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Aboveground and belowground biodiversity responses to seed mixtures and mowing in a long-term set-aside experiment

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ABSTRACT

Set-asides sown to wildflowers are introduced to promote agrobiodiversity. Often, sown seed mixtures have been used to enhance aboveground biodiversity while belowground biodiversity has received less attention. We studied in a 15-year-old set-aside experiment, the impact of seed mixtures (grass vs. meadow) and mowing (mown vs. unmown) on the abundance and diversity of plants, two aboveground invertebrate groups (pollinators and natural enemies of pest species) and one key belowground group, earthworms. We also studied the treatment effects on selected soil chemical properties. In general, a sown meadow seed mixture mostly benefitted aboveground biodiversity, whereas the impacts of late-season mowing were most discernible for earthworms. Plant species richness or coverage did not differ between seed mixtures, but plant coverage showed a positive response to mowing, while the impact on species richness was minor. The meadow seed mixture was dominated by *Centaurea jacea*. A non-mown meadow treatment supported the highest earthworm density and species richness, while the values were lowest in the mown meadow, where earthworm total mass was also at its lowest. In a grass seed mixture of intermediate density and richness, the mowing had no measurable effect on the earthworm community. Topsoil carbon, nitrogen and soluble phosphorus concentrations showed a typical gradient for non-inverted soils, with the highest concentrations in the 0–2.5 cm layer. The two uppermost soil layers (to 5 cm depth) had higher soluble phosphorus content under grass than under meadow seed mixture. Abundance of natural enemies of pests was not significantly different between the treatments, but for carabids there was a marginally significant positive response to mowing. Bumblebee species richness and the abundance of bumblebees and honeybees were highest in the mown meadow seed mixture plots. Butterfly species richness was marginally significantly higher in mown than in non-mown treatments in both seed mixtures. The results showed the potential of set-asides to promote both aboveground and belowground biodiversity through increased plant diversity.

1. Introduction

Decline in agrobiodiversity has been documented in many countries (FAO, 2019). Intensification of arable land use has both decreased the area and lowered the quality of habitats for invertebrates. Various non-cropped habitats, such as set-asides and fallows (Alanen et al., 2011; Toivonen et al., 2013), wildflower strips (Haaland et al., 2011) and perennial field margins (Critchley et al., 2006; Tarmi et al., 2011) have been introduced to compensate for the habitat loss in agricultural environments. Because plant species richness enhances diversity of higher trophic levels (e.g. Siemann et al., 1998; Ekroos et al., 2013), sowing various seed mixtures improves the quality of non-cropped habitats for invertebrates (Alanen et al., 2011; Toivonen et al., 2013). Often, sown seed mixtures have been used to enhance pollinators and other aboveground invertebrates, while belowground biodiversity, including earthworms, has received less attention.

Earthworms constitute a key faunal group in arable soils (Bertrand et al., 2015) and in grasslands the low physical disturbance of soil supports their abundance and diversity (Curry, 1993; Fraser et al., 1996). Plant diversity provides the resource base for the soil decomposer community through litter deposition and root exudates, thereby moderating the interaction between above and belowground ecosystems

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(Wardle et al., 2004; Fuji et al., 2020). The inputs vary in quality and quantity according to plant community features, making seed mixtures a potential regulator of soil biodiversity. Earlier findings showed higher plant diversity to be associated with more abundant and/or diverse earthworm communities, although the effects have differed (Eisenhauer, 2009 and refs. therein). Often, the positive effect on earthworms does not result from diversity per se but is due to the presence of single influential species in diverse plant mixtures, particularly legumes (Milcu et al., 2008; Eisenhauer et al., 2009), which produce high N content litter, preferred by earthworms (Curry and Schmidt, 2007). High aboveground biomass in diverse treatments (Spehn et al., 2000), or the higher abundance of fine roots and their rhizodeposition (Zaller and Arnone, 1999), can also be the enhancing factor.

In wildflower seed mixture experiments, earthworm communities have rarely been studied with aboveground invertebrates. Therefore, it is largely unknown whether the same seed mixtures and mowing treatments that have proved beneficial for pollinators (Alanen et al., 2011) and natural enemies of pests (Toivonen et al., 2018), also benefit earthworms. Such information would be valuable for the development of multi-functional biodiversity measures for agri-environmental schemes. Often the elevated earthworm abundance and species richness in diverse grassland treatments has been due to the increase of soil surface foraging epi-anecic earthworms, which particularly benefit from the input of highly nutritive litter (Spehn et al., 2000; Milcu et al., 2008; Eisenhauer et al., 2009). In arable grassland, the management regime (mowing frequency and timing, treatment of cuttings) regulates the input of surface litter, but to our knowledge its influence on earthworm communities has not been investigated. Earthworm communities respond to field treatments by changes in growth rates of resident populations and by migration. Due to the low rate of spread of earthworms (often less than 10 m yr^{-1}; Edwards and Bohlen, 1996), immigration related responses may be slow and addressing these questions requires data from long-term field experiments.

In the present study, we aimed to study the impact of seed mixtures and mowing on the abundance and diversity of three invertebrate groups important for ecosystem service provision – pollinators, natural enemies of pest species and earthworms – in a long-term set-aside experiment. The seed mixtures used in the experiment (grass vs. meadow) differed in terms of the number of sown plant species. Earlier studies regarding the first six years of the experiment showed the meadow seed mixture to benefit pollinators and insect groups comprising bird chick-food, whereas the impact of mowing was minor (Alanen et al., 2011; Huusela-Veistola, 2007; Hyvönen and Huusela-Veistola, 2011). Currently, 15 years since the establishment of the experiment, we expected the abundance and diversity of aboveground invertebrates, as well as of earthworms, to be higher in meadow than in grass seed mixtures due to differences in plant species diversity and species composition (Eisenhauer et al., 2009; Haaland et al., 2011). Furthermore, we expected mowing to impact earthworm abundance and diversity due to increase in the amount of plant residues on the soil surface (Bertrand et al., 2015). Since phosphorus, carbon and nitrogen liberate as reactive substances upon decomposition of cut biomass left on soil surface and partly associate with soil minerals in the topmost soil layer, we also expected that mowing facilitates their accumulation (Díaz-Zorita and Grove, 2002; Franzluebbers, 2002). A positive impact of mowing was also expected on aboveground biodiversity (Grandchamp et al., 2005; Bruppacher et al., 2016). The impact was expected to be greater than that found in the first six years of the experiment due to documented long-term impacts (Tälle et al., 2016, 2018).

2. Methods

2.1. Experimental design

The field experiment was established in 2003 on a 7 ha field parcel. The experiment was a strip plot design with four replicate blocks containing the six treatment combinations for the two study factors (seed mixture and mowing), resulting in a total of 24 experimental plots (see Alanen et al., 2011). In the present study, one seed mixture was excluded (see below), resulting in a total of 16 experimental plots. While establishing the experiment, mowing treatments were first randomly assigned to each experimental plot by columns and then the three seed mixture treatments by rows. The experimental plots were 0.25 ha (50 m × 50 m) in size. The experiment, located in Ypäjä, southern Finland (ETRS-TM35FIN N 6745551 E 299807), lies in a landscape dominated by spring cereal production, with scattered areas of coniferous forest.

The soil type of the experiment site was silty clay (eutric Cambisol), with an average clay (<0.0002 mm) content of 42% (26–56%, $n = 24$) and soil pH of 5.8–6.4 (1:2.5 vol/vol water slurry). Mean soil clay content of the mowed treatment plots (45%) was slightly, although not statistically significantly, higher than in other treatments (37–42%) due to inherent within-field variability of soil textural properties (Fig. S1A). Annual precipitation at the location is 627 mm and the mean temperature + 4.6 °C (climatological normal period data 1981–2010 from Jokioinen, 10 km from the site; Finnish Meteorological Institute, 2012). The warmest month is July (mean +16.7 °C) and the coldest February (−5.3 °C). Between 2009 and 2020 soil frost occurred at a nearby experiment site (Nummela) typically from mid-December to early April, in most years to a maximum depth exceeding 50 cm (Äijö et al., 2021). Crop rotation preceding the establishment of the experiment was as follows: 2002, spring barley; 2001, winter rye; 1997–2001, grassland, and 1996, spring wheat.

The two seed mixture treatments were a grass mixture (grass seed mixture) and a diverse nectar and pollen plant seed mixture (meadow seed mixture). The grass seed mixture included *Agrostis capillaris* L. and *Festuca ovina* L. The meadow seed mixture included, *A. capillaris* and *F. ovina* sown together with 12 nectar and pollen plant species (see Alanen et al., 2011 for further details) of which *Centaurea jacea* L. became the dominant species during the experiment. In both seed mixtures, there was some *Phleum pratense* L. as a contaminant. The third seed mixture was excluded in the present study because its species composition had developed over the experiment to resemble closely the grass seed mixture, and the number of sample plots had to be limited because of the labor intensity of earthworm sampling. The mowing treatment was either late summer mowing (conducted with a mower/-chopper annually between 28th August and 5th October; cuttings left on the field) or no mowing.

2.2. Sampling of earthworms

Three soil samples were taken from the central area of each experimental plot to establish earthworm content. The samples were positioned at the vertices of an equilateral triangle with 5 m sides. In a few plots, the sampling area was moved slightly away from the plot center if the vegetation there was highly unrepresentative of the treatment, for instance when only grasses were present in the meadow treatment.

Sampling was done on 12th–24th September 2018, before autumn mowing. The sampling proceeded block by block to avoid possible bias caused by earthworm activity changes over the field work period. The soil temperature at 5 cm depth ranged between + 8 and + 12.5 °C, based on daily readings next to the sampling sites. Soil moisture content was measured at 0–15 cm depth, next to each sampling pit on the day of sampling (TDR; Trase System, Model no. 6050 ×1 Soilmoisture Equipment Corporation, Santa Barbara, California, USA). The median soil moisture content was 33% (range 21–39%). The topsoil conditions during the sampling were thus favorable for earthworm activity and effective earthworm sampling.

Earthworms were sampled with combined hand sorting and AITC (mustard-oil) extraction (ISO 23611–1, 2018), with small modifications (Nuutinen, 2019). A soil sample of 25 cm × 25 cm and a depth of 20 cm was taken with a spade and placed on a white sheet. The sample was taken so that one of its vertical surfaces remained unbroken. The surface was photographed prior to the hand sorting to document earthworm activity-related differences, particularly in the litter layer. Earthworms were hand sorted from the samples. Simultaneously with the hand sorting, AITC liquid was poured into the bottom of the pit to obtain deep burrowing *Lumbricus terrestris* L. The extraction was continued for 25 min, adding liquid according to its infiltration rate. The total volume applied was typically close to 5 L. During the hand sorting and chemical extraction, the earthworms were collected in cool tap water and then stored in 4% formalin.

After storage of 17 weeks in formalin, the samples were transferred to 70% ethanol. All specimens were subsequently weighed, identified to species or genus level (Sims and Gerard, 1999) and their developmental stage recorded (juveniles, sub-adults, adults). Of incomplete specimens only head sections were used in the estimation of earthworm total density. All specimens were used in biomass estimation. For unit area total density and mass estimates, the hand sorting and chemical extraction samples were combined, and the total value multiplied by sixteen. The mean of the three samples for each plot was used in the statistical analyses. When only juveniles of a given earthworm genus were present, the genus was included as one species in the calculation of species richness. To compare the ecological group composition of the treatments, the species were combined into endogeic (all *Aporrectodea*) and epigeic + epi-anecic (all *Lumbricus*) groups and their proportions of all individuals calculated based on the combined three samples from each plot.

2.3. Sampling of other taxa

The sampling of plants and pollinators was conducted in the growing season of 2018 by following the procedures described in Alanen et al. (2011). The plant sampling was conducted by recording all the plant species in each experimental plot and by estimating their coverage by species as a percentage of the area of the entire plot (50 × 50 m) using a nine-step scale: $1 = x < 0.125\%$, $2 = 0.125\% < x < 0.5\%$, $3 = 0.5\% < x < 2\%$, $4 = 2\% < x < 4\%$, $5 = 4\% < x < 8\%$, $6 = 8\% < x < 16\%$, $7 = 16\% < x < 32\%$, $8 = 32\% < x < 64\%$ and $9 = x > 64\%$. Before statistical analyses, the classes used in the field were transformed into the mean coverage values for each class: 1 = 0.0625%, 2 = 0.3125%, 3 = 1.25%, 4 = 3%, 5 = 6%, 6 = 12%, 7 = 24%, 8 = 48% and 9 = 82%. The sum of mean coverage values of all species was used as a measure of plant coverage for each experimental plot in the statistical analyses.

The sampling of pollinators (bumblebees, honeybee, butterflies and diurnal moths) was carried out using the standard line-transect method (Pollard and Yates, 1993). A 250 m transect passed through each experimental plot in a serpentine manner. A permanent route was walked at a steady speed and all individuals within a 5 × 5 m square ahead were recorded. The counts were carried out four times during the summer at approximately two-week intervals under weather conditions allowing insect activity (for minimum weather requirements, see Pollard and Yates, 1993), the first count being made in the first half of June and the last count at the end of July (See TableS1 for species list.). Flower visits of pollinators were also recorded. The sum of four counts was used as a measure of pollinator abundance in the statistical analyses.

Sampling of ground-dwelling insects was conducted by pitfall trapping. The traps consisted of plastic cups with a diameter of 9.5 cm and depth of 5.7 cm. The trapping liquid was concentrated NaCl liquid (300 g l^{-1}). Three pitfalls were placed in a line (at three meters distance) in the center of each experimental plot. Three one-week sampling periods were conducted in May–June, June–July and July–August, respectively. The trap catches were stored in 70% alcohol and thereafter sorted into families (Carabidae, Staphylinidae) or order (Araneae) and their numbers were calculated, and their pooled abundances were used as a measure of biological control ecosystem service.

2.4. Soil sampling and analyses

Soil samples were taken in May 2019 with 20 cm slotted steel cylinders that were hammered to 18.5 cm depth under relatively dry conditions to avoid compaction. The soil cores were divided into four layers (at 0–2.5, 2.5–5, 5–10 and 10–18.5 cm depths) that were analyzed separately. Laboratory analyses were done on one soil sample per plot and a given depth, each sample being combined from 6 to 9 subsamples. Chemical soil testing involved agronomic soil test phosphorus (P-Ac) according to the national Finnish method described in Vuorinen and Mäkitie (1955); ammonium acetate at pH 4.65 extracts readily soluble soil P in similar amounts as deionized water at 1:60 soil-to-solution ratio. Total soil C and N were analyzed with a LECO CN-2000 analyzer (LECO corp., St. Joseph, MI, USA); the soil did not contain free $CaCO_3$ and total C content thus corresponds to organic C. Soil particle separates (percent content < 0.002 mm (clay), 0.002–0.006, 0.006–0.02, 0.2–0.6, 0.6–2, > 2 mm particles) were determined using a pipette method described in Elonen (1971).

2.5. Statistical analyses

We built a linear mixed model (LMM) separately for each response variable: natural enemies of pests (i.e. total abundance of spiders, carabids and staphylinids, and each of them separately); pollinators (i.e. total abundance of honeybees and bumblebees, and both of them separately, as well as species richness of bumblebees, butterflies and moths); earthworm density, mass and species richness; plant species richness and coverage all plants, dicots, grasses and *C. jacea*; soil variables (carbon, nitrogen, phosphorus and clay content). Coverages of all plants and *C. jacea* were log N + 1-transformed before the analyses due to non-normal data distribution. All presented estimates were transformed back to the original scale. Statistical modeling was based on a strip plot experimental design. Seed mixture, mowing and interaction of seed mixture and mowing were included as fixed explanatory factors and the replicate block (n = 4) and its interaction with seed mixture and mowing as random factors in the LMMs. In addition, two pairwise comparisons were included: comparison between grass and meadow seed mixtures under non-mowing treatment and the same comparison under mowing treatment. Analyses were performed using the SAS/PROC MIXED or SAS/PROC GLIMMIX procedures.

3. Results

3.1. Belowground biodiversity and soil properties

Earthworm variables responded to both interaction between mowing and seed mixture (density and species richness) and mowing alone (biomass) (Table 1). Total density differed significantly between seed mixtures in mown but not in non-mown treatments (Fig. 1a). The non-mown meadow treatment supported the highest earthworm density while the lowest density occurred in the mown meadow. Regarding earthworm mass, the significant main effect of mowing indicated higher biomass in non-mowed treatments, mainly because of the very low mass recovered from mowed meadow (Fig. S2). Earthworm species richness was greatest in the non-mown meadow treatment and it differed significantly from the lowest richness in the mown meadow (Fig. 1b). In the grass seed mixture, the mowing had no discernible effect on earthworm richness. Altogether, five species, representing all three main ecological groups of earthworms, were present in the field (Table S2): endogeic *Aporrectodea caliginosa* and *A. rosea*, epigeic *Lumbricus rubellus* and L. *castaneus* and epi-anecic L. *terrestris*. A notable pattern in the distribution of adult individuals was the absence of litter-feeding (epigeic and epi-anecic) species from the mown meadow treatment (Table S2). There were no clear differences between the treatments in the age composition of the community: in the data pooled by the treatments the proportion of juvenile earthworms varied between 55%

Table 1

Effects of seed mixture and mowing and their interaction (F-values and the level of significance: ns=non-significant, °$p < 0.1$, *$p < 0.05$, **$p < 0.01$) on studied variables and estimates of least square means and 95% confidence limits (in parentheses) for each treatment. Degrees of freedom: Num DF= 1, Den DF= 3 for all except earthworm species richness Num DF= 1 Den DF= 6.

	Effect			Estimates of LSM by treatments			
	Seed mixture	Mowing	Seed mixture × Mowing	Grass	Meadow	Non-mown	Mown
BELOWGROUND							
Earthworm density	0.4 ^{ns}	19.9*	17.7*	178.8 (108.8, 248.7)	162.3 (92.3, 232.2)	234.6 (160.9, 308.3)	106.4 (32.7, 180.1)
Earthworm biomass	3.6 ^{ns}	22.6*	5.5 ^{ns}	102.5 (51.9, 153.2)	67.0 (16.3, 117.6)	121.0 (73.2, 168.8)	48.5 (0.67, 96.3)
Earthworm species richness	1.0 ^{ns}	4.2 ^{ns}	81.0***	2.9 (2.2, 3.6)	3.0 (2.3, 3.7)	3.4 (2.4, 4.3)	2.5 (1.5, 3.5)
Soil clay content (%)	0.3 ^{ns}	9.86°	1.8 ^{ns}	40.3 (32.3, 48.2)	42.1 (34.2, 50.1)	37.3 (30.2, 44.3)	45.1 (38.1, 52.2)
Soil phosphorus (0–2.5 cm)	33.6*	0.4 ^{ns}	8.4°	19.9 (14.8, 25.0)	16.4 (11.3, 21.5)	18.6 (13.0, 24.2)	17.6 (12.0, 23.2)
Soil phosphorus (2.5–5 cm)[1])	21.1*	0.2 ^{ns}	0 ^{ns}	13.6 (10.0, 17.3)	10.6 (6.9, 14.3)	12.5 (8.0, 17.0)	11.7 (7.2, 16.1)
Soil carbon (0–2.5 cm)[2])	0.1 ^{ns}	33.2*	3.3 ^{ns}	5.0 (3.9, 6.1)	4.9 (3.8, 6.0)	4.5 (3.4, 5.6)	5.4 (4.4, 6.5)
Soil nitrogen (0–2.5 cm)[2])	0.4 ^{ns}	90.0**	0.4 ^{ns}	0.4 (0.28, 0.43)	0.3 (0.27, 0.42)	0.3 (0.24, 0.38)	0.4 (0.31, 0.46)
ABOVEGROUND							
Plant species richness	3.8 ^{ns}	12.8 *	3.2 ^{ns}	23.6 (19.7, 27.5)	26.1 (22.2, 30.0)	23.6 (20.2, 27.1)	26.1 (22.7, 29.6)
Plant coverage	0.8 ^{ns}	0.22 ^{ns}	0.04 ^{ns}	95.4 (47.8, 189.6)	123.6 (62.0, 245.3)	103.9 (57.1, 188.4)	113.6 (62.5, 205.9)
Dicot coverage	10.0°	0.3 ^{ns}	2.9 ^{ns}	34.8 (4.0, 65.6)	77.2 (46.4, 108.0)	52.1 (20.8, 83.5)	59.9 (28.6, 91.2)
Grass coverage	1.2 ^{ns}	0.3 ^{ns}	0.8 ^{ns}	81.1 (4.3, 157.8)	47.7 (−29.1, 124.5)	70.0 (1.3, 138.7)	58.7 (−10.0, 127.4)
Centaurea jacea coverage	73.8**	7.7°	4.7 ^{ns}	1.6 (0.1, 5.1)	49.5 (20.4, 117.9)	6.2 (2.1, 15.8)	17.3 (6.8, 41.8)
Pollinator species richness	3.1 ^{ns}	6.9°	0.5 ^{ns}	19.9 (15.8, 23.9)	22.9 (18.8, 26.9)	19.3 (15.3, 23.2)	23.5 (19.5, 27.5)
Bumblebee species richness	13.1*	2.1 ^{ns}	0.7 ^{ns}	3.8 (1.8, 5.7)	6.0 (4.0, 8.0)	4.1 (1.8, 6.5)	5.6 (3.3, 8.0)
Butterfly species richness	0.1 ^{ns}	15.0*	0.1 ^{ns}	5.3 (2.9, 7.6)	5.6 (3.2, 8.0)	4.4 (2.5, 6.3)	6.5 (4.6, 8.4)
Moth species richness	0.1 ^{ns}	0.5 ^{ns}	0 ^{ns}	9.6 (7.4, 11.8)	9.9 (7.7, 12.1)	9.4 (7.0, 11.8)	10.1 (7.7, 12.5)
Pollinator abundance	6.8°	4.8 ^{ns}	2.2 ^{ns}	37.1 (−54.7, 128.9)	127.6 (35.8, 219.4)	56.0 (−26.9, 138.9)	108.8 (25.9, 191.6)
Bumblebee abundance	2.8 ^{ns}	0.3 ^{ns}	1.0 ^{ns}	11.0 (−0.4, 22.4)	19.5 (8.1, 30.9)	14.0 (2.6, 25.4)	16.5 (5.1, 27.9)
Honeybee abundance	7.5°	4.5 ^{ns}	2.9 ^{ns}	26.1 (−60.4, 112.7)	108.1 (21.6, 194.7)	42.0 (−39.4, 123.4)	92.3 (10.8, 173.7)
Natural enemy abundance	4.5 ^{ns}	2.1 ^{ns}	0 ^{ns}	138.0 (103.0, 173.0)	160.3 (125.3, 195.2)	135.1 (91.5, 178.6)	163.2 (119.6, 206.7)
Carabid abundance	9.4°	5.9°	0.3 ^{ns}	59.0 (25.5, 92.5)	89.0 (55.5, 122.5)	58.2 (22.0, 94.4)	89.8 (53.6, 126.0)
Staphylinid abundance	4.1 ^{ns}	0 ^{ns}	3.1 ^{ns}	15.8 (10.5, 21.2)	11.3 (6.0, 16.7)	13.6 (7.9, 19.3)	13.5 (7.9, 19.2)
Spider abundance	0.5 ^{ns}	0.3 ^{ns}	0.01 ^{ns}	63.2 (50.3, 76.2)	59.9 (46.9, 72.9)	63.3 (48.6, 77.9)	59.9 (45.2, 74.5)

[1])No significant differences were detected for the depths of 5–10 cm or 10–18 cm. [2])No significant differences were detected for the depths of 2.5–5 cm, 5–10 cm or 10–18 cm.

and 63%, with the lowest reading in non-mowed grass and highest in non-mowed meadow.

The topsoil in the mown meadow treatment often differed from that in the other treatments by having an uppermost darker layer with poorly decomposed plant litter (Fig. S3). In the topmost soil layer (0–2.5 cm), organic carbon and nitrogen contents were higher in mown than in non-mown treatments, while phosphorus content of the two upper layers (0–2.5 and 2.5–5 cm) was highest in the grass seed mixture (Table 1, Fig. 2a–c). In all plots, total C and N, and soil test P, concentrations were higher in the topmost soil layer than in deeper sampled layers (Fig. S1B). In the grass topmost layer, pH was similar in mowing treatments while in the meadow, pH was notably higher in the non-mown treatment, where pH was at its highest (Fig. 2d, Table 1).

3.2. *Aboveground biodiversity*

Total plant coverage did not differ between the treatments (Table 1, Fig. 1c), but the coverage of dicot species was higher in the mown meadow than in the mown grass seed mixture treatment ($F_{1,3}$ =11.8, $p = 0.041$). *C. jacea* was more abundant in the meadow than in the grass seed mixture in both mowing treatments (Fig. S4, Table 1). The lowest plant species richness was associated with the non-mown grass seed mixture treatment, while the other treatments did not differ from each other (Fig. 1d).

Abundance of natural enemies of pests did not show any significant differences between the treatments (Table 1, Fig. 1e). A marginally significant difference was found for carabids between mowing treatments. Carabid beetles were most abundant in the mown meadow seed mixture, differing significantly from abundance in the non-mown grass mixture (Fig. 1f).

Abundance of pollinators was marginally significantly different between the seed mixtures (Table 1). However, significantly higher abundances of pollinators (Fig. 1g) and honeybees (Fig. S5) were found from the mown meadow seed mixture than from the non-mown grass seed mixture. Honeybee comprised the majority of the pollinator observations. Total species richness of pollinators showed marginally significant difference between mowing treatments (Table 1, Fig. 1h). However, bumblebee species richness was affected by seed mixture; the highest species richness was found in the mown meadow seed mixture treatment, which differed from the mown (Fig. S6) and was marginally significantly from the non-mown ($p = 0.054$) grass mixture. Butterfly species richness was marginally significantly higher in the mown than in the non-mown treatments for both seed mixtures (grass: $p = 0.071$; meadow: $p = 0.054$) (Fig. S6).

4. Discussion

Our results indicated notable variation in the response of aboveground and belowground biodiversity and soil properties to seed mixture treatments. Furthermore, the differing impacts of mowing highlighted the importance of set-aside management in regulating the responses to seed mixtures.

We expected the meadow seed mixture and mowing in both seed mixtures to enhance species diversity and abundance, both aboveground and belowground, but this was not the case. Aboveground, no consistent effects were found for natural enemies, while the seed mixture was important for some pollinator variables. Belowground, seed mixture affected topsoil phosphorus accumulation. Mowing appeared to affect earthworm abundance and the concentration of carbon and nitrogen in the soil surface layer.

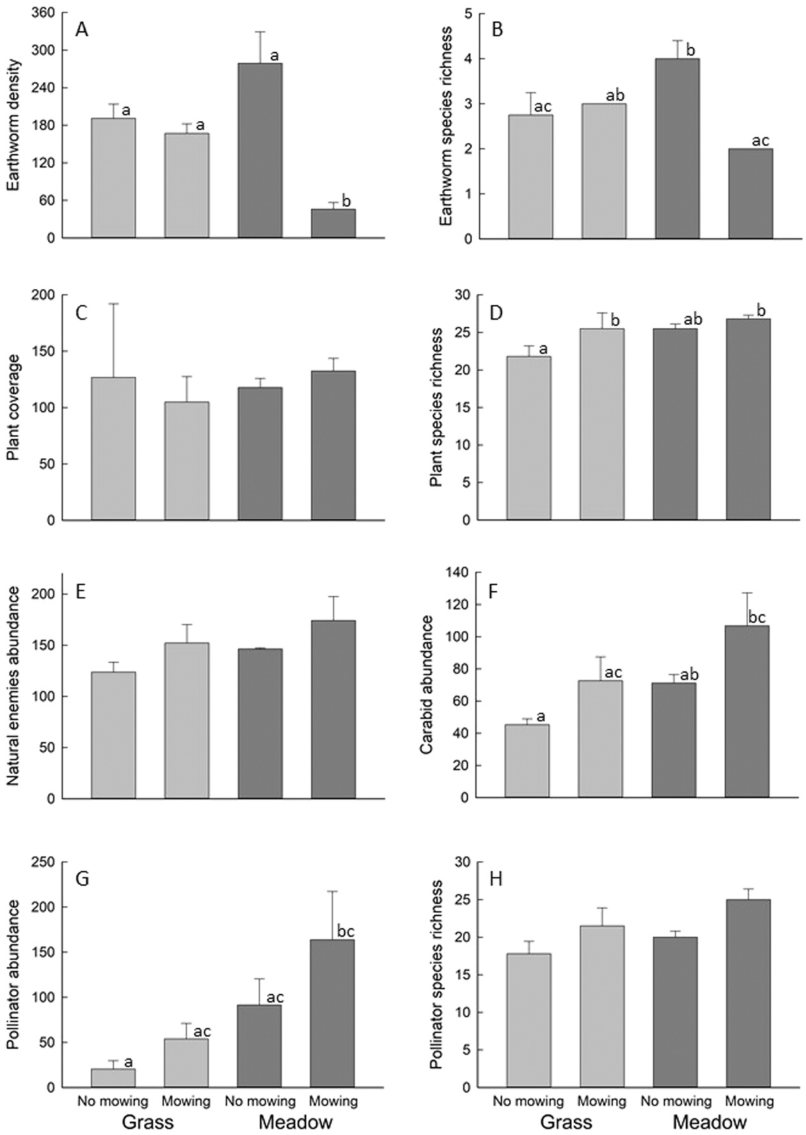

Fig. 1. Mean values (+SE) of belowground (earthworm density and earthworm species richness) aboveground (plant coverage, plant species richness, natural enemy abundance, carabid abundance, pollinator abundance and pollinator species richness) biodiversity variables in the treatments. Letters denote statistically significant differences between the treatments ($p < 0.05$, $N = 4$). Units for species richness and abundance variables are species or individuals per 0.25 ha experimental plot, expect for earthworm density (individuals per m^2) and for plant coverage (% of 0.25 ha experimental plot). See Materials and methods for data pooling an calculations of each variable.

4.1. Belowground biodiversity and soil properties

While the seed mixtures did not differ regarding plant species richness, they did differ by there being greater coverage of dicot plant species in the meadow treatment. This may have contributed to the relatively high earthworm density and diversity in non-mown meadow through production of litter with relatively high nutrient value and low lignin content compared with grass dominated swards (Edwards and Bohlen, 1996 and refs. therein). It is also possible that in the grass seed mixture the dense swards and root mats physically limited earthworm foraging and ultimately their population growth, as suggested by Eisenhauer et al. (2009). Although not studied here, the quality and quantity of cutting remnants may have resulted in differences in soil moisture and temperature regimes between seed mixtures (Yahdjian et al., 2007). Those differences would be reflected, for example, in the depth and length of frost, which are important factors that limit earthworm activity under local conditions.

No support was found for our expectation that mowing and leaving of the cuttings on the soil surface increased earthworm abundance or diversity by providing a rich food source, particularly for surface feeding epigeic and epi-anecic species. The finding that the lowest earthworm density, biomass and richness was associated with the mown meadow seed mixture was unexpected. One explanation for this could lie in the chemical characteristics of the litter of the dominant plant species, *C. jacea*, in the meadow seed mixture. It is, for instance, possible that the *Centaurea* cuttings are an unsuitable food resource for earthworms. The possibility of a negative chemical impact is underlined by some *Centaurea* species exhibiting strong allelopathy, which affects both plants and soil microbes (Hierro and Callaway, 2003; Vivanco et al., 2004). There is also evidence that herbivory increases extraction of allelopathic root exudates in *Centaurea* (Thelen et al., 2005) and an additional possibility is that mowing would similarly enhance the extraction. In our experiment, *C. jacea* was abundant also in the non-mown meadow seed mixture, but the putative negative effects of its litter on earthworms in that treatment may have been substantially lower. To our knowledge, the effects of allelopathy on earthworms has not been studied, and considering the known negative response of earthworms to plant secondary compounds (Wardle et al., 1998), and motivated by the present findings, closer investigation of allelopathic impacts of *Centaurea* on earthworms would be worthwhile.

The absence of adult surface-foraging earthworms in the mown meadow seed mixture could have lowered the level of bioturbation and incorporation of surface residues and this may explain the accumulation of an undecomposed litter layer in this treatment. A similar type of accumulation of litter was observed by Clements et al. (1991) after a 20-year absence of earthworms from grassland. As such, litter

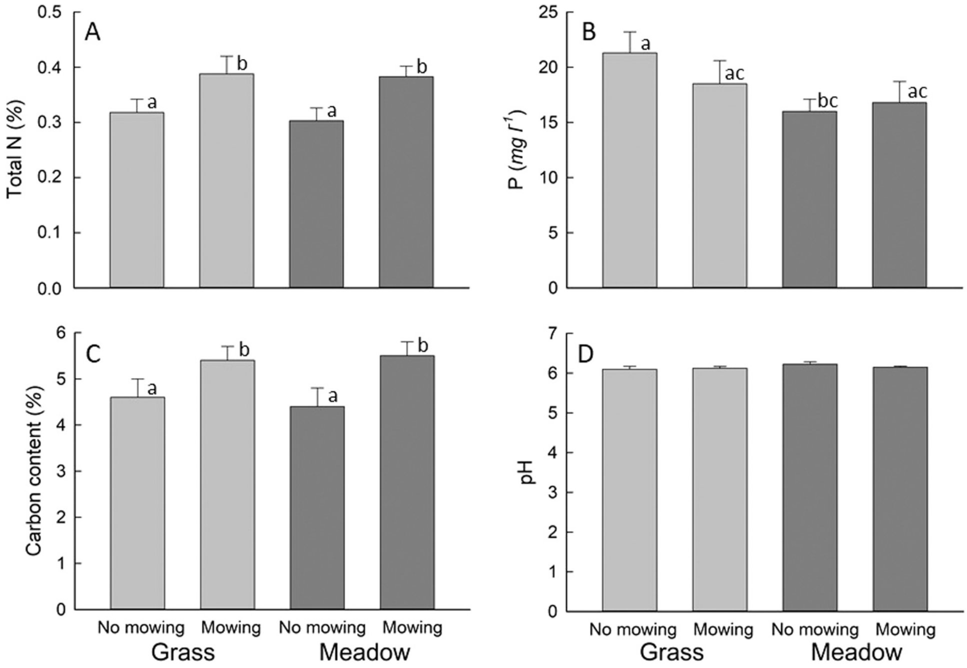

Fig. 2. Mean values (+SE) for soil variables (total N, P, carbon content and pH) in the treatments. Letters denote statistically significant differences between the treatments ($p < 0.05$, $N = 4$).

accumulation on the soil surface does not necessarily mean greater carbon accumulation within the whole soil profile (Luo et al., 2010), but the knowledge regarding carbon supply deeper in the soil by different plants as a separate factor is scarce. Because mixing of litter with mineral soil as a result of bioturbation likely increases the share of mineral-protected soil organic matter (Bossuyt et al., 2005; Sheehy et al., 2019) a more stable compartment than undecomposed litter, lower earthworm activity and less bioturbation may be coupled with lower stability of soil organic matter. The higher carbon and nitrogen contents recorded for mowed treatments may have been biased because of somewhat higher mean clay contents in mowed plots; increasing clay content is often associated with an increase in soil organic matter (e.g. Dexter et al., 2008, Feng et al., 2013).

4.2. *Aboveground biodiversity*

Established patterns of above ground biodiversity largely followed the earlier results from the initial six years of the experiment (Alanen et al., 2011; Hyvönen and Huusela-Veistola, 2011). Plant and butterfly species richness showed a positive response to mowing, which was contrary to earlier findings from the experiment but in accordance with findings from elsewhere (Bruppacher et al., 2016; Tälle et al., 2016, 2018). However, regarding plant species richness, the impact was a result of low species richness of non-mown grass mixtures compared with other treatments. Mowing was conducted late in autumn without removing the cuttings and the finding of a minor impact of mowing is in accordance with earlier findings where mowing without removing the cuttings was shown to be ineffective in increasing plant species richness (Tarmi et al., 2011). This is due to litter accumulation, also recorded in our mown treatments, which may prevent establishment of herb seedlings (Tilman, 1993; Foster and Gross, 1998).

While the differences in plant species richness between seed mixtures remained low, the coverage of *C. jacea* was higher in the meadow than in the grass seed mixture. *C. jacea* was the most abundant of the sown meadow species. It was also the most popular plant species among honeybees and bumblebees, representing 80% of the observed flower visits, and the positive association between *Centaurea* and bumblebees increased during the experiment (see Alanen et al., 2011 Appendix Table 1). The findings are in accordance with previous results of Korpela et al. (2013) from experimentally established wildflower strips in which *Centaurea* abundance was the best predictor of bumblebee abundance. The currently observed high level of persistence of *C. jacea* in its sown areas 15 years after its sowing demonstrates that it is a good choice in wildflower seed mixtures targeted at pollinators in strips that are kept in place for many years.

For butterfly species richness, mown treatments supported higher species richness than non-mown treatments in both seed mixtures (marginally significant difference). Previous studies have shown that mowing may have both negative and positive effects on butterflies, depending on the timing and other details of how mowing is conducted (Valtonen et al., 2006; Konvicka et al., 2008; Bruppacher et al., 2016). Overall, the management of our experimental set-aside field included two aspects that were previously reported to be positive for butterflies by Valtonen et al. (2006) and Bruppacher et al. (2016), namely late timing of mowing and leaving half of the experimental areas not mown. At the level of experimental treatments, our observation of a marginally positive effect of mowing on butterfly species richness might have been due to a generally positive effect of mowing on nectar plant richness and abundance (Tälle et al., 2018). It is notable that the approximately 20 grassland specialist butterfly and day-active moth species that colonized the experimental set-aside area during its first 6–9 years (Alanen et al., 2011; Kuussaari et al., 2014), were still present in the set-aside 15 years after its establishment. This suggests that long-term set-asides may provide significant habitats for numerous grassland Lepidoptera species.

Natural enemies of pests consisted of three species groups whose responses to the treatments were minor. Carabid beetles represented the only group which responded both to seed mixture and mowing (marginally significant response). Earlier, carabids did not respond to either treatment in the experiment (Huusela-Veistola, 2007) but showed significant annual variation in abundance. Earlier studies established clear impacts of seed mixture (Toivonen et al., 2018) and mowing (Moreby and Southwood, 2000) on carabids and spiders. Their abundance has been reported to be reduced by mowing (Moreby and Southwood, 2000) and the timing of mowing strengthens the impact (Morris, 1981). In our experiment, late mowing without removing the cuttings likely reduced the impact of mowing on natural enemies of pests.

4.3. Set-asides for multiple environmental goals

Our experiment has shown that set-aside sown with meadow seed mixture can support agrobiodiversity and maintain a high level of biodiversity. Regarding pollinators, the detected level of diversity was higher compared with that in arable fields (see also Steffan-Dewenter and Tscharntke, 1997; Kuussaari et al., 2011). The abundance and diversity of earthworms in this study were high for boreal arable fields, except for the low values associated with the mown meadow, possibly related to the specific nature of *Centaurea* litter. For instance, in a country wide arable field survey in Finland the mean density of earthworms was close to one hundred individuals per square meter and the mean richness two species (Nieminen et al., 2011). In general, the abundance and richness were close to those typically reported for uncultivated field margins where the values are often twice as high as inside the fields (Nieminen et al., 2011). Our results are therefore in line with many earlier findings on the favorability of grasslands for earthworms (e.g. Postma-Blaauw et al., 2010; Ponge et al., 2013).

In agro-environmental management, wildflowers are sown both in strips of various widths and larger field parcels. Pollinators have been shown to be able to colonize both types of landscape elements within a few years (Alanen et al., 2011; Korpela et al., 2013). The colonization of earthworms takes longer. It is likely that the length of time that our experiment had been established was sufficient to allow for the immigration and settlement of the initially absent earthworm species in all parts of the field. However, particularly in the case of epi-anecic *L. terrestris*, with measured rates of spread of only 4–5 m year^{-1} (Hoogerkamp et al., 1983; Nuutinen et al., 2011) one cannot rule out the possibility that the dispersal inside the field was ongoing. For the support of earthworm communities within a short-time scale, wildflower strips of a smaller size may therefore be more efficient than set-asides. The growth of earthworm population will often occur by recruitment from the indigenous community present in the field (Roarty and Schmidt, 2013). However, there is evidence that uncultivated, vegetated field margins can function as earthworm dispersal routes and source areas in agricultural fields when a species is initially absent (Nuutinen et al., 2011). Under such circumstances, placement of wildflower strips mid-field could support earthworm movement to fields.

The measures included in agri-environmental schemes are assumed to enhance several environmental goals in order to improve their cost-efficiency. Therefore, supporting biodiversity is not the only target but also other environmental goals, such as carbon sequestration and nutrient leaching, should be considered. Long-term set-aside is listed as a potentially efficient means of carbon sequestration (NASEM, 2019). However, in the short term, carbon enrichment of the topmost soil layer can only occur without detectable increase in the whole soil profile carbon sequestration (Luo et al., 2010, Heikkinen et al., 2021). Soil carbon measurements were not conducted at the beginning of our experiment, so we are unable to determine whether or not set-aside has changed the carbon content of the soil during the duration of the experiment. The current measurements, however, indicated that mowing treatments increased carbon accumulation in the uppermost topsoil layer. It remains an open question as to whether the management treatments applied in our experiment had any significant effect on carbon sequestration. In contrast, the recorded accumulation of phosphorus in the topsoil layer may increase the risk of leaching to watersheds (see Christianson et al., 2016). This risk could be reduced by removing the mowed cuttings, which is common practice in buffer zones in Finland (Uusi-Kämppä et al., 2000). Mowing and removing cuttings would also be expected to support plant and pollinator diversity (Bruppacher et al., 2016; Tälle et al., 2016, 2018), thereby further enhancing the role of set-asides as a multifunctional tool for reaching topical agri-environmental goals.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107656.

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