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Mid-term effect of active grassland restoration methods with soil disturbance on ground-dwelling spiders

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Abstract

Grasslands are among the most diverse terrestrial biomes in terms of plants and arthropods. Unfortunately, nowadays many are degraded due to the last decades of intensive management which led to a dramatic decline in their biodiversity. To restore degraded grasslands, active seed addition is often necessary because of the depleted local seed bank, but it requires that the grasslands are ploughed or harrowed beforehand. It was already demonstrated that such soil disturbances, when regularly applied like in croplands, negatively impact the ground-dwelling fauna. However less is known about their effects in permanent grasslands when applied only once. In our experiment, we investigated the mid-term effect (after one year) of four active grassland restoration treatments with two methods of soil disturbance, namely harrowing and ploughing, on the abundance, species richness and community assemblage of ground-dwelling spiders. Results showed that the restoration treatments had no significant impact on spider abundance and species richness when compared to control undisturbed grasslands, but some changes were observed regarding the community within the ploughed grasslands which harbored a smaller and more mobile spider community after restoration. This was mainly driven by the higher abundance of some pioneer species typically found in frequently disturbed habitats. In addition, all the restored grasslands had more hygrophilous species than the control grasslands suggesting that the microclimate conditions changed after restoration. We also investigated if the response of the ground-dwelling spiders could be influenced by the proportion of undisturbed herbaceous areas adjacent to the restored grasslands. These potential adjacent refuge areas had no significant effect on spider abundance and community recovery. Overall, no negative impact of the active restoration treatments was observed, suggesting that local ground-dwelling spiders are quite resilient to the punctual soil disturbance event necessary when restoring species-poor grasslands.

Introduction

In Europe, the development of intensive agricultural practices have strongly impacted farmland biodiversity due to the constant increase in field size, implementation of monocultures and an excessive use of fertilizers and pesticides (Haddad, Haarstad, and Tilman 2000; Benton et al. 2002; Wesche et al. 2012; Lessard-Therrien et al. 2018). Awareness about this farmland biodiversity crisis increased in the 1980s already and in order to address the issue with the attempt to stop the decline, agri-environment schemes (AES) were introduced throughout Western Europe (Switzerland included) at the beginning of the 1990s (Kleijn and Sutherland 2003), which was followed by Eastern EU countries about a decade latter (Batáry et al. 2015; Sutcliffe et al. 2015). AES financially support farmers to adopt less intensive agricultural practices with the main aim to reduce pressure on the environment and biodiversity in particular. Extensively managed grasslands are by far the most popular and abundant (in terms of hectare) type of AES (Kleijn and Sutherland 2003; Humbert et al. 2018). However, despite the implementation of these schemes in Europe, there is still little evidence of a positive impact on biodiversity which calls for more effective alternative solutions (Knop et al. 2006; Aviron et al. 2009; Concepción et al. 2012; Batáry et al. 2015). In fact, the extensification of grasslands management through passive measures such as the reduction of fertilizers and pesticides input or delaying the first cut of the meadows did not result in a drastic change in terms of species richness as it was expected (Kleijn et al. 2001; van Klink et al. 2017). This limited effectiveness could be the result of a locally depleted seed bank due to previous years of intensive management (Bekker et al. 1997; Walker et al. 2004; Waldén and Lindborg 2016).

In this context, active restoration methods through direct seed addition have gained interest in the last two decades to re-create or promote biodiversity in species-poor meadows (Dobson, Bradshaw, and Baker 1997; Losvik and Austad 2002; Jongepierová, Mitchley, and Tzanopoulos 2007; Slodowicz, Humbert, and Arlettaz 2019). As demonstrated in Schmiede et al. (2012), it is recommended to plough or harrow the meadows prior to seed addition to open the soil and reduce plant competition to increase the probability of (new) plant establishment. In fact, their experiment resulted in the re-establishment of 101 species in total including 28 from the Red List species after three years on 12 restored plots of 10 m^2. Similar results were obtained in wet grasslands with a higher proportion of newly established plants after harrowing compared to undisturbed seeded meadows (Poschlod and Biewer 2005). While active restoration methods with ploughing or harrowing beforehand have already shown some efficiency to restore plant diversity, less is known about the effect of such soil disturbances on ground-dwelling arthropods in permanent grasslands (but see Thorbek and Bilde 2004; Liu et al. 2016). Though, negative impacts of soil work on epigeal arthropods have been shown in arable lands known to be frequently disturbed (Thorbek and Bilde 2004; Attwood et al. 2008; Navntoft et al. 2016). Note that the impacts are mainly measured a few weeks after the disturbance which can be seen more as the short-term effect of soil disturbance on arthropod community.

The aim of this study was to investigate the mid-term impact (after one year) of active grassland restoration methods with soil disturbance on ground-dwelling arthropods. Specifically on the ground-dwelling spider community of extensively managed, but relatively plant species-poor, meadows. We tested the effect of two level of soil work, harrowing which breaks up the soil surface and ploughing that goes deeper into the ground being slightly more destructive.

Spiders are good bioindicators for restoration monitoring due to their high mobility and rapid regeneration time allowing them to respond faster to environmental disturbances than plants making them a valuable model for our research aim (Mortimer, Hollier, and Brown 1998; Wheater, Cullen, and Bell 2000). Moreover, they are a highly diverse taxon of generalist predators playing a crucial role in the food web as both predators and preys (DiCarlo and DeBano 2019). Indeed, they keep the arthropod population under control by removing pests for example but they also represent a great source of food for small mammals and birds (Hunter and Price 1992; Nyffeler and Sunderland 2003).

It was already shown that spiders responded negatively to soil disturbance caused by ploughing and harrowing. Some mobile species from the Linyphiid family were shown to be particularly affected (Thorbek and Bilde 2004; Kosewska et al. 2018; Pfingstmann et al. 2019). The negative impact on the spider community was not only due to direct mortality from the mechanical disturbance but also through the loss of resources and destruction of the habitat (James R. Bell, Wheater, and Cullen 2001). These cumulative indirect effects were actually more detrimental to spider abundance than direct mortality itself (Thorbek and Bilde 2004). In addition, ploughing and harrowing was shown to have an impact on other soil invertebrates such as collembola which reduces the number of preys available for these predators indirectly impacting spider density as a negative bottom-up effect (Wise et al. 1999; Liu et al. 2016).

In our experiment, we tested the effect of four active restoration treatments on the abundance and species richness of spiders. In addition, we also addressed more specifically:

1) Spider functional diversity in order to investigate any potential changes in their community. It was already shown that some specific species such as small agrobionts or big active hunters can be favored after habitat disturbance, switching the community assemblage according to their body size, foraging strategy and mobility (Rushton, Luff, and Eyre 1989; James R. Bell, Wheater, and Cullen 2001; Bonte et al. 2003; Öberg and Ekbom 2006; Kosewska et al. 2018; Klink et al. 2019).
2) The influence of undisturbed herbaceous areas adjacent to the restored grasslands that could provide a stable and safe refuge for spiders after the soil disturbance event, as well as intact population sources for the (re-)colonization of the restored grassland. Indeed, leaving refuges after mowing was shown to be beneficial for arthropods in grasslands (Humbert et al. 2012; Buri, Arlettaz, and Humbert 2013; Buri et al. 2016) and spiders

used natural shelters surrounding their habitat after tillage in vineyards (Pfingstmann et al. 2019). Thus, having such undisturbed adjacent areas close to their habitat might influence ground-dwelling spider abundance and species richness response to the restoration treatments.

According to the literature cited above, we hypothesized that (a) soil disturbance should have a negative impact on both the abundance and species richness and that (b) the functional diversity and assemblage of the population should be affected after the disturbance. We also expected to see (c) a positive influence of the adjacent undisturbed areas on both spider abundance and species richness. This research was part of the grassland restoration project launched in 2018 by the division of Conservation Biology at the University of Bern in Switzerland and that is still running.

Materials and Methods

Study sites and experimental design

The present research was conducted on the Swiss lowland Plateau within extensively managed meadows registered as Swiss AES. The Swiss AES regulations for extensively managed meadows imply that the first cut cannot be done before 15 June and that no pesticides or fertilizers can be applied. In 2018, 60 of such AES meadows were selected within twelve lowland regions of the Swiss Plateau (12 x 5 meadows = 60). The main conditions were that all meadows should have been extensively managed since at least 2013 and relatively species-poor in term of plant diversity. In addition, the five meadows within each region were at least 330 m away from each other and located within a 3 km radius. These twelve regions were situated between 450 and 720 m in altitudes and separated by at least 5 km going from the Canton of Vaud up to Luzern (Fig. 1).

In May and June 2019, four restoration treatments were randomly assigned to four meadows within each region and one meadow was left untreated as a control (Fig. 2). The treatments were: (i) hay transfer from a species-rich donor meadow on a harrowed meadow (abbreviated HH); (ii) hay transfer from a species-rich donor meadow on a ploughed meadow (abbreviated HP); (iii) sowing of a commercial seed mixture on a ploughed meadow (abbreviated SC); and (iv) sowing of seeds collected from a species-rich donor meadow on a ploughed meadow (abbreviated SN). Harrowing was done with a rotatory harrow and ploughing with a ploughing machine both pulled by a tractor. A BACI-design (before-after-control-intervention) was applied (Underwood 1991). All meadows were sampled in 2018 (baseline data), meadows were actively restored in 2019 and then resampled in 2020. This allowed us to compare the results before and after the restoration as well as against control undisturbed grasslands.

One restored meadow sown with natural seeds from a species rich donor meadow (SN) in Puidoux failed. This failure potentially happened following heavy rains in 2019 just after the seeding that flooded the meadow or because the seed mixture initially used was of poor quality. In addition, the high presence of *Rumex obtusifolius* also partially explained this outcome. Therefore, this meadow was discarded from the analysis and the final total number of meadows was of 59 in 2020.

Spider sampling

In 2018 and 2020, ground-dwelling arthropods were sampled in all meadows using pitfall traps. Two sampling sessions of one week each occurred before mowing the restored meadows and again after mowing, resulting in four sessions of one week in total. After each session, pitfalls were emptied and new ones were placed for the following week. The sampling session started in mid-May and ended in July.

Pitfall traps were made of plastic cups of 90 mm in diameter put in the soil with the top of the plastic cup being at ground level. Each cup was labelled with the date, ID of the meadow (two first letters of the region and abbreviation of the treatment applied) and the sampling session. Four pitfalls were placed in each meadow arranged in a 10 x 10 m square, 20 m away from a random permanent point previously placed at the beginning of the project (Fig. 3A). The setup scheme was adapted if needed to make sure pitfalls did not end outside of the sampling area (Fig. 3B). Pitfalls were filled with a mix of propylene glycol diluted in water (2:1 ratio) as a killing and preserving agent with a pinch of detergent (sodium dodecyl) to reduce surface tension. A transparent cover was added 5 cm above each pitfall to protect them from the rain (Fig. 4). In addition, a small wire mesh was also placed on top of each cup to prevent mammals or reptiles to fall into the traps (Fig. 4). Once collected, the pitfalls were emptied and sorted in the lab in three groups: Staphylinidae, Carabidae and Spiders. All the groups were counted and conserved in small jars filled with 60% ethanol for later identification. The abundance was calculated using all the pitfalls of the four sessions while the identification was only done for one pitfall of two sessions.

Spider identification and ecological traits

Spiders were identified to species level using the identification key of Nentwig et al. (2010). Identification was made only using one of the four pitfalls placed on each meadow of the session 1 and 3 (1/8 of total pitfalls). Functional diversity was determined using three ecological traits: body size, humidity preference and mobility (Table 1). Body size was taken as a continuous variable defined as the mean body length in mm of the smallest and biggest size of each species without considering the sex from Nentwig et al. (2010). Humidity preference was also taken as a continuous value found between 0 and 1, respectively going from spider preference to very moist (0) habitat up to very dry (1) habitat (Cardoso et al. 2011; Entling et al. 2007). Lastly, mobility was defined by the frequency of a species to use aerial dispersal also known as "ballooning" which is the most efficient way to disperse across long distances and to recolonize a new habitat (Weyman 1993). To do so, spiders sense the electrical fields in the environment and evaluate if the weather conditions are good enough for them to disperse through the air using threads of silk (Cho et al. 2018). The frequency of a species to use ballooning was therefore defined as (1) for rare, (2) for occasional and (3) for frequent (Macías-Hernández et al. 2020).

Refuge opportunities

During the restoration of the meadows, some areas directly adjacent to the ploughed or harrowed parts of the meadows were left untouched due to mechanical constrains or because the meadows were close to the forest (Fig. 5). Thus, we investigated if these undisturbed areas could potentially be used as a refuge after the disturbance since they could provide a stable and safe habitat for spiders. To see if the undisturbed refuge area influenced spider-community to scope with soil disturbance, we calculated a refuge ratio for each meadow. This refuge ratio was calculated as the ratio of the undisturbed area divided by the total area of the meadow. A 50 m buffer around large meadows was also considered for the analysis. The resulting value obtained was between 0 and 1, with 0 meaning the whole meadow was restored (ploughed or harrowed) and no refuge was left, and 1 meaning that no disturbance was applied (control).

Statistical analysis

All the analyses were done using R statistical software version 3.6.1 (R Core Team 2019). Spider abundance was calculated as the mean abundance per meadow before mowing (sessions 1 and 2) and after mowing (sessions 3 and 4). Using the mean abundance and not the sum allowed us to take into consideration the meadows where some traps were disregarded due to the presence of mice or lizards. Species richness was represented by the number of independent species recorded per meadow with their abundance in session 1 and 3 pooled together.

To investigate and compare the effect of the restoration treatments on the abundance, species richness and ecological traits in 2018 and 2020, data were analyzed using linear mixed-effect models LMMs using the "lme4" package (Bates et al. 2014). Treatments were integrated as the fixed effect and regions as the random effect to consider the differences between them. Both variables were defined as factors. Firstly, to assess if there was any potential year effect between 2018 and 2020, control meadows were compared. Specifically, LMM models were run only on the control meadows including data of 2018 and 2020 with year as the fixed effect. If there was a significant signal, statistical models were applied on the difference between the years (2020 data minus 2018 data) to account for this year effect. Otherwise, models were applied on 2020 and 2018 data separately. Refuge opportunities were analyzed using LMMs as well with the refuge ratio as the fixed effect and treatments as random effect for the explanatory variables.

The abundance and species richness were used as response variables as well as the mobility since low mobile species might benefit more from these potential refuges.

Species diversity was calculated using the Shannon-Wiener index (H') which accounts for both the abundance and evenness of the species present (Magurran 1988) using the "vegan" package (Oksanen et al. 2007). The ecological trait analysis was made using the community-weighted mean (CWM). CWM calculates the mean trait value weighted by the abundance of the species present in the community, giving us an insight of the community structure. The equations for these two analyses were the following:

$$\text{Shannon-Wiener Index (H)} = -\sum_{i=1}^{S} p_i \ln p_i$$

$$\text{Community-weighted mean (CWM)} = \sum_{i=1}^{n} \frac{N_i}{N_{tot}} * SI_i$$

Results

In 2018, a total of 35’288 spiders were collected and 3’835 adults identified to species level while the abundance was lower in 2020 with 27’641 spiders and 3’281 adults identified (see Appendix Table S1). The sampled individuals represented 14 families, 40 genera and 61 species. Juveniles, sub-adults or individuals in bad shape that were only identified up to family or genus level were not included in the analysis. The most abundant species was *Pardosa palustris* from the Lycosidae family representing 50% of the total identified spiders in both years (see Appendix S1 and S2). Before mowing, the mean abundance and SD of spiders per meadow was of 48.03 ± 27.12 in 2018 and of 38.11 ± 21.65 in 2020. Spider mean abundance and SD was lower after mowing with a total of 20.83 ± 12.61 spiders in 2018 and 23.63 ± 17.44 in 2020. Regarding species richness, an average of 8.80 ± 2.54 species were found per meadow in 2018 for an average of 8.29 ± 2.23 in 2020.

Abundance and species richness of spiders

In 2020, none of the restoration treatments had a significant effect on spider abundance before mowing when compared to the control (Appendix Fig. S3). However, the abundance in the SC treatment was significantly higher than the control (C) after mowing (Fig. 6 and Table S3). Regarding species richness, no effect was detected (see Appendix Fig. S4 and Table S3). Some rare families represented by low abundant species (singleton) in 2018 were missing after restoration and one new rare family was found in 2020. Despite these changes, the Shannon index did not significantly differ between treatments and years (see Appendix Fig. S5).

In order to investigate if rare species responded differently to the treatments, models were applied on the least abundant species that made up for 5% of the samples (see Appendix Fig. S1 and S2). Note that the term rare species was used to define the low abundant species in our samples and do not refer to the degree of rareness of the species in the country. For the species richness, HH and SC were significantly different than C with an average of one species missing in the treatments (see Fig. 7 and Appendix Table S3). Overall, there was no pattern of one specific species missing only in these two treatments and not on the others. No effect was observed when the models were applied on the abundance before and after mowing.

Ecological traits

The CWM for body size differed between treatments after restoration. HP and SC were significantly different than the control with a higher abundance of small species in the treatments (Fig. 8A). When comparing the treatments between them, the difference in SC was also significant compared to HH that had fewer small species. This higher abundance of small species especially came from an increase of *Erigone dentipalpis* and *Oedothorax apicatus* in all treatments which was more pronounced in the ploughed meadows (HP, SN and SC) (Fig. 9). Note that, no effect was detected in SN despite the clear difference seen in the three treatments (Fig. 9). After looking more into detail the species present in the three ploughed treatment, we realized that *Pardosa palustris* abundance was slightly higher in SN compared to HP and SC. As a reminder, *Pardosa palustris* was the most abundant species in our samples and is a rather big species measuring between 5 and 7 mm. The higher abundance of this species in SN could explain why no effect was detected with this bigger species potentially hiding the signal. Thus, the CWM analysis was rerun without *Pardosa palustris* and all the three ploughed meadows HP, SC and SN had significantly more smaller species than C (Fig. 8B).

Regarding the CWM for humidity preference, all the treatments were significantly different than the control in 2020 with more hygrophilous species in the treatments especially in the ploughed meadows HP, SN and SC (Fig. 10A). No difference was detected among treatments. Results did not differ when the analysis was done without *Pardosa palustris* (Fig. 10B).

Finally, a year effect was detected for the CWM of mobility when the models were applied only on the control of both years. Thus, the analyses were applied on the difference of the CWM for mobility between 2020 and 2018 (2020 data minus 2018 data). The difference of CWM for mobility in HP and SC was significant compared to C, with more mobile species in 2020 than 2018 in the treatments (Fig. 11). SC had also more mobile species when compared to HH in 2020. As observed for the CWM of the body size, after removing *Pardosa palustris* a signal was detected in SN as well as in HP and SC, with these three ploughed treatments having more mobile species compared to the control in 2020 (Fig. 11B).

Refuge opportunities

There was no significant effect of the refuge ratio on spider abundance and species richness (Appendix Fig. S6). Models were also applied on the CWM for mobility since these refuges might be more beneficial for low mobile species, but no significant effect was detected.

Discussion

In this study, the mid-term effect (after one year) of two mechanical soil disturbance methods, namely harrowing or ploughing, on the community of ground-dwelling spiders were investigated. The study was conducted within the framework of an active grassland restoration experiment which included four different restoration treatments where seed addition was performed together with some soil work and a control (unseeded and undisturbed) grassland. Overall, no general effect was detected except in the ploughed treatment that was sown with the commercial seed mixture (SC) where spider abundance increased after mowing compared to the other treatments and control. Though, spider community did slightly change after the restoration in ploughed treatments, with a higher abundance of two species commonly found in disturbed habitat and an increase of hygrophilous species in in all the restoration treatments compared to the controls. Lastly, we also tested whether untreated areas adjacent to the restored meadows could provide some refuge opportunities for spiders after disturbance but no significant effect was detected.

Effect on ground-dwelling spider abundance and species richness

Spider abundance was sampled twice, both before and after mowing, and was not significantly impacted by the soil disturbance caused by the restoration treatments applied in the meadows, expect for one treatment. In fact, the abundance after mowing significantly increased in the meadows that were ploughed and seeded with a commercial seed mixture (SC) when compared to untreated meadows. This increase was observed in 10 of the 12 regions suggesting that it was a general tendency. Since this positive effect was not observed in the other similar (ploughed) treatments, it is difficult to conclude if it results from a direct impact of the soil work or an indirect effect from the seeded mixture. The higher abundance observed in SC could potentially reflect a change in terms of vegetation that positively impacted spiders. Unfortunately, this hypothesis cannot be confirmed as we did not conduct any vegetation survey that would have allowed us to compare plant population before and after restoration.

The results obtained differ from previous studies that observed a negative impact on spider abundance after soil disturbance (Pernille Thorbek and Bilde 2004; Attwood et al. 2008; Navntoft et al. 2016). However, the cited literature measured the short-term effect by sampling spiders a few weeks following soil work. The fact that we did not observe a negative effect in the abundance suggest that spider community are resilient to soil harrowing or ploughing and that they were able to successfully recover after one year. This was also observed in previous disturbance studies showing that one year was enough to recover from a controlled fire in xeric grassland (Hamřík and Košulič 2021) and only a few weeks after tillage in vineyards (Pfingstmann et al. 2019). Thus, abundances might have decrease directly after the restoration action but the effect could not be detected anymore after one year. In addition, the soil disturbance was applied only once in our experiment compared to arable lands that are frequently disturbed which suggest that the population could recolonize and reproduce without being strongly disturbed systematically. Finally, some species were favored after harrowing and ploughing and their increase in abundance might have compensate some lower numbers in other species which could explains why no signal was detected.

Similar results were observed for the species richness, with no significant effect detected after the restoration. Despite that, three rare families such as the Zodariidae, Clubionidae and Atypidae were missing after the restoration that were represented by singletons in 2018 and one new family was found in 2020 (Agelenidae) represented by only two individuals of the same species. This could suggest that these rare families might respond differently to the treatments applied but that the effect was hidden by the other abundant ones. When the models were run only on the rare species representing 5% of the total catch, the harrowed meadows (HH) and seeded meadows with a commercial mixture (SC) had significantly less rare species than the control. However, the difference observed was of only one species missing in HH and SC (Fig. 7 and Table S3) and it was not the same species that seemed to be impacted in both treatments. Indeed, the species missing greatly differed between the regions and treatments suggesting that it was not a species-specific response. Thus, it is difficult to conclude anything from these results and the rare species missing in some meadows might not reflect a direct negative impact from the disturbance caused by the treatments.

The difference observed in terms of low abundant species could come from the stochastic process of the sampling method used. In fact, pitfalls are efficient to capture active species and measures the activity density rather than the effective abundance of spiders itself making this method less efficient to capture rare species (Topping and Sunderland 1992; Lang 2000; Work et al. 2002; Gardarin and Valantin-Morison 2021). The diversity calculated with the Shannon Index did not significantly differ between years and treatments which can confirm the above hypothesis.

Ecological trait

Regarding the CWM for body size, a higher abundance of smaller species was found after restoration on two of the three ploughed treatments. When the CWM analysis was done without *Pardosa palustris*, all the ploughed meadows had a significantly higher amount of small species compared to the control. This difference in small species abundance was mainly driven by an increase of *Erigone dentipalpis* and *Oeodothorax apicatus* from the Linyphiid family which are often found in disturbed habitats such as arable lands (Rushton, Luff, and Eyre 1989; Bell, Wheater, and Cullen 2001).

These two pioneer species are known to have a greater capacity of recolonization and, compared to other species form the same family, they do not use webs to catch their preys but actively hunt on the ground. This hunting strategy makes them less dependent on the structure of their habitat (Bishop 1990; Samu and Szinetár 2002; Blandenier 2009). Having a higher abundance of these two species in the community should not cause any problem for the other species or families. Indeed, interspecific competition and cannibalism within spider community seem to be rare, especially in simple ecosystems such as agricultural habitats (Wise 1993; Marshall and Rypstra 1999).

Similar results were obtained for the CWM of mobility and body size with the ploughed meadows having more mobile species when compared to the control or the harrowed ones. The fact that we observe the same result for the body size and the mobility is not surprising. Smaller species are known to be more efficient when ballooning due to their lightweight (Weyman 1993; Thomas, Brain, and Jepson 2003). They have a better control when they use aerial dispersal and have less chances to end up in a risky place. Thus, smaller species will use this dispersal method more frequently than bigger spiders which is highly beneficial to escape from a disturbance and recolonize new habitats.

Another change was also observed for the CWM of humidity preference. All the treatments had more hygrophilous species compared to the control with the effect being stronger in the ploughed meadows (HP, SN and SC). Removing the most abundant species *Pardosa palustris* did not change the outcome. These results suggest that the microclimate conditions of the meadows changed after the restoration which could be due to a change in vegetation structure (Humbert, Delley, and Arlettaz 2021). Such results were also obtained for carabids but with a decrease in xerophilous species in two of the ploughed treatments (Auberson 2021).

Refuge opportunities

Some adjacent parts of our meadows were not restored and could potentially be used as undisturbed refuges by spiders or simply act as a population source for the (re-)colonization of the restored but disturbed meadow. The refuge was defined as the ratio of these unrestored grassland areas divided by the total area (restored plus unrestored). Leaving such undisturbed areas could mimic the uncut refuges left in grasslands after mowing which have already been demonstrated to have a positive impact on invertebrates (Humbert et al. 2012; Buri, Arlettaz, and Humbert 2013). In our experiment, and contrary to our original hypothesis, the refuge ratio did not have any significant influence on the spider responses to the restoration treatment with soil disturbance. This refuge ratio was also tested on the CWM of mobility since they could be more useful for low mobile species but no significant signal was detected.

The fact that the refuge ratio had no effect on spider community could be a matter of scale. Indeed, spiders are highly mobile arthropods and can easily cover distances of hundred meters rapidly either through the air or in the ground. This suggests that having a refuge adjacent to their habitat does not matter that much if the landscape overall can provide them suitable and safe habitat opportunities after the disturbance to survive (Samu, Sunderland, and Szinetár 1999; Bonte et al. 2003; Reynolds, Bohan, and Bell 2007). The ploughing or harrowing certainly caused direct mortality of part of the population but their rapid regeneration time and great mobility allowed them to recolonize the meadows once the disturbance was over.

Conclusion and management recommendations

The results obtained in our study suggest that the ground-dwelling local spider communities are resilient to the active restoration of the flora of degraded grasslands that necessitates some soil disturbance beforehand. Nevertheless, some species-specific response as well as small changes in some community traits were observed. For example, more smaller and mobile species were found in the ploughed meadows reflecting the higher abundance of pioneer species from the Linyphiid family. These pioneer species should not represent any threat for the other spider species and families. In addition, an observed increase of hygrophilous spiders in the ploughed meadows also suggest that the microclimate of the meadows became more humid after the restoration. No vegetation surveys were done to confirm this hypothesis but this humidity change could be the result of a more dense and higher vegetation in the restored meadows. This is a known vegetation response as soil disturbance releases nutrients that favor plant growth, but the effect is temporary (Khurshid et al. 2006). Altogether, the results obtained support that extensive grasslands can be restored using soil disturbance without risking damage to the local already existing ground-dwelling fauna.

Despite no evidence of a positive effect of the undisturbed refuge areas on spiders, leaving such refuge is still recommended for other invertebrates. This is especially the case for low mobile species that can use these adjacent natural shelters in order to increase their chances of survival which was seen for carabids after ploughing for example (Auberson 2021).

As further research steps, we recommend to continuously monitor spider population to see if it stabilizes with time especially since there was a higher number of pioneer species after restoration. We also recommend to sample plant-dwelling spiders (and other invertebrates) using suction sampling to provide a more accurate representation of the arthropod community present.

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Tables

Table 1. Summary of the ecological traits used for the spider community analysis. Body size was taken as a continuous value, mean between the smallest and biggest size of each species (Nentwig et al. 2010). Humidity preference was also taken as a continuous value found between 0 and 1 (Cardoso et al. 2011; Entling et al. 2007). Mobility was categorical and defined as the frequency of a species to use aerial dispersal known as ballooning (Bonte et al. 2003; J.R. Bell et al. 2005; Blandenier 2009; Macías-Hernández et al. 2020).

Variable	**Unit**
Body size	Continuous: mm
Humidity preference	Continuous: between 0 (moist) and 1 (dry)
Mobility (ballooning)	Categorical: (1) rare; (2) occasional; (3) frequent

Figures

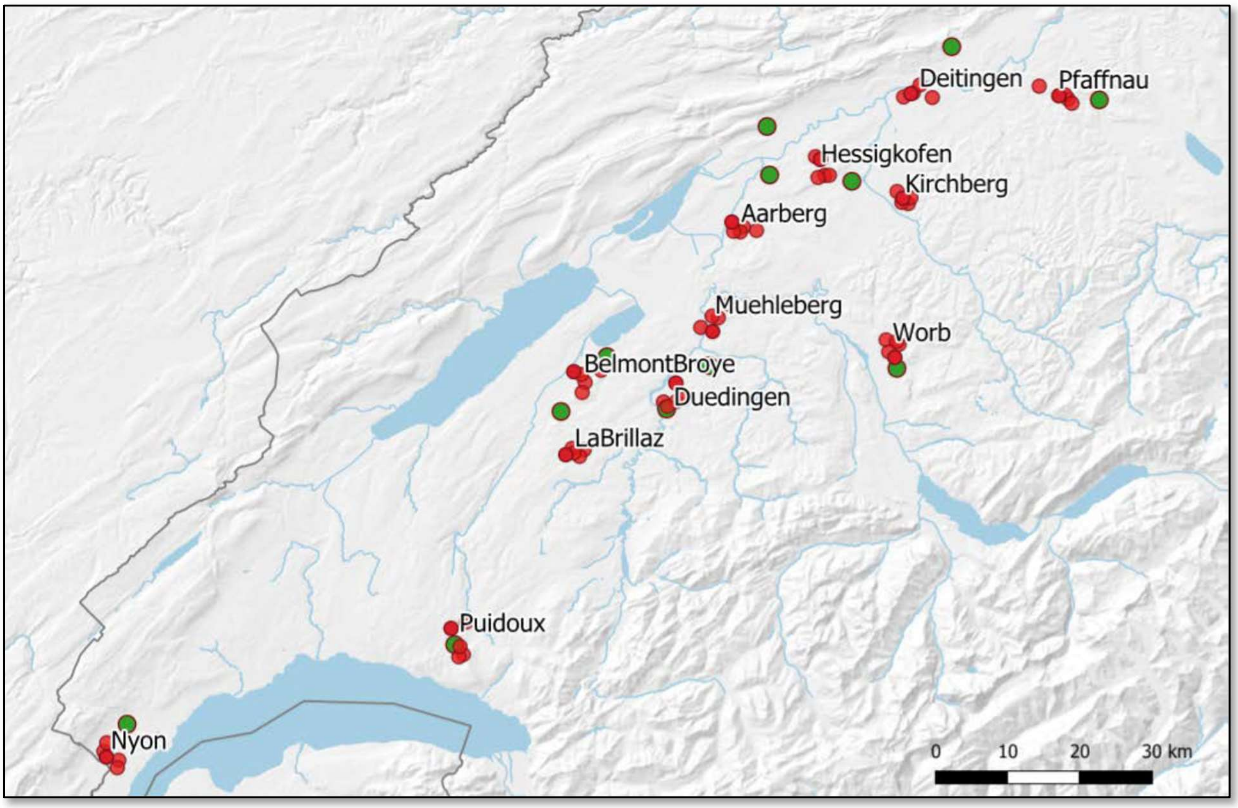


Figure 1. Study sites. Map with all the 12 sampling regions from the cantons of Vaud (Nyon) to Luzern (Pfaffnau). Five extensively managed meadows were selected within each region (red dots). The green dots are the donor meadows (origin of the seed for three of the restoration treatments).

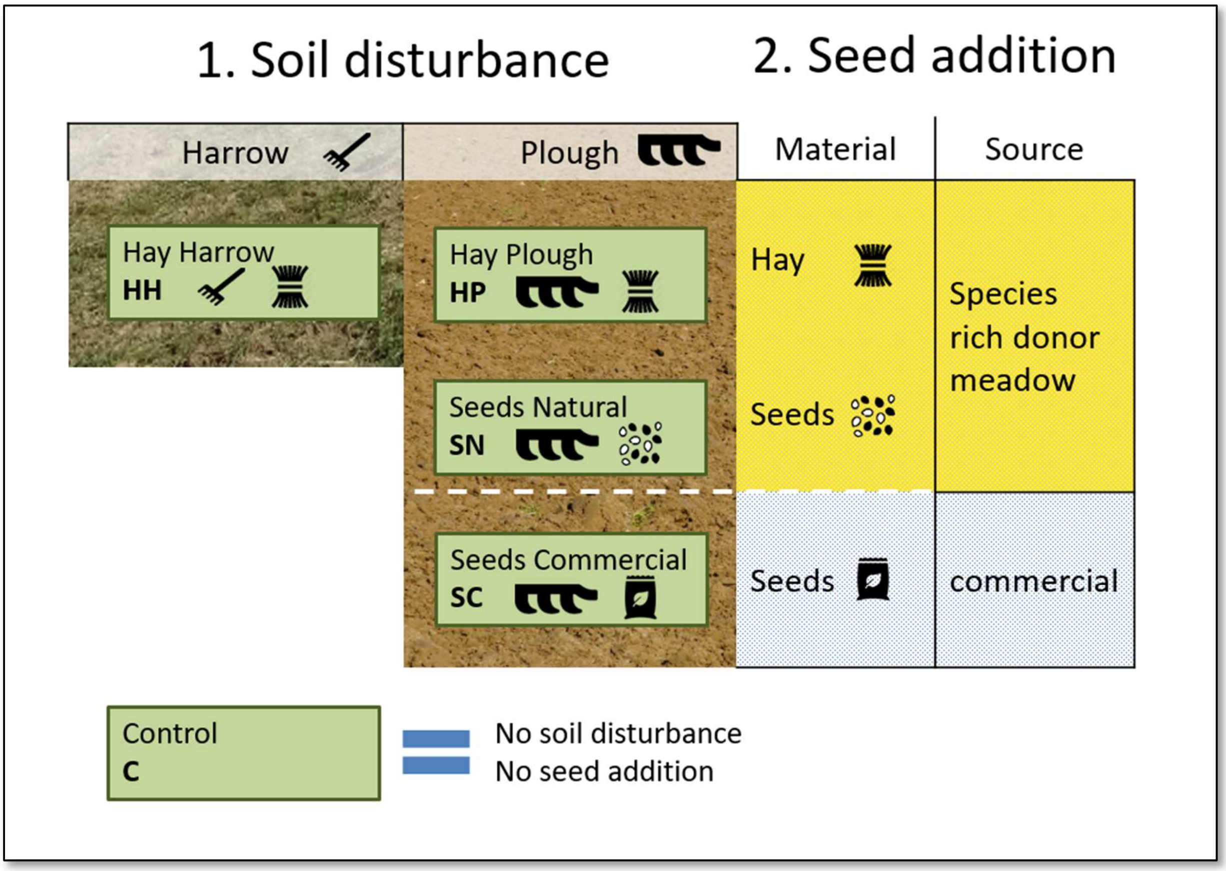


Figure 2. Experimental design. Four restoration treatments and a control were applied (green rectangles). The main restoration factors were: 1) Soil disturbance, meadows were either harrowed or ploughed; and 2) Seed addition, seeds were either directly sown or added using hay transfer. Seeds came from a species-rich donor meadow or from a commercial mixture. Altogether this led to the following four restoration treatments: (i) hay transfer from a species-rich donor meadow on a harrowed meadow (abbreviated HH); (ii) hay transfer from a species-rich donor meadow on a ploughed meadow (abbreviated HP); (iii) sowing of a commercial seed mix on a ploughed meadow (abbreviated SC); and (iv) sowing of seeds collected from a species-rich donor meadow on a ploughed meadow (abbreviated SN).

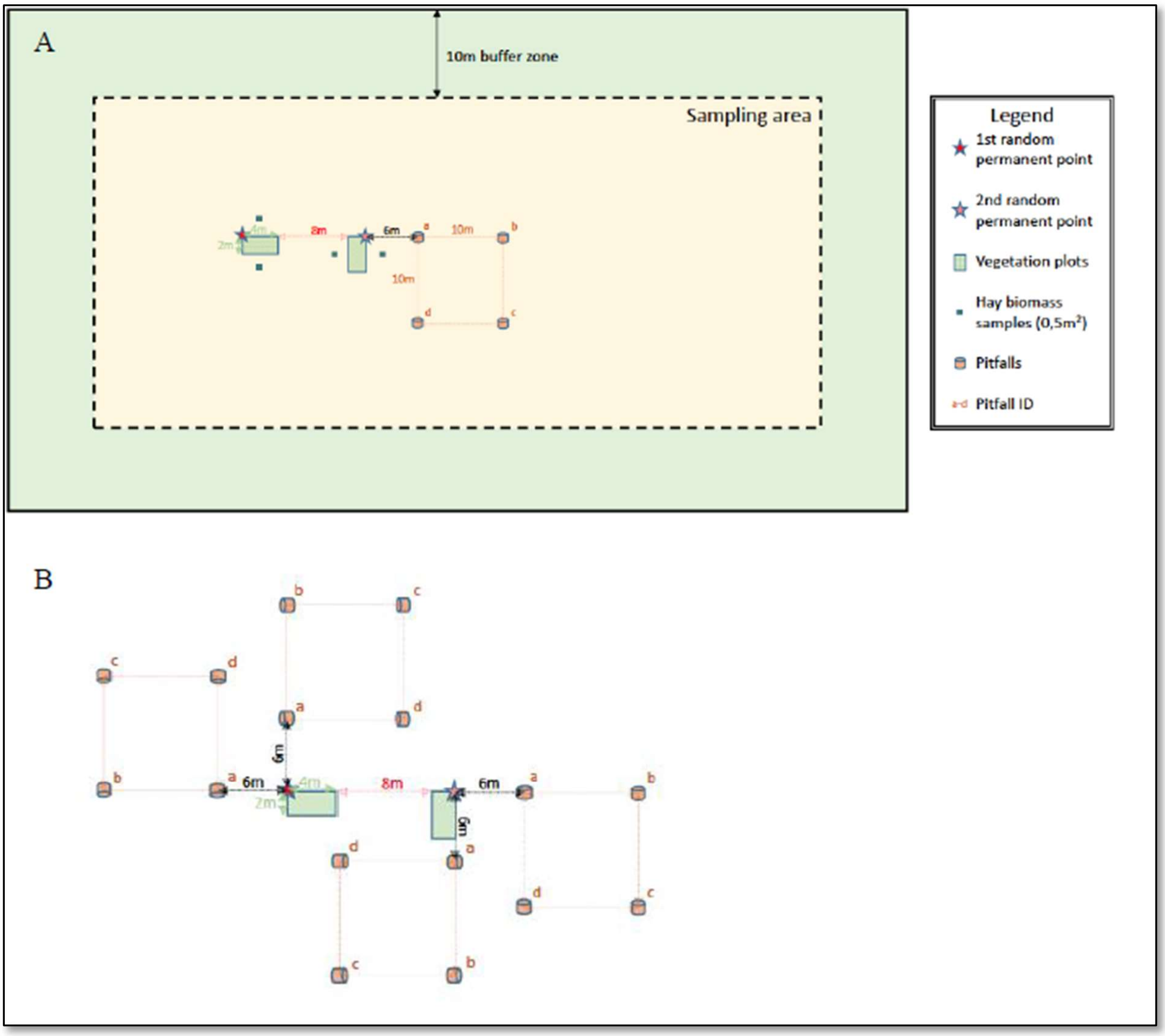


Figure 3. Pitfall setup in the meadows. A) Original scheme for the setup of the four pitfalls, and B) alternative options if one pitfall ends up outside of the sampling area under scheme A.

Figure 4. Pitfall trap. Pitfalls were made of a plastic cup put into the ground filled with water and propylene glycol (2:1). Traps were protected from the rain by placing a transparent cover on top and a wire mesh was added to avoid any mammals or reptiles to fall into the cups.

Figure 5. Refuge opportunities. Some parts of the restored meadows were left untouched during the experiment (highlighted in green) due to mechanical constrains or proximity with forests. Such areas could potentially act as a refuge after the disturbance caused by the restoration. The analysis was run on the ratio of these undisturbed areas divided by the total size of the meadow. A 50 m buffer around large meadows was also took into consideration for the total size.

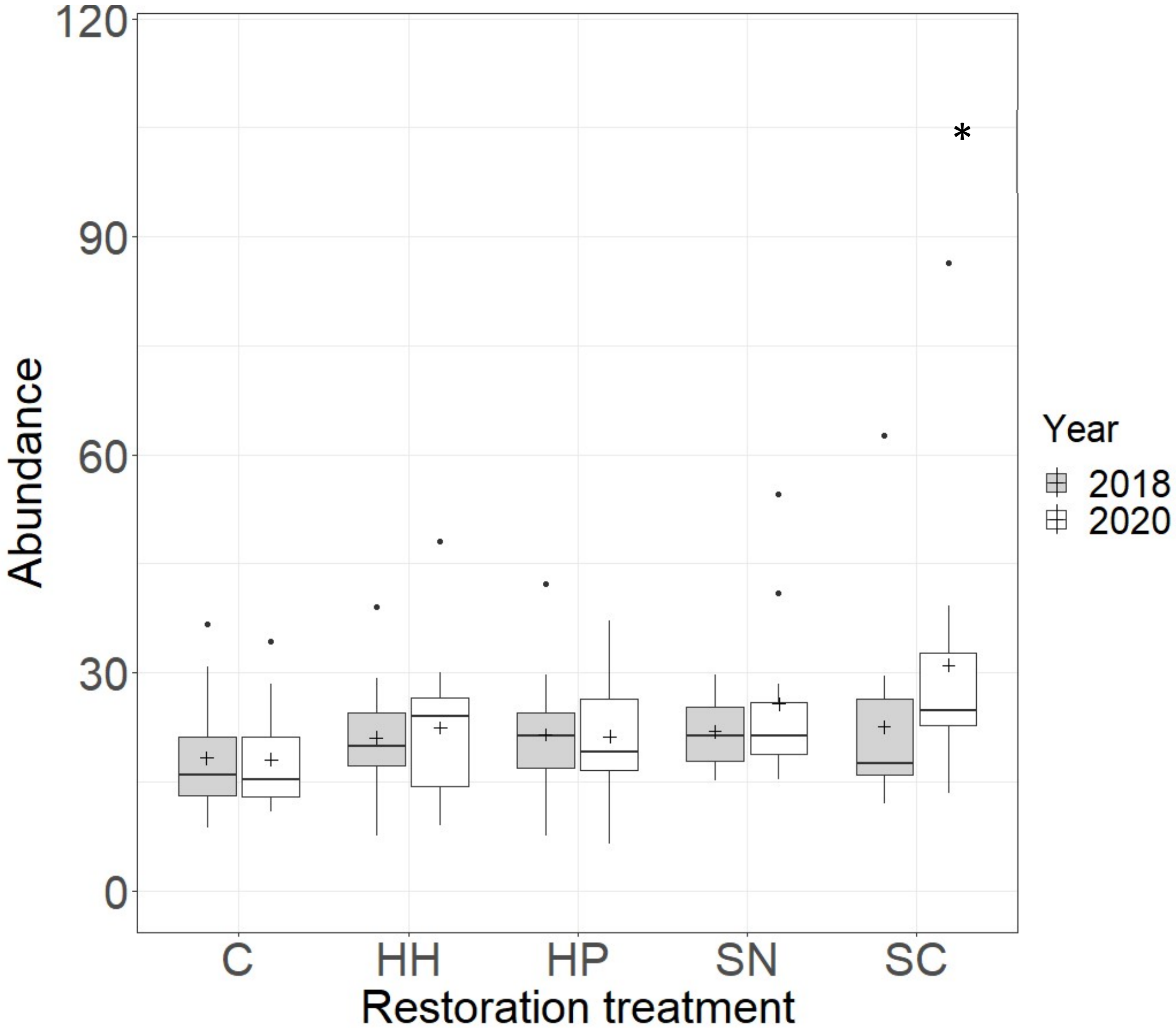


Figure 6. Spider abundance (mean per pitfall per meadow) after mowing in 2018 and 2020 for each restoration treatment. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. In 2020, abundance was significantly higher in seed commercial (SC) compared to the control (C) . No year effect was detected. Codes for significant differences (treatment compared to control) are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

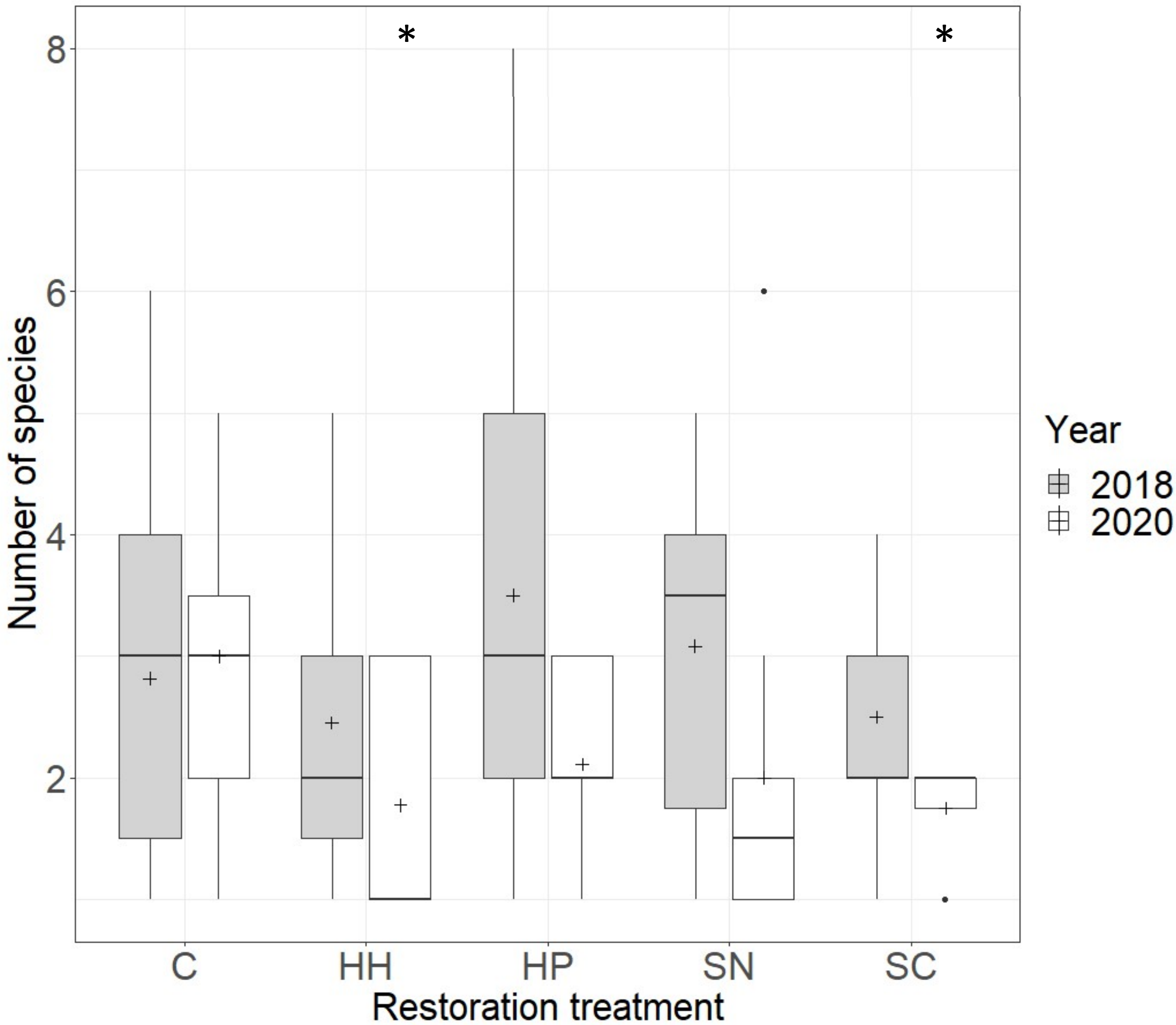
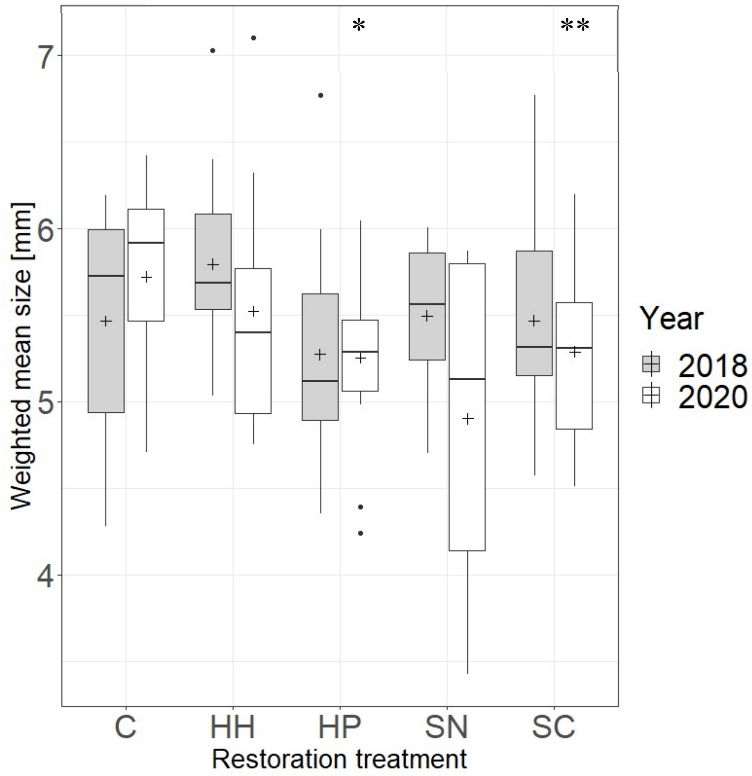


Figure 7. Spider species richness (mean per pitfall per meadow) of the least abundant species representing 5% of the entire catch in 2018 and 2020, per treatments. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. HH and SC were significantly different compared to the control in 2020 with less rare species in the treatments . Codes for significant differences (treatment compared to control) are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

A)



B)

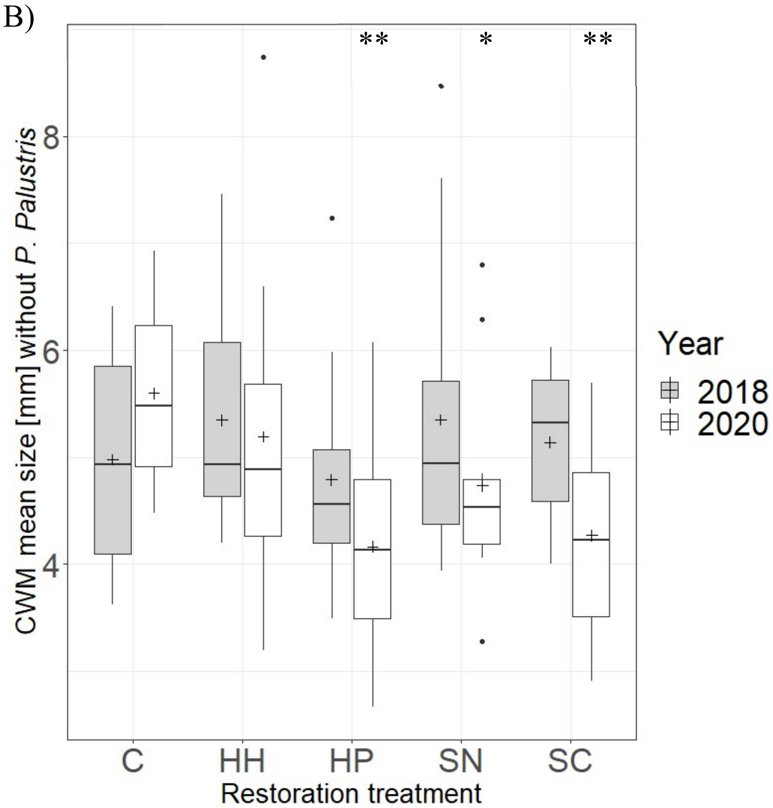


Figure 8. Spider community weighted mean for body size in 2018 and 2020 per treatments. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. Figure A) is for all the species and B) without the most abundant species *Pardosa palustris*. A) HP and SC had more smaller species compared to C in 2020; B) Without *P. Palustris*, HP, SN and SC had more smaller species compared to C in 2020. Codes for significant differences (treatment compared to control) are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

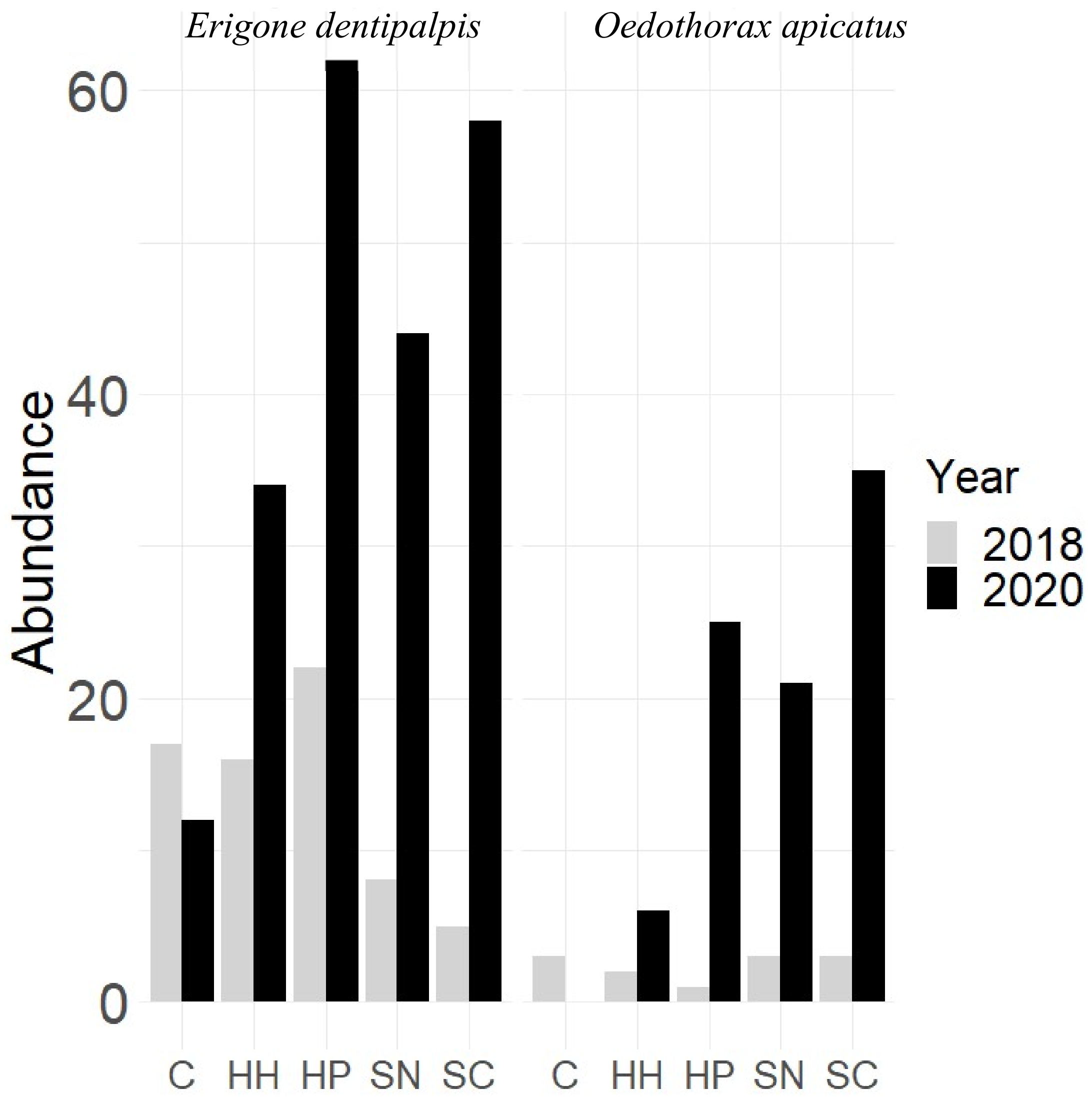
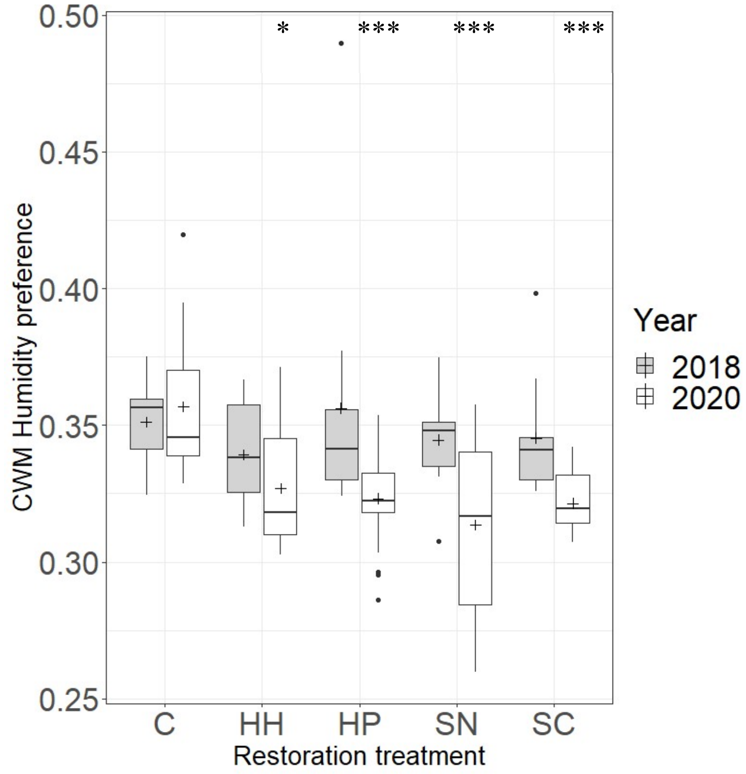


Figure 9. Abundance of the two small pioneer species *Erigone dentipalpis* and *Oedothorax apicatus* in 2018 and 2020, per treatment. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial.

A)



B)

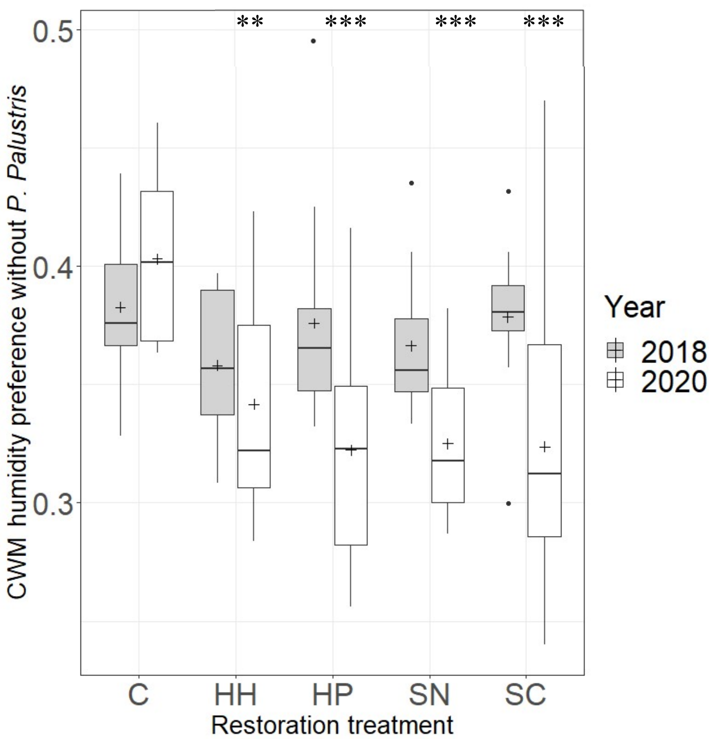


Figure 10. Spider community weighted mean for humidity preference in their habitat (moist = 0; dry = 1) in 2018 and 2020 per treatments. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. A) All treatments had significantly more hygrophilous species compared to the control in 2020; B) Results did not differ without the most abundant species *Pardosa palustris*. Codes for significant differences (treatment compared to control) are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

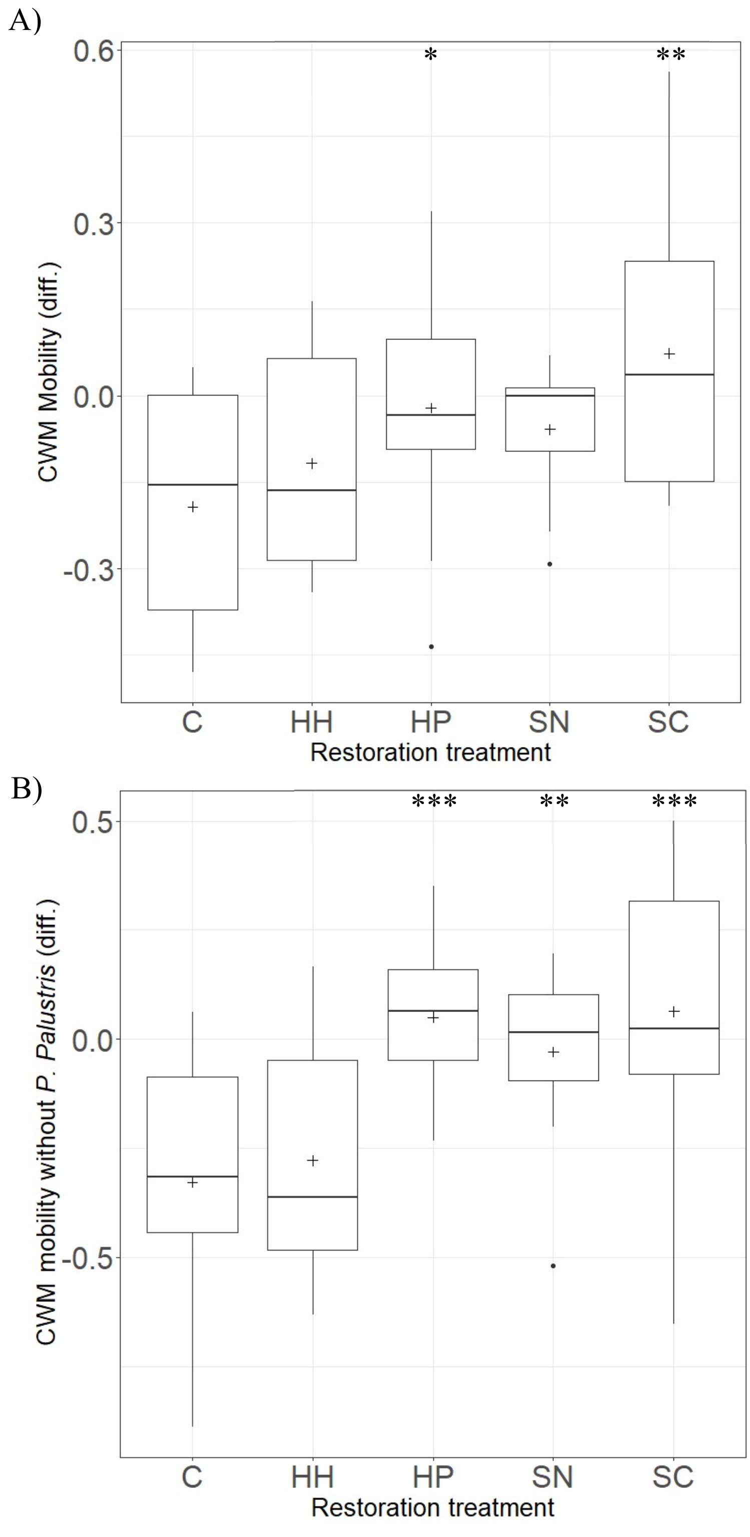


Figure 11. Difference between 2018 and 2020 in the spider community weighted mean for mobility per treatment (2020 data minus 2018 data). Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. Mobility was defined as the frequency a species use aerial dispersal (1 = rare; 2 = occasional; 3 = frequent). A) The difference in HP and SC were significant when compared to the difference in the control, there was more mobile species in 2020 in the treatments; B) Without the most abundant species *Pardosa palustris*, the differences in the three ploughed meadows were significant (HP, SN, SC), there was more mobile species in the treatments in 2020. Codes for significant differences (treatment compared to control) are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Appendix

Fig. S1: Species ranking in 2020.

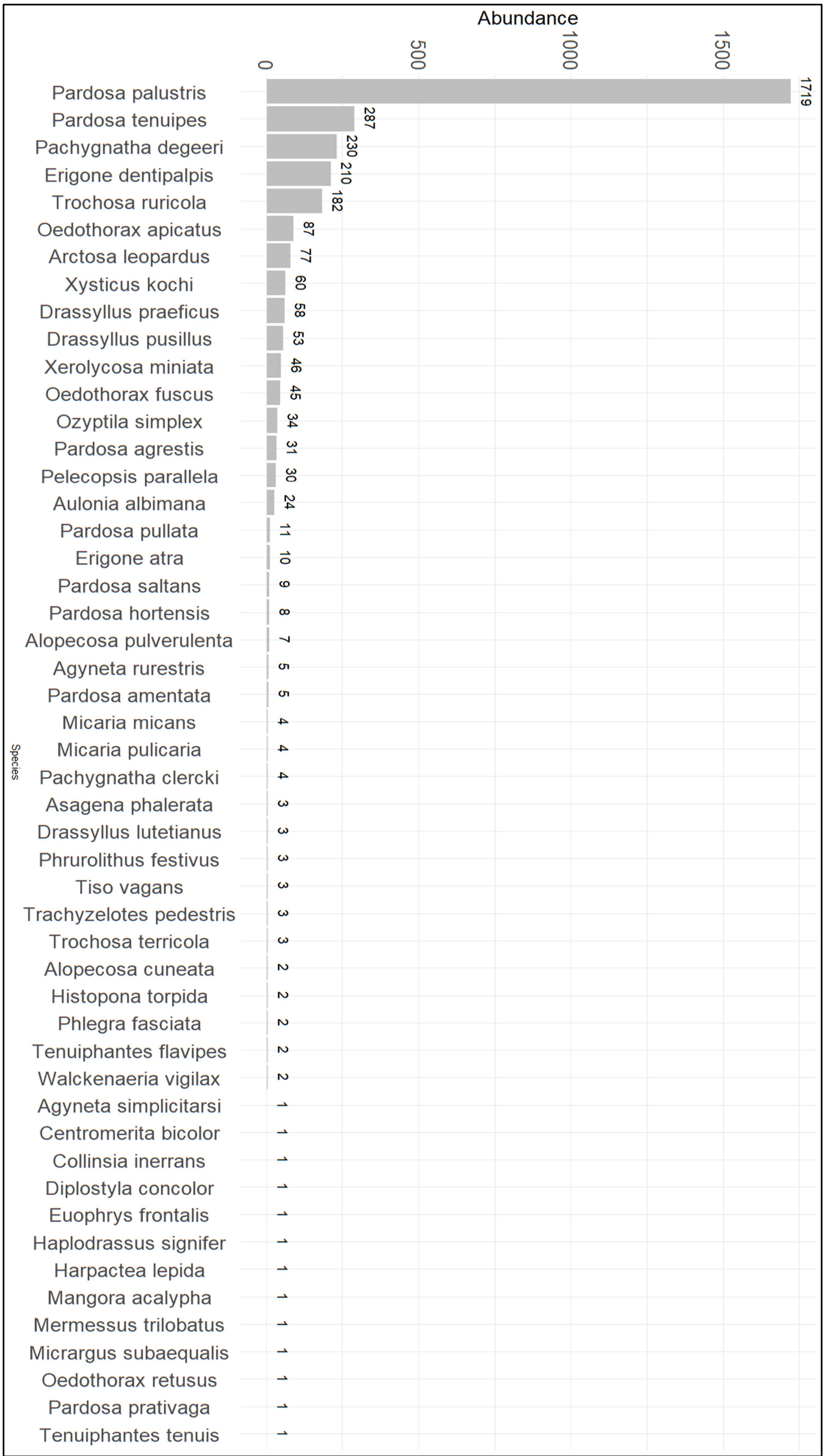


Fig. S2: Species ranking in 2018.

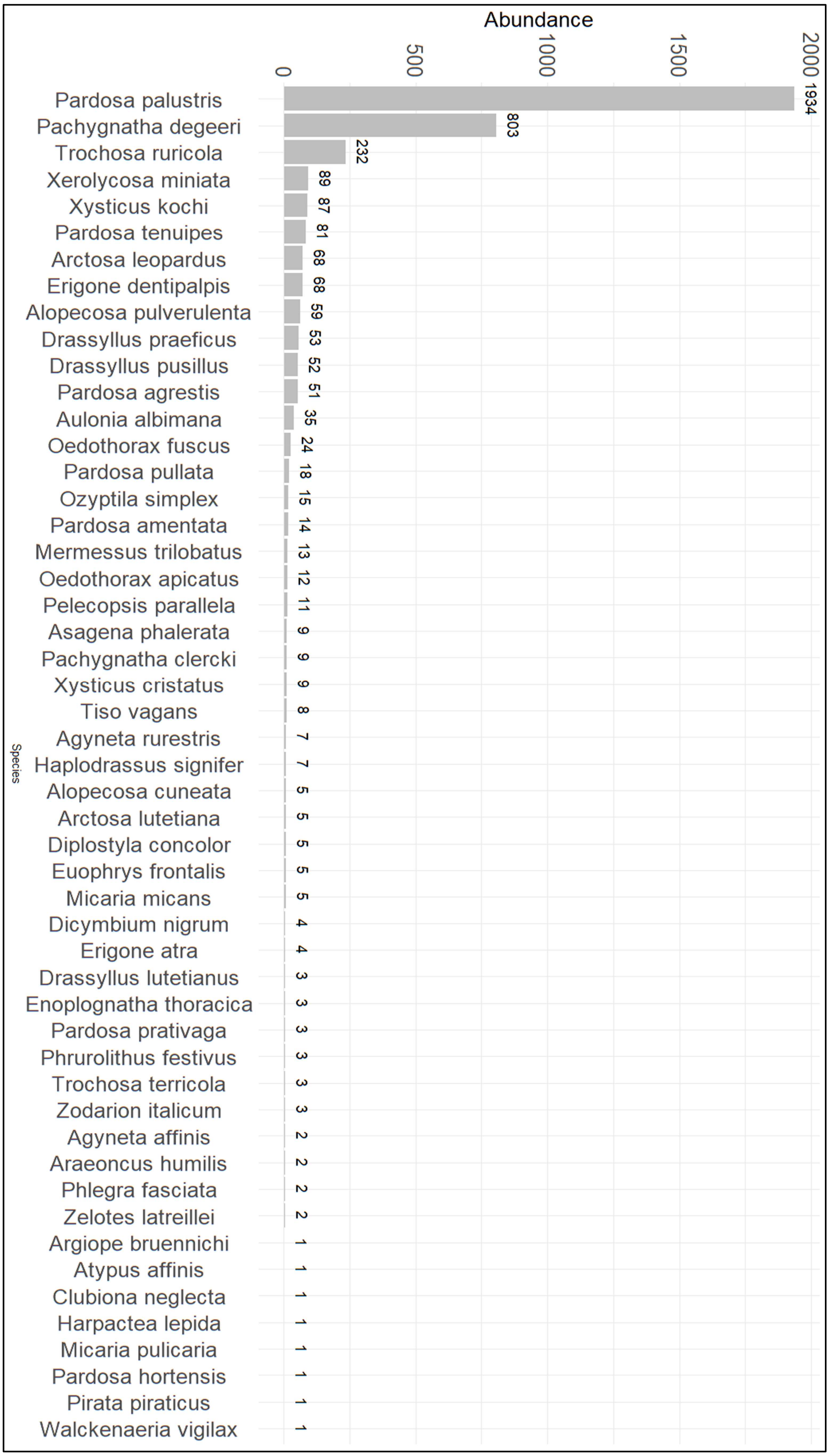


Fig. S3: Spider abundance (mean per pitfall per meadow) before mowing in 2018 and 2020 per treatments. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. No significant differences compared to the controls were detected.

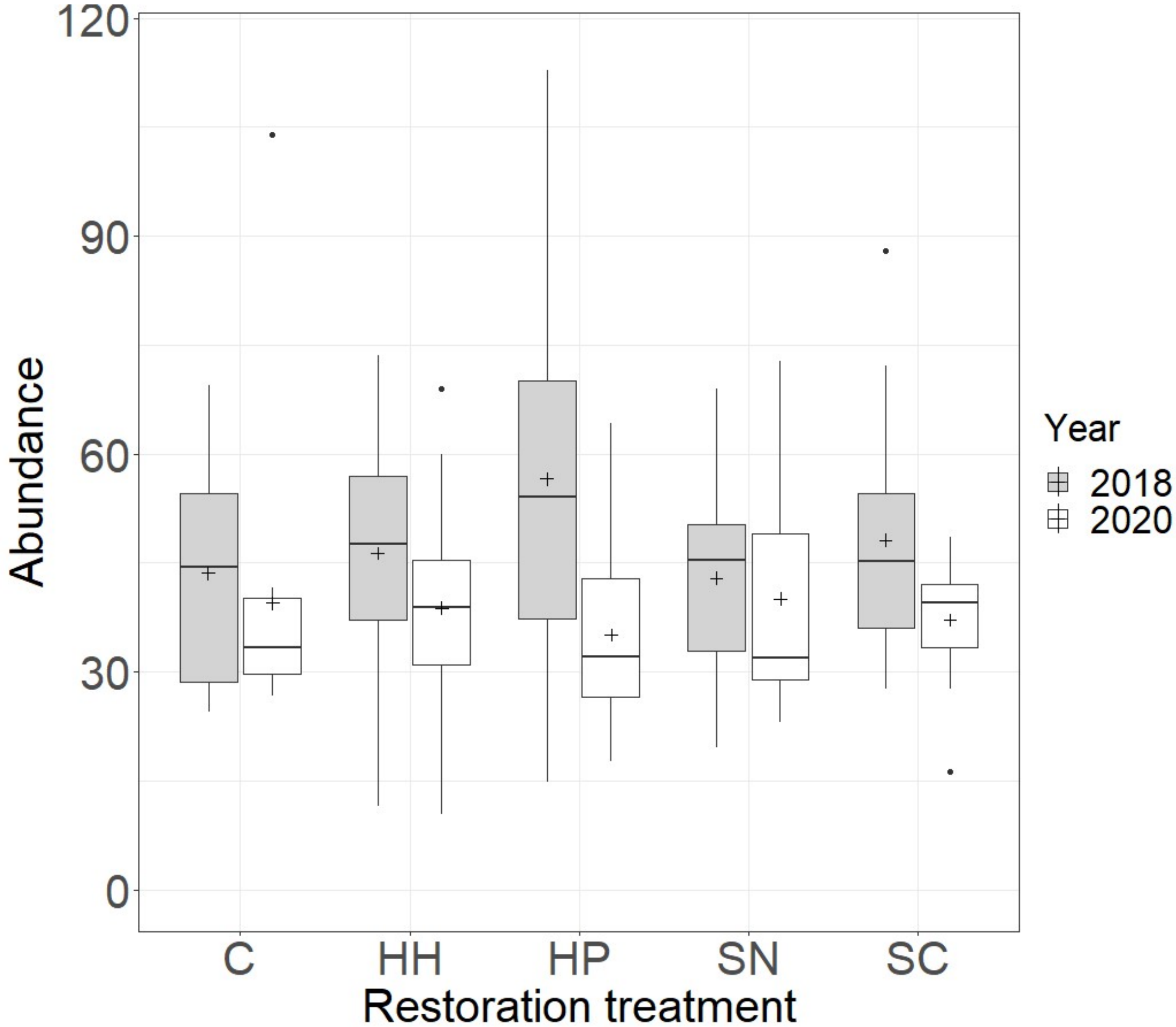


Fig. S4: Spider species richness (mean per pitfall meadow) in 2018 and 2020 per treatments. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. No significant differences compared to the controls were detected.

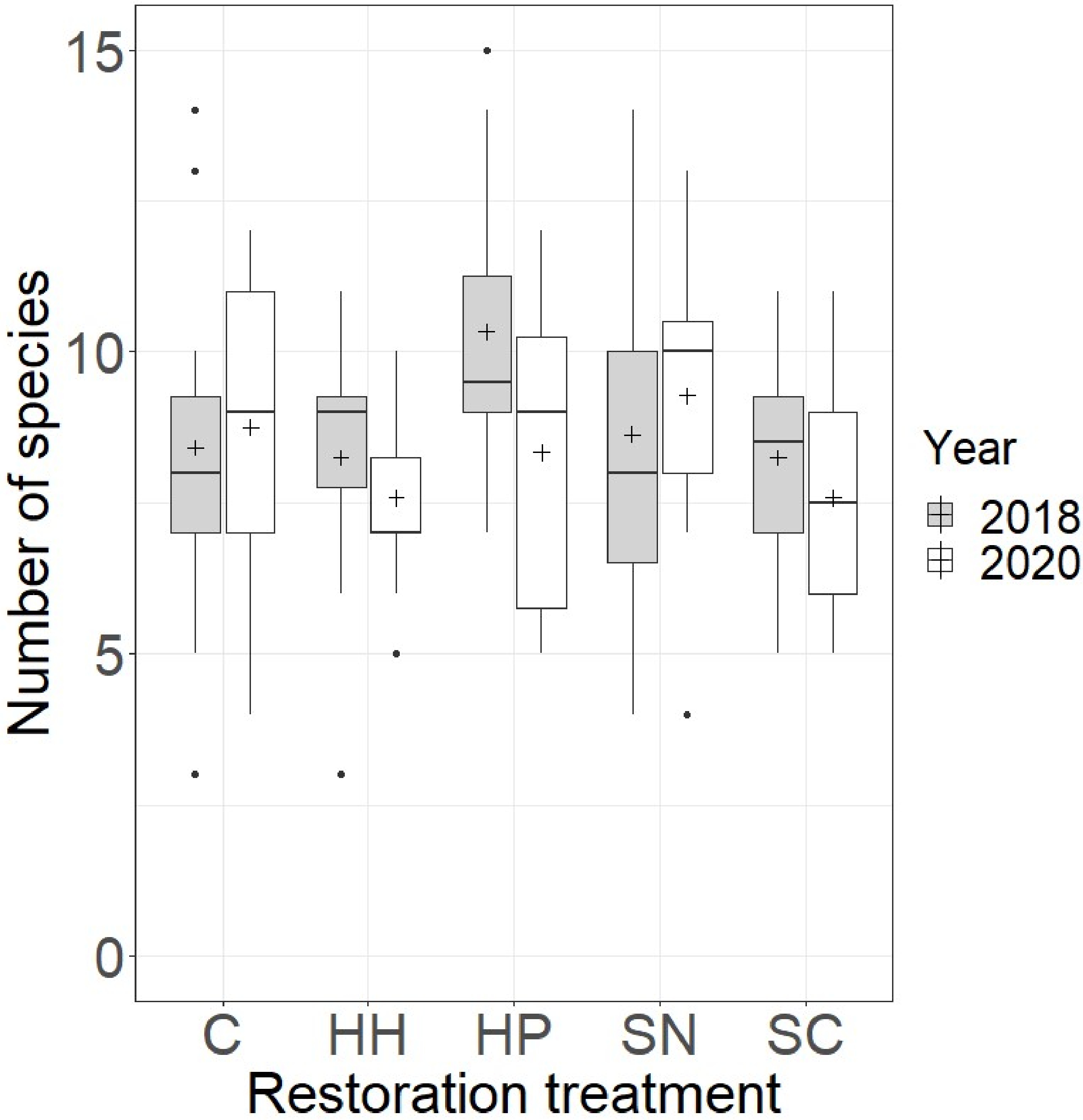


Fig. S5: Spider diversity in 2018 and 2020 per treatments, calculated using the Shannon-Index. The higher the index value, the more diverse the community is. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. No significant differences compared to the controls were detected.

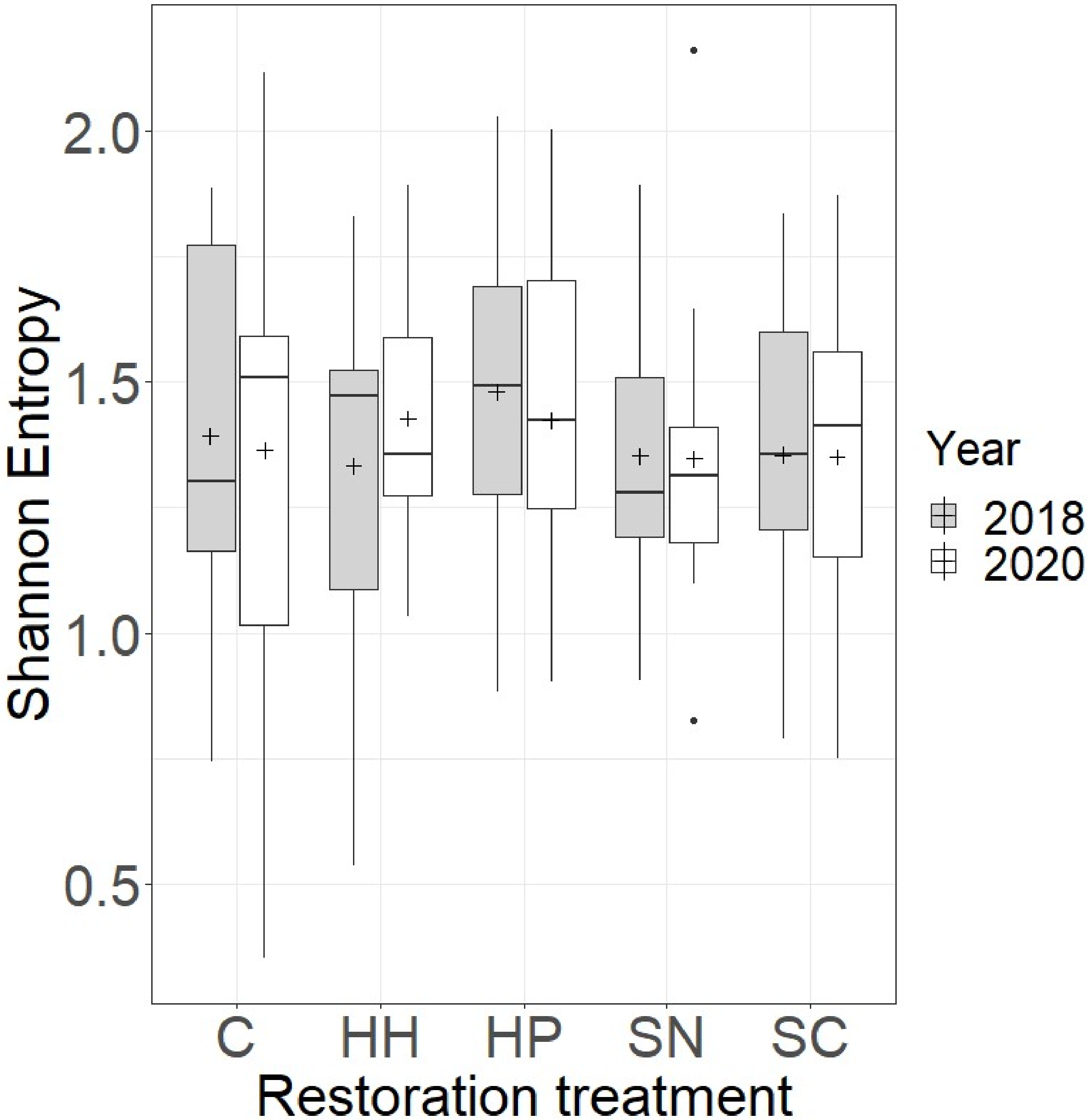


Fig. S6: Impact of the refuge ratio on spiders: A) abundance before mowing; B) abundance after mowing; C) species richness; and D) CWM for mobility. Refuge ratio of a meadow was defined as the undisturbed areas around the part of the meadow restored (with soil disturbance) divided by the total size of the meadow. A ratio equal to 0 means that the entire meadow was restored (disturbed) while a ratio equal to 1 means that the entire meadow was left untouched. No significant correlations were detected.

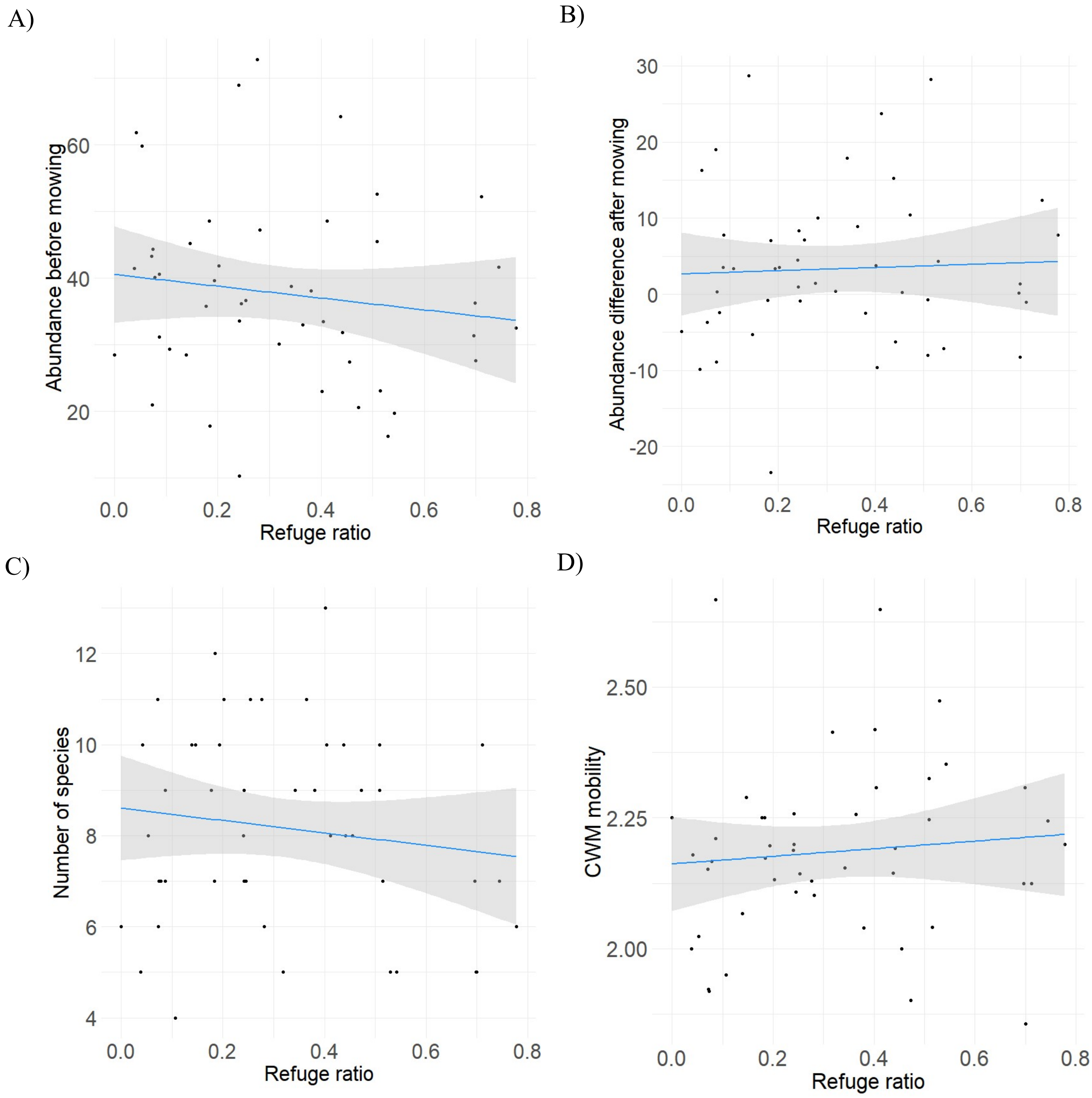


Table S1: Table with all spider species collected in 2018 and 2020 in the control and treated meadows. Sorted by alphabetic order with their respective abundance each year and ecological traits. Body size was taken as a continuous variable determined as the mean body length in mm from Nentwig et al. (2010). Humidity preference was also taken as a continuous value respectively going from preference to moistest (0) up to driest (1) habitat based on Cardoso et al. (2011) and Entling et al. (2007). Lastly, mobility was defined as the frequency of a species to use aerial dispersal also known as "ballooning", classified as (1) for rare, (2) for occasional and (3) for frequent based on Bonte et al. (2003), J.R. Bell et al. (2005), Blandenier (2009) and Macías-Hernández et al. (2020) studies. NAs represent missing values.

Species	**Amount 2018**	**Amount 2020**	**Size [mm]**	**Humidity Preference**	**Mobility**
Agyneta affinis	2	0	1.50	0.51	3
Agyneta rurestris	7	5	2.10	0.38	3
Agyneta simplicitarsi	0	1	1.65	0.68	3
Alopecosa cuneata	5	2	7.50	0.59	2
Alopecosa pulverulenta	59	7	9.00	0.42	2
Araeoncus humilis	2	0	1.40	0.31	3
Arctosa leopardus	68	77	3.40	0.28	2
Arctosa lutetiana	5	0	9.00	0.53	2
Argiope bruennichi	1	0	14.40	0.44	3
Asagena phalerata	9	3	5.00	0.81	2
Atypus affinis	1	0	11.00	0.70	NA
Aulonia albimana	35	24	3.80	0.52	2
Centromerita bicolor	0	1	3.25	NA	3
Clubiona neglecta	1	0	6.50	NA	1
Collinsia inerrans	0	1	2.25	0.30	3
Dicymbium nigrum	4	0	1.80	0.31	3
Diplostyla concolor	5	1	2.50	0.32	3
Drassyllus lutetianus	3	3	5.70	0.50	1
Drassyllus praeficus	53	58	6.50	0.50	1
Drassyllus pusillus	52	53	4.00	0.50	1
Enoplognatha thoracica	3	0	5.60	0.65	2
Erigone atra	4	10	1.90	0.29	3
Erigone dentipalpis	68	210	2.20	0.23	3
Euophrys frontalis	5	1	3.20	NA	2
Haplodrassus signifer	7	1	8.20	0.60	1
Harpactea lepida	1	1	6.00	NA	1
Histopona torpida	0	2	9.20	0.39	NA
Mangora acalypha	0	1	4.50	0.62	3
Mermessus trilobatus	13	1	1.60	NA	3
Micaria micans	5	4	NA	NA	1
Micaria pulicaria	1	4	3.20	0.36	1
Micrargus subaequalis	0	1	1.90	0.38	3
Oedothorax apicatus	12	87	2.50	0.28	3
Oedothorax fuscus	24	45	2.50	0.22	3
Oedothorax retusus	0	1	2.60	NA	3
Ozyptila simplex	15	34	3.50	0.39	2
Pachygnatha clercki	9	4	5.00	0.26	3

Pachygnatha degeeri	803	230	3.50	0.38	3
Pardosa agrestis	51	31	4.50	0.30	2
Pardosa amentata	14	5	6.50	0.26	2
Pardosa hortensis	1	8	5.00	NA	2
Pardosa palustris	1934	1719	6.00	0.32	2
Pardosa prativaga	3	1	6.20	0.26	2
Pardosa pullata	18	11	5.00	0.36	2
Pardosa saltans	0	9	5.60	NA	2
Pardosa tenuipes	81	287	4.80	NA	2
Pelecopsis parallela	11	30	1.00	0.31	3
Phlegra fasciata	2	2	5.80	0.54	2
Phrurolithus festivus	3	3	2.70	0.43	2
Pirata piraticus	1	0	7.00	NA	2
Tenuiphantes flavipes	0	2	2.15	NA	3
Tenuiphantes tenuis	0	1	3.15	0.31	3
Tiso vagans	8	3	1.90	0.34	3
Trachyzelotes pedestris	0	3	7.00	NA	1
Trochosa ruricola	232	182	10.50	0.32	2
Trochosa terricola	3	3	10.50	0.43	2
Walckenaeria vigilax	1	2	2.00	0.28	3
Xerolycosa miniata	89	46	5.20	0.43	2
Xysticus cristatus	9	0	5.80	0.42	2
Xysticus kochi	87	60	7.00	0.42	2
Zelotes latreillei	2	0	7.00	0.50	1
Zodarion italicum	3	0	2.60	0.46	1
Total	**3835**	**3281**			

Table S3: Effect of the restoration treatments on spider abundance, species richness, diversity index and the CWM of the ecological traits in 2020. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. Significant p-values are highlighted in bold.

Response variable		Estimate	SE	P-value
Abundance				
Abundance before mowing	HH vs C	-0.682	6.412	0.916
	HP vs C	-4.361	6.412	0.499
	SN vs C	0.616	6.556	0.926
	SC vs C	-2.290	6.412	0.722
	HP vs HH	-3.679	5.267	0.490
	SN vs HH	1.350	5.267	0.804
	SC vs HH	-1.608	5.267	0.762
	SN vs HP	4.946	5.327	0.363
	SC vs HP	2.071	5.202	0.695
	SN vs SC	2.906	5.361	0.594
Abundance after mowing	HH vs C	4.397	4.610	0.346
	HP vs C	3.176	4.610	0.495
	SN vs C	7.514	4.723	**0.007**
	SC vs C	13.030	4.610	0.119
	HP vs HH	-1.221	4.777	0.800
	SN vs HH	3.128	4.900	0.528
	SC vs HH	8.633	4.777	0.080
	SN vs HP	4.444	5.633	0.439
	SC vs HP	9.854	5.503	0.088
	SN vs SC	-0.143	0.166	0.407
Species richness	HH vs C	-0.167	0.829	0.166
	HP vs C	-0.417	0.829	0.618
	SN vs C	0.463	0.849	0.589
	SC vs C	-0.167	0.829	0.166
	HP vs HH	0.750	0.807	0.360
	SN vs HH	1.674	0.827	0.051
	SC vs HH	0.000	0.807	1.000
	SN vs HP	0.922	0.835	0.281
	SC vs HP	-0.750	0.813	0.366
	SN vs SC	-1.769	0.562	**0.010**
Biodiversity indice				
Shannon index	HH vs C	0.063	0.131	0.634
	HP vs C	0.059	0.131	0.656
	SN vs C	-0.035	0.134	0.796
	SC vs C	-0.014	0.131	0.917
	HP vs HH	-0.004	0.103	0.968
	SN vs HH	-0.090	0.106	0.401
	SC vs HH	-0.077	0.103	0.461

	SN vs HP	-0.085	0.113	0.459
	SC vs HP	-0.073	0.110	0.515
	SN vs SC	0.005	0.082	0.952
Traits analysis				
CWM body size	HH vs C	-0.189	0.247	0.448
	HP vs C	-0.606	0.247	**0.018**
	SN vs C	-0.387	0.253	0.133
	SC vs C	-0.809	0.247	**0.002**
	HP vs HH	-0.416	0.241	0.094
	SN vs HH	-0.198	0.247	0.430
	SC vs HH	-0.620	0.241	**0.015**
	SN vs HP	-0.222	0.248	0.380
	SC vs HP	-0.204	0.242	0.410
	SN vs SC	0.430	0.260	0.127
CWM Moisture	HH vs C	-0.025	0.009	**0.010**
	HP vs C	-0.033	0.009	**0.001**
	SN vs C	-0.034	0.010	**0.000**
	SC vs C	-0.041	0.009	**0.001**
	HP vs HH	-0.008	0.009	0.380
	SN vs HH	-0.009	0.010	0.379
	SC vs HH	-0.016	0.009	0.104
	SN vs HP	0.000	0.010	0.998
	SC vs HP	-0.007	0.009	0.442
	SN vs SC	0.007	0.010	0.473
CWM Mobility	HH vs C	0.064	0.063	0.310
	HP vs C	0.181	0.063	**0.006**
	SN vs C	0.123	0.064	**0.001**
	SC vs C	0.229	0.063	0.061
	HP vs HH	0.116	0.066	0.087
	SN vs HH	0.058	0.068	0.395
	SC vs HH	0.165	0.066	**0.017**
	SN vs HP	-0.058	0.072	0.429
	SC vs HP	0.049	0.071	0.498
	SN vs SC	-0.106	0.079	0.194
Trait analysis without *Pardosa palustris*				
CWM Body size	HH vs C	-0.409	0.413	0.329
	HP vs C	-1.434	0.413	**0.001**
	SN vs C	-0.879	0.423	**0.044**
	SC vs C	-1.328	0.413	**0.003**
	HP vs HH	-1.026	0.431	**0.023**
	SN vs HH	-0.466	0.442	0.299
	SC vs HH	-0.920	0.431	**0.041**
	SN vs HP	0.568	0.398	0.163
	SC vs HP	0.106	0.389	0.787

	SN vs SC	0.474	0.351	0.204
CWM Mobility	HH vs C	0.093	0.120	0.441
	HP vs C	0.394	0.120	**0.002**
	SN vs C	0.275	0.123	**0.029**
	SC vs C	0.360	0.120	**0.004**
	HP vs HH	0.301	0.123	**0.019**
	SN vs HH	0.182	0.126	0.156
	SC vs HH	0.267	0.123	**0.036**
	SN vs HP	-0.119	0.133	0.377
	SC vs HP	-0.034	0.130	0.798
	SN vs SC	-0.085	0.135	0.534
CWM Humidity	HH vs C	-0.061	0.018	**0.002**
	HP vs C	-808.000	0.018	**0.000**
	SN vs C	-0.078	0.019	**0.000**
	SC vs C	-0.079	0.018	**0.000**
	HP vs HH	-0.019	0.019	0.321
	SN vs HH	-0.017	0.020	0.398
	SC vs HH	-0.018	0.019	0.356
	SN vs HP	0.003	0.020	0.891
	SC vs HP	0.001	0.020	0.944
	SN vs SC	0.001	0.021	0.953
Models on most abundant species				
Species richness	HH vs C	-0.500	0.700	0.479
	HP vs C	0.083	0.700	0.906
	SN vs C	0.506	0.717	0.484
	SC vs C	-0.750	0.700	0.290
	HP vs HH	0.583	0.696	0.408
	SN vs HH	1.041	0.713	0.154
	SC vs HH	-0.250	0.696	0.722
	SN vs HP	0.441	0.795	0.585
	SC vs HP	-0.833	0.778	0.296
	SN vs SC	1.320	0.633	0.063
Abundance before mowing	HH vs C	-0.254	0.225	0.265
	HP vs C	-0.275	0.225	0.227
	SN vs C	-0.111	0.230	0.632
	SC vs C	-0.680	0.225	**0.004**
	HP vs HH	0.000	7.397	1.000
	SN vs HH	5.167	7.591	0.501
	SC vs HH	-0.138	7.397	0.072
	SN vs HP	5.137	7.440	0.497
	SC vs HP	-13.750	7.252	0.072
	SN vs SC	18.348	7.576	**0.025**
Abundance after mowing	HH vs C	2.905	6.288	0.646

	HP vs C	2.989	6.288	0.637
	SN vs C	9.575	6.436	0.144
	SC vs C	14.239	6.288	**0.029**
	HP vs HH	0.083	6.439	0.990
	SN vs HH	6.743	6.602	0.315
	SC vs HH	11.333	6.439	0.088
	SN vs HP	6.623	7.740	0.401
	SC vs HP	11.250	7.553	0.151
	SN vs SC	-4.611	9.481	0.636
Models on least abundant species				
Species richness	HH vs C	-1.078	0.518	**0.045**
	HP vs C	-0.907	0.531	0.096
	SN vs C	-0.689	0.518	0.192
	SC vs C	-1.213	0.495	**0.019**
	HP vs HH	0.200	0.477	0.677
	SN vs HH	0.400	0.464	0.394
	SC vs HH	-0.133	0.445	0.766
	SN vs HP	0.200	0.478	0.679
	SC vs HP	-0.333	0.459	0.473
	SN vs SC	0.533	0.472	0.272
Abundance before mowing	HH vs C	0.223	0.368	0.548
	HP vs C	-0.161	0.381	0.675
	SN vs C	-0.213	0.367	0.565
	SC vs C	-0.441	0.339	0.203
	HP vs HH	-2.117	1.594	0.197
	SN vs HH	-2.295	1.534	0.149
	SC vs HH	-3.229	1.427	**0.034**
	SN vs HP	-0.060	0.353	0.866
	SC vs HP	-0.285	0.329	0.396
	SN vs SC	0.841	0.905	0.366
Abundance after mowing	HH vs C	-0.022	0.257	0.931
	HP vs C	-0.182	0.228	0.435
	SN vs C	0.061	0.240	0.801
	SC vs C	0.223	0.257	0.396
	HP vs HH	-0.333	0.465	0.485
	SN vs HH	0.100	0.483	0.839
	SC vs HH	0.250	0.509	0.631
	SN vs HP	0.433	0.408	0.178
	SC vs HP	0.583	0.382	0.279
	SN vs SC	-0.150	0.504	0.775

Table S4: Effect of restoration the treatments on the difference of the CWM for mobility between 2020 and 2018 (2020 data minus 2018 data) in order to take into consideration the year effect. Treatment abbreviations: C = control, HH = hay harrow, HP = hay plough, SN = seed natural, SC = seed commercial. Significant p-values are highlighted in bold.

Response variable		**Estimate**	**SE**	**P-value**
Traits analysis				
CWM mobility	HH vs C	0.075	0.078	0.340
	HP vs C	0.171	0.078	**0.034**
	SN vs C	0.132	0.080	0.106
	SC vs C	0.265	0.078	**0.001**
	HP vs HH	0.096	0.080	0.239
	SN vs HH	0.059	0.082	0.477
	SC vs HH	0.190	0.080	**0.022**
	SN vs HP	-0.039	0.081	0.632
	SC vs HP	0.094	0.079	0.246
	SC vs SN	0.131	0.080	0.117
Traits analysis without *Pardosa palustris*				
CWM mobility	HH vs C	0.050	0.108	0.644
	HP vs C	0.379	0.108	**0.001**
	SN vs C	0.300	0.111	**0.009**
	SC vs C	0.392	0.108	**0.001**
	HP vs HH	0.328	0.104	**0.003**
	SN vs HH	0.249	0.106	**0.023**
	SC vs HH	0.342	0.104	**0.002**
	SN vs HP	-0.079	0.102	0.445
	SC vs HP	0.013	0.100	0.895
	SN vs SC	-0.119	0.127	0.358