Grassland restoration and soil disturbance: the effects of harrowing and ploughing on ground beetle communities

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Abstract

Semi-natural grasslands are hotspots of biodiversity but since a few decades they are disappearing at an alarming rate due to land-use changes and agricultural intensification. Those grasslands that are still extensively managed moreover suffer from ecological degradation, notably impoverishment of species diversity. One of the most common techniques applied for restoring grasslands consists in reseeding its plant community. This usually requires a preliminary soil disturbance, via either harrowing or ploughing, to enable the germination and establishement of the added plants that would otherwise be hampered via out-competition by extant ground vegetation. It is still poorly understood, however, to which extent such highly disturbing operations negatively impact biodiversity. The aim of this study was to assess the mid-term effects (after one year) of harrowing and ploughing on ground beetle communities. Twelve sites of the Swiss lowlands were selected to carry out our experimental manipulations. In every study site, four different restoration treatments plus a control were randomly allocated to one out of five extensively managed hay meadows. The treatments consisted in: 1) hay harrow: hay transfer from a species rich donor meadow onto a meadow that had been harrowed beforehand; 2) hay plough: same but the hay was transferred onto a meadow ploughed beforehand; 3) seed natural: sowing of a seed mixture collected by hand from a species-rich donor meadow onto a meadow ploughed beforehand; 4) seed commercial: sowing of a commercial seed mixture on a ploughed meadow. Ground beetles were sampled one year before (in 2018) and one year after the restoration (in 2020) operations using pitfall traps.

We detected no significant effects of soil disturbance on ground beetle species richness and abundance in 2020, but restored meadows that had undergone some soil disturbance harboured a higher beetle diversity (Shannon index) compared to control meadows. Small changes regarding species-specific traits were also observed in the beetle community namely a higher community body size in ploughed meadows compared to controls, a higher community trophic

level in hay plough meadows compared to controls and a higher community humidity preferences in seed natural meadows compared to both hay harrow and control meadows. In addition, a positive correlation was found in restored, ploughed meadows between ground beetles abundance and the amount of unrestored grasslands in the surroundings of the experimental meadow, which is attributed to a refuge effect. Our results suggest a fairly high resilience of the ground beetle communities to the soil disturbance operations that typically accompany the active restoration of plant species-poor grasslands.

Introduction

Semi-natural grasslands are a hotspot for the faunal and floral diversity of agricultural land (Wilson *et al.* 2012; Habel *et al.* 2013). However, since the 1940s, major changes in the agricultural practices at the European scale (e.g. through intensification) have led to a dramatic decrease in farmland biodiversity (Donald, Green & Heath 2001; Stoate *et al.* 2001; Robinson & Sutherland 2002). In Switzerland for example, grasslands have been particularly impacted, losing up to 95% of the original dry meadows and pastures surfaces and up to 98% of the original *Arrhenatherion* surfaces within the last one hundred years (Lachat *et al.* 2010). To counter these negative tendencies, agri-environment schemes (AES) have been implemented during the 1990s throughout Europe and in 1998 in Switzerland (OPD 2013). The aim of AES is to promote biodiversity by financially supporting the farmers to use more biodiversity-friendly agricultural practices.

The positive effects of these schemes (e.g. hedgerows, wildflower strips or extensively managed grasslands) on the farmland biodiversity remained so far limited. Indeed, Kleijn *et al.* (2006), as well as Chaudron *et al.* (2020), which studied a broad range of organisms (including vascular plants, birds, bees, grasshoppers, ground beetles and crickets) across Europe found only neutral to moderately positive effects of the schemes on biodiversity. At the Swiss scale, Aviron *et al.* (2011) showed an increase in butterflies generalist species in AES wildflower strips but the specialist species remained out of the positive influence of this scheme. Considering the plant species richness of AES extensively managed hay meadows, Van Klink *et al.* (2017) found no change within a five years period, meaning that passive restoration (limited to a cessation of fertiliser applications and a late first cut) did not provide the necessary conditions for new species to establish. This poor output is linked to the fact that grasslands harbouring little variety in terms of plant species often suffer from a depleted seed bank due to decades of intensive exploitation (Bakker *et al.* 1996; Bekker *et al.* 1997; Schmiede, Otte &

Donath 2012). The active restoration of these ecosystems becomes thus increasingly important (e.g. Anderson 1995; Walker *et al.* 2004; Baur 2014; Waldén & Lindborg 2016).

One of the most efficient method to actively restore grasslands consists in the addition of seeds (Rey Benayas & Bullock 2012). Though, disturbing the soil surface prior to restoration (e.g. via harrowing or ploughing) is necessary to achieve a successful plant restoration using this technique (Edwards *et al.* 2007; Kiehl *et al.* 2010), especially as it provides new germination niches (Coulson *et al.* 2001). However, soil tillage is a severe disturbance that impacts deeply the ground-dwelling fauna (Kladivko 2001). As this kind of disturbance is uncommon in grasslands managed under extensive practices, its effects have not been much studied yet. Improving the restoration process in extensively managed grasslands is thus tighlty linked to a deeper understanding of the impacts of soil tillage on ground-dwelling organisms and to the description of the least harmful methods for the invertebrates.

In this respect, ground beetles (Coleoptera: Carabidae) were chosen as study group. These beetles are known to be a good indicator taxon when considered together with other beetles families or spiders (Rainio & Niemela 2003; Koivula 2011) and they are important arthropods for the grassland ecosystem. Indeed, they are useful for the primary production of agricultural lands, acting as control agents against undesirable plants or animals like aphids (Thiele 1977; Luff 1987). They also represent an important link in the food-chain, as many vertebrates depend on them as a food resource (e.g. amphibians, reptiles, bats, birds; Lovei & Sunderland 1996; Dietz & Kiefer 2014).

Tillage can affect carabid beetles in two ways: either directly by killing or lethally wounding them or indirectly by making the habitat inhospitable. Shearin, Reberg-Horton and Gallandt (2014) studied the direct mortality induced by different tillage techniques on ground beetles in grasslands. A 50% decrease in activity density was demonstrated in both ploughing and harrowing treatments. In cropland, Kromp (1999), as well as Thorbek and Bilde (2004), investigated the indirect mortality due to tillage one month after the treatment. Both studies could not demonstrate any negative effect of harrowing on ground beetle populations, but it was shown that ploughing does harm both species richness and abundance. Additionnally, Woodcock *et al.* (2008) showed a higher restoration success (defined as the replication of the community of a species-rich grassland) of a phytophagous beetles community using a harrowing treatment compared to untouched controls.

Species richness and abundance are not the only variables that characterize a community. Species-specific traits, such as body size, trophic level or humidity preferences also give useful hints on the impacts of the restoration (Barber *et al.* 2017). It was demonstrated that smaller beetles prevail after a strong disturbance (e.g. tilling, mowing or grazing events; Blake *et al.* 1994; Rainio & Niemela 2003; Hanson *et al.* 2016) and it is known that whereas predatory beetles are more abundant in intensively managed habitats (e.g. cropland), herbivorous species are favoured mostly in extensively managed, grassy areas (Woodcock *et al.* 2010a; Birkhofer, Wolters & Diekötter 2014; Hanson *et al.* 2016). Considering humidity preferences, it was shown that soil water content determines the carabids species assemblage (Eyre, Luff & Rushton 1990). Hygrophilous beetles will thus be attracted by moist areas whereas a dry soil will harbour a xerophilous community. However, regarding the effect of tillage on the soil water content itself, no clear trend could be demonstrated (Strudley, Green & Ascough II 2008). Still, Khurshid *et al.* (2006) showed that in a corn field, ploughing leads to the highest levels in soil moisture content and vegetation height. Regarding overwintering habitat preferences, it is widely accepted that adult ground beetles choose mostly grasslands while larvae tend to select arable lands for spending winter (Purvis & Fadl 2002; Holland, Birkett & Southway 2009). Moreover, it was shown that *Pterostichus melanarius* (Illiger, 1798), a larval overwinterer, experienced a strong decrease detectable up to six months after spring tillage (Purvis & Fadl 1996).

The aim of this study was to investigate the mid-term effects of a soil disturbance (harrowing or ploughing) on the carabid beetle community. These impacts were assessed one year after the disturbance linked to the active restoration of extensively managed hay meadows. The following hypotheses were formulated mainly according to the above-cited cropland literature: H1) ploughing would negatively affect the species richness and abundance of ground beetles, whereas the harrowing treatment would show no effect; H2) ploughing would induce changes in the community according to species-specific traits (e.g. a decrease of the mean community body size and an increase of the predatory, hygrophilous and larval overwinterer beetle abundance). In addition, we expected to find more carabids in restored meadows presenting a high proportion of undisturbed grassland surface surrounding the restored area (H3). This last hypothesis is based on studies showing that in cropland, carabids species richness and abundance is positively correlated with the percentage of natural or semi-natural habitats in the surrounding landscape (e.g. Lys, Zimmermann & Nentwig 1994; Purtauf *et al.* 2005; Boetzl *et al.* 2019). Thus, the amount of non-restored extensively managed grassland adjacent to the disturbance area, acting as a refuge or simply as intact source population for future (re)colonisation, might influence positively the response of ground beetles abundance to the restoration event.

This study was conducted within the framework of the Grassland restoration project launched in 2018 by the Division of Conservation Biology (University of Bern, Switzerland). This project investigates experimentally the long-term effects of different restoration methods (including two soil disturbance levels and three seed addition techniques) on the plant and invertebrate populations of relatively species-poor extensively managed grasslands.

Materials and methods

Study sites and experimental design

The study was conducted within twelve sampling regions located in the Swiss lowlands and distributed between Nyon (VD) and Pfaffnau (LU) (Fig. 1). All of these regions were at least 10 km apart. Within each region, five meadows, found at an elevation between 450 and 720 m a.s.l., were selected in 2018. They were comprised in a radius of 3 km but were at least 400 m apart. All these meadows presented a relatively low plant species richness and were registered as BPA (the Swiss AES) extensively managed hay meadows since at least 2012. This implied that the first hay cut could not be done before 15th June and that no pesticide or fertilizer was applied. The mowing frequency lied between two and three cuts per year, whereof the last cut could be replaced by autumn grazing.

In 2019, the four following restoration treatments, plus a control without any intervention, were randomly assigned to the five meadows of each region:

1) Sowing of a commercial seed mixture on a ploughed meadow; abbreviated SC
2) Sowing of a hand-collected seed mixture on a ploughed meadow; SN
3) Hay transfer from a species rich donor meadow on a ploughed meadow; HP
4) Hay transfer from a species rich donor meadow on a harrowed meadow; HH
5) Control: no seed addition and no soil disturbance; C

For all the sowing treatments and the hay transfer on a ploughed meadow treatment (SC, SN and HP), the area had to be ploughed in early spring. Then, it was regularly harrowed (every four to six weeks) in order to prevent the growth of unwanted vegetation. Finally, shortly before sowing, which occurred in May, respectively transferring the hay, which occurred in June, the meadow was once more harrowed to level the soil.

For the hay transfer on a harrowed meadow, the grass was cut approximately one week before the treatment. Then, a few days before the sowing, the soil was superficially harrowed two to three times. A graphical overview of the experiment is presented in the Figure S1.

Ground beetles sampling

The project was constructed as a before-after-control-intervention (BACI) experiment. It started in 2018 with the selection of the study site and ground beetles were sampled in all 60 meadows. In 2019, meadows were restored and in 2020, only 59 meadows were sampled for invertebrates as one field had to be set aside due to a restoration failure. This was probably caused by a strong storm that washed the freshly sown seeds away. Pitfall traps were used to collect carabids. Two trapping sessions were defined following the method applied by Van Klink *et al.* (2019): the first session was planned before and the second after the first mowing event, which could not happen before 15th June under the BPA regulations. The first pitfall traps were placed in mid-May and the last were collected by the end of July. Each session was divided in two one-week trapping periods. After the first week, the traps were emptied and new ones were placed for one more week. To build the pitfall traps, white plastic cups were used (diameter = 90 mm, volume = 550 ml). Water (0.083 litres) and propylene glycol (0.166 litres) were poured in each cup in order to kill and preserve the carabids. A pinch of detergent (sodium dodecyl sulphate) was added to reduce the surface tension. The pitfalls were protected from rainfall by a transparent plastic cover (18 x 18 cm) that was placed 5 cm upon the cup. Moreover, to prevent small mammals or reptiles to fall in the traps, a metal grid was installed all around it (Fig. 2).

Every meadow was sampled with four pitfalls, which were set up in the corners of a 10 x 10 m square. Permanent points have been randomly placed at the beginning of the project in each meadow. These served as beacon and the pitfall square was placed 30 m away from it. The resulting 1904 pitfalls were brought to the lab for sorting and identification. After sorting, the insects were conserved in jars containing 60% ethanol. The abundance was counted for each pitfall but due to time constraints, only one quarter of the samples (one pitfall per meadow and per trapping week) could be identified up to the species level (Trautner & Geigenmüller 1987; Müller-Motzfeld 2004).

Biodiversity index

To measure biodiversity, we used the Shannon index (*H*). It was calculated as follows:

$$H = \sum_{i=1}^{n} \frac{N_i}{N_{tot}} * ln \frac{N_i}{N_{tot}}$$

Where N_i is the number of individuals of the species i and N_{tot} is the summed abundance of all species for the sample.

Community indices

We chose to investigate four traits (body size, trophic level, humidity preference and hibernation stage) to describe the impact of treatments on the community. The trait categorization of each species was based mostly on Luka *et al.* (2009) but if data was missing, other sources where used to complete our trait database (Marggi 1992; Fazekas 1997; Cole *et al.* 2002; Müller-Motzfeld 2004; Lundgren 2009). Changes in the community were described using the following trait-based community weighted means (Table 1):

- Community body size index (CBI): The community weighted mean for the body size was calculated per meadow. The mean species size (mm) was taken for the calculation.

- Community trophic index (CTI): Two discrete species-specific trophic categories were used: 1 = herbivore; 2 = predator. The few omnivorous beetles were attributed to either one of both classes according to their main feeding habit.
- Community humidity preference index (CHPI): Three discrete species-specific humidity preference categories were used: 1 = xerophilous; 2 = mesophilic; 3= hygrophilous.
- Community hibernation index (CHI): Three discrete species-specific hibernation stage categories were used: 1 = overwintering as larvae only, 2 = overwintering either as larvae or as adults; 3 = overwintering as adults only.

The community indices CI were calculated as follows:

$$CI = \sum_{i=1}^{n} \frac{N_i}{N_{tot}} * SI_i$$

Where N_i is the abundance of the species i, N_{tot} is the summed abundance of all species and SI_i is the specific index of the species i.

The use of discrete categories created gradients. Thus, ground beetles communities featuring low indices harboured smaller or more herbivorous / xerophilous / larval overwintering beetles compared with communities presenting higher indices which sheltered hence bigger or more predatory / hygrophilous / adult overwintering beetles.

Refuge opportunities

Due to size discrepancies between the donor and the receiver surfaces or to the proximity of hedgerows or forest hedges, some of the study meadows were not entirely restored. Thus, the grassland parts that were neither ploughed nor harrowed might have served as refuge areas for invertebrates, similarly to what is observed during mowing events (e.g. Humbert *et al.* 2012;

Buri, Arlettaz & Humbert 2013; Kühne *et al.* 2015). To analyze the effect of this refuge opportunity, we calculated a ratio by dividing the non-restored area by the entire meadow area. Note that when the meadow was very large, a maximum of 50 m distance from the restored area was taken into account as entire meadow area. The ratio results in a value between 0 and 1, with 0 meaning the whole meadow was ploughed (no refuge opportunity) and higher values meaning a higher proportion of the initial meadow was not disturbed and could thus offer a potential refuge for ground beetles.

Statistical analysis

For all the analyses, either linear mixed-effects or generalized linear mixed-effects models (LMMs or GLMMs; R package lme4; Bates *et al.* 2007) were used. The region (12 levels) was always integrated as random factor to correct for region-specific differences and the treatments were set as explanatory variables in all models except the one analyzing the refuge ratio. Year effects were systematically tested by analysing the controls 2018 and 2020. If they were significantly different, the analysis was run on the difference between 2020 and 2018 values (i.e. 2020 data minus 2018 data) and not on the data 2020. All the analyses were performed using the statistical software R 4.0.2. (R Core Team 2020).

The species richness data of the first and second trapping sessions (with a total of 8'387 individuals) were pooled, resulting in a species richness variable per year and per meadow. This was then used as a response variable to analyse the effects of treatments on species richness and diversity (Shannon index) with GLMMs models and a poisson distribution. To describe the effects of treatments on the abundance of beetles, all the collected pitfalls (for a total of 31'209 individuals; generally, four pitfalls per meadow) were pooled per meadow either before or after mowing. The analyses on the abundance were thus run on the mean abundances per meadow and per session. LMMs were applied with the mean abundance as response variable.

The four different community indices were considered per year and taken as response variables. We used LMMs or GLMMs to compare the effects of harrowing and ploughing on the ground beetle community. Additionally, a multivariate regression was run on the 18 species present in at least eight regions and at least once in each of the five treatments in total. It was performed using the R package gllvm (Niku *et al.* 2017) in order to account for individual variations at the species level in response to treatments. Finally, the response of species richness and abundance to the refuge ratio, considered as the explanatory variable, was analysed using LMMs.

Results

Overall, 1904 pitfalls were processed, of which 66 were removed, mainly because of the presence of small mammals. In total, we caught 31’209 carabids, out of which 8’387 were identified to the species level. We found 73 species in our samples (see Fig. S2 and Table S1 for a complete species list with their different traits and abundances). *Amara fulvipes* (Audinet-Serville, 1821) was by far the most common species, with 938 individuals for the year 2018 and 1’012 in 2020, making up alone some 23% of the identified catch (22% in 2018 and 24% in 2020). The 10 most common species (including *A. fulvipes*) reached around 80% (83% in 2018 and 78% in 2020) of the identified catch.

As the treatments were randomly allocated within a region, we did not expect to find any difference between control and treatments or within treatments before the restoration event. Nevertheless, considering the stochasticity that might arise in a natural system, some exceptions to this rule are possible. Hence, in order to alleviate the following section, the only results presented for 2018 are these particular exceptions. Moreover, the output values of the analyses (estimates, standard errors and p-values) are presented only in the Tables S2 (2018) and S3 (2020).

Ground beetle species richness, abundance and diversity

In 2018, the mean ± standard deviation (SD) ground beetle species richness per meadow was 10.56 ± 3.21, whereas it reached 12.46 ± 3.22 in 2020. The difference between the controls 2018 and 2020 revealed no statistically significant year effect (Table S4) thus, species richness analyses were run on the 2018 and 2020 data separately. No significant effect of the treatments compared to the control or within the treatments could be detected (Fig. S3).

In 2018 before mowing, the mean ground beetle abundance ± SD per trap was 25.51 ± 14.30 and in 2020, it was 25.29 ± 13.92. After mowing, the mean ground beetle abundance per trap was 8.39 ± 6.35 in 2018 and 9.10 ± 5.85 in 2020. The difference between the controls 2018 and 2020 revealed no statistically significant year effect (Table S4), thus, abundance analyses were run on the 2018 and 2020 data separately. No significant effect of the treatments compared to the control or within the treatments could be detected (Fig. S4).

The widespread species *A. fulvipes* makes up almost a quarter of the ground beetles caught. This abundant species might have blurred the detection of potential impacts of treatments on other species. Thus, the analyses on the abundance was carried out again excluding this species. So then, without *A. fulvipes* and before mowing, the mean ground beetle abundance per trap was 19.85 ± 14.26 in 2018 and 17.89 ± 11.16 in 2020 and after mowing, the mean ground beetle abundance per trap was 6.94 ± 5.19 in 2018 and 9.42 ± 10.29 in 2020. Significantly more beetles were found in SC-meadows compared to HH- and SN-meadows in 2018 before mowing. In 2020 before mowing, in the contrary, there were significantly more beetles in HH-meadows than in SC-meadows. No effect could be detected after mowing.

Considering the Shannon index, the first analysis revealed no significant year effect (Table S4). The subsequent analyses were thus run on the 2018 and 2020 data separately. It is to be highlighted that HP-meadows harboured already a significantly higher index compared to SC-meadows in 2018, but the most interesting finding concerning this index is that all treatments presented a significantly higher diversity than C-meadows in 2020 (Fig. 3).

Community indices

Considering the community body size (CBI), the difference between the controls 2018 and 2020 revealed no significant year effect (Table S4) and the analyses were thus run on the 2018 and 2020 data separately. The ground beetle CBI of HP-meadows was significantly bigger than in the HH-, C- and SC-meadows in 2020. Moreover, the SN-community was significantly bigger than the C-meadows community (Fig. 4A). The same analysis was run without *A. fulvipes*, which belonged to the big species with a mean size of 10.5 mm. In 2020, the community of the HP-meadows stayed significantly bigger than the HH-, C- and SC-meadows communities. Moreover, the SN- community became significantly bigger than the C-, HH- and SC-meadow community (Fig. 4B).

Regarding the trophic level, the beetles were assigned to either the herbivore guild (1) or to the predator guild (2). The CTI of the C-meadows were significantly higher in 2018 compared to 2020 (Table S4; Fig. 5A), indicating a significant year effect. A correction was applied by subtracting 2020 and 2018 values and running the analysis again on this difference. The CTI difference was significantly higher in HP- compared to C- meadows (Table S5; Fig. S5A). The same analysis was run without *A. fulvipes*, which belongs to the herbivore guild. No significant effect could be detected anymore (Fig. 5B and S5B).

To analyse the humidity preferences of the beetles (CHPI), they were distributed in 3 classes: xerophilous (1), mesophilic (2) and hygrophilous (3). The CHPI of the C-meadows were significantly higher in 2018 compared to 2020 (Table S4; Fig. 6A). This year effect was corrected by running the analysis on the difference between 2020 and 2018 values. The CHPI difference in SN-meadows was significantly higher compared to C- and HH-meadows (Table

S5; Fig. S6A). The same analysis was run without *A. fulvipes*, which is a xerophilous beetle. There, we found that HP- and SN-meadows harboured a significantly higher CHPI difference compared to HH-meadows (Fig. 6B and S6B).

Finally, no significant difference could be observed between the controls 2018 and 2020 considering the CHI (Table S5), meaning the subsequent analysis was run on the data 2018 and 2020 separately. No significant effect of the treatments or within treatments could be detected considering the ground beetle hibernation stage (larvae = 1; both = 2; adult = 3; Fig. 7A). The same analysis was run without *A. fulvipes*, which overwinters as imago. The absence of significant effect of treatments on the index stayed (Fig. 7B).

Multivariate regression

Whereas the HH-treatment did not impact negatively any species, *Microlestes minutulus* (Goeze, 1777), *Anisodactylus binotatus* (Fabricius 1787) and *Poecilus cupreus* (Linné, 1758) benefitted from it. HP-treatment negatively impacted *A. fulvipes* and *Amara lunicollis* (Schiødte, 1837), whereas *A. binotatus, P. cupreus* and *Harpalus (Pseudoophonus) rufipes* (De Geer, 1774) benefitted from it. SC-treatment impacted negatively *A. lunicollis* but it promoted *Diachromus germanus* (Linné, 1758)*, Bembidion (Metallina) properans* (Stephens, 1828), *A. binotatus* and *P. cupreus.* Finally, SN-treatment, similarly to HP-, had negative effects on *A. fulvipes* and *A. lunicollis* but boosted *D. germanus, H. rufipes, Harpalus affinis* (Schrank, 1781)*, A. binotatus* and *P. cupreus* (Fig. 8). *A. binotatus* and *P. cupreus* presented a higher abundance across all treatments compared to controls. An output table containing all the estimates, standard errors and p-values is presented in the Table S6.

Refuge opportunities

If we consider the restoration treatments individually, no significant effect of the refuge ratio on ground beetle abundance was detected. Though, when grouping the ploughing treatments (i.e. HP, SC and SN), the proportion of refuge area was positively correlated to the carabids abundance after mowing (Fig. 9). No significant effect could be detected before mowing on abundance nor on species richness.

Discussion

In this study, we investigated the response of ground beetles to two soil disturbance actions (harrowing or ploughing) carried out within a grassland restoration experiment. The study was conducted in 60 extensively managed hay meadows in the Swiss lowlands. Baseline data were collected in 2018, in 2019 the sites were restored and finally, in 2020, data were sampled again. Whereas some effects due to ploughing were demonstrated considering specific traits, no significant effect on the species richness nor on the abundance could be detected one year after the soil disturbance event. The harrow did not seem to impact the carabids community in any way, this machine should therefore be prioritized whenever possible when restoring grasslands. These results, discussed in detail in the following subsections, suggest a high resilience of the ground beetle community after grassland soil disturbance on the mid-term (one year after the treatment). To the best of our knowledge, this study is the first investigating these aspects of active grassland restoration.

Species richness, abundance and biodiversity index

First, it is to be highlighted that a high abundance was registered across both sampling years (15’520 individuals caught in 944 pitfalls for the year 2020; 16,4 individuals per trap in average). In comparison, Lischer *et al.* (2016) which similarly studied extensively managed hay meadows, collected 4'553 ground beetles using 752 traps (6 individuals per trap in average). This difference highlights the huge year effects that can arise in arthropods populations, as already observed in other studies (e.g. Woodcock *et al.* 2008), along with the need to correct for it.

Whereas a negative impact of ploughing on the ground beetles species richness and abundance one month after the disturbance was found by Thorbek and Bilde (2004) and in contrast with our hypothesis, we did not detect any significant effect of these treatments on both variables. Shearin, Reberg-Horton and Gallandt (2014) observed a more than 50% increase in mortality immediately after grassland tillage and it was thus expected that a similar proportion of ground beetles would die in 2019 following the disturbance. However, no significant difference in terms of abundance or species richness could be observed between the treatment and the control meadows in 2020. We thus argue that the negative impacts of tillage were already compensated one year after the treatment by ground beetles that survived the treatment and by the recolonization of the disturbed zone by beetles coming from nearby semi-natural areas. Still, we chose to redo the analysis without the widespread beetle *A. fulvipes*, as the abundance of this single species might have prevented the detection of potential impacts of the treatments on the other ground beetles. In this configuration, a slight difference was found between HH- (hay harrow) and SC- (seed commercial) meadows, the latter sheltering significantly less individuals. While this difference might be seen as an evidence for the greater impacts linked to ploughing on the fauna compared to harrowing, we prefer to stay cautious as no significant differences were observed between the other ploughed meadows (HP – hay plough, and SN – seed natural) and HH-meadows. We thus argue that this significance arose randomly from the important amount of tests that were run in this study.

After restoration, all the treatment meadows presented a higher Shannon index compared to controls, meaning that within treatment, both the species richness and evenness tended to be higher. This positive response of diversity towards disturbance might be explained by the fact that the dominance of a few species, allowed by the relative stability of the conditions before treatment, was challenged by the disturbance. Indeed, this event wiped the slate clean, loosening thus the interspecific competition (Darwin 1859) and favouring many other less competitive species. This might also be related to the intermediate disturbance hypothesis (Grime 1973; Connell 1978). This controversial theory (Fox 2013) states that the highest species richness is found at medium disturbance levels as generalists and widespread species populations diminish letting hence opportunities for rare and specialist species to prosper. We can argue that this effect, rarely observed in arthropods, was partially observed within our experiment as *A. fulvipes*, which is the most abundant beetle across both sampling years, and *A. lunicollis*, which is respectively the second most abundant beetle in 2018 and the sixth most abundant beetle in 2020, were negatively impacted by the ploughing, leaving thus space for other species to thrive.

Trait analysis

Four different species-specific traits were analysed within this study, namely the body size, the trophic level, the humidity preference and the hibernation stage. Regarding the community body size index (CBI), the beetle community harboured slightly larger species in HP-meadows than in C-, HH- and SC-meadows after the restoration and in SN-meadows compared to C-meadows. The multivariate regression revealed that this size increase is linked to a significant increase in the abundance of *A. binotatus*, *P. cupreus* and *H. rufipes.* Those are big carabids, ranging from 9 to 13.5 mm (while the average is 7.75 mm). This result contradicts our hypothesis, which was based on several studies showing a decrease in the ground beetles community body size with an increasing disturbance (e.g. tilling, mowing or grazing events; Blake *et al.* 1994; Ribera *et* *al.* 2001; Hanson *et al.* 2016). One reflection to explain this contradiction might be in the experimental designs used: indeed, whereas we investigated the changes in CBI across time but on single sites, e.g. we studied the changes occurring in a single community across time, the previously cited authors studied the change in ground beetle community body size across a land-use gradient, e.g. they compared different ground beetle communities in different habitats presenting different disturbance levels on the same time-scale. This variation in the approaches might thus partly explain the discrepancy observed between the results as the authors studied well-established communities whereas we observed transitional stages.

The community trophic index (CTI) increased in HP-meadows compared to controls, showing a higher proportion of predatory ground beetles in HP- compared to C-meadows. This result is linked to a significant increase of *P. cupreus* and *B. properans* which are predators and a decrease of *A. fulvipes* and *A. lunicollis* which are herbivores. If we compare our disturbed meadows with cropland, this result is in line with several studies which showed that predatory carabids are more abundant in cropland compared to grasslands (Woodcock *et al.* 2010a; Birkhofer, Wolters & Diekötter 2014; Hanson *et al.* 2016). Though, none of these studies considered the so-called "pitfall of pitfalls" (Lang 2000) which states that pitfalls present the drawback of measuring the activity density of insects rather than their effective abundance on the meadow. As the ground cover (bare vs vegetated ground) hugely influences the activity of beetles (Honek 1988), it also influences the catching rate (Lang 2000; Thomas, Brown & Kendall 2006). In our study, we compared similar habitats and were hence not prone to fall in this pitfall..

Considering the humidity preferences index (CHPI), we found less xerophilous beetles in C- and HH- than in SN-meadows. This result, partly in line with our hypothesis, indicates a real impact of ploughing on the microhabitat of the meadows and is linked to a significant decrease of the dominant and xerophilous species *A. fulvipes* in SN-meadows. The problem that arise here is to understand why the HP- and SC-communities, which similarly experienced the ploughing treatment, did not react as SN-communities. Whereas this result might arise randomly like for the abundance results, other explanations (e.g. overrepresentation of one species, vegetation differences, etc.) have to be considered. Some hints are given further down on this topic.

We could not demonstrate any significant effect of the treatments on the community hibernation index (CHI). This absence of significance is probably due to counterbalancing forces: 1) it is expected that strictly adult overwinterers prefer grasslands and would thus reject the freshly disturbed meadows for spending the winter 2020-2021 (Purvis & Fadl 2002; Holland, Birkett & Southway 2009); 2) it was shown that larval overwinterers are more affected by spring tillage compared to adult overwinterers (Purvis & Fadl 1996). Hence, it is probable that whereas the treatment impacted more severely larval overwinterers in 2019, this negative effect could not be observed in the 2020 catch as these same species preferred the treated meadows as overwintering fields in 2020-2021.

As for the abundance, we ran again the entire trait analyses without *A. fulvipes.* Whereas the CTI and the CHI effects disappeared, the effects observed on the CBI became even stronger. Indeed, HP- and SN-meadows harboured a significantly higher CBI than the other three treatments. Considering the CHPI, a shift was observed: whereas the effects between SN and C disappeared, a new significant difference was observed between HP- and HH-meadows, with HP- showing a higher CHPI difference compared to HH-meadows. Here, it is to be noted that all of the four community indices stayed at stable levels in HP- and SN-treatments after the removal of *A. fulvipes* while the CBI dropped and the CTI, CHPI and CHI rose in the three other treatments (e.g. C, HH and SC). This means that *A. fulvipes* hugely influences the C-, HH- and SC-treatments and was therefore much more present in these three treatments compared to HP- and SN- meadows in 2020. This implies that HP- and SN- treatments had a higher negative impact on *A. fulvipes* and this effect was confirmed by the multivariate regression. This result is difficult to fully unfold. As a hint, it is to be considered that whereas ploughing suppressed all vegetation from the ploughed meadows, harrowing allowed a certain amount of the litter to stay rooted in the meadows. Controls obviously offered undisturbed vegetated conditions. This higher plant availability in HH- and C-meadows directly after the treatment might explain the prevalence of the herbivorous *A. fulvipes* in these two meadow types, as this species might have suffered less there. However, explaining the difference between SC- and HP-/SN-meadows is not as straightforward. We have to keep in mind that the origin of the seeds was the same for HP- and SN-meadows, whereas it differed for SC-meadows. Thus, one possible explanation would be that the vegetation of HP- and SN- meadows (be it in terms of species richness, height or density) differs somehow from the SC-treatment, the last being more favourable to *A. fulvipes*. Unfortunately, this statement remains a hypothesis as no extensive vegetation surveys were carried out in 2020.

As revealed by the multivariate regression, the effects presented within this section were mainly linked to the increase of maximum five species or by the decrease of one or two single species. These reactions can be explained by the very recent soil disturbance. Indeed, whereas all species which benefitted from the treatments are considered as pioneers, *A. lunicollis* and *A. fulvipes* are restricted to healthy grasslands, with the latest being even stenotopic (Luka *et al.* 2009). Thus, the discrepancies observed between our results and the literature (e.g. body size increase instead of a decrease in treatments) and the significant effects in general are expected to resorb with the time as the disturbance applied in our experiment is punctual. As a matter of fact, it is expected that the soil microstructure and micro-climatic conditions will transition back to their initial state and it is hence possible that the previously dominant ground beetle species, and particularly *A. fulvipes*, will thrive again, reversing the trends observed.

Refuge opportunities

As some of the study meadows were only partly restored, the adjacent unploughed or unharrowed surfaces offered valuable refuges for the ground beetles. We found a significantly positive correlation between refuge opportunities (ratio of non-restored area divided by the entire meadow area) and the beetle abundance after mowing on ploughed meadows (i.e. HP, SN and SC). Letting a refuge by avoiding to restore the entire meadow surface is by all means beneficial for invertebrates, as already demonstrated in the context of mowing disturbance (Humbert *et al.* 2012; Buri, Arlettaz & Humbert 2013; Kühne *et al.* 2015). Though, the positive impacts we could demonstrate on the ground beetles remained limited. The temporal restriction (only after mowing) is tricky to explain. It is to be considered that the refuge areas probably sheltered more beetles in 2020 compared to disturbed surfaces. Thus, whereas the abundance difference before mowing between high and low refuge ratio meadows was not significant because the ground beetles probably stayed rather sedentary as sufficient resources were present, this difference became statistically significant after mowing as the beetles became more mobile in order to find those resources (e.g. food, shelter, etc.). Moreover, shorter grass and open ground patches probably allowed to register a higher activity-density after the mowing event. If this phenomenon really underlies the observed effect, it will probably disappear after a few years following the settlement of the system.

The "ploughing only" restriction is in the contrary much easier to understand. Indeed, harrowing represents a very shallow disturbance with only around 40% of the grass cover removed (Woodcock *et al.* 2008) while the plough goes much deeper in the soil and weeds entirely the surface. Thus, the harrowing treatment offers much more survival opportunities to ground beetles compared to ploughing. This explains why the unharrowed surface had no impact on ground beetle abundance while the ploughed meadows offering a refuge sheltered significantly more beetles.

Conclusion and management recommendations

This study suggested that ground beetle species inhabiting semi-natural grasslands are resilient to the soil disturbance event required while restoring these valuable habitats. Whereas no impact of harrowing was found, some changes considering the community weighted mean of specific traits were observed one year after the restoration in ploughed treatments compared to controls: the ground beetle community was bigger in ploughed meadows, more predaceous in HP- and more hygrophilous in SN-meadows. These effects were all linked to a significant increase of a few indigenous pioneer species and on the long term, these species will probably settle back to lower abundance levels. In the contrary, species strictly linked to grasslands (e.g. *A. lunicollis* and *A. fulvipes*) are expected to thrive again with the progressive resettlement of the initial micro-climatic and structural state of the grasslands. Our results were not entirely in line with previous cropland studies. An explanation for these discrepancies is that recurrent disturbances occurring in cropland drive the installation of disturbance-resistant beetle species. This community features the characteristics of being more diverse and to harbour more exotic species compared to the ground beetles community found in grassland where soil disturbances represent punctual and isolated events (Cárcamo, Niemalä & Spence 1995).

To effectively restore plant species richness in extensive grasslands, a soil disturbance (either harrowing or ploughing) is necessary (Kiehl *et al.* 2010) but these invasive techniques might negatively impact the ground-dwelling organisms. In the light of our results, we recommend privileging the harrow for restoring extensively managed meadows as it appears that this technique does not impact the ground beetle community. Besides, it was suggested that harrowing is more beneficial to restore hay meadows plant diversity than ploughing (Edwards *et al.* 2007). In a lesser extent, and in case the usage of a plough is unavoidable, we recommend leaving parts of the initial meadow surface undisturbed as this might help to mitigate the damages caused by the treatment on ground beetles. As the establishment of a target floral community will additionally impact the ground beetles and in order to cover all the aspects of the grassland restoration, we recommend a long-term monitoring of the development of the carabid beetles population as well as a comparison with the donor community.

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Tables

Table 1. Summary table of the four different community indices used in the analyses. Whereas the actual size in mm was used to calculate the CBI, the three other community weighted means had numbers attributed to their different levels.

Code	**Variable**	**Unit**
CBI	Body size	mm
CTI	Trophic level	Categorical: 1 herbivore, 2 predator
CHI	Hibernation state	Categorical: 1 larva only, 2 larvae or adult, 3 adults only
CHPI	Humidity preference	Categorical: 1 xerophilous, 2 mesophilic, 3 hygrophilous

Figures

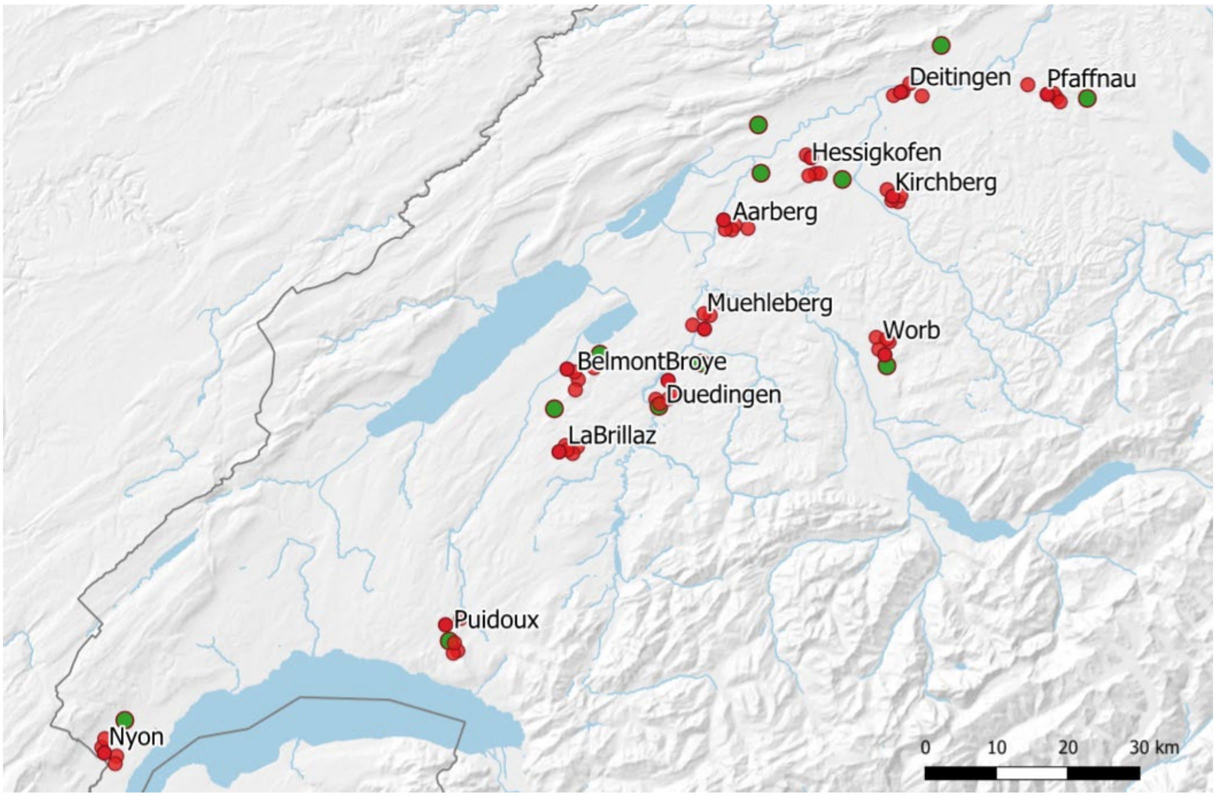


Figure 1. Map of the twelve study regions located between Nyon (VD) in the S-W and Pfaffnau (LU) in the N-E of Switzerland. The species rich donor meadows (one per site) are in green and the meadows (to be restored or kept as control) are in red.

Figure 2. Picture of the set-up of pitfall traps in the field. The plastic cover avoids the filling of the cup due to rainfall and the metal grid prevents small mammals and reptiles to fall in the trap.

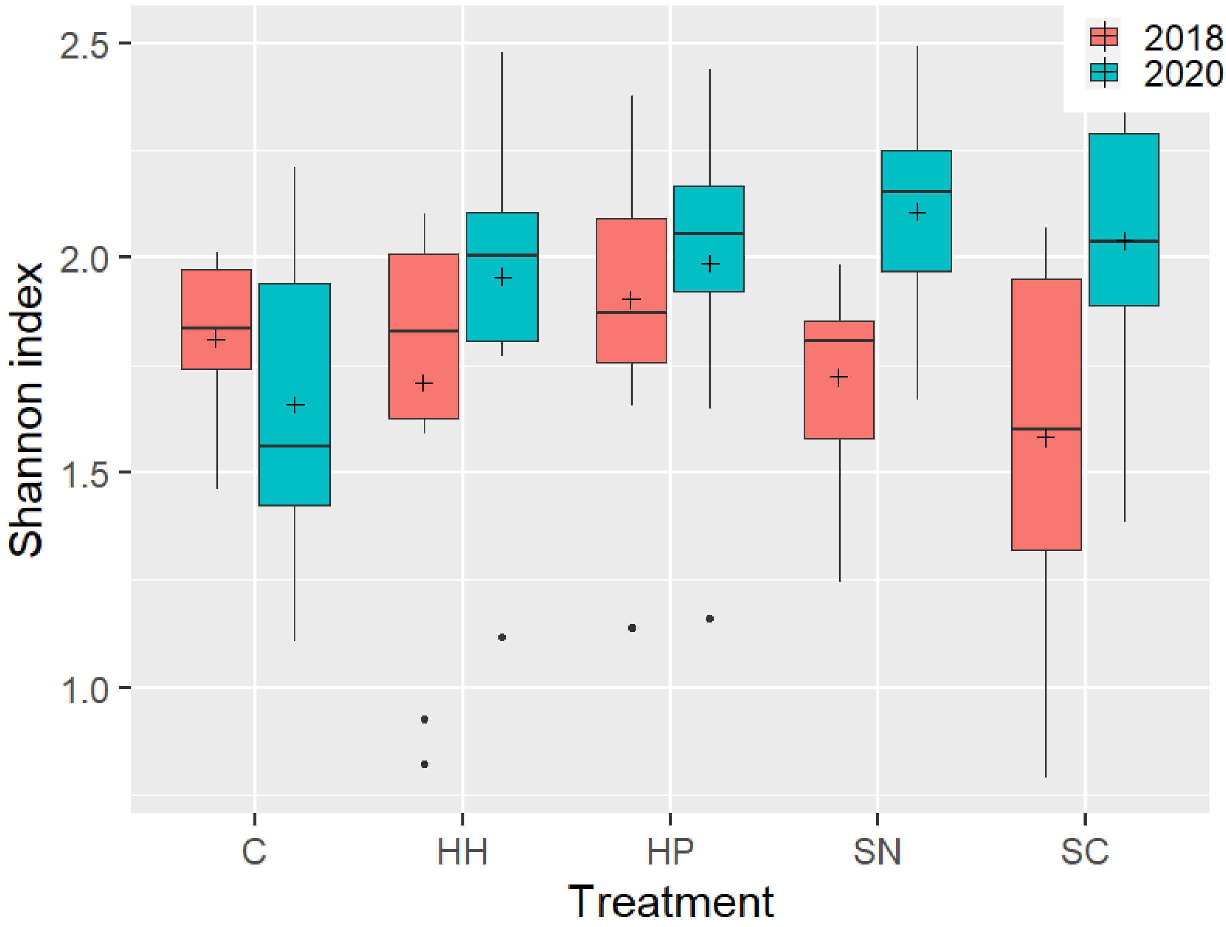


Figure 3. Shannon index per restoration treatment. In 2020, all treatments presented a significantly higher Shannon index compared to the control. Abbreviations for treatments: C = control; HH = hay harrow; HP = hay plough; SN = seed natural and SC = seed commercial.

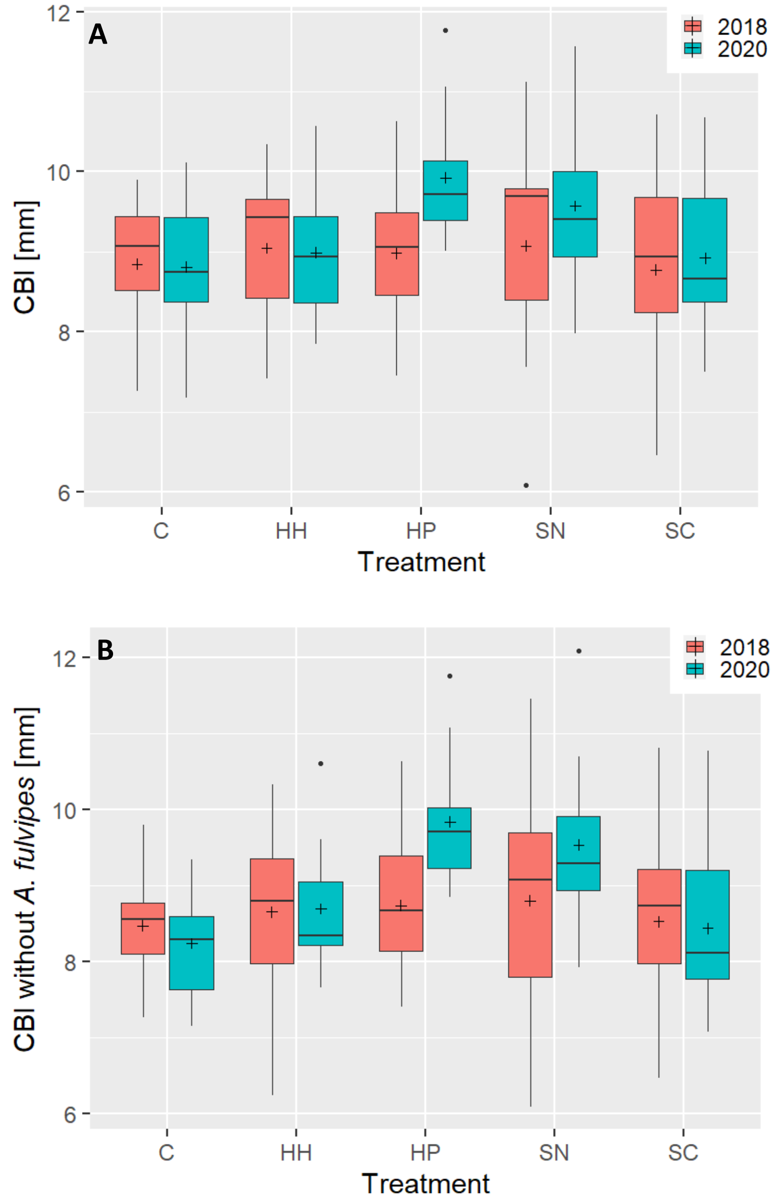


Figure 4. (A) Community body size index (CBI) including *A. fulvipes*. In 2020, the community of the HP-meadows was significantly bigger than the HH-, C- and SC-meadows communities. Moreover, the SN community was significantly bigger than the C-community. (B) CBI without *A. fulvipes.* In 2020, the community of the HP- and SN-meadows was significantly bigger than the HH-, C- and SC-meadows communities. Abbreviations as in Figure 3. More details (estimates, standard errors and p-values) are provided in Table S3.

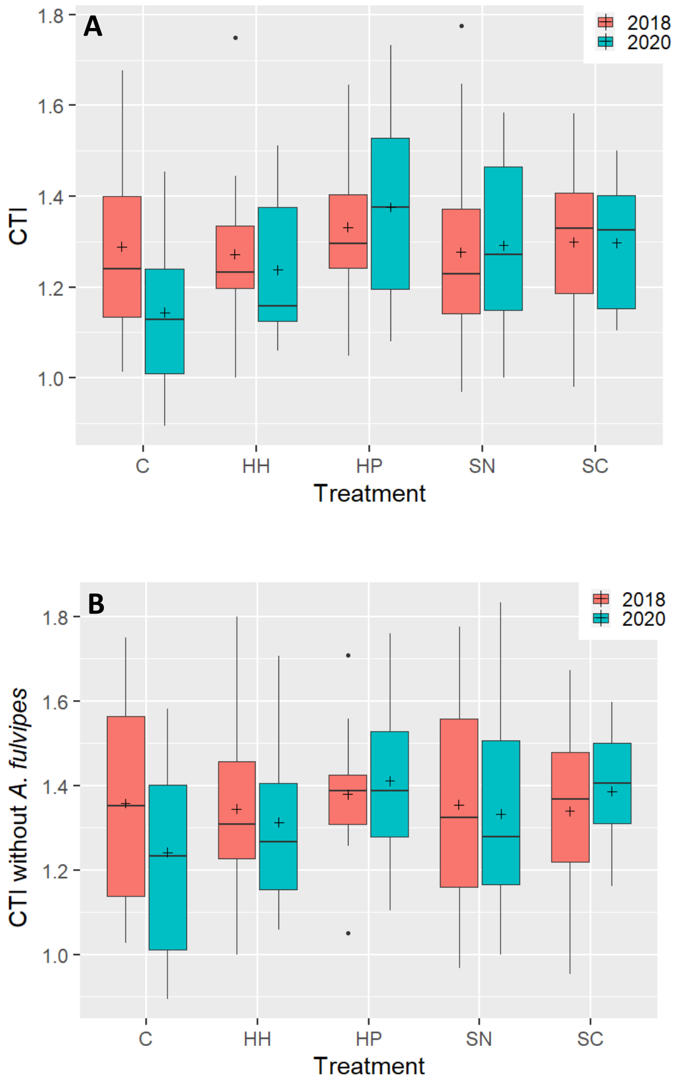


Figure 5. (A) Community trophic index (CTI) including *A. fulvipes*. The beetles were distributed in two classes: herbivore (1) and predator (2). The controls 2018 presented a significantly higher CTI compared to the 2020 controls, showing a year effect. Thus, the analysis was run on the difference between 2020 and 2018 values. The CTI difference was significantly lower in C- compared to HP-meadows. (B) CTI without *A. fulvipes*. After the removal of this widespread species, no significant effect could be found anymore on the difference between 2020 and 2018 values. Abbreviations as in Figure 3. More details (estimates, standard errors and p-values) are provided in Tables S4 and S5.

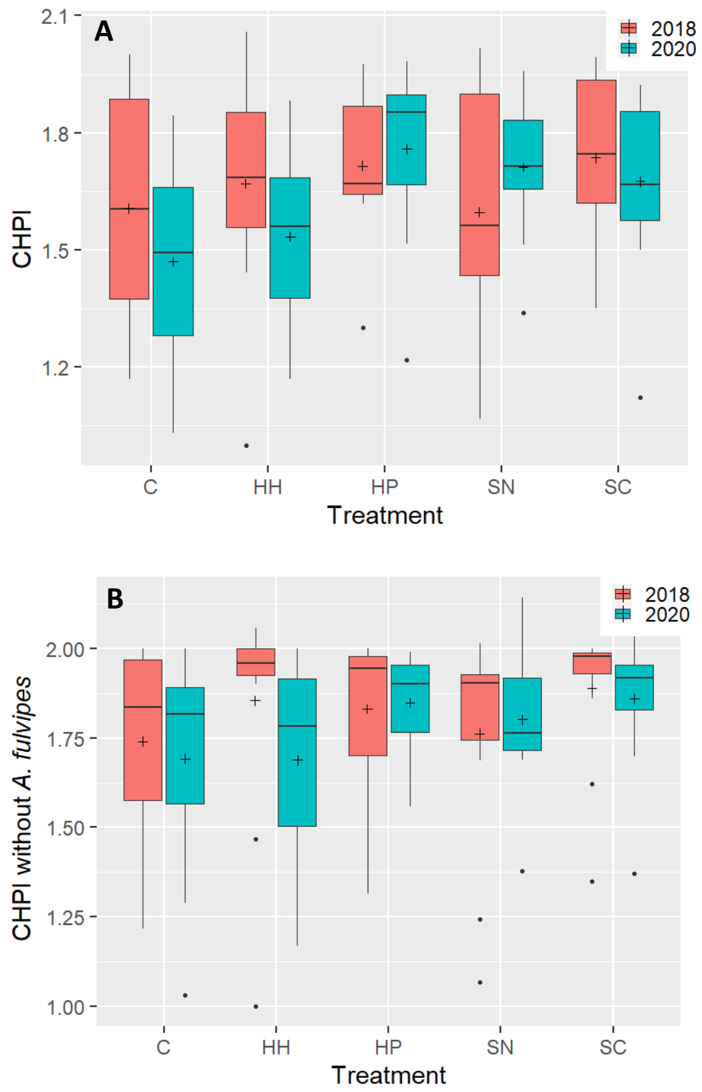


Figure 6. (A) Community humidity preference index (CHPI) including *A. fulvipes*. The beetles were distributed in three classes: xerophilous (1), mesophilic (2) and hygrophilous (3). The controls 2018 presented a significantly higher CHPI compared to the 2020 controls, showing a year effect. Thus, the analysis was run on the difference between 2020 and 2018 values. The CHPI difference was significantly lower in C- and HH- meadows compared to SN-meadows. (B) CHPI without *A. fulvipes*. After the removal of this widespread species, the CHPI difference was significantly lower in HH- meadows compared to HP- and SN-meadows. Abbreviations as in Figure 3. More details (estimates, standard errors and p-values) are provided in Tables S4 and S5.

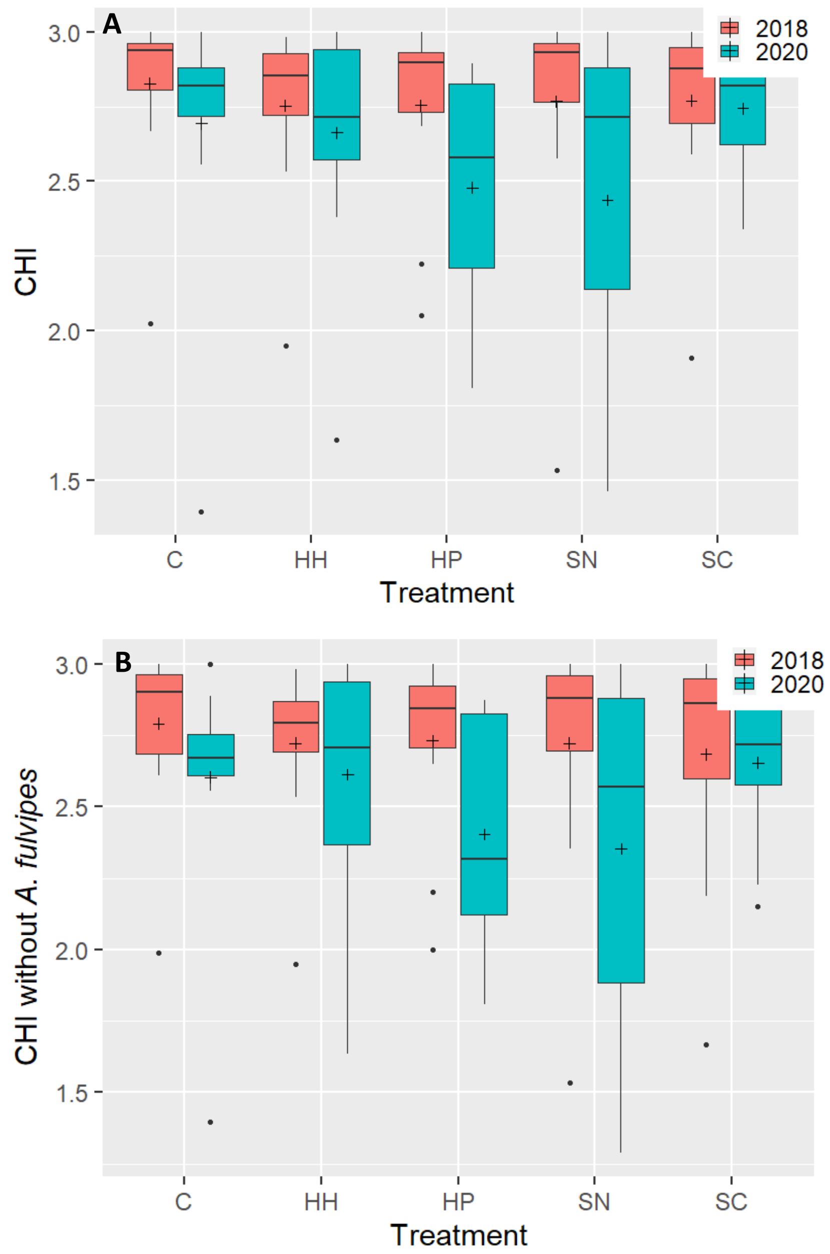


Figure 7. (A) Community hibernation index (CHI) including *A. fulvipes.* The beetles were distributed in three classes: larvae (1), both (2) and adults (3). No significant effect of the treatments or within treatments could be detected. (B) Community hibernation index without *A. fulvipes*. After the removal of this widespread species, no significant effect could be detected. Abbreviations as in Figure 3. More details (estimates, standard errors and p-values) are provided in Table S3.

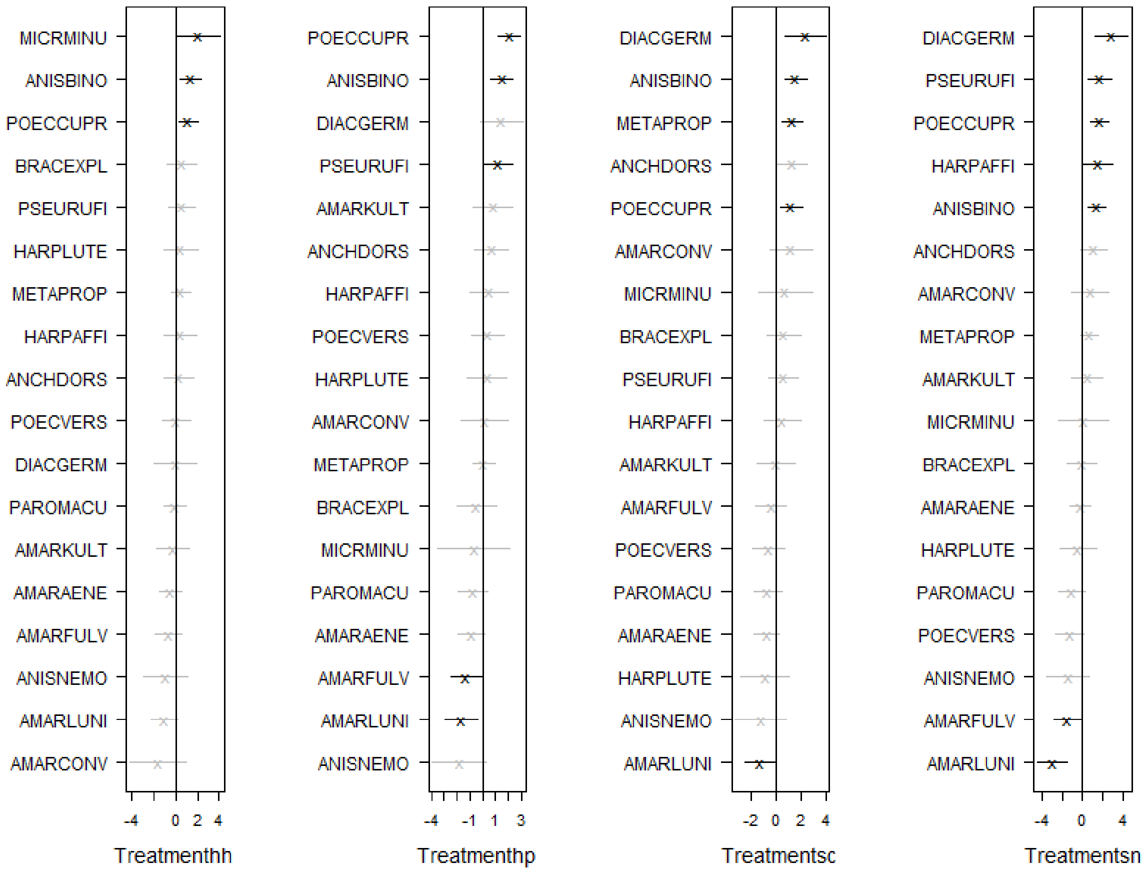


Figure 8. A multivariate regression was run on the 18 species present in at least eight regions and across all treatments. Significant effects (either positive or negative) are highlighted in black, whereas non-significant results are depicted in grey. The HH-treatment did not present any negative effect on the species whereas it was beneficial to three species. In the contrary, all ploughing treatments affected at least one species (*A. fulvipes* and/or *A. lunicollis*) and they beneficiated three to five species. Abbreviations as in Figure 3. More details (estimates, standard errors and p-values) are provided in Table S6.

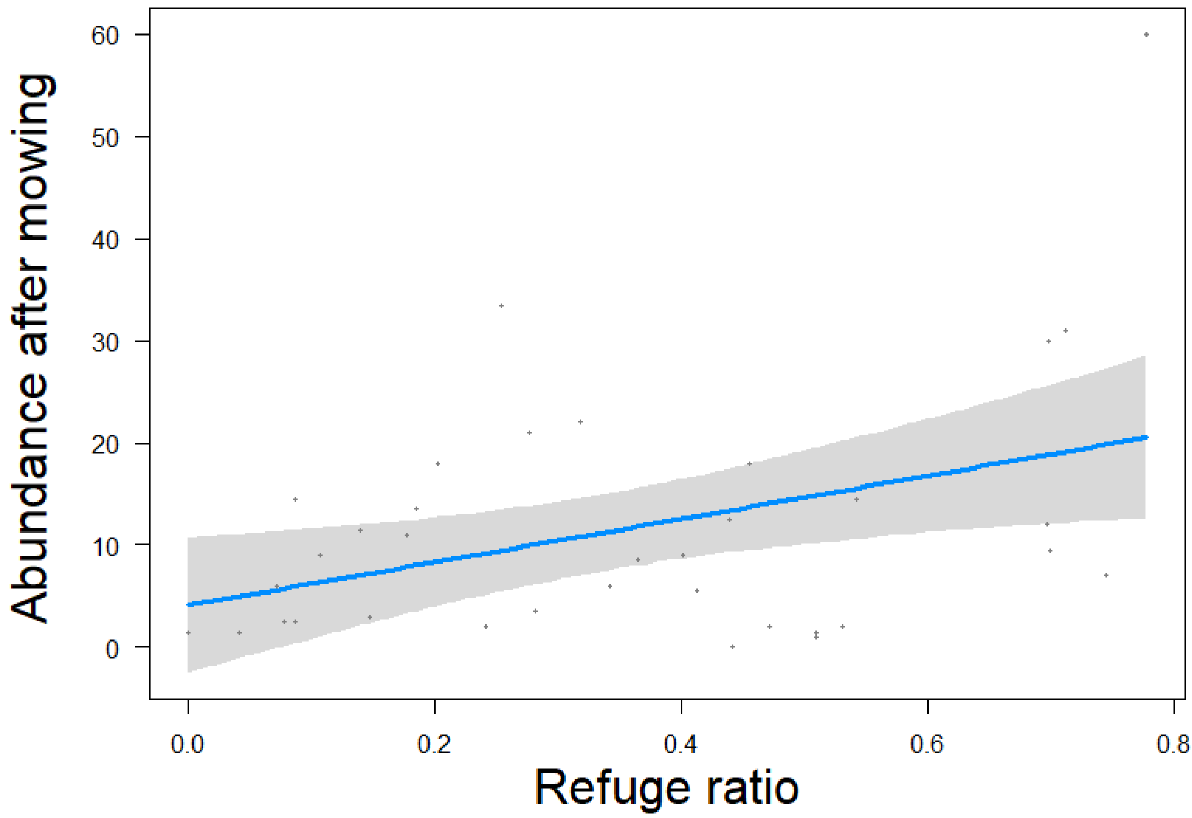


Figure 9. The ratio of the non-restored area / the whole meadow area when considering only the ploughing treatments (i.e. HP, SN and SC) was positively correlated with ground beetle abundance after mowing (in 2020). The value 0 means the whole meadow was ploughed (no refuge) and higher values mean that a proportion of the initial meadow was not ploughed (for example non-restored buffer zone was left near the forest edge). More details (estimates, standard errors and p-values) are provided in Table S3.

Appendix

Table S1. List of the ground beetle species with the abundances before (in 2018) and after (in 2020) restoration. The table also provides all species-specific traits: mean body size; trophic level; humidity preferences; hibernation stage (Marggi 1992; Fazekas 1997; Cole *et al.* 2002; Müller-Motzfeld 2004; Luka *et al.* 2009; Lundgren 2009).

Species	Abundance 2018	Abundance 2020	Size [mm]	Trophic level	Humidity preferences	Hibernation stage
Abax ovalis (Duftschmid, 1812)	4	0	13	predator	hygrophilous	imago
Abax parallelepipedus (Piller & Mitterpacher, 1783)	1	0	20	predator	mesophilic	NA
Acupalpus meridianus (Linnaeus, 1760)	0	2	3.5	predator	mesophilic	imago
Agonum muelleri (Herbst, 1784)	10	1	8	predator	mesophilic	imago
Agonum sexpunctatum (Linnaeus, 1758)	1	0	8.5	predator	mesophilic	imago
Agonum viridicupreum (Goeze, 1777)	1	0	9	predator	hygrophilous	imago
Amara aenea (DeGeer, 1774)	228	379	7.5	herbivore	xerophilous	imago
Amara communis (Panzer, 1797)	28	23	7	herbivore	mesophilic	both
Amara convexior (Stephens, 1828)	78	38	8	herbivore	mesophilic	imago
Amara familiaris (Duftschmid, 1812)	4	25	6.5	herbivore	mesophilic	imago
Amara fulvipes (Audinet-Serville, 1821)	938	1012	10.5	herbivore	xerophilous	imago
Amara kulti (Fassati, 1947)	137	294	9.5	herbivore	mesophilic	larvae
Amara lucida (Duftschmid, 1812)	3	1	5.75	herbivore	mesophilic	imago
Amara lunicollis (Schiødte, 1837)	619	278	7.5	herbivore	mesophilic	imago
Amara montivaga (Sturm, 1825)	7	17	8.5	herbivore	xerophilous	imago
Amara nitida (Sturm, 1825)	8	0	8	herbivore	mesophilic	imago
Amara ovata (Fabricius, 1792)	0	12	8.75	herbivore	mesophilic	imago
Amara plebeja (Gyllenhal, 1810)	5	7	7	herbivore	mesophilic	imago
Amara similata (Gyllenhal, 1810)	0	16	8.75	herbivore	mesophilic	imago
Anchomenus dorsalis (Pontoppidan, 1763)	14	62	6.8	predator	mesophilic	imago
Anisodactylus binotatus (Fabricius, 1787)	282	299	11	herbivore	mesophilic	imago
Anisodactylus nemorivagus (Duftschmid, 1812)	138	75	9	herbivore	xerophilous	imago
Anisodactylus signatus (Panzer, 1796)	0	4	11.75	herbivore	mesophilic	larvae
Badister bullatus (Schrank, 1798)	1	0	5.5	predator	mesophilic	imago
Bembidion guttula (Fabricius, 1792)	0	1	3.3	predator	hygrophilous	imago
Bembidion lampros (Herbst, 1784)	3	16	3.4	predator	mesophilic	imago
Bembidion obtusum (Audinet-Serville, 1821)	0	1	3.2	predator	mesophilic	imago
Bembidion properans (Stephens, 1828)	336	266	3.95	predator	mesophilic	imago
Bembidion quadrimaculatum (Linnaeus, 1760)	7	0	3.05	predator	xerophilous	imago
Brachinus crepitans (Linnaeus, 1758)	1	0	8.7	predator	xerophilous	NA
Brachinus elegans (Chaudoir, 1842)	7	8	7.75	NA	mesophilic	imago
Brachinus explodens (Duftschmid, 1812)	42	49	6	predator	xerophilous	imago
Calathus fuscipes (Goeze, 1777)	1	4	12.25	predator	mesophilic	both
Calathus melanocephalus (Linnaeus, 1758)	1	0	7.5	predator	xerophilous	both
Carabus auratus (Linnaeus, 1761)	5	3	23.5	predator	mesophilic	NA
Carabus cancellatus carinatus (Charp. 1825)	0	1	23	predator	mesophilic	NA

Carabus coriaceus (Linnaeus, 1758)	0	1	37	predator	hygrophilous	both
Carabus granulatus (Linnaeus, 1758)	0	2	19.5	predator	hygrophilous	imago
Carabus monilis (Fabricius, 1792)	52	24	24.5	predator	mesophilic	both
Clivina fossor (Linnaeus, 1758)	5	4	6.25	predator	mesophilic	imago
Diachromus germanus (Linnaeus, 1758)	118	96	8.45	herbivore	mesophilic	imago
Harpalus affinis (Schrank, 1781)	13	69	10.5	herbivore	mesophilic	imago
Harpalus dimidiatus (P.Rossi, 1790)	20	66	12.5	herbivore	xerophilous	imago
Harpalus distinguendus (Duftschmid, 1812)	7	53	9.55	herbivore	xerophilous	both
Harpalus latus (Linnaeus, 1758)	7	6	9.5	herbivore	mesophilic	both
Harpalus luteicornis (Duftschmid, 1812)	64	25	6.75	herbivore	mesophilic	imago
Harpalus marginellus (Gyllenhal, 1827)	1	0	10.65	herbivore	mesophilic	NA
Harpalus rubripes (Duftschmid, 1812)	21	9	10	herbivore	mesophilic	both
Harpalus serripes (Quensel, 1806)	8	30	10.5	herbivore	xerophilous	imago
Harpalus smaragdinus (Duftschmid, 1812)	0	2	9.25	herbivore	xerophilous	both
Harpalus subcylindricus (Dejean, 1829)	57	127	6.75	herbivore	xerophilous	NA
Harpalus tardus (Panzer, 1796)	13	3	9.45	predator	xerophilous	NA
Loricera pilicornis (Fabricius, 1775)	2	1	7.4	predator	hygrophilous	imago
Microlestes minutulus (Goeze, 1777)	3	25	3.1	predator	xerophilous	imago
Nebria brevicollis (Fabricius, 1792)	1	10	12	predator	hygrophilous	both
Nebria salina (Fairmaire & Laboulbène, 1854)	0	3	11	predator	mesophilic	both
Notiophilus palustris (Sturm, 1826)	0	3	4.75	predator	hygrophilous	imago
Ophonus azureus (Fabricius, 1775)	2	2	7.5	herbivore	xerophilous	imago
Panagaeus cruxmajor (Linnaeus, 1758)	2	0	8.25	predator	hygrophilous	imago
Parophonus maculicornis (Duftschmid, 1812)	86	61	6.65	NA	mesophilic	imago
Poecilus cupreus (Linnaeus, 1758)	132	283	11	predator	mesophilic	imago
Poecilus lepidus (Leske, 1785)	1	4	12	predator	xerophilous	larvae
Poecilus versicolor (Sturm, 1824)	542	252	9.75	predator	mesophilic	imago
Pseudoophonus griseus (Panzer, 1796)	0	3	10.5	herbivore	xerophilous	larvae
Pseudoophonus rufipes (De Geer, 1774)	33	140	13.5	herbivore	mesophilic	both
Pterostichus melanarius (Illiger, 1798)	12	17	15	predator	hygrophilous	both
Pterostichus niger (Schaller, 1783)	1	0	18.5	predator	hygrophilous	NA
Pterostichus ovoideus (Sturm, 1824)	1	0	6.75	predator	hygrophilous	imago
Pterostichus vernalis (Panzer, 1796)	16	7	6.85	predator	mesophilic	imago
Semiophonus signaticornis (Duftschmid, 1812)	1	1	6.5	herbivore	xerophilous	larvae
Stenolophus teutonus (Schrank, 1781)	8	11	6.25	predator	mesophilic	imago
Syntomus truncatellus (Linnaeus, 1760)	7	6	3.15	predator	mesophilic	imago
Trechus quadristriatus (Schrank, 1781)	0	1	4	predator	mesophilic	larvae
Total abundance	**4146**	**4241**				

Table S2. Effects of the treatments on the species richness, abundance, biodiversity index and species-specific traits in 2018. Significant p-values are highlighted in bold. Abbreviations as in Figure 3.

Response variable		**Estimate**	**SE**	***P***
SPECIES RICHNESS				
Species richness				
	HH vs C	0.008	0.124	0.951
	HP vs C	0.015	0.124	0.902
	SC vs C	-0.088	0.127	0.486
	SN vs C	-0.064	0.126	0.614
	HP vs HH	0.008	0.123	0.951
	SC vs HH	-0.096	0.127	0.448
	SN vs HH	-0.071	0.126	0.572
	SC vs HP	-0.104	0.126	0.412
	SN vs HP	-0.079	0.126	0.530
	SN vs SC	0.025	0.129	0.847
ABUNDANCE				
Abundance before mowing				
	HH vs C	-1.482	5.149	0.775
	HP vs C	-1.485	5.149	0.774
	SC vs C	2.661	5.149	0.608
	SN vs C	-1.284	5.149	0.804
	HP vs HH	-0.003	5.149	1.000
	SC vs HH	4.143	5.149	0.425
	SN vs HH	0.198	5.149	0.970
	SC vs HP	4.146	5.149	0.425
	SN vs HP	0.201	5.149	0.969
	SN vs SC	-3.945	5.149	0.448
Abundance after mowing				
	HH vs C	-2.021	2.553	0.433
	HP vs C	-2.994	2.553	0.247
	SC vs C	-1.076	2.553	0.675
	SN vs C	-1.890	2.553	0.463
	HP vs HH	-0.973	2.553	0.705
	SC vs HH	0.945	2.553	0.713
	SN vs HH	0.131	2.553	0.959
	SC vs HP	1.918	2.553	0.456
	SN vs HP	1.104	2.553	0.667
	SN vs SC	-0.814	2.553	0.751

Abundance before mowing without *A. fulvipes*				
	HH vs C	-1.750	4.854	0.720
	HP vs C	0.917	4.854	0.851
	SC vs C	8.958	4.854	0.072
	SN vs C	-2.208	4.854	0.651
	HP vs HH	2.667	4.854	0.586
	SC vs HH	10.708	4.854	**0.033**
	SN vs HH	-0.458	4.854	0.925
	SC vs HP	8.042	4.854	0.105
	SN vs HP	-3.125	4.854	0.523
	SN vs SC	-11.167	4.854	**0.026**

Abundance after mowing without *A. fulvipes*				
	HH vs C	-1.083	2.063	0.602
	HP vs C	-0.042	2.063	0.984
	SC vs C	1.125	2.063	0.588
	SN vs C	0.125	2.063	0.952
	HP vs HH	1.042	2.063	0.616
	SC vs HH	2.208	2.063	0.290
	SN vs HH	1.208	2.063	0.561
	SC vs HP	1.167	2.063	0.575
	SN vs HP	0.167	2.063	0.936
	SN vs SC	-1.000	2.063	0.630

BIODIVERSITY INDEX

Shannon index				
	HH vs C	-0.103	0.136	0.452
	HP vs C	0.091	0.136	0.507
	SC vs C	-0.230	0.136	0.096
	SN vs C	-0.090	0.136	0.511
	HP vs HH	0.193	0.136	0.160
	SC vs HH	-0.127	0.136	0.352
	SN vs HH	0.013	0.136	0.924
	SC vs HP	-0.321	0.136	**0.022**
	SN vs HP	-0.180	0.136	0.189
	SN vs SC	0.140	0.136	0.306

TRAIT ANALYSIS

Body size				
	HH vs C	0.201	0.436	0.647
	HP vs C	0.138	0.436	0.752
	SC vs C	-0.071	0.436	0.871

	SN vs C	0.230	0.436	0.601
Body size without *A. fulvipes*				
	HH vs C	0.179	0.461	0.700
	HP vs C	0.266	0.461	0.566
	SC vs C	0.054	0.461	0.907
	SN vs C	0.329	0.461	0.479
Hibernation state				
	HH vs C	-0.074	0.130	0.572
	HP vs C	-0.073	0.130	0.579
	SC vs C	-0.058	0.130	0.659
	SN vs C	-0.060	0.130	0.649
Hibernation state without *A. fulvipes*				
	HH vs C	-0.068	0.141	0.632
	HP vs C	-0.059	0.141	0.676
	SC vs C	-0.106	0.141	0.455
	SN vs C	-0.069	0.141	0.630

Table S3. Effects of the treatments on the species richness, abundance, biodiversity index and traits as well as effect of the refuge ratio on the species richness and abundance in 2020. Significant p-values are highlighted in bold. Abbreviations as in Figure 3.

Response variable		**Estimate**	**SE**	***P***
SPECIES RICHNESS				
Species richness				
	HH vs C	0.113	0.119	0.343
	HP vs C	0.086	0.120	0.474
	SC vs C	0.177	0.117	0.130
	SN vs C	0.163	0.120	0.175
	HP vs HH	0.008	0.123	0.951
	SC vs HH	-0.096	0.127	0.448
	SN vs HH	-0.071	0.126	0.572
	SC vs HP	0.092	0.114	0.424
	SN vs HP	0.077	0.117	0.511
	SN vs SC	-0.014	0.115	0.900
ABUNDANCE				
Abundance before mowing				
	HH vs C	1.755	5.000	0.727
	HP vs C	-7.700	5.000	0.131
	SC vs C	-5.256	5.000	0.299
	SN vs C	-7.891	5.127	0.131
	HP vs HH	-9.455	5.000	0.065
	SC vs HH	-7.011	5.000	0.168
	SN vs HH	-9.646	5.127	0.067
	SC vs HP	2.444	5.000	0.628
	SN vs HP	-0.192	5.127	0.970
	SN vs SC	-2.635	5.127	0.610
Abundance after mowing				
	HH vs C	-0.305	2.099	0.885
	HP vs C	3.673	2.099	0.087
	SC vs C	2.756	2.099	0.196
	SN vs C	3.527	2.152	0.109
	HP vs HH	3.978	2.099	0.065
	SC vs HH	3.061	2.099	0.152
	SN vs HH	3.832	2.152	0.082
	SC vs HP	-0.917	2.099	0.665

	SN vs HP	-0.146	2.152	0.946
	SN vs SC	0.771	2.152	0.722
Abundance before mowing without *A. fulvipes*				
	HH vs C	3.042	3.834	0.432
	HP vs C	-4.167	3.834	0.283
	SC vs C	-4.792	3.834	0.218
	SN vs C	0.115	3.933	0.977
	HP vs HH	-7.208	3.834	0.067
	SC vs HH	-7.833	3.834	**0.047**
	SN vs HH	-2.927	3.933	0.461
	SC vs HP	-0.625	3.834	0.871
	SN vs HP	4.282	3.933	0.282
	SN vs SC	4.907	3.933	0.219
Abundance after mowing without *A. fulvipes*				
	HH vs C	-1.958	4.181	0.641
	HP vs C	5.875	4.181	0.166
	SC vs C	3.583	4.181	0.395
	SN vs C	3.701	4.275	0.391
	HP vs HH	7.833	4.181	0.066
	SC vs HH	5.542	4.181	0.191
	SN vs HH	5.659	4.275	0.191
	SC vs HP	-2.292	4.181	0.586
	SN vs HP	-2.174	4.275	0.613
	SN vs SC	0.117	4.275	0.978

BIODIVERSITY INDEX Shannon index				
	HH vs C	0.297	0.132	**0.029**
	HP vs C	0.328	0.132	**0.016**
	SC vs C	0.382	0.132	**0.006**
	SN vs C	0.448	0.135	**0.002**
	HP vs HH	0.031	0.132	0.814
	SC vs HH	0.085	0.132	0.524
	SN vs HH	0.151	0.135	0.268
	SC vs HP	0.054	0.132	0.686
	SN vs HP	0.120	0.135	0.378
	SN vs SC	0.067	0.135	0.625

TRAIT ANALYSIS

Body size				
	HH vs C	0.179	0.336	0.596
	HP vs C	1.116	0.336	**0.002**
	SC vs C	0.114	0.336	0.736
	SN vs C	0.781	0.344	**0.028**
	HP vs HH	0.937	0.336	**0.008**
	SC vs HH	-0.065	0.336	0.847
	SN vs HH	0.602	0.344	0.087
	SC vs HP	-1.002	0.336	**0.005**
	SN vs HP	-0.335	0.344	0.335
	SN vs SC	0.667	0.344	0.059

Body size without *A. fulvipes*				
	HH vs C	0.457	0.361	0.213
	HP vs C	1.602	0.361	< **0.001**
	SC vs C	0.200	0.361	0.582
	SN vs C	1.318	0.370	< **0.001**
	HP vs HH	1.145	0.361	**0.003**
	SC vs HH	-0.257	0.361	0.481
	SN vs HH	0.862	0.370	**0.025**
	SC vs HP	-1.402	0.361	< **0.001**
	SN vs HP	-0.284	0.370	0.447
	SN vs SC	1.118	0.370	**0.004**

Hibernation state				
	HH vs C	-0.030	0.152	0.845
	HP vs C	-0.215	0.152	0.166
	SC vs C	0.051	0.152	0.739
	SN vs C	-0.250	0.156	0.117
	HP vs HH	-0.185	0.152	0.233
	SC vs HH	0.081	0.152	0.597
	SN vs HH	-0.220	0.156	0.167
	SC vs HP	0.266	0.152	0.088
	SN vs HP	-0.035	0.156	0.823
	SN vs SC	-0.301	0.156	0.061

Hibernation state without *A. fulvipes*				
	HH vs C	0.010	0.160	0.952
	HP vs C	-0.199	0.160	0.220
	SC vs C	0.051	0.160	0.753
	SN vs C	-0.245	0.164	0.143
	HP vs HH	-0.209	0.160	0.199
	SC vs HH	0.041	0.160	0.799
	SN vs HH	-0.254	0.164	0.129
	SC vs HP	0.250	0.160	0.126
	SN vs HP	-0.045	0.164	0.784

	SN vs SC	-0.295	0.164	0.079

REFUGE RATIO

Abundance before mowing

	ratio HH	4.510	26.166	0.867
	ratio HP	8.299	16.070	0.617
	ratio SC	4.274	6.975	0.554
	ratio SN	-37.200	20.430	0.102
	ratio all ploughed meadows	-5.344	8.432	0.531

Abundance after mowing

	ratio HH	0.846	5.802	0.887
	ratio HP	26.326	12.238	0.057
	ratio SC	28.000	17.049	0.132
	ratio SN	1.110	16.724	0.949
	ratio all ploughed meadows	21.123	8.626	**0.020**

Table S4. The controls sampled in 2018 were tested against the 2020 controls in order to point out potential year effects. Significant p-values are highlighted in bold. In case of significant results, the subsequent analysis was run on the difference 2020 minus 2018 to correct for the year effect (see Table S5).

Response variable		**Estimate**	**SE**	***P***
SPECIES RICHNESS				
Species richness				
	20 vs 18	0.030	0.123	0.806
ABUNDANCE				
Abundance before mowing				
	20 vs 18	3.104	3.711	0.421
Abundance after mowing				
	20 vs 18	-2.823	2.598	0.300
Abundance before mowing without *A.fulvipes*				
	20 vs 18	0.333	3.546	0.927
Abundance after mowing without *A.fulvipes*				
	20 vs 18	0.292	2.088	0.891
BIODIVERSITY INDEX				
Shannon index				
	20 vs 18	-0.153	0.115	0.196
TRAIT ANALYSIS				
Body size				
	20 vs 18	-0.036	0.290	0.904
Body size without *A.fulvipes*				
	20 vs 18	-0.235	0.153	0.134
Trophic level				
	20 vs 18	-0.145	0.047	**0.010**
Trophic level without *A.fulvipes*				
	20 vs 18	-0.117	0.066	0.105
Humidity preferences				
	20 vs 18	-0.136	0.049	**0.018**
Humidity preferences without *A.fulvipes*				
	20 vs 18	-0.048	0.035	0.194

Hibernation stage				
	20 vs 18	-0.135	0.121	0.290
Hibernation stage without *A.fulvipes*				
	20 vs 18	-0.188	0.120	0.145

Table S5. Effects of the treatments on the differences in trophic level and humidity preferences between 2020 and 2018. Significant p-values are highlighted in bold. Abbreviations as in Figure 3.

Response variable		Estimate	SE	*P*
DIFFERENCES 2020-2018				
Trophic level				
	HH vs C	0.111	0.088	0.215
	HP vs C	0.189	0.088	**0.037**
	SC vs C	0.143	0.088	0.111
	SN vs C	0.176	0.090	0.057
	HP vs HH	0.079	0.088	0.376
	SC vs HH	0.032	0.088	0.714
	SN vs HH	0.066	0.090	0.469
	SC vs HP	-0.046	0.088	0.601
	SN vs HP	-0.013	0.090	0.887
	SN vs SC	0.033	0.090	0.712
Trophic level without *A. fulvipes*				
	HH vs C	0.085	0.091	0.354
	HP vs C	0.148	0.091	0.110
	SC vs C	0.164	0.091	0.079
	SN vs C	0.121	0.093	0.201
	HP vs HH	0.063	0.091	0.492
	SC vs HH	0.079	0.091	0.392
	SN vs HH	0.036	0.093	0.704
	SC vs HP	0.016	0.091	0.864
	SN vs HP	-0.027	0.093	0.771
	SN vs SC	-0.043	0.093	0.647
Humidity preferences				
	HH vs C	0.000	0.093	1.000
	HP vs C	0.179	0.093	0.060
	SC vs C	0.075	0.093	0.421
	SN vs C	0.252	0.095	**0.011**
	HP vs HH	0.179	0.093	0.060
	SC vs HH	0.075	0.093	0.421
	SN vs HH	0.251	0.095	**0.011**

	SC vs HP	-0.104	0.093	0.268
	SN vs HP	0.072	0.095	0.450
	SN vs SC	0.176	0.095	0.070
Humidity preferences without *A. fulvipes*				
	HH vs C	-0.118	0.078	0.136
	HP vs C	0.065	0.078	0.407
	SC vs C	0.019	0.078	0.808
	SN vs C	0.101	0.080	0.210
	HP vs HH	0.183	0.078	**0.023**
	SC vs HH	0.137	0.078	0.085
	SN vs HH	0.219	0.080	**0.009**
	SC vs HP	-0.046	0.078	0.556
	SN vs HP	0.036	0.080	0.652
	SN vs SC	0.082	0.080	0.308

Table S6. Output table of the multivariate regression run on the 18 species that were present in at least eight regions and across all treatments. This table shows the effects of the treatments on these 18 individual species for 2020. Significant p-values are highlighted in bold. Abbreviations as in Figure 3.

Response variable		**Estimate**	**SE**	***P***
SPECIES				
Amara aenea				
	HH vs C	-0.229	0.448	0.609
	HP vs C	-0.864	0.452	0.056
	SC vs C	-0.422	0.464	0.363
	SN vs C	-0.096	0.452	0.832
Amara convexior				
	HH vs C	-1.561	1.272	0.220
	HP vs C	0.317	0.880	0.719
	SC vs C	1.208	0.824	0.143
	SN vs C	0.995	0.847	0.240
Amara fulvipes				
	HH vs C	-0.699	0.611	0.252
	HP vs C	-1.395	0.581	**0.016**
	SC vs C	-0.279	0.599	0.641
	SN vs C	-1.196	0.596	**0.045**
Amara kulti				
	HH vs C	-1.454	0.864	0.093
	HP vs C	0.339	0.718	0.636
	SC vs C	0.207	0.682	0.761
	SN vs C	-0.022	0.764	0.977
Amara lunicollis				
	HH vs C	-1.035	0.620	0.095
	HP vs C	-1.681	0.615	**0.006**
	SC vs C	-1.449	0.620	**0.020**
	SN vs C	-2.952	0.710	**<0.001**
Anchomenus dorsalis				
	HH vs C	0.288	0.692	0.677
	HP vs C	0.693	0.661	0.294
	SC vs C	1.204	0.635	0.058
	SN vs C	1.068	0.652	0.101

Anisodactylus binotatus				
	HH vs C	1.401	0.459	**0.002**
	HP vs C	1.484	0.458	**0.001**
	SC vs C	1.511	0.457	**0.001**
	SN vs C	1.365	0.468	**0.004**
Anisodactylus nemorivagus				
	HH vs C	-0.876	1.028	0.395
	HP vs C	-1.792	1.076	0.096
	SC vs C	-1.281	1.044	0.220
	SN vs C	-1.417	1.077	0.188
Bembidion (Metallina) properans				
	HH vs C	0.486	0.411	0.237
	HP vs C	0.096	0.421	0.819
	SC vs C	1.178	0.395	**0.003**
	SN vs C	0.674	0.419	0.108
Brachinus explodens				
	HH vs C	0.766	0.654	0.242
	HP vs C	-0.376	0.744	0.613
	SC vs C	0.426	0.656	0.516
	SN vs C	-0.038	0.709	0.957
Diachromus germanus				
	HH vs C	0.040	0.959	0.967
	HP vs C	1.446	0.809	0.074
	SC vs C	2.202	0.792	**0.005**
	SN vs C	2.904	0.812	**0.000**
Harpalus affinis				
	HH vs C	0.461	0.047	**<0.001**
	HP vs C	0.565	0.047	**<0.001**
	SC vs C	0.466	0.047	**<0.001**
	SN vs C	1.521	0.047	**<0.001**
Harpalus luteicornis				
	HH vs C	0.470	0.788	0.551
	HP vs C	0.337	0.799	0.674
	SC vs C	-0.916	0.998	0.359
	SN vs C	-0.424	0.918	0.644
Harpalus (Pseudoophonus) rufipes				
	HH vs C	0.598	0.601	0.320
	HP vs C	1.157	0.583	**0.047**

	SC vs C	0.547	0.603	0.365
	SN vs C	1.696	0.582	**0.004**
Microlestes minutulus				
	HH vs C	2.079	1.035	**0.045**
	HP vs C	-0.693	1.418	0.625
	SC vs C	0.693	1.122	0.537
	SN vs C	0.087	1.238	0.944
Parophonus maculicornis				
	HH vs C	-0.032	0.500	0.949
	HP vs C	-0.802	0.564	0.155
	SC vs C	-0.757	0.551	0.170
	SN vs C	-1.076	0.608	0.077
Poecilus cupreus				
	HH vs C	1.152	0.462	**0.013**
	HP vs C	2.086	0.441	**<0.001**
	SC vs C	1.166	0.455	**0.010**
	SN vs C	1.656	0.455	**<0.001**
Poecilus versicolor				
	HH vs C	0.088	0.611	0.885
	HP vs C	0.462	0.621	0.457
	SC vs C	-0.623	0.628	0.322
	SN vs C	-1.424	0.674	**0.035**

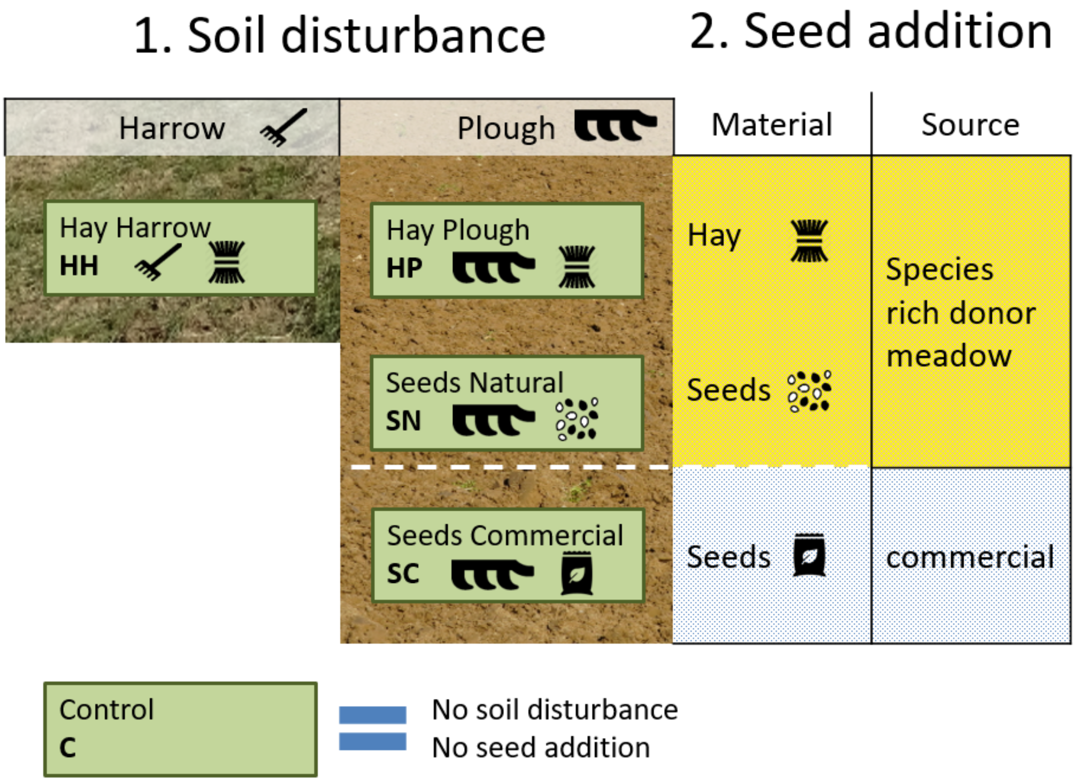
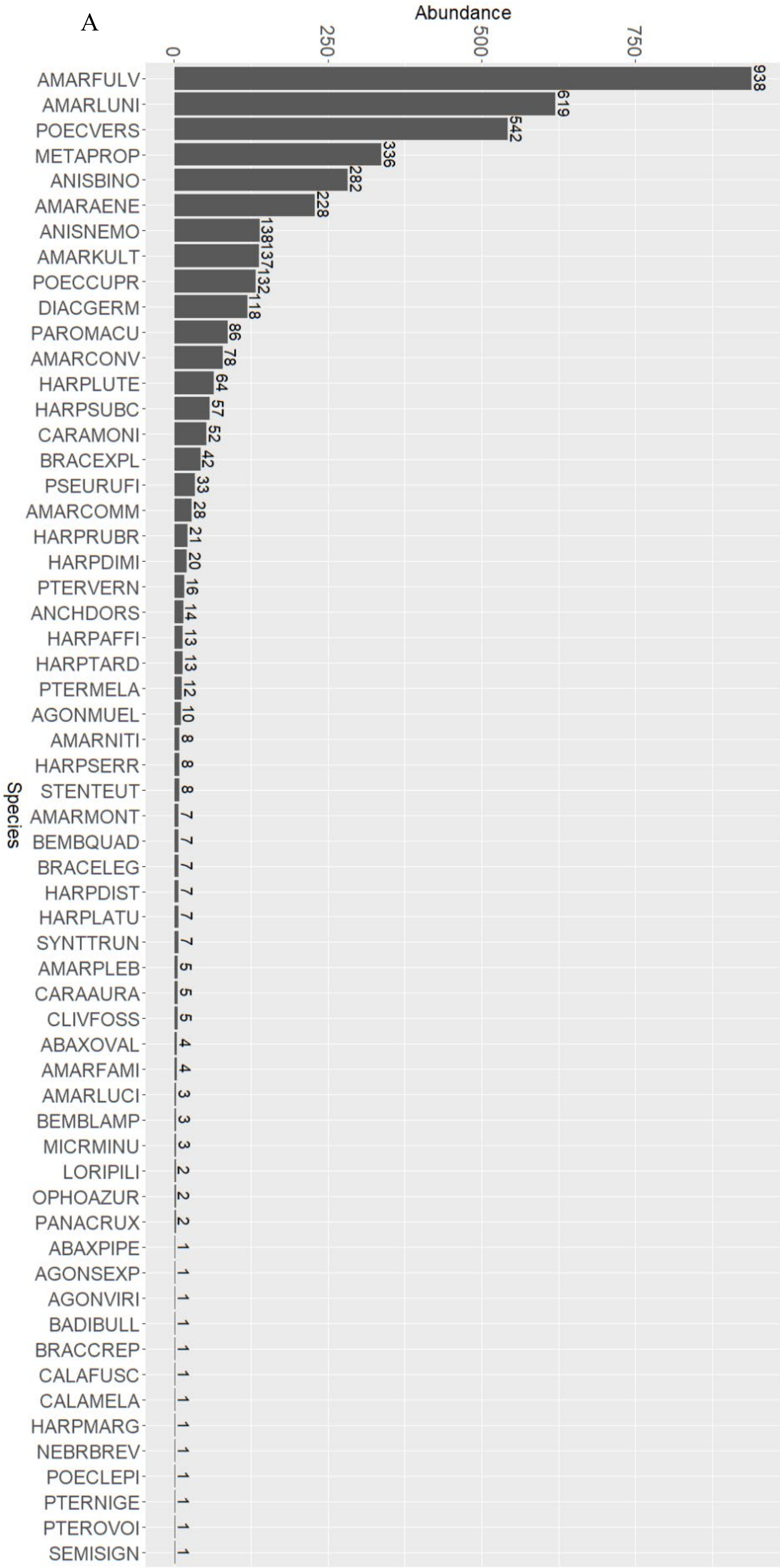


Figure S1. Overview of the experiment with the four restoration treatments plus the control.

A



Abundance
0
250
500
750
Species
AMARFULV 938
AMARLUNI 619
POECVERS 542
METAPROP 336
ANISBINO 282
AMARAENE 228
ANISNEMO 138
AMARKULT 137
POECCUPR 132
DIACGERM 118
PAROMACU 86
AMARCONV 78
HARPLUTE 64
HARPSUBC 57
CARAMONI 52
BRACEXPL 42
PSEURUFI 33
AMARCOMM 28
HARPRUBR 21
HARPDIMI 20
PTERVERN 16
ANCHDORS 14
HARPAFFI 13
HARPTARD 13
PTERMELA 12
AGONMUEL 10
AMARNITI 8
HARPSERR 8
STENTEUT 8
AMARMONT 7
BEMBQUAD 7
BRACELEG 7
HARPDIST 7
HARPLATU 7
SYNTTRUN 7
AMARPLEB 5
CARAAURA 5
CLIVFOSS 5
ABAXOVAL 4
AMARFAMI 4
AMARLUCI 3
BEMBLAMP 3
MICRMINU 3
LORIPILI 2
OPHOAZUR 2
PANACRUX 2
ABAXPIPE 1
AGONSEXP 1
AGONVIRI 1
BADIBULL 1
BRACCREP 1
CALAFUSC 1
CALAMELA 1
HARPMARG 1
NEBRBREV 1
POECLEPI 1
PTERNIGE 1
PTEROVOI 1
SEMISIGN 1

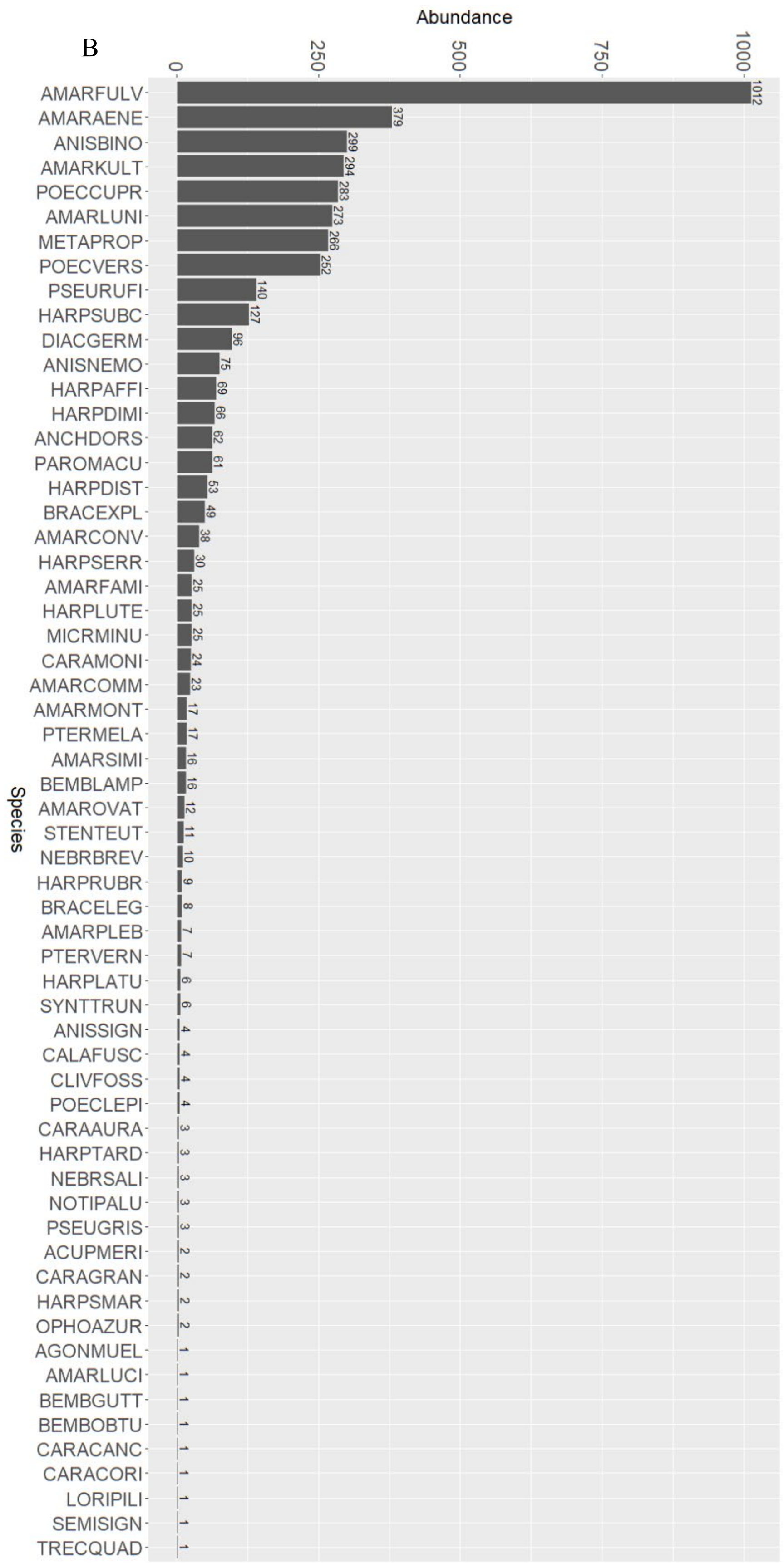


Figure S2. Ground beetles abundance in 2018 (A) and 2020 (B). The abbreviations correspond to the first four letters of the genus and species.

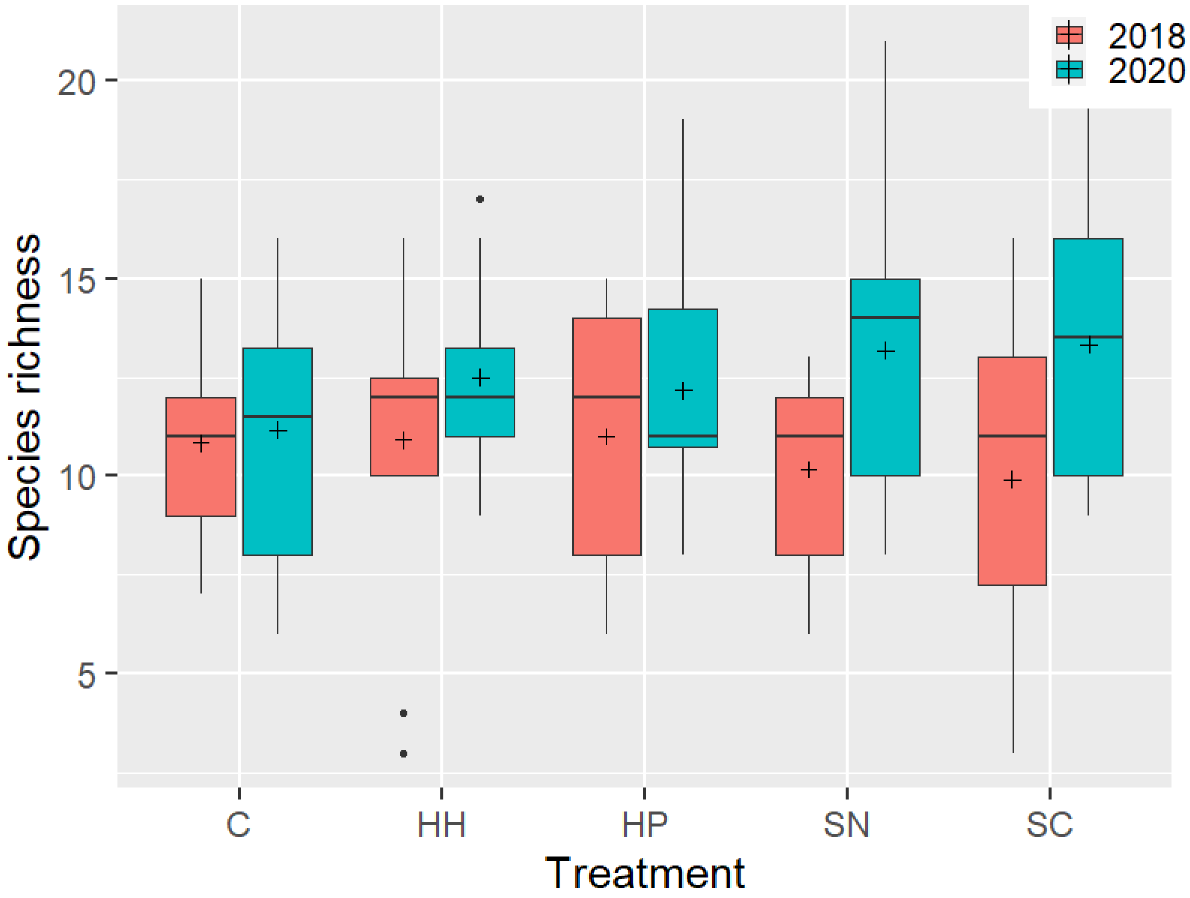


Figure S3. Ground beetles species richness per year and per meadow. No significant effect of the treatments could be detected neither in 2018 nor in 2020. Abbreviations as in Figure 3.

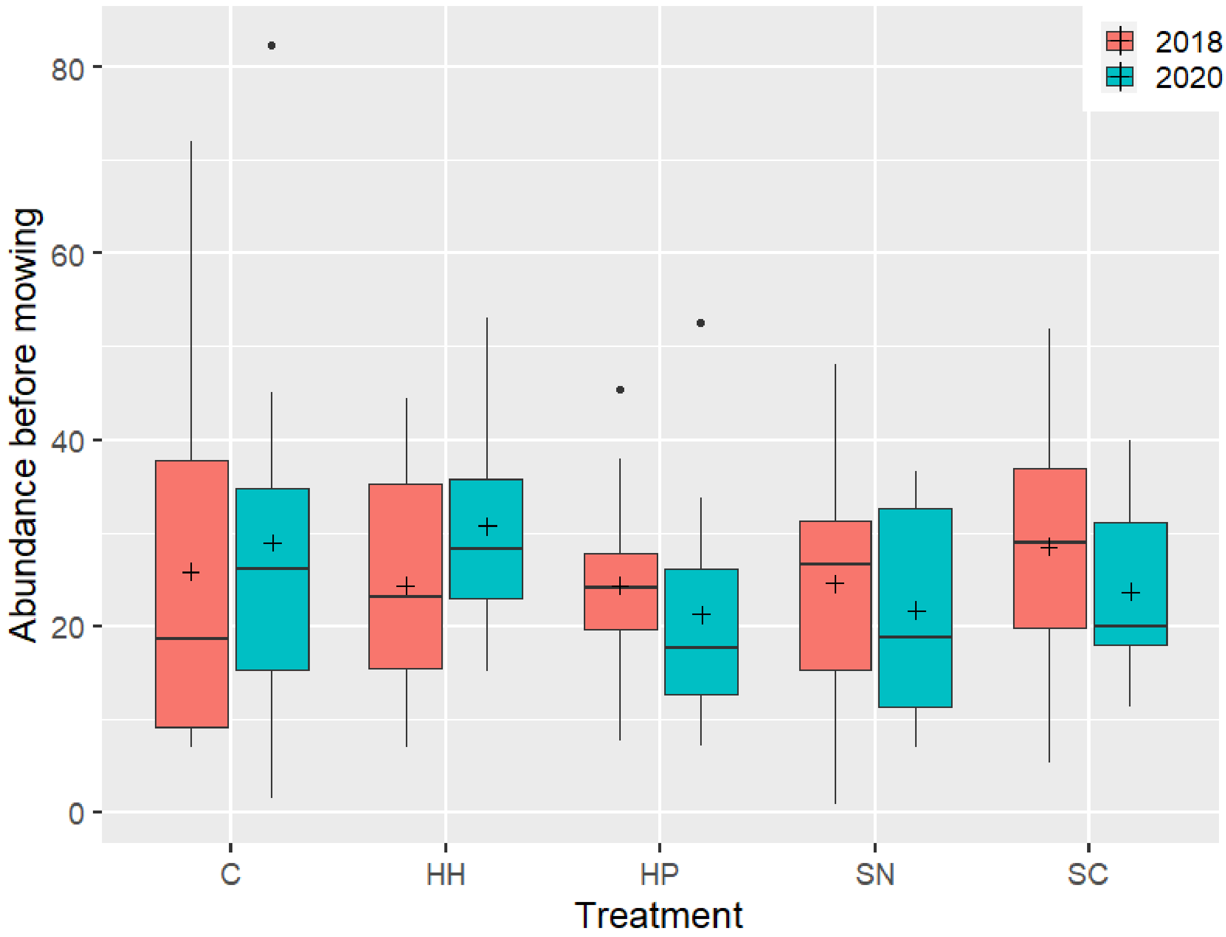


Figure S4. Ground beetles mean abundance per meadow before mowing. No significant effect of the treatments could be detected. Abbreviations as in Figure 3.

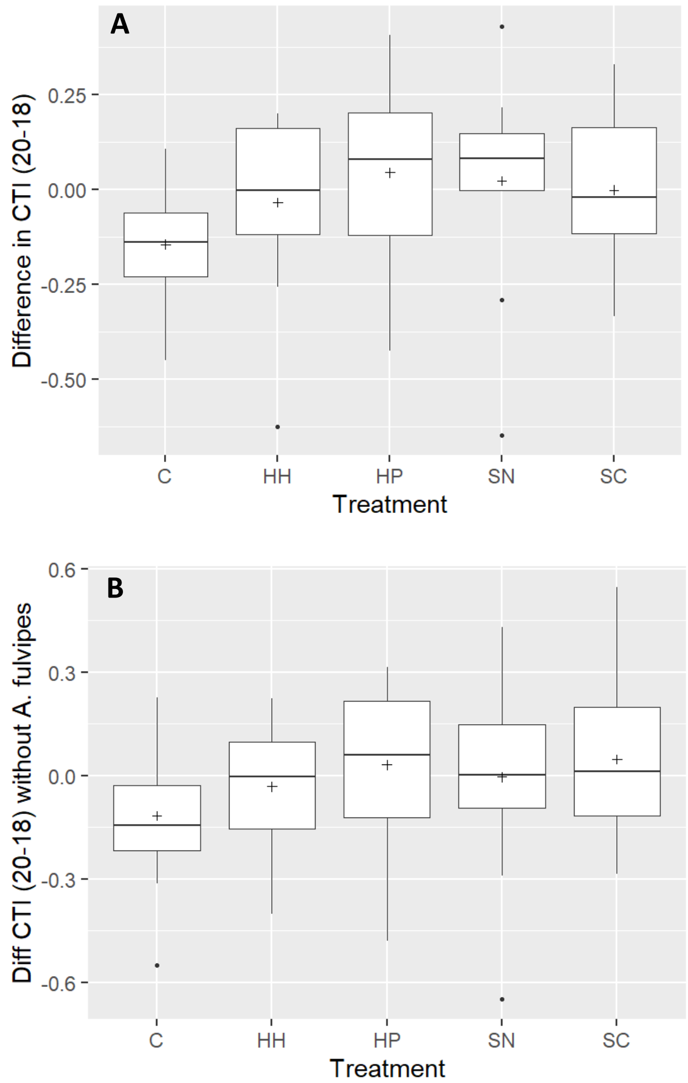


Figure S5. Difference between the 2020 and the 2018 CTI values. While the HP-meadows had a significantly higher difference compared to controls when considering all species (A), no significant effect of the treatments could be detected after the removal of *A. fulvipes* (B). Abbreviations as in Figure 3.

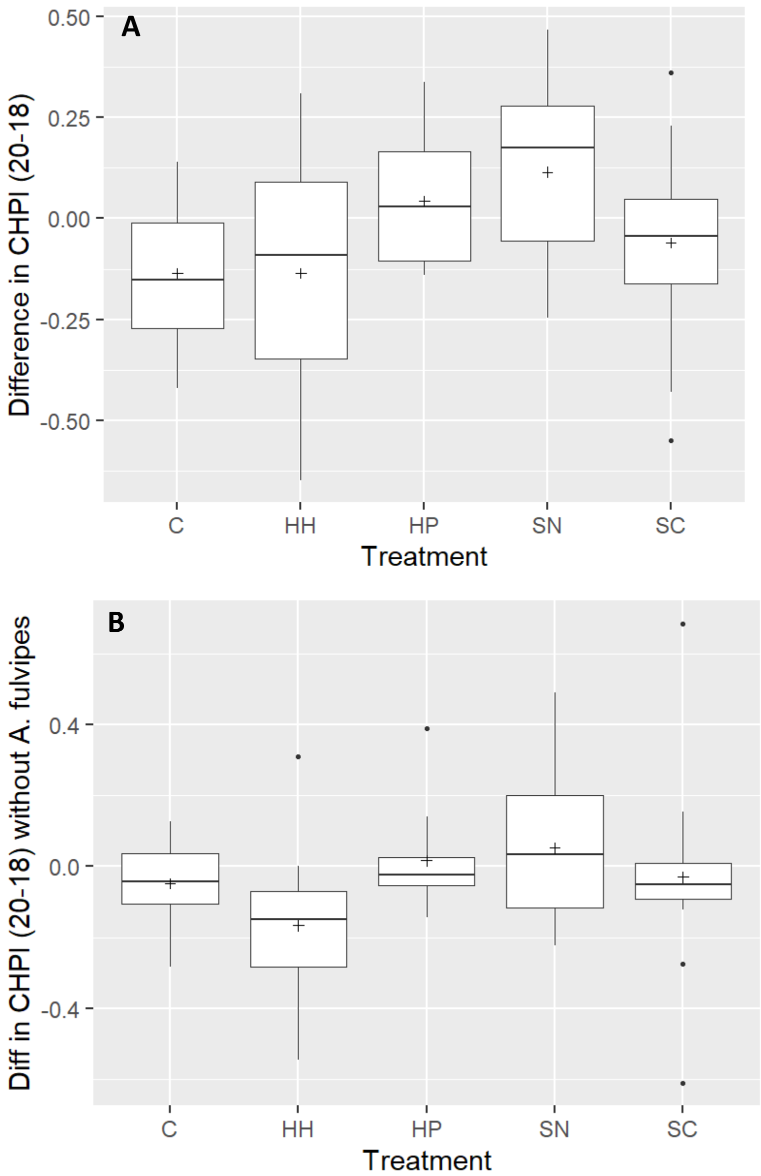


Figure S6. Difference between the 2020 and the 2018 CHPI values. While the SN-meadows had a significantly higher difference compared to C- and HH-meadows when considering all species (A), HP- and SN-meadows harboured a higher difference compared to HH-meadows after the removal of *A. fulvipes* (B). Abbreviations as in Figure 3.