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RESEARCH PAPER

Effects of uncut grass refuges on the plant community of extensively managed hay meadows

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A B S T R A C T

Invertebrates inhabiting grasslands benefit from uncut grass refuges, yet effects on the plant community have not been properly quantified. We experimentally investigated the effects on the vegetation of two different types of refuges. While both consisted in not mowing 10–20% of a meadow area, they differed in their rotation frequency: (1) in within-year rotational refuges (WYRR), the location of the refuge within a meadow was changed at each mowing operation, usually twice a year; (2) in between-years rotational refuges (BYRR), the refuge changed location only between years. A third mowing regime without any refuge was included as control (C) for comparison. The study was conducted in thirty extensively managed meadows across the Swiss lowlands. The vegetation was sampled at two 1-m^2 plots within each of the four strata defined by a stratified random design that accounted for the spatial location of the uncut refuge over the years. There were no overall significant negative effects of WYRR on plant species richness and composition at the meadow scale, although a small negative effect was detected locally (i.e. at the refuge scale) where a WYRR had been implemented more than once in the preceding three years. Leaving BYRR negatively impacted plant species richness (-11%), even reducing the number of indicator plant species by 22% (from 4.5 to 3.5 per 2 m^2), regardless of when and where refuges were left uncut. A beta-diversity analysis revealed no difference at community level between the two refuge types and control meadows. Previous studies had evidenced positive effects of uncut refuges on herbivore and pollinator communities, while this study shows that the plant community is not affected as long as the location of the refuge is changed at each mowing operation. We thus recommend this measure for promoting biodiversity in extensively managed grasslands.

Introduction

Semi-natural extensively managed hay meadows have long characterized the cultural landscapes of Europe although they have faced dramatic declines since World War II (Boch et al., 2020). In contrast to intensively managed meadows, they are not fertilized, or only loosely with organic manure, and usually experience no application of herbicides and insecticides. In meadows, mowing operations are requisite to maintain the grassland habitat open in the long term (Grime, 1973; Milberg et al., 2017), although the mechanic impact of the harvesting process itself may eliminate a large fraction of the invertebrate fauna: for instance, up to 65−85% of the orthopteran populations (Humbert et al., 2010a, 2010b).

To mitigate this detrimental impact of mowing on invertebrates, it has been recommended to leave 10−20% of the area of a meadow as an uncut grass refuge at each hay harvest (Humbert et al., 2018). Leaving an uncut grass refuge within hay meadows registered under Swiss agri-environment schemes (AES) has already been implemented in most Swiss cantons as a voluntary measure and the uptake by farmers was high (e.g. see (Hold et al., 2022), for the canton of Bern). It will also most likely be mandatory in the next Swiss Agricultural Policy. This recommendation was drawn from a synthesis of several of our studies carried out in extensively managed meadows on the effects of the so-called rotational refuges (by definition, their location within a meadow change at each cut) on the arthropod community (Humbert et al., 2018). We showed that: (1) species richness of specialist butterflies was higher in meadows exhibiting an uncut grass refuge compared to control meadows without any refuge (Bruppacher et al., 2016; see also Konvicka et al., 2008); (2) orthopteran densities were twice as high and species richness 23% higher on meadows with a refuge than on control meadows (Buri et al., 2013); and (3) wild bee and hoverfly abundance and species richness were also greater on meadows with refuges, thanks

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to an enhanced and prolonged availability of resources, notably pollen and nectar (Meyer et al., 2017). Other studies had shown that the community of spiders in wet litter meadows benefit from yearly uncut grass strips that stay at the same place for at least one year, thus providing overwintering habitat (Cattin et al., 2003; Frenzel et al., 2022; Schmidt et al., 2008). Similarly, Dennis et al. (1994) established that the predatory beetle species *Tachyporus hypnorum* reaches higher densities in areas with taller winter vegetation height (see also Pywell et al., 2005). Sward architecture is a primary factor to promote phytophagous and predatory field invertebrate species (Woodcock et al., 2009) and arthropod biomass in general (Andrey et al., 2014), which ultimately calls for a minimum continuity of standing vegetation during the growing season.

Despite the accumulating evidence for positive effects of uncut grass refuges on the meadow's arthropod community, it is not yet clear how the plant community is affected by such a measure. A study of our research group, conducted in the same experimental setup described in Humbert et al. (2018) did not find any significant difference between the plant and bryophyte communities of meadows with and without a rotational uncut refuge (van Klink et al., 2017). However, plots for vegetation relevés had been placed at random in any given study meadow, regardless of where the uncut grass refuge had been previously left on the meadow, while a 10-m buffer zone without relevés was respected at the meadow periphery. Therefore, conclusions of van Klink et al. (2017) are drawn at the meadow scale and not necessarily related to the area where the rotational refuges were located. Nevertheless, the plant community could, locally, be negatively affected by the maintenance of an uncut grass refuge, especially depending on the type of refuge that is being implemented (rotational versus yearly, see below). For instance, the accumulation of dead plant material (i.e. litter) may: (1) constitute a mechanical barrier that impedes the emergence of seedlings (Foster & Gross, 1998; Ruprecht et al., 2010); (2) reduce light availability (Jensen & Gutekunst, 2003); (3) alter soil humidity (Eckstein & Donath, 2005) and (4) increase soil nutrients content (Wardle et al., 1997). Such modifications of micro-environmental conditions may exacerbate interspecific competition for access to light and other resources, leading to an impoverished plant community (Hautier et al., 2009; Loydi et al., 2013). While long-term land abandonment is known to negatively impact the vegetation (e.g. Riedener et al., 2014; Valkó et al., 2018), short-term cessation of cutting (1–2 years without management) might have little or no effect on the plant community depending on the grassland type, with oligotrophic grasslands being more resistant (Klimes et al., 2013; Pavlů et al., 2011).

In Switzerland, after a dramatic decline in the last century, the area of meadowland that is managed extensively has increased in the first two decades of this millennium, reaching a total area of 85,080 ha in 2020, which represented 8.1% of the total utilized agriculture area, compared to 39,000 ha in 2000 and 63,000 ha in 2010 (FOAG, 2021). The maintenance of these meadows is financially supported by the main Swiss AES for the promotion of farmland biodiversity (Swiss Federal Council, 2013). Two payment schemes exist. First, there are the so-called "Quality I" contributions (hereafter QI) which consist of an input-based (also called action-based) financial support for farmers managing their meadows extensively, respecting certain criteria, in particular absence of fertilization and first mowing not before 15 June. Second, beside the QI-contributions, extensively managed meadows can qualify for the output-based (also called results-based) "Quality II" contributions (hereafter QII). To be eligible for the QII-contributions, a minimum of six indicator plant species have to be present within a 3-m radius plot set in a representative part of the meadow (Swiss Federal Council, 2013). This latter, more recent and higher financial incentive motivates farmers to reach QII, and to avoid losing that required minimum plant diversity once they have achieved that target. Such hybrid schemes, i.e. with certain management conditions and an potential output-based payment, are nowadays popular in the European Union too (Elmiger et al., 2023; Herzon et al., 2018).

The aim of this study was to investigate and compare the effects on the plant community of two ways to create uncut grass refuges in extensively managed meadows, namely within-year rotational grass refuges and between-years rotational refuges. In contrast to the approach by van Klink et al. (2017), here we relied on a stratified random sampling design. More specifically, we carried out vegetation relevés at either the exact places where refuges had been kept, or at sites where no refuges had been left. This enabled studying the effects on the plant community of uncut refuges at both the refuge scale and at the meadow scale. Based on the above considerations, we put forward three hypotheses. First, we predicted that no type of refuge would affect the plant community composition at meadow scale. Second, we predicted that overall plant species richness and the number of QII indicator plant species would show lower values where within-year rotational refuges had been implemented in the previous year(s) and even further lower values at the locations where refuges had not been alternated spatially within a year (between-years rotational refuge). Third, as leaving uncut a fraction of a meadow increases spatial habitat heterogeneity, we hypothesised that this would be reflected in an increased plant beta diversity compared to a meadow without any refuge (Bonari et al., 2017).

This study is a follow-up of van Klink et al. (2017) and was conducted at the same study sites. It was motivated by an advisory group of stakeholders (including policy-makers, field biologists and farmers, see Introduction in Buri et al., 2013) who were concerned by the potential negative consequences for floral diversity of implementing vegetation refuges within meadowland.

Materials and methods

Study sites and experimental design

The meadows used in this study were selected in 2010 across the Swiss Plateau by a research team of the Division of Conservation Biology at the University of Bern (Appendix A). The Swiss Plateau is a typical Western European lowland intensively used landscape where semi-natural habitats like hedgerows and forest patches are still present but constitute usually < 20% of the matrix (Zingg et al., 2018). Annual precipitation ranges from 850 to 1150 mm and mean annual temperature from 8 to 12 °C. Selected meadows were located between 390 and 830 m elevation and belonged to the *Molinio-Arrhenatheretea* phytosociological class. They were all registered under Swiss AES as extensively managed hay meadows since at least 2004 and followed the standard management requirements, i.e. no application of fertilizer, a first cut not before 15 June and aftermath grazing allowed only between 1 September and 30 November (Swiss Federal Council, 2013). Although there is no restriction on the number of annual cuts, these AES meadows are usually mown twice a year.

Originally, 48 meadows spread over twelve regions were randomly allocated to four different mowing regimes. With these mowing regimes farmers had to: (i) delay the first cut by one month (15 July instead of 15 June); (ii) cut the meadow not more than twice a year, with a gap of eight weeks between the cuts; or (iii) leave 10–20% of the meadow area uncut each time the meadow was mown. The fourth mowing regime was the control (see van Klink et al., 2017, for more details on the mowing regimes). Early 2016, the meadows with the 8-week mowing regime and the meadows with the uncut grass refuge were pooled together and randomly allocated to two new mowing regimes. These two new mowing regimes consisted of (1) within-year rotational refuges (abbreviated hereafter as WYRR); and (2) between-years rotational refuges (BYRR). Both regimes involved leaving 10–20% of a meadow area uncut at every mowing operation, forming a refuge, but differed in the rotation frequency of the refuge. In meadows with a WYRR mowing regime, the area left unmown changed at each hay harvest (usually twice a year) while in BYRR meadows, the location of the unmown refuge changed only from one year to another, i.e. the refuge implemented in the year t was cut only in the year t_{+1}, at the first mowing operation of the season.

During the course of time, some of the meadows selected in 2010 were unfortunately lost due to land-use conversion, resulting in a slightly unbalanced design with 10 BYRR-meadows, 9 WYRR-meadows and 11 C-meadows (C for control, i.e. meadows not harbouring any refuge). In the years 2016, 2017 and 2018, after each mowing, the uncut grass refuges of every study meadow were mapped and digitalized in QGIS (Quantum GIS Development Team, 2018).

Vegetation sampling

The vegetation was sampled in spring 2019 (9 May–14 June) based on a stratified random design that accounted for the spatial location and time-frequency of the uncut refuges left in the previous years (hereafter called refuge frequency). Specifically, sampling areas were classified in four strata: (1) areas where the farmer never implemented a refuge in 2016–2018, abbreviated *never*; (2) areas where an uncut grass refuge was left in the year 2017 but not in the other years, (*R2017*); (3) areas where a refuge was left in 2018 but not in the other years (*R2018*); and (4) areas where a refuge was occurring in at least two out of the three study years (abbreviated *more than once*; see Appendix B for an illustration). To be able to disentangle the effects of the refuges from those of other confounding environmental factors potentially affecting meadow plant communities, the vegetation was also sampled in control meadows. However, as there were no uncut grass refuges in C-meadows, three fictive uncut grass refuges per meadow, with an area representing 10−20% of the area of the focal meadow, were drawn on QGIS for the years 2016, 2017 and 2018, respectively. These fictive refuges were typically placed next to a forest or a river, in a corner or a steeper part of the meadow where mowing is more difficult, i.e. where farmers naturally place them for practical reasons. The vegetation was then sampled in the same strata as mentioned above for WYRR- and BYRR-meadows. In WYRR-meadows, where the location of the refuge changed from the first to the second yearly cut, we selected the strata based on the location where the refuge had been left after the first cut.

In each of the above-described refuge frequency strata (*never, R2017, R2018, more than once*), two locations were selected at random, representing the southwest corner of a 1 m x 1 m plot used for vegetation sampling. While this summed to a total number of eight vegetation relevés per meadow, in some meadows the stratum *more than once* was present in different combinations (like 2016/2018 and 2017/2018) and in a few other meadows the strata *R2017* did not occur (see Table A.1 in Appendix A, where the coordinates of each vegetation relevés are provided).

All vascular plant species were recorded and their respective cover was estimated visually in each of the 224 vegetation plots. The coverage of litter, mostly herbaceous, was also estimated visually in each plot. In order to further disentangle the potentially confounding effects exerted by the shade generated by nearby trees (forest or hedges) and buildings (Erdős et al., 2019), the daily average sunshine duration (in hours) theoretically experienced (as actual weather conditions were not accounted for) at each vegetation plot from March to May was estimated (see Appendix F for more details on the methodology).

Statistical analysis

The data collected at the two 1-m^2 vegetation plots from each of the above-described refuge frequencies were merged to obtain a single measure per 2 m^2. While plant species richness was pooled considering species identity, species and litter coverages as well as sunshine duration were averaged between the two plots. The effects of leaving an uncut refuge were then investigated at two different scales. First, at meadow scale, using for that the mean of all 2-m^2 merged plots within a given meadow, while comparing these means across mowing regimes. Second, at the refuge scale, where the four refuge frequencies were compared within the same mowing regime.

Data were analysed with linear mixed-effect models (LMM) using the *lmer* function of the *lme4* package (Bates et al., 2015). The response variables were the total plant species richness per 2 m^2, QII indicator plant species richness, plant functional group richness (grasses, forbs and legumes) and coverage of herbaceous litter. The explanatory variables (fixed effects) were the three different mowing regimes (WYRR, BYRR and C) or the four different refuge frequencies (*never, R2017, R2018* and *more than once*). In every model, the region was included as a random effect. The relationship between average daily sunshine duration in March–May and the four different refuge frequencies was investigated similarly. Furthermore, linear regressions were run between total plant species richness or QII indicator plant species richness versus coverage of herbaceous litter or average daily sunshine duration. All models were fitted using Gaussian error distribution and the response variables were log-transformed where necessary to achieve a normal distribution of the residuals (as indicated in Table C.1 and D.1 in Appendix C, respectively D).

Finally, community variability (beta diversity) was calculated using the Bray-Curtis dissimilarity index integrated in the function *betadisper* of the *vegan* package (Oksanen et al., 2020). The Bray-Curtis dissimilarity index is a modified version of the Sørensen index that allows the inclusion of abundance (or coverage for plant) data (Anderson et al., 2011). Statistical analyses were run in R version R 4.1.0 (R Core Team, 2021).

Results

Total plant species richness

The highest number of plant species recorded per 2 m^2 was 38, the lowest 8 and the mean number of species (± standard deviation SD) across all meadows and sampled strata was 22.3 (± 5.0). At 1 m^2 scale, the highest number of plant species was 28, the lowest 6, while we found an average of 16.0 (± 4.1) plant species per m^2. The difference in total number of plant species between WYRR-meadows (22.3 ± 4.6) and C-meadows (23.5 ± 4.7) was not significant (Fig. 1A). Nevertheless, there was a significantly lower number of plant species in BYRR-meadows (20.9 ± 4.6) compared to C-meadows ($P = 0.003$).

Refuge frequency did not have any significant effect on plant species richness in C-meadows and BYRR-meadows (Fig. 2B and Fig. D.1A in Appendix D). Nevertheless, on WYRR-meadows there were fewer plant species where refuges were left more than once in the previous years compared to areas where a refuge was left in 2017 (Fig. 2A).

Indicator plant species richness

The number of QII indicator plant species ranged from 0 to 14 per 2 m^2. On average, fewer indicator species were found in BYRR-meadows (3.5 ± 2.9) compared to both C-meadows (4.5 ± 2.8, $P = 0.003$) and WYRR-meadows (5.1 ± 2.8, $P = 0.001$; Fig. 1B).

Refuge frequency did not have a significant effect on QII indicator plant species in C-meadows and BYRR-meadows (Fig. 2D and Fig. D.1B in Appendix D). Nevertheless, on WYRR-meadows there were fewer indicator species where refuges had been left more than once between 2016 and 2018 (5.0 ± 2.9), compared to areas where there had never been a refuge (5.8 ± 3.2, $P = 0.045$) and compared to the refuge frequency *R2017* (Fig. 2C).

Grass, legume and forb species richness

Mowing regime had no effect on grass species richness (Fig. 3A). Regarding legumes, there were fewer species in BYRR-meadows (mean = 2.4 ± 1.4) compared to C-meadows (3.1 ± 1.4, $P = 0.008$) and WYRR-meadows (2.9 ± 1.4, $P = 0.018$; Fig. 3B). Similarly, there was a lower number of forb species in BYRR-meadows (11.1 ± 3.4) compared to C-

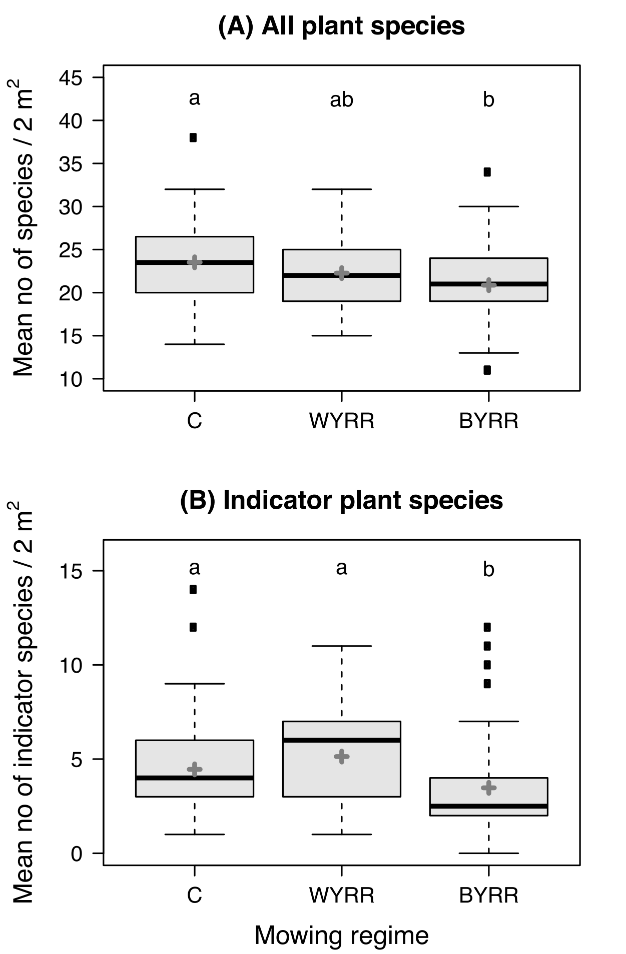

Fig. 1. Mean number of total plant species (A) and mean number of QII indicator plant species (B) with respect to the mowing regime (C = control meadows, WYRR = within-year rotational refuges and BYRR = between-years rotational refuges). Different letters indicate significant differences among mowing regimes at an alpha-rejection level of 0.05. Bold transversal bars represent medians and gray crosses means. The box boundaries represent the first and the last quartiles, whiskers the interquartile distance multiplied by 1.5, while outliers are shown as open dots. See Appendix C for statistical analyses.

meadows (13.1 ± 2.6, $P < 0.001$) and WYRR-meadows (12.6 ± 3.7, $P < 0.001$; Fig. 3C).

Herbaceous litter, sunshine duration and beta diversity

The percentage cover of herbaceous litter present in the vegetation plots ranged from 0 to 63.5%. On average, there was significantly less litter on C-meadows (4.7 ± 6.9%) compared to WYRR-meadows (7.5 ± 9.1%, $P = 0.042$) and BYRR-meadows (10.0 ± 13.9%, $P = 0.013$; Fig. E.1 Appendix E). In WYRR-meadows there was much more litter in areas where a refuge had been left in 2018 (11.7 ± 11.8%) compared to areas where there had never been a refuge (4.9 ± 8.8, $P = 0.044$, Fig. E.2A in Appendix E). In BYRR-meadows it was in the areas where refuges were left more than once over the years, that litter accumulated the most (19.4 ± 22.3%) compared to refuge frequency *never* (3.7 ± 5.0%, $P = 0.004$, Fig. E.2B in Appendix E). A further analysis showed that the total number of plant species correlated negatively with the percentage of herbaceous litter (LMM with the region included as random effect: estimate on log scale = -0.085, SE = 0.018, df = 108, $P < 0.001$).

Average number of daily sunshine hours (March to May) was high in the majority of the vegetation plots (median = 11.3; 25% quartile = 10.2, 75% quartile = 12). It did not significantly differ among sampling strata with different refuge frequencies (Fig. F.2 in Appendix F). Both the total number of plant species and the number of indicator species did not significantly correlate with sunshine duration (Appendix F). Finally, beta diversity did not significantly differ among mowing regimes (Appendix G).

Discussion

This is the first study that quantitatively investigates how different types of rotational uncut grass refuges implemented in grassland influence the plant community. At the scale of a meadow, rotational refuges that change location only from one year to another (BYRR, for between-years rotational refuges) exert a negative impact on the plant community, reducing overall plant species richness as well as the number of specific indicator plant species. In contrast, refuges whose location changes at every mowing operation (WYRR, for within-year rotational refuges) did not have any negative impact, neither on overall plant species richness nor on indicator plant species richness, but only as long as the refuge had not been placed more than once at the same location in the preceding three years. Note that these results obtained in mesic grasslands may contrast with studies in drier low-productive communities where relaxed management regimes (e.g. biennial mowing) may have no effect on the plant species richness (Klimes et al., 2013; Zhao et al., 2020). Altogether our findings emphasize that seasonally alternated, rotational uncut refuges can be recommended without restrictions to promote the mesic grassland entomofauna (Humbert et al., 2018), without being worried about counter negative effects on the vegetation community.

Meadow scale

In accordance with our hypothesis, the total number of plant species on WYRR-meadows (22.3 per 2 m^2) did not differ significantly from the number of species on control (C) meadows (23.5), within which no refuge had been implemented earlier on. The same was true regarding the number of QII indicator plant species (C-meadows: 4.5 per 2 m^2; WYRR-meadows: 5.1). Nevertheless, BYRR-meadows had fewer plant species (20.9) and QII indicator plant species (3.5) than C-meadows (23.5 and 4.5, respectively). Although the absolute difference between the number of QII indicator species on BYRR-meadows and C-meadows was relatively small (-1 species), it still represents a reduction of 22.2%. In addition, remember that ≥ 6 indicator plant species per 3-m radius plot qualify a meadow for the better endowed output-based QII financial contributions of the Swiss AES. This means that just one indicator plant species less on a given meadow can substantially diminish the payment the farmer receives, which in turn might dissuade participation to the input-based scheme too (Wuepper & Huber, 2022).

Similar results were found for the number of legume and forb species, which were both lower on BYRR-meadows compared to C-meadows and WYRR-meadows, while no effect was evidenced for grass species. As most of the official QII indicators belong to forbs and legumes, we conclude that the plant species lost in BYRR-meadows were in fact QII indicator species.

On BYRR-meadows, the percentage cover of herbaceous litter (10.0%) was, on average, higher than on C-meadows (4.7%). This was mostly driven by particularly high litter accumulation in areas where refuges were left more than once during the previous three years (19.4%). A dense litter layer decreases light availability at ground level, negatively affecting seed germination and the establishment of seedlings (Foster & Gross, 1998). This can to a large extent explain the lower plant species richness observed in BYRR-meadows. The cover of herbaceous litter in WYRR-meadows (7.5%) was also statistically higher than in C-meadows (BYRR- and WYRR-meadows did not differ in this respect), but apparently insufficient to affect the vegetation of WYRR-meadows, in line with earlier findings of Loydi et al. (2013).

Finally, the variation in beta-diversity (based on Bray-Curtis

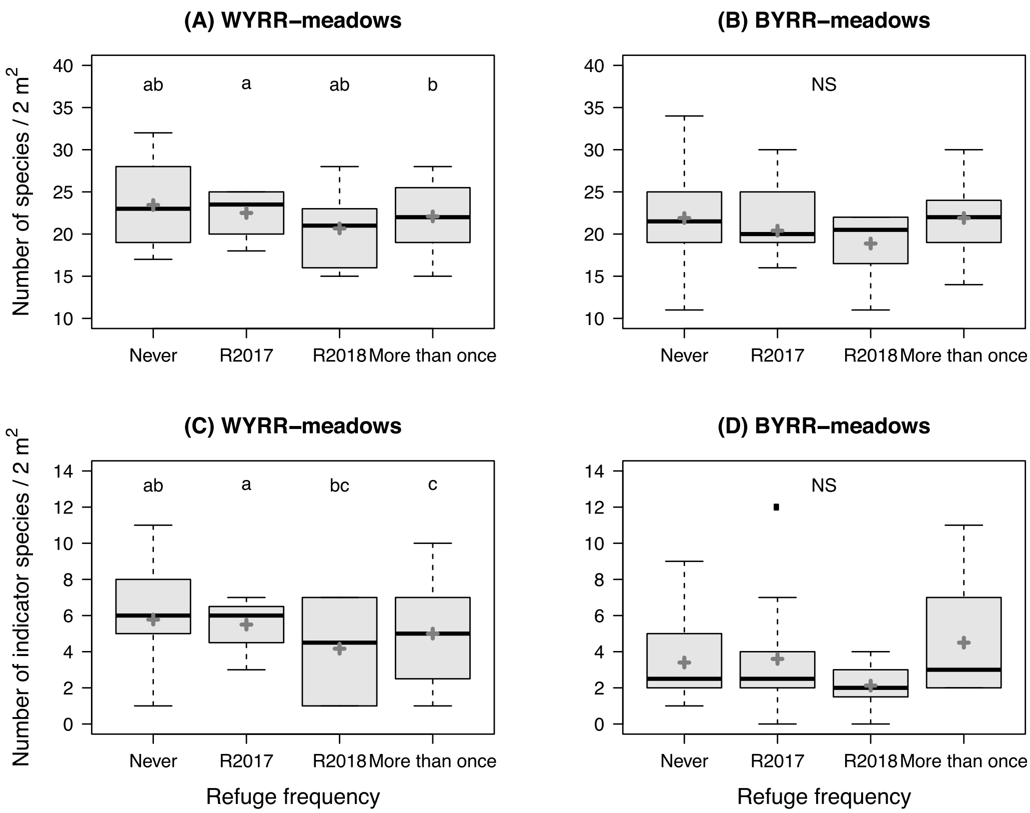

Fig. 2. Number of plant species in relation to the four different refuge frequencies (i.e. the four strata based on the location where an uncut refuge had been left the previous years) in WYRR-meadows (A) and BYRR-meadows (B), as well as the number of QII indicator plant species in relation to the four different refuge frequencies in WYRR-meadows (C) and BYRR-meadows (D). NS stands for no significant difference. Abbreviations, boxplot features and statistical symbols as in Fig. 1. See Appendix D for statistical analyses.

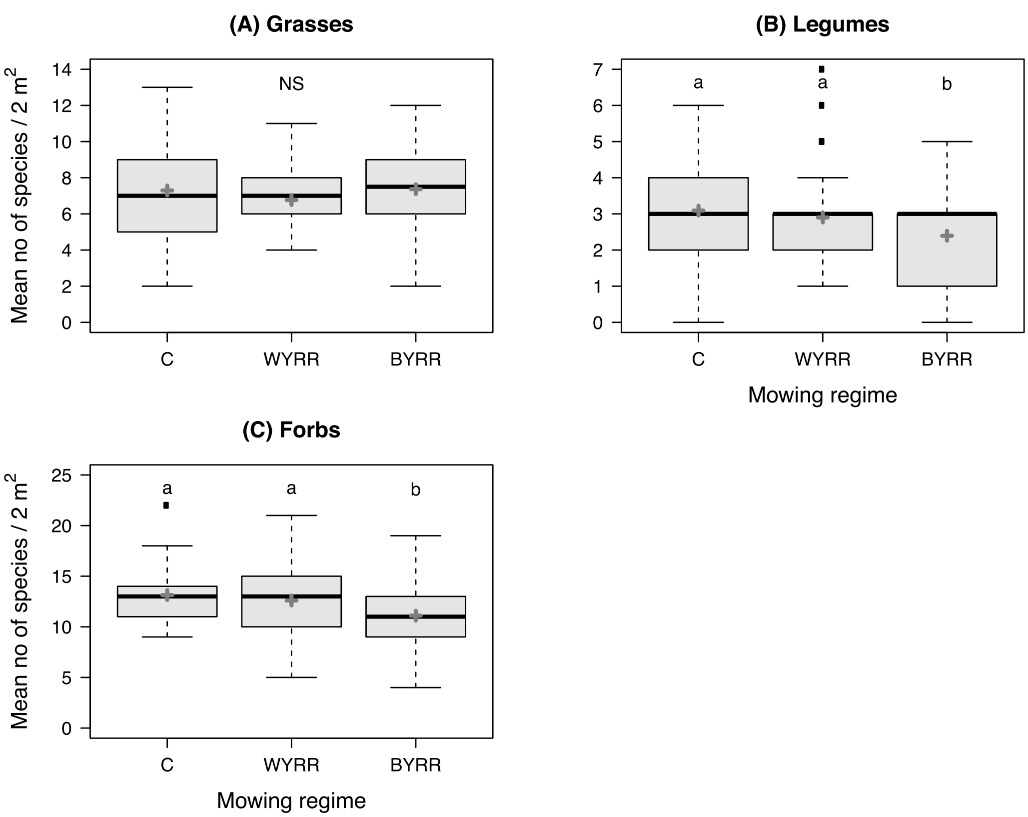

Fig. 3. Mean number of grass (A), legume (B) and forb (C) species with respect to the mowing regime. Abbreviations, boxplot features and statistical symbols as in Fig. 1 (with NS = no significant difference). See Appendix C for statistical analyses.

distances) was similar among the three mowing regimes, contradicting our prediction. It indicates that the above-mentioned differences were likely too marginal to be discernible at the plant community level.

Refuge scale

We had hypothesised that refuges would negatively impact the vegetation if located more than once at the same place during the three years of the experiment. This was confirmed only for WYRR-meadows, but not for BYRR-meadows. In WYRR-meadows, QII indicator species richness was lower in areas where refuges had been placed at the same place more than once, compared to either areas void of any refuge (*never*) during the course of the experiment, or areas with a refuge in 2017 (*R2017*, i.e. two years before the vegetation relevés). When considering the total number of plant species instead of just indicators species, a similar pattern was observed: fewer species were recorded for refuge *more than once,* compared to *never* or *R2017*, but the differences were not always statistically significant. Hence, although within-year rotational refuges have slight short-term negative effects on the vegetation, the plant community will fully recover two years later, providing that the refuge area has been mown in the meantime and located at different places (Zhao et al., 2020).

We had assumed that farmers leave vegetation refuges primarily in shadier areas (e.g. adjacent to a forest edge), which could have biased the observed effects (Erdős et al., 2019). However, daily average sunshine duration did not differ between areas where a refuge was left once, or more than once in the previous years, compared to areas without any refuge. Our initial assumption was thus wrong. Furthermore, total plant species richness and the number of QII indicator plant species were not significantly affected by sunlight availability, which might be explained by the fact that 77% of all our study plots received more than 10 h of sunlight per day (averaged over March−May). We thus conclude that light availability was not a limiting and possibly confounding factor in our experiment.

Conclusion and management recommendations

Our experiment establishes that the installation of vegetation refuges within mown grassland does not impact negatively plant species richness and indicator plant species richness, but insofar that the refuge's location within a meadow is changed at every mowing operation, i.e. twice within a given vegetation period, and is never placed at the same location more than once over a period of two consecutive years. The minor negative effects observed when rotational refuges stayed at the same place within the same season (-11% overall plant species richness; -22% indicator plant species richness) were only detected at the meadow scale but not at the refuge scale. This suggests that this measure has carry-over effects (cumulative from one year to another) on a given meadow plant community, which, again, can easily be avoided by changing the location of a refuge at each mowing operation.

This research confirms earlier findings on both vascular plants and bryophytes van Klink et al. (2017) that within-year rotational refuges (WYRR) do not impact the plant diversity of extensively managed meadows. Given that positive effects of WYRR have already been evidenced for grassland herbivore and pollinator communities (Humbert et al., 2018; van Klink et al., 2019), this measure can be applied widely for promoting meadowland biodiversity, in particular where invertebrate populations are of concern. However, further research must elucidate to which extent between-years rotational refuges (BYRR) could represent an advantage for the overall insect community, providing them notably with valuable overwintering sites, as they do for some beetles and spiders (as suggested in Pywell et al., 2005). Annual and biennial mowing, instead of traditional European temperate grasslands mowing regime which includes two cuts per year, has also been recommended for the persistence of endangered *Maculinea* butterfly species (Johst et al., 2006).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.07.003.

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