Plant occurrence in space and time: the importance of land use, habitat structure, and pollination mode

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Chapter 4

Dutch landscapes are losing insect-pollinated plants

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Abstract

Aim: The interruption of plant-pollinator interactions may threaten global plant diversity, food security and ecosystem stability. Recent reports of strong declines of both insects and plants seem to point to insect decline as a driver of plant decline. However, it is still unknown whether these trends are linked and to what extent plant declines are related to insect-pollination, as plants often produce seeds without the need for insect pollinators. In this study, we hypotheses that the decline of pollinators may have shifted our plant communities away from insect-pollination over time.

Location: The Netherlands

Taxon: Pollinated plants

Methods: We combine 625,247 vegetation plot data from 1930 to 2017 and plant traits to assess the changes in occurrences of plants pollinated by different modes.

Results: The proportion of obligately insect-pollinated plants has declined ~10.4% while obligately wind-pollinated plants have increased ~9.6% over the last 87 years. The proportion of facultatively insect-pollinated plants has declined ~6.4% while facultatively wind-pollinated plants have increased ~9.6%. This proportional change reflects an absolute decline in the number of insect-pollinated species and increase in the number of wind-pollinated species over time in the Netherlands.

Main conclusion: In conclusion, Dutch landscapes are losing insect-pollinated plant species, which are being replaced by wind-pollinated species, due to declines in pollination service. Based on our results, we encourage policies to address the conservation of insect pollinators to mitigate the decline of plants.

Significance statement: Studies have reported alarming declines in insect or bee-pollinated plants at national scale. However, it remains unknown whether and to what extent insect-pollinated species have declined in our ecosystem at the community level. Here we show declines in pollinator has shifted natural plant community away from insect-pollination.

Keywords: Temporal trends, Plant diversity, Plant community composition, Plant-insect interaction, Pollination modes, Insect-pollination decline, Natural landscapes

Introduction

Plant-pollinator interactions rate among the most critical relationships in our planet's ecosystems (Potts et al., 2016a; Potts et al., 2016b). Pollinator-dependent plants are an important component of global plant biodiversity and provide humans with 85% of the most important crops (Potts et al., 2010; Huang et al., 2021; Tscharntke, 2021; Dicks et al., 2021; Wei et al., 2021). Evidence suggests that approximately 80% of flowering plants are pollinated by insects, and that half would suffer over 80% reductions in seed production despite the fact that plants can often produce seed by wind or selfing (Ollerton et al., 2011; Rodger et al., 2021).

In parallel, other studies show strong declines in the richness of terrestrial insects (Janzen & Hallwachs, 2021), hoverflies (Hallmann et al., 2021) and butterflies (Warren et al., 2021), in the abundance of terrestrial insects (van Klink et al., 2020), hoverflies(Hallmann et al., 2021) and butterflies (Forister et al., 2021; Warren et al., 2021), and in the biomass of flying insects (Hallmann et al., 2021). This has raised the interest in understanding the role of insects in our ecosystems, in insect-plant interactions and insect conservation (Harvey et al., 2020). Biesmeijer et al. (2006) found evidence of declines in bees and insect-pollinated plants between two periods at the national scale in the Netherlands and the UK. Moreover, bee species decline is linked to loss of their preferred food plants (Scheper et al., 2014); plant species in the diet of declining bumblebee species were themselves declining, in contrast to those in the diet of stable and increasing species (Kleijn & Raemakers, 2008). It remains unclear, however, whether the declines in insects and insect-pollinated plants are linked, and to what extent the relative and absolute occurrence of insect-pollinated plants have shifted in relation to plants pollinated through selfing or by wind in natural ecosystems at the level of plant communities over time.

Here we assess whether the pollination mode of plants (insect, wind, selfing) is correlated with their past and present occurrence in Dutch landscapes, hypothesising that the decline of pollinators may have shifted our plant communities away from insect-pollination. We assume that this shift might be more crucial to obligate outcrossers (Biesmeijer et al., 2006), therefore we analyse obligate (i.e. a species only pollinated by a single mode, Table S1) and facultative (i.e. a species pollinated by more than one mode, Table S1) pollination separately. To adequately 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). The 625,247 plots are spread over the Netherlands (Figure S1), and they span 87 years (1930 to 2017), with 1,425 native plant species included in the analysis. Some plots have been recorded multiple times (named resampled plots). We use them to assess fixed-site vegetation shifts.

Materials and Methods

Plant plot data

We obtained vegetation plot data representing complete vascular plant species composition across the Netherlands from 1930-2017, from the Dutch Vegetation Database (Hennekens, 2018). Plot sizes vary with habitat types and they reflect those traditionally used by European phytosociology (Westhoff et al., 1978). All spore plants were excluded since they do not reproduce via pollination. In a small number of cases, data are 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.

Pollination modes

Data of pollination modes were extracted from Biobase (2003), and included the pollination modes (insect, wind and selfing) of all native Dutch vascular plants. In this study, we used two pollination groups: obligate pollination (i.e. a species only pollinated by one mode) and facultative pollination (i.e. a species pollinated by more than one mode, e.g. a species is pollinated by insect, but also with other modes like wind or selfing as complementary in its pollination service), which represent different pollination strategies. Firstly, pollination modes were classified into insect-pollination, wind-pollination and self-pollination, and all plants were assigned a facultative classification for each of the three pollination modes (Table S1). Facultative pollination mode includes all species and each species may be assigned to one or more than one of the 3 categories (e.g. if a species is both insect and self-pollinated). Obligate pollination includes plants that only exhibit a single pollination mode (i.e. obligate insect-pollination, obligate wind-pollination and obligate self-pollination). Species which exhibit more than one pollination mode (facultative) are excluded in the obligate pollination categorization.

The proportions of plants pollinated by different modes change over time

From 1930 on, all plant plot data was classified into eight time periods: [1930, 1939], [1940, 1949], [1950, 1959], [1960, 1969], [1970, 1979], [1980, 1989], [1990, 1999], [2000-2017]. In each time period, for either facultative or obligate group, 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 used a generalized linear model (GLM) with a logit distribution to assess temporal trends in the proportion of each pollination mode (P_i) over the 8 time periods. Since we only measure the proportion of each pollination mode in each plot, we excluded the effect of plot sizes and locations. The final GLM formula is: The proportion of plant species pollinated by each mode ~ Time period*Pollination mode. These analyses were conducted in R version 4.0.3 (R Core Team, 2020) using the glmmTMB (Brooks et al., 2017) packages.

The richness of plants pollinated by different modes change over time

In each of the eight time periods, we calculated the species richness of each pollination mode in each plot. Due to the species-area relationship, we only kept plots which included sample size information, which will be treated as a random effect in the statistical models.

We used a generalized linear mixed model (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. The plot size was treated as a random effect in the model. The final GLMM formula is: The richness of plant species pollinated by each mode ~ Time period*Pollination mode + (1|plot size). Analyses were conducted in R version 4.0.3 (R Core Team, 2020) using the glmmTMB (Brooks et al., 2017) packages.

Comparison of the Ellenberg values (nitrogen) of plants pollinated by different modes

The Ellenberg values were obtained from JUICE (https://www.sci.muni.cz/botany/juice/). Ellenberg values were assigned to species in our study. Finally, we got 1,071 species with Ellenberg values from JUICE. Tata was tested with a Kruskal-Wallis test and a post hoc multiple comparison test.

Results and Discussion

To disentangle the percentage changes of pollination modes in vegetation communities, we performed generalized linear models with a logit distribution. Results show a shift at community level of -1.3% for obligately insect-pollinated plants and +1.2% increase for obligately wind-pollinated plants per decade (Figure 1 a-b). Compared to obligate insect-pollination, we found a weaker but still significant decline in the occurrence of facultative insect-pollination which we estimated to be decreasing by ~0.8% per decade (Figure 1 c-d), although these species are less vulnerable to declines in insect-pollination services (Aguilar et al., 2006). The proportion of obligately self-pollinated plant species increased (~0.1% per decade), but facultatively self-pollinated plants decreased (~0.5% per decade) over time (Figure 1), due to the fact that most insect-pollinated plants are also facultative selfers. Our fixed-site analysis based on plots recorded multiple times shows the same trend (Figure S2-3).

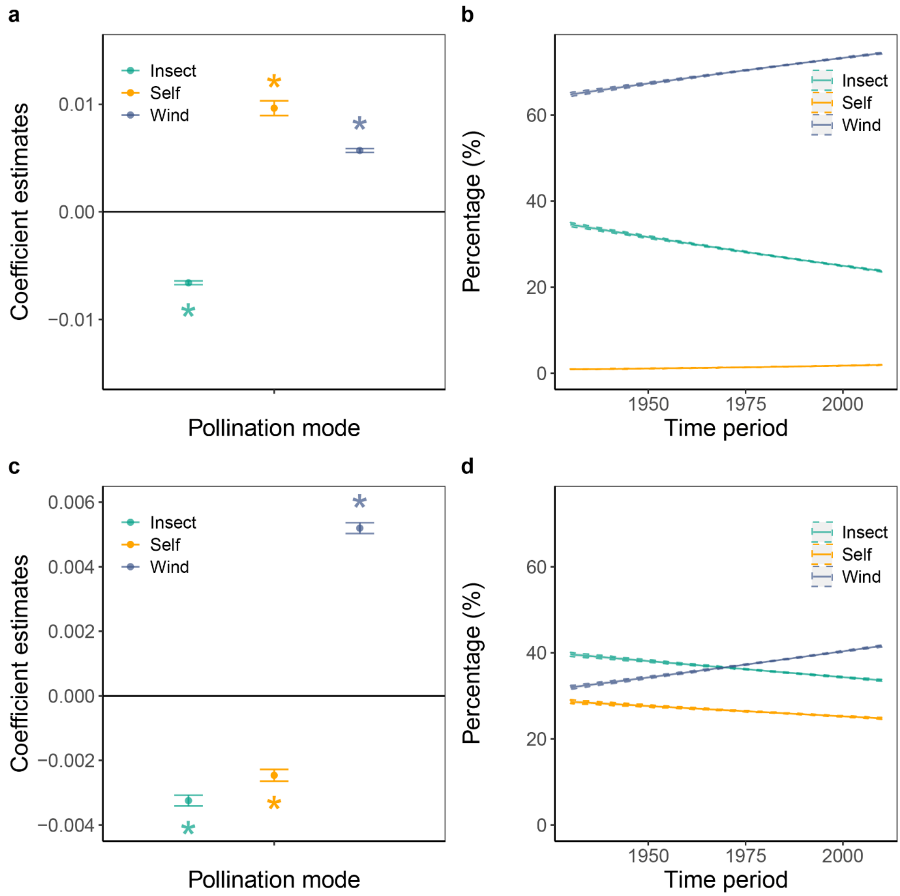

Figure 1 Shifts in the occurrence of pollination modes over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) for obligate pollination, and model coefficient estimates (± s.e. indicated by bars) (c) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (d) for facultative pollination, both from the generalized linear model (GLM) with a logit distribution (Table S2). In a and c, asterisks mean statistically significant ($P < 0.05$).

To find out whether the shift of pollination modes in vegetation communities is due to changes in plant richness, we performed generalized linear mixed models with a negative binomial distribution. We show that, on average, vegetation plots in the Netherlands have lost three species during the 87 year period (Figure S7). Insect-pollinated plants account for most of the loss, with wind-pollinated plants showing a slight increase in richness over time (Figure 2 c-d). Plants that are obligate insect, wind or self-pollinated show similar patterns, with a gain in obligate wind pollinators (mostly grasses) and loss of insect-pollinated species, adding up to a slight increase of plants with obligate pollination modes overall (Figure 2 a-b, Figure S6). The decreasing trend for insect-pollinated species is consistent with previous findings from NW Europe (Biesmeijer et al., 2006; Carvalheiro et al., 2013; Goulson et al., 2015) and may result from a deficiency of insect pollinators (Lennartsson, 2002; Pauw & Hawkins, 2011). In summary, Dutch landscapes are losing insect-pollinated plant species, which are being replaced by wind-pollinated species. This is probably also happening in other areas of the world where pollinating insects are also declining. Since insect-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. Results from analysis based on resampled plots (fixed sites) also show a great decline in facultative insect-pollination and self-pollination while increase in facultative and obligate wind-pollination (Figure S4-5, 8-9).

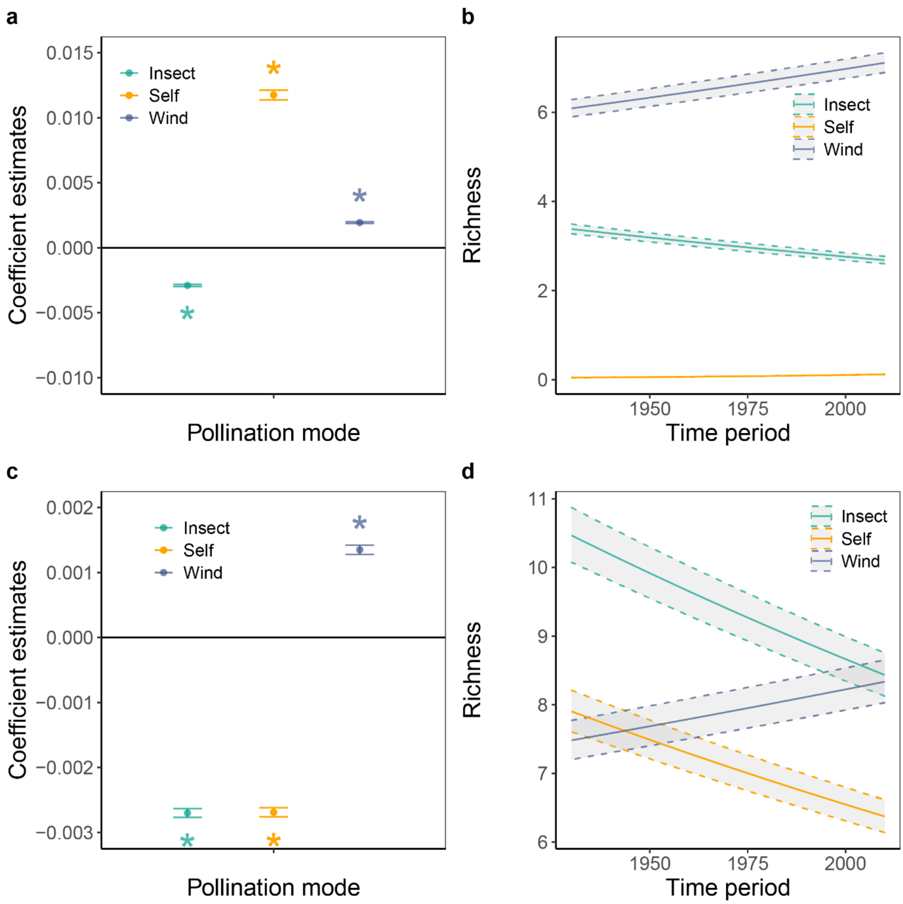

Figure 2 Shifts in the richness of pollination modes over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) for the obligate pollination, and model coefficient estimates (± s.e. indicated by bars) (c) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (d) for facultative pollination, both from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S3). In a and c, asterisks mean statistically significant (*P* < 0.05).

Our estimates of 1.3% decline in obligate insect-pollinated plants and 0.8% decline in facultative insect-pollinated plants per decade in the Netherlands reveal that plant communities have shifted away from insect-pollination in the last 87 years. This estimated loss rate fills the critical knowledge gap of quantifying the extent of 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 declined at the national scale between two periods.

Such a decline raises concern given the critical role of plant-pollinator networks for ecosystem functioning. Changes in plants within these networks may reflect the declines observed for some bee and hoverfly pollinators (Potts et al., 2010; Dicks et al., 2021). Even though a correlative study such as ours cannot definitively assign causality, the confluence of findings from controlled experiments of changes in plant-pollinator interactions over different period (Lennartsson, 2002), historical pollination rates from specimen (Pauw & Hawkins, 2011), and species occurrence tracked through time (Biesmeijer et al., 2006), all suggest that the decline of insect pollinators alter plant community composition. Moreover, the absence of a correlation between plant pollination modes and their Ellenberg values for nitrogen indicates that the observed decline of insect-pollinated plants is not simply explained by nitrogen change tolerance of plants (Figure 3-4). Carvalheiro et al. (2020) found a greater decline in richness of plants that are dependent on pollinators and prefer nutrient-rich environments than plants that are not dependent on pollinators and prefer nutrient-rich environments, which supports our conclusion.

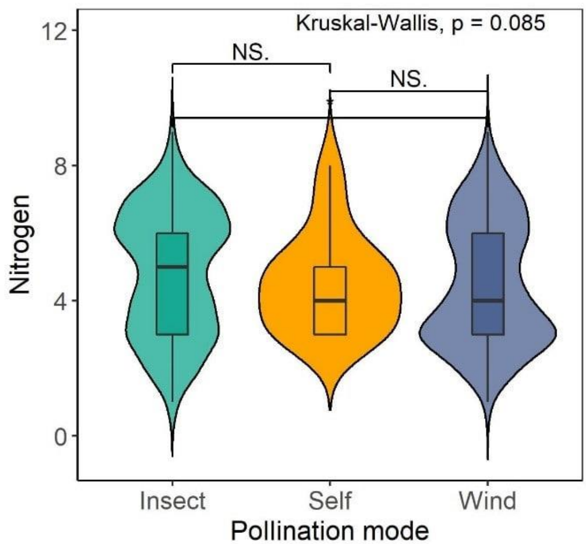

Figure 3 Comparison of the Ellenberg values (nitrogen) of plants obligately pollinated by different modes (n = 527, d.f. = 2, $\chi2$ = 4.942). Boxplots show the range of Ellenberg values calculated across 1,071 plant species. Upper and lower box bounds represent the

75th and 25th percentiles, respectively, and the horizontal line represents the median value. Observed values are shown with asterisks. The database of Ellenberg values is from JUICE (https://www.sci.muni.cz/botany/juice/).

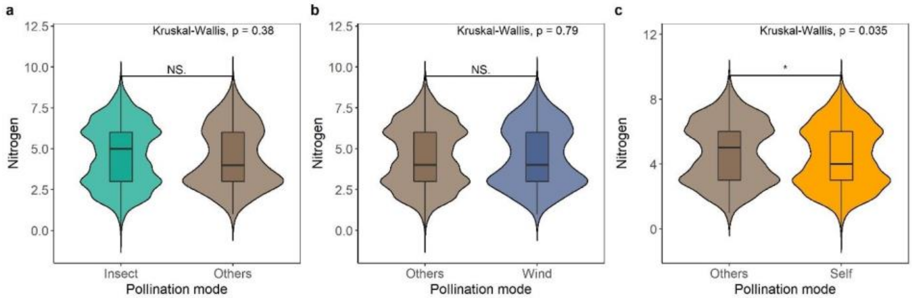

Figure 4 Comparison of the Ellenberg values (nitrogen) of plants facultatively pollinated by different modes. a, nitrogen values between facultive insect-pollination and other pollination modes (n = 1,071, d.f. = 1, $\chi2$ = 0.785). b, nitrogen values between facultive wind-pollination and other pollination modes (n = 1,071, d.f. = 1, $\chi2$ = 0.069). c, nitrogen values between facultive self-pollination and other pollination modes (n = 1,071, d.f. = 1, $\chi2$ = 4.449). Boxplots show the range of Ellenberg values calculated across 1,071 plant species. Upper and lower box bounds represent the 75th and 25th percentiles, respectively, and the horizontal line represents the median value. Observed values are shown with asterisks. The database of Ellenberg values is from JUICE (https://www.sci.muni.cz/botany/juice/).

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These results suggest that insect-pollination is important for plant persistence and for the composition of plant communities. Without mitigation efforts, declines of insect-pollinated plants and their pollinators may continue in natural communities. This implies that policies should take effective strategies (e.g. habitat protection and reduce chemical pollution (Stefanescu et al., 2004; Goulson et al., 2015; Warren et al., 2021; Aguirre-Gutiérrez et al., 2017)) to protect insect pollinators and mitigate declines in insect-pollinated plants. An inspiration for this could be the IPBES pollinator report (Potts et al., 2016b), 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).

Conflict of Interest

The authors declare no competing interests.

Data availability

Plot data for analysis during this study is from public domain resource, which is indicated in this article. Data of plant trait will be made available in the Zenodo upon acceptance for publication.

Code availability

The R code used in this study will be made available in the Zenodo upon acceptance for publication.

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Biosketch

Kaixuan Pan is a PhD candidate at Leiden University. His research focuses on the temporal and spatial dynamics of plant species and their interactions with pollinators.

Author contributions

K.P., G.R. de S. and K.B. conceived the idea and designed the study. L.M. and K.B. developed the idea of results validating by resampled plots. K.B. provided the trait data. K.P. conducted all analysis. L.M. checked the model developed by K.P. K.P. wrote the first manuscript draft. K.B. and G.R. de S. further contributed to the interpretation of results and K.B. contributed to the writing of discussion in the final manuscript. All authors commented on and edited the manuscript. G.R. de S. and K.B. jointly supervised the study.

Supplementary Information

Temporal trends in the proportions of plants pollinated by different modes in resampled grid cells at 1 km resolution in the same location (fixed sites) and recorded in different years

To further support our analysis and test whether observed changes in the proportion of pollination modes is consistent at the site scale, we selected plots with georeferenced information and matched them with grid cells at 1 km resolution covering the whole Netherlands. Only grid cells that were sampled at multiple time points were retained (resampled grid cells). Since there might be more than one plot in each grid cell, we first calculate the average number of each pollination mode AN_i in each grid cell. Then, at each grid cell in each year, the proportion of each pollination mode (GP_i) in each grid cell was calculated

$GP_i = AN_i / \sum AN_i$

We used a generalized linear mixed model (GLMM) with a logit distribution to assess temporal trends in the proportion of each pollination mode. The grid cell location was treated as a random effect in the model. The final GLMM formula is: The proportion of plant species pollinated by each mode ~ Year*Pollination mode + (1|grid cell location). Analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

Temporal trends in the richness of plants pollinated by different modes in resampled plots with the same size and within the same grid cell at 1 km resolution (fixed sites) and recorded in different years

In each grid cell at 1 km resolution, for each plot size category, we kept a set of plots that shared the sample plot size and were recorded in multiple years. Those plot size categories that were only recorded once were excluded. For each set of resampled plots, we calculated the species richness of each pollination mode in each plot.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to assess temporal trends in the richness of each pollination mode. The plot size and location were treated as random effects in the model. The final GLMM formula is: The richness of plant species pollinated by each mode ~ Year*Pollination mode + (1|plot size) + (1|plot location). These analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

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

To test whether the total richness of species which exhibit multiple pollination modes (facultative) and exhibit only one mode (obligate) in vegetation plots change over time, in each of the eight time periods defined ([1930, 1939], [1940, 1949], [1950, 1959], [1960, 1969], [1970, 1979], [1980, 1989], [1990, 1999], [2000-2017]), we calculated the total species richness of facultative or obligate pollination plants in each plot. Due to the species-area relationship, we only kept plots which included sample size information, which will be treated as a random effect in the statistical models.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to assess temporal trends in the total richness. The plot size was treated as a random effect in the model. The final GLMM formula is: The total richness ~ Time period + (1|plot size). These analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

Temporal trends in the total richness of pollination plants in resampled plots with the same size and within the same grid cell at 1 km resolution (fixed sites) and recorded in different years

In each grid cell at 1 km resolution, for each plot size category, we kept a set of plots that shared the sample plot size and were recorded in multiple years. Those plot size categories that were only recorded once were excluded. For each set of resampled plots, we calculated the total species richness of facultative or obligate pollination plants in each plot.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to assess temporal trends in the total richness. The plot size and location were treated as random effects in the model. The final GLMM formula is: The total richness ~ Year + (1|plot size) + (1|plot location). These analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

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

Group	Pollination_mode	Freq	Definition
Obligate	Insect	411	all plants only with insects as their pollination
Obligate	Wind	310	all plants only with wind as their pollination
Obligate	Self	32	all plants only with selfing as their pollination
Facultative	Insect	1055	all plants with insect as one of their pollination modes
Facultative	Wind	387	all plants with wind as one of their pollination modes
Facultative	Self	674	all plants with selfing as one of their pollination modes

Table S2 Significance of the factor year in GLMs testing effects on the proportion of plants pollinated by different modes based on all plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Proportions of obligate plants ~ year*pollination mode (binomial distribution) : n = 1,857,282;	Intercept (insect)	33.93	<0.001	12.09 ± 0.356
	Year (insect)	-36.74	<0.001	-0.007 ± 0
	Intercept (wind)	-29.618	<0.001	-10.397 ± 0.351
	Year (wind)	32.252	<0.001	0.006 ± 0
	Intercept (self)	-17.04	<0.001	-23.292 ± 1.367
	Year (self)	14.0153	<0.001	0.01 ± 0.001
Proportions of facultative plants ~ year*pollination mode (binomial distribution) : n = 1,875,741;	Intercept (insect)	17.6243	<0.001	5.841 ± 0.331
	Year (insect)	-19.438	<0.001	-0.003 ± 0
	Intercept (wind)	-32.627	<0.001	-10.784 ± 0.331
	Year (wind)	31.2261	<0.001	0.005 ± 0
	Intercept (self)	10.6327	<0.001	3.837 ± 0.361
	Year (self)	-13.541	<0.001	-0.002 ± 0

Table S3 Significance of the fixed factor year in GLMMs testing effects on the richness of plants pollinated by different modes based on all plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligate plants ~ year*pollination mode (negative binomial distribution) : n = 1,313,091;	Intercept (insect)	43.0383	<0.001	6.801 ± 0.158
	Year (insect)	-36.589	<0.001	-0.003 ± 0
	Intercept (wind)	-14.487	<0.001	-1.938 ± 0.134
	Year (wind)	29.0493	<0.001	0.002 ± 0
	Intercept (self)	-34.38	<0.001	-25.762 ± 0.749
	Year (self)	31.2262	<0.001	0.012 ± 0
Richness of facultative plants ~ year*pollination mode (negative binomial distribution) : n = 1,324,680;	Intercept (insect)	56.1556	<0.001	7.558 ± 0.135
	Year (insect)	-40.29	<0.001	-0.003 ± 0
	Intercept (wind)	-4.1996	<0.001	-0.592 ± 0.141
	Year (wind)	19.208	<0.001	0.001 ± 0
	Intercept (self)	51.5003	<0.001	7.257 ± 0.141
	Year (self)	-38.296	<0.001	-0.003 ± 0

Table S4 Significance of the fixed factor year in GLMMs testing effects on the proportion of plants pollinated by different modes based on resampled plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Proportions of obligate plants ~ year*pollination mode (binomial distribution) : n = 364,683;	Intercept	15.1599	<0.001	10.814 ± 0.713
	Year (insect)	-16.446	<0.001	-0.006 ± 0
		-14.106	<0.001	-9.986 ± 0.708
	Year: wind	15.333	<0.001	0.005 ± 0
		-5.6421	<0.001	-20.29 ± 3.596
	Year: self	4.36778	<0.001	0.008 ± 0.002
Proportions of facultative plants ~ year*pollination mode (binomial distribution) : n = 366,669;	Intercept (insect)	7.76959	<0.001	5.254 ± 0.676
	Year (insect)	-8.5825	<0.001	-0.003 ± 0
	Intercept (wind)	-15.917	<0.001	-11.004 ± 0.691
	Year (wind)	15.1676	<0.001	0.005 ± 0
	Intercept (self)	5.58468	<0.001	4.121 ± 0.738
	Year (self)	-6.9958	<0.001	-0.003 ± 0

Table S5 Significance of the fixed factor year in GLMMs testing effects on the richness of plants pollinated by different modes based on resampled plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligate plants ~ year*pollination mode (negative binomial distribution) : n = 382,122;	Intercept (insect)	9.6639	<0.001	2.68 ± 0.277
	Year (insect)	-6.2071	<0.001	-0.001 ± 0
	Intercept (wind)	-22.701	<0.001	-5.371 ± 0.237
	Year (wind)	30.3959	<0.001	0.004 ± 0
	Intercept (self)	-7.0754	<0.001	-9.477 ± 1.339
	Year (self)	5.13044	<0.001	0.003 ± 0.001
Richness of facultative plants ~ year*pollination mode (negative binomial distribution) : n = 384,525;	Intercept	21.624	<0.001	4.7 ± 0.217
	Year (insect)	-12.37	<0.001	-0.001 ± 0
		-27.246	<0.001	-6.267 ± 0.23
	Year: wind	35.8696	<0.001	0.004 ± 0
		25.202	<0.001	5.784 ± 0.23
	Year: self	-17.783	<0.001	-0.002 ± 0

Table S6 Significance of the factor year in GLMMs testing effects on the total richness of pollinated plants based on all plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligately pollinated plants ~ year (negative binomial distribution) : n = 437,697;	Intercept	12.47	<0.001	1.511 ± 0.121
	Year	6.14	<0.001	0 ± 0
Richness of facultatively pollinated plants ~ year (negative binomial distribution) : n = 441,560;	Intercept	44.52	<0.001	5.935 ± 0.133
	Year	-20.94	<0.001	0.001 ± 0

Table S7 Significance of the fixed factor year in GLMMs testing effects on the total richness of pollinated plants based on resampled plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligately pollinated plants ~ year (negative binomial distribution) : n = 127,374;	Intercept	-7.4	<0.001	-1.634 ± 0.221
	Year	17.18	<0.001	0.002 ± 0
Richness of facultatively pollinated plants ~ year (negative binomial distribution) : n = 128,175;	Intercept	13.529	<0.001	3.246 ± 0.24
	Year	-0.986	0.324	0 ± 0

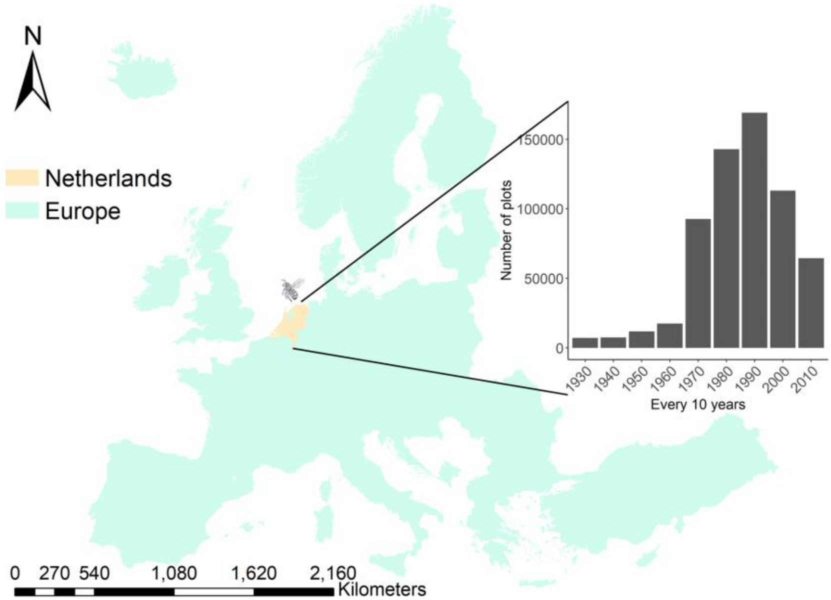

Figure S1 Numbers of vegetation plots over time in the Netherlands.

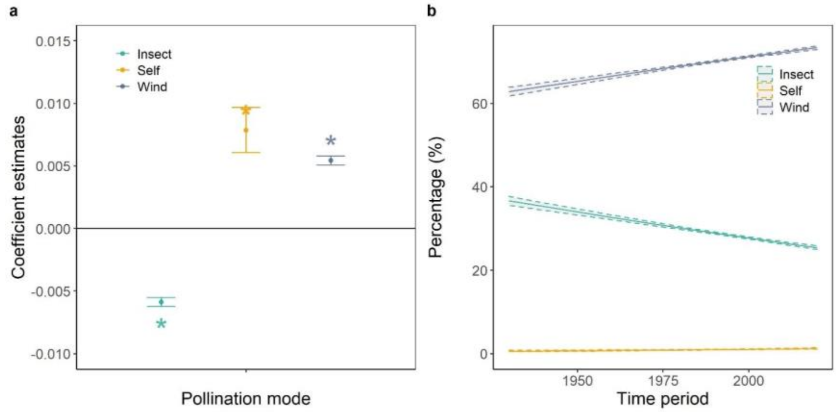

Figure S2 Shifts in the occurrence of obligate pollination modes (obligate insect-, wind- and self-pollination) in resampled grid cells over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a logit distribution (Table S4). In a, asterisks mean statistically significant ($P < 0.05$).

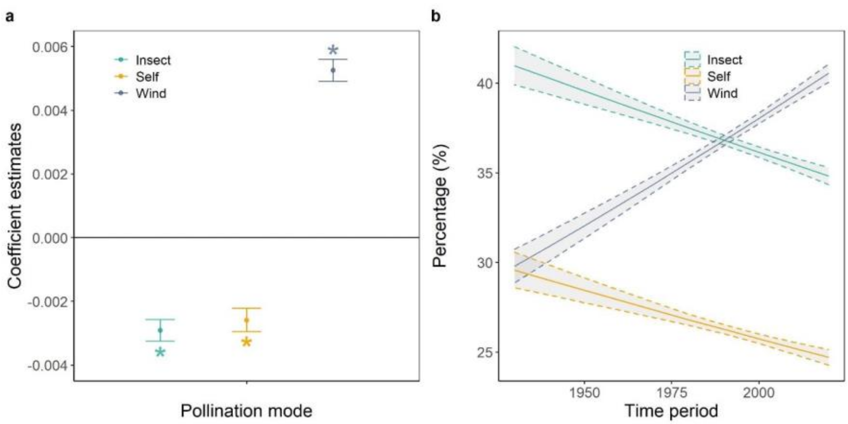

Figure S3 Shifts in the occurrence of facultative pollination modes (facultative insect-, wind- and self-pollination) in resampled grid cells over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a logit distribution (Table S4). In a, asterisks mean statistically significant ($P < 0.05$).

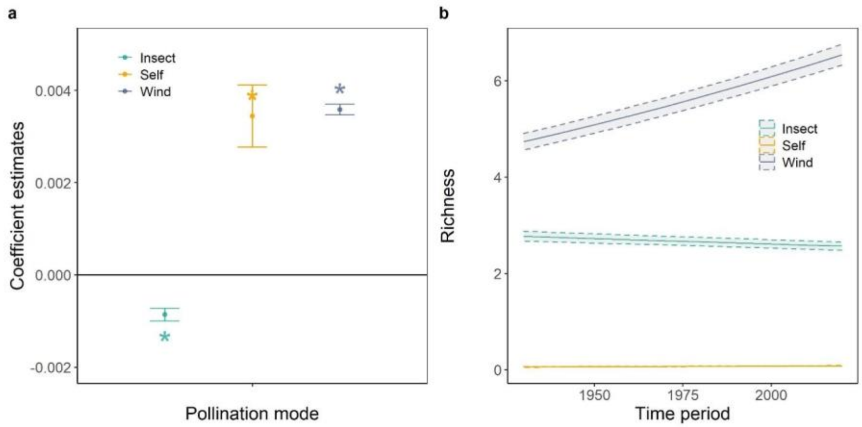

Figure S4 Shifts in the richness of obligate pollination modes in resampled plots over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S5). In a, asterisks mean statistically significant ($P < 0.05$).

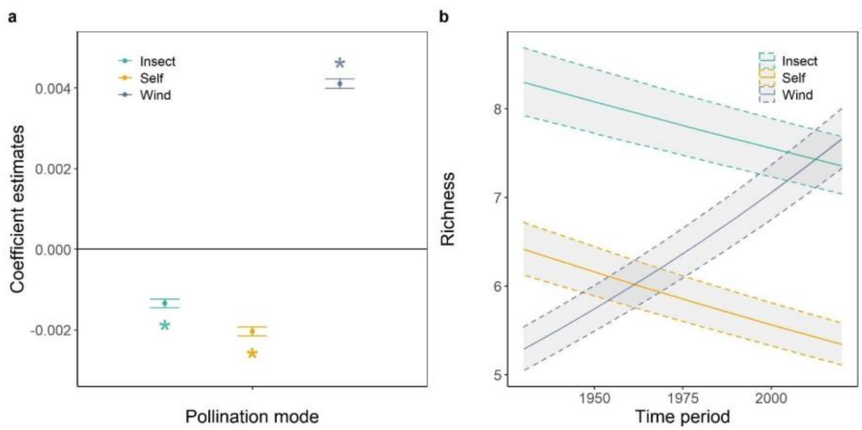

Figure S5 Shifts in the richness of facultative pollination modes in resampled plots over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S5). In a, asterisks mean statistically significant ($P < 0.05$).

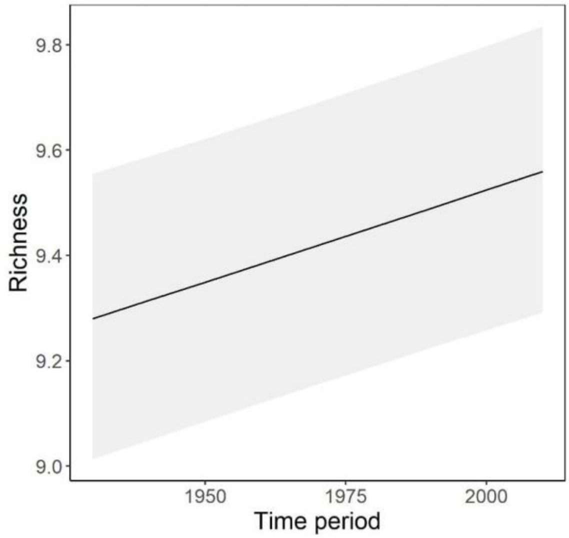

Figure S6 The total richness of three obligate pollination modes (obligate insect-, wind- and self-pollination) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S6).

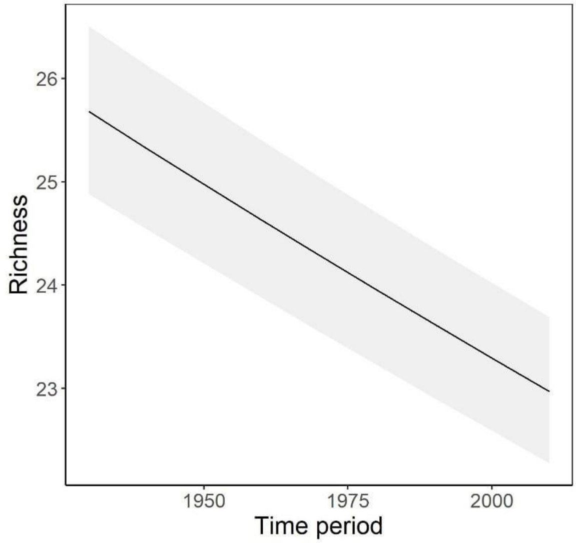

Figure S7 The total richness of three facultative pollination modes (facultative insect, wind and self) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S6).

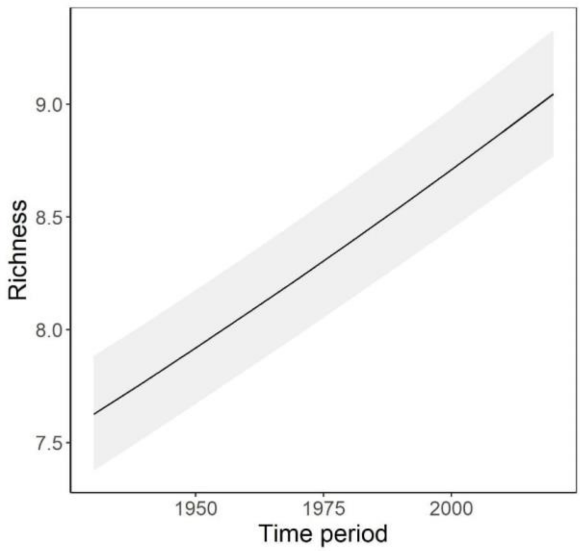

Figure S8 The total richness of three obligate pollination modes (obligate insect-, wind- and self-pollination) in resampled plots (same location but recorded in different years) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S7).

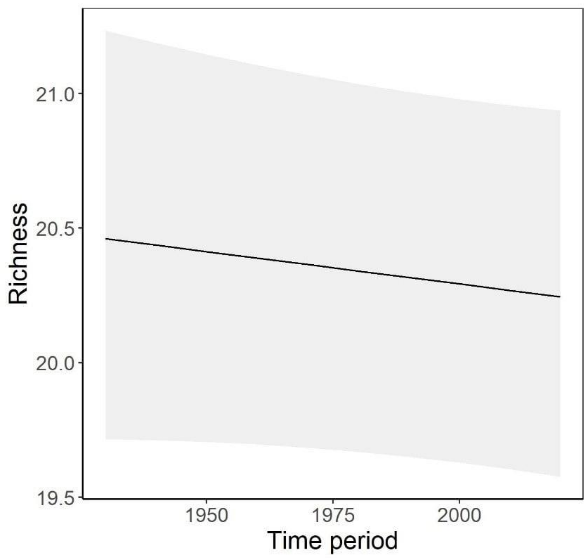

Figure S9 The total richness of three facultative pollination modes (facultative insect, wind and self) in resampled plots (same location but recorded in different years) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S7).

References

R Core Team (R Foundation for Statistical Computing, 2020). *R: A language and environment for statistical computing*.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M. & Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *RJ*, **9**, 378–400.