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RESEARCH ARTICLE

Dutch landscapes have lost insect-pollinated plants over the past 87 years

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Abstract

1. The interruption of plant-pollinator interactions may threaten global plant diversity, food security and ecosystem stability. Recent reports of strong declines in both insects and plants point to insect decline as a driver of plant decline. However, it is still unknown whether these trends are related as plants often produce seeds without the need for insect pollinators, and to what extent insect-pollinated plants have declined in relation to plants not pollinated by insects.

2. In this study, we hypothesise that natural plant communities have shifted away from insect-pollination. We combined 365,768 vegetation plots from 1930 to 2017 in the Netherlands and plant traits to assess the changes in occurrences of plants pollinated by different modes. Furthermore, we included key drivers in plant decline—specifically nitrogen, moisture and habitat types—as interaction factors to explore the persistence of the observed changes under different environmental conditions.

3. The proportion of insect-pollinated plants has declined while that of wind-pollinated plants has increased over the last 87 years. This proportional change reflects an absolute decrease in the number of insect-pollinated species and an increase in the number of wind-pollinated species.

4. *Synthesis and applications.* This study implies that Dutch landscapes are losing insect-pollinated plant species, which is likely due, at least in part, to the decline in pollination services. Our results of quantifying the decline in insect-pollinated plants support the necessity and urgency of taking conservation initiatives. Several management strategies and policy recommendations could be applied to alleviate the decline of insect-pollinated plants and ensure crop safety. For example, conserving natural environments by reducing nitrogen deposition may support local plants and insect pollinators. Additionally, there is a particular need for focused efforts to protect natural grasslands, as these areas harbour many insect-pollinated plants, which have experienced declines. Finally, monitoring and assessing the state of both pollinators and (insect-pollinated) plants is needed to assess the progress of conservation measures. While recognising the interdependence of pollinators and pollinated plants, it is crucial to extend efforts beyond pollinator

1 | INTRODUCTION

In the past decades, plant diversity has shown declines in Europe (Eichenberg et al., 2020; Jandt et al., 2022). Of the 350,000 flowering plant species in the world, around 82%–90% are dependent on insects like bees, beetles, moths and flies for reproduction compared to only around 10% that are pollinated by wind (Hoshiba & Sasaki, 2008; Ollerton et al., 2011; Rodger et al., 2021). Those pollinator-dependent plants are an important component of global plant biodiversity and also provide humans with 85% of their most important crops (Dicks et al., 2021; Huang et al., 2021; Klein et al., 2007; Potts et al., 2010; Tscharntke, 2021; Wei et al., 2021). Evidence suggests that approximately half of insect-pollinated plants would suffer over 80% reductions in seed production when not pollinated by insects despite the fact that plants can often produce seed by wind or selfing (Ollerton et al., 2011; Rodger et al., 2021). Furthermore, several studies have reported strong declines in the richness (Biesmeijer et al., 2006; Hallmann et al., 2021; Janzen & Hallwachs, 2021; Warren et al., 2021), abundance (Forister et al., 2021; Hallmann et al., 2021; Van Klink et al., 2020; Warren et al., 2021) and biomass (Hallmann et al., 2021) of insects from multiple continents. If these trends are representative, some plant species may face increased extinction risk due to reduced pollinator service.

However, the threat posed to plant species by the decline in pollinators is contingent upon the plants' dependency on them. This issue has persisted as an open question because many plants generate seeds independently of pollinators, either through self-pollination (auto-fertility) or wind-pollination. In scenarios where plants produce seeds without insect pollinators, a decline in insect-pollinators may not necessarily elevate the risk of extinction for plant species. To quantify the contribution of different pollination modes to the decline of plant species, it is necessary to compare the reduction in species richness between those reliant on biotic pollination and those dependent on abiotic pollination. Previous studies have primarily focused on insect-pollinated plants at a large scale. For instance, declines in pollinators and pollinated plants at the national level in the Netherlands and the UK (Biesmeijer et al., 2006). However, plants have also been shown to decline due to abiotic drivers. Nitrogen, pH, and moisture have emerged as prominent drivers of semi-natural vegetation in the Netherlands and Western Europe (Bakker & Berendse, 1999; de Graaf et al., 2009; Kleijn & Raemakers, 2008; Tamis et al., 2005; Van Landuyt et al., 2008). Thus, it remains unclear: (1) whether the declines in plants are linked to their pollination modes, (2) to what extent the relative and absolute occurrence of insect-pollinated plants have shifted over time in comparison to plants that reproduce by selfing or by wind-pollination, particularly at the community-level, and (3) whether the extent of change in insect-pollinated plants is solely due to abiotic factors.

Here, we assess whether the pollination mode of plants (insect, wind, selfing) is correlated with their past and present occurrence in Dutch landscapes. We hypothesise that (i) the proportion of plants with different pollination modes in (semi-)natural plant communities has changed since the 1930s. (ii) This shift may be due to changes in the richness of insect- and wind-pollinated species, resulting in either a decline in insect-pollinated species and an increase in wind-pollinated species, or a decline in both types of species with a steeper decline in insect-pollinated species. We assume that this shift might be more crucial to obligate outcrossers (Biesmeijer et al., 2006). Therefore, we separately analyse (a) all plants pollinated by each mode (insect, wind, and selfing; Table S1), and (b) a subset of obligate outcrossers (i.e. a species only pollinated by a single mode, Table S1). To demonstrate such a shift, for each group, we evaluate temporal changes in both relative (i.e. proportion) and absolute richness of plants pollinated by different modes at the vegetation plot level by using long-term plot monitoring data of plant assemblages in the Netherlands (Hennekens, 2018). Additionally, we incorporated nitrogen, moisture, and habitat types, identified as key factors influencing changes in plant species (Bakker & Berendse, 1999; Buscardo et al., 2008; de Graaf et al., 2009; Ganuza et al., 2022; Kleijn & Raemakers, 2008; Tamis et al., 2005; Van Landuyt et al., 2008; Veldman et al., 2015), as interaction factors to investigate whether the observed changes persist under different environmental conditions. The 365,768 plots are spread across the Netherlands (Figure S1) and span 87 years (1930 to 2017), with 1332 native plant species included in the analysis.

2 | MATERIALS AND METHODS

Figure S2 summarises the workflow used to perform the analysis in this study.

2.1 | Plant plot data

We obtained vegetation plot data representing complete vascular plant species composition across the Netherlands from 1930 to 2017,

from the Dutch Vegetation Database (Hennekens, 2018). To ensure strict adherence to the geographical confines of the Netherlands, we excluded all plots located near the boundary but outside the country (about 2% of all plots). All plots were sampled in (semi-)natural habitats. Plot sizes ranged from 1 to 1000 m², and they reflected those traditionally used by European plant sociologists (Westhoff et al., 1978). Only plots with coordinates were retained to include the effects of spatial locations in further analysis. All spore plants were excluded since they do not reproduce via pollination. In a small number of cases, data were reported for subspecies, but we conducted analyses at the level of taxonomic species, thus trinomials were collapsed to binomials in the dataset before further analyses. We assigned the same plot ID to plots sharing identical coordinates and plot sizes. We refer to the Supporting Information for a detailed description of the data (Text S1).

2.2 | Pollination modes

Data of pollination modes were extracted from CBS (2003), which includes the pollination modes (insect, wind, and selfing) of all native Dutch vascular plants. In this study, we analysed pollination modes in two separate ways: (i) all plants with a pollination mode (i.e. all species pollinated by one or more modes; this includes plants with both obligate pollination+facultative pollination strategies) and (ii) only obligately pollinated plants (i.e. only species pollinated by a single mode). First, the pollination modes were classified into insect, wind and self-pollination (Table S1). The analysis for all plants included species that could be assigned to one or more of the three modes. Obligate pollination included plants that only exhibited a single pollination mode (i.e. obligate insect-pollination, obligate wind-pollination or obligate self-pollination). Species that exhibited more than one pollination mode (facultative) were excluded from the obligate pollination categorization.

2.3 | Selection of other drivers as interaction terms

To investigate whether temporal trends in plants pollinated by different modes persist under different environmental conditions, we introduced additional interaction terms to assess the correlation between temporal trends of plant species and pollination modes. The selection of these terms was informed by a review of relevant Dutch and other European studies, aiming to identify potential key drivers of plant diversity change. Notably, nitrogen, pH and moisture emerged as prominent drivers of semi-natural vegetation in the Netherlands and Western Europe (Bakker & Berendse, 1999; de Graaf et al., 2009; Kleijn & Raemakers, 2008; Tamis et al., 2005; Van Landuyt et al., 2008).

Moreover, grassland and forest tend to differ substantially in plant diversity (Buscardo et al., 2008; Veldman et al., 2015) and pollinator availability (Ganuza et al., 2022; Vujanović et al., 2023). Consequently, we incorporated habitat types of grassland and forest as interaction terms to assess whether the diversity of plants with different pollination modes exhibits distinct trends in these habitats.

2.3.1 | Mean Ellenberg values of nitrogen, pH and moisture in each plot

To account for abiotic variables, we incorporated nitrogen (eutrophication), pH (acidification) and moisture (desiccation) as alternative explanatory variables. We calculated the mean Ellenberg values of nitrogen, pH and moisture of all species in each plot indicating the abiotic preferences of the plant community by using the methods outlined by Tichý et al., 2023. The Ellenberg values were obtained from different sources (https://www.sci.muni.cz/botany/juice/, Hill et al., 1999; Tichý et al., 2023; Tyler et al., 2021), and mean values of nitrogen, pH and moisture values were calculated for each species. We obtained Ellenberg values for 1332 species. Plots, in which no pollinated species could be assigned an Ellenberg value, were removed. Finally, 365,768 plots were retained. For each plot, we calculated the mean Ellenberg values for nitrogen, pH and moisture of all species.

2.3.2 | Forest plots and grassland plots

As we restricted our study to (semi-)natural habitats, our ability to measure the effects of land-use on plant diversity was limited. However, the transition of habitats from grassland to forest could potentially alter biodiversity (Buscardo et al., 2008; Veldman et al., 2015) and influence pollinator availability (Ganuza et al., 2022; Vujanović et al., 2023). Since the inception of phytosociology in the early 20th century (Becking, 1957), European vegetation surveys have adhered to standardised methodologies. Accordingly, we further classified our plots into grassland (sampled at [1 to 100] m²) and forest ([101 to 1000] m²) according to the method described by Večeřa et al., 2021, and tested whether habitat types (forest or grassland) drive the temporal trends in the diversity of plants pollinated by various modes. This classification aligns with plot sizes conventionally used in European phytosociology (Westhoff et al., 1978; Willner & Faber-Langendoen, 2021).

2.4 | Modelling temporal changes in vegetation plots

To test whether the proportions of plants pollinated by different modes changed over time (since 1930, we classified all plot data into nine time periods: [1930, 1939], [1940, 1949], [1950, 1959], [1960, 1969], [1970, 1979], [1980, 1989], [1990, 1999], [2000–2009], [2010–2017]). In each time period, for either (i) all species or (ii) obligately pollinated species, we calculated the proportion of plant species pollinated by each of three modes (P_i) in each plot,

$$P_i = N_i / N$$

N_i is the number of species pollinated by mode i (i.e. insect, wind or selfing). N is the sum of the number of insect, wind and self-pollinated species in each plot.

We then transformed the observed proportions by taking the logarithms of ratios of proportions, breaking the unit sum constraint, and used the generalised linear mixed models (GLMM) with a gaussian distribution to assess temporal trends in the proportion of biotic and abiotic pollination mode (P_i) across time following the methodology outlined by Kühn et al., 2006. Here, we have chosen to use the proportion of self-pollination as the denominator in the log-ratios. To enhance the accuracy of explanatory variable effects (Dormann et al., 2007; Kühn et al., 2006; Mielke et al., 2020), we incorporated spatial structure into the model using the Stochastic Partial Differential Equation approach, as implemented by the sdmTMB package (version 0.4.1; Anderson et al., 2022), to address spatial autocorrelation effects. Additionally, plot ID was introduced as a random factor. We tested different mixed-effects models with and without spatial autocorrelation structures, including the plot ID as a random factor. Since we only measured the proportion of each pollination mode in each plot, we excluded the effect of plot size, as proportional data is scale-independent. Preliminary results based on AIC indicated that the model with the spatial autocorrelation structure and plot ID as a random factor performed the best.

The final model formula: The proportion of plant species pollinated by each mode ~ Time period + (1|plot ID) + spatial structure. These analyses were conducted in R version 4.0.3 (R Core Team, 2020) using the sdmTMB package (version 0.4.1; Anderson et al., 2022), which has been used in many ecological studies to account for spatial autocorrelation (Barbato et al., 2023; Liu et al., 2023; Ohyama et al., 2023).

To test whether the richness of plants pollinated by different modes changed over time, we calculated the species richness of each pollination mode in each plot in each of the nine time periods for either (i) all species or (ii) obligately pollinated species. The models were run individually for each pollination mode, resulting in a total of 8 separate models (all species × 4 pollination modes, obligately pollinated species × 4 pollination modes, Figure S2).

We used GLMM with a negative binomial distribution, which deals with overdispersion in a Poisson distribution, to assess temporal trends in the richness of each pollination mode. Spatial structure was included in the model using the stochastic partial differential equation approach, as implemented by the sdmTMB package (version 0.4.1; Anderson et al., 2022), to exclude the effects of spatial autocorrelation. The plot size was also treated as a covariate in the models, as there was a significant, but weak correlation between coordinates and plot sizes (−0.1, Table S2). The plot ID was included as the random factor. The inclusion of a spatial component, plot size and plot ID was tested using AIC for each of the eight separate models. The final GLMM was: The richness of plant species ~ time period + plot size + (1|plot ID) + spatial structure.

To identify whether the temporal changes observed in the richness of plants pollinated by different modes may be due to abiotic factors (e.g. nitrogen), we identified four potential drivers (mean Ellenberg nitrogen in each plot, mean Ellenberg pH in each plot, mean Ellenberg moisture in each plot and habitat type of each plot) expected to drive plant diversity changes over time. Each of the four drivers was included as a fixed effect interacting with the period in a GLMM with a negative binomial distribution. We fit models with different dependent variables (i) plant richness of all species or (ii) plant richness of obligately pollinated species. As with the other models, the plot sizes were treated as covariates, the plot ID was treated as the random factor, and the spatial structure was included in the model. Due to a high collinearity between habitat type and plot size ($r=0.7$; Table S2), and the collinearity between the mean Ellenberg nitrogen and the mean Ellenberg pH ($r=0.8$), only habitat type and mean Ellenberg nitrogen were included in the model. To enhance the simplicity and interpretability of the model, Ellenberg nitrogen and moisture were reclassified into three categories. For nitrogen, these categories were defined as high (value class 7–8), moderate (value class 3–6), and low (value class 1–2). Similarly, for moisture, the categories were designated as high (value class 9–12), moderate (value class 5–8), and low (value class 1–4). The formula of the model was: The richness of plant species ~ time period*nitrogen + time period*moisture + time period*habitat type + (1|plot ID) + spatial autocorrelation. The model was run individually for each pollination mode. GLMM analyses were conducted in R version 4.0.3 (R Core Team, 2020) and using the sdmTMB function in the sdmTMB (version 0.4.1; Anderson et al., 2022) packages.

3 | RESULTS

The results of the GLMM (with proportions of plants as the dependent variable) showed a shift at the community level, namely a decline in obligately insect-pollinated plants (coefficient for insect-pollination: −0.014) and an increase in obligately wind-pollinated plants over time (coefficient for wind-pollination: 0.015; Figure 1a). We also found a significant decline in the occurrence of all insect-pollinated plant species (coefficient for insect-pollination: −0.019, and coefficient for wind-pollination: 0.032; Figure 1b), although these species are suggested to be less vulnerable to declines in insect-pollination services.

The model to test whether the shift of pollination modes in vegetation communities is due to changes in plant richness showed that, on average, vegetation plots in the Netherlands have lost one species over the past 87 years (Text S2, Figure S3, Table S5). Insect-pollinated plants accounted for most of the loss, with wind-pollinated plants showing a slight increase in richness over time (Figure 2b, Table S4). Overall, plants with obligate pollination modes showed almost no change (Figure S4, Table S5), with a slight increase observed in obligate wind pollinators (mostly grasses) and a loss of insect-pollinated species (Figure 2a).

Due to the nature of our correlative study, it is not possible to confirm the loss of pollination services as the driver of observed

declines. Therefore, we also evaluated whether the observed trends in species richness of insect-pollinated and wind-pollinated plants interacted with differences in nitrogen, pH, moisture, and habitat type averaged at the plot level. All factors have been previously established as drivers of plant change in the Netherlands (Section 2). We assume that if the decline in insect-pollinated plants was solely attributable to factors such as moisture, nitrogen or habitat types, then insect-pollinated plants should exhibit the same trends over time as wind-pollinated plants, provided they are subject to the same moisture and nitrogen levels or come from the same habitat type. Moisture levels had a strong effect, similar for both insect- and wind-pollinated species (Figure 3a,b, Table S6). The main effect was that plant richness declined mostly in dryer areas while there was no change or slight increase in high moisture areas. However, it appears that the decline in insect-pollinated plants was not solely due to moisture levels, as they declined across two of three moisture levels (low and moderate). In contrast, wind-pollinated plants only showed a slight decline at moderate moisture levels. This suggests that other factors beyond moisture levels may be driving the decline in insect-pollinated plants. Similar results were found at different nitrogen levels when comparing insect- and wind-pollinated plants. At different nitrogen levels from high to low, the richness of insect-pollinated plants declined more than wind-pollinated plants (Figure 3c,d, Table S6). It means that the shortage of insect-pollination services over time may cause an additional decline in insect-pollinated plants. However, the small but significant differences (Figure 3c, Table S6) in the decline over time of the richness of insect-pollinated plants at different nitrogen levels also reflect the role nitrogen plays in regulating plant richness at the local level. The richness of insect-pollinated plants has declined similarly in both forests and grasslands, but the richness of wind-pollinated plants only declined in forests (Figure 3e,f). This may be explained by the fact that many wind-pollinated species in the Netherlands are trees in forests (Pan et al., 2022). Similarly, for obligately pollinated species, moisture showed strong effects on insect-pollinated and wind-pollinated species, with most species declining in drier areas (Figure 4a,b, Table S6). The effects of nitrogen on plant richness varied with pollination modes: although the extent of the decline in the richness of insect-pollinated plants varied, higher declines in insect-pollinated plants than wind-pollinated plants over different nitrogen levels (Figure 4c,d, Table S6). The richness of insect-pollinated plants has declined both in grasslands and forests, whereas the richness of wind-pollinated plants showed a very slight increase in forests and grasslands (Figure 4e,f).

4 | DISCUSSION

Our analysis of the occurrence and frequency of obligate and all insect-pollinated plants in plant communities in the Netherlands

FIGURE 1 Shifts in the occurrence of pollination modes over time. Model coefficient estimates (±SE indicated by bars) are shown (a) for obligate pollination, and (b) for all species in each pollination mode group, both from the GLMM (with proportions of plants as the dependent variable; Table S3). In (a and b), asterisks indicate statistical significance ($p < 0.05$). Self-pollination was taken as the reference category and thus omitted.
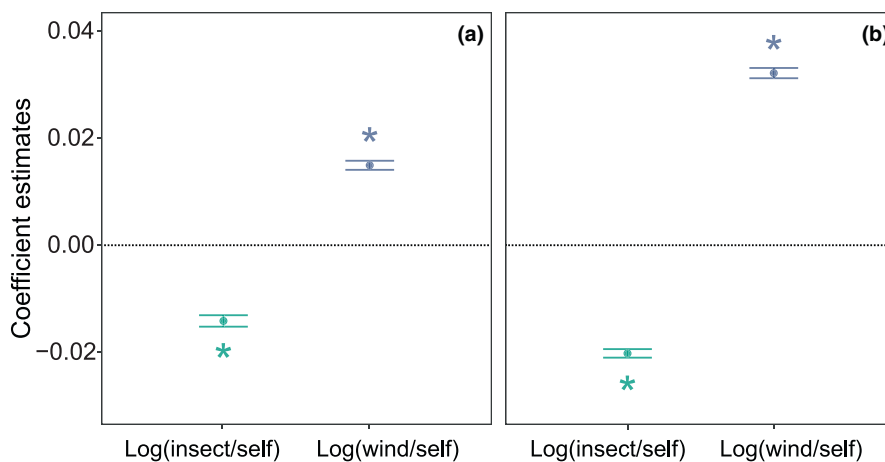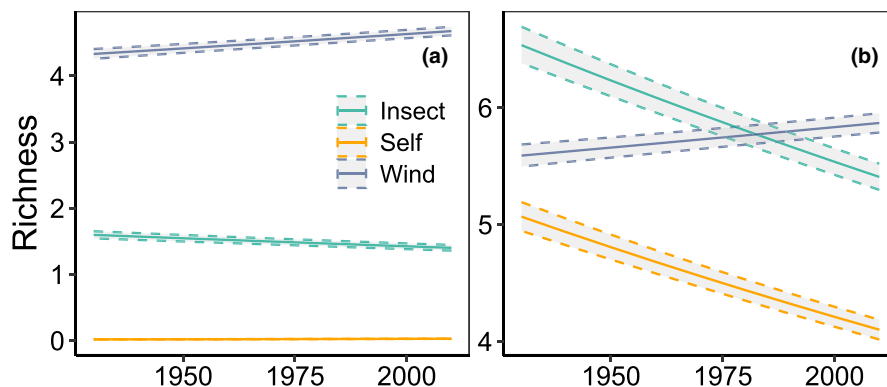

FIGURE 2 Shifts in the richness of pollination modes over time. Given are model best fits with solid lines indicating estimated changes in species richness and dashed lines indicating 95% CIs for obligate pollination (a), and for all species in each pollination mode group (b), all from the generalised linear mixed model (GLMM) with a negative binomial distribution (Table S4).
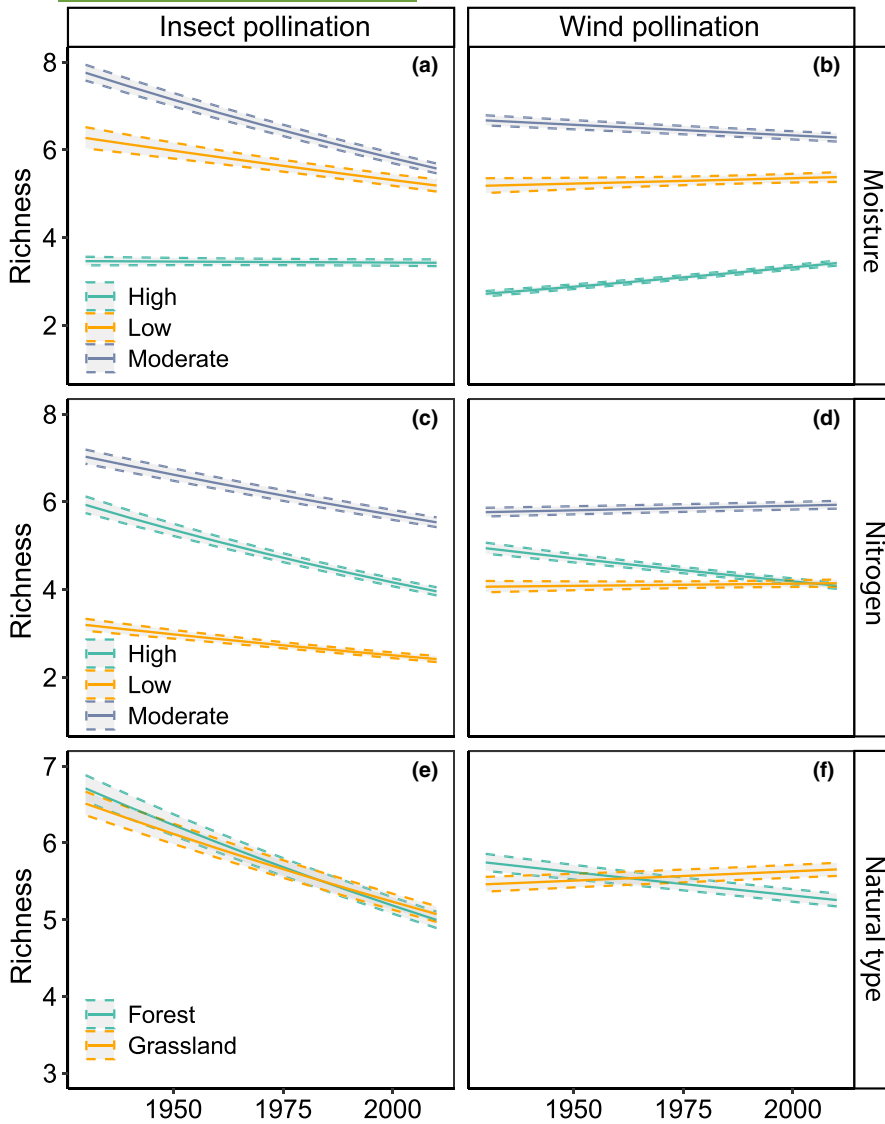
FIGURE 3 Shifts in species richness of pollination modes over time for communities with different average levels of moisture (a, b) and nitrogen (c, d), and habitat type (e, f). Given are model best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs for communities with different moisture levels over time for all (a) insect-pollinated plants, (b) wind-pollination plants, and communities with different nitrogen preferences for all (c) insect-pollinated plants and (d) wind-pollination plants. The last panels show the relation with habitat types for all (e) insect-pollinated plants and (f) wind-pollinated plants (Table S6). To make the comparison between biotic pollination and abiotic pollination simple, insect and wind-pollinations were compared in this figure. Most self-pollinated species are also insect-pollinated, thus self-pollinated species showed similar trends as insect-pollinated species, and these results can be found in Figure S5.

revealed that these communities have on average lost insect-pollinated plants in the last 87 years. This finding fills a critical knowledge gap in terms of quantifying the extent of the decline in insect-pollination at a level of plant communities (vegetation plot level) compared to previous findings (Biesmeijer et al., 2006), where bees and insect-pollinated plants showed parallel declines at the national scale before and after 1980. In summary, Dutch landscapes are losing insect-pollinated plant species, which are being replaced by wind-pollinated species. Similar trends may be observed in other regions where pollinating insects are declining. Since animal-pollinated plants represent ~80% of the earth's flowering plants (Ollerton et al., 2011; Rodger et al., 2021), such a loss may greatly affect the future of our ecosystems and the services they provide.

These findings are also concerning given the critical role of plant-pollinator networks in ecosystem functioning. Changes in plants within these networks may reflect the declines observed for some bee and hoverfly pollinators (Dicks et al., 2021; Potts et al., 2010), as well as the effects of other factors, for example nitrogen and moisture, which are indicated as major drivers in the reduction of, or shifts in, plant diversity (Bakker & Berendse, 1999; de Graaf et al., 2009; Kleijn & Raemakers, 2008). Our results indicated that moisture, nitrogen and habitat types showed different effects on plants with different pollination modes, which means the change in plant richness appears to be driven by the combination and interaction between pollination modes and abiotic factors. In more detail, a more pronounced decline in the richness of insect-pollinated plants compared to wind-pollinated plants within the same nitrogen or habitat category (e.g. nitrogen level 1 or grassland) indicates that insect-pollinated plants are more severely affected, likely due to the shortage of insect pollination, as many plants exhibit pollen limitation (Bennett et al., 2020; Thomann et al., 2013). With increasing evidence of the decline in insect pollinators (Forister et al., 2021; Janousek et al., 2023; Powney et al., 2019; Warren et al., 2021), it is becoming more likely that plants that rely on insect pollinators are experiencing pollen limitation due to a shortage of insect-pollination services. Even though a correlative study such as ours cannot definitively assign causality, our results indicate that the observed decline of insect-pollinated plants is not simply explained by tolerance

FIGURE 4 Shifts in species richness of obligate pollination modes over time for communities with different levels of moisture (a, b), nitrogen (c, d) and habitat type (e, f). Given are model best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs for communities with different moisture levels over time for obligately (a) insect-pollinated plants, (b) wind-pollination plants, and communities with different nitrogen preferences for obligately (c) insect-pollinated plants, (d) the wind-pollinated plants. The last panels show the relation with habitat types for obligately (e) insect-pollinated plants and (f) wind-pollinated plants (Table S6). In this figure, biotic (insect) and abiotic (wind) pollination modes were compared. Results for self-pollinated plants can be found in Figure S6.
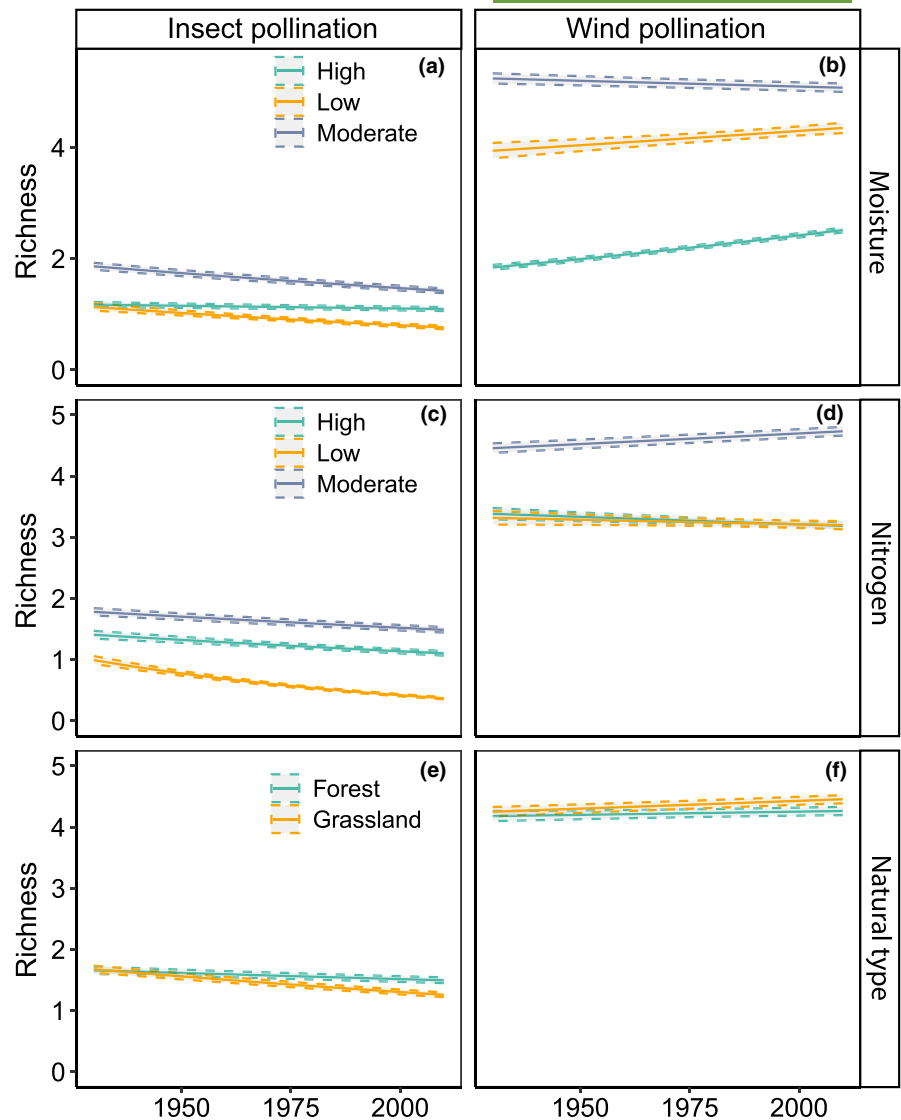
to nitrogen or moisture change of plants, even though these abiotic factors play a role in driving changes in plant diversity over time (Berendse et al., 2021; Roth et al., 2015).

Although our study included the complete flowering-plant composition and a vast number of plots from (semi-)natural habitats across the Netherlands, there are limitations to our analysis. Therefore, we remain cautious about generalising our hypothesis that the decline in insect-pollinated plants may be attributed to a decline in insect-pollination. First, these plots might be sampled in different (semi-) natural habitats, and plant richness may slightly vary with these habitats. Although we classified the plots into grassland and forest habitats according to plot size based on Večeřa et al., 2021, detailed information about the various habitat types is not available as the individual plots in the database were not assigned to specific habitat types. However, it is noteworthy that grassland and forest represent two primary drivers shaping the distribution of plants pollinated by insects and wind. By incorporating habitat type as an interaction term, we aim to prudently conclude the trends in insect- and wind-pollinated plants in the Netherlands. Second, despite our discovery

of a shift in pollination modes in (semi-)natural communities and observed different responses of insect and wind-pollinated plants when they are members of plant communities with different average Ellenberg values for nitrogen, moisture and habitat type (forest or grassland), there was no direct evidence indicating the difference is related to pollinator decline. It is plausible that this difference is due to a decline in pollination services. Notably, the calculation of EIV is based on species, not abundance as only a few plots give abundance data. Last, due to the collinearity between plot size and habitat, as well as nitrogen and pH, it is therefore difficult to separate these effects on plants.

These results suggest that Dutch landscapes have shifted away from insect-pollination. Without mitigation efforts, declines of insect-pollinated plants and their pollinators may continue in (semi-) natural communities. This highlights the need for policies to implement effective strategies (e.g. habitat protection and reduce chemical pollution; Aguirre-Gutiérrez et al., 2017; Goulson et al., 2015; Stefanescu et al., 2004; Warren et al., 2021) to protect insect pollinators and mitigate declines in insect-pollinated plants. Inspiration

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for this could be the IPBES pollinator report (Potts et al., 2016), the EU Pollinator Initiative (https://ec.europa.eu/environment/nature/conservation/species/pollinators/policy_en.htm) and other initiatives such as the Coalition of the Willing on Pollinators (https://promotepollinators.org/) and the Dutch Delta Plan for Biodiversity Recovery (https://www.samenvoorbiodiversiteit.nl/themas). With these initiatives, governments, companies, NGOs and other parties aim to improve knowledge of pollinator decline and make plans for safeguarding sustainable pollinator and plant populations. However, these efforts alone may prove insufficient, as the majority focuses primarily on pollinators. Our findings indicate that the decline in insect-pollinated plants is not solely attributable to a reduction in insect-pollination services; other factors such as nitrogen, moisture and habitat types also contribute to the phenomenon. To address these complexities, policymakers and relevant stakeholders can consider the following actions:

1. Mitigate nitrogen deposition: decrease nitrogen deposition, recognising it as a critical driver of plant diversity change. Identify areas with species preferring low nitrogen levels and implement measures to reduce nitrogen deposition in these regions.
2. Promote habitat recovery: Encourage habitat recovery in both forest and grassland, given the decline in insect-pollinated plants in both ecosystems. Place heightened emphasis on the restoration of insect pollinators and insect-pollinated plants in grasslands, particularly those that are obligately insect-pollinated.
3. Advocate for long-term monitoring and assessment of the status of insect-pollinated plants to safeguard plant biodiversity and crop safety. While several pollinator monitoring platforms exist (e.g. Global Pollinator Watch, Pollinator Species Monitoring—EUPoMS, The Bee Hub, UK Pollinator Monitoring Scheme, and the bee diversity map from the Dutch Atlas Natural Capital), there is a notable gap in platforms addressing the other side of the plant-insect interaction relationship.

Furthermore, in the realm of scientific inquiry, there is a wealth of global studies on insects and pollinators, but comparatively fewer studies on biotic- and abiotic-pollinated plants and their dynamics. Therefore, a concerted effort is needed to conduct more relevant studies to safeguard plant diversity and crop safety. Our results of quantifying the decline in insect-pollinated plants support the necessity and urgency of taking this conservation initiative.

AUTHOR CONTRIBUTIONS

Kaixuan Pan, Geert R. de Snoo and Jacobus C. Biesmeijer conceived the idea and designed the study. All authors contribute to the design of the methodology. Jacobus C. Biesmeijer and Kaixuan Pan collected the data. Kaixuan Pan conducted all the analysis. Leon Marshall assisted with model development. Kaixuan Pan wrote the first manuscript draft. Leon Marshall, Jacobus C. Biesmeijer and Geert R. de Snoo further contributed to the interpretation of results and the writing of discussion in the final manuscript. All authors contributed critically to the drafts and gave final approval for publication. Geert R. de Snoo and Jacobus C. Biesmeijer jointly supervised the study.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via Zenodo https://doi.org/10.5281/zenodo.10848426 (Pan et al., 2024).

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SUPPORTING INFORMATION

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

Text S1. The description of the plot data.

Text S2. Temporal trends in the total richness of obligate and facultative pollination groups.

Table S1. Number of plant species with different pollination modes included in the analysis.

Table S2. Spearman's test for all variables included in the model of identifying drivers of temporal trends in the richness of plants pollinated by different modes.

Table S3. Significance of the factors in GLMMs testing effects on the proportion of plants pollinated by different modes.

Table S4. Significance of factors in GLMMs testing effects on the richness of plants pollinated by different modes.

Table S5. Significance of the factors in GLMMs testing effects on the total richness of pollinated plants.

Table S6. Significance of the factors nitrogen, moisture and habitat type in GLMMs testing effects on driving temporal trends of the richness of plants pollinated by different modes.

Figure S1. Distribution of plots in the Netherlands (a) and the numbers of vegetation plots over time in the Netherlands (b).

Figure S2. Workflow used to do analysis in this study.

Figure S3. The total richness of all species in each of the three pollination modes (insect, wind and self) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S5).

Figure S4. The total richness of three obligate pollination modes (obligate insect, wind and self-pollination) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S5).

Figure S5. Shifts in the richness of all species (obligate pollination+facultative pollination) over time for communities with different levels of a, moisture, b, nitrogen and c, natural type.

Figure S6. Shifts in species richness of obligate pollination modes over time for communities with different levels of a, moisture, b, nitrogen and c, natural type.

Figure S7. Validation of the model with the proportion of plant species pollinated by each mode (insect, wind and self-pollination)~Time period+(1|Plot ID)+spatial structure.

Figure S8. Validation of the models with the richness of plant species (obligate pollination)~Time period+Plot size+(1|Plot ID)+spatial structure.

Figure S9. Validation of the models with richness of plant species (all species: obligate+facultative)~Time period+plot size+(1|Plot ID)+spatial structure.

Figure S10. Validation of the model with the total richness of pollinated plant species (insect+wind+self)~Time period+plot size+(1|Plot ID)+spatial structure.

Figure S11. Validation of the model with the richness of plant species (obligate pollination)~Time period*Nitrogen+Time period*Moisture+Time period*Habitat type+(1|Plot ID)+spatial structure.

Figure S12. Validation of the model with the richness of plant species (all species)~Time period*Nitrogen+Time period*Moisture+Time period*Habitat type+(1|Plot ID)+spatial structure.