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Microarthropod communities and their ecosystem services restore when permanent grassland with mowing or low-intensity grazing is installed

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ABSTRACT

The current focus on intensification and maximizing productivity in agriculture can endanger soil biota and the ecosystem services they provide in such a way that it acts counterproductive and increases the dependence on external inputs. In this study, we aimed to identify the factors that are most limiting for the restoration of soil biota and their ecosystem services on sandy soils. To this end, we assessed microarthropod communities, their relationship with the aboveground food web and their effect on organic matter decomposition, in two land-use types: grasslands with agricultural land use and grasslands with nature land use. The latter are grasslands converted from agricultural land use, for the development of the Dutch National Ecological Network. For these land-use types, we took into account two main factors of disturbance: the number of years since the last tillage (i.e., plowing event), and the current grassland management (mowing or grazing). We found that the diversity of microarthropods was higher in nature grasslands than in agricultural grasslands. The abundance of microarthropods increased with time since last tillage for grasslands that were mown, but not for grasslands that were grazed. An agricultural grassland without tillage since 39 years had a microarthropod abundance similar to reference natural grasslands reported in previous research. The number of predatory beetles increased with a higher microarthropod abundance in mown grasslands, but not so in grazed grasslands. The number of fungivorous and herbofungivorous grazer microarthropods positively influenced the decomposition of soil organic matter as measured with the Tea Bag Index. Furthermore, we found a negative effect of Difenyl and total fungicide concentrations in the soil on (herbo)fungivorous grazers. Contrary to our expectations, we found more pesticide residues in nature grasslands than in agricultural grasslands. In conclusion, to restore the soil microarthropods and the ecosystem services they contribute to, the best practice is to strive for permanent grassland (without tillage) with mowing or low-intensity grazing (without compaction of the topsoil).

1. Introduction

To sustain the economic viability of agriculture, there is an increased focus on cost reduction through the intensification of agricultural production. This process of intensification conflicts not only with the management and conservation of belowground and aboveground biodiversity, but also with biodiversity-related long-term ecosystem services (Siepel, 2018; WNF, 2015; EEA, 2015; Hallmann et al., 2017). Therefore, the focus on intensification and maximizing productivity may endanger different ecosystem services, leading to an increased dependence on external inputs such as fertilizers and pesticides (Erisman et al., 2015; Foley et al., 2005; Geiger et al., 2010; Buckwell et al., 2014). To restore the balance between food production, biodiversity and related ecosystem services, there is a development towards sustainable agricultural systems which include organic, nature-inclusive, regenerative and circular farming (Erisman et al., 2016; LNV, 2018; EU, 2020; Schreefel et al., 2020). However, there are major knowledge gaps concerning the direction and speed of restoration of belowground and aboveground biodiversity of grasslands on presently or previously intensively used agricultural fields.

Soil microarthropods can be important indicator species for regeneration, and they can be used to study the effects of both agricultural

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extensification and management practices on biodiversity and related ecosystem services. Soil microarthropods form a large and species-rich group of the soil biota, with a function in aboveground biodiversity as food source for the aboveground food web. They are prey for larvae and adults of a range of aboveground macrofauna, including ground beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneida) (e.g., Siepel et al., 1989). Predator-prey interactions are a critical component of ecosystems, shaping both belowground and aboveground food webs. Grassland ecosystems are regulated by both bottom-up and top-down effects. Top-down regulation may affect the speed of decomposition as the fungivorous grazers among the microarthropods, which facilitate the decomposition of fungi, are kept at a lower population level; however, in a bottom-up regulation, these microarthropod densities are a function of food quality and abundance. Continuous removal of the vegetation by grazing creates a warmer microclimate in the topsoil, which is favourable for organisms of increasing body size and hence increasing development time. Thus, larger predators will have an advantage here compared to smaller prey in terms of development and population density, making top-down control more likely. This is why elucidating the relative strength of top-down and bottom-up forces in complex and tight interactions between belowground and aboveground biota has been a major focus of research on grassland ecosystems. Currently, there is consensus that both of these play a role (Denno et al., 2003; Lenoir et al., 2007); however, it is not yet clear whether these processes affect predator-prey dynamics involving soil microarthropods differently, what factors underlie this potential variation, and how they influence ecosystem services.

Besides their importance for biodiversity, microarthropods are important for soil ecosystem services. Microarthropods play a role in the decomposition of organic matter and in nutrient recycling (Bruckner, 1998; Kautz et al., 2006). More specifically, Siepel and Maaskamp (1994) suggest that different feeding guilds of microarthropods have specific roles in these processes: both fungivorous and herbofungivorous grazers have a stimulating effect on microbial respiration, while fungivorous browsers and opportunistic herbofungivores have an inhibiting effect. The stimulating effect that the (herbo)fungivorous grazers (i.e. the sum of fungivorous and herbofungivorous grazers) have on microbial respiration could be of importance for organic, regenerative and circular farming systems with a reduced use of external inputs. It is therefore essential to take factors into account that might limit soil microarthropod abundance.

In addition to fertilization and disturbance, pesticide residues could play a role. In recent decades, the widespread use of pesticides in combination with high soil persistence and toxicity of the residue has resulted in soil contamination. A study by Silva et al. (2019) found one or more pesticide residues in 83% of the 317 tested agricultural soils. Buijs and Mantingh (2019; 2020) detected pesticide residues in agricultural and natural soils which had previously been used for agriculture. Non-target microarthropod populations may decline in the presence of pesticide residues, especially in sandy soils; nevertheless, toxicity or resistance has been found to vary among microarthropod species (Joy and Chakravorty, 1991; Siepel, 1995; Chelinho et al., 2014).

Soil microarthropods have been widely used to study the effect of differences in land use (Sousa et al., 2004; Parisi et al., 2005; Minor and Cianciolo, 2007). In a soil biology monitoring program throughout the Netherlands, Rutgers et al. (2009) showed a gradient of abundance of microarthropods on sandy soils from arable land to dairy grasslands to semi-natural grasslands. In an explorative study, Siepel (2018) found a 90% lower abundance of microarthropods in current agricultural soils on sandy soils (both grassland and arable land) compared to a reference of less intensively used semi-natural grasslands (mown twice a year, density around 200,000 individuals m^{-2}), whereas unmanaged natural grasslands showed even higher densities (>300,000 individuals m^{-2}). In addition to land-use intensity (agriculture versus nature), soil disturbance by tillage and grazing can also negatively affect the abundance of microarthropods (Siepel and van de Bund, 1988; Siepel, 1996a; Kinneara and Tongway, 2004; Gulvik et al., 2007; de Groot et al., 2016).

In order to identify the factors that limit the restoration of soil biota and their ecosystem services in grasslands on sandy soils, we studied 40 grasslands, 20 of which with agricultural land use and 20 with nature land use. The latter have been converted from agricultural land use, for the development of the Dutch National Ecological Network. Rather than labeling them as 'natural' sites, we use the term 'nature grasslands' to refer to these grasslands, so as to stress the current management. We considered two key factors related to disturbance: the number of years since the last tillage (i.e., plowing event) and the current grassland management (mowing versus grazing). We focused on microarthropods as indicators of soil biota and soil biodiversity, their relation to the aboveground food web, and their effect on soil organic matter decomposition, which is an ecosystem service. We hypothesize that the abundance, species diversity, and functional diversity of microarthropods in grassland soils is higher under nature management than under agricultural management. Moreover, we expect that an increase in the number of years since last tillage results in increasingly higher microarthropod abundance, species diversity, and functionality. In addition, we expect that mowing has a less disrupting effect than grazing on soil microarthropod species diversity, abundance, and functionality. We expect more predators with agricultural land use due to higher productivity, and more predators in grazed grasslands as an example of top-down regulation, due to cattle-grazing by controlling the standing-crop. Related to ecosystem services, we expect an increase in the decomposition of recalcitrant organic matter when (herbo)fungivorous grazers are stimulated. As there is a history of former arable cropping on the nature grasslands and incidental use of herbicides on the agricultural sites, we expect to detect pesticide residues, but in low concentrations that do not affect soil microarthropod abundance and diversity.

2. Materials and methods

2.1. Site selection

We selected 40 grasslands: 20 agricultural grasslands and 20 nature grasslands which were managed as nature reserves since last tillage. The agricultural grasslands were fertilized with slurry manure and artificial fertilizer, with amounts varying between 300 and 495 available N ha^{-1}. The nature grasslands were not fertilized (Table 1). For each of these two land-use types, two different kinds of grassland management were used: mowing and grazing. The number of cuts on agricultural grasslands under mowing management varied between 3 and 6 cuts per year, while for nature grasslands under mowing management this was only 2 cuts. Agricultural grasslands under grazing management were cut 1–4 times, in combination with grazing management. Nature grasslands under grazing management were only grazed. Of each of the four combinations of land use and management, we selected ten grasslands with a wide range of years since last tillage; this range varied from 4 to 70 years. The locations of the selected grasslands sites were in the Veluwe region in a 10 km radius around Terlet (latitude 52.0567241 and longitude 5.9405045). All grasslands were located on sandy soils (Typic Haploquod and Plaggeptic Haploquod; Soil Survey Staff, 1999) with a deep water table to rule out dispersal of soil fauna during waterlogging (Siepel, 1996b; Jabbour and Barbercheck, 2008).

2.2. Vegetation and insect surveys

In each grassland, we used a 5 × 5 m monitoring plot for plant cover surveys, insect and soil microarthropod sampling, and soil analyses (see Appendix A1). The vegetation surveys were carried out at the end of May and in early June of 2019, using the Braun-Blanquet method (Braun-Blanquet, 1932). In June 2019, soil-surface dwelling insects were sampled with pitfall traps (Wiggers et al., 2015). To this end, three pitfall traps (8 cm diameter, ca. 20 cm deep) were placed in each plot.

Table 1
Results of the different parameters measured for each land use (agriculture or nature) and management (mowing or grazing) combination. Means, and standard deviations between brackets, of the 10 sites of each combination are given. Per parameter different letters indicate significant difference according to post-hoc Tukey tests ($P < 0.05$).

		Agriculture		Nature	
Parameter	Unit	Mowing	Grazing	Mowing	Grazing
Years since last tillage event		17 (21)[a]	15 (15)[a]	22 (15)[a]	21 (10)[a]
Fertilization level	kg Available N ha^{-1}	406 (73)[a]	338 (35)[a]	–	–
Number of cuts mown		4.6 (0.97)[c]	2.5 (0.85)[b]	2.0 (0)[b]	0[a]
Grazing days	LU days ha^{-1} yr^{-1}	–	624 (409)[b]	–	181 (332)[a]
N	mg 100 g^{-1}	2645 (442)[ab]	3294 (1164)[b]	2233 (832)[ab]	2115 (1013)[a]
P-Al	mg P_2O_5 100 g^{-1}	34 (19)[ab]	46 (21)[b]	25 (13)[a]	38 (15)[ab]
K	mg K kg^{-1}	89 (22)[b]	160 (74)[c]	34 (9)[a]	70 (39)[a]
pH		5.3 (0.3)[b]	5.3 (0.2)[b]	4.8 (0.3)[a]	4.8 (0.3)[a]
Organic matter	%	6.1 (1.0)[a]	6.9 (1.8)[a]	5.2 (1.4)[a]	6.1 (1.7)[a]
Clay	%	4.0 (2.1)[a]	3.7 (1.9)[a]	3.7 (2.4)[a]	2.0 (0.5)[a]
Plant species	Number 25 m^{-2}	6.0 (3.1)[a]	4.6 (1.3)[a]	11.3 (3.7)[b]	13.3 (5.2)[b]
Forb species	Number 25 m^{-2}	3.5 (3.0)[a]	2.0 (1.6)[a]	7.5 (3.0)[b]	10.2 (4.2)[b]
Springtails and mite individuals	Number m^{-2} (*1000)	85.5 (62.8)[a]	55.5 (30.8)[a]	103.0 (37.8)[a]	85.3 (43.5)[a]
Springtails and mite species	Number m^{-2}	28.3 (4.8)[a]	25.6 (4.5)[a]	36.1 (5.7)[b]	38.1 (8.7)[b]
Springtails and mites diversity	Shannon index	2.6 (0.2)[ab]	2.3 (0.2)[a]	2.7 (0.2)[b]	2.8 (0.3)[b]
(Herbo)fungivorous grazers	Number m^{-2} (*1000)	8.8 (15.3)[ab]	1.0 (1.8)[a]	21.7 (11.3)[b]	17.0 (25.0)[ab]
Insects in pitfall traps	Number	393 (179)[a]	591 (170)[a]	401 (138)[a]	576 (225)[a]
Predators (including spiders)	Number	314 (131)[a]	506 (154)[b]	232 (123)[a]	391 (197)[ab]
Decomposition rate		0.022 (0.009)[b]	0.017 (0.006)[ab]	0.013 (0.003)[a]	0.013 (0.002)[a]
Litter stabilization factor		0.165 (0.053)[a]	0.185 (0.038)[a]	0.152 (0.033)[a]	0.171 (0.026)[a]
Pesticides	Number	2.3 (1.8)[a]	2.3 (2.1)[a]	1.5 (1.1)[a]	4.8 (2.5)[b]
Avicides	μg kg dm^{-1}	2.0 (2.6)[a]	1.4 (2.3)[a]	2.1 (1.9)[a]	3.6 (1.5)[a]
Fungicides	μg kg dm^{-1}	4.2 (4.7)[a]	23.6 (46.4)[a]	3.4 (5.4)[a]	32.7 (73.4)[a]
Insecticides	μg kg dm^{-1}	0.0 (0.0)[a]	11.9 (21.2)[a]	2.4 (5.2)[a]	51.7 (34.9)[b]
Herbicides	μg kg dm^{-1}	4.8 (8.3)[a]	0.2 (0.6)[a]	0.3 (0.9)[a]	0.7 (1.2)[a]
Pesticides	μg kg dm^{-1}	11.0 (11.7)[a]	37.1 (47.5)[ab]	8.3 (8.2)[a]	88.7 (80.4)[b]

The traps were half filled with a solution of water and glycol (3:1) and 3% Extran soap. A plexiglass cover 20 cm above the trap prevented rainfall diluting the liquid. The traps were removed and emptied after seven days. Insects were identified and grouped at the order level, but predator groups (carabid and staphylinid beetles, ants and spiders) were identified to the species level in order to group them by their feeding guild. Carabidae larvae and adults were assigned as general predators, but without the tribes Zabrini and Harpalini (herbivores), and Staphylinidae, and without the subfamily Aleocharinae (fungivorous). Carabidae tribes Notiophilini and Loricerini were assigned as specialists in hunting and feeding on epigeic springtails. Ants were considered general predators, as were spiders, although in the latter group the Linyphiidae (s.l., thus including Erigonidae) were assigned as specialist in hunting and feeding springtails.

2.3. Soil chemical and pesticide sampling and analysis

On 8, 9, and 16 October 2019, a bulk soil sample of 50 soil cores (0–10 cm) was collected from each 5 × 5 m monitoring plot (see Appendix A1). After homogenization, a sub-sample was analyzed for soil-chemical parameters. Prior to this analysis, samples were oven-dried at 40 °C. Soil acidity of the oven-dried samples was measured in 1 M KCl (pH-KCl). Soil Organic Matter (SOM) was determined by loss-on-ignition (Ball, 1964). Ammonium-lactate-extractable P (PAL) was determined according to the standard method (Bronswijk et al., 2003). Total K in solution was determined using flame photometry after extraction of soil with HCl (0.1 M) and oxalic acid (0.5 M) in a 1:10 M:V ratio and filtration (Bronswijk et al., 2003). Clay (<2 μm diameter) content was determined through density fractionation (NEN 5753, 2018). Another soil sub-sample was sent to Eurofins Zeeuws-Vlaanderen for pesticide/residue analysis. All samples were freeze-dried and homogenized prior to analysis. Homogenized samples were extracted with acetone, petroleum ether and dichloro-methane, using an optimized mini-Luke method. A total of 664 pesticides and pesticide residues were analyzed with gas chromatography (Agilent) and liquid chromatography (LC-chromatograph (Agilent) and MSMS (Sciex)). Glyphosate, its residue AMPA and glufosinate were analyzed using single residue analysis. The detection limit (LOD) was 0.1 mg per kg sample.

2.4. Soil microarthropods sampling and determination

On 8, 9 and, 16 October 2019, grasslands were also sampled for microarthropods, taking three cores per 5 × 5 m monitoring plot (see Appendix A1). Cores were 5 cm in diameter and 5 cm deep mineral soil plus upper litter. Cores were taken from the middle of the monitoring plots, at 1 m distance from each other. Cores were extracted on a Tullgren funnel for 7 days. During this period, the temperature was increased from 35° to 45°C. Ethanol 70% was used as conservation fluid, and the microarthropods obtained were put into lactic acid 30% for clarification and identification (Siepel and van de Bund, 1988). Identification of the main groups was performed according to Weigmann (2006) for Oribatida, Karg (1993) for Gamasina, and Karg (1989) for Uropodina. Nomenclature was according to Siepel et al. (2009) for Oribatida, Siepel et al. (2016) for Astigmatina, and Siepel et al. (2018) for Mesostigmata.

2.5. Litter decomposition

To determine the potential decomposition of soil organic matter on each grassland, the Tea Bag Index (TBI) was used (Keuskamp et al., 2013). In each grassland, four Green tea and four Rooibos tea bags were buried at an 8 cm depth in the 5 × 5 m monitoring plots in May 2019 (see Appendix A1). After 90 days, the tea bags were collected and stored at 4 °C prior to drying at 70 °C for 48 h. After drying, any remaining sand and fine plant roots were carefully removed, and the teabags were weighed to determine weight loss. The decomposition rate (*k*) and the litter stabilization factor (*S*) were calculated using the Tea Bag Index (Keuskamp et al., 2013): $k = \ln(x)/t$ with t = number of days that the tea bags were buried and $x = ar/(Wt - (1 - ar))$ with $ar = Hr(1 - S)$ where $Hr = 0.552$ (the hydrolysable fraction of Rooibos tea), Wt = the fraction of Rooibos tea that remained (tea weight after 90 days/initial tea weight). $S = 1 - (ag/Hg)$ where ag = the fraction of green tea that decomposed (initial tea weight – tea weight after 90 days)/(initial tea weight) and Hg = 0.842 (the hydrolysable fraction of Green tea).

2.6. Data analysis

Principal component analysis (PCA) was used to explore the multivariate distribution of the abundance of microarthropod species across sites, using the *vegan* package in R (Oksanen et al., 2019). Counts were log-transformed after adding 1, and then normalized per species. Besides this species-level PCA, we also performed a PCA on counts per life-history strategy. We illustrated to what degree the sites with nature or agricultural land use were identifiable as separate clusters on the first two principal components. In the same way, we identified whether mown and grazed sites form distinct clusters.

For a wide variety of soil and soil life variables, we tested for differences in measured values between each of the four combinations of use (agriculture or nature) and management (mowing or grazing). A post-hoc Tukey was performed to test for statistical significance of differences, using the *glht* function of the Multcomp package (Hothorn et al., 2008).

The number of microarthropod individuals per site (sum of the three cores) was analyzed using negative-binomial generalized linear models (GLM, using the function *glm.nb* of the MASS package; Venables and Ripley, 2002) with three explanatory variables: the natural log of the years since the last plowing event, and the factors land use (agriculture or nature) and management (mowing or grazing). We fitted 19 models with all possible combinations of these three variables and all their two-way and three-way interactions, with the restriction that if an interaction was included, the model also contained the underlying interactions and main effects. We used the dredge function of the MuMIn package (Bartoń, 2020) to run the 19 models, and then selected the most parsimonious model (lowest AIC). The subset of fungivorous or herbo-fungivorous grazer microarthropods was analyzed in exactly the same way.

Before analyzing the pitfall trap catches, we first removed certain groups from the counts because pitfall traps are not well-suited to catch them systematically; these groups were Acari, Collembola, Psocoptera, Thysanoptera, Trichoptera, Lepidoptera, Siphonaptera, Diptera, Symphyta, Apocrita, and Parasitica. The remaining 62.0% of the individuals caught were surface-dwelling animals, and their totals (of the three pitfall traps per site) were analyzed with negative binomial GLM. We also analyzed the subset of predators (73.6% of the surface dwellers).

To test the hypothesized relationships between aboveground predators and belowground microarthropods, we analyzed (i) the number of sheet weavers (Linyphiidae s.l., including dwarf spiders Erigonidae) in pitfall traps as a function of the number of springtails (Collembola) in soil samples from the same site, as these spiders specifically hunt springtails (Harwood et al., 2001); similarly, we analyzed (ii) the sum of predatory ground and rove beetles (Carabidae and Staphylinidae, excluding herbivores and fungivores) as a function of total microarthropods, as these beetles prey on soil microarthropods (e.g., Pollet et al., 1989). In both cases we used a negative-binomial GLM, and explored interaction with land use and management.

The decomposition rate (k) and the litter stabilization factor (S), based on the weight loss of the buried tea bags, were analyzed with linear regression models. All data are archived in van Eekeren et al. (2021).

3. Results

3.1. Field site characteristics

The number of days that animals grazed ha^{-1} year^{-1} (calculated in Livestock Units (LU)) were higher for grazed agricultural grasslands than for the grazed nature grasslands (Table 1). On average, agricultural grasslands sites tended to have a higher soil nutrient level (significantly so for K, and also for certain combinations of management for N and P) than nature grasslands. Consistently, pH was lower in nature grasslands. Soil organic matter and clay content were not significantly different for the land-use types. Plant species richness, especially for forbs, was significantly higher on nature grasslands.

3.2. Microarthropod abundance, richness and diversity

A total of 19,759 soil microarthropods were caught and identified as belonging to 119 species. Higher numbers of microarthropods (mites and springtails) were caught in nature grasslands than in agricultural grasslands (but not significantly so, due to strong variation among grasslands; Table 1). The diversity of microarthropods was significantly higher on nature grasslands than on agricultural grasslands. Land use and management affected the species and guild abundance (see Appendix C1). The density of microarthropods increased with time since last tillage for grasslands that were mown, but not for grasslands that were grazed (Fig. 1a). Time since last tillage can be seen as the time to recover from large-scale disturbance of the soil. The positive relationship in mown grasslands with time since tillage holds both for grasslands with nature management and for grasslands in agricultural use (as permanent grassland). In the latter category, one grassland (without tillage since 39 years) had a microarthropod density within the range of reference natural grasslands surveyed in Siepel (1996a), which were located in the same area, on dry sandy soils.

We also investigated the subset of feeding guilds of microarthropods that have a positive influence on the decomposition of organic matter (Siepel and Maaskamp, 1994), i.e., the (herbo)fungivorous grazers. Nature grassland contained more (herbo)fungivorous grazers (significant for mown sites). Their abundance increased strongly with years

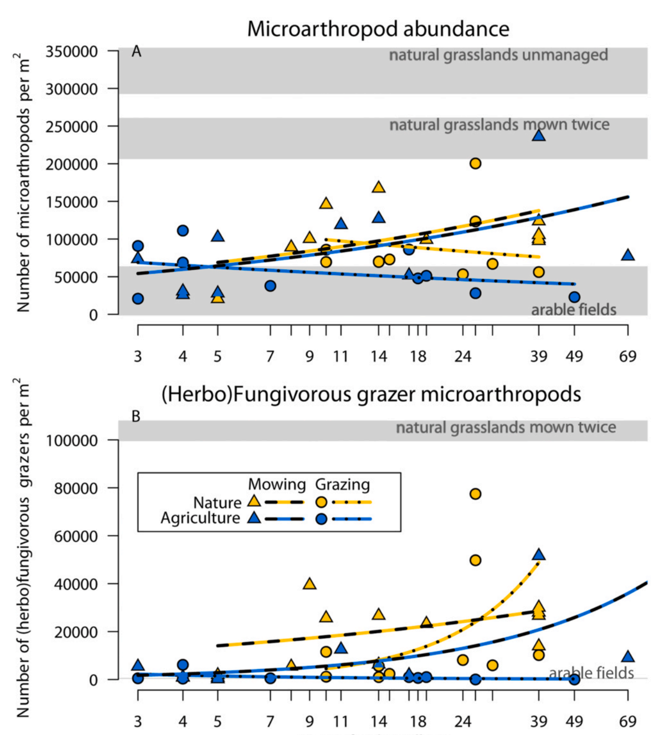

Fig. 1. A) Total number of soil microarthropods and B) number of (herbo) fungivorous grazer soil microarthropods found in each of the 40 grasslands, here extrapolated to 1 m^2 (5 cm deep). In mown grasslands, numbers increased with years since last tillage (note the ln-transformed axis), but not in grazed grasslands. Grey areas indicate reference values for arable fields and natural grasslands (either unmanaged or mown twice per year): mean ± standard deviation as found by Siepel (1996a). For details of the fitted models see Appendix B1 and B2.

since last tillage, especially on mown grasslands (Fig. 1b; interaction effect: $P < 0.01$). However, no site had densities high enough to be in the range of the densities in reference natural grasslands (Fig. 1b). The category of grazed grasslands with agricultural management remained at the level of the reference of arable land, while mown grasslands with agricultural management show a positive response to the number of years since last tillage. For grazed grasslands, we found a negative relationship between the number of grazing days per ha and the abundance of microarthropods (see Appendix C2). Classifying the microarthropods in drought-tolerant groups (Siepel, 1996b; Berg et al., 2004) showed clear differences among the sensitive and mesotolerant groups, which were significantly less abundant on grazed grasslands (23.0% agriculture and 16.7% nature) than on mown grasslands (30.9% agriculture and 31.1% nature)(Fig. 2).

3.3. Belowground and aboveground interactions

Split per grassland type, the number of predatory insects and spiders were lower on nature grasslands than on agricultural grasslands (312 ± 180, $z = -1.78$ vs 410 ± 170se, $P = 0.075$). Although not significant, more predatory insects were captured in pitfall traps on the grazed grasslands compared to the mown grasslands (Table 1). The number of predatory beetles and the number of soil microarthropods per grassland interacted with management (Fig. 3). On grazed grasslands, there was a negative correlation between the number of predatory beetles and the number of microarthropods: the higher the number of

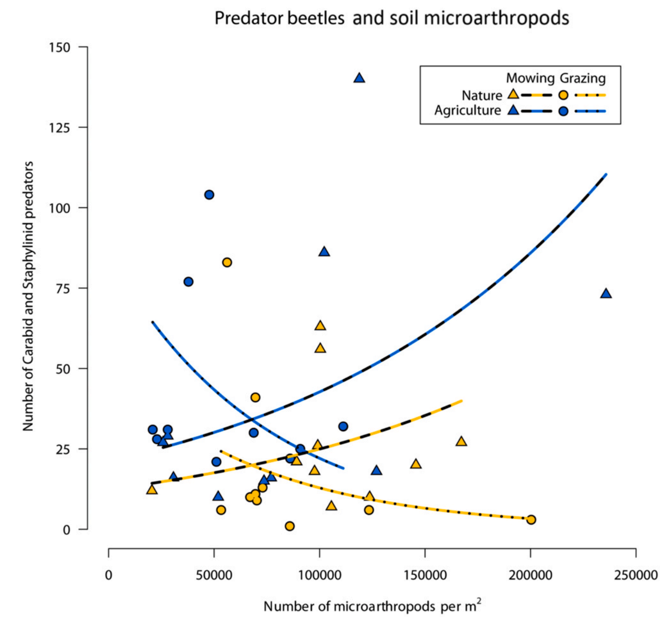

Fig. 3. Number of Carabid and Staphylinid beetles (predators only) in pitfall traps, as a function of the number of soil microarthropods in the same grasslands. For details of the fitted models see Appendix B4.

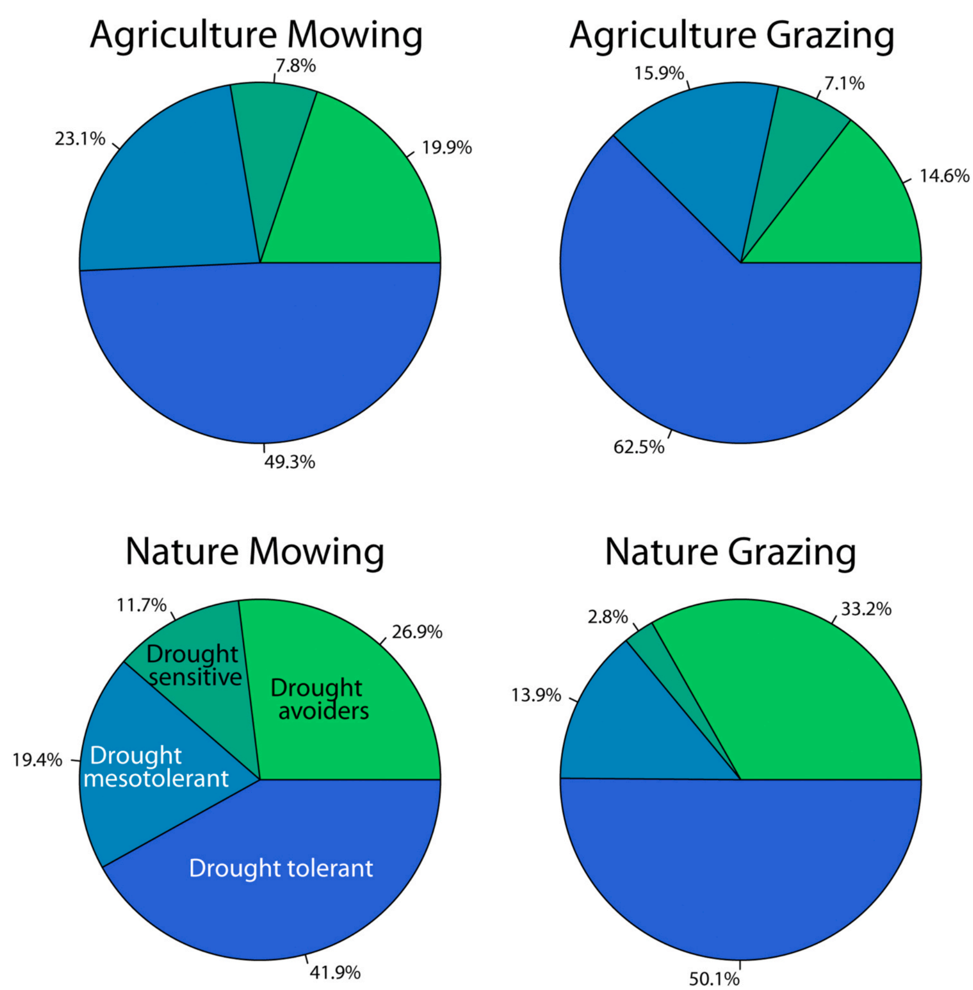

Fig. 2. Proportions of soil microarthropods that are categorized as being drought avoiders, drought sensitive, drought mesotolerant, or drought tolerant, in nature and agricultural grasslands that are either mown or grazed. Classification according to Siepel (1996b); Berg et al. (2004). All differences are significant (Chi-square tests, $P < 0.001$). For details of statistics see Appendix B3.

predatory beetles, the lower the number of microarthropods. On mown grasslands, the opposite was true: the higher the number of microarthropods, the higher the number of predatory beetles.

3.4. Potential effects on decomposition and carbon cycling

The TBI showed significant differences in decomposition rate (k) between grasslands with agricultural and grasslands with nature land use (Table 1). Thus, more easily metabolized organic matter was broken down in agricultural grasslands than in nature grasslands. Although not significant, average values of the litter stabilization factor (S; indicating decomposition of recalcitrant organic compounds) were higher in agricultural (S: 0.175) than in nature sites (S: 0.162). Within the different management types, mowing had a non-significant higher k but lower S (k: 0.0173; S: 0.158) than grazing (k: 0.0149; S: 0.178). The litter stabilization factor (S) decreased over time since last tillage (see Appendix C3). A subgroup within the microarthropods, the feeding guild of (herbo)fungivorous grazers can stimulate fungal growth by grazing hyphae. Thus, they can impact the decomposition rate and stabilization of carbon in the soil. There was a negative trend ($P = 0.05$) between the litter stabilization (S) and the number of (herbo)fungivorous grazers per site: the litter stabilization factor (S) decreased with higher numbers of (herbo)fungivorous grazers (Fig. 4).

3.5. Effect of pesticide residues

A significantly higher number and concentration of pesticides were found in soils of grazed grasslands with nature land use (Table 1). The concentrations of pesticides were higher with grazing than with mowing. The total amount of pesticide in the soil declined with the number of cuts. This decline was weaker in agricultural grasslands, but the total amount of pesticide was significantly lower in grasslands with nature management that were mown twice a year than in unmown grasslands (see Appendix C4). A total of 27 different pesticides or residues were detected. The main insecticides detected were Dieldrin, DDT, and its metabolites such as DDD. The main incidence of fungicides were Difenyl and Tetrahydrofthalimide. Only one avicide, Antraquinon, was found. Herbicides such as Chloropropham, 2_4-D 1, Fluroxypyr n1, and MCPA 1 were mainly found in agricultural grasslands. No glyphosate or metabolites like Ampa were detected in the soil samples analyzed. The incidence of the pesticides Difenyl and Antraquinon, which may also originate from bad combustion of fossil fuels, was tested in relation to the distance to the nearest highway or other national road. In the data set, 16 out of 40 locations had Difenyl concentrations above the detection limit, indicating that Difenyl concentrations were not higher closer to a highway or another national road (see Appendix C5). The concentration of Antraquinon, which was detected in 25 out of 40 locations, was significantly higher when a grassland was closer to a highway or another national road (see Appendix C6).

Concentrations of insecticides in the soil above their detection limit were found in 13 of the 40 grasslands. The abundance of soil microarthropods in general, and microarthropods with asexual reproduction in particular, and of aboveground predator rove and ground beetles were not significantly influenced by the cumulative soil insecticide concentrations. The abundance of (herbo)fungivorous grazer microarthropods was negatively influenced by both Difenyl (on 16 out of 40 locations) and the total fungicide concentration (on 25 of the 40 locations) in the soil (Fig. 5a and b). The decomposition rate and the litter stabilization factor of the TBI were not influenced by the concentrations of the different pesticides.

4. Discussion

4.1. Land-use effects and time since last tillage

Our goal was to study the effect of land use and land management on microarthropod communities and their function. In line with our hypotheses, we found a higher diversity of microarthropods in nature grasslands than in agricultural grasslands as well as an increase in abundance with mowing management over the years since last tillage. According to different studies, soil disturbance by tillage is the main cause of the decline in microarthropods, due to a redistribution of organic matter and changes in the temperature, humidity, and pore size

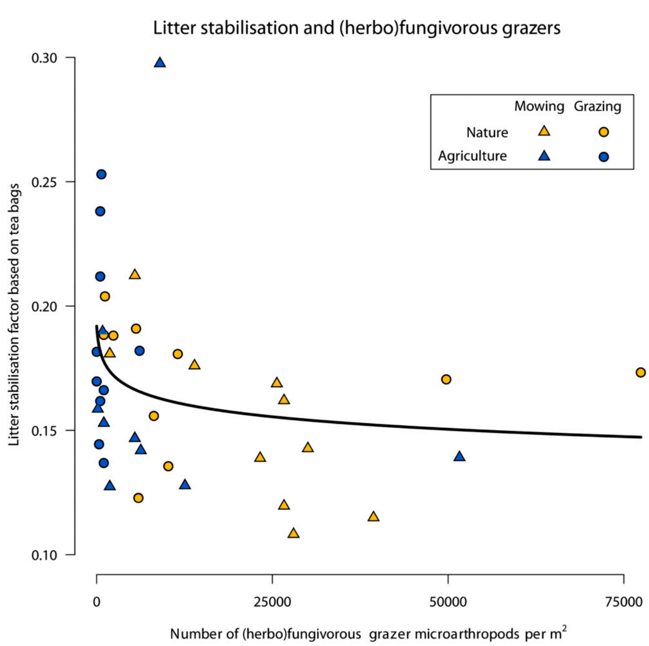

Fig. 4. Litter stabilization factor the based on Tea Bag Index, as a function of the number of (herbo)fungivorous grazer microarthropods. For details of the fitted model see Appendix B5.

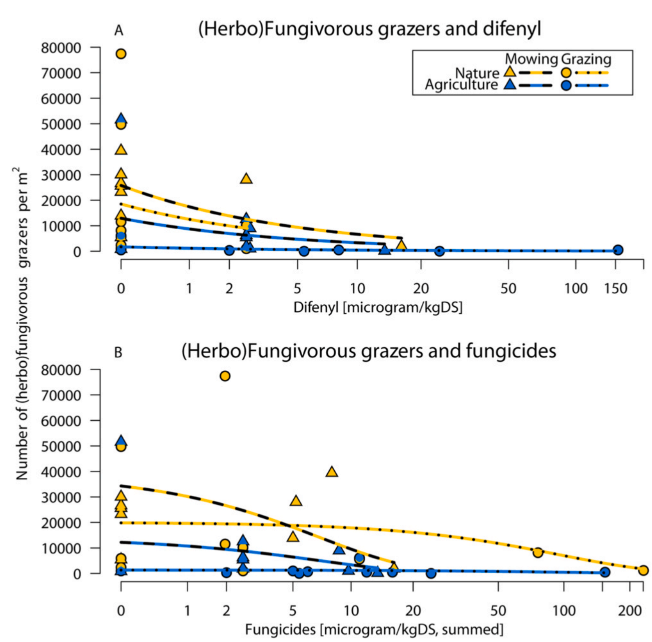

Fig. 5. Abundance of (herbo)fungivorous grazer soil microarthropods as a function of A. difenyl concentrations and B. total fungicides concentrations. Difenyl accounts for 39% of the fungicides sum. Difenyl had non-zero concentrations in 16 of the 40 sites. The sum of the other fungicides was non-zero in 15 sites. Difenyl and the sum of the other fungicides were not significantly correlated ($c = -0.065$, $P = 0.69$). For details of the fitted models see Appendix B6 and B7.

distribution in the microhabitat (Loring et al., 1981; Blevins et al., 1984; Perdue and Crossley, 1990). This suggests that time since last tillage could be an important factor explaining differences in microarthropod communities, including (herbo)fungivorous microarthropods. This view is also confirmed by one of the agricultural grasslands in our research, which had not been tilled since 39 years and which had a microarthropod density within the range of reference natural grasslands (Siepel, 1996a; Siepel, 2018). Other parts of the soil food web such as ectomycorrhizal fungi (EMF) and arbuscular mycorrhiza fungi (AMF) required 25–30 years (EMF, Boerner et al., 1996) or even 45 years (Roldan et al., 1997) for recovery. A study on 26 Dutch soils into the effect of land-use transition from arable to nature-managed grasslands on fungal biomass (van der Wal et al., 2006) and a study on a chronosequence on soil-food web interactions (Morriën et al., 2017) also selected soils from the Veluwe region. Both studies suggest that restoration of former arable land takes place in different stages and requires changes in abiotic soil properties and food web interactions (van der Wal et al., 2006; Morriën et al., 2017). This implies that our selected fields, of which 38 out of 40 were last plowed less than 40 years ago, could be still in the succession process; this may be one of the explanations why the numbers of microarthropods found in this study are lower than previously reported for reference natural grasslands (Siepel, 1996a, Siepel, 2018).

4.2. Management effects

Somewhat to our surprise, we saw consistent and striking differences in the total numbers both of microarthropods and of the feeding guilds of (herbo)fungivorous grazers, between management types and over time since last tillage. On mown grasslands, there was a positive relationship with time since last tillage, which shows a tendency of recovery towards the levels of reference natural grasslands. However, this relationship was absent or even negative in grazed grasslands, with a negative correlation between the abundance of microarthropods and the number of grazing days. This would imply that besides the number of years since last tillage, grazing is causing low microarthropod densities in the investigated grassland ecosystems. Starting with a plowed soil (no compaction), grazing and trampling tend to compact the upper layer of the soil (0–5 cm). This compaction of the topsoil and a change in pore size distribution make it difficult to enter deeper soil layers, at least for the larger species (diameter larger than 100 μm) (Siepel, 1996b). Species susceptible to desiccation in these grasslands must either be small to avoid desiccation by moving down in the profile or will disappear because avoidance is impossible due to their size. Thus, the combination of compaction in the upper layer with grazing and the microarthropods' susceptibility to desiccation could be the main explanation for the lower abundance of microarthropods on grazed grasslands on dry sandy soils. This is supported by our findings: when we compared the grazed and mown grasslands, it was especially the fractions of drought-intolerant and mesotolerant species that declined. There could also be a relationship with the accumulation of pesticides in grazed grasslands directly or indirectly (via the food-web) affecting the soil microarthropods; however, we could not establish this relationship in our study (see Sections 3.5 and 4.5). In contrast to grazing, mowing may result in a restoration of microarthropod density that nearly approaches the reference densities of natural grasslands mown twice a year, both in nature and in agricultural land use. This may be due to the limited disturbance, lower compaction of the upper soil layer, and an increase in organic matter input in permanent grassland than on arable farming land (Soussana et al., 2010). A higher abundance of soil microarthropods in soils with high organic matter content has been reported by Scheu and Schulz (1996). Furthermore, Gulvik et al. (2007) reported that different taxa of microarthropods correlate positively with the continuity of land use. They also report that a meadow site under management (mowing, hay removal and aftermath grazing with sheep) can have increased numbers of microarthropods.

4.3. Aboveground-belowground relationships

The restoration of belowground components of the ecosystem can be impacted by aboveground processes and biodiversity, including plant growth and insect diversity. Therefore, not only land-use and management choices should be considered in restoration projects, but also aboveground-belowground linkages (Kardol and Wardle, 2010). Grazing and mowing are the most common ways of grassland management (Tälle et al., 2016). We expected to find more predators in agricultural land use due to higher productivity, and more predators in grazed grasslands due to higher expected temperatures in more open vegetation. Our results corresponded with our expectation that on average larger predators are found more abundantly in grazed grassland, and in combination with lower densities of microarthropods. This is why we conclude here that grazed grasslands may have a top-down regulation, whereas mown grasslands have higher microarthropod densities and a lower density of predators, and may thus have a more bottom-up controlled system. Grazing affects the grassland ecosystem, including selective feeding on grassland plants. Conversely, grass or hay removal under mowing is not selective for plants, and may thus impact the plant diversity and the accumulation of litter (Beltman et al., 2003). Therefore, different grassland management methods affect the dominant control processes in the food web. In addition, other research has shown that top-down effects on insect abundance are known to exist both in grassland (Sanders and Platner, 2007) and in some arable land (Wilby and Orwin, 2013; Woodcock et al., 2016). However, there are similarly convincing examples of bottom-up effects on insect abundance both in grassland (Duffey, 1975; Ritchie, 2000) and in arable land (Hawes et al., 2009), thus leading to the conclusion that we may not be able to generalize by habitat. Our evidence for shifts from bottom-up control to top-down control thus indicates a potential mechanism accounting for the variation in soil fauna found with different types of grassland management. Moreover, given the recent reports of declines in arthropod biomass (e.g., Hallmann et al., 2017; Wepprich et al., 2019), understanding the ongoing regulation of insect populations with different types of grassland management takes on new importance.

4.4. Potential effects on decomposition and carbon cycling

As hypothesized, we measured a negative trend ($P = 0.05$) between litter stabilization (S) and the number of (herbo)fungivorous grazers, indicating a higher ability to break down recalcitrant organic material with a higher number of (herbo)fungivorous grazers. Moreover, we found that the average decomposition rate k, which determines the mass loss of soluble compounds (e.g., non-lignified cellulose and hemicellulose), was higher in agricultural sites, indicating that the turnover of easily degradable compounds is higher in agricultural grasslands. In general, the decomposition of litter is mainly controlled by biotic factors (Gavazov, 2010), as well as by temperature and moisture. Differences in decomposition between agriculture and nature might indicate that there are differences in soil biota that impact the carbon cycling in the two land-use types. This is supported by our finding that the number of (herbo)fungivorous grazers correlates with litter stabilization, and higher numbers of (herbo)fungivorous grazers in nature grasslands corresponds to lower organic matter stabilization. Research on agricultural grasslands in the north of the Netherlands also showed a negative correlation with the number of species of soil biota and the litter stabilization factor (Iepema et al., 2015). This is in line with the findings of Morriën et al. (2017), who concluded that in the process of restoration, soil networks become more connected, and subsequently the carbon uptake becomes more efficient. In addition, they also found an increase in fungivorous mites and a substantial shift in microbial consumers (Morriën et al., 2017). The review by Nielsen et al. (2011) summarizes that soil microarthropods stimulate soil decomposition, and that interactions between soil biota can change decomposition and carbon cycling.

4.5. Pesticides

Due to the history of former arable cropping in the nature grasslands and the incidental use of herbicides on the agricultural grasslands, we expected to detect pesticide residues. To our surprise, we found that the average concentration of pesticide residues was twice as high in nature grasslands as in agricultural grasslands, namely 48.5 and 24.1 μg kg dm^{-1}, respectively. Furthermore, in grazed nature grasslands, the average concentration was ten times higher than in mown nature grasslands (8.3 and 88.7 μg kg dm^{-1} for mowed and grazed grasslands, respectively). In the same Dutch province (Gelderland), Buys and Mantingh (2019; 2020) found very similar values in nature grasslands (an average of 46.1 μg kg dm^{-1}); however, in agricultural grasslands, they found an average of 64.8 μg kg dm^{-1} total pesticides in 2019, which might be partly due to a difference in soil type and sampling methodology.

We hypothesized to find low concentrations of pesticide residues that do not affect the soil microarthropod abundance and diversity. Indeed, we did not find an effect of pesticide residues on total abundance or diversity; however, we did find a negative effect of Difenyl and total fungicide concentrations in the soil on (herbo)fungivorous microarthropods, especially when concentrations increased. We could not find other effects of the pesticide concentrations measured on the microarthropods or aboveground insects. This may be partly due to low concentrations. However, although the total pesticide concentration did not significantly affect the number of microarthropods, specific compounds may still impact specific species and feeding guilds, directly or indirectly. For example, Siepel (1995) found a significant effect of DDT and its residues on asexually reproducing microarthropods in experimental fields. However, the DDT concentrations in these fields were about 40 times higher than found in our study.

Pesticide residues can contaminate the soil directly or indirectly, via recent or historical use on seeds, crops and animals, via manure, via irrigation of contaminated surface water, via use of pesticides on crops used for concentrates, and via chemical processes such as poor combustion of fossil fuels (Farrar et al., 2004; IARC, 2013; Lea-Langton et al., 2013). In our research, the presence of the persistent DDT (banned in the Netherlands since 1973) and its metabolites shows that historical use of pesticides can be an important source. This is in line with research in for example Germany (Hofmann et al., 2019). For Antraquinon, the relation with the distance to highways and other national roads (see Appendix C6) shows that traffic and poor combustion of fossil fuels may also be a source, in addition to historical use. The incidence of Difenyl could not be related with the distance to highways or other national roads, as was mentioned in studies by Farrar et al. (2004) and Lea-Langton et al. (2013).

Our study found that the amount of pesticide decreased with the number of cuts, which is a potential explanation for the higher pesticide concentrations in grazed nature grasslands. Thus phyto-extraction and phytoremediation (Pilon-Smits, 2005; Timmermans and van Eekeren, 2016)—via uptake of pesticides in the grass and subsequent removal by mowing—may well be an important route to reduce the accumulation of pesticides in the soil. The lower soil nutrient levels (P and K) in nature grasslands under mowing management compared to grazing support this route (Table 1).

5. Conclusions and implications for practice

The major objective of this research was to identify the factors that are most limiting for the restoration of soil life and their ecosystem services under grasslands on sandy soils with a low groundwater table. For soil microarthropods and their ecosystem, the best practice for regeneration is stopping the disturbance by tillage and compaction of the topsoil (0–5 cm), or in other words, striving for permanent grassland with mowing or low-intensity grazing management with minimal soil compaction (which depends on factors such as the choice of animal type, timing of grazing during the season, grazing system, and grazing efficiency etc. (Gulvik et al., 2007; Hoekstra et al., 2019; Schils et al., 2019). An additional possibility is the restoration of microarthropods via adjacent habitats to the grasslands, such as permanent grass strips or hedges, where there is less disturbance and from which microarthropods disperse over time (Siepel, 2015). Moreover, the restoration of specific microarthropods may be accelerated by species introduction through the application of topsoil and sod from late successional stages (de Groot et al., 2016). For certain ecosystems services (e.g., decomposition), it should be investigated whether there are other biota in the soil food web in the process of restoration that can take over the function of (herbo) fungivorous grazers. Iepema et al. (2015) have shown that the litter stabilization factor decreases with a higher number of species of biota, which suggests that other species can also break down recalcitrant organic matter. We linked total fungicide concentrations to reduced (herbo)fungivorous grazing microarthropods. Contamination with pesticides via different direct and indirect routes should be stopped, and routes of contamination should be further investigated. Phytoremediation and phyto-extraction via the uptake of pesticides in the grass and subsequent mowing is an important measure to reduce historical contamination.

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.2021.107682.

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Appendices

Appendix A. Additional information on Materials & Methods.

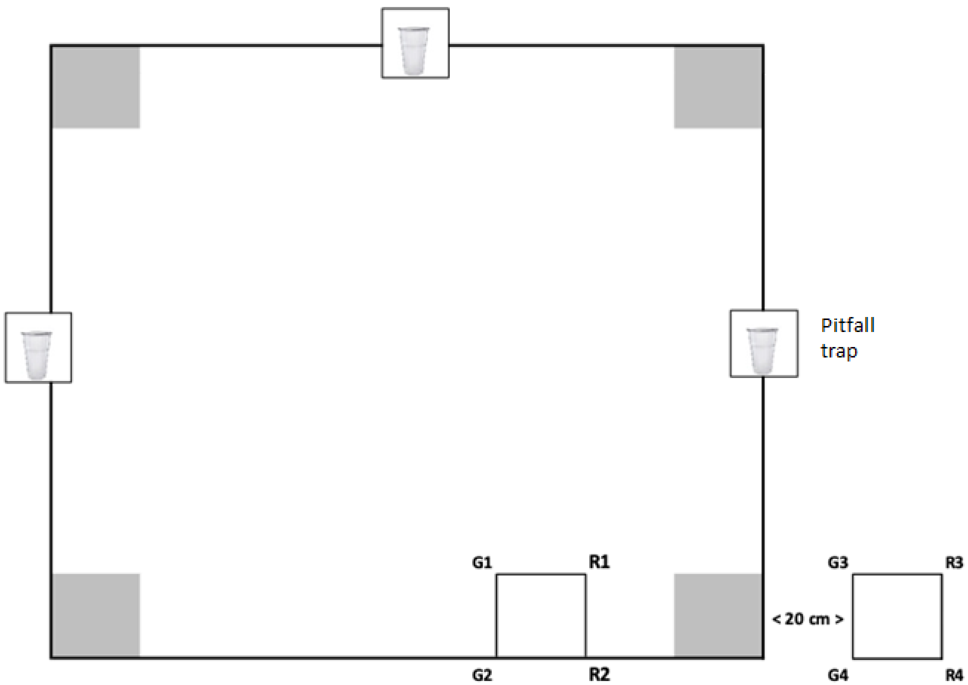

Figure A.1 Schematic overview of the 5 by 5 meter monitoring plot for insect and vegetation surveys, for decomposition measurements and soil and pesticide residue sampling.

Appendix B. Details of the statistical models plotted in the figures in the main text.

Table B.1 Selected (based on lowest AIC) model (negative binomial regression with log-link) for the total abundance of soil microarthropods in the soil samples per grassland (Fig. 1a in the main text).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	6.2184	0.3597	17.289	< 2e-16	***
Land use	0.5962	0.2345	2.542	0.01102	*
Management	-0.8224	0.4787	-1.718	0.08583	.
log(Years after last tillage)	-0.1931	0.1436	-1.345	0.17865	
Land use:Management	-0.5278	0.3247	-1.626	0.10402	
Management:Years after last tillage)	0.5300	0.1878	2.822	0.00478	**

Table B.2 Selected (based on lowest AIC) model (negative binomial regression with log-link) for the abundance of (herbo)fungivorous soil microarthropods in the soil samples per grassland (Fig. 1b in the main text).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	3.4849	0.8382	4.158	3.21e-05	***
Land use	-4.2383	2.1629	-1.960	0.050054	.
Management	-2.2021	1.1340	-1.942	0.052148	.
log(Years after last tillage)	-0.8195	0.3613	-2.268	0.023325	*
Land use:Management	6.8181	2.5795	2.643	0.008214	**
Land use:log(Years after last tillage)	2.5705	0.7622	3.373	0.000745	***
Management:log(Years after last tillage)	1.7814	0.4711	3.781	0.000156	***
Land use:Management:log(Years after last tillage)	-3.1874	0.9129	-3.492	0.000480	***

Tabel B.3 Differences in the distribution of individuals over four drought strategies (species were classified as drought avoiders, drought sensitive, drought mesotolerant or drought tolerant) were analyzed with Pearson's Chi-square tests (see Fig. 2 in the main text).

	Avoiders	**Sensitive**	**Mesotolerant**	**Tolerant**
Agriculture Mowing	989	387	1147	2453
Agriculture Grazing	473	230	515	2030
Nature Mowing	1632	710	1179	2542
Nature Grazing	1653	138	692	2496

X-squared = 939.85, df = 9, p-value < 2.2e-16

Mowing	2621	1097	2326	4995
Grazing	2126	368	1207	4526

X-squared = 389.77, df = 3, p-value < 2.2e-16

Agriculture	1462	617	1662	4483
Nature	3285	848	1871	5038

X-squared = 377.11, df = 3, p-value < 2.2e-16

Table B.4 Selected (based on lowest AIC) model (negative binomial regression with log-link) for the number of Carabid and Staphylinid beetles (predators only) in pitfall traps per grassland (Fig. 3 in the main text).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	4.4473273	0.3510544	12.668	< 2e-16	***
Land use	-0.5377560	0.2383909	-2.256	0.024085	*
Microartropods	-0.0022963	0.0007935	-2.894	0.003805	**
Management	-1.3911794	0.4920962	-2.827	0.004698	**
Microartropods:Management	0.0034824	0.0009423	3.695	0.000219	***

Table B.5 Selected (based on lowest AIC) model (simple linear regression) for the abundance of (herbo)fungivorous grazers in the soil samples per grassland as a function with the litter stabilization factor based on the Tea Bag Index (Fig. 4 in the main text).

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	0.191875	0.013116	14.629	<2e-16 ***
log((Herbo)fungivourous grazers + 1)	-0.007283	0.003597	-2.025	0.0502 .

Table B.6 Selected (based on lowest AIC) model (negative binomial regression with log-link) for the abundance of (herbo)fungivorous grazers in the soil samples per grassland as a function of difenyl concentrations (Fig. 5a. in the main text).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.3194	0.4054	5.721	1.06e-08***
Land use	2.3721	0.5057	4.691	2.72e-06***
Management	2.0132	0.4886	4.121	3.78e-05***
log(Difenyl + 1)	-0.5654	0.1807	-3.129	0.00176**
Land use:Management	-1.6810	0.6714	-2.504	0.01229*

Table B.7 Selected (based on lowest AIC) model (negative binomial regression with log-link) for the abundance of (herbo)fungivorous soil microarthropods in the soil samples per grassland as a function of total fungicide concentrations (Fig. 5b. in the main text)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.065811	0.367354	5.623	1.87e-08 ***
Land use	2.695430	0.491867	5.480	4.25e-08 ***
Management	2.209436	0.538578	4.102	4.09e-05 ***
Fungicides	-0.010441	0.004352	-2.399	0.0164 *
Land use:Management	-1.662086	0.683507	-2.432	0.0150 *
Management:Fungicides	-0.117562	0.049829	-2.359	0.0183 *

Appendix C. Additional figures.

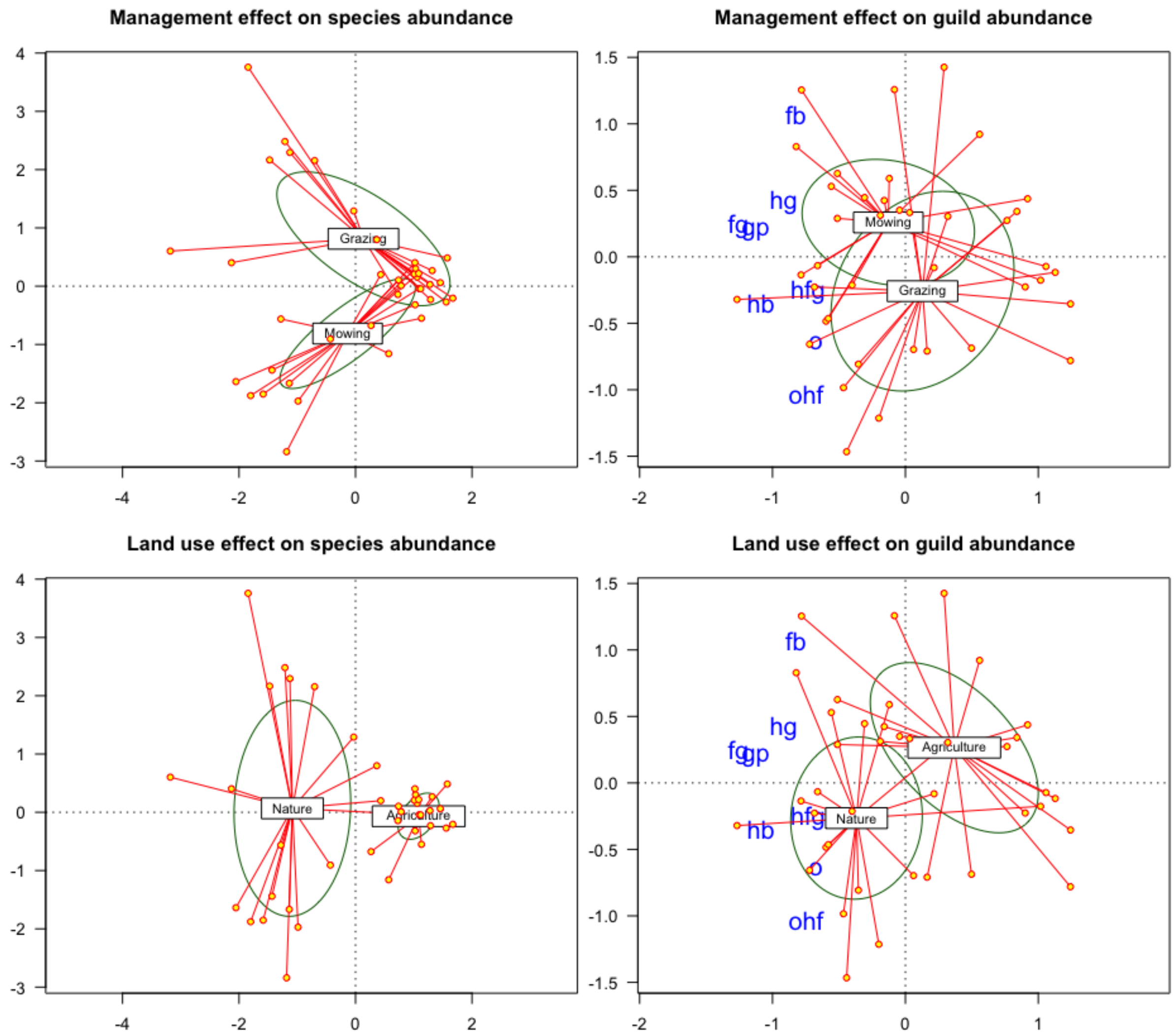

Figure C1. Multivariate analyses of the variation in species abundance (left panels) and abundance of the feeding guilds in which species are grouped (right panels). Top row shows how sites with different management (mowing vs grazing) differ in their positions on the first two axes, while differences between nature and agricultural sites are shown in the bottom row. Abundances are ln-transformed after adding 1. b:bacterivorous, fb:fungivorous browser, fg:fungivorous grazer, gp:general predator, hb:herbivorous browser, hfg(herbo)fungivorous grazer, hg:herbivorous grazer, o:omnivore, ohf:opportunistic herbo-fungivore

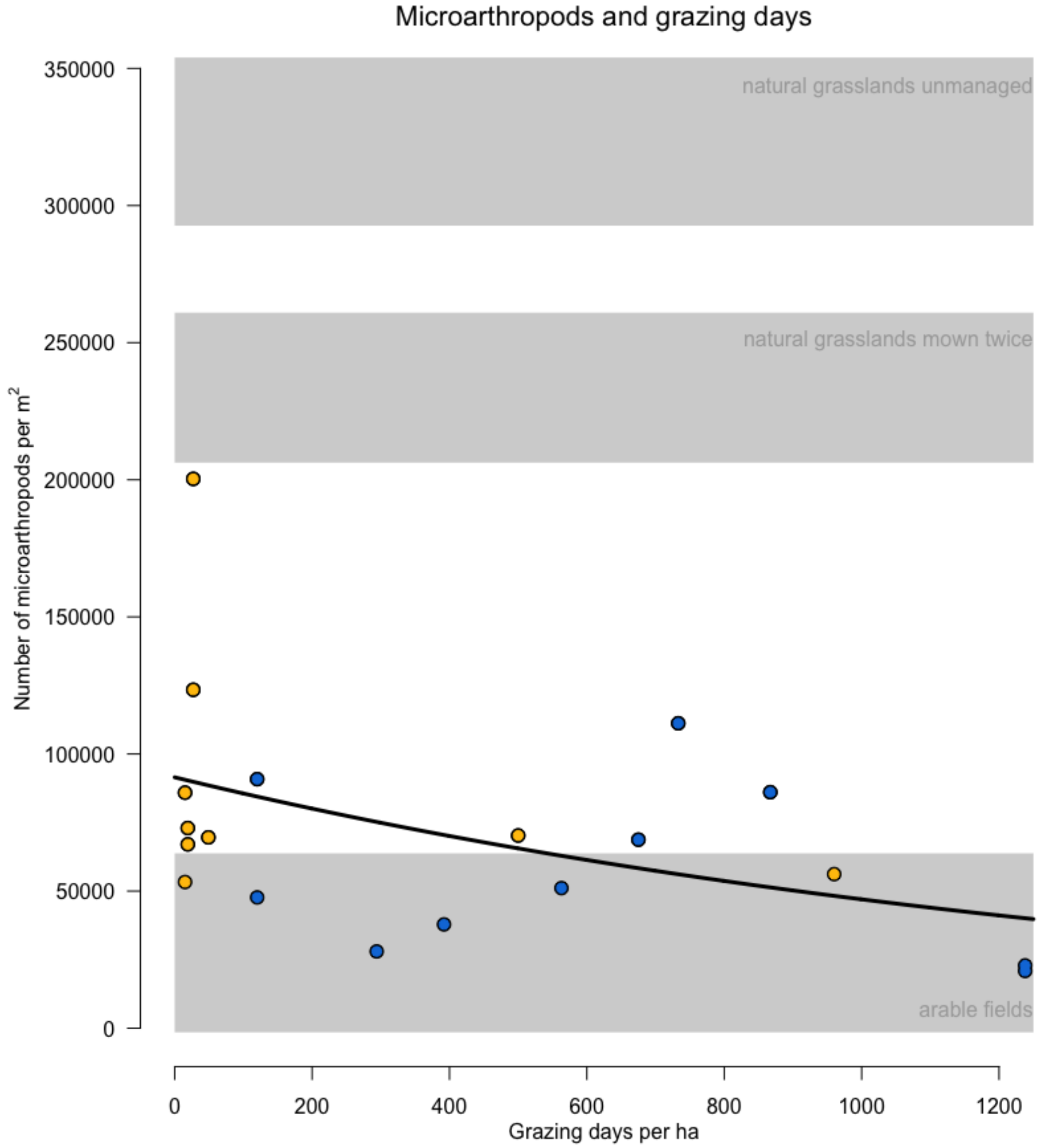

Figure C2. Number of microarthropods (5cm deep) found in each of the grazed sites. One grazed site was left out because the grazing days per ha were unknown. Green circles are nature grasslands and brown circles are agricultural grasslands. Grey areas indicate reference values for arable fields and natural grasslands (either unmanaged or mown twice per year): mean +/- standard deviation as found by Siepel (2018).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	6.2896568	0.1512193	41.593	< 2e-16 ***
Grazing.days.per.ha	-0.0006661	0.0002577	-2.584	0.00976 **

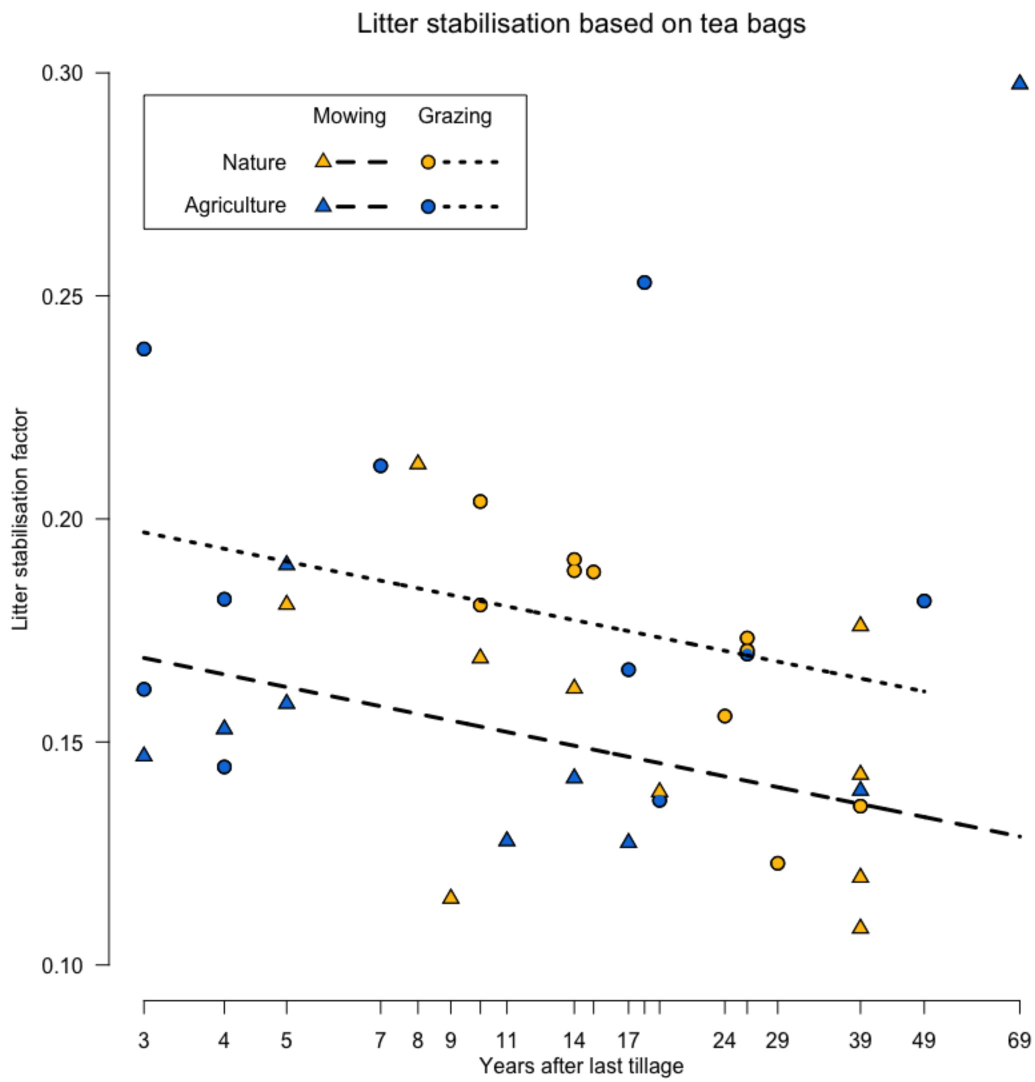

Figure C3. Litter stabilization factor based on Tea Bag Index. Note that the axis with years since last tillage is ln-transformed. The point in the top right corner was identified to have high leverage and removed from the plotted regression model. Based on the complete dataset and without this outlier this resulted in the following model.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	
(Intercept)	0.21100	0.01590	13.270	3.21e-15	***
log(Years after last tillage)	-0.01277	0.00559	-2.283	0.02859	*
Management	-0.02816	0.00933	-3.018	0.00472	**

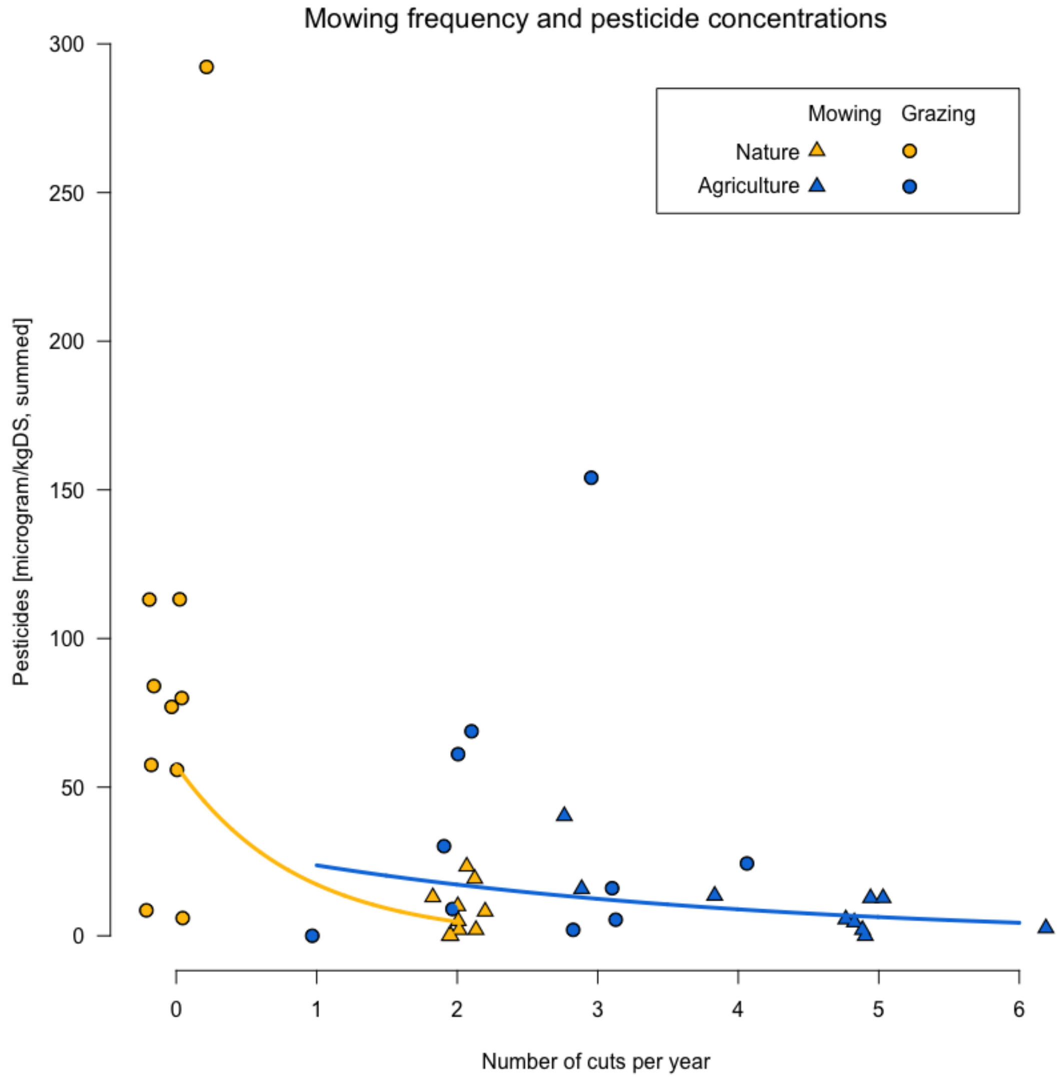

Figure C4. Summed pesticide concentrations as a function of the number of mown cuts per year. Concentrations of all measured insecticides, herbicides, fungicides and avicides were summed. As a response variable the natural log of the summed pesticide concentration was used after adding 1.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	3.5117	0.7723	4.547	5.94e-05	***
nCutsMown	-0.3047	0.2032	-1.500	0.1424	
Land use	0.5539	0.8654	0.640	0.5262	
nCutsMown:Land use	-0.8559	0.3428	-2.497	0.0173	*

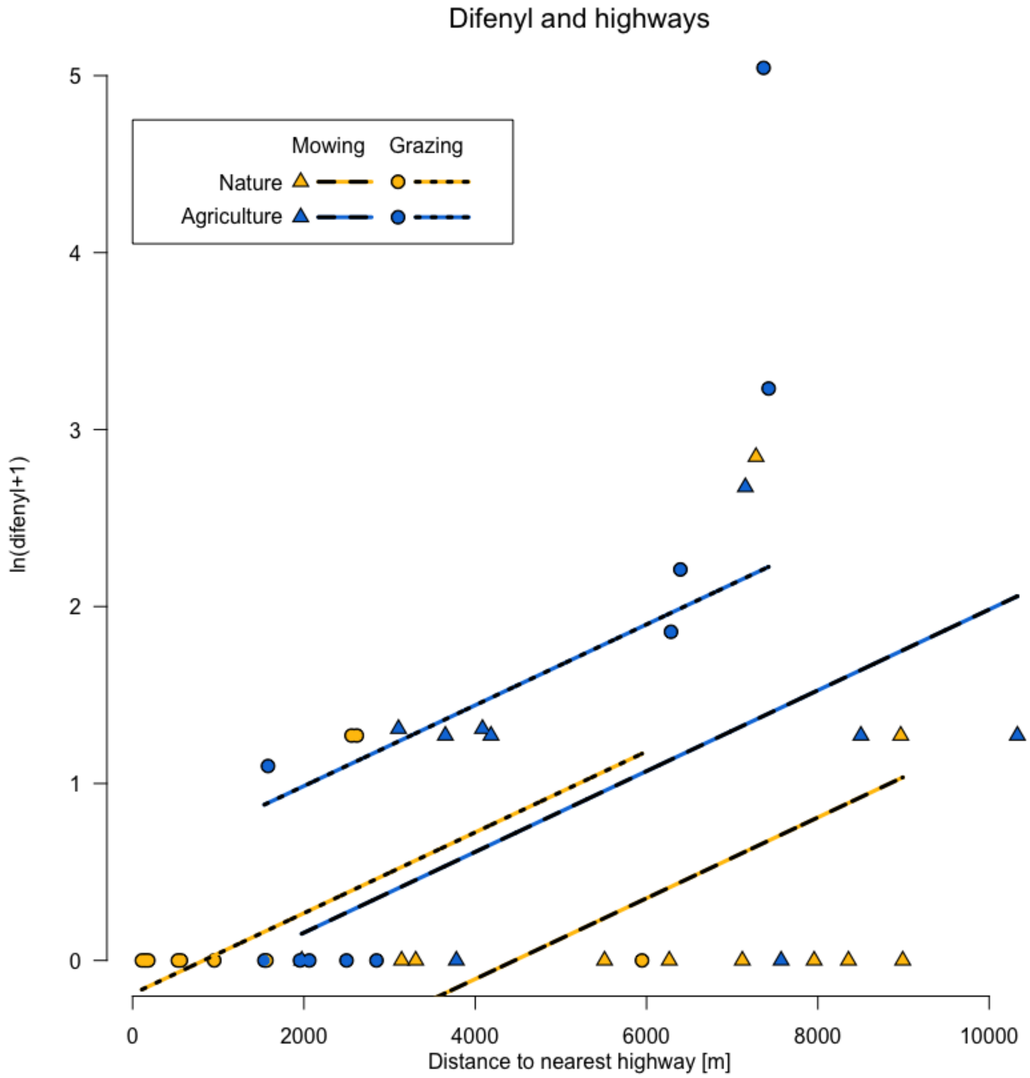

Figure C5. Relationship between Difenyl concentrations and the distance to the nearest highway. No indication was found that Difenyl levels were closer to highways. No interaction effects explored, as 'only' 16 of 40 Difenyl measurements were above detection limit.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	
(Intercept)	5.291e-01	3.243e-01	1.631	0.11155	
distHighway	2.283e-04	6.279e-05	3.636	0.00086	***
Management	-8.290e-01	3.661e-01	-2.264	0.02967	*
Land use	-7.183e-01	3.040e-01	-2.363	0.02368	*

Also when analysing the chance that any Difenyl is found or not (binomial), a positive relationship with distance to a highway is found:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	-1.2243254	0.8716271	-1.405	0.1601	
distNational road	-0.0010813	0.0006599	-1.639	0.1013	
distHighway	0.0006742	0.0003086	2.185	0.0289	*
Land use	-1.6611120	0.8818750	-1.884	0.0596	.

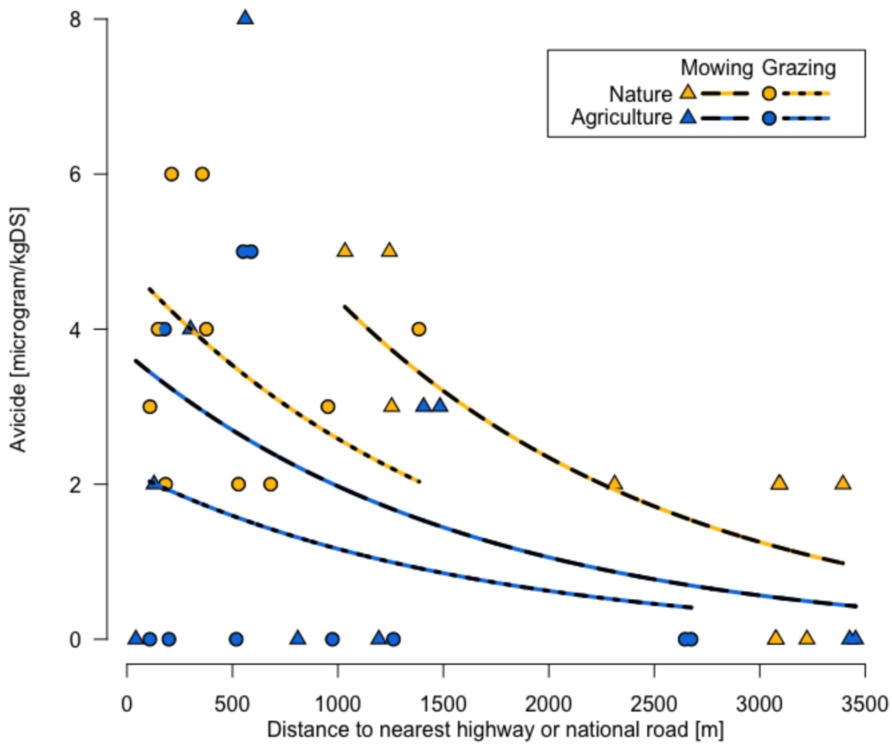

Figure C6. Relationship between avicide concentrations and the distance to the nearest highway or other national road.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	0.7783123	0.2156905	3.608	0.000308	***
distNational road or Highway	-0.0006248	0.0001429	-4.372	1.23e-05	***
Management	0.5263333	0.2578197	2.041	0.041203	*
Land use	0.7965708	0.2360450	3.375	0.000739	***