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Unequal pollinator benefits from partial mowing regimes in a field experiment

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Abstract

1. Studies suggest that partial mowing, where unmown refuges are left for insects after mowing, promotes arthropods in semi-natural grasslands. However, studies comparing community development in refuges to unmown controls are scarce, particularly for insect pollinators. As competition for floral resources is a central driver in pollinator community composition, the potential increase in pollinator density within unmown refuges is likely to filter ecological communities.
2. We here present a partial mowing field experiment on dike grasslands to study how pollinator communities develop in unmown strips (refuges) within mown dike locations compared to unmown controls. We collected data on flower visitation frequency (counting 28,553 unique visitation events) and community composition from transect counts (identifying 4530 pollinators to the species level) in three periods: before (four days), directly after (four days) and later (until four weeks) after mowing.
3. Pollinator visitation frequency (+85%) and abundance (+25%) increased in partially mown grasslands directly after mowing, but three weeks later pollinators had abandoned refuges, resulting in lower numbers than in control vegetation. These declines were not equally divided over pollinator groups, with significant non-*Bombus* wild bee abundance and species richness decline (−82% and −70%, respectively), whereas honeybees maintained high abundance. Subsequently, rank-abundance curves reveal a disproportionate decline of intermediately common and rare species at partially mown sites, with no compensatory appearance of later-season species, which we did observe at unmown controls.

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4. *Synthesis and applications:* We conclude that, although unmown refuges under partial mowing provide initial relief for insects, they do not substitute unmown vegetation. Our results suggest that they primarily benefit common pollinators, such as honeybees, and might not sustain pollinator diversity as a whole.

KEYWORDS
competition, grassland, linear landscape elements, nature restoration, partial mowing, pollinators

INTRODUCTION

Native grasslands are biodiverse habitats that can harbour rich arthropod communities (Ghazoul, 2006; Sexton & Emery, 2020; Veen et al., 2009). Although fully natural grasslands are rare in the Western Palearctic, maintained grasslands through human activity are widespread. Examples of these include road verges and dike grasslands that, just like natural grasslands, can harbour rich arthropod communities (e.g., Bátori et al., 2016; Phillips et al., 2020). To prevent succession, both in interest of sustaining open grassland and their anthropogenic functions, mowing management is applied (Bochniak et al., 2024; Milberg et al., 2017). This mowing management, which results in the sudden removal of all vegetation, conflicts with the needs of arthropods that require year-round vegetation (Steidle et al., 2022).

Studies show that alternative ways of mowing (e.g., using different material or delaying the first cut) can benefit arthropods (Berger et al., 2024; Humbert et al., 2010b; Humbert et al., 2012). Nevertheless, these don't mitigate the sudden loss of vegetation. As such, more recent work suggests adopting partial (or mosaic) mowing regimes, where unmown refuge patches are left after mowing (Révész et al., 2025). The core idea is to spread mowing events over the year, while leaving unmown vegetation every time that can function as refuge to arthropods. Studies report increased abundance and species richness of many arthropod groups (e.g., orthopterans, butterflies, true bugs, spiders and beetles) in unmown refuges compared to mown vegetation and different mowing regimes, suggesting partial mowing can aid conservation of different arthropod groups (Biella et al., 2025; Bruppacher et al., 2016; Meyer et al., 2017; Wintergerst et al., 2021).

Nevertheless, comparing arthropod order level abundance and species richness in unmown refuges to completely mown controls runs the risk of oversimplifying conservation outcomes as community changes in these refuges may be overlooked. Just like traditional mowing regimes, partial mowing can filter arthropod communities (Buri et al., 2013; van Klink et al., 2019), but short-term community dynamics in unmown refuges after mowing are understudied. Nevertheless, the aggregation of individuals in unmown refuges after mowing might well result in community level changes. For instance, Lebeau et al. (2015) show that density increases in unmown refuges of *Maniola jurtina*, a common grassland butterfly, were followed by partial refuge abandonment and changes in foraging behaviour of this species. Comparing community development in unmown refuges at different stages after partial mowing to developments in unmown controls is thus important to further our understanding of how partial mowing filters communities.

Flower visiting insects (or pollinators) are an especially relevant but relatively understudied group in this context, while the few studies looking at pollinators in the context of partial mowing report varying responses (Révész et al., 2025). While these (generally) mobile insects suffer relatively few casualties through direct mowing (Fluri et al., 2001), pollinator community formation is thought to be driven by competition for available resources and subsequent niche partitioning (Brosi, 2016; Fründ et al., 2013; Valdovinos et al., 2016). This niche partitioning arises when generalist pollinators shift their foraging towards relatively underutilized floral resources, which reduces resource use overlap with specialist foragers, thereby promoting coexistence within the pollinator community (Brosi, 2016; Valdovinos et al., 2013). However, the division of resources could be disrupted when resources suddenly decline (Biella et al., 2019; Biella et al., 2020) as is the case in partial mowing. Some species within pollinator communities might thus respond differently to partial mowing than other species, explaining the varying responses observed so far. However, to our knowledge, no studies have looked at short-term community-wide changes in a well-established pollinator community when switching to a partial mowing regime.

Here, we set up a field experiment to study changes in visitation frequency and community composition of well-established pollinator communities in unmown strips (refuges) within mown vegetation. We selected experimental locations on semi-natural dike grasslands and compared to control locations where the entire vegetation was left unmown which allowed us to isolate the effects of partial mowing from other phenological changes. Specifically, we ask three questions; (1) How does pollinator visitation frequency, abundance and species richness change in unmown refuges directly and later after partial mowing? (2) Are changes in visitation frequency, abundance and diversity evenly distributed over different pollinator groups? and (3) How do changes translate to pollinator species abundance distribution? We expect that directly after mowing pollinators will aggregate in unmown refuges (as recently reviewed for other arthropods (Révész et al., 2025)), leading to increased visitation frequency and abundance of the species present. Further, we hypothesize that remaining vegetation at partially mown sites is unable to sustain this higher pollinator abundance for a prolonged time as pollinators are generally suggested to be resource limited (e.g., Sponsler et al., 2023), resulting in declines later after partial mowing not observed in control sites. These declines will likely not be equal for all groups, as species with higher competitive strength are more likely to persist in resource limited conditions.

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MATERIALS AND METHODS

Location

We selected five south-facing dike sections that were at least 300 m long along the southern Waal dike near Nijmegen (Appendix S1), where we established five quadrats (1.5 × 1.5 m) per location (25 in total). All dike sections shared vegetation type (namely *Arrhenaterion* grasslands, a typical flower-rich dike grassland vegetation in the Netherlands) and management practice; they were mown twice each year (mid/late-June and September), with the intent to facilitate biodiversity while ensuring dike functioning (Liebrand, 1999). From previous monitoring work we also know that these sites host rich solitary bee communities adapted to early availability of floral resources (Swinkels et al., 2025). Both flower and pollinator community composition showed no significant differences between experimental and control locations before mowing (Appendices S2 and S3). The closest locations were 330 meters apart with no direct sight lines towards each other, with on average 1068 meters between locations, accounting for the flight ranges of most pollinating insects (Zurbuchen et al., 2010). We tested all models for spatial autocorrelations using DHARMa-based Moran's I tests, finding no consistent signs of spatial autocorrelation (Appendix S4).

Experimental set-up

The experiment took place from the 30th of May until the 28th of June, 2023. It consisted of three periods: four days *Before* mowing (30th of May until the 2nd of June), four days *After* mowing (4th until the 7th of June) and a *Later* period (from the 8th until the 28th of June, on average 14.2 days later), where visits were spread over a longer time depending on favourable weather conditions (at least 18°C, max three on the Beaufort scale (BFT) and at least 50% clear skies). We marked five 1.5 × 1.5 m plots in the middle of each dike section, with a 75 m long transect running above and below the plots so that the area between the two transects was about 33% of the total vegetation (Figure 1). The five quadrats were representative for the dike grassland vegetation.

To study pollinator community dynamics in unmown refuges we adopted a Before-After Control-Impact (BACI) design, with the control consisting of unmown vegetation (Green, 1979). Grassland was mown at three dike sections (15 quadrats) on the 3rd of June, using a bar mower. Bar mowers are generally considered to cause the least number of insect casualties, with results suggesting around 5% loss of honeybees (Fluri et al., 2001) and 20% of more sedentary arthropods (Humbert et al., 2010a). Mowing occurred between 9 AM and 3 PM with good weather conditions, as most pollinators are active at that time providing them the opportunity to escape. We mowed roughly

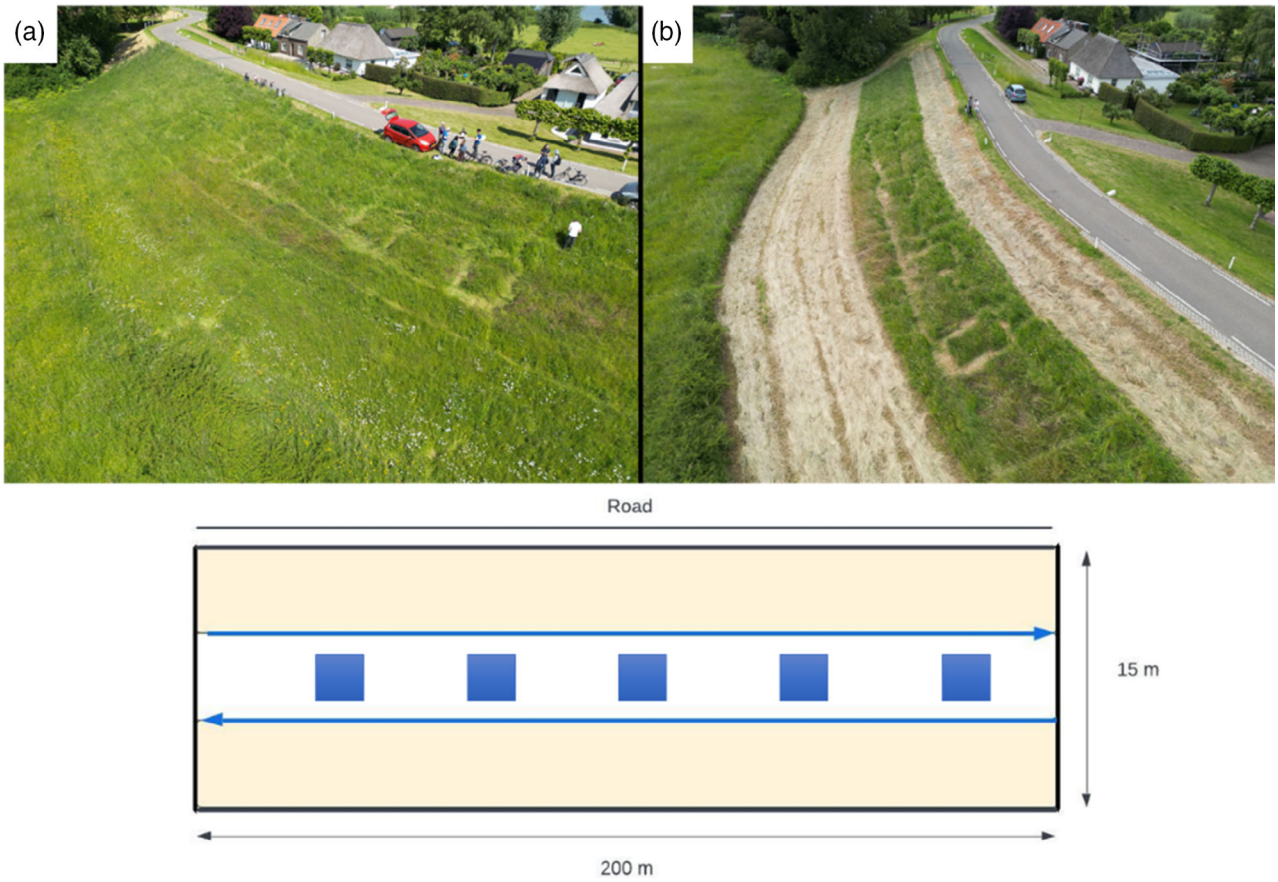


FIGURE 1 Example of an experimental location before (a) and after (b) mowing. Below the pictures is the schematic set-up, with blue squares indicating the plots for visitation counts, blue arrows the transect lines and the white area representing the unmown area.

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66% of the vegetation, both at the top and bottom of the dike, leaving an unmown strip in the middle (33%). These percentages are representative, but on the larger end of the spectrum, for partial mowing practices (Révész et al., 2025). This choice was thus conservative, leaving more vegetation for remaining arthropods. Cuttings were not collected directly after mowing so that pollinators that got trapped between the cuttings had the opportunity to escape.

Vegetation sampling

Within each of the established quadrats, flowering floral units per species, a flower or set of flowers that a pollinator can reach without having to fly (Baldock et al., 2015; Carvalheiro et al., 2008; Tew et al., 2023), were counted on the first and last day of the Before and After periods, and quantities were interpolated between the two counts (see Appendix S5 for a list of flower species and considered floral units). In the later period, floral units were counted during each visitation survey as these surveys were more irregular. As counts were partly performed by trained students, the similar looking and closely related *Centaurea jacea* and *Centaurea scabiosa* were treated as one group, as well as *Trifolium dubium* and *Medicago lupulina*.

Pollinator visitations

Between 9 AM and 5 PM, pollinator visitations were counted by experts and trained students. Students always performed surveys in pairs to minimize misidentifications. On sampling days, each quadrat at a location was observed for 20 min in randomized order, both in the morning and afternoon (40 mins per quadrat total, 200 min per dike section per day). In the four days before and after mowing, all locations were monitored simultaneously every day to account for weather and insect activity effects (thus meaning dike sections were monitored for 800 min, or 13.33 h, both before and directly after mowing). In the Later period, observations were spread out over time, but each location was at least visited on three separate days. As fewer observers were available, only three quadrats per dike section were observed in the later period (on average, dike sections were monitored for 403.8 min, or 6.73 h, in this period of the experiments).

During the surveys, each pollinator – floral unit interaction was registered. Pollinators were assigned to one of ten groups: honeybees, bumblebees, other wild bees, syrphid flies, other flies, ants, wasps, beetles, bee flies and butterflies, or recorded as unidentified without certain identification. The groups share similar life strategies and are at the same time easy to identify for trained volunteers. Flowers were identified to the species level (but see Methods – *vegetation sampling*).

Transect counts

Pollinator species were counted at each dike section along two parallel 75 m long transects with a 2 m sampling width extending into the vegetation from the transect line (at experimental locations following the upper edge and lower edge of the unmown strip for 75 m each). Each transect was sampled during 15 min of active searching time. While identifying, chasing or handling pollinators, time was paused. All transect counts throughout the experiment were completed by the same two people to minimize observer bias. Pollinators that could not be identified in the field were caught and transferred to the lab. Transects were surveyed four times per period, in the morning and afternoon on two separate days. We chose two days rather than all four to reduce the chance that collecting individuals would lead to local depletion of populations.

Environmental data

In addition to data on vegetation and pollinators, we recorded the time, temperature, wind speed and the percentage of clouds for each survey.

Analysis of floral visitation data

All statistical analysis were performed in R version 4.2.2. (R Core Team, 2022). To study how floral unit availability and visitation frequency changed over time we used the total number of floral units and visitations per survey. We then constructed GLMM (Generalized linear mixed models) with number of floral units or visitations as dependent variable following a Negative binomial error distribution. We included the interaction effect of the period (before mowing, after mowing or later) and treatment (partially mown vegetation or unmown vegetation) as primary interest and corrected for cloud coverage as a proxy for weather conditions in visitation models. As baseline floral unit counts and visitation frequency differed between quadrats, we included the quadrat-specific mean pre-treatment value of the corresponding response variable as an offset in each respective model. This ensured that floral unit counts and visitation frequency were each standardized relative to their own pre-treatment baseline distributions. Finally, we accounted for nested observations by including location as a random variable. Models additionally including Quadrat as a nested random effect failed to converge, likely because persistent differences among quadrats were already captured by the quadrat-specific pre-treatment offset.

We then explored a single negative binomial GLMM including the three-way interaction between Treatment, Period and pollinator group to compare responses of different pollinator groups. However, this model failed to converge. We therefore fitted separate pollinator group level models, following a similar structure as described above. These models still allow us to assess temporal responses within each pollinator group, but do not allow direct statistical comparisons of responses between pollinator groups. We present results for bumblebees, honeybees, beetles and wild bees as other groups were recorded too infrequently for reliable analysis. Including a pre-treatment offset resulted in disproportionately large relative (fold-change) effects for

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quadrants where pre-treatment average visitation frequency for individual pollinator groups was low. Therefore, we also tested alternative group-level models, without the offset, that we present in the appendix.

The *emmeans* package (Lenth et al., 2025) was used to compute estimated marginal means (Searle et al., 1980) for between-treatment and between-periods effects within treatment, with pairwise comparisons assessed using *t*-tests. *p*-Values were obtained from a post-hoc Tukey test.

Analysis of transect data

To study pollinator abundance and species richness, we constructed a similar model to the ones described above with pollinator abundance or species richness (Poisson distributed) per transect survey as dependent variable. We then constructed models at the group level to calculate group-level contributions to the larger patterns (without the offset). Groups with low abundance or few species (e.g., 'honeybees' is only one species) were excluded from the group-level species richness analysis. We plot the estimated change in abundance or species richness per group as a proportion of that group, since there are large differences in abundance between groups.

To answer our third question and study how the changes analysed above translate to species abundance distribution, we constructed rank-abundance curves per period of the experiment. Such curves are commonly presented to capture the dominance, abundance and species richness that shape communities (e.g., Habel & Schmitt, 2018). To correct for the different number of surveys among treatments (i.e., three vs. two locations), we constructed rank-abundance curves per location and show the average curve by fitting a loess curve with 95% confidence interval.

RESULTS

In total we counted 28,553 visitation events during 167 observation hours and identified 4570 pollinator individuals to the species level (94 species) from transect counts. In both the visitation and transect datasets, honeybees (38.7% and 46.7% respectively) and bumblebees (42.7% and 31.2%) were the most abundant, followed by beetles (6.9% and 7.2%) and wild bees (6.3% and 9.0%). A full overview of the data is given in appendices S6 and S7.

Floral unit availability

Floral unit availability in the plots decreased significantly over time (Figure 2a, Appendix S8). This decline was stronger in unmown refuges compared to unmown vegetation, resulting in a significant difference in floral unit availability in the later period of the experiment (IRR = 2.44, 95% CI: 1.47–4.07, $p < 0.001$).

Visitation frequency

In line with our first hypothesis, visitation frequency increased nearly twofold (from 42.1 visitations per twenty minutes to 75.91) in the first four days after mowing in partially mown vegetation (IRR = 1.63, 95% CI: 1.25–2.12, $p < 0.001$, Figure 2b, Table 1 and Appendix S8). We observed no change in unmown control vegetation (IRR = 1.02, 95% CI: 0.83–1.25, NS). Consequently, the average number of visitations and the relative increase were significantly higher in partially mown locations compared to unmown ones (IRR = 1.61, 95% CI: 1.17–2.22, $p < 0.01$ and IRR = 1.63, 95% CI: 1.25–2.12, $p < 0.001$, respectively).

Trends reversed towards the Later period (up to four weeks after mowing), with a non-significant increase observed in unmown locations (IRR = 1.24, 95% CI: 0.95–1.62, $p > 0.05$) and twofold decrease in partially mown locations (IRR = 0.52, 95% CI: 0.42–0.64, $p < 0.001$) compared to the first four days after mowing. As a result, in the Later period, the average visitation frequency in control plots was significantly higher than in experimental plots (57.4 versus 38,5, IRR = 1.49, 95% CI: 1.04–2.13, $p < 0.05$).

An alternative model examining visitation frequency per floral unit also found higher visitation rates at partially mown sites immediately after mowing, followed by a decline in the Later period (Appendix S9).

Group level visitation patterns

At the group level, relative floral unit visitation frequency of all four major groups (honeybees, bumblebees, non-*Bombus* wild bees and beetles), similar to the total pattern, increased at partially mown locations (Figure 3a–d, Appendix S10). This increase was significant for honeybees, wild bees and beetles (Table 2). The higher variation at the group level did result in fewer significant differences between treatments at the pollinator group level.

Trends at the group level again reversed towards the Later period, with significant decreases in visitation frequency observed for honeybees, bumblebees and beetles (Table 2). These decreases were not observed in unmown vegetation, where all groups but beetles increased. When comparing between treatments, the number of bumblebee visitations was significantly higher in unmown vegetation during this Later period (IRR = 1.67, 95% CI: 1.00–2.77, $p < 0.05$). A model not comparing to baselines provided largely similar patterns (Appendices S11 and S12).

Transect counts

In the first four days after mowing, pollinator abundance increased significantly at partially mown locations (IRR = 1.25, 95% CI: 1.01–1.56, $p < 0.05$, Figure 4a, Appendix S13). A similar increase in unmown vegetation was non-significant (IRR = 1.26, 95% CI: 0.96–1.64, $p > 0.05$). Abundance changes were not equally divided over pollinator groups, with the abundance increase in partially mown

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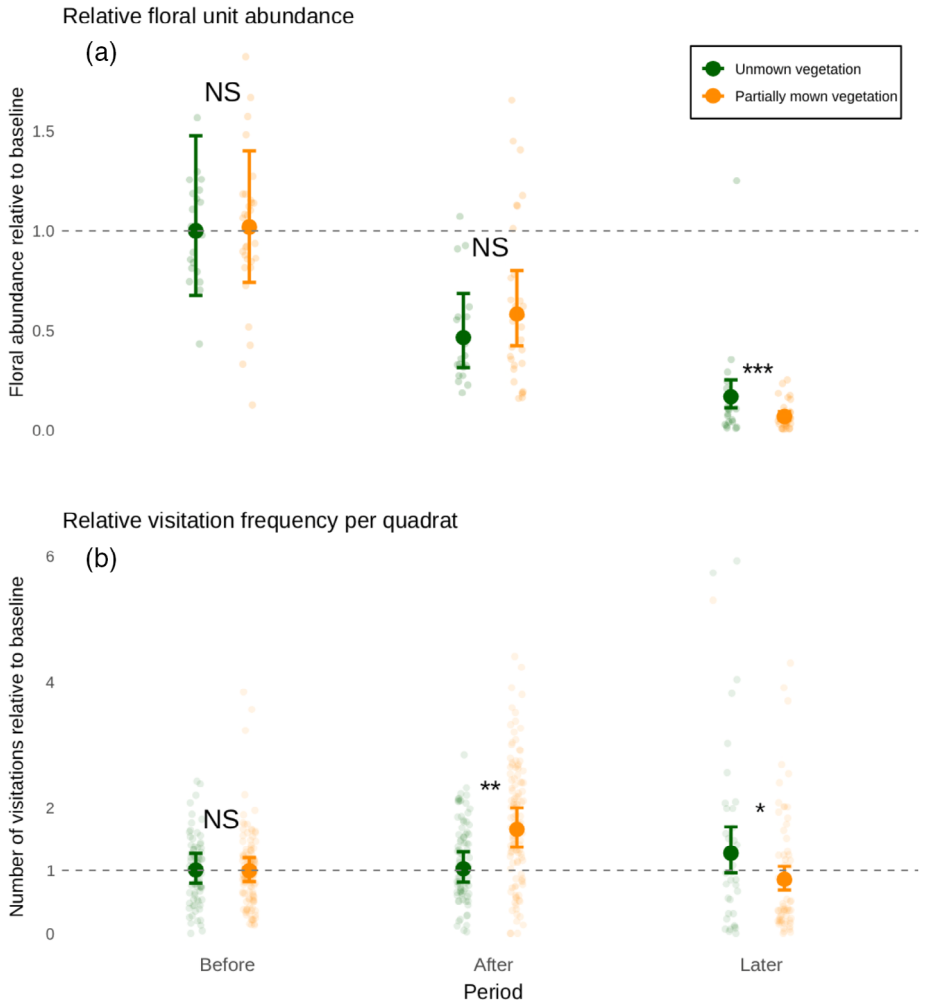


FIGURE 2 Model estimates (marginal means with 95% confidence intervals) of relative floral unit availability (a) and relative visitation frequency (b) to a pre-mowing baseline per period of the experiment (x-axis). Unmown vegetation is shown in green, partially mown vegetation in orange. Between treatment differences per period are indicated in text ($p > 0.05$ = NS, $0.01 < p < 0.05$ = *, $0.001 < p < 0.01$ = **, $p < 0.001$ = ***).

TABLE 1 Within-treatment pairwise comparisons between periods for total flower availability and visitation frequency.

Variable	Treatment	Contrast	Effect (95% CI)	Significance
Floral abundance	Unmown	Before – After	0.46 (0.30–0.71)	**
Floral abundance	Unmown	After – Later	0.36 (0.24–0.56)	***
Floral abundance	Unmown	Before – Later	0.17 (0.11–0.26)	***
Floral abundance	Partially mown	Before – After	0.57 (0.41–0.81)	**
Floral abundance	Partially mown	After – Later	0.12 (0.08–0.17)	***
Floral abundance	Partially mown	Before – Later	0.07 (0.05–0.10)	***
Visitation frequency	Unmown	Before – After	1.02 (0.83–1.25)	NS
Visitation frequency	Unmown	After – Later	1.24 (0.95–1.62)	NS
Visitation frequency	Unmown	Before – Later	1.26 (0.97–1.64)	NS
Visitation frequency	Partially mown	Before – After	1.66 (1.40–1.96)	***
Visitation frequency	Partially mown	After – Later	0.52 (0.42–0.63)	***
Visitation frequency	Partially mown	Before – Later	0.86 (0.70–1.05)	NS

Note: Significance levels are based on contrasts of estimated marginal means from the fitted models (NS: $p \geq 0.5$; *: $0.01 \leq p < 0.05$; **: $0.001 \leq p < 0.01$; ***: $p < 0.001$).

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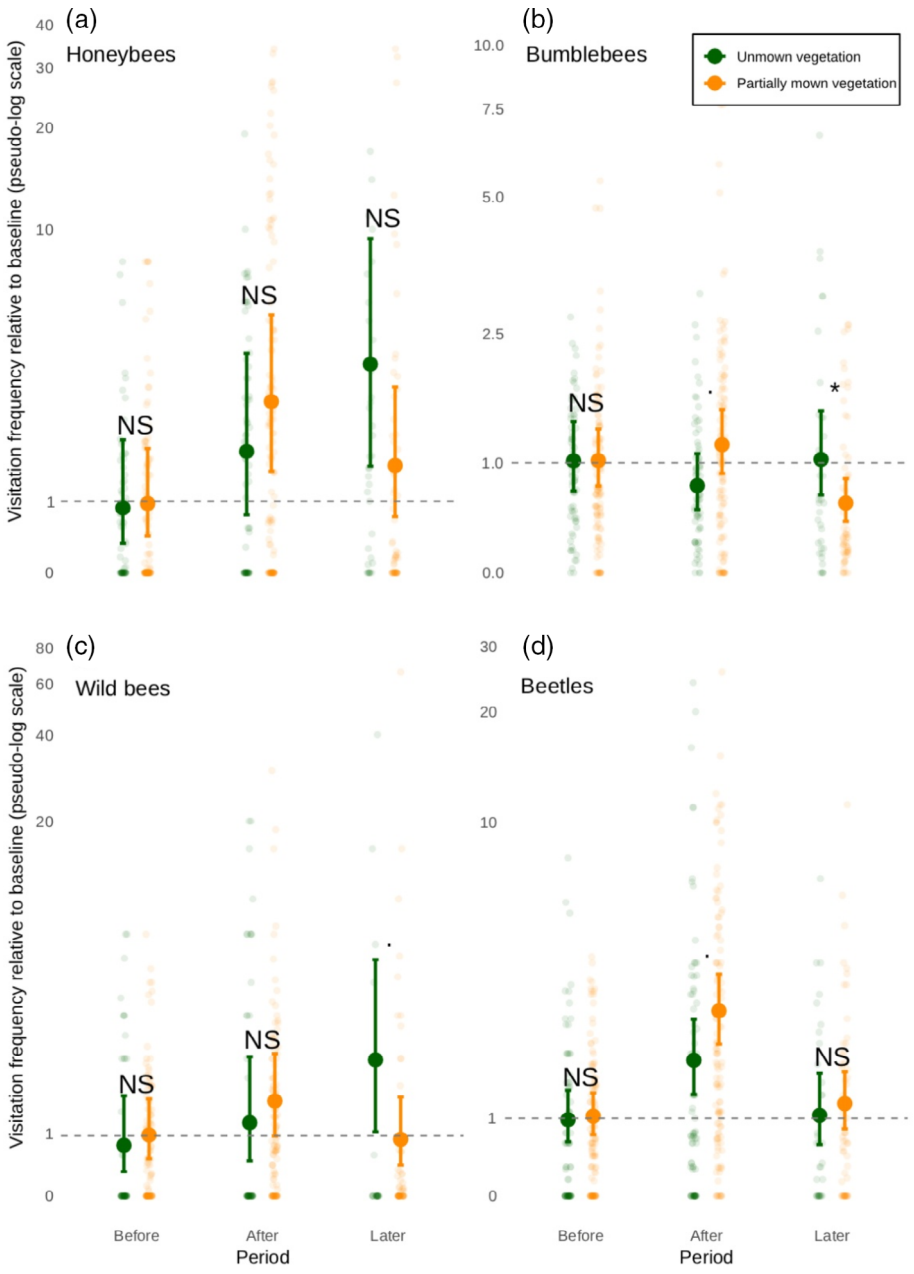


FIGURE 3 Model estimates (marginal means with 95% confidence intervals) of pollinator group level relative visitation frequency for honeybees (3A), bumblebees (3B), wild bees (3C) and beetles (3D) to a pre-mowing baseline per period of the experiment (x-axis). Unmown vegetation is shown in green, partially mown vegetation in orange. Between treatment differences per period are indicated in text ($p > 0.05$ = NS, $0.01 < p < 0.05$ = *, $0.001 < p < 0.01$ = **, $p < 0.001$ = ***).

vegetation mostly explained by an increase in honeybee and beetle abundance (IRR = 2.01, 95% CI: 1.74–2.32, $p < 0.001$ and IRR = 2.12, 95% CI: 0.92–4.92, NS respectively), whereas other groups showed no significant changes (Figure 5a). At control locations, we also observed an increase in honeybee abundance (IRR = 3.42, 95% CI: 2.78–4.21, $p < 0.001$), together with a decline in bumblebee and syrphid abundance (IRR = 0.61, 95% CI: 0.43–0.87 and IRR = 0.25, 95% CI: 0.11–0.56 respectively, both $p < 0.001$).

In the later period, pollinator abundance decreased at partially mown locations in the Later period (IRR = 0.56, 95%, CI: 0.45–0.70, $p < 0.001$, Figure 4a), while pollinator abundance increased in unmown vegetation (IRR = 1.37, 95% CI: 1.05–1.78, $p < 0.05$). Consequently, pollinator abundance became significantly higher in unmown vegetation than in partially mown vegetation in the later period (IRR = 2.49, 95% CI: 1.87–3.30, $p < 0.001$). At the group level, abundance declines in partially mown vegetation during the later stage of the experiment were observed for all groups, but was especially strong in non-*Bombus* wild bees (IRR = 0.18, 95% CI: 0.10–0.34, $p < 0.001$, Figure 5a,c). In unmown vegetation, no groups showed significant abundance declines, while bumblebees (IRR = 1.16, 95% CI:

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TABLE 2 Within-treatment pairwise comparisons between experimental periods for visitation frequency of different insect groups.

Taxon	Treatment	Contrast	Effect (95% CI)	Significance
Honeybees	Unmown	Before – After	2.02 (1.06–3.85)	*
Honeybees	Unmown	After – Later	2.10 (0.93–4.76)	NS
Honeybees	Unmown	Before – Later	4.24 (1.93–9.34)	***
Honeybees	Partially mown	Before – After	2.95 (1.75–4.98)	***
Honeybees	Partially mown	After – Later	0.55 (0.31–0.98)	*
Honeybees	Partially mown	Before – Later	1.63 (0.88–3.00)	NS
Bumblebees	Unmown	Before – After	0.77 (0.55–1.06)	NS
Bumblebees	Unmown	After – Later	1.32 (0.87–2.01)	NS
Bumblebees	Unmown	Before – Later	1.01 (0.67–1.54)	NS
Bumblebees	Partially mown	Before – After	1.15 (0.88–1.52)	NS
Bumblebees	Partially mown	After – Later	0.53 (0.38–0.73)	***
Bumblebees	Partially mown	Before – Later	0.61 (0.44–0.84)	***
Wild bees	Unmown	Before – After	1.49 (0.59–3.77)	NS
Wild bees	Unmown	After – Later	2.12 (0.70–6.42)	NS
Wild bees	Unmown	Before – Later	3.15 (1.06–9.38)	*
Wild bees	Partially mown	Before – After	1.64 (1.01–2.67)	*
Wild bees	Partially mown	After – Later	0.56 (0.29–1.09)	NS
Wild bees	Partially mown	Before – Later	0.92 (0.47–1.82)	NS
Beetles	Unmown	Before – After	1.51 (1.20–1.89)	***
Beetles	Unmown	After – Later	0.59 (0.43–0.82)	***
Beetles	Unmown	Before – Later	0.89 (0.63–1.25)	NS
Beetles	Partially mown	Before – After	2.51 (2.15–2.91)	***
Beetles	Partially mown	After – Later	0.50 (0.42–0.59)	***
Beetles	Partially mown	Before – Later	1.25 (1.02–1.52)	*

Note: Significance levels are based on contrasts of estimated marginal means from the fitted models (NS: $p \geq 0.5$; *: $0.01 \leq p < 0.05$; **: $0.001 \leq p < 0.01$; ***: $p < 0.001$).

1.02–1.32, $p < 0.05$) and syrphids (IRR = 1.37, 95% CI: 0.55–3.40, NS) increased. Overall, group-level abundance changes were smaller in unmown vegetation (Appendix S14).

The pollinator abundance increase in the period directly after mowing was not paired with an increase in pollinator species richness, but pollinator species richness did decline with pollinator abundance at partially mown locations later on (IRR = 0.74, 95% CI: 0.57–0.95, $p < 0.001$, Figure 4b). This resulted in significantly higher species richness in unmown vegetation compared to partially mown locations in the Later period ($p < 0.001$, IRR = 1.79, 95% CI: 1.36–2.36). Group-level species richness changes largely mimicked those observed in abundance, with again a strong decline in non-*Bombus* wild bee species richness during the Later period (IRR = 0.33, 95% CI: 0.21–0.52, $p < 0.001$, Figure 5b,d).

Community composition

Rank-abundance curves revealed that the species abundance distributions (log-scale) were similar in the Before and After periods in both partially mown and unmown vegetation, with overlapping 95% confidence intervals (Figure 6). In the Later period, however, we observed contrasting dynamics at unmown and partially mown sites. In partially mown vegetation, moderately common pollinator species (those in the middle of the curve) declined in abundance, accompanied by a reduction in the number of observed species, resulting in a steeper rank-abundance curve. This illustrates that the observed abundance decline (see results above) was unevenly distributed over species, with the most common pollinator species persisting in partially mown vegetation. Meanwhile, in unmown vegetation, we observed an abundance increase of moderately common species and the appearance of new species, resulting in a more gradual rank-abundance curve. Thus, the observed increase in abundance was distributed more evenly over species. A full table of all species level abundances is given in Appendix S7.

DISCUSSION

Partial mowing, where unmown refuge vegetation remains available to arthropods, could be a valuable alternative to traditional mowing, where all vegetation is mown at once (Révész et al., 2025).

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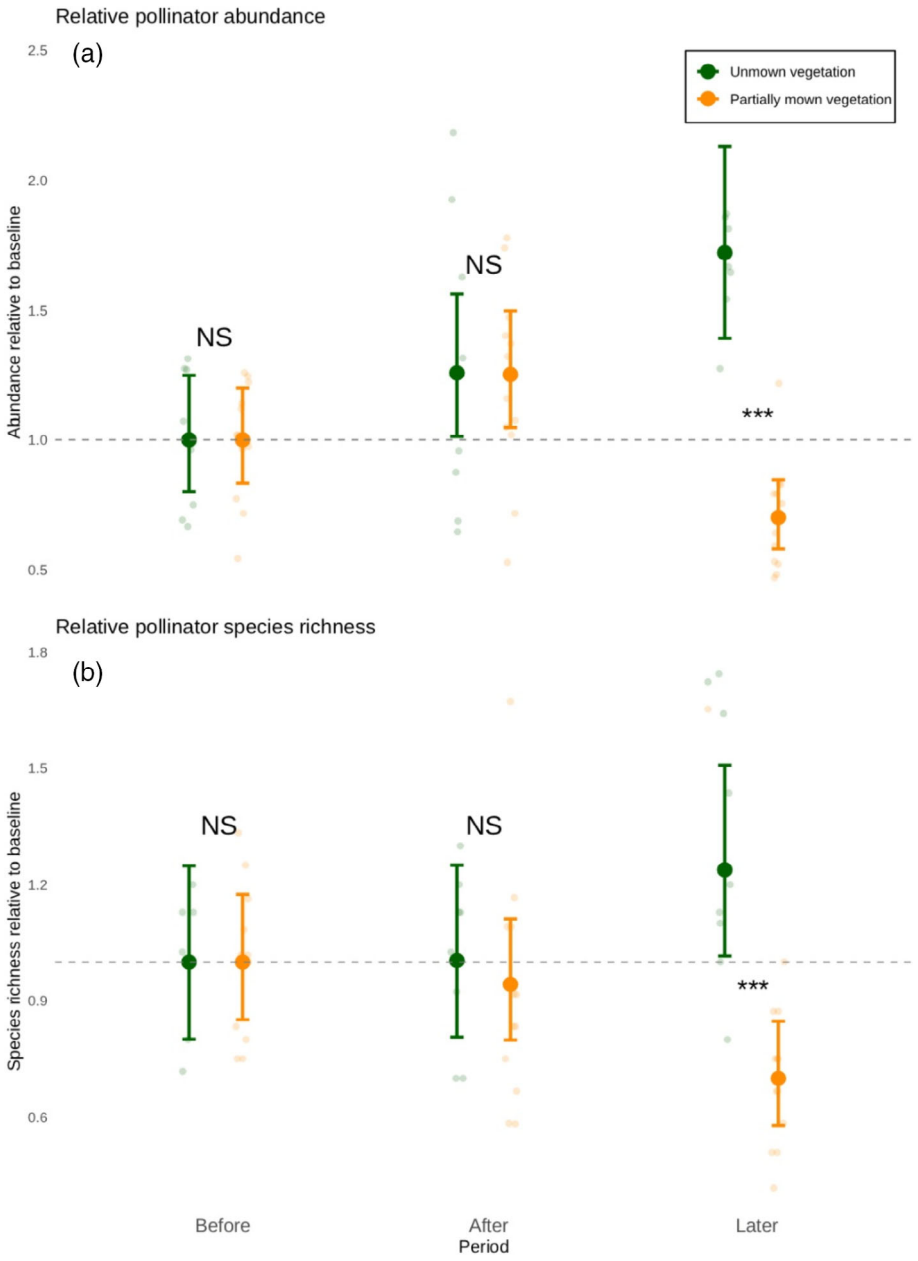


FIGURE 4 Model estimates (marginal means with 95% confidence intervals) of relative pollinator abundance (4A) and species richness (4B) to a pre-mowing baseline per period of the experiment (x-axis). Unmown vegetation is shown in green, partially mown vegetation in orange. Between treatment differences per period are indicated in text ($p > 0.05$ = NS, $0.01 < p < 0.05$ = *, $0.001 < p < 0.01$ = **, $p < 0.001$ = ***).

Nevertheless, studies on community development in refuge vegetation compared to unmown vegetation are scarce, whereas these are crucial to understand how partial mowing affects arthropod communities. Our study shows that, for pollinators in our system, initial aggregation in refuge vegetation is followed by a decline in abundance and species richness only a few weeks later. These developments were not visible in unmown controls, where communities largely stayed the same. This points out that, despite the positive effects of partial mowing compared to fully mown vegetation, partial mowing does filter arthropod communities.

Total density and activity

In remaining vegetation strips on mown locations we observed that pollinator abundance and activity significantly increased after mowing, but later on declined to roughly pre-mowing levels. On the one hand this is consistent with the broad consensus that partial mowing can benefit arthropods (Buri et al., 2014; Meyer et al., 2017), on the other hand it shows that unmown refuges do not sustain all pollinator individuals previously present at the location. This contrasts with other arthropod groups, such as spiders, true bugs and beetles, which are reported to

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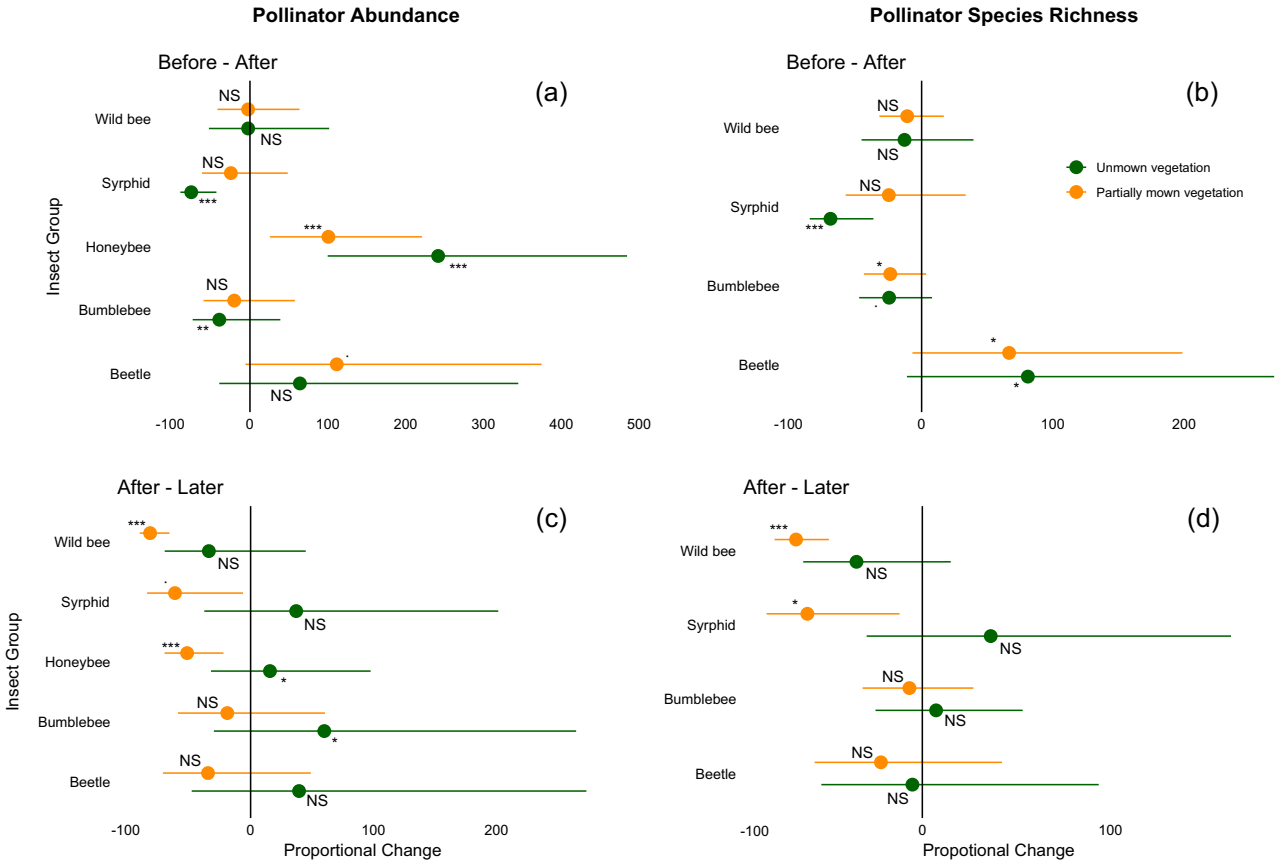


FIGURE 5 Within treatment proportional group-level responses in abundance (A,C) and species richness (B,D) for the comparison between the *Before* versus *After* periods (A,B) and *After* versus *Later* periods (C,D). Control locations are shown in green, experimental locations in orange. Points indicate the estimated marginal means from the fitted model and bars the 95% confidence interval. Significance is given in text ($p > 0.05$ = NS, $0.01 < p < 0.05$ = *, $0.001 < p < 0.01$ = **, $p < 0.001$ = ***).

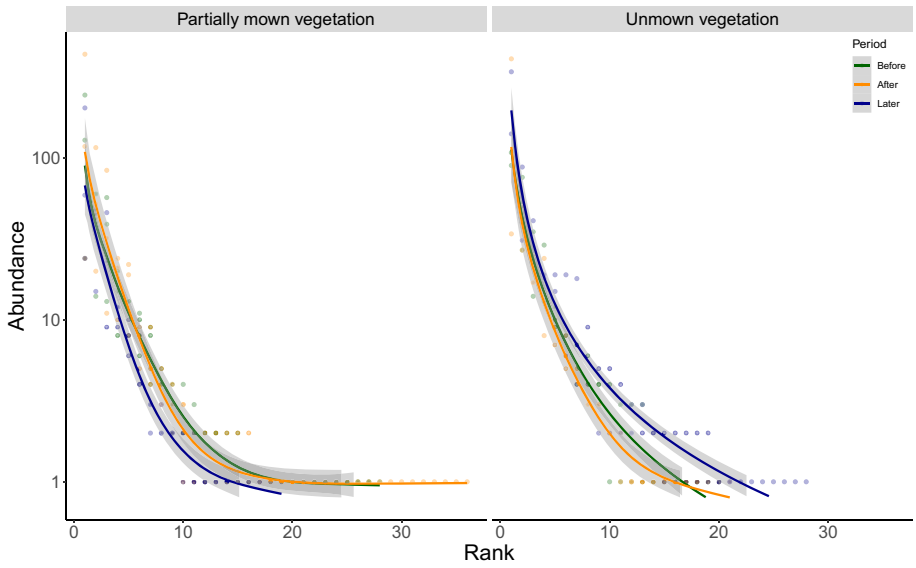


FIGURE 6 Averaged rank-abundance curves (visualized with a loess curve) of the pollinator communities during the Before (dark green), After (orange) and Later (dark blue) periods from experimental treatments and controls. Grey areas give the 95% confidence interval.

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maintain higher abundance and species richness (Révész et al., 2025). We did not observe these increases and decreases in unmown controls, where floral unit visitation frequency and pollinator abundance were significantly higher than at partially mown sites in the Later period. Together, this suggests that the remaining vegetation in unmown refuges is unable to sustain all pollinators previously present at the location.

Remarkably, floral unit availability per quadrat was lower in unmown strips than in fully unmown controls during the final period of the experiment. This pattern may have resulted from elevated floral unit visitation at experimental sites immediately following mowing. It has long been recognized that increased pollinator visitation can accelerate senescence of individual flowers and floral units, particularly in long-lived flowers such as many of the perennials included in this study (Stead, 1992). More recently, a case study of *Sabatia angularis* demonstrated that pollination-induced senescence is pollen dose–dependent but independent of pollen source (Spigler, 2017). This finding suggests that increased visitation frequency alone, regardless of floral constancy, can advance the onset of senescence. Accelerated floral senescence potentially reduces the availability of floral resources later in the season, intensifying competition among pollinators for the remaining flowers. Such dynamics could have contributed to the developments observed in this study.

Group-level responses

The initial increase and later decrease in pollinator abundance in unmown refuges were not shared equally among pollinator groups. Compared to pre-mowing conditions, only honeybees and beetles maintained similar numbers, whereas pollinator groups relevant to nature management (non-*Bombus* wild bees, bumblebees) showed abundance and species richness declines not observed at unmown control locations. Such differing responses have been shown before, as other groups within arthropod communities also responded differently to partial mowing over a 5-year period (van Klink et al., 2019).

Visitation frequency increased roughly twofold more than pollinator abundance directly after mowing. Such disproportionate visitation frequency increase has been proposed as a proxy for increased competition for floral resources (Forster et al., 2023). This higher competition in turn could explain later pollinator abundance and species richness decreases, as pollinators might relocate to less competed flowers elsewhere in the landscape. This is also consistent with our findings that, for pollinators, filtering likely occurs only after pollinator aggregation rather than as an immediate effect of the mowing itself. Although Swinkels et al. (2025) suggest that floral resource limitation on dike grasslands is quickly relieved, our results thus nevertheless suggest that competition for floral resources was elevated in partially mown vegetation. Click or tap here to enter text. Meanwhile, it is unlikely that these differences result from differential mortality through mowing, as (1) literature for our groups does not suggest between-group differences in mortality by mowing and (2) expected mortality lies between 5% and 20%, far below observed increases (Fluri et al., 2001; Humbert et al., 2010a).

In addition, increased competition might also explain different responses between pollinator groups, as some will be more resistant to increased competition than others. The persistence of honeybees in our study, that display high patch fidelity (Fragoso & Brunet, 2023) and are generally described as strong competitors that can outcompete other pollinators in resource limiting conditions (Henry & Rodet, 2018; Valido et al., 2019), is consistent with this idea. The initial high abundance of honeybees present in our system may also explain the contrast with other studies that observe stable numbers of wild bees and hoverflies in refuge strips but report lower numbers of honeybees (Buri et al., 2014; Meyer et al., 2017). Whether honeybee abundance predicts the effectiveness of partial mowing remains an open question.

Species richness and community composition

The group-level changes resulted in an overall decline in species richness at experimental locations, as opposed to unmown controls where we observed a (non-significant) increase. This finding conflicts with other studies that generally show a smaller response of species richness in unmown refuges (Révész et al., 2025) and with studies on wild bees (Buri et al., 2014) and hoverflies (Meyer et al., 2017) specifically which show no changes in species richness. This difference might partially result from the inclusion of the whole pollinator community, where small group-level changes cumulate to an overall significant effect. In addition, our system boasted a high initial proportion of honeybees (38.7% of all visitations and 46.7% of all individuals). An increasing number of studies link high honeybee abundance to increased competition and subsequent decline of other pollinators (Cappellari et al., 2022; Valido et al., 2019). As such, the high proportion of honeybees in our system, especially after partial mowing, could potentially explain why non-*Bombus* wild bee species richness declined most.

Closer inspection of rank-abundance curves provides support for the cumulative effect of small changes as at experimental locations not only rare species disappear, but also common species become less abundant. This results in a decreased detection rate, lowering the number of species encountered per survey. Steeply declining rank-abundance curves, where both rare and semi-common species decline, have been described by Habel and Schmitt (2018) to explain widespread insect decline (Hallmann et al., 2017). That we observe it here in miniature tied to the loss of suitable habitat is in line with Habel and Schmitt's contention connecting steeper rank-abundance curves to smaller and isolated nature areas.

In addition, we observed no compensatory appearance of later-season species at partially mown locations, given that species richness declined in partially mown locations and increased at unmown ones (also see Appendix S7). So far, unmown refuges were thought to specifically benefit those species with a later phenology. Of course, recovery of communities can take multiple decades, and it could well be that species with later phenology did not find refuges within one year (Hirayama et al., 2025). Nevertheless, van Klink et al. (2019)

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report that, after five years of partially mowing in Swiss meadows, species richness of species with later phenology did not increase. In addition, we do observe the appearance of species with later phenology in control vegetation, suggesting that species with later phenology are potentially limited in unmown refuges.

Conservation outlook

Our results suggest that unmown refuges, despite facilitating more individuals than fully mown meadows, act as an ecological filter just like many other types of management (e.g. Bergholz et al., 2022; Larkin and Stanley, 2021. For conservation, this implies that unmown refuges after partial mowing are no substitute for the entire vegetation, and thus that deliberate management decisions need to be made just like with other mowing regimes. We know that delayed mowing generally benefits arthropods (Humbert et al., 2012), and this could be combined with partial mowing. In addition, Révész et al. (2024) show that unmown vegetation proportion and width of unmown areas interact and influence conservation outcomes, indicating the significance of the size and shape of the refuge. Nevertheless, generally speaking, the factors that influence the carrying capacity of unmown refuges are understudied and thus an important topic for future research.

In addition to local management choices, the abandonment of refuge patches observed in our study highlights the importance of a landscape scale approach as pollinators need suitable habitat to escape towards (e.g., Meyer et al., 2017; Schmidt et al., 2008). Wild bee abundance on dikes, as well as total insect abundance at hedgerows and flowerstrips, are positively affected by the presence of natural protected areas nearby (Lexmond et al., 2026; Swinkels et al., 2025). Although, to our knowledge, there are no studies on the implementation of landscape scale partial mowing, Johansen et al. (2019) show that in traditional mowing agricultural management in Romania, heterogenous mowing times of meadows dictated where pollinators foraged at the landscape scale. How pollinators use the landscape after partial mowing, and how a landscape-level partial mowing regime can be implemented are thus important avenues for future research.

Finally, like many others (e.g., Biella et al., 2020, Biella et al., 2019; Maia et al., 2019), our study was conducted at a limited number of sites within a single study system. With a large number of simultaneous observations, a mowing treatment at a realistic management scale, and no signs of spatial autocorrelation (Appendix S4), the observed responses most likely reflect realistic treatment effects. Future studies should test whether these responses generalize across a broader range of landscapes and environmental contexts.

CONCLUSION

We conclude that partial mowing, although it is a promising management regime that allows a wide variety of arthropods to benefit from remaining vegetation, did not sustain pollinator diversity as a whole in our experiment. In grasslands dominated by generalists (and especially honeybees) such as at our dikes, partial mowing led to a loss of pollinator species richness, especially for (vulnerable) wild bees that are often a conservation target. While preferable to full vegetation mowing, conservation authorities should realize that partial mowing does significantly modify the pollinator community. Experiments with leaving larger areas unmown for a year, in combination with refuge areas in the surrounding landscape, are called for to examine the effects on the flowering plant community and pollinating insects alike.

AUTHOR CONTRIBUTIONS

Constant Swinkels: Conceptualization; methodology; investigation; formal analysis; writing – original draft. **Ilona de Weert:** Conceptualization; investigation; methodology; writing – review and editing. **Paolo Biella:** Writing – review and editing; conceptualization; methodology. **Eelke Jongejans:** Formal analysis; writing – review and editing. **Hans de Kroon:** Supervision; writing – review and editing. Our study brings together authors from different countries, and was locally setup in close collaboration with the water authorities, the local dike manager and the contractor doing the mowing. Water authorities and the local dike manager were informed about the outcomes, while the mowing method was determined together with the contractor to reflect realistic and feasible practice.

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CONFLICT OF INTEREST STATEMENT

The authors confirm that they had no conflicts of interest in this study. This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.crjdfn3k1 (Swinkels et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Map of the Ooijpolder near Nijmegen, the Netherlands. The green line represents the dike running through the area. Green points are the control locations, yellow points the experimental locations. An overview of the Netherlands is given in the right upper corner, with the blue point indicating the location of the Ooijpolder within the Netherlands.

Appendix S2: NMDS of floral unit availability composition, with location as 'strata' to correct for nestedness (multiple floral unit quadrants and counts for one location). Experimental locations are presented in orange, controls in green. Point shape indicates the location. We observed no significant differences in composition ($p > 0.05$).

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Appendix S3: NMDS of pollinator community composition from transect counts, with location as 'strata' to correct for nestedness (multiple floral unit quadrants and counts for one location). Experimental locations are presented in orange, controls in green. Point shape indicates the location. We observed no significant differences in composition ($p > 0.05$).

Appendix S4: Outcomes of DHARMa Moran's I spatial autocorrelations tests for the four main models presented in text (first column). Spatial autocorrelations tests were both implemented at the location level (column 2 and 3) and (where applicable) at the quadrat level (column 4 and 5).

Appendix S5: Table with all flower species encountered during our study, and what was considered as a floral unit.

Appendix S6: Table of visitation data at experimental locations and control locations per period. Numbers represent the number of unique visits of an individual of the given group to a flower within the observation quadrant.

Appendix S7: Number of individuals per species observed in transect counts at experimental locations and control locations per period.

Appendix S8: Model outcomes for total number of floral units and visitations as response variable. for each explanatory variable the regression coefficient, Chi squared and significances (as given by a likelihood-ratio test) are indicated, as well as the emmeans estimates, *Z*-value and significances (Wald Test) for period comparisons. Significant outcomes are given in bold.

Appendix S9: Model estimates of visitation frequency corrected for flower availability per period of the experiment (x-axis). Controls are shown in green, experimental locations in orange. Violins represent the distribution of model predicted values based on the available datapoints (i.e., values corrected for quadrant level baseline differences), points the model estimate and error bars the 95% confidence interval. Between treatment differences per period are indicated in text ($p > 0.05$ = NS, $0.01 < p < 0.05$ = *, $0.001 < p < 0.01$ = **, $p < 0.001$ = ***), changes between periods per treatment are indicated by lines (solid = significant, dotted = insignificant).

Appendix S10: Model outcomes for visitation frequency per pollinator group as response variable. For each explanatory variable the regression coefficient, Chi squared and significances (likelihood-ratio test) are indicated, as well as the emmeans estimates, *Z*-value and significances (Wald Test) for period comparisons. Significant outcomes are given in bold.

Appendix S11: Model estimates (marginal means with 95% confidence intervals) of pollinator group level visitation frequency for honeybees (a), bumblebees (b), wild bees (c) and beetles (d). Unmown vegetation is shown in green, partially mown vegetation in orange. Between treatment differences per period are indicated in text ($p > 0.05$ = NS, $0.01 < p < 0.05$ = *, $0.001 < p < 0.01$ = **, $p < 0.001$ = ***).

Appendix S12: Within-treatment pairwise comparisons between experimental periods for visitation frequency of different insect groups. Significance levels are based on contrasts of estimated marginal means from the fitted models (NS: $p \geq 0.5$; *: $0.01 \leq p < 0.05$; **: $0.001 \leq p < 0.01$; ***: $p < 0.001$).

Appendix S13: Model outcomes for pollinator abundance and species richness from transects as response variable. For each explanatory variable the regression coefficient, Chi squared and significances (likelihood-ratio test) are indicated, as well as the emmeans estimates, *Z*-value and significances (Wald Test) for period comparisons. Significant outcomes are given in bold.

Appendix S14: Proportional changes in group level abundance (a) and species richness (b) in unmown refuges (orange) and controls (green) in the before mowing situation and later period.

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