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# Rewilding with large herbivores: Direct effects and edge effects of grazing refuges on plant and invertebrate communities

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## ABSTRACT

Natural grazing refuges can contribute significantly to plant and animal diversity in grazed ecosystems, particularly when herbivore densities are high. When natural grazing refuges are absent, artificial refuges could be created, for example by means of fencing. It remains, however, unclear how grazing refuges affect the diversity of various taxa in their surroundings. Edge effects can be expected to be positive for biodiversity because at these edges minimal disturbance is combined with beneficial light conditions for plant diversity. This can be expected to decrease with increasing distance and to differ between matrix vegetation types.

Here, we investigated the impact of herbivore exclusion through fencing on communities of plants and various invertebrate taxa in a rewilding area on very productive soil, the Oostvaardersplassen, The Netherlands. The area is grazed year round by Heck cattle, konik horses and red deer, at a combined density of approximately 2.4 animal $\text{ha}^{-1}$. Ten exclosures (13 × 12 m) were erected in 2010 and plant communities were monitored for three years. In the third year, pitfall trapping, earthworm counts and plant surveys were performed in the centre, at the edge, at 10 m and at 20 m distance from each exclosure.

Plant species richness declined strongly at the centre of the exclosures, but remained high outside the exclosures and at their edges. Earthworm, isopod, myriapod and ground beetle diversity increased in the exclosures, but showed small or no differences in species composition, while weevils showed a decrease. Spider, true bug, and leafhopper diversity did not differ, but showed large changes in species composition. For leaf-, dung and click beetles, neither diversity nor species composition differed systematically between treatments. For all taxa, diversity at the exclosure edges was as high as in the most diverse treatments, thus, combining all taxa to calculate multidiversity showed species richness to peak at the edge of the exclosures, but this positive edge-effect extended less than 10 metres.

We conclude that when natural grazing refuges are not present, the creation of grazing refuges may thus be an effective management tool to increase diversity. Because exclosure edges support the highest multidiversity, maximising the edge length will have most beneficial effects for grassland flora and fauna, which can be achieved by creating many small, rather than few large refuges, or by creating serrated rather than straight edges. Such positive effects can be expected to be beneficial to higher trophic levels such as birds and other vertebrates.

## 1. Introduction

Grazing by large mammalian herbivores has historically and prehistorically been a major structuring force in almost all terrestrial ecosystems (Bakker et al., 2015), affecting plant and animal communities. Grazing is under certain conditions beneficial to plant species richness (Milchunas et al., 1988; Olff and Ritchie, 1998), but is damaging to ecosystems and biodiversity when large herbivore densities are high (Côté et al., 2004; Morris, 1967; Smith, 1940). Herbivores can reach high densities in the absence of top down control, which can happen on isolated islands, after extermination of large carnivores, or among feral herds (e.g. Boyd et al., 1964; Smith et al., 2003). Under such conditions, the presence of grazing refuges is important for tree recruitment (Smit et al., 2006), maintenance of populations of grazing-sensitive plants (Chollet et al., 2013; Rebollo et al., 2002; Shitzer et al., 2007), and animal diversity (Foster et al., 2014; van Klink et al., 2015). Grazing refuges can be of geological (e.g. rock outcrops or water bodies) or

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biological origin (e.g. spiny shrubs) (Milchunas and Noy-Meir, 2002).

In Western Europe, grazing by large herbivores is a commonly applied management type in nature restoration projects, which increasingly takes place on abandoned agricultural lands. Here, heterogeneity in abiotic conditions is typically absent, since agricultural practices have increased productivity and removed underlying geological and hydrological features (Benton et al., 2003). As such, abiotic grazing refuges are often not present, while also biotic refuges are typically absent through consistent historical removal. Biotic grazing refuges are characterized by the presence of chemically or mechanically defended plant species that can serve as protective structures for grazing-sensitive species. When protective species are present, spatial differentiation in grazing will occur where large herbivores will return to previously used feeding stations, while locations with chemically or mechanically defended plant species are avoided (Smit et al., 2006). An additional factor determining the emergence of biotic grazing refuges is the density of large herbivores. When herbivore densities are high, also defended species are unable to establish, decreasing the chances for their protégés (Smit et al., 2015) and grazing-sensitive fauna. This interaction between abiotic and biotic heterogeneity and the presence of grazing refuges is especially relevant in the context of rewilding, which in Europe is typically considered on such abandoned agricultural lands (Merckx and Pereira, 2014; Navarro and Pereira, 2012). The general aim of rewilding is to restore and maintain natural processes with minimal human intervention (Navarro and Pereira, 2012; Sandom et al., 2013), although interventions to push the system into the desired direction are usually implemented (Sandom et al., 2013). Typically, this involves reintroductions of keystone species, such as large herbivores.

In the absence of natural grazing refuges, artificial refuges, for example in the form of wildlife exclosures, water bodies, or coarse woody debris, can assume their role in protecting grazing sensitive plant and animal species (Beever and Brussard, 2000). These have been shown to be beneficial to species richness of gastropods (Suominen, 1999), spiders (Warui et al., 2005), herbivorous insects (Den Herder et al., 2004; Roininen et al., 1997), beetles (Barton et al., 2011), soil organisms (Wardle et al., 2001) and abundance of small mammals (Beever and Brussard, 2000). On plant diversity, contrasting effects of herbivore exclusion have been reported, mediated by site productivity (Bakker et al., 2006). Under nutrient-rich conditions, the exclusion of large herbivores can result in light competition among plant species, with a subsequent decline in plant species richness. Under nutrient poor conditions, competitive exclusion is expected to be less important in determining plant species richness (Bakker et al., 2006; Olff and Ritchie, 1998; but see Shitzer et al., 2007).

In contrast to the interior areas of grazing refuges, however, competitive exclusion among plant species can be expected to be of less importance at their edges. Here, disturbance through trampling and defoliation are minimal, while beneficial light conditions for plants are maintained. For invertebrates, this should result in an increased abundance and diversity of resources at these edges, caused by a tall-statured, species-rich plant community with a well-developed litter layer. Additionally, these transition zones will have a warmer microclimate than the exclosure interiors, while providing shelter from weather extremes and predators. Mobile species can also make use of resources both in- and outside the exclosures (Dennis and Fry, 1992; Ries et al., 2004). In analogy with forest–grassland ecotones (Ewers and Didham, 2006; Harper et al., 2005; Łuczaj and Sadowska, 1997) or crop–boundary ecotones (Saska et al., 2007), we thus expect overall diversity to peak at the exclosure edges and to decrease with distance from the exclosures. The magnitude of the edge effect is expected to depend on the contrast between the vegetation types (Harper et al., 2005).

In a highly productive rewilding area (Oostvaardersplassen, The Netherlands) with high densities of large herbivores (red deer, konik horses and Heck cattle), we tested two concrete predictions: (i) the effect of fencing out large herbivores on species richness ($\alpha$-diversity) and species composition will differ between taxa, where plant diversity is expected to decrease, with a concomitant decrease in diversity of herbivorous taxa, while diversity of detritivorous taxa is expected to increase, followed by an increase in diversity of carnivorous taxa. Diversity of dung feeding species is expected to decrease under herbivore exclusion. (ii) The edges of the exclosures will be most species rich. These predictions were tested in two different, but adjacent vegetation types, which differed in vegetation height and composition: short grazed lawn (SL) vegetation and tall herbaceous (TH) vegetation. We assessed the response of plant, earthworm, soil macrofauna (myriapods and isopods), spider, plant-and leafhopper, true bug, ground beetle, dung beetle, click beetle, leaf beetle and weevil species richness and community composition, where we take an taxonomic rather than a functional approach to enhance comparability with previous and future literature, which usually focuses on one or a few taxonomic groups (van Klink et al., 2015).

## 2. Methods

### 2.1. Study site

The experiment was performed in the Oostvaardersplassen (OVP; N52°26′, E5°21′), a 5600 ha nature reserve located in the province of Flevoland, The Netherlands, which was embanked in 1969 and is surrounded by water on all sides. The site is located at some 5 m below sea level and has a temperate oceanic climate with a mean annual temperature of 10.1 °C and an average of 833 mm precipitation annually. Heck cattle (*Bos taurus*), konik horses (*Equus ferus caballus*) and red deer (*Cervus elaphus*), were introduced in the reserve in 1983, 1984 and 1992 respectively. These populations are not human-regulated, although an early-reactive management is applied to minimize animal suffering. Concretely, individual animals that are not likely to survive are shot, which typically occurs at the end of winter (ICMO2, 2010). Since their introduction, the herds have grown until a density of 2.58 heads per hectare (0.18 Heck cattle $ha^{-1}$, 0.61 Konik horses $ha^{-1}$, 1.79 Red deer $ha^{-1}$) in 2012 (Cornelissen et al., 2014b). These herds have decreased shrub cover and increased cover of homogeneous grassland (Cornelissen et al., 2014a,b; Vulink et al., 2000). This grassland is best described as productive, wet grassland on clay soil, dominated by nitrophilous grasses and forbs. In addition to the large herbivores, considerable numbers of geese visit the OVP during winter and early spring (predominantly *Branta leucopsis*, ca. 20,000), while (not introduced) Roe deer (*Capreolus capreolus*) and hare (*Lepus europaeus*) are currently very rare. The red fox (*Vulpes vulpes*) is the largest mammalian carnivore in the study area.

### 2.2. Experimental setup

In April 2010 (year 1), ten exclosures (13 m × 12 m) with adjacent control plots were erected in a 1 km × 1 km area in the south of the reserve. At this location, grazing by the large herbivores mainly occurs between October and May, when food is scarce. During the summer months grazing is concentrated in other parts of the reserve. The exclosures were placed in two SE–NW directed rows, divided over the two dominant vegetation types: the short lawn (SL) vegetation dominated by grasses (mostly *Lolium perenne*), and the tall herbaceous (TH) vegetation dominated by reed (*Phragmites australis*) and forbs such as *Carduus crispus* and *Sysimbrium officinale* (Fig. 1, also see Smit et al., 2015). The placement of each of the exclosures was selected based on homogeneity of the 35 × 12 m area needed for each exclosure—control combination, and the absence of coarse woody debris. There were small but significant differences in soil properties between the vegetation types, detailed in Appendix A. In the TH vegetation, organic carbon and soil moisture concentrations were higher, whereas the SL vegetation contained a higher fraction of silt (particles $< 63\ \mu m$). Additionally there was a slight increase in soil pH from east (pH 7.4) to west (pH 7.7), but only in the grazed controls (Appendix A).

Each exclosure consisted of a 2 m high fence, surrounded by an electric wire at 40 cm from the fence. A control plot of 8 × 12 m was located at the north-westward side of the exclosure, with a 5 m buffer between the exclosure and the control plot (Fig. 1). The control plot was visually equal to the neighbouring exclosure at the time of placement, but no pre-treatment vegetation recordings were made. In a parallel experiment, tree saplings were planted in these exclosures and the control plots (see Smit et al., 2015).

### *2.3. Sampling design*

In each exclosure and in the control plots a permanent plot (1 m × 1 m) for vegetation recordings was established at the start of the experiment (see Fig. 1). Here, vegetation recordings were made by estimating cover of all species on the decimal scale inside each permanent plot in years 1 (June 2010), 2 (July 2011) and 4 (August 2013). The vegetation inside the exclosures grew rapidly, which may have hampered detection of small species in the first years, however, all of these had disappeared inside the exclosures after three years. In year four recordings were made late in the season, which may have caused species with an early phenology to be missed. Vegetation height was measured at all occasions, and additionally four months after the erection of the exclosures by lowering a Styrofoam drop disk (65 g, ø 24 cm) onto the vegetation, except inside the exclosures in year 4, because the vegetation was too high (>150 cm) for the drop disk.

To examine the effects of the grazing exclusion on the invertebrate community, arthropods were trapped by means of pitfall trapping and earthworms by hand-sorting soil in year 4. Four pitfalls filled with a 4% formaldehyde solution were placed at each exclosure/control combination: one at the centre close to the permanent plot, one at the edge of the exclosure, one trap at 10 m from the exclosure and one at 20 m (Fig. 1). The positions of the traps at the edge, 10 m and 20 m in relation to the exclosure were randomized in such a way that each of these traps was located at a different edge of the exclosure, always avoiding the north-western side of each exclosure, since here an additional 1 m high exclosure was located (Fig. 1, see Smit et al., 2015). The traps were protected by rebar constructs with a plastic roof to prevent entry of rain water and trampling by large grazers, and covered with mesh to prevent capture of small rodents and other vertebrates.

The traps were operational for two five-week periods, covering the complete months of May and August. During these two periods, both species that overwinter as larva or pupa (spring breeders) and species that overwinter as egg (summer breeders) can be caught. The following groups were identified to species level: arachnids (Araneae and Opiliones), soil macrofauna (Myriapoda and Isopoda), plant- and leafhoppers (Hemipera: Auchenorrhyncha, including one species of jumping plant lice Hemiptera: Psylloidea), true bugs (Hemiptera: Heteroptera), ground beetles (Coleoptera: Carabidae), dung beetles (Coleoptera: Scarabaeoidea), click beetles (Coleoptera: Elateridae), weevils (Coleoptera: Curculionoidea) and leaf beetles (Coleoptera: Chrysomelidae). Additionally, plant communities were recorded similarly to the permanent plots in a 1 $m^2$ area around each pitfall trap. Earthworms were collected by hand-sorting 27,000 $cm^2$ (30 × 30 × 30 cm) of soil in May of year 4, at the same distances from the exclosures as the pitfall traps were located, but at different sides of the exclosures (Fig. 1).

On two occasions the presence of foxes (*Vulpes vulpes*) disrupted sampling. Young foxes were present in one of the exclosures during the sampling of earthworms. For this reason worms were not sampled in the centre and edge of that exclosure and these samples were therefore omitted from the analysis of

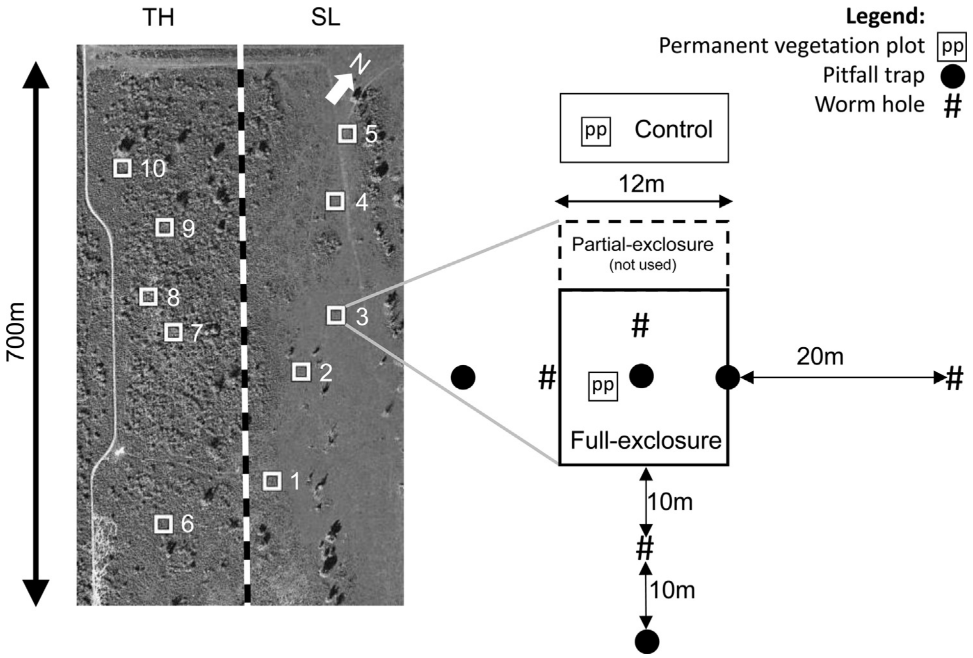

**Fig. 1.** Overview of the experimental setup with an example of the positioning of pitfall traps and worm holes around an exclosure. Permanent plots were used for vegetation recordings. The positions of the traps and worm holes in relation to the exclosures was randomised in such a way that no two traps of the same type were located at the same side of the exclosure. Image from Bing maps© 2013.

earthworms. In August, one pitfall trap at the centre of an exclosure was dug out and upended. As this meant a loss of three weeks' worth of data, this location was omitted from all analyses of the pitfall catches.

### *2.4. Statistical analysis*

#### *2.4.1. Species richness*

All invertebrate species known to be associated with trees (four beetle species and a leafhopper species) were excluded from analysis, as they had colonized the planted tree species (see Smit et al., 2015). Differences in mean species richness per sample (permanent plot, pitfall trap or wormhole) between the distance treatments (centre, edge, 10 m and 20 m) and the vegetation types were tested using Poisson distributed mixed effects models (GLMM). In these models exclosure number was entered as random variable, and vegetation type, distance treatment, and their interaction as fixed variables. Post-hoc Tukey tests were used to test for differences between the distance treatments.

To attain a synthetic measure of biodiversity over all taxa, multidiversity (Allan et al., 2014) was calculated. Multidiversity is a novel metric which sums average proportional species richness across all taxonomic groups. Treatment effects on multidiversity were tested using mixed effects models with a normal distribution and the same fixed and random structure as the models for species richness of the different taxa.

#### *2.4.2. Community composition*

To test for effects of the exclosures on community composition of all taxa, pairwise β-diversity between the grazed controls and the edges and centres of the exclosures was calculated using the Morisita–Horn index. This abundance based index was recommended after a recent comparison between 29 β-diversity metrics (Barwell et al., 2015). An additional reason to choose this metric was that it produced fewer errors due to low numbers of individuals than the conceptually similar Morisita-index.

Because β-diversity is known to be strongly affected by both differences in species richness (number of species in the two compared samples) and differences in γ-diversity (total size of the species pool) (Chase et al., 2011; Kraft et al., 2011), we corrected for these biases by subtracting the expected β-diversity based on the given α- and γ-diversity, from the observed β-diversity following Kraft et al. (2011). If the observed β-diversity is equal to the expected β-diversity (corrected β-diversity = 0), this indicates that differences in community composition are driven by differences in numbers of individuals, and not by turnover of species. Conversely, if corrected β-diversity > 0, this indicates species sorting, whereas if corrected β-diversity < 0, this indicates clumping of individuals within locations (Chase et al., 2011).

To calculate the expected β-diversity, a null-model approach based on Kraft et al. (2011) was used. Here, the expected β-diversity is calculated for each pairwise comparison based on the number of individuals observed per sample and the observed species-abundance distribution (SAD) of the species pool of the given taxon (see below). From this SAD, communities are drawn with the observed number of individuals of each of the compared samples, and β-diversity is calculated. The mean of 1000 iterations is then taken as the expected β-diversity, and subtracted from the observed β-diversity. In the original null model (Kraft et al., 2011), the mean corrected β-diversity is divided by its standard deviation in order to obtain a β-deviation standardized effect size (SES). This can, however, significantly affect the outcome of β-diversity correction, and even inverse patterns (Qian et al., 2013). Additionally, the interpretation of β-diversity is hampered by this procedure, as the traditional bounds between 0 and 1 are abandoned. For these reasons we report the original corrected β-diversity in the main text, while the SES results can be found in Appendix C. Qualitatively, the outcome as SES was the same.

When using such a null model, it is of extreme importance to use an appropriate species pool (Lessard et al., 2012). Here, we delineated the species pools using multivariate permutational anova (Permanova) (see also Appendix B,Table B1 and Fig. B1). There were highly significant differences between the communities of the two vegetation types for plants (Permanova: $F = 23.4$, $p < 0.001$) and pooled arthropods (Permanova: $F = 15.08$, $p < 0.001$). Hence, we used separate species pools for the two vegetation types.

Because no differences in species composition were found between the samples at 10 m and 20 m from the exclosures in either vegetation type for both plants (Permanova $F = 0.93$, $p = 0.45$) and arthropods (Permanova $F = 1.23$, $p = 0.24$), samples from both distances were used as grazed control samples (Table B1). Additionally, there was no strong evidence for spatial autocorrelation of the traps surrounding an exclosure (Plants: Permanova $F = 1.37$, $p = 0.16$, arthropods: $F = 1.45$, $p = 0.07$), therefore all pairwise comparisons between exclosures and grazed plots in each vegetation type were used to calculate mean β-diversity.

Because the corrected β-diversities showed no approximation of any parametric distribution, non-parametric sign tests were used to assess whether the median deviated from 0, and Wilcoxon

**Table 1**

Summary statistics of effects of distance from exclosure and vegetation type ofspecies richness of 11 taxa according to GLMM. Plant and animal diversity was measured 3 years after 10 exclosures were erected, divided over two vegetation types, in a rewilding area in The Netherlands. Ns = not significant ($p > 0.05$).

| Taxon | Number of individuals | Total number of species | Distance treatment | | Vegetation type | | Treatment × veg type | | Model | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | $\chi^2$ | $P$ | $\chi^2$ | $P$ | $\chi^2$ | $P$ | $\chi^2$ | $P$ | $r^2$ |
| Plants | | 31[a] | 84.00 | <**0.001** | | ns | | ns | 84.28 | <**0.001** | 0.80 |
| Earthworms | 264[b] | 4 | 12.73 | **0.01** | 13.17 | <**0.001** | | ns | 25.18 | <**0.001** | 0.45 |
| Soil fauna | 1083 | 13 | 24.05 | <**0.001** | 10.02 | <**0.01** | | ns | 73.98 | <**0.001** | 0.49 |
| Arachnids | 6732 | 59 | | ns | | ns | | ns | 2.79 | ns | |
| Plant- and leafhoppers | 969 | 20 | 8.05 | **0.05** | | ns | | ns | 8.05 | **0.05** | 0.20 |
| True bugs | 762 | 21 | | ns | | ns | | ns | 2.58 | ns | |
| Ground beetles | 6208 | 49 | 33.98 | <**0.001** | | ns | | ns | 33.98 | <**0.001** | 0.48 |
| Dung beetles | 230 | 14 | | ns | 4.81 | **0.03** | | ns | 4.81 | **0.03** | 0.14 |
| Click beetles | 2064 | 5 | | ns | | ns | | ns | 0.6 | ns | |
| Leaf beetles | 617 | 24 | | ns | | ns | | ns | 6.41 | ns | |
| Weevils | 1372 | 23 | 14.73 | <**0.01** | | ns | | ns | 14.73 | <**0.01** | 0.34 |
| Multidiversity | 20310[c] | 263 | 37.29 | <**0.001** | 4.19 | **0.04** | | ns | 43.29 | <**0.001** | 0.69 |

[a] Found in year 3.

[b] Excluding juveniles.

[c] Excluding plants.

rank sum tests were used to test for differences in β-diversity between the two vegetation types for all taxa. In order to avoid false positives due to the large number of tests performed (48 tests for deviation from 0, and 24 tests for differences between the vegetation types), we report *p*-values adjusted by FDR (Benjamini and Hochberg, 1995). All analyses were performed using R (Core Team, 2014), making use of the Vegan package for multivariate anova and β-diversity calculation (Oksanen et al., 2014), the Multcomp package for post hoc testing (Hothorn et al., 2008), the lme4 package for mixed effect models (Bates et al., 2014), the BSDA package for sign tests, and the lmerTest package (Kuznetsova et al., 2014) for obtaining p-values based on Satterthwaite's approximation from the mixed effects models.

## 3. Results

Over three years sampled, in total 47 plant species were recorded (Table 1), of which in the fourth year 6 were only found in the grazed controls and 9 were only found at the edge of the exclosures. Four species of earthworms were found, represented by 581 individuals, of which 317 juveniles. In the grazed SL vegetation earthworms were only found in one plot. Therefore earthworm β-diversity was not analysed for the SL vegetation. Of arthropods, 20,109 individuals were identified to 228 species (see Table 1). Of these, 69 species were only found in the exclosures, and 33 species only in the grazed controls. A complete species list is available in Appendix D.

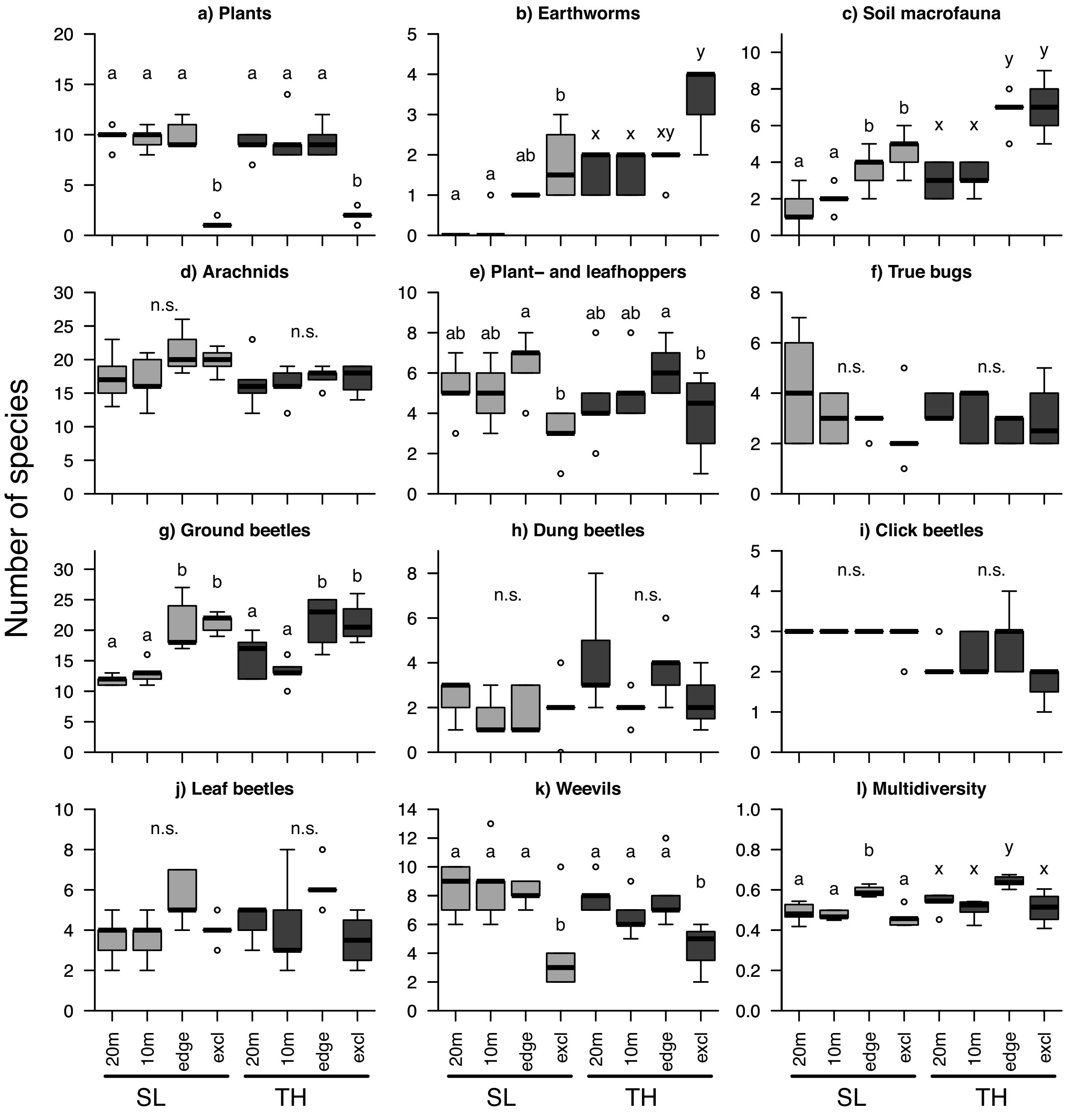

**Fig. 2.** Mean species richness (α-diversity) per sample taken at 20 m, 10 m, at the edge and at the centre (excl) of 10 exclosures divided over two vegetation types (short lawn [SL] vegetation, and tall herbaceous [TH] vegetation). Plant species richness was assessed per $m^2$, earthworm species richness per 30 × 30 × 30 cm hand-sorted soil, all arthropod groups per two times 5 weeks of pitfall trapping (spring and late summer). Different letters denote differences ($p < 0.05$) according to GLMM between treatment levels. For taxa where species richness differed significantly between vegetation types, this is denoted by use of *x* and *y*.

### *3.1. Species richness*

Over the three years of the experiment, plant species richness declined sharply at the centre of all exclosures of both vegetation types, until in the fourth year, a homogeneous stand of stinging nettle (*Urtica dioica*), with a few stems of reed (*P. australis*) was present. In the grazed control plots plant species richness did not change much over time. There was no difference in plant species richness between the edges of the exclosures, 10 m distance, and 20 m distance (Fig. 2a). During this period, vegetation height increased strongly inside the exclosures. After one month, the vegetation inside the exclosures was on average 5 cm taller in the SL vegetation and 12 cm taller in the TH vegetation. After four months (at peak standing crop) the difference had increased to 30 cm in the SL and 50 cm in the TH vegetation. Three and a half years after the start of the experiment, the vegetation inside the exclosures was approximately 180 cm tall in the TH vegetation, and 150 cm in the SL vegetation. By contrast, the grazed controls were on average 12 cm in the SL vegetation and 15 in the TH vegetation. In the SL vegetation, 26% of plant species and 34% of arthropod species were exclusively found in the exclosures, and in the TH vegetation this was 34% and 30% respectively.

Species richness of the various invertebrate groups showed contrasting responses to the exclusion of large herbivores. As expected, the detritivorous groups, earthworms and soil macrofauna, showed highest species richness at the centre and edge of the exclosures (Table 1 and Fig. 2b and c), but dung beetles showed no significant response (Table 1 and Fig. 2h). The mostly carnivorous groups responded differently, where arachnids showed no difference in richness between treatments (Fig. 2d), but ground beetles were most species rich inside the exclosures (Fig. 2g). The (predominantly) herbivorous groups also showed varying responses, in contrast to our expectations. The only group showing the expected decrease in diversity, following the decrease in plant species richness inside the exclosures were weevils (Fig. 2k), whereas true bugs, click beetles, and leaf beetles showed no differences in species richness between the distance treatments (Table 1 and Fig. 2f, i and j). Plant- and leafhoppers were significantly more species rich at the exclosure edge than in the centre, but showed no significant effects in any of the other comparisons (Fig. 2e). Multidiversity was higher at the edges of the exclosures than at the centre or the grazed controls at either distance (Fig. 2l), but no interaction between distance treatment and vegetation type was found, indicating no difference in the magnitude of the edge effect.

A significant difference in species richness between the SL and the TH vegetation was found for earthworms, soil macrofauna and dung beetles (Table 1 and Fig. 2b,c and h), and for multidiversity (Table 1 and Fig. 2l), where in all cases species richness was higher in the TH vegetation.

### *3.2. Community composition*

There were also strong differences in the effects of the exclosures on community composition of the different taxa. Plants showed the strongest change in community composition at the centre of the exclosures in both vegetation types, followed by arachnids, plant- and leafhoppers and true bugs (Fig. 3a). Other groups showed less strong changes in community composition, but only earthworms (SL: N/A; TH: $p = 0.49$), dung beetles (SL: 0.09; TH: $p = 0.16$) and click beetles (SL: $p = 0.21$; TH: $p = 0.63$) showed no significant effects in either vegetation type, indicating that for these groups poorer communities were random draws from the richer ones.

The difference in community composition between the grazed plots and the exclosure edges was generally smaller than the difference between grazed plots and exclosure centres (Fig. 3). Again, plants, arachnids, plant- and leafhoppers and true bugs showed strongest changes in community composition and dung beetles again showed no difference ($p = 0.06$). Here, however earthworms and click beetles showed weakly significant deviations from 0 (earthworms TH: $p = 0.03$, SL: n/a; click beetles TH: $p = 0.03$, SL: $p = 0.11$). Corrected β-diversity of all other groups showed highly significant deviations from 0.

For some taxa also differences in the effect size in community change were found between vegetation types (Fig. 3). In most cases this meant larger differences in community composition in the SL vegetation than in the TH vegetation. Only for arachnids and dung beetles compared to the edge of the exclosure, and for plants compared to the centre of the exclosure, were the changes in community composition larger in the SL vegetation (Fig. 3).

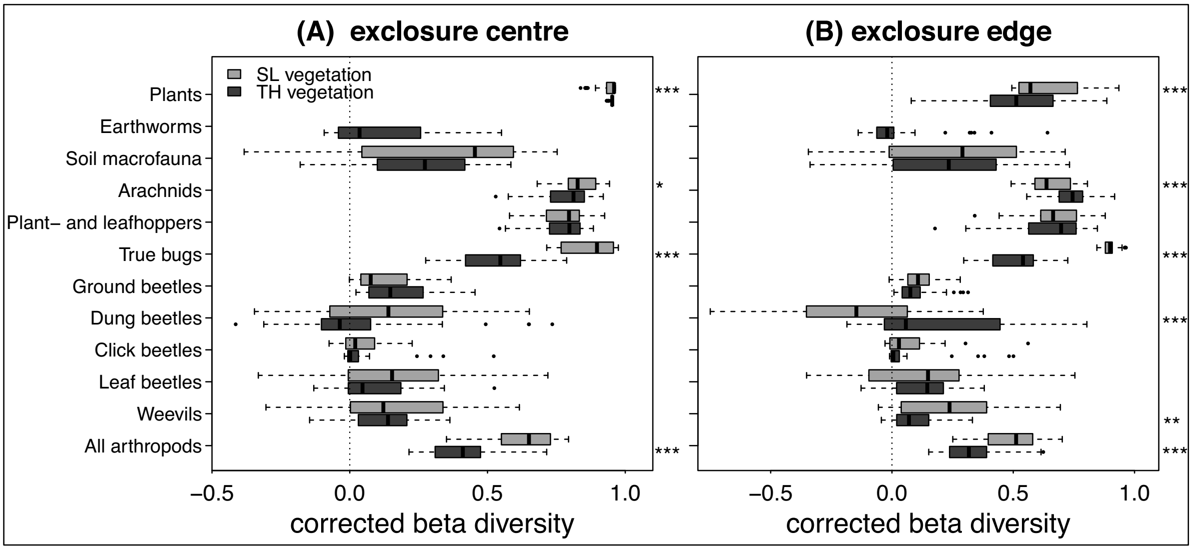

**Fig. 3.** Difference in community composition (Morisita–Horn index corrected for differences in $\alpha$- and $\gamma$-diversity between groups and traps) between the grazed controls and the exclosure centre (A) and between the grazed controls and the exclosure edge (B) over the two vegetation types. Stars indicate adjusted *p*-values of the difference between the vegetation types * $p < 0.05$, **$p < 0.01$, ***$p < 0.001$. All taxa except earthworms, dung beetles and click beetles in both vegetation types in A, and earthworms, dung beetles in TH and click beetles in TH in B deviated significantly from zero.

## 4. Discussion

Within only three years, the exclusion of large herbivores led to strong, but often contrasting effects on species richness and/or community composition of almost all studied groups in both vegetation types. The two starting vegetation types harboured differing communities of plants and arthropods, but differences in species richness were only found for earthworms, soil macrofauna, ground beetles and multidiversity, where richness was higher in the TH vegetation. This higher overall species richness might be explained by the higher productivity, owing to the taller vegetation both in- and outside the exclosures, and possibly by lower disturbance frequencies in the TH vegetation.

The null-model based on Kraft et al. (2011) was successful in correcting the observed β-diversity for differences in number of individuals and species, demonstrating that several groups showed no or very limited differences in community composition between treatments. This can, however, be indicative of two distinct ecological processes. First, the taxon in question may indeed show no or very limited response to the treatments, but rather show an increase or decrease of the number of individuals. This was in our experiment the case for the earthworms, soil macrofauna, and ground beetles, which all showed increases in species richness inside the exclosures and no or very small difference in species composition, and especially for the click beetles, which showed neither differences in species richness nor in community composition. The second possible process is the presence of vagrant individuals in either of the treatments. If these vagrant individuals are a random subset of the whole community, no differences in community composition will be detected. This was likely the case for the dung beetles and leaf beetles, of which substantial numbers were found inside the exclosures, even though their resource base was not present. Dung beetles feed on ungulate dung, which was obviously not present inside the exclosures, and of the leaf beetle species caught, none feed on *U. dioica*. That for these mobile taxa no differences were found in either α- or β-diversity, shows the limitations of the applied experimental design in terms of exclosure size and the use of activity dependent traps. Indeed, when species that are, based on their resource use, unlikely to survive at the exclosure centres were to be excluded, it is likely that total species richness here would be significantly lower than at the edges or in the grazed controls. When interpreting the results of such random draw models, these possible processes should be considered, where knowledge of the life-history characteristics of the species can be helpful.

For other groups we detected strong changes in species composition after erection of the exclosures. The plant community was completely replaced by *U. dioca*. This development was reflected in the communities of weevils, plant- and leafhoppers, and true bugs, which all showed a replacement of species specialized on forbs and grasses by species specialized on *U. dioica*. Also spiders showed strong turnover in species, where inside the exclosures large numbers of wolf spiders (Lycosidae) were found, while in the control plots mostly dwarf spiders (Linyphiidae) were found. Such differences in composition are often reported (e.g. Gibson et al., 1992; Noel and Finch, 2010), and are most likely related to the high tolerance of disturbance by certain dwarf spider species, and positive response to increased habitat complexity of the mostly spring-active wolf-spider species (Langellotto and Denno, 2004).

Over all groups combined (measured as multidiversity), there was no difference in species richness between the centre of the exclosures and the grazed controls, since the positive effects on some groups were balanced out by negative effects on other groups. Although positive effects of grazing on invertebrate diversity are sometimes reported (Suominen et al., 2003; Woodcock et al., 2006), our result contrasts three recent meta-analyses that show general negative responses of arthropod abundance (Foster et al., 2014; Takagi and Miyashita, 2014) and species richness (Foster et al., 2014; van Klink et al., 2015) to large herbivore grazing. For most groups this can be attributed to direct resource competition with the large herbivores, habitat simplification, trampling and ingestion (van Klink et al., 2015), leading to a decrease in total number of individuals and, hence, species. All three meta-analyses show large variation in arthropod response to grazing, but obvious differences between most of the analysed studies and the present study are the timing and the intensity of grazing. At our experimental location, there was a high grazing intensity in winter and early spring, whereas during summer grazing was concentrated elsewhere in the reserve. Many invertebrate species overwinter as egg or pupa, and therefore are unlikely to be strongly affected by grazing during this period. Other species however, overwinter as larva or adult in diapause, and often benefit from protective vegetation cover (Dennis et al., 1994; Sotherton, 1984), as was present in our exclosures. Effects of grazing may thus depend on the overwintering strategy of a species or group in relation to the timing of grazing.

We found a positive edge effect on multidiversity, in line with our second hypothesis, but no difference in edge effects between vegetation types, contrasting Harper et al. (2005). This edge effect could be explained by the co-occurrence of groups that peaked in the exclosures and groups that peaked under grazing. Such positive edge effects on diversity of invertebrates have been reported over larger scales, such as forest–grassland ecotones (Bedford and Usher, 1994; Tothmeresz et al., 2014; van Halder et al., 2010) and crop field boundaries (Saska et al., 2007). We, however, found no indications that this positive edge effect extended far outside the exclosures, since between 10 and 20 m no differences in either species richness or community composition were found. This is possibly partially due to the relatively sharp border between the grazed and ungrazed conditions, but also suggests that diurnal or seasonal migrations are hard to detect. Previous studies reported edge effects extending between 3 m for Orthoptera (Ewers and Didham, 2006) until well over 100 m for the same as well as other arthropod taxa (Albrecht et al., 2010), while for plants the effects generally extend less than 25 m (Harper et al., 2005). Although the difference in community composition between the grazed and control plots was larger in the SL than in the TH vegetation, no differences in magnitude of the edge effect were found. These somewhat contrasting findings suggest that in both vegetation types the creation of grazing refuges has similar positive effects on diversity.

## 5. Conclusion

In productive systems such as ours, the exclusion of grazing is highly likely to rapidly cause a decrease in plant species richness due to an increase in light competition. However, the edges of the grazing refuges proved beneficial to both plant and animal diversity. For grazing-sensitive species, such edges can be beneficial, and if the aim of the creation of grazing refuges is to benefit such species, it can be recommended to maximise the edge length, for example by creation of many small exclosures, rather than few large ones, or by creating serrated or bent, rather than straight edges on larger exclosures. If the use of fencing is undesirable, other, more natural ways of creating grazing refuges can be explored. For example, the deposition of coarse woody debris was shown to be beneficial to abundance and species richness of invertebrates (Barton et al., 2011), reptiles (Manning et al., 2013) and for tree recruitment (Smit et al., 2012), although these effects will disappear when the wood has decayed. In ecosystems with a high ground water table, the creation of water bodies to isolate grassland patches could be considered. Either way – by fencing or by more natural means – our study shows that creating grazing refuges is a simple but very effective tool for biodiversity conservation, particularly in areas with high herbivore densities.

## Acknowledgements

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## Appendix A. : Soil physical properties

### *A1. Methods*

We measured four properties of the soil inside (mixed sample from the entire surface) and outside (mixed sample at 20 m from each exclosure) all exclosures. Soil samples were collected in November 2013 by taking soil to a depth of 15 cm using a ø 2 cm gauge auger. Samples were taken until approximately 100 g of fresh soil was collected.

Of this soil, some 20 g were used to measure soil moisture and organic carbon content. Soil moisture was measured by weighing the samples before and after drying for 24 h at 70 °C. Organic carbon was measured by weighing the dried samples again after loss on ignition for 4 h at 550 °C. Another 20 g were used to measure pH, and the remaining ca. 50 g were used for grain size analysis. Before grain-size analysis, all samples were freeze–dried and sieved over 1 mm mesh. Hereafter, the samples were treated with hydrogen peroxide ($H_2O_2$) to remove all organic matter and salts. Grain size was measured by laser-diffraction, using the Mastersizer 2000 (Malvern Instruments, Worcestershire, United Kingdom). Percentages of five particle fractions are reported: coarse sand (500–1000 μm), medium sand (250–500 μm), fine sand (125–250 μm), very fine sand (62.5–125 μm) and silt (<63 μm).

### *A1.1. Statistical analysis*

All properties (Organic C, soil moisture, pH, all grain-size fractions) were tested for differences between the vegetation types, exclosure treatment, and exclosure position along the east-west gradient using general linear mixed models. In these models exclosure id (factorial) was taken as random variable, and vegetation type, exclosure position (numeric) and exclosure treatment (grazed/exclosure) as fixed variables. Because for pH all measurements were duplicated, an additional random variable linking these duplicates was included. Model selection was based on AIC and the Anova command for comparing alternative models.

Because the grain size fractions are not independent, we additionally performed a multivariate permutational anova. Here, vegetation type, exclosure id, exclosure treatment and all their interactive effects were used as fixed variables.

### *A2. Results*

Soil moisture and organic carbon were higher in the TH vegetation than in the SL vegetation (Table A1 and Fig. A1), but did not differ between the exclosure and control plots or along the east-west gradient. By contrast, pH did not differ between the two vegetation types, but increased somewhat to the west in the grazed control plots, but not in the exclosure plots (Table A1 and Fig. A2).

The grain size distribution showed only small differences between the vegetation types, with a significantly higher fraction of medium to fine sand (125 μm–500 μm), but a lower fraction of silt (<63 μm) in the TH vegetation (Table A1 and Fig. A3).

**Table A1**
Effects of exclosure treatment, vegetation type: short grazed (SL) or tall herbaceous (TH) vegetation, and position along the east-west gradient on soil physical properties and grain-size distribution according to mixed effects models. Only significant differences are shown.

| Property | Exclosure treatment | | Vegetation type | | E–W position | | Interactive effects | | | Model | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *t* | *p* | *t* | *p* | *t* | *P* | | *t* | *P* | $\chi^2$ | *P* |
| Soil moisture (%) | | | 4.27 | <**0.001** | | | | | | 12.39 | <**0.001** |
| Organic C (g/100 g) | | | 3.71 | **0.002** | | | | | | 10.62 | **0.001** |
| pH | −3.03 | **0.02** | | | | | Treatment × position | 3.333 | **0.01** | 17.24 | <**0.001** |
| coarse sand (0.5–1 mm) (%) | 2.38 | **0.03** | | | | | | | | 5.21 | **0.02** |
| medium sand (250–500 μm) (%) | | | 2.68 | **0.018** | | | | | | 6.23 | **0.01** |
| fine sand (125–250 μm) (%) | | | 3.68 | **0.002** | | | | | | 10.14 | **0.001** |
| very fine sand (63–125 μm) (%) | | | −2.59 | **0.02** | | | Vegetation type × treatment × position | −2.45 | **0.037** | 33.36 | <**0.001** |
| silt (<63 μm) (%) | | | | | | | Vegetation type × treatment × position | 1.84 | 0.098 | 26.9 | <**0.001** |

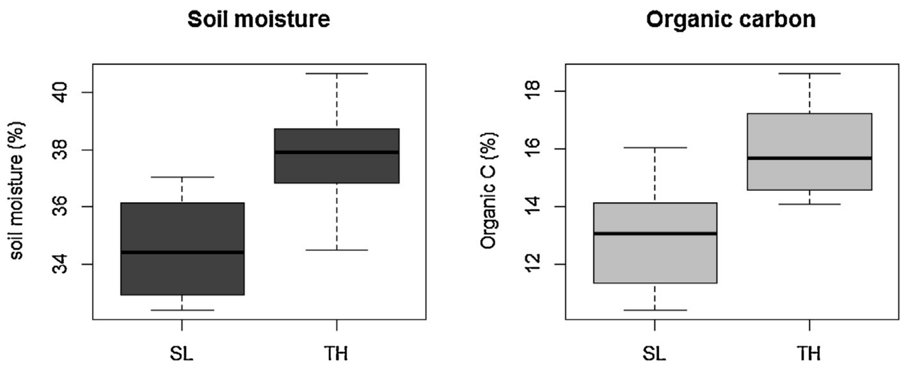

**Fig. A1.** Significant differences in soil moisture and organic carbon contents between the short-grazed (SL) and the tall herbaceous (TH) vegetation types.

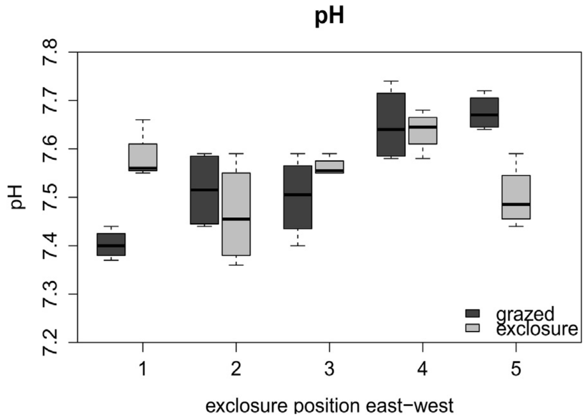

**Fig. A2.** Soil pH increased somewhat from east to west, but only under grazing. In the absence of grazing, pH differed between exclosures, but not in a systematic way. This difference is possibly caused by bioturbation by earthworms in the exclosures. The number refer to the order of the exclosures along the east–west gradient.

Additionally, there were complex interactions with exclosure position, exclosure treatment and vegetation type, where especially the second exclosure pair seemed to differ from the others, complicating interpretation (Table A1 and Fig. A3). Multivariate anova showed that both vegetation type ($F = 9.17$, $p = 0.006$, $R^2 = 0.29$) and exclosure id ($F = 5.50$, $p = 0.35$, $R^2 = 0.17$) were significant factors, but treatment ($p > 0.4$), nor any of the interactive effects were significant (all $p > 0.1$).

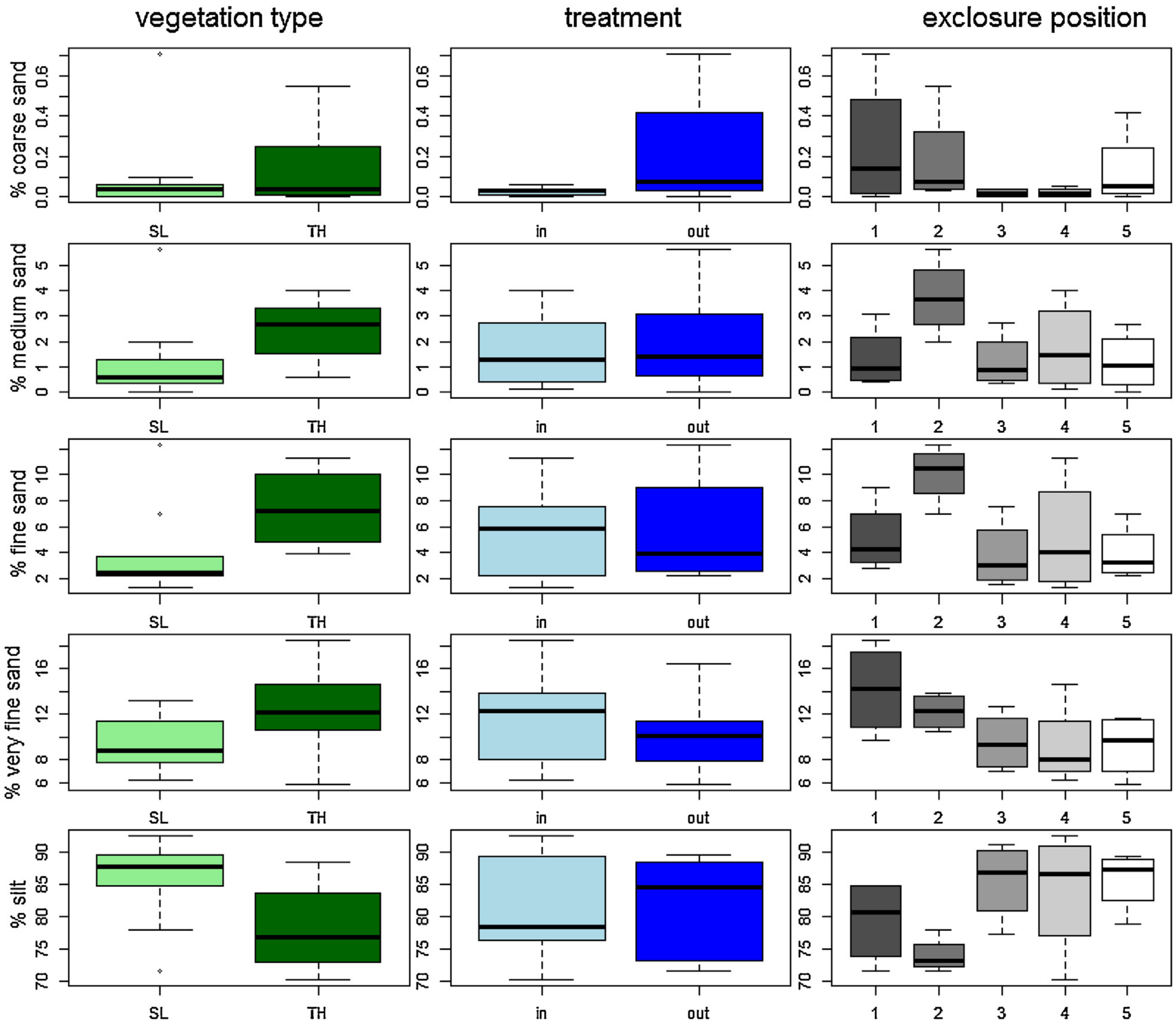

**Fig. A3.** Grain size distribution over the vegetation types, exclosure treatments and exclosure position along the east-west gradient. Particle sizes: coarse sand (500–1000 μm), medium sand (250–500 μm), fine sand (125–250 μm), very fine sand (62.5–125 μm) and silt (<63 μm).

## Appendix B.

See Table B1 and Fig B1.

**Table B1**
Permuational Multivariate anova results for species pool delineation shows strong differences in the species pools of the SG and the TH vegetation for plants and arthropods, but no differences between samples taken at 10 m and 20 m from the exclosures or systematic differences between the exclosures (see also Fig. B1).

| | | Distance treatment | | Vegetation type | | Distance × vegetation | | Exclosure id | |
|---|---|---|---|---|---|---|---|---|---|
| | | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Plants | All samples | 23.4 | <**0.001** | 4.34 | **0.01** | 2.15 | **0.04** | 1.37 | 0.16 |
| | 10–20 m | 0.93 | 0.45 | 4.57 | **0.006** | | ns | 1.22 | 0.28 |
| All arthropods | All samples | 15.08 | <**0.001** | 9.12 | <**0.001** | 2.05 | **0.03** | 1.45 | 0.07 |
| | 10–20 m | 1.23 | 0.24 | 8.09 | <**0.001** | | ns | 1.46 | 0.07 |

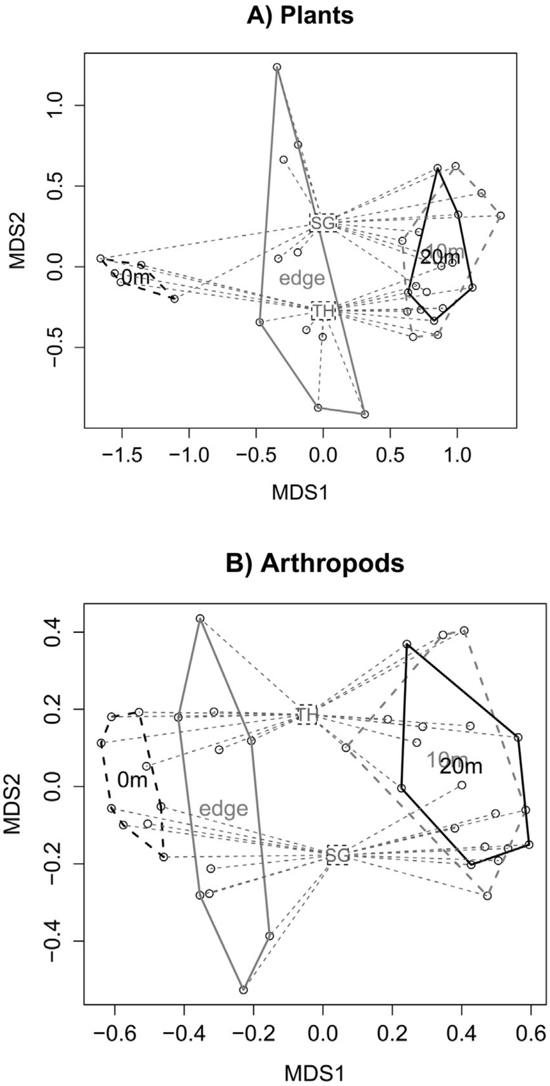

**Fig. B1.** NMDS biplots of Morisita–Horn dissimilarities for plants (a) and arthropods (b), showing clear differences between the vegetation types and effects of the exclosures.

## Appendix C.

See Fig. C1.

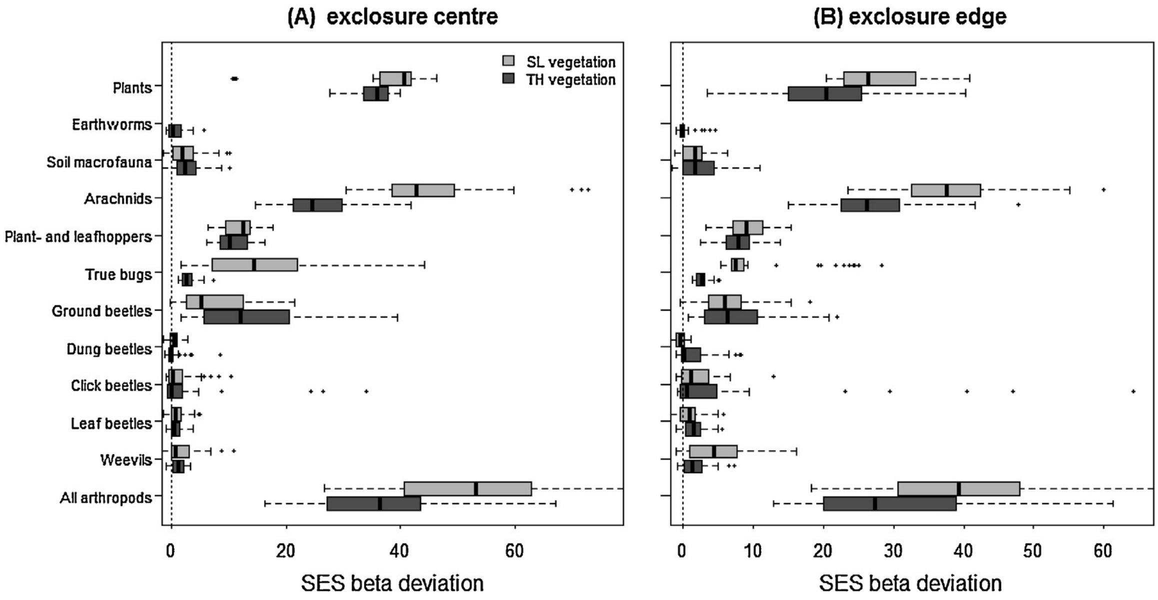

**Fig. C1.** Standardized effect size SES (mean $\beta_{corrected}$/sd $\beta_{expected}$) of corrected β-diversity (Morisita–Horn index) between the grazed controls and the exclosure centre (A) and between the grazed controls and the exclosure edge (B) over the two vegetation types short lawn (SL) and tall herbaceous (TH) vegetation.

## Appendix D. : Species list

See Table D1.

**Table D1**
Frequency (number of plots in which a species was found) of all plant and invertebrate species in year 3 of the investigation. The grazed plots are pooled since no difference in species composition was detectable between 10 and 20 m distance from the exclosures.

| | Exclosure centre (*n* = 10) | Exclosure edge (*n* = 10) | Grazed (*n* = 20) | Total incidence (*n* = 40) |
|---|---|---|---|---|
| Plants | | | | |
| *Anisantha sterilis* | | 1 | | **1** |
| *Arabidopsis thaliana* | | | 1 | **1** |
| *Capsella bursa-pastoris* | | | 12 | **12** |
| *Carduus crispus* | 1 | 8 | 15 | **24** |
| *Cerastium fontanum* | | 1 | 3 | **4** |
| *Cirsium arvense* | | 2 | 7 | **9** |
| *Dactylis glomerata* | | 3 | 2 | **5** |
| *Galeopsis bifida* | | 3 | | **3** |
| *Lactuca serriola* | | 3 | | **3** |
| *Lolium perenne* | | 8 | 20 | **28** |
| *Matricaria chamomilla* | | 4 | 11 | **15** |
| *Matricaria discoidea* | | | 7 | **7** |
| *Odontites vernus* | | 2 | | **2** |
| *Phleum pratense* | | 4 | 4 | **8** |
| *Phragmites australis* | 4 | 5 | | **9** |
| *Plantago lanceolata* | | 2 | | **2** |
| *Plantago major* | | 8 | 18 | **26** |
| *Poa annua* | | 1 | 9 | **10** |
| *Poa pratensis* | | | 1 | **1** |
| *Polygomum aviculare* | | 9 | 20 | **29** |
| *Sisymbrium officinale* | 1 | 8 | 19 | **28** |
| *Sonchus asper* | | 4 | 4 | **8** |
| *Sonchus oleraceus* | | 2 | | **2** |
| *Stellaria aquatica* | | 6 | | **6** |
| *Stellaria media* | | | 3 | **3** |
| *Taraxacum officinale* | | | 5 | **5** |
| *Trifolium pratense* | | 1 | 1 | **2** |
| *Trifolium repens* | | 2 | 18 | **20** |
| *Tripleurospermum maritimum* | | 1 | 1 | **2** |

**Table D1** (*Continued*)

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| *Urtica dioica* | 10 | 9 | | **19** |
| *Veronica persica* | | | 10 | **10** |
| Total number of species | | | | **31** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Lumbricidae (earthworms) | | | | |
| *Allolobophora chlorotica* | 6 | 5 | 10 | **21** |
| *Aporrectodea rosea* | 4 | | | **4** |
| *Lumbricus castaneus* | 5 | | 2 | **7** |
| *Lumbricus rubellus* | 9 | 8 | 5 | **22** |
| Juveniles | 10 | 11 | 18 | **39** |
| Total number of species | | | | **4** |
| – | | | | |
| Isopoda (wood lice) | | | | |
| *Phyloscia moscorum* | 3 | 3 | 1 | **7** |
| *Pocellio scaber* | 2 | 1 | 1 | **4** |
| *Trachelipus rathkii* | 3 | 2 | 1 | **6** |
| *Trichoniscus pusillus* | | | 1 | **1** |
| Total number of species | | | | **4** |
| – | | | | |
| Chilopoda (centipedes) | | | | |
| *Lamyctes emarginatus* | 1 | | | **1** |
| *Lithobobius forficatus* | 10 | 9 | 17 | **36** |
| Total number of species | | | | **2** |
| – | | | | |
| Diplopoda (millipedes) | | | | |
| *Brachydesmus superus* | 4 | 3 | | **7** |
| *Brachyiulus pusillus* | 10 | 9 | 12 | **31** |
| *Craspedosoma rawlinsii* | 10 | 10 | 7 | **27** |
| *Cylindroiulus britannicus* | | 1 | | **1** |
| *Julus scandinavicus* | 5 | 6 | 4 | **15** |
| *Polydesmus denticulatus* | 7 | 7 | 6 | **20** |
| *Polydesmus inconstans* | 2 | 1 | | **3** |
| Total number of species | | | | **7** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Arachnids Araneae (spiders) | | | | |
| Araneidae | | | | |
| *Larinioides cornutus* | 1 | 5 | 1 | **7** |
| – | | | | |
| Clubionidae | | | | |
| *Clubiona phragmitis* | 7 | 7 | 3 | **17** |
| *Clubiona reclusa* | 4 | 2 | | **6** |
| – | | | | |
| Gnaphosidae | | | | |
| *Micaria pulicaria* | 2 | 4 | 3 | **9** |
| *Zelotes latreillei* | 1 | | | **1** |
| – | | | | |
| Linyphiidae | | | | |
| *Bathyphantes gracilis* | 8 | 10 | 20 | **38** |
| *Centromeria bicolor* | 1 | | | **1** |
| *Collinsia inerrans* | 5 | 5 | 19 | **29** |
| *Dicymbium nigrum* | 9 | 8 | 1 | **18** |
| *Diplocephalus cristatus* | | | 2 | **2** |
| *Diplocephalus latifrons* | 10 | 10 | 13 | **33** |
| *Diplostyla concolor* | 10 | 10 | 14 | **34** |
| *Dismodicus bifrons* | 2 | 3 | | **5** |
| *Erigone atra* | 7 | 10 | 20 | **37** |
| *Erigone dentipalpis* | 4 | 7 | 20 | **31** |
| *Erigone longipalpis* | | | 2 | **2** |
| *Gnathonarium dentatum* | | 1 | | **1** |
| *Gongylidiellum vivum* | | 1 | | **1** |
| *Gongylidium rufipes* | 1 | | | **1** |
| *Hypomma bituberculatum* | 1 | | | **1** |
| *Leptyphantes flavipes* | | | 1 | **1** |
| *Meioneta rurestris* | 2 | 1 | 20 | **23** |
| *Mermessus trilobatus* | 1 | 2 | 9 | **12** |
| *Micrargus hebigradus* | | 1 | | **1** |
| *Microlinyphia impigra* | | 2 | 3 | **5** |
| *Neriene clathrata* | 1 | 2 | 1 | **4** |
| *Neriene montana* | | | 1 | **1** |
| *Oedothorax apicatus* | | | 9 | **9** |
| *Oedothorax fuscus* | 6 | 3 | 17 | **26** |
| *Oedothorax retusus* | 1 | | | **1** |
| *Porrhomma microphtalmum* | 1 | 1 | 8 | **10** |
| *Porrhomma oblitum* | | | 2 | **2** |

**Table D1** (*Continued*)

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| *Porrhomma pygmaeum* | | | 1 | **1** |
| *Stemonyphantes lineatus* | | | 1 | **1** |
| *Tapinocyba insecta* | | | 3 | **3** |
| *Tenuiphantes tenuis* | 8 | 3 | 18 | **29** |
| *Tiso vagans* | 3 | 1 | 4 | **8** |
| *Troxochrus scabriculus* | 8 | 10 | 19 | **37** |
| – | | | | |
| Lycosidae | | | | |
| *Alopecosa pulverulenta* | | 1 | | **1** |
| *Pardosa agrestis* | | 2 | 7 | **9** |
| *Pardosa amentata* | 10 | 10 | 13 | **33** |
| *Pardosa palustris* | | | 3 | **3** |
| *Pardosa prativaga* | 10 | 10 | 16 | **36** |
| *Piratula hygrophila* | 9 | 7 | 5 | **21** |
| *Trochosa ruricola* | 8 | 8 | 7 | **23** |
| – | | | | |
| Mimetidae | | | | |
| *Ero cambridgei* | | | 1 | **1** |
| *Ero furcata* | 1 | 1 | | **2** |
| – | | | | |
| Pisauridae | | | | |
| *Pisaura mirabilis* | 1 | 1 | | **2** |
| – | | | | |
| Salticidae | | | | |
| *Marpissa muscosa* | | 1 | | **1** |
| – | | | | |
| Tetragnathidae | | | | |
| *Pachygnatha clercki* | 9 | 10 | 19 | **38** |
| *Pachygnatha degeeri* | 5 | 10 | 19 | **34** |
| *Tetragnatha cf. extensa* | 2 | 2 | | **4** |
| – | | | | |
| Theridiidae | | | | |
| *Enoplognatha ovata* | 1 | 2 | | **3** |
| *Robertus lividus* | 2 | 4 | 8 | **14** |
| – | | | | |
| Thomisidae | | | | |
| *Ozyptilla praticola* | 1 | 1 | | **2** |
| *Xysticus ulmi* | 8 | 7 | 1 | **16** |
| Total number of species | | | | **56** |
| | | | | |
| Opiliones (harvestmen) | | | | |
| *Mitopus morio* | | 1 | 1 | **2** |
| *Oligolophus tridens* | 7 | 6 | 1 | **14** |
| *Rilaena triangularis* | 1 | | 1 | **2** |
| Total number of species | | | | **3** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Auchenorrhyncha (plant- and leafhoppers) | | | | |
| Aphrophoridae | | | | |
| *Philaenus spumarius* | 1 | 2 | | **3** |
| | | | | |
| Cicadellidae | | | | |
| *Anoscopus flavostriatus* | 4 | 7 | 9 | **20** |
| *Anoscopus serratulae* | | 9 | 9 | **18** |
| *Aphrodes makarovi* | 9 | 10 | 16 | **35** |
| *Arthaldeus pascuellus* | 1 | 3 | 7 | **11** |
| *Cicadula persimilis* | | 2 | | **2** |
| *Deltocephalus pulicaris* | | 1 | 10 | **11** |
| *Errastunus occelaris* | | 1 | | **1** |
| *Eupteryx aurata* | 5 | 3 | 3 | **11** |
| *Eupteryx urticae* | | 2 | | **2** |
| *Euscelis lineolatus* | | | 2 | **2** |
| *Macrosteles cristatus* | 3 | 5 | 20 | **28** |
| *Macrosteles variatus* | 4 | 1 | | **5** |
| *Streptanus aemulans* | | 2 | 3 | **5** |
| *Streptanus sordidus* | | 2 | 6 | **8** |
| | | | | |
| Cixidae | | | | |
| *Cixius spec* | | 1 | | **1** |
| | | | | |
| Delphacidae | | | | |
| *Javesella dubia* | 5 | 6 | 13 | **24** |
| *Javesella pelucida* | | 1 | 1 | **2** |
| | | | | |
| Typhlocybinae | | | | |
| *Zyginidia scutelaris* | | | 1 | **1** |

**Table D1** (*Continued*)

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Total number of species | | | | **19** |
| | | | | |
| Psylloidea (jumping plant lice) | | | | |
| Triozidae | | | | |
| *Trioza urticae* | | 3 | | **3** |
| Total number of species | | | | **1** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Heteroptera (true bugs) | | | | |
| Anthocoridae | | | | |
| *Anthocoris nemorum* | 2 | | | **2** |
| *Orius majusculus* | 2 | 2 | 3 | **7** |
| | | | | |
| Lygaeidae | | | | |
| *Lygus rugulipennis* | | | 6 | **6** |
| | | | | |
| Miridae | | | | |
| *Adelphocoris quadripunctatus* | | 2 | | **2** |
| *Apolygus spinolae* | 1 | | | **1** |
| *Chlamidatus saltitans* | 1 | | 10 | **11** |
| *Conostethus venustus* | | | 5 | **5** |
| *Liocoris tripustulatus* | | 1 | | **1** |
| *Megaloceroea recticornis* | | | 1 | **1** |
| *Plagiognathus arbustorum* | 1 | | | **1** |
| *Scolopostethus affinis* | 9 | 6 | | **15** |
| *Scolopostethus thomsoni* | 9 | 7 | 2 | **18** |
| *Stenodema calcarata* | | 2 | | **2** |
| *Trigonotylus caelestialium* | | 1 | 14 | **15** |
| | | | | |
| Nabidae | | | | |
| *Nabis ferus* | | | 13 | **13** |
| *Nabis limbatus* | 1 | | | **1** |
| | | | | |
| Saldidae | | | | |
| *Saldula fucicola* | | | 1 | **1** |
| *Saldula orthochila* | | | 12 | **12** |
| *Saldula saltatoria* | | 2 | 1 | **3** |
| | | | | |
| Tingidae | | | | |
| *Tingis ampliata* | | 2 | | **2** |
| *Tingis cardui* | | 2 | 1 | **3** |
| Total number of species | | | | **21** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Coleoptera | | | | |
| Carabidae (ground beetles) | | | | |
| *Acupalpus exiguus* | 6 | 7 | 5 | **18** |
| *Acupalpus meridianus* | 1 | | 2 | **3** |
| *Acupalpus parvulus* | 1 | | | **1** |
| *Agonum fuliginosum* | 1 | 1 | | **2** |
| *Agonum muelleri* | 1 | 1 | 3 | **5** |
| *Amara aenea* | 9 | 9 | 13 | **31** |
| *Amara aulica* | 9 | 9 | 6 | **24** |
| *Amara bifrons* | 2 | 2 | 9 | **13** |
| *Amara communis* | 2 | 1 | | **3** |
| *Amara familiaris* | 3 | 4 | 4 | **11** |
| *Amara lunicollis* | | 1 | 1 | **2** |
| *Amara ovata* | | 2 | | **2** |
| *Amara similata* | 4 | 3 | 7 | **14** |
| *Anchomenus dorsalis* | 10 | 10 | 20 | **40** |
| *Anisodactylus binotatus* | 1 | | | **1** |
| *Badister bullatus* | 7 | 9 | 7 | **23** |
| *Badister lacertosus* | 10 | 4 | | **14** |
| *Badister sodalis* | 8 | 6 | 4 | **18** |
| *Bembidion aeneum* | 8 | 7 | 4 | **19** |
| *Bembidion bigutattum* | 10 | 5 | 4 | **19** |
| *Bembidion bipunctatum* | | 2 | | **2** |
| *Bembidion guttula* | 1 | | | **1** |
| *Bembidion lampros* | 4 | 8 | 17 | **29** |
| *Bembidion lunulatum* | 2 | 2 | | **4** |
| *Bembidion obtusum* | | 3 | 1 | **4** |
| *Bembidion properans* | 1 | 4 | 14 | **19** |
| *Blemus discus* | 2 | 3 | | **5** |
| *Calathus melanocephalus* | | | 1 | **1** |
| *Calathus rotundicollis* | 1 | 1 | | **2** |
| *Carabus granulatus* | 10 | 10 | 11 | **31** |

**Table D1** (*Continued*)

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| *Chlaenius nigricornis* | 1 | | | **1** |
| *Clivina fossor* | 7 | 5 | 7 | **19** |
| *Dyschirius globosus* | 3 | 4 | 2 | **9** |
| *Harpalus affinis* | 6 | 10 | 16 | **32** |
| *Harpalus laevipes* | 1 | | | **1** |
| *Harpalus rufipes* | 10 | 10 | 20 | **40** |
| *Leistus terminatus* | | 1 | | **1** |
| *Loricera pilicornis* | 7 | 3 | 5 | **15** |
| *Nebria brevicollis* | | 3 | | **3** |
| *Ophonus rufibarbis* | 2 | | | **2** |
| *Oxypselaphus obscurus* | 3 | 3 | 2 | **8** |
| *Poecilus cupreus* | 4 | 8 | 5 | **17** |
| *Pterostichus melanarius* | 10 | 10 | 20 | **40** |
| *Pterostichus niger* | 10 | 10 | 17 | **37** |
| *Pterostichus strenuus* | 10 | 9 | 16 | **35** |
| *Pterostichus vernalis* | 10 | 10 | 19 | **39** |
| *Stomis pumicatus* | 1 | 1 | | **2** |
| *Syntomus foveatus* | | 1 | | **1** |
| *Trechus obtusus* | 8 | 9 | 7 | **24** |
| Total number of species | | | | **49** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Scarabaeoidea (dung beetles) | | | | |
| *Aphodius ater* | 1 | 1 | 3 | **5** |
| *Aphodius depressus* | | | 1 | **1** |
| *Aphodius foetens* | | | 7 | **7** |
| *Aphodius fossor* | | 1 | 1 | **2** |
| *Aphodius granarius* | 1 | 1 | 2 | **4** |
| *Aphodius luridus* | 7 | 9 | 20 | **36** |
| *Aphodius plagiatus* | | 1 | | **1** |
| *Aphodius prodromus* | 1 | 1 | 3 | **5** |
| *Aphodius pusillus* | | 1 | 1 | **2** |
| *Aphodius rufipes* | 1 | 2 | 1 | **4** |
| *Aphodius rufus* | 2 | 1 | | **3** |
| *Aphodius sphacelatus* | | | 2 | **2** |
| *Geotrupus spiniger* | 1 | 6 | 6 | **13** |
| *Oxyomus sylvestris* | 8 | 4 | 4 | **16** |
| Total number of species | | | | **14** |
| – | | | | |
| Elateridae (click beetles) | | | | |
| *Agriotes lineatus* | 9 | 10 | 20 | **39** |
| *Agriotes obscurus* | 10 | 10 | 20 | **40** |
| *Agriotes sputator* | 4 | 8 | 12 | **24** |
| *Ampedus cinnabarinus* | | 1 | | **1** |
| *Dalopius marginatus* | | | 1 | **1** |
| Total number of species | | | | **5** |

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Chrysomelidae (leaf beetles) | | | | |
| *Aphtona euphorbiae* | 1 | | | **1** |
| *Cassida flaveolus* | | 3 | 1 | **4** |
| *Cassida rubiginosa* | 1 | 3 | | **4** |
| *Cassida vittata* | | 1 | | **1** |
| *Chaetocnema concinna* | 3 | 7 | 6 | **16** |
| *Chaetocnema hortensis* | | 2 | 6 | **8** |
| *Crepidodera aurata* | 3 | | | **3** |
| *Crepidodera fulvicornis* | 1 | | | **1** |
| *Crepidodera plutus* | 1 | | | **1** |
| *Gastrophysa polygoni* | | | 4 | **4** |
| *Longitarsus atricillus* | | | 1 | **1** |
| *Longitarsus luridus* | 1 | | 3 | **4** |
| *Longitarsus melanocephalus* | | 5 | 12 | **17** |
| *Longitarsus parvulus* | | 1 | | **1** |
| *Longitarsus suturellus* | 1 | 1 | | **2** |
| *Oulema melanopus* | | 1 | | **1** |
| *Phyllotreta exclamationis* | | 1 | | **1** |
| *Phyllotreta nemorum* | 10 | 10 | 16 | **36** |
| *Phyllotreta nigripes* | | | 1 | **1** |
| *Phyllotreta undulata* | 5 | 6 | 4 | **15** |
| *Psylliodes chrysocephala* | | | 1 | **1** |
| *Psylloides chalcomera* | 4 | 7 | 7 | **18** |
| *Psylloides cuprea* | 10 | 10 | 15 | **35** |
| *Sphaeroderma testaceum* | | 1 | 1 | **2** |
| Total number of species | | | | **24** |

**Table D1** (*Continued*)

| | Exclosure centre ($n = 10$) | Exclosure edge ($n = 10$) | Grazed ($n = 20$) | Total incidence ($n = 40$) |
|---|---|---|---|---|
| Curculionidae/Curculionoidea (weevils) | | | | |
| *Amalus scortillum* | | 5 | 10 | **15** |
| *Ceratapion gibbirostre* | | 2 | | **2** |
| *Ceratapion onopordi* | | 4 | 2 | **6** |
| *Ceutorhynchus chalybaeus* | 5 | 10 | 17 | **32** |
| *Ceutorhynchus erysimi* | 9 | 10 | 20 | **39** |
| *Ceutorrhynchus pyrrhorhynchus* | 3 | 2 | 2 | **7** |
| *Ceutorrhynchus typhae* | 6 | 10 | 14 | **30** |
| *Hadroplontus litura* | 1 | 4 | 3 | **8** |
| *Hypera nigrirostris* | | 1 | 4 | **5** |
| *Ischnopterapion virens* | | 1 | 10 | **11** |
| *Microplontus rugulosus* | | 2 | 1 | **3** |
| *Nedyus quadrimaculatus* | 4 | 3 | 1 | **8** |
| *Parethelcus pollinarius* | 2 | | | **2** |
| *Pelenomus quadritruberculatus* | 7 | 10 | 19 | **36** |
| *Phyllobius pomaceus* | 2 | 1 | 2 | **5** |
| *Phyllobius pyri* | | 1 | | **1** |
| *Protapion fulvipes* | 1 | 2 | 7 | **10** |
| *Rhinoncus perpendicularis* | 1 | 6 | 7 | **14** |
| *Sitona hispidulus* | | 2 | 17 | **19** |
| *Sitona lepidus* | 1 | 4 | 20 | **25** |
| *Tanymecus palliatus* | | | 1 | **1** |
| *Trichosirocalus troglodytes* | | 1 | 1 | **2** |
| *Tychius picirostris* | | 1 | 1 | **2** |
| Total number of species | | | | **23** |

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