Surviving the detrimental effects of mowing through regrowth: the impact of phased mowing on vegetation and pollinators on Dutch river dykes

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December 2025

Illustration by Jeroen Smit

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This thesis is submitted in partial fulfilment of the degree of MSc. Biology

at Wageningen University & Research,

The Netherlands

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In collaboration with waterschap Hollandse Delta

The author declares

1) that this work is his own and

2) that he had adhered to The Netherlands

Code of Conduct for Academic Practice

Abstract

Immense insect losses have been recorded in 2017, and with that (insect–pollinated) plants get lost. Biodiversity is rapidly decreasing, although its benefits are crucial to us. Moreover, grasslands are known to have a high biodiversity potential, with mowing regime as one of the main drivers of vegetation composition. Mowing also has serious impacts on pollinators. As partial mowing enhances floral resources for pollinators throughout the flowering season. Given that grasslands on river dykes can form long stretches of habitat for a wide variety of species, leads to the following research question:

What is the impact of phased mowing and regrowth on vegetation- and pollinator composition on Dutch river dykes?

Vegetation surveys were done on nine dykes over four years to investigate vegetation composition changes. Within one flowering season, flower cover and pollinators (bees & butterflies) were investigated on seven dykes, once before and thrice after (partial) mowing. After mowing, investigations were done either in mown or unmown dyke parts.

Results showed the following: over four years, plant species richness increased, herb cover decreased and grass cover increased. Phased mowing heavily impacted flower cover and pollinators by vegetation removal. Regrowth after mowing caught up to levels of unmown dyke parts and possibly overtook unmown levels after the last data collection, partly due to decreased light competition. Regrowth positively impacted pollinators because of increased floral resources. Later in the season, pollinators were more abundant in regrown patches than unmown patches.

In conclusion, the impact of phased mowing and regrowth on vegetation- and pollinator composition is vast. The impact is mainly embodied by flower cover, thereby affecting pollinators. In mown dyke parts, phased mowing had a negative impact on flower cover and pollinators directly and a suggested positive impact on flower cover and pollinators later in the flowering season. Regrowth of mown dyke parts strongly attracts pollinators, while unmown dyke parts can function as refuges and sustain the pollinators after mowing.

By implementing a phased mowing regime, the flowering season could be extended, and pollinators could benefit from floral resources and nesting habitat throughout the year. Floral resources could function as an indicator for pollinator community (Segre et al., 2023). Thereby, this management tool could contribute to halting pollinator biodiversity loss. This is essential as biodiversity delivers benefits necessary to sustain our livelihoods.

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1. Introduction

The planetary boundary of biosphere integrity is known to be transgressed by both of its control variables (Richardson et al., 2023). One of these control variables is genetic diversity. Further, insect biomass has declined by 76% in 27 years in Germany, with its biggest cause possibly being the agricultural intensification (Hallmann et al., 2017). A reduction of insects and especially pollinators may explain the decline of insect-pollinated plants found over the past 87 years (Pan et al., 2024). Also, Biesmeijer et al. (2006) found a connection between a reduction in plants and their functionally linked pollinator species. This implies that the decline in insect biomass is related to reduction in plant species and is harmful because it affects pollination.

Grasslands are known to have a high biodiversity potential (Sloat et al., 2025). Biodiversity has a wide array of benefits, which are crucial for sustaining our livelihood (Duffy, 2009;Guo et al., 2010). In grasslands, mowing regime is one of the main drivers of vegetation composition (Schrama et al., 2013). Mowing has been studied increasingly because of its impact on plants and the availability of resources for herbivores (Halbritter et al., 2015). In grasslands, mowing is needed at least once a year to prevent woody growth, depending on site conditions (Milberg & Tälle, 2023). Moreover, different mowing regimes have serious impacts on the ecosystem by disturbing the primary production (Schulz et al., 2024). Mowing can have positive impacts on the plant diversity by the removal of nutrients via phytoextraction (Timmermans & van Eekeren, 2016). Limited amounts of nutrients create higher species richness than no nutrient limitations (Palpurina et al., 2019). As mowing impacts seed setting, it determines the future vegetation composition (Leng et al., 2011). Mowing in grasslands can increase plant species diversity and herb cover, decrease grass cover, and increase bare soil cover (Hoekstra et al., 2023;Antonsen & Olsson, 2005; Halassy et al., 2025). Phased or partial mowing is known to have positive impacts on the vegetation composition and pollinator community, higher floral species richness, and flower cover as well as >170% higher pollinator abundance (Hemmings et al., 2022;Morrison et al., 2025). In this work, phased and partial mowing are used interchangeably, although phased mowing emphasises having multiple (partial) mowing events, while partial mowing emphasises mowing only a part of the vegetation, often combined with mowing in more phases.

Mowing is known to seriously affect arthropods, including the (insect) pollinators. The abundance of arthropods is lowest directly after mowing, showing direct mortality (Berger et al., 2024). Reduced mowing combined with partial mowing is known to increase biomass, abundance, diversity, and reproduction of insects. Leaving areas uncut in winter is also important to maintain habitat for hibernation (Wintergerst et al., 2021). Despite its essence for hibernating insects, dead winter vegetation is becoming rare (Unterweger et al., 2018). A systematic review on 22 articles showed that leaving uncut refuges by partial mowing often increases arthropod abundance (69% of the time), and species richness (64% of the time) inside refuges compared to outside refuges (Révész et al., 2025). Furthermore, partial mowing is known to enhance the number of blooming plants throughout the season, resulting in more continuous resources for pollinators (Johansen et al., 2019). The regrowth of the vegetation increases hiding places for different species, including diurnal moths. However, floral resources for butterflies take longer to regenerate (Valtonen et al., 2006). The timing of mowing is also a complex issue, depending on what species are considered. For instance, within Lepidoptera (butterflies), species differ in life cycles which make it impossible to mow without harming juveniles of one of the species (Valtonen et al., 2006).

Mowing regimes in linear landscape elements have promising potential to improve biodiversity and connectivity. Adapted mowing regimes are being developed in several grassland types such as road verges and dykes. The latter have a large potential for biodiversity. Additionally, vegetation on dykes should become more herb-rich to increase floral resources. Because stability of dykes is justifiably a major concern, it is important to mention that herb rich river dykes are still safe dykes (Rooijen et al., 2024). River dykes in The Netherlands can be an important habitat for bees (Swinkels et al., 2020). Grasslands on river dykes can form long stretches of habitat for a wide variety of species. Therefore, river dykes might improve connectivity between habitat patches and can be used for multiple purposes. In one of the most water rich waterboards in The Netherlands, there is approximately 1000 km of river dykes, showing the abundance of this potential habitat (*Waterschap Rivierenland - Dijken in Ons Rivierengebied*, n.d.). Considering the densely populated area surrounding the dykes, most of them have a vital function now and in the future, making dyke grasslands relevant in the future as well.

As aforementioned, insects are declining and insects are closely related to the vegetation, which is heavily impacted by mowing. Mowing regimes are being adapted by governmental institutions to minimise detrimental effects and improve biodiversity. However, evidence of the impact of phased mowing on the vegetation of river dykes is limited, especially in the Netherlands. That being said, a perennial study found that flower species richness is a useful cue for bee richness on Dutch river dykes (Swinkels et al., 2020). Furthermore, flower availability together with phenology determine bee community on Dutch river dykes (Swinkels et al., 2025). Research is mainly conducted in non-dyke grasslands and other biotopes. Yet, it remains unknown what the impact of phased mowing on dykes is on the vegetation and flower availability and with that on pollinators, within a flowering season as well as over multiple years. Moreover, barely any evidence exists on the impact of regrowth after mowing on pollinators. Hence, the objective of this study is to obtain insight into the impacts of phased mowing and regrowth on the vegetation composition and pollinator composition on Dutch river dykes.

To reach this aim, the following research questions were composed: 1) How does the vegetation composition develop over four years under phased mowing, and what is the influence of phased mowing on flower cover within the flowering season? 2) What is the effect of phased mowing on pollinator abundance and diversity within the flowering season? 3) What is the effect of regrowth of mown dyke parts on pollinator abundance and diversity?

Results are hypothesised as follows: first, the species richness under phased mowing is expected to increase over the years, while the grass cover is expected to decrease, the herb cover and the bare soil cover are expected to increase. During the growing season it will take time for the regrowth to reach flowering stage again, first flowering might start after several weeks, slowly increasing the flower cover. Thus, it is expected that the mown plots will have a higher flower cover again later in the season and extend the flowering season compared to unmown plots. However, it is not expected to exceed the flower cover of the unmown parts. Second, the abundance and diversity of pollinators in the mown parts will be decreased drastically directly after mowing. A substantial part of the pollinators is expected to be killed during mowing, and most of the pollinators still alive will migrate to the unmown plots. In the unmown parts of the dyke, the pollinator abundance and diversity are expected to stay the same or even increase due to immigration of pollinators from mown parts. Third, the pollinator abundance and diversity in the mown parts will slowly recover over time, as a reaction to the regrowth of the vegetation, and later floral resources. The extending of the flowering season will also increase the pollinators abundance in the end of the season because of an increase in floral resources.

2. Methods

2.1. Study area

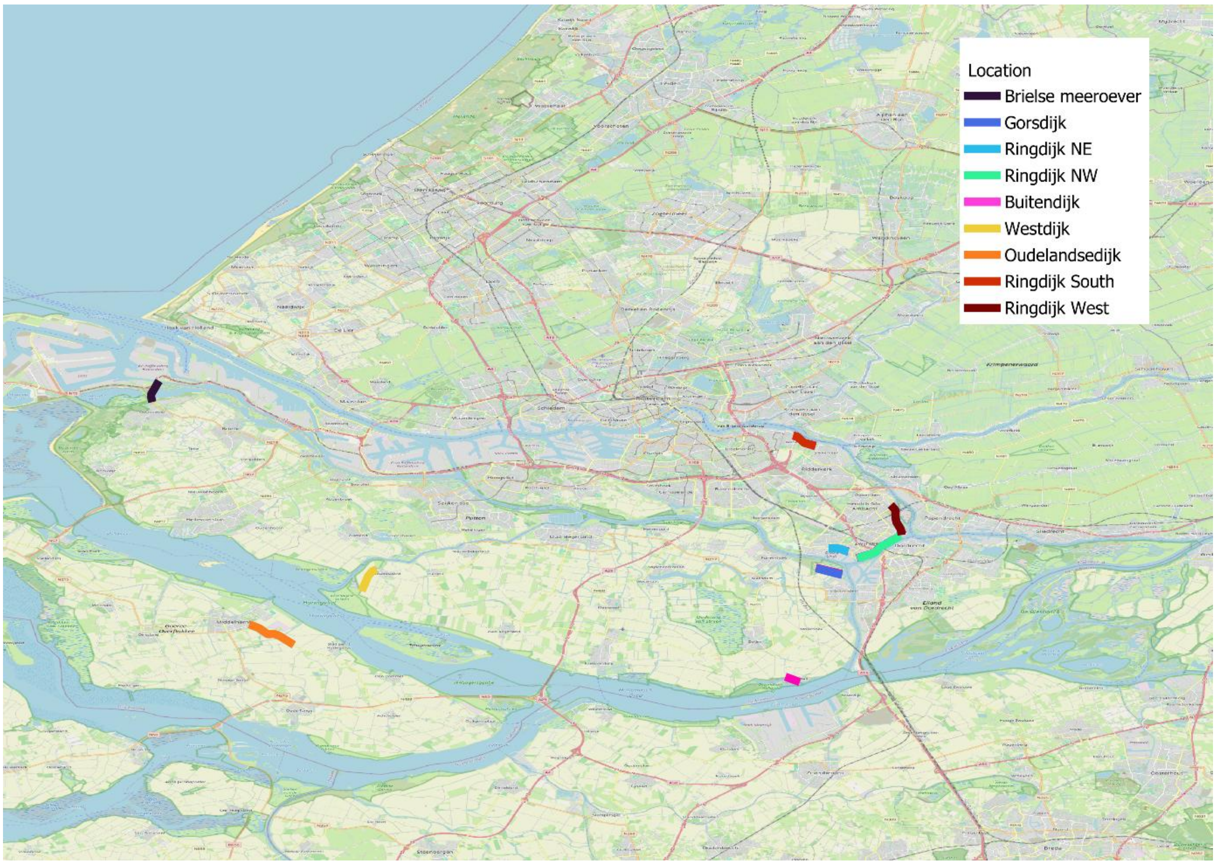

Figure 1. study area

This study took place on nine dykes part of waterboard Hollandse Delta (WSHD), located South of Rotterdam, in The Netherlands. The Netherlands has a temperate oceanic climate. The province Zuid-Holland, containing all dykes except for Oudelansedijk, has 831 mm of precipitation annually and 10.74 degrees average mean surface temperature (average from 1991-2020) (*Climate Change Knowledge Portal - World Bank Group*, 2021). These dykes are: Brielse meeroever, Gorsdijk, Oudelandsedijk, Buitendijk, Westdijk, and Ringdijk, which consist of Ringdijk South, Ringdijk North-West, Ringdijk North-East, and Ringdijk West. All dykes consist of a sandy core and an outer layer of clay. Gorsdijk and Buitendijk are sown with an herb rich seed mixture in 2017 (see appendix A). The other dykes are sown in a conventional way, with grass. Oudelandsedijk also has trees in its vegetation.

2.1.1. Mowing regimes

In this study, different timing of mowing was not investigated, simplifying the experiments set-up. Since 2021 all the dykes are managed using a phased mowing method. Mowing takes places twice a year, in June and September, leaving approximately 25% of the vegetation unmown each round. Every patch of vegetation is mown at least once a year. Gorsdijk, Buitendijk and Westdijk are aimed to be mown in blocks (ecoplan), while the other dykes are mown in a sinusoidal pattern. The mown vegetation is taken away within five days after mowing, to create nutrient-poor conditions.

2.2. Vegetation surveys

This study was part of a research project which is ongoing since 2021. The project has focused on the impacts of phased mowing on the vegetation. Yet, only in dykes sown with an herb rich seed mixture, an increase in diversity was found.

On all dykes, sixteen plots of 1x1 meter were placed on the inner slope in 2021 and marked with a herring. Except for Ringdijk North-West, Ringdijk North-East, and Ringdijk West, on those dykes eight plots were placed as it is one dyke with three orientations. This resulted in 120 plots distributed over all nine dykes. The plots were randomly assigned to different heights to account for the effect of height on the dyke. The vegetation in those plots was surveyed for grass, herb, moss, and bare ground coverage. All species present were identified using Heukels' Flora (Duistermaat, 2020) and field guide Nederlandse Flora (Eggelte, 2021), and coverage per species was estimated. Plots were surveyed in August 2021, spring 2022, August 2023, and in May 2025.

2.3. Transect counts

For the pollinator transects, all dykes were used, except for the Ringdijk North-West and Oudelandsedijk. Ringdijk North-West was excluded to ensure spatial independence. Excluding Ringdijk North-West created a minimal distance of three kilometres instead of one kilometre from dyke to dyke. Oudelandsedijk was excluded because of the presence of trees on the dyke.

The species included in this study were bees (*Anthophila*) and butterflies (*Lepidoptera*). Bees are of undeniable importance as pollinators (Tepedino, 1979); (Klein et al., 2007). While butterflies are charismatic species which have been studied intensively, creating opportunities to compare results. To assess effects of mowing and regrowth on bees and butterflies, transect counts were conducted. Transect counts were performed two weeks prior to mowing, one week after mowing, three weeks after mowing, and seven weeks after mowing. Mowing took place in the third week of June. In total, seven transects were walked per dyke. One before mowing, and two for every round after mowing, one in the mown parts and one in the unmown parts. All rounds after mowing were done in the same transect locations. The order of transects was shuffled every round, to minimalize effects of the diurnal pattern. Transect counts were conducted between 9:00 a.m. and 18:00 p.m., while weather conditions were suitable: dry, > 15°C, and wind speeds not higher than 5 Beaufort.

Within each transect round bees and butterflies were counted. For bee sampling we used standardised transect walks of 150x1 m, divided in three 50 m parts. For the first transect round the length of the dyke was divided in three parts of equal length. The midpoint of each part became the mid of a 50 m transect. For the transect rounds after mowing, the transect selection was more complicated because of the mowing dynamics. In that case, the transect were distributed differently, ensuring a total length of 150 m, mimicking the distribution over the dyke as before mowing as close as possible. A decision chart can be found in appendix – B.

Per 50 m section, five minutes were used, summing up to 15 minutes of transect walking for 150 m (Scheper et al., 2015). Bees that could not be identified immediately were identified later in the laboratory. All plants in the bee transect that flowered at the time of the survey were counted per species to calculate flower cover in the transect. This was done by counting the number of flowers per inflorescence per species, multiplied by the number of inflorescences per individual, and the number of flowering individuals present. Flower cover is used as an indicator for floral resources. For butterfly transect counts we used the standardised butterfly monitoring method (Sevilleja et al., 2019), also known as 'Pollard walks' (Pollard & Yates, 1993). Because of the elongated and narrow configuration of the dykes, we were restricted to butterfly transects of only 3 m wide, instead of the standard 5 m. The butterfly transects were placed on the same spots as bee transects, in a way that the bee transects lie in the exact middle of the butterfly transect (see figure 2). The butterfly transect and bee transect both had a length of 150 m. The flower survey (150x1) was used as a cue for bee and butterfly abundance and diversity. Pollinator species richness was used as a cue for diversity.

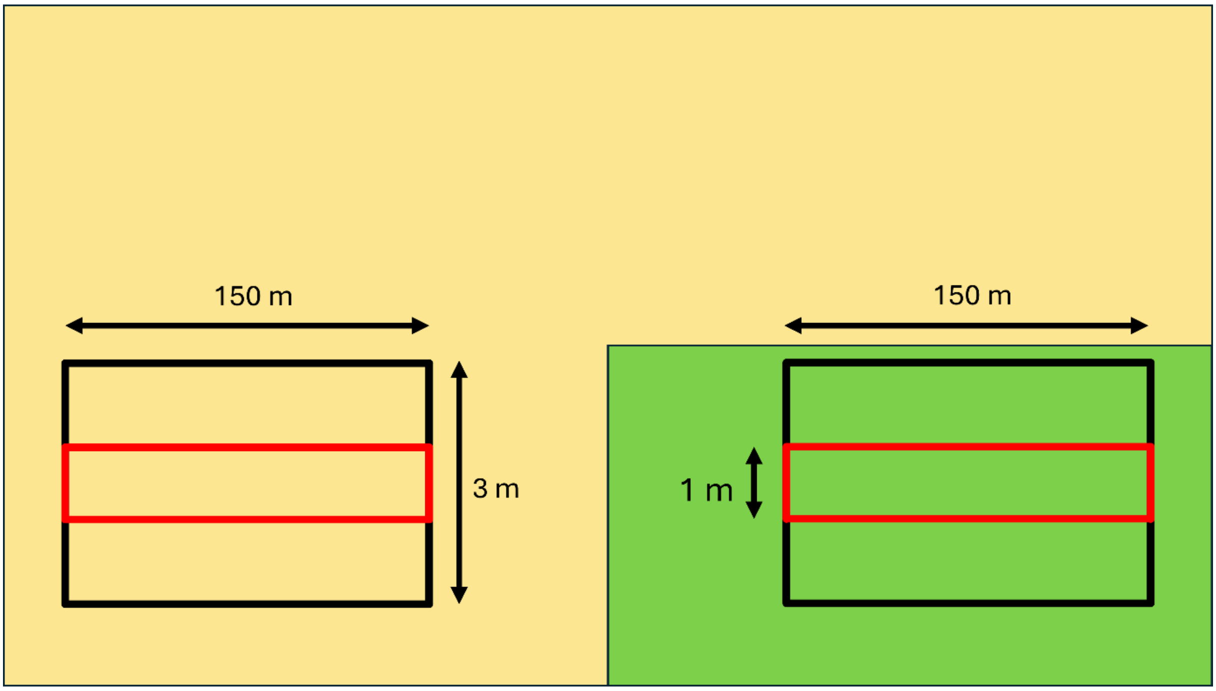

Figure 2. Schematic representation of pollinator transects on dyke. Green colour represents unmown parts while yellow colour represents mown dyke parts. Red rectangle represents bee transect and black rectangle represents butterfly transect.

2.4 Morphological identification of pollinator species

For identification of bee species, a field guide by Falk & Lewington (2017) was used. For identification of butterfly species, a field guid by Richard Lewington (2017) was used. *Bombus terrestis* and closely related species are complicated to distinguish based on morphology. Therefore, *Bombus terrestris complex* was treated as one species.

2.5 Data analysis

Plant species richness for all years and dykes was obtained from vegetation surveys. To test the change in vegetation composition over time, a linear mixed model (LMM) was fitted. The model included year (centred at 2021), sown status (sown and unsown), and their interactions as fixed effects and dyke as random factor with plot nested in dyke. Normality assumption was met, visual checks showed homogeneity of variance when the test was inconclusive (p = 0.059).

Changes in moss-, herb-, and bare soil cover, were analysed using generalized estimating equations (GEE), because model assumptions could not be met. Plot identity was used as the clustering variable to account for repeated measures. Year (centred at 2021), sown status, and their interaction were used as fixed effects and an exchangeable correlation structure was used.

To analyse the changes in grass cover, a LMM was fitted using the nlme package (Pinheiro & Bates, 2023). Year, sown status, and their interaction were used as fixed effects, dyke and plot nested in dyke were used as random effects. Heteroscedasticity across year and sown status combinations was modelled by using a varIdent variance structure, and restricted maximum likelihood (REML) was used for fitting. Normality assumption was doubtful (p = 0.058), but visual inspection of QQ-plot did not show large anomalies. Homogeneity of variance assumption was met.

Flower cover and pollinators were analysed in two parts, because the unbalanced design (absence of round 1 mown) complicated estimating interactions. For rounds 1-2, a generalized linear mixed model (GLMM) with a beta distribution was fitted, using the glmmTMB package (Brooks et al., 2017). For rounds 2-4, flower cover was logit transformed: $log\ x/(1-x)$, and a LMM was fitted using lme4 package (Bates et al., 2015). Models were chosen based on model fit, and ability to cope with zeros. For both models fixed effects were round, sown status, mown status, and their interactions, with dyke as random effect. Both models on flower cover were evaluated using the DHARMa package (Hartig, 2024); The model met all assumptions.

For pollinator abundance, both parts (1-2, 2-4) were analysed using a zero-inflated negative binomial GLMM, utilizing the glmmTMB package. Both models had mown status, round, and their interaction as fixed effects and dyke as random effect. Pollinator species richness in rounds 1-2 was analysed using a LMM with mown status and round as fixed effects and the interaction was left out because no interaction was found. Dyke was omitted as random factor because it had zero variance. For round 2-4, a LMM was fitted with square-root transformed species richness as response, using the lme4 package. The model had mown status, round, and their interaction as fixed effects, and dyke as random effect. Sown status was excluded from the pollinator models because it did not improve model fit. Model selection for all pollinator models was based on model fit and ability to cope with zeros. For all pollinator models, model fit and assumptions were evaluated and confirmed using DHARMa diagnostics.

To analyse the effect of flower cover on pollinators the flower cover data and pollinator data was combined. Pollinator abundance was analysed using a zero inflated negative binomial GLMM, and for pollinator species richness a negative binomial GLMM was fitted. Both models had flower cover and mown status as fixed effects and dyke as random factor. Both models were fit using the glmmTMB package, and model assumptions were checked using the DHARMa package, no deviations were found. Wald z tests were used to assess significance of fixed effects. All post hoc analyses were performed using the emmeans package, and all statistical analyses were done with R version 4.5.0. (Lenth, 2024; *R: The R Project for Statistical Computing, 2025)*.

3. Results

3.1.1 Vegetation composition

Mean plant species richness over four years and all dykes is found to be 9.88 per plot. Lowest average species richness is found on Brielse meeroever with 8.95, highest average species richness is found on Ringdijk South with 11.4. Lowest species richness found per plot is 3, found in three plots, on three different dykes: Ringdijk South, Westdijk, and Brielse meeroever. Highest species richness found per plot is 19, found in a plot on Ringdijk South.

Plant species richness increased with 0.92 species per plot yearly for sown dykes ($t = 6.480$, $p < 0.0001$) and increased with 0.076 species per plot yearly for unsown dykes ($t = 5.091$, $p < 0.0001$), see figure 3. Additionally, species richness was 2.22% higher on unsown dykes ($t = 2.460$, $p = 0.0378$). Dyke ($SD = 0.962$) and plot nested in dyke ($SD = 1.246$) as random effects accounted for additional variation. From 2021 towards 2025, the percentage grass species from all plant species found on the dykes increased; 15.22%, 16.98%, 18.42%, 19.32%. In the same period, the proportion herb species fluctuated, and might decrease; 76.09%, 79.23%, 77.19%, 73.86%.

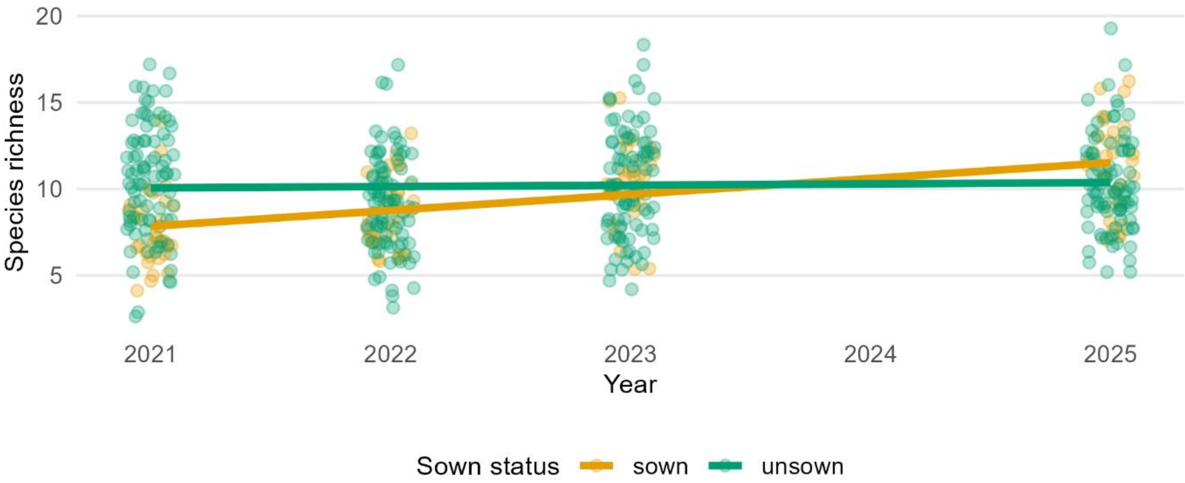

Figure 3. Species richness of vegetation for sown and unsown dykes. Lines in graph show fitted trends from a linear mixed model. Points reflect raw data; points are offset slightly for improved visibility. 2024 is missing because no data was collected that year.

Grass cover increased with 2.63 % yearly for sown dykes and increased with 7.51% yearly for unsown dykes, see figure 4A ($t = 2.11$, $p < 0.05$, interaction: $t = 3.51$, $p < 0.001$). Moreover, grass cover was 25.65% higher on unsown dykes compared to sown dykes ($t = 2.79$, $p < 0.05$). Random factors variances were 10.8 for dyke and 2.31 for plots within dykes, indicating decent variability between locations.

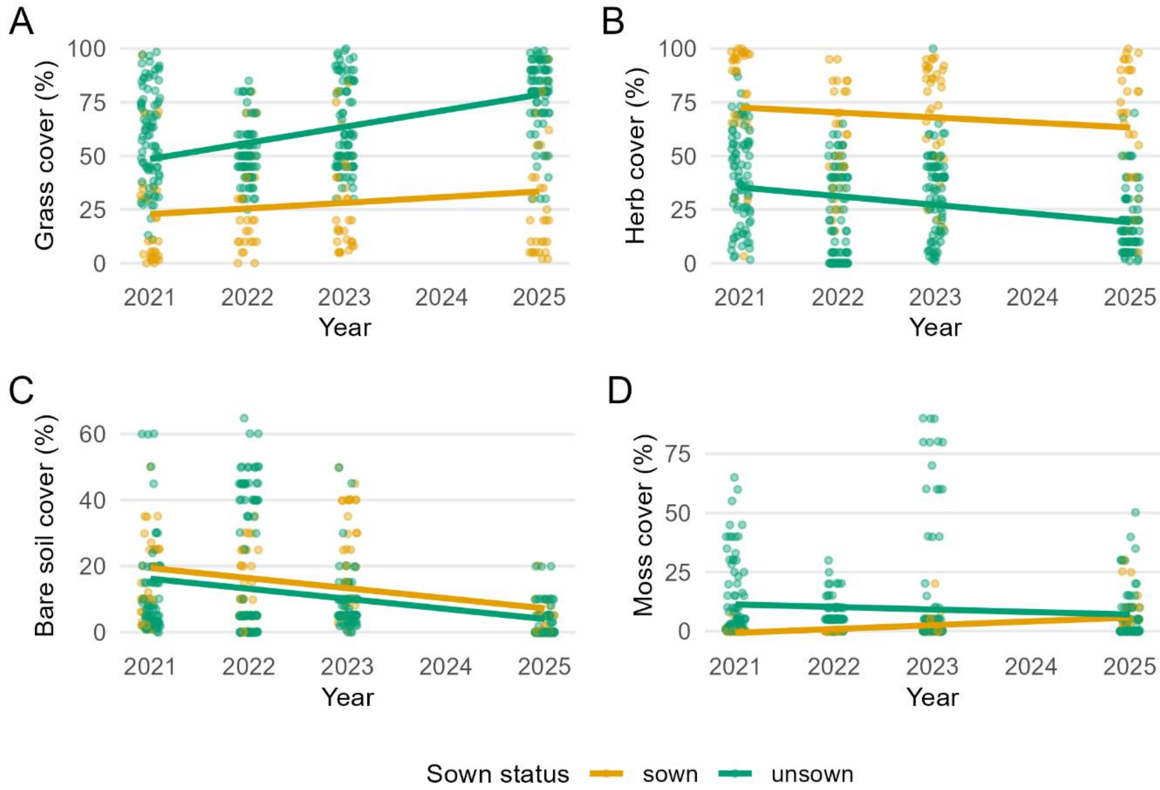

Figure 4. Trends in cover (%) data for moss cover (A), herb cover (B), bare soil cover (C), and grass cover (D). Lines represent fitted trends from models. Points represent raw data and are offset slightly for improved visibility. 2024 is missing because no data was collected that year.

Herb cover decreased on both sown and unsown dykes by 3.60% yearly (Wald's Chi-square 44.2, $p < 0.0001$) and was 40.29% higher on sown dykes (Wald's Chi-square 135.8, $p < 0.0001$, interaction: Wald's Chi-square 1.82, $p = 0.177$), see figure 4B. The correlation within plots was small ($\alpha = 0.122$, SE = 0.050), indicating weak similarity under repeated measurements within plots. Bare soil cover decreased with 3.05% yearly on both sown and unsown dykes (Wald's Chi-square 116.68, $p < 0.0001$, interaction: Wald's Chi-square 0.06, $p = 0.81$) and was 3.22% higher on sown dykes (Wald's Chi-square 5.67, $p = 0.017$), see figure 4C. The correlation within plots was effectively zero ($\alpha = -0.00058$, SE = 0.031), indicating no similarity under repeated measurements within plots. Moss cover increased with 1.62% yearly on sown dykes and decreased with 1.07% yearly on unsown dykes, see figure 4A (Wald's Chi-square 24.2, $p < 0.0001$, interaction: Wald's Chi-square 32.7, $p < 0.0001$). Moss cover was 12.02% higher on unsown dykes (Wald's Chi-square 73.32, $p < 0.0001$). The correlation within plots was moderate ($\alpha = 0.296$, SE = 0.050), indicating that repeated measurements within plots were positively associated.

3.1.2 Flower cover

The five species with highest flower cover for sown dykes were: *Galium mollugo*, *Galium verum*, *Daucus carota*, *Centaurea jacea*, and *Senecio jacobea*. For unsown dykes: *Daucus carota*, *Foeniculum vulgare*, *Senecio jacobea*, *Picris hieracioides*, and *Heracleum sphondylium* were the five species with highest flower cover.

On sown dykes, flower cover decreases with 47.6% (back-transformed predicted proportion) from round one to two if no mowing took place ($p < 0.001$). However, if mowing took place, almost all flowers were gone (-99.7%, $p < 0.0001$). Nonetheless, on unsown dykes, flower cover is estimated to increase by 166.0% when mowing did not take place, although results only suggest the difference ($p = 0.056$). But a drastic decrease (-86.5%) when mowing took place ($p < 0.001$).

Flower cover from rounds 2-4 depends on round (Chisq 32.43, $p < 0.0001$), on mowing (Chisq 23.70, $p < 0.0001$), and on sown status (Chisq = 17.78, $p < 0.0001$). The effect of mowing on flower cover depends on round (Chisq 22.44, $p < 0.0001$), and round and sown status tend to interact (Chisq 5.93, $p = 0.051$) as well as mowing and sown status (Chisq 3.12, $p = 0.077$). Flower cover is found to be higher on sown dykes than on unsown dykes in all cases, except for round three. Differences varied from 0.019% higher (mown) to 1.91% higher (unmown) in round two, and 3.79% higher (mown) to a suggested ($p = 0.086$) difference of 0.61% (unmown) in round four (percentages in this subsection represent back-transformed estimated marginal means). Thus, a bigger difference is observed between sown and unsown dykes in flower cover in round four.

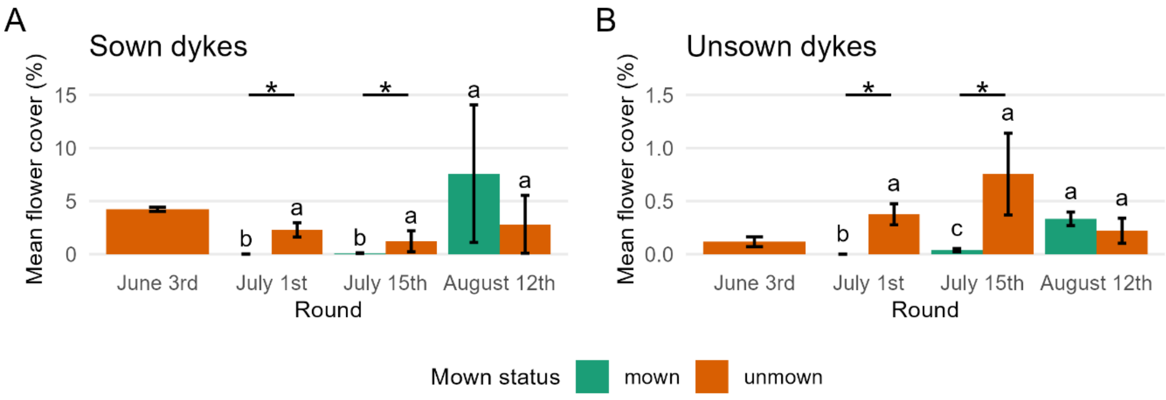

Figure 5. Mean flower cover (%) on sown (A) and unsown (B) dykes over four transect rounds. Only results of model on round 2-4 are shown. Different letters indicate significance within mown status, between rounds. Asterisks indicate significance within round, between mown/unmown. Error bars represent standard errors. Pay attention to differently scaled Y-axis. Time interval between rounds is not equal.

Within sown dykes, on mown dyke parts, flower cover increased 4.01% from round three to four. Within sown dykes, on unmown dyke parts, flower cover is not found to differ significantly (figure 5A). Within unsown dykes, on mown dyke parts, flower cover increased by 0.02% from round two to three and increased by 0.29% from round three to four. Within unsown dykes, on unmown dyke parts, flower cover is not found to differ significantly (figure 5B).

Within sown and unsown dykes, flower cover was higher in unmown dyke parts compared to mown dyke parts in round two and three. Test results suggest that flower cover was 3.37 higher in mown dyke parts in round four ($p = 0.084$) on sown dykes and test results weakly indicate that flower cover was 0.18% higher in mown dyke parts in round four on unsown dykes as well ($p = 0.16$).

3.2 Pollinator abundance and species richness

Within the same four rounds, pollinators were counted and identified, resulting in a total of 386 pollinators and 28 species. 249 pollinators were found in sown dykes, of which 201 on Gorsdijk, and 137 were found on unsown dykes. 15 unique species were found on sown dykes, and 24 unique species were found on unsown dykes. Total bee abundance was 166, and 14 bee species were observed. Total butterfly abundance was 217, and 14 butterfly species were observed. Most abundant butterfly species found were: *Maniola jurtina* (116), and *Pieris rapae* (30), *Pyronia tithonus* (21), *Polyommatus icarus* (21), and *Vanessa cardui* (5). Most abundant bee species were: *Bombus terrestris* c. (50), and *Apis mellifera* (46), *Bombus pascuorum* (29), *Bombus lapidarius* (22), and *Bombus campestris* (5), see full species list in appendix – C. Bar chart of abundance and species richness per round and mown status for bees and pollinators separately can be found in appendix – D. Mean pollinator abundance per transect (150 m2) per round was 16.13 on sown dykes vs 3.85 on unsown dykes. Mean pollinator species richness per transect per round was 3.81 on sown dykes and 2.30 on unsown dykes.

Pollinator abundance increased enormously from round one (3.76) to round two (17.31), in unmown dyke parts ($p < 0.001$). From round one to round two in mown dyke parts, a decrease was found (0.70; $p = 0.013$). The effect of mowing depended on round (interaction: Chisq = 44.47, $p < 0.0001$), and pollinator abundance depended on mowing (Chisq 10.81, $p = 0.001$), but not on round (Chisq 3.47, $p = 0.17$). Mown dyke parts had less pollinators than unmown dyke parts in round two and three, in round four however, the effect reversed, see figure 6A. In mown dyke parts, abundance increased over time, while abundance decreased over time in unmown dyke parts, see figure 6A. In mown dyke parts, round two is found to be lower than round three and four, estimated abundances for round two, three, and four were 0.54, 2.36, and 5.16. In unmown dyke parts a decrease is found from round two to three, and from round three to four, estimated abundances for rounds two, three, and four were: 14.20, 8.76, and 2.68, respectively.

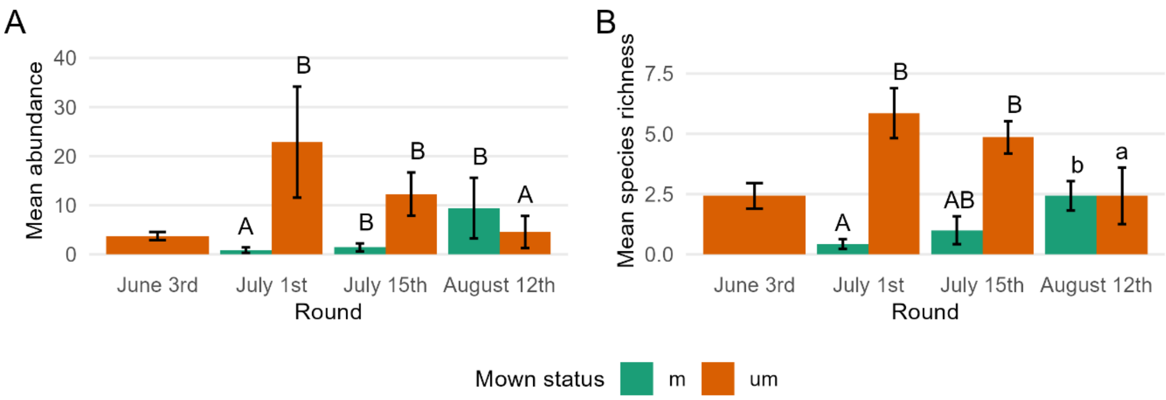

Figure 6. Mean pollinator abundance (A) and mean pollinator species richness (B) over four transect rounds. Only results of models on round 2-4 are shown to prevent confusion. Capital letters indicate significant differences within round, between mown status. Different letters indicate significant differences within mown status, between rounds. Error bars represent standard errors. Pay attention to differently scaled Y-axis. Time interval between rounds is not equal.

Pollinator species richness increased from 2.43 in round one to 5.86 in round two unmown ($p = 0.01$). From round one towards round two mown 0.43, the decrease was not found to be significant ($p = 0.20$). For pollinator species richness, the effect of mowing depended on round (Chisq = 23.73, $p < 0.0001$), and species richness depended on mowing (Chisq 28.93, $p < 0.0001$), but not on round (Chisq 0.028, $p = 0.99$), as it does for pollinator abundance. Pollinator species richness in mown dyke parts increased over time, while it decreased over time in unmown dyke parts, see figure 6B. In mown dyke parts, species richness in round four is found to be higher than round two (-2.08) and suggested to be higher than round three ($\beta = -1.86 \pm 0.804$ SE, $t = -2.315$, $p = 0.067$). While in unmown dyke parts round four was found to be 4.08 lower than round two, and 3.21 lower than round three. In round four the species richness of unmown and mown transects end up being not significantly different.

3.3 Effect of regrowth on pollinator abundance and diversity

Flower cover had a positive relation with pollinator abundance ($\beta = 1.26 \pm 0.120$ SE, Wald $z = 2.44$, $p < 0.05$), see figure 7A. With every increase of 1% in flower cover, pollinator abundance increased by 26%. Mowing also influenced pollinator abundance, as unmown plots were found to have an estimated 4 times higher pollinator abundance ($\beta = 4.21 \pm 1.45$ SE, Wald $z = 4.18$, $p < 0.0001$).

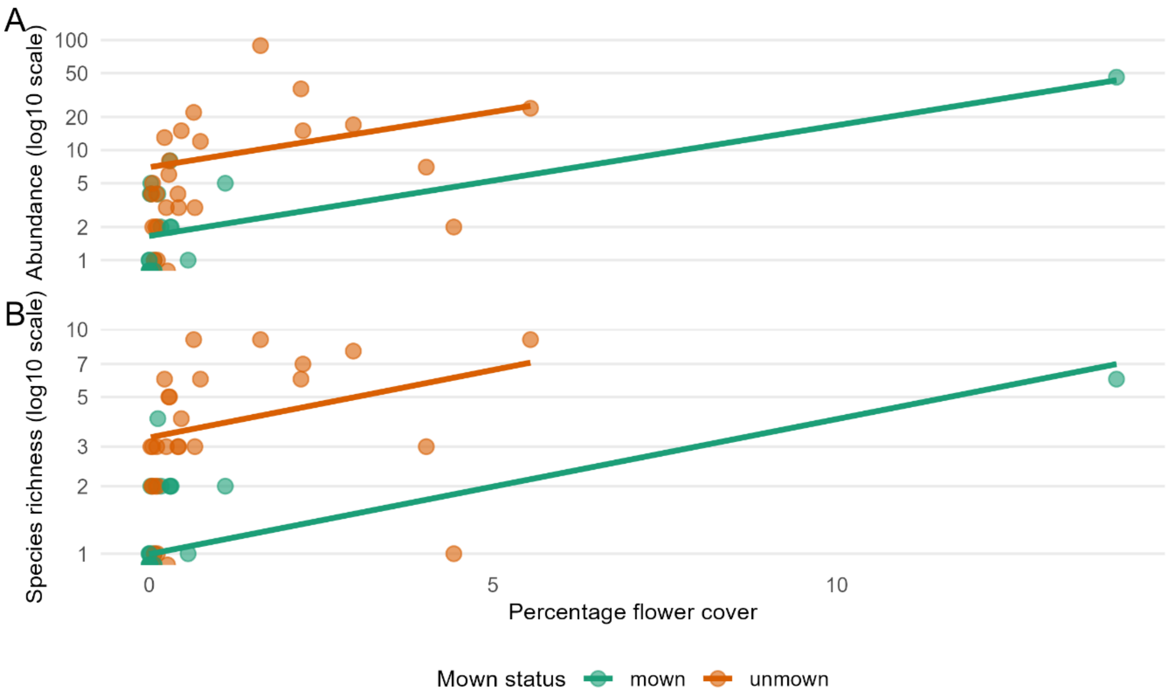

Figure 7. Predicted lines of (A) pollinator abundance (log10 scale) vs flower cover (%) and (B) pollinator species richness (log10 scale) vs flower cover (%). Points represent raw data points.

Flower cover had a positive relation with pollinator species richness ($\beta = 1.15 \pm 0.042$ SE, Wald z = 3.79, $p < 0.001$), see figure 7B. With every increase of 1% in flower cover, pollinator species richness increased by 15%. Unmown dyke parts were found to have higher pollinator species richness than mown dyke parts ($\beta = 3.31 \pm 0.824$ SE, Wald z = 4.81, $p < 0.00001$).

4. Discussion

After the introduction of phased mowing from 2021 up to 2025, plant species richness increased, as did grass cover. However, herb cover decreased. In the season of 2025, phased mowing clearly impacted flower cover, with a striking increase in mown parts of the dykes late in the season. Pollinators were strongly impacted by phased mowing in 2025, both in numbers and in species richness. Lastly, flower cover had a strong effect on pollinators, in the mown dyke parts showing the positive effect of regrowth. In the last round, more pollinators were observed in mown dyke parts than in unmown dyke parts.

4.1.1 Vegetation composition

As expected, plant species richness on the dykes increased over the years. Unexpectedly, grass cover increased and herb cover and bare soil cover decreases. Both might decrease as a result from increasing grass cover. The increase in species richness is not in correspondence with a study of Parmentier et al. (2024), where a more complicated sinusoidal phased mowing experiment increased floral diversity and increased number of unique plant species blooming, compared to phased mowing in straight lines. Conflicting with our results, it suggests that the proportion of grass species increases, instead of herb species. However, low mowing intensity is found to increase plant species richness in agricultural grasslands in Germany (Schulz et al., 2024), confirming the results. However, mowing should take place because mowing increases plant diversity compared to no mowing (Smith et al., 2018; Sundberg, 2012). Repeated physical disturbance, like mowing, could be a helpful tool in reducing dominant species, creating opportunities for other species (Mälson et al., 2010). In our data, sown dykes start with fewer species than unsown dykes. Because before phased mowing started in 2021, few herb species dominated the sown dykes, and management was not performed regularly. When the management started using the phased mowing method, species in the seed bank could easily germinate when conditions were opportune. Higher herb cover compared to grass cover create better conditions for new species, as herbs do not make as impenetrable swards as grassed do (Kiss et al., 2021). This paves the way for new species to colonize the dyke, resulting in higher increase of species richness.

Grass cover appears to contradict findings from Antonsen & Olsson (2005), where grass cover is found to decrease under full mowing twice a year. Although, the strongly increasing grass cover here could be caused by the nutrient-rich clay soil where the dykes consist of. Additionally, increased nitrogen deposition could worsen this (Lu et al., 2021), which is relevant for our research as The Netherlands are known to have high nitrogen deposition compared to other European countries (W. de Vries et al., 2023).

The reduced herb cover found under a phased mowing regime is partly in correspondence with research of Smith et al. (2018). They did not find herb cover to increase with mowing compared to unmown control plots. The results could have been in line with Hoekstra et al. (2023) and Antonsen & Olsson (2005), where herb cover was found to benefit from extensive mowing. Nevertheless, we found a contradicting trend. If a more intensive treatment was present, a positive effect might have been observed. Although the bare soil cover is found to decrease, a study of Moinardeau et al. (2019) did not find differences between presence or absence of mowing over a period of three years. Here, the decrease in bare soil cover is expected to be caused by an increasing grass cover. This is unfortune, because bare soil cover positively affects bees (Tsiolis et al., 2022). Mosses could have decreased in unsown dykes because of extremely hot and quite dry summers. Mosses might also be replaced by grasses. On sown dykes, mosses might increase because there is still more bare soil to colonise and more herbs which do not make as thick and impenetrable swards as grasses do (Kiss et al., 2021). Bryophytes, including mosses, were found to be maintained by mowing compared to a lack of mowing, and were found to be more stable under mowing than grasses (Ross et al., 2019). This could confirm the results of this study, as no strong effects were observed. In calcareous grassland, moss cover is even found to increase by mowing, although at the expense of other species (Vanderpoorten et al., 2004).

Concluding, in terms of plant species richness, dykes are getting more diverse. Although, this increase is likely due to grass species. Additionally, grass cover is strongly increasing at the cost of herb cover and bare soil cover. This might imply a future continuation of the decrease in herb biodiversity.

4.1.2 Flower cover

Flower cover was higher on sown dykes, however not in all round and mowing combinations. As expected, flower cover was almost absent in the first round after mowing and flower cover in mown plots increased later in the season. In line with the hypothesis, in round two and three unmown dyke parts have higher flower cover than mown dyke parts and results suggest that on sown dykes in round four mown dyke parts had higher flower cover. Unexpectedly, in round two flower cover on sown dykes decreased in unmown plots compared to round one. Furthermore, flower cover on unsown dykes increased compared to round one.

The increase in flower cover from round one to two (in unmown plots) on unsown dykes is in line with the June gap phenomenon (Timberlake et al., 2019). Higher flower cover in round two might also be caused by the extremely dry and warm spring, because water limitation can delay flowering (KNMI - Zachte, Zeer Droge En Zeer Zonnige Lente, 2025; Gallagher & Campbell, 2021). However, another study found that the maximum flower cover occurs in end of May, with minimum flower cover in mid-June (Bishop et al., 2024). This is in line with our drop in flower cover (in unmown plots) on sown dykes, from round one to two. This opposition can be explained by the actual species where the flower cover is determined by. *Galium mollugo* and *Galium verum* are two of the species contributing most to the flower cover of sown dykes. *Galium mollugo* an *Galium verum* have early flowering times, explaining the high flower cover on sown dykes in the first round. *Foeniculum vulgare* and *Picris* *hieracioides* are among the species contributing most to the flower cover of unsown dykes. They have later flowering times, explaining increasing flower cover in the first rounds, together with the absence of the *Galium* species (Duistermaat, 2020).

Flower cover seems to swiftly increase in mown dyke parts. Regrowth is triggered by the mechanical damage, and the quick rate of regrowing might be caused by decreased light competition (Lennartsson & Oostermeijer, 2001). An increase in flower cover later in the season agrees with Johansen et al. (2019) and Jantunen et al. (2007). However, Johansen et al. (2019) even found that mown areas had more floral resources than unmown areas. A striking difference is that the decrease in floral resources in unmown areas, as Johansen et al. (2019) found is not observed in this study. This decrease in floral resources naturally occurs in meadows during August, when most species finish their reproduction (Dahlström et al., 2008). The results suggest that flower cover in the late summer can be improved by phased mowing, but do not yet show so. This is possibly caused by high variation and timing of fourth transect round. Thus, our results are partly in agreement with these studies.

Finally, phased mowing has a major impact on flower cover, removing flower cover completely in mown dyke parts early in the season, causing a regrowing flower cover later in the season, up to the level of unmown dyke parts and possibly exceeding that level.

4.2 Pollinator abundance and species richness

Regarding pollinators the hypothesis is partly accepted: after mowing decrease in pollinator abundance was observed. However, for pollinator species richness no significant decrease was found after mowing. Another disagreement with the hypothesis is the substantial increase of pollinators in unmown plots in round two. Moreover, results are consistent with Valtonen et al. (2006), where a decline in butterfly abundance was observed, because of mowing. Mowing decreases nectar, and breaks down the vegetation structure, which could lead to a depletion of host plants suitable for egg deposition (Valtonen et al., 2006).

After mowing, the pollinators possibly migrated from mown to unmown dyke parts, but this study did not investigate the extent of migration. However, round one is visibly lower than the average of round two, indicating that migration is not the only mechanism at work. The opposite result would have been more logical because mowing is expected to kill some pollinators (Berger et al., 2024). Most important mechanisms explaining the low amounts of pollinators in round one are the ‘June gap’, and a dip in floral resources. The June gap is a phenomenon describing the period in which spring butterflies are gone, and summer butterflies are not present yet, or slowly appearing (Halsch et al., 2024; Fox, 2025). In addition, the flower resources naturally dip in June as well (Timberlake et al., 2019), when, the first transect round was conducted. Another transect round three weeks prior to the first could give valuable insights into these dynamics.

The lower abundance and species richness of pollinators in mown dyke parts compared to unmown dyke parts directly after mowing, as well as higher pollinator abundance, but not species richness in mown dyke parts later in the season are confirmed by Biella et al. (2025). They reported comparable results but for a wider range of insects. The recovery of pollinator composition after mowing is also consistent with a study of Berger et al. (2024); where a gradual recovery of arthropods was found after mowing.

Especially abundance is first slowly recovering and increasing rapidly in the end of the season. Species richness appears to gradually recover in mown dyke parts. The different reaction between abundance and species richness is minor. Clear different trends might be lacking due to the small dataset and low numbers for species richness. 14 bee species were found, a small number, compared to the 331 species in The Netherlands (*Basisrapport Voor de Rode Lijst Bijen*, 2018). Also 14 butterfly species were found, a relatively bigger share of the total 53 species in The Netherlands (*De Vlinderstichting | Dagvlinder of Nachtvlinder*, 2025). Additionally, bees and butterflies could be affected differently by mowing, however data exploration does not show clear patterns, see appendix - D. A study of J. P. R. de Vries et al. (2026) did find difference between abundance and species richness as well as differences between arthropod orders under grassland productivity. Therefore, further investigation of this might yield valuable insights.

Abundance in round four even gets overtaken by abundance of mown dyke parts, although species richness was not found to be higher for mown dyke parts in round four. Flower cover is not explaining the decreasing trend in unmown dyke parts, as flower cover is not found to decrease in unmown dyke parts (see figure 5). The increase of pollinators in mown dyke parts in combination with a decrease of pollinators in unmown dyke parts, could imply a (back) migration from unmown dyke parts to the freshly vegetated mown dyke parts.

Thus, mowing heavily impacts pollinators by vegetation removal. Pollinators in mown plots increase later in the season, while pollinators in unmown plots decrease later in the season. Pollinator numbers in mown plots overtake the pollinator numbers in unmown plots in round four.

4.3 Effect of regrowth on pollinator abundance and diversity

In line with the expectations, pollinators gradually recovered as a reaction to the increasing flower cover. Pollinator abundance and species richness both follow the flower cover closely. As a result, a positive effect of flower cover on both pollinator abundance and species richness was found, albeit the effect was stronger for abundance compared to species richness. Ecologically, this means that more food results in more pollinators present and more species of pollinators present. The positive effect of flower cover on species richness is in correspondence with Segre et al. (2023). Although, they did only find a positive relation between flower cover and bee richness but not for butterfly richness. Although the pollinators species richness might be impacted more by flower species richness than the numbers of pollinators (Segre et al., 2023). Flower cover is found to be predicting bumblebee abundance stronger than solitary bees (Bishop et al., 2024). Unfortunately, in this research, pollinator counts were low, and almost all bees found were social bees, making such a distinction impossible. Either with or without a mowing treatment, pollinator composition is strongly driven by floral resources, corresponding with previous research (Cole et al., 2015; Scheper et al., 2013).

Flower cover graphs suggest that flower cover later in the season is higher because of mowing, causing an extension of the flowering season and a possible positive effect on pollinators. Pollinator abundance is already higher in round four, confirming the hypothesis, see figure 4.A. With the suggested extension of the flowering season, pollinator species richness in mown dyke parts is likely to also overtake unmown dyke parts. This creates a positive effect of regrowth on pollinator community in late summer by extending the flowering season, which reveals the potential of phased mowing to be advantageous to pollinators late in the season. Noordijk et al. (2009) found that floral resources caused by re-flowering (due to mowing) were important to pollinators late in the season confirming this potential.

In conclusion, flower cover and pollinators are positively related. Regrowth strongly attracts pollinators later in the season. In the end of the flowering season, more pollinators are present in regrown vegetation than in unmown vegetation. Therefore, regrowth of mown dyke parts positively impacts both pollinator abundance and species richness.

4.4 Strengths & limitations

Studies on regrowth after mowing combined with pollinators are rare, emphasizing the importance of this work. River dykes as potential pollinator habitat is a promising topic due to its abundance, and extensive management, underlining the importance of performed investigations. A long-term dataset is essential to account for yearly variations and can give valuable insight to future vegetation developments under phased mowing.

First, the observational character of the study had some drawbacks. Variation between dykes was high. Especially Gorsdijk had extremely high values for flower cover and pollinator data, see appendix – E for a flower cover box plot per dyke. To account for this, dyke is used as random factor. In addition, dykes differed in size and figuration. At Buitendijk for example, is a particularly small dyke, almost all unmown dyke parts were used for transects. For dykes larger in size, however, a smaller proportion of the unmown (and mown) dyke parts were used for transects. Another difference that arises from this, was the distance between unmown dyke parts and therewith between transects. As pollinators rarely travel large distances, especially bees, the distance could impact results. Zurbuchen et al. (2010) showed that 50 % of females of three solitary bee species did not forage further than 100-300 m. Incorporating patch distance and connectivity between patches in analysis, could yield insight into whether distances between unmown refuges impact pollinators. Fragmentation effects in an elongated habitat like dykes could impair the corridor function they possibly have.

The observational character of the study caused that the timing of mowing and pick-up was not in our control. Mowing was supposed to happen in the third week of June; however, it took longer for all the dykes to be mown. The main problem was that not all the mown vegetation got removed in the amount of time expected. On Buitendijk and Westdijk, the vegetation was not even (completely) removed. Causing the second transect round to take longer. Because the regrowth started after some time without the vegetation being removed, transects were conducted. Leaving the cut material is undesirable, since removal can promote plant diversity (Andraczek et al., 2023). The round subsequent to mowing did for all dykes happen at approximately the same number of days after vegetation pick-up (if applicable). But still, there is variation in time. However, no visible pattern in regrowth because of this variation was observed between dykes. Therefore, impact on results is expected to be minor. Because of variation in time intervals, round is treated as a factor in the models. Due to this variation, the mortality caused by mowing is complicated to extract. In an experimental setting, transects could be walked directly before mowing and after mowing and vegetation removal.

Another drawback complicating extracting mortality of mowing is the June gap phenomenon. A dip in flower resources in June complicates extracting the pollinator mortality due to mowing (Timberlake et al., 2019). Because flower resources naturally dip in June, when the first transect round was conducted. Moreover, adult butterflies are mainly present during April-June and July-September (Halsch et al., 2024). Between those two periods, a dip in butterflies occurs, also called the June-gap (Fox, 2025). This complicates the measurement of mortality of mowing additionally. The effect of the June dip impacted the results of the first transect round although different effects are observed between sown and unsown dykes.

Furthermore, due to time restrictions, flower cover and pollinators were only investigated for one season. Continuation for multiple seasons may yield valuable insights concerning the multiple year effects, as for instance flower abundance is found to be correlated with butterfly abundance and richness in the next year (Segre et al., 2023). This may provide insights that clarify fluctuations in pollinator data. More transect rounds would give a higher resolution of the flower cover and pollinator dynamics. Three-week intervals would be preferable, smaller interval if time is not restraining.

Lastly, visiting the same transects every round minimizes variation. However, repeated visiting of the same transects might impact the flower cover by trampling. Especially during the vegetation surveys, marks were left due to trampling. Some trampled vegetation from the vegetation survey was still visible in first transect rounds. Although, those effects are not expected to be substantial.

4.5 Recommendations

Floral resource and pollinator dynamics are not completely understood, especially late in the flowering season. Therefore, recommendations mainly concern investigating these dynamics in late summer. Firstly, we would recommend researching the flower cover in August and September under a phased mowing regime, as regrowing dyke parts are expected to overtake unmown patches soon after our last transect round. If expectations are proven, phased mowing in early summer would be underlined and management could be adapted matching pollinators needs. Secondly, with data collected during this study, flower species richness in regrowing vegetation could be analysed. Impacts of flower species richness on pollinators could be evaluated as well, either pollinator abundance or species richness could be considered. Distinguishing the impact of floral resources on bees and butterflies could also yield valuable insights. Finally, the investigation of other pollinators and insect taxa is urgent and should not be overlooked. Only adapting management towards bees and butterflies could impair other taxa, because phenology and life cycles differ seriously between taxa. Conserving bees and pollinators should not go at the cost of losing biodiversity of other insects, keeping the goal of increasing biodiversity in mind.

4.6 Management implications

Mowing should be performed in early summer, to allow for mown vegetation to regrow. Thereby a decent flower cover in late summer and an herb layer for winter can be established. Management should include making sure that mown vegetation gets picked up, enabling vegetation to start regrowing swiftly.

Furthermore, results show the importance of partial mowing to extend flower cover and enhance pollinators in late summer. The partial mowing is crucial to keep refuges throughout summer and winter (Wintergerst et al., 2021). Results once again show the importance of flower cover for pollinators confirming previous research. Together with the finding that sown dykes can sustain enormously high numbers of pollinators, this emphasises the undeniable importance of flower rich grasslands. As the first and most important goal of dykes is ensuring safety, it is highly important to keep in mind that herb rich river dykes are as safe as conventional grass dykes (Rooijen et al., 2024). Consequently, future management should incorporate a focus on flower rich grasslands. Phased mowing and sowing native flower mixtures could be concrete and feasible management implications to reach this goal. By implementing these tools, landowners and decision-makers could contribute to conserving and increasing biodiversity. Increased biodiversity delivers benefits essential for our livelihoods, thus making it relevant for all of us.

4.7 Conclusion

To conclude, the impact of phased mowing and regrowth on vegetation- and pollinator composition is vast. The impact is embodied by the flower cover and thereby affecting the pollinators. Mowing has a negative impact on flower cover and pollinators directly after mowing, and a suggested positive impact on flower cover and pollinators later in the season. Regrowth of mown dyke parts strongly attracts pollinators. By implementing a phased mowing regime, the flowering season could be extended. Subsequently, pollinators could benefit from floral resources and nesting habitat throughout the year. Floral resources could function as an indicator for pollinator community (Segre et al., 2023). Thereby, this management tool could contribute to halt insect biodiversity loss and maintain biodiversity-based benefits necessary to sustain our livelihoods.

Acknowledgements

First, I would like to thank my supervisor José van Paassen for the incredible amount of help, valuable insights, and guidance throughout the process. Secondly, I want to thank Marije Smits for collaboration during a substantial part of the vegetation surveys. Next, I want to thank Remco Ploeg for instructions on the bee transects walking and flower counting and Reinier de Vries for help with developing the experimental set-up, both from the chair group Plant Ecology and Nature conservation (PEN). In addition, thanks go out to Femke van Beersum and Henk Martens (PEN) for providing field and laboratory materials. Further, I want to thank Ronald Ykema, Rene Snip, and Rachid Abraimi from waterboard Hollandse Delta for collaboration and the information about the dykes and their management. Lastly, I want to thank Jeroen Smit for creating the illustration for the cover page.

AI acknowledgement

During the preparation of this work the author used ChatGPT5 (accessible via chatgpt.com) in order to generate R codes or fix errors in R. After using this tool, the author reviewed and edited the content as needed and takes full responsibility for the content of the report.

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Appendices

Appendix - A

Herbs mixture sown in Buitendijk and Gorsdijk

Achillea millefolium, Agrimonia eupatoria, Alopecursus pratensis, Anthriscus sylvestris, Barbarea vulgaris, Campanula rotundifolia, Centaurea cyanus, Centaurea jacea, Chrisanthemum leucanthemum, Cichorium intybus, Crepis biennis, Daucus carota, Galium mollugo, Gallium verum, Knautia arvensis, Lathyrus pratensis, Leucanthemum vulgare, Lotus corniculatus, Malva moschata, Origanum vulgare, Pastinaca sativa, Pimpinella major, Ranunculus repens, Reseda lutea, Saponaria officinalis, Silene pratensis, Tanacetum vulgare, Tragopogon pratensis, Trifolium pratensis, Verbascum nigrum.

Appendix - B

Transect rounds 2-4 (And for dykes which have already been mown for *Galium mollugo* dominance before first round):

1. Is there 150x3 m unmown?
- Yes → question 2
- No→ use all the unmown length (minimal 3 m of width)
2. Is it possible to walk three transects of 50x3 m (unmown and mown)?
- Yes → question 3
- No → Try to approach the three transects of 50 m as good as possible (e.g. 50, 58 and 42 m)
3. Is it possible to be 7 m from the top of the dyke on average?
- Yes → Distribute the transect parts as good as possible over the length of the dyke (a transect in every third). And the height distributed to an average of 7 m from the top of the dyke
- No → Try to approach the average of 7 m from the top of the dyke as good as possible

Appendix – C

Buitendijk:
Bombus terrestris complex, Bombus pascuorum, Bombus campestris, Bombus lapidarius, Apis mellifera, Maniola jurtina, Pyronia tithonus, Pararge aergeria, Vanessa cardui, Aglais io, Polyommatus icarus, Macroglossum stellatarum, Vanessa atalanta, Aricia agestis
Brielse meeroever:
Bombus lapidarius, Andrena bimaculata, Andrena flavipes, Sphecode gibbus, Maniola jurtina, Pyronia tithonus, Coenonympha pamphilus, Aglais io, Polyommatus icarus, Pieris rapae
Gorsdijk:
Bombus terrestris complex, Bombus pascuorum, Bombus campestris, Bombus lapidarius, Apis mellifera, Maniola jurtina, Pyronia tithonus, Aglais io, Polyommatus icarus, Pieris rapae, Macroglossum stellatarum, Papilio machaon, Aricia agestis
Ringdijk North-East:
Bombus terrestris complex, Bombus pascuorum, Bombus lucorum, Apis mellifera, Maniola jurtina, Pararge aergeria, Pieris rapae
Ringdijk South:
Bombus terrestris complex, Bombus ruderarius, Bombus pascuorum, Bombus hortorum, Bombus lapidarius, Apis mellifera, Pararge aergeria, Polyommatus icarus, Pieris rapae, Aricia agestis, Lycaena phlaeas
Ringdijk West:
Bombus terrestris complex, Bombus lapidarius, Apis mellifera, Polyommatus icarus, Pieris rapae, Lycaena phlaeas
Westdijk:
Bombus terrestris complex, Bombus pascuorum, Bombus campestris, Bombus lapidarius, Andrena nitidiuscula, Andrena ventralis, Andrena rosae, Maniola jurtina, Pyronia tithonus, Polyommatus icarus, Pieris rapae, Thymelicus lineola

Appendix – D

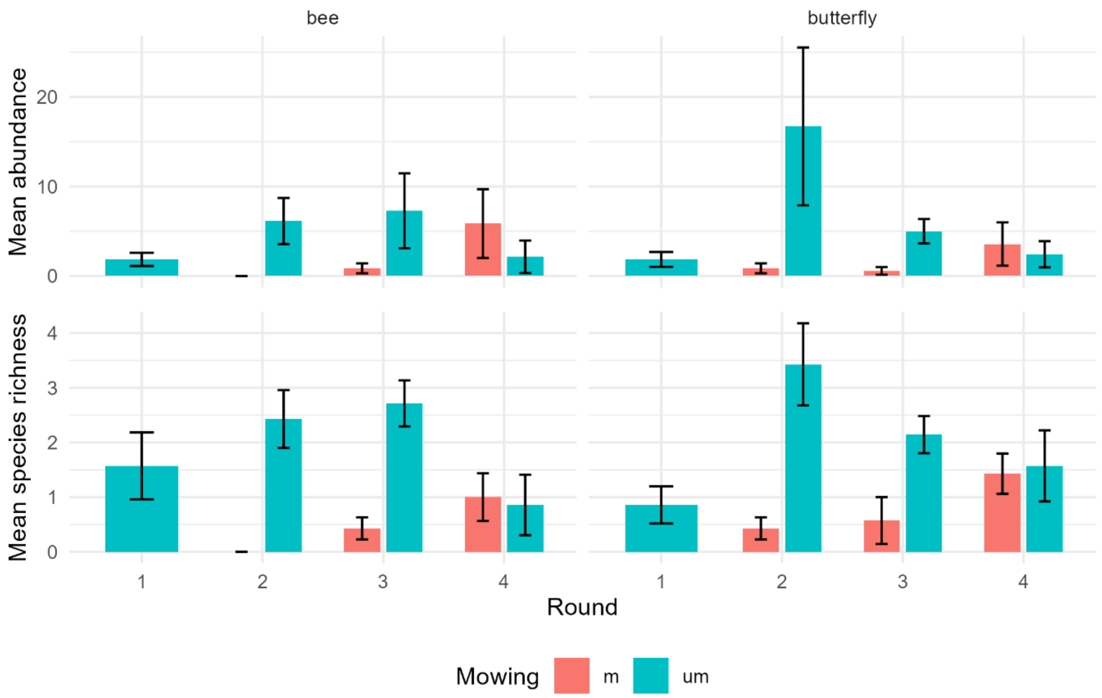

__Figure 8.__ Mean abundance and mean species richness for bees and butterflies over all rounds, separated by mown status. Error bars represent standard errors.

Appendix – E

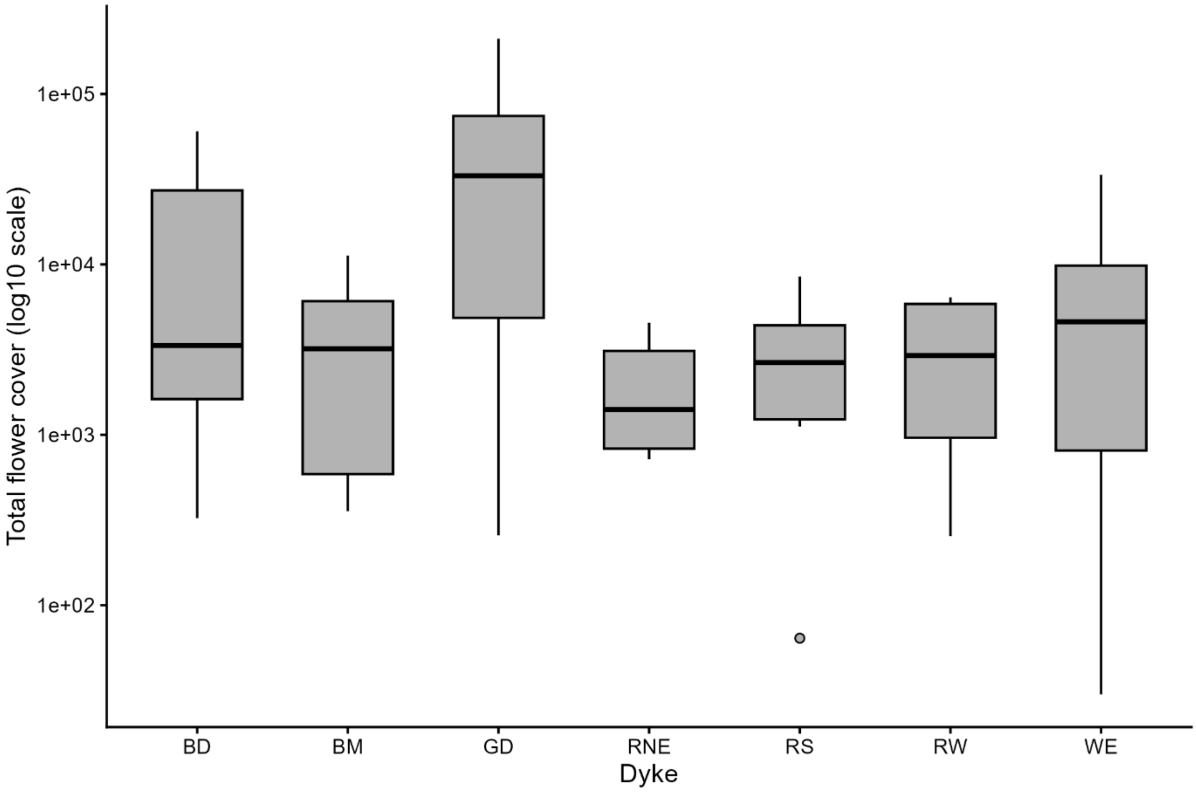

Figure 9. *Total flower cover of all rounds combined per dyke. Pay attention to log10 scale on Y-axis*