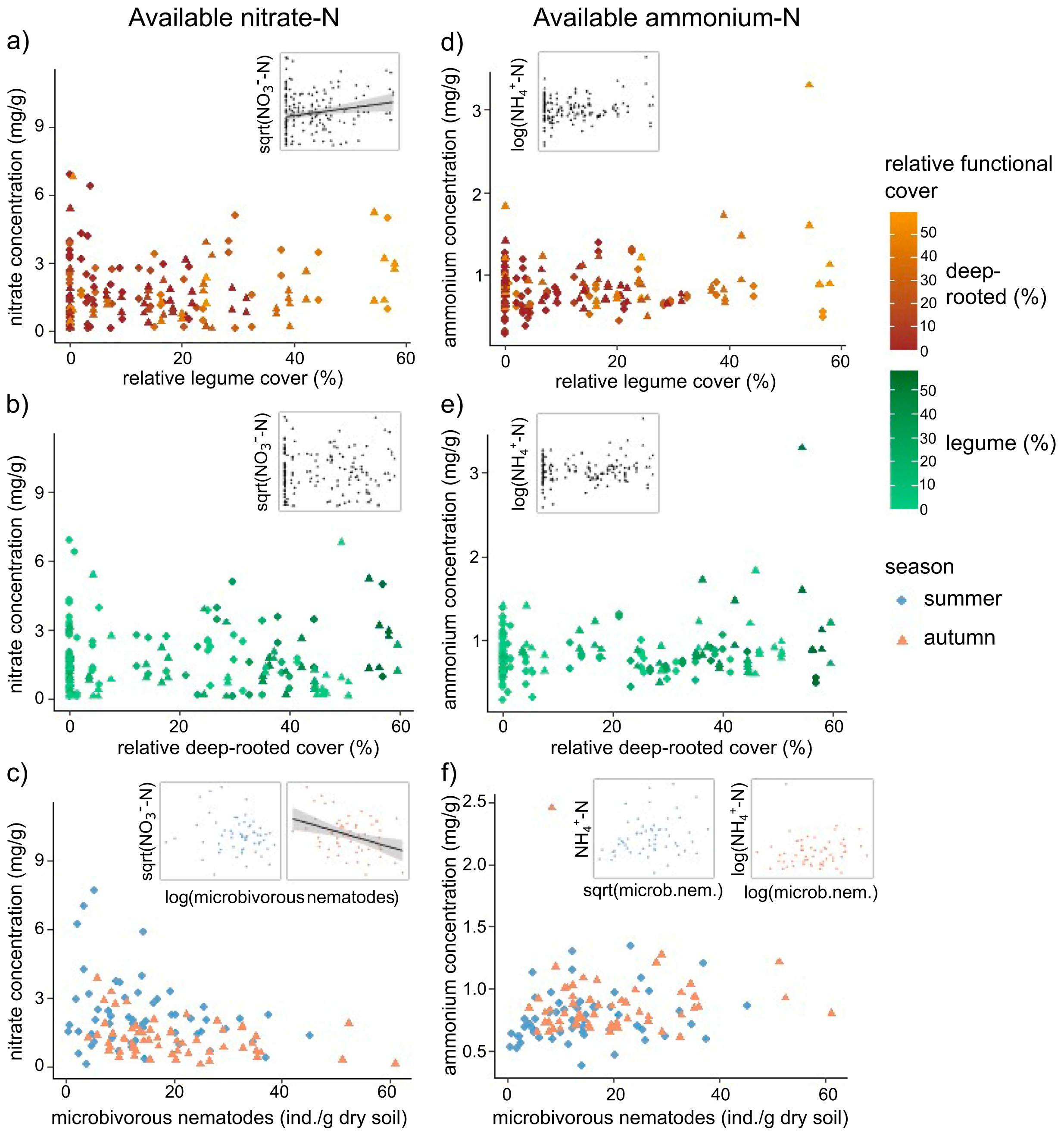

Fig. 2. Effect of cover crop functional traits on nitrate and ammonium availability (as concentration per resin dry mass) in topsoil from 44 cover crop plots (a-b, d-e), and the relationship between microbivorous nematodes and N-forms from 60 plots (c,f). Insets with trendlines indicate statistically significant ($0.001 < P < 0.01$) linear effects.

exoskeletons (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 the monocultures.

The total aboveground biomass of cover crops and weeds correlated positively with the abundance of earthworms and within-vegetation arthropods, 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 plant and non-barley biomass (Fig. S3).

3.3. *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. 4a, Table S5) and the average resin concentrations of NO_3^--N (Fig. 2a, Table S5). The relative deep-rooted cover associated positively with within-vegetation arthropods, bacterivorous nematodes, and earthworm abundance and biomass (Fig. 4b, Table S5). Legume cover increased NH_4^+-N when deep-rooted cover crops were abundant (Fig. 2d,e, Table S5). Among within-vegetation arthropods, the proportions of predatory and herbivorous taxa increased, and neutral taxa decreased with increasing legume cover (Fig. 4a, Table S5), while increasing the deep-rooted cover increased neutral taxa at the expense of herbivores (Fig. 4b, Table S5). Cover crop species richness did not affect the

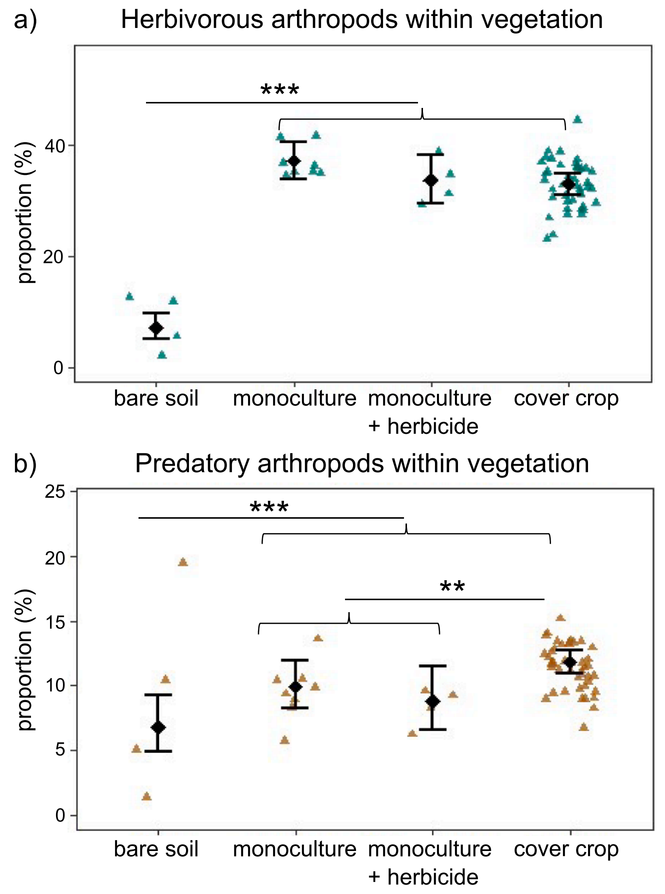

Fig. 3. Proportion of a) herbivores and b) predators in arthropods suction-sampled from bare soil (n = 4), monoculture (without and with herbicide; n = 8 and n = 4, respectively) and cover crop plots (n = 44). Averages over three samplings per plot (points), modelled estimates (diamonds), 95% confidence intervals (error bars), and significant contrasts ($0.01 < p < 0.05$ *, $0.001 < p < 0.01$ ** or $p < 0.001$ ***) are shown.

invertebrate abundances or resin N concentrations (Fig. 4c, Fig. S1s,t, Table S5).

4. Discussion

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

4.1. 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 and Wall, 2011). Invertebrate abundances on bare soil were very low only two years after last cultivation. The strong positive link between the simple monoculture vegetation and the fauna that we found (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 in our study (see also García-Pérez et al., 2016; Gaupp-Berghausen et al., 2015).

Periods with uncultivated bare soil can cause nutrient leaching and erosion (Scavo et al., 2022) due to the absence of efficient nutrient uptake by vegetation (Hooper and Vitousek, 1998; Niklaus et al., 2006). This was also clearly shown in our study, where the barley monoculture

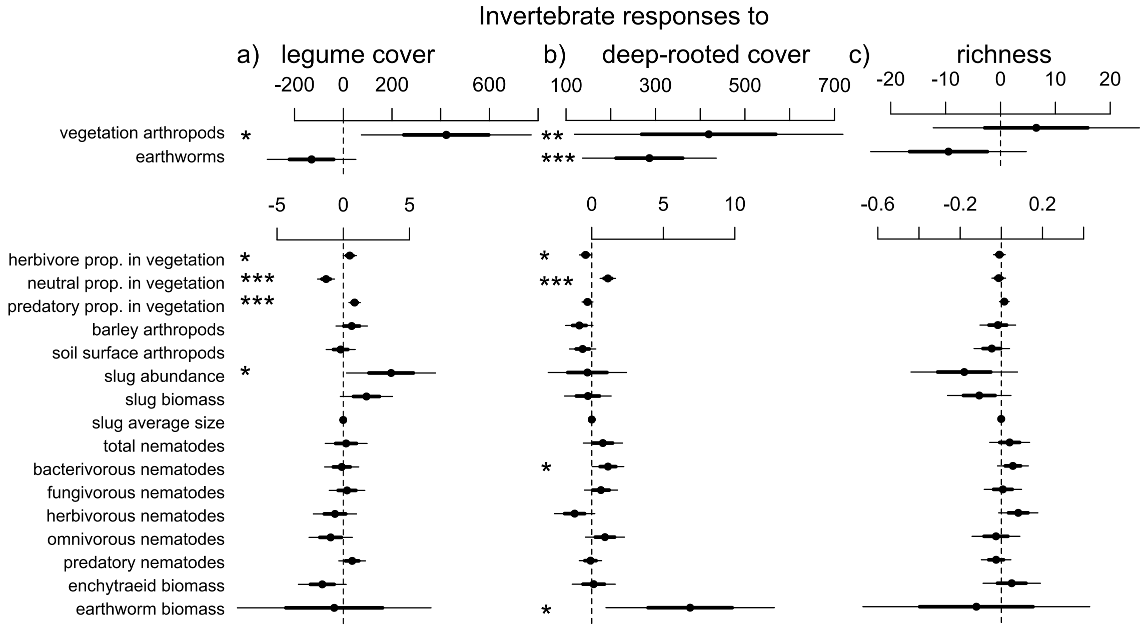

Fig. 4. Effects of relative a) legume cover, b) deep-rooted cover and c) cover crop richness on invertebrates from cover crop plots (n = 44; responses are abundance when not otherwise mentioned; prop. equals proportion). Standard error (wide whiskers) and 95% confidence interval (narrow whiskers) of estimates (dots), and statistically significant effects are shown at $0.01 < p < 0.05$ (*), $0.001 < p < 0.01$ (**) or $p < 0.001$ (***).

or vegetation efficiently reduced inorganic N availability in the soil. Seasonal increase in plant biomass likely explains the decreased NO_3^--N availability from summer to autumn, while the fast nitrification in agricultural soils explains the lack of responses in NH_4^+-N.

4.2. Cover crops sustain invertebrates and enhance the herbivore control potential

The positive effect of cover crops on within-vegetation arthropods aligns with earlier reported vegetation diversity effects (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 an earlier study in the same site (Shrestha et al., 2025) highlights the fast responses of soil communities to diversified vegetation. Contrasting earlier studies (Abalos et al., 2021; Hooper and 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 does not necessarily decrease nutrient availability (Tilman et al., 1997). This could partly be explained by 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 and Setälä, 1998), but disentangling the different mechanisms is difficult when the inorganic N released by animals is instantly assimilated by plants and microbes.

Even when higher vegetation diversity affects the entire food web (Buzhdygan et al., 2020), contrasting effects may be detected at different trophic levels. Often, the strongest positive effects are detected on herbivores (Balvanera et al., 2006; Ebeling et al., 2018; Scherber et al., 2010), but in our study, cover crops increased the proportion of predatory arthropods in vegetation. Decreased herbivore abundance (Letourneau et al., 2011) and increased biological control (Beaumelle et al., 2021; Iverson et al., 2014; Scherber et al., 2010) have earlier been recorded in diversified plant communities, especially in productive systems where predators can reach high abundances (Koricheva et al., 2000; Oksanen et al., 1981; Srivastava and Lawton, 1998; Welti et al., 2020). Supporting these observations, neither the leaf-sucking herbivores counted from barley, nor the herbivore damage measured from barley leaves (unpublished data) increased in our study despite more arthropods being found with cover crops. 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), thus implying 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.

Recent analyses have highlighted invertebrate abundance as an early and sensitive indicator of local biodiversity changes (van Klink et al., 2023; Susi et al., 2026). Although we did not directly quantify invertebrate biodiversity, our results, combined with these findings, suggest that cover cropping might also influence the diversity of other organisms than plants in the grain field that we studied.

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

While the cover crop presence influenced invertebrate abundances, their species richness (with 1–8 added species) did not affect invertebrate abundance. Instead, following the earlier studies that stress the importance of plant community composition (Haddad et al., 2009; Sylvain and 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 the fact that herbivores generally prefer legumes over the main crop can alleviate the problem. As a result, intercropping with legumes can increase the probability of win-win yield- and biocontrol scenarios in dense vegetation (Iverson et al., 2014). In recent studies originating from our experiment, Cappelli et al., (2024) and Shrestha et al., (2025) showed legumes also suppressed disease in barley and among soil fungi. In spite of this, however, legumes did not influence barley yield (Cappelli et al., 2024: Fig. S6). Contrasting the earlier results (Abalos et al., 2021; Eisenhauer, 2012), we did not find legume cover to increase earthworm abundances. NO_3^--N availability still increased, illustrating the potential of legumes to reduce the need of inorganic fertilisers (Li et al., 2020) in addition to their positive effects for vegetation and soil surface food webs. Clearly, selecting N_2-fixing 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.

In contrast to an earlier study that found no effects of rooting depth on grassland soil arthropods (Beugnon et al., 2019), we found that increasing the deep-rooted cover increased faunal abundances both above- and belowground (Fig. 4b). This supports our hypothesis of enhanced consumer resources and habitats with deep-rooted plants. Looser soil structure or the quality of plant residues (Cooledge et al., 2022) could explain the positive association of earthworms with deep-rooted plants (Katsvairo et al., 2007). Larger soil volume affected by root exudates with deep-rooted plants may also increase soil microbial activity (Jansson et al., 2021), and accordingly in our experiment, the deep-rooted plants increased both the abundance of bacterivorous nematodes (this study) and the most abundant soil bacteria (manuscript in preparation). The surprising effect of plant root architecture on the aboveground invertebrate composition could be mediated by the aboveground traits of deep-rooted species.

Overall, we found trait-specific effects of cover crops on invertebrates in different habitats, suggesting distinct effects on ecosystem services. It appears 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 plant cover during growing season is crucially important for maintaining invertebrate fauna in agroecosystems. It appears that cover crops, besides potentially reducing soil C loss, increase the invertebrate abundances above levels maintained by crop monocultures, as well as the possibility of biological pest control. Cover crops affect soil invertebrates, but this does not seem to 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 show that cover crops can maintain the abundance of aboveground and belowground invertebrates, thus supporting their potential role in pest control and soil functioning. Notably, when appropriate plant functional traits are included, high plant species richness is not needed to achieve these effects.

CRediT authorship contribution statement

Paula Thitz: Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Mikko Tiusanen:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

Seraina Lisa Cappelli: Writing – review & editing, Visualization, Investigation, Data curation. **Stephanie Gerin:** Writing – review & editing, Investigation. **Rashmi Shrestha:** Writing – review & editing, Investigation. **Marleena Hagner:** Writing – review & editing, Investigation. **Jussi Heinonsalo:** Writing – review & editing, Resources, Project administration, Funding acquisition. **Anna-Liisa Laine:** Writing – review & editing, Resources, Funding acquisition. **Juha Mikola:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Krista Raveala, John Allen, Anna Välkki, Lauri Kettunen, Johanna Vielmaa, Simo Väänänen, Helena Wirta and Tuomas Kankaanpää for field help; Visa Nuutinen, Ilkka Sarikka, Juho Paukkunen and Sampsa Malmberg for species identification; and Annalea Lohila for financial support of resin capsule analyses. The work was financially supported by Maj and Tor Nessling Foundation (grant number 2218) and Academy of Finland (STN MULTA; grant number 327222).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110490.

Data availability

Data and scripts are available in Zenodo (https://doi.org/10.5281/zenodo.19663879).

References

Abalos, D., de Deyn, G.B., Kuyper, T.W., van Groenigen, J.W., 2014. Plant species identity surpasses species richness as a key driver of emissions from grassland. Glob. Change Biol. 20 (1), 265–275. https://doi.org/10.1111/gcb.12350.

Abalos, D., de Deyn, G.B., Philippot, L., Oram, N.J., Oudová, B., Pantelis, I., Clark, C., Fiorini, A., Bru, D., Mariscal-Sancho, I., van Groenigen, J.W., 2021. Manipulating plant community composition to steer efficient N-cycling in intensively managed grasslands. J. Appl. Ecol. 58, 167–180. https://doi.org/10.1111/1365-2664.13788.

Abrahamsen, G., 1973. Studies on body-volume, body-surface area, density and live weight of Enchytraeidae (Oligochaeta)*). Pedobiologia 13 (1), 6–15. https://doi.org/10.1016/S0031-4056(23)02073-5.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agric. Ecosyst. & Environ. 74, 19–31. https://doi.org/10.1016/S0167-8809(99)00028-6.

Andow, D.A., 1991. Vegetational diversity and arthropod population response. Annu. Rev. Entomol. 36 (1), 561–586. https://doi.org/10.1146/annurev.en.36.010191.003021.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9 (10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x.

Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y., Connolly, J., De Deyn, G.B., de Kroon, H., Isbell, F., Milcu, A., Roscher, C., Scherer-Lorenzen, M., Schmid, B., Weigelt, A., 2019. The future of complementarity: Disentangling causes from consequences. Trends Ecol. Evol. 34, 167–180. https://doi.org/10.1016/j.tree.2018.10.013.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beaumelle, L., Auriol, A., Grasset, M., Pavy, A., Thiéry, D., Rusch, A., 2021. Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context. Ecol. Solut. Evid. 2 (3), 1–12. https://doi.org/10.1002/2688-8319.12086.

Beugnon, R., Steinauer, K., Barnes, A.D., Ebeling, A., Roscher, C., Eisenhauer, N., 2019. Chapter Five—Plant functional trait identity and diversity effects on soil meso- and macrofauna in an experimental grassland. In: Eisenhauer, N., Bohan, D.A., Dumbrell, A.J. (Eds.), Advances in Ecological Research, 61. Academic Press, pp. 163–184. https://doi.org/10.1016/bs.aecr.2019.06.004.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Edwards, P. j, 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. J. Appl. Ecol. 45 (1), 141–150. https://doi.org/10.1111/j.1365-2664.2007.01393.x.

Blaise, C., Mazzia, C., Bischoff, A., Millon, A., Ponel, P., Blight, O., 2022. Vegetation increases abundances of ground and canopy arthropods in Mediterranean vineyards. Sci. Rep. 12, 3680. https://doi.org/10.1038/s41598-022-07529-1.

Boetzl, F.A., Douhan Sundahl, A., Friberg, H., Viketoft, M., Bergkvist, G., Lundin, O., 2023. Undersowing oats with clovers supports pollinators and suppresses arable weeds without reducing yields. J. Appl. Ecol. 60 (4), 614–623. https://doi.org/10.1111/1365-2664.14361.

Borer, E.T., Seabloom, E.W., Tilman, D., 2012. Plant diversity controls arthropod biomass and temporal stability. Ecol. Lett. 15 (12), 1457–1464. https://doi.org/10.1111/ele.12006.

Brooks, M., Kristensen, E., Benthem, K., van, K., J., Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9 (2), 378. https://doi.org/10.32614/RJ-2017-066.

Buzhdygan, O.Y., Meyer, S.T., Weisser, W.W., Eisenhauer, N., Ebeling, A., Borrett, S.R., Buchmann, N., Cortois, R., de Deyn, G.B., de Kroon, H., Gleixner, G., Hertzog, L.R., Hines, J., Lange, M., Mommer, L., Ravenek, J., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Petermann, J.S., 2020. Biodiversity increases multitrophic energy use efficiency, flow and storage in grasslands. Nat. Ecol. Evol. 4 (3), 393–405. https://doi.org/10.1038/s41559-020-1123-8.

Buzhdygan, O.Y., Tietjen, B., Petermann, J.S., Eisenhauer, N., Hines, J., Schmid, B., Baldauf, S., Ebeling, A., Scherber, C., Buchmann, N., Borrett, S.R., de Kroon, H., Weisser, W., Meyer, S.T., 2025. Plant diversity facets differentially affect energy dynamics in grasslands depending on trophic contexts. Ecol. Monogr. 95 (1), e70004. https://doi.org/10.1002/ecm.70004.

Cappelli, S.L., Domeignoz-Horta, L.A., Loaiza, V., Laine, A.-L., 2022. Plant biodiversity promotes sustainable agriculture directly and via belowground effects. Trends Plant Sci. 27 (7), 674–687. https://doi.org/10.1016/j.tplants.2022.02.003.

Cappelli, S.L., Domeignoz Horta, L.A., Gerin, S., Heinonsalo, J., Lohila, A., Raveala, K., Schmid, B., Shrestha, R., Tiusanen, M.J., Thitz, P., Laine, A.-L., 2024. Potential of undersown species identity versus diversity to manage disease in crops. Funct. Ecol. 38 (7), 1497–1509. https://doi.org/10.1111/1365-2435.14592.

Cooledge, E.C., Chadwick, D.R., Smith, L.M.J., Leake, J.R., Jones, D.L., 2022. Agronomic and environmental benefits of reintroducing herb- and legume-rich multispecies leys into arable rotations: a review. Front. Agric. Sci. Eng. 9 (2), 245–271. https://doi.org/10.15302/J-FASE-2021439.

Cozim-Melges, F., Ripoll-Bosch, R., Veen, G.F., Ciska, Oggiano, P., Bianchi, F.J.J.A., van der Putten, W.H., van Zanten, H.H.E., 2024. Farming practices to enhance biodiversity across biomes: a systematic review (Article). Npj Biodivers. 3 (1), 1. https://doi.org/10.1038/s44185-023-00034-2.

Culman, S.W., Snapp, S.S., Ollenburger, M., Basso, B., DeHaan, L.R., 2013. Soil and water quality rapidly responds to the perennial grain kernza wheatgrass. Agron. J. 105 (3), 735–744. https://doi.org/10.2134/agronj2012.0273.

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D.K., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5 (10), eaax0121. https://doi.org/10.1126/sciadv.aax0121.

Domeignoz-Horta, L.A., Cappelli, S.L., Shrestha, R., Gerin, S., Lohila, A.K., Heinonsalo, J., Nelson, D.B., Kahmen, A., Duan, P., Sebag, D., Verrecchia, E., Laine, A.-L., 2024. Plant diversity drives positive microbial associations in the rhizosphere enhancing carbon use efficiency in agricultural soils. Nat. Commun. 15 (1), 8065. https://doi.org/10.1038/s41467-024-52449-5.

Ebeling, A., Hines, J., Hertzog, L.R., Lange, M., Meyer, S.T., Simons, N.K., Weisser, W.W., 2018. Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. Basic Appl. Ecol. 26, 50–63. https://doi.org/10.1016/j.baae.2017.09.014.

Eisenhauer, N., 2012. Aboveground–belowground interactions as a source of complementarity effects in biodiversity experiments. Plant Soil 351, 1–22. https://doi.org/10.1007/s11104-011-1027-0.

Eisenhauer, N., Milcu, A., Sabais, A.C.W., Bessler, H., Weigelt, A., Engels, C., Scheu, S., 2009. Plant community impacts on the structure of earthworm communities depend on season and change with time. Soil Biol. Biochem. 41 (12), 2430–2443. https://doi.org/10.1016/j.soilbio.2009.09.001.

Emerman, S.H., Dawson, T.E., 1996. Hydraulic lift and its influence on the water content of the rhizosphere. Oecologia 108, 273–278.

Eriksen-Hamel, N.S., Whalen, J.K., 2007. Impacts of earthworms on soil nutrients and plant growth in soybean and maize agroecosystems. Agric. Ecosyst. & Environ. 120 (2–4), 442–448. https://doi.org/10.1016/j.agee.2006.11.004.

García-Pérez, J.A., Alarcón, E., Hernández, Y., Hernández, C., 2016. Impact of litter contaminated with glyphosate-based herbicide on the performance of *Pontoscolex corethrurus*, soil phosphatase activities and soil pH. Appl. Soil Ecol. 104, 31–41. https://doi.org/10.1016/j.apsoil.2016.03.007.

Gaupp-Berghausen, M., Hofer, M., Rewald, B., Zaller, J.G., 2015. Glyphosate-based herbicides reduce the activity and reproduction of earthworms and lead to increased soil nutrient concentrations. Sci. Rep. 5 (1), 12886. https://doi.org/10.1038/srep12886.

Gebremikael, M.T., Steel, H., Buchan, D., Bert, W., De Neve, S., 2016. Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. Sci. Rep. 6 (1), 32862. https://doi.org/10.1038/srep32862.

Geisen, S., Wall, D.H., van der Putten, W.H., 2019. Challenges and opportunities for soil biodiversity in the Anthropocene. Curr. Biol. 29 (19), R1036–R1044. https://doi.org/10.1016/j.cub.2019.08.007.

Gerin, S., Kulmala, L., Korkiakoski, M., Shrestha, R., Rautakoski, H., Thitz, P., Liski, J., Heinonsalo, J., Lohila, A., 2026. Barley intercropped with undersown species in northern Europe: a modest yet positive impact on CO2 uptake during the shoulder seasons. Agric. Ecosyst. Environ. 401, 110265. https://doi.org/10.1016/j.agee.2026.110265.

Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M., Knops, J.M.H., 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. Am. Nat. 158 (1), 17–35. https://doi.org/10.1086/320866.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H., Tilman, D., 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecol. Lett. 12, 1029–1039. https://doi.org/10.1111/j.1461-0248.2009.01356.x.

Halbritter, A.H., De Boeck, H.J., Eycott, A.E., Reinsch, S., Robinson, D.A., Vicca, S., Berauer, B., Christiansen, C.T., Estiarte, M., Grünzweig, J.M., Gya, R., Hansen, K., Jentsch, A., Lee, H., Linder, S., Marshall, J., Peñuelas, J., Kappel Schmidt, I., Stuart-Haëntjens, E., Vandvik, V., 2020. The handbook for standardized field and laboratory measurements in terrestrial climate change experiments and observational studies (ClimEx). Methods Ecol. Evol. 11 (1), 22–37. https://doi.org/10.1111/2041-210X.13331.

Hooper, D.U., Vitousek, P.M., 1998. Effects of plant composition and diversity on nutrient cycling. Ecol. Monogr. 68 (1), 121–149. https://doi.org/10.1890/0012-9615(1998)068[0121:EOPCAD]2.0.CO;2.

Iverson, A.L., Marín, L.E., Ennis, K.K., Gonthier, D.J., Connor-Barrie, B.T., Remfert, J.L., Cardinale, B.J., Perfecto, I., 2014. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. J. Appl. Ecol. 51 (6), 1593–1602. https://doi.org/10.1111/1365-2664.12334.

Jansson, C., Faiola, C., Wingler, A., Zhu, X.-G., Kravchenko, A., de Graaff, M.-A., Ogden, A.J., Handakumbura, P.P., Werner, C., Beckles, D.M., 2021. Crops for carbon farming. Front. Plant Sci. 12, 636709. https://doi.org/10.3389/fpls.2021.636709.

Jokinen, P., Pirinen, P., Kaukoranta, J.-P., Kangas, A., Alenius, P., Eriksson, P., Johansson, M., Wilkman, S., 2021. Finnish Meteorological Institute. Til. Suom. Ilma ja Meres ä 1991-2020 (Rep. No. 8 Finn. Meteorol. Inst. 169. ⟨https://helda.helsinki.fi/server/api/core/bitstreams/4a090295-f4a7-4b55-a3e4-39a0e370f5b9/content⟩.

Katsvairo, T.W., Wright, D.L., Marois, J.J., Hartzog, D.L., Balkcom, K.B., Wiatrak, P.P., Rich, J.R., 2007. Cotton roots, earthworms, and infiltration characteristics in sod–peanut–cotton cropping systems. Agron. J. 99 (2), 390–398. https://doi.org/10.2134/agronj2005.0330.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Shen, M., Swengel, S.R., Chase, J.M., 2023. Disproportionate declines of formerly abundant species underlie insect loss. Nature 628, 359–364. https://doi.org/10.1038/s41586-023-06861-4.

Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J., Huss-Danell, K., 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. Oecologia 125 (2), 271–282. https://doi.org/10.1007/s004420000450.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Le Provost, G., Schenk, N.V., Penone, C., Thiele, J., Westphal, C., Allan, E., Ayasse, M., Blüthgen, N., Boeddinghaus, R.S., Boesing, A.L., Bolliger, R., Busch, V., Fischer, M., Gossner, M.M., Hölzel, N., Jung, K., Kandeler, E., Klaus, V.H., Kleinebecker, T., Manning, P., 2022. The supply of multiple ecosystem services requires biodiversity across spatial scales. Nat. Ecol. & Evol. https://doi.org/10.1038/s41559-022-01918-5.

Lees, K.J., McKenzie, A.J., Newell Price, J.P., Critchley, C.N., Rhymer, C.M., Chambers, B.J., Whittingham, M.J., 2016. The effects of soil compaction mitigation on below-ground fauna: How earthworms respond to mechanical loosening and power harrow cultivation. Agric. Ecosyst. Environ. 232, 273–282. https://doi.org/10.1016/j.agee.2016.07.026.

Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Rrez, C.G., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? A synthetic review. Ecol. Appl. 21 (1).

Li, C., Hoffland, E., Kuyper, T.W., Yu, Y., Zhang, C., Li, H., Zhang, F., van der Werf, W., 2020. Syndromes of production in intercropping impact yield gains. Nat. Plants 6 (6), 653–660. https://doi.org/10.1038/s41477-020-0680-9.

Lipowsky, A., Roscher, C., Schumacher, J., Michalski, S.G., Gubsch, M., Buchmann, N., Schulze, E.D., Schmid, B., 2015. Plasticity of functional traits of forb species in response to biodiversity. Perspect. Plant Ecol. Evol. Syst. 17 (1), 66–77. https://doi.org/10.1016/j.ppees.2014.11.003.

Loranger, H., Weisser, W.W., Ebeling, A., Eggers, T., De Luca, E., Loranger, J., Roscher, C., Meyer, S.T., 2014. Invertebrate herbivory increases along an experimental gradient of grassland plant diversity. Oecologia 174 (1), 183–193. https://doi.org/10.1007/s00442-013-2741-5.

Mamabolo, E., Pryke, J.S., Gaigher, R., 2024. Soil fauna diversity is enhanced by vegetation complexity and no-till planting in regenerative agroecosystems. Agric. Ecosyst. & Environ. 367, 108973. https://doi.org/10.1016/j.agee.2024.108973.

McCary, M.A., Schmitz, O.J., 2021. Invertebrate functional traits and terrestrial nutrient cycling: Insights from a global meta-analysis. J. Anim. Ecol. 90 (7), 1714–1726. https://doi.org/10.1111/1365-2656.13489.

Meyer, S.T., Scheithe, L., Hertzog, L., Ebeling, A., Wagg, C., Roscher, C., Weisser, W.W., 2017. Consistent increase in herbivory along two experimental plant diversity gradients over multiple years. Ecosphere 8 (7), e01876. https://doi.org/10.1002/ecs2.1876.

Mikola, J., Setälä, H., 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. Ecology 79, 153–164.

Mikola, J., Bardgett, R.D., Hedlund, K., 2002. Biodiversity, ecosystem functioning and soil decomposer food webs. In: Loreau, In.M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and ecosystem functioning: Synthesis and perspectives. Oxford Univ. Press.

Neff, F., Prati, D., Achury, R., Ambarlı, D., Bolliger, R., Brändle, M., Freitag, M., Hölzel, N., Kleinebecker, T., Knecht, A., Schäfer, D., Schall, P., Seibold, S., Staab, M., Weisser, W.W., Pellissier, L., Gossner, M.M., 2023. Reduction of invertebrate herbivory by land use is only partly explained by changes in plant and insect characteristics. Ecol. Monogr. https://doi.org/10.1002/ecm.1571.

Niklaus, P.A., Wardle, D.A., Tate, K.R., 2006. Effects of plant species diversity and composition on nitrogen cycling and the trace gas balance of soils. Plant Soil 282 (1), 83–98. https://doi.org/10.1007/s11104-005-5230-8.

Nuutinen, V. (2018). 11. Earthworm sampling. In H*andbook on wp4 protocols for sampling, sample procedure and analysis*. Diverfarming. ⟨http://www.diverfarming.eu/images/deliverables/D4_1.pdf#page=114⟩.

Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. Am. Nat. 118 (2), 240–261. https://doi.org/10.1086/283817.

Osler, G.H.R., 2007. Impact of fauna on chemical transformations in soil. Soil Biological Fertility—A Key to Sustainable Land Use in Agriculture. Springer, p. 267.

Pampolino, M.F., Hatano, R., 2000. Comparison between conventional soil tests and the use of resin capsules for measuring P, K, and N in two soils under two moisture conditions. Soil Sci. Plant Nutr. 46 (2), 461–471. https://doi.org/10.1080/00380768.2000.10408799.

R Core Team, 2025. R: a language and environment for statistical computing. R. Found. Stat. Comput. ⟨https://www.R-project.org/⟩ (Vienna, Austria).

Scavo, A., Fontanazza, S., Restuccia, A., Pesce, G.R., Abbate, C., Mauromicale, G., 2022. The role of cover crops in improving soil fertility and plant nutritional status in temperate climates. A review. Agron. Sustain. Dev. 42 (5), 93. https://doi.org/10.1007/s13593-022-00825-0.

Scherber, C., Milcu, A., Partsch, S., Scheu, S., Weisser, W.W., 2006. The effects of plant diversity and insect herbivory on performance of individual plant species in experimental grassland. J. Ecol. 94 (5), 922–931. https://doi.org/10.1111/j.1365-2745.2006.01144.x.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.D., Roscher, C., Weigelt, A., Allan, E., Beler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Tscharntke, T., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468 (7323), 553–556. https://doi.org/10.1038/nature09492.

Sekiya, N., Yano, K., 2004. Do pigeon pea and sesbania supply groundwater to intercropped maize through hydraulic lift? - Hydrogen stable isotope investigation of xylem waters. Field Crops Res. 86 (2–3), 167–173. https://doi.org/10.1016/j.fcr.2003.08.007.

Shrestha, R., Huusko, K., Sietiö, O.-M., Schmid, B., Cappeli, S.L., Thitz, P., Gerin, S., Laine, A.-L., Lohila, A., Heinonsalo, J., 2025. Impacts of diverse undersown cover crops on seasonal soil microbial properties. FEMS Microbiol. Ecol., fiaf068 https://doi.org/10.1093/femsec/fiaf068.

Siemann, E., Tilman, D., Haarstad, J., Ritchie, M., 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. Am. Nat. 152 (5), 738–750. https://doi.org/10.1086/286204.

Silva, E.B., Franco, J.C., Vasconcelos, T., Branco, M., 2010. Effect of ground cover vegetation on the abundance and diversity of beneficial arthropods in citrus orchards. Bull. Ѐntomol. Res. 100 (4), 489–499. https://doi.org/10.1017/S0007485309990526.

Srivastava, D.S., Lawton, J.H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am. Nat. 152 (4), 510–529.

Steinauer, K., Fischer, F.M., Roscher, C., Scheu, S., Eisenhauer, N., 2017. Spatial plant resource acquisition traits explain plant community effects on soil microbial properties. Pedobiologia 65, 50–57. https://doi.org/10.1016/j.pedobi.2017.07.005.

Susi, H., Thitz, P., Hagner, M., Raveala, K., Ekroos, J., Laine, A.-L., 2026. Impacts of carbon farming practices on biodiversity at the farm scale. Agric. Ecosyst. & Environ. 400, 110230. https://doi.org/10.1016/j.agee.2026.110230.

Sylvain, Z.A., Wall, D.H., 2011. Linking soil biodiversity and vegetation: Implications for a changing planet. Am. J. Bot. 98 (3), 517–527. https://doi.org/10.3732/ajb.1000305.

Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379 (6567), 718–720. https://doi.org/10.1038/379718a0.

Tilman, D., Lehman, C.L., Thomson, K.T., 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proc. Natl. Acad. Sci. 94 (5), 1857–1861. https://doi.org/10.1073/pnas.94.5.1857.

Unsicker, S.B., Baer, N., Kahmen, A., Wagner, M., Buchmann, N., Weisser, W.W., 2006. Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. Oecologia 150 (2), 233–246.

Wan, N.-F., Fu, L., Dainese, M., Kiær, L.P., Hu, Y.-Q., Xin, F., Goulson, D., Woodcock, B. A., Vanbergen, A.J., Spurgeon, D.J., Shen, S., Scherber, C., 2025. Pesticides have negative effects on non-target organisms. Nat. Commun. 16, 1360. https://doi.org/10.1038/s41467-025-56732-x.

Welti, E.A.R., Prather, R.M., Sanders, N.J., de Beurs, K.M., Kaspari, M., 2020. Bottom-up when it is not top-down: predators and plants control biomass of grassland arthropods. J. Anim. Ecol. 89 (5), 1286–1294. https://doi.org/10.1111/1365-2656.13191.

Wright, A.J., Wardle, D.A., Callaway, R., Gaxiola, A., 2017. The overlooked role of facilitation in biodiversity experiments. Trends Ecol. & Evol. 32 (5), 383–390. https://doi.org/10.1016/j.tree.2017.02.011.

Yeates, G.W., Bongers, T., de Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera – An outline for soil ecologists. J. Nematol. 25 (3), 315–331.

Zaret, M., Kinkel, L., Borer, E.T., Seabloom, E.W., 2023. Soil nutrients cause threefold increase in pathogen and herbivore impacts on grassland plant biomass. J. Ecol. 111 (8), 1629–1640. https://doi.org/10.1111/1365-2745.14111.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. https://doi.org/10.1086/648138.