



Royal Netherlands Academy of Arts and Sciences (KNAW) KONINKLIJKE NEDERLANDSE AKADEMIE VAN WETENSCHAPPEN

The distributions of insect, wind and self pollination of plants in the Netherlands in relation to habitat types and 3D vegetation structure.

Pan, Kaixuan; Marshall, Leon; Biesmeijer, Koos; de Snoo, Geert R.

published in

Journal of Pollination Ecology
2022

DOI (link to publisher)

[10.26786/1920-7603\(2022\)684](https://doi.org/10.26786/1920-7603(2022)684)

document version

Publisher's PDF, also known as Version of record

document license

CC BY

[Link to publication in KNAW Research Portal](#)

citation for published version (APA)

Pan, K., Marshall, L., Biesmeijer, K., & de Snoo, G. R. (2022). The distributions of insect, wind and self pollination of plants in the Netherlands in relation to habitat types and 3D vegetation structure. *Journal of Pollination Ecology*, 30(3), 16-28. [https://doi.org/10.26786/1920-7603\(2022\)684](https://doi.org/10.26786/1920-7603(2022)684)

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the KNAW public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the KNAW public portal.

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

pure@knaw.nl

THE DISTRIBUTIONS OF INSECT, WIND AND SELF POLLINATION OF PLANTS IN THE NETHERLANDS IN RELATION TO HABITAT TYPES AND 3D VEGETATION STRUCTURE

Kaixuan Pan^{1*}, Leon Marshall^{2,3}, Koos Biesmeijer^{1,2}, Geert R. de Snoo^{1,4}

¹*Institute of Environmental Sciences, Leiden University, Leiden, The Netherlands*

²*Naturalis Biodiversity Center, Leiden, The Netherlands*

³*Agroecology Lab, Université libre de Bruxelles (ULB), Brussels, Belgium*

⁴*Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands*

Journal of Pollination Ecology,
31(3), 2022, pp 16-28

DOI: [10.26786/1920-7603\(2022\)684](https://doi.org/10.26786/1920-7603(2022)684)

Received 28 December 2021,
accepted 16 March 2022

*Corresponding author:
k.pan@cml.leidenuniv.nl

Abstract—Plants can be pollinated in many ways, with insect, wind and selfing as the most common modes. While it seems likely that the occurrence of pollination modes is correlated with environmental conditions, e.g. vegetation structure, and this remains uncertain. Here, we mapped the composition of pollination modes of different plant groups (woody species, herbs, and grasses) across (semi-)natural habitats and their distributions in relation to 3D vegetation structure in the Netherlands. We found insect pollination is the most common mode across (semi-)natural habitats for woody species and herbs. Woody species pollinated by insects showed an even higher percentage in dune, river swamp and swamp peat than in other habitat types, whereas herbs showed a higher percentage of insect pollination in dune than in other habitat types. Grasses were always pollinated by wind or wind-self in all habitats. Woody plants pollinated by wind showed a positive relationship with canopy densities in three different strata from 2 to 20 m vegetation, while insect pollination showed a positive relationship with the canopy density of 0.5 to 2 m vegetation. All grass presented negative relationships with canopy density. Herbs showed different relationships with canopy densities of different strata dependent on pollination modes. Insect-pollinated species increased with canopy densities of low strata but decreased with canopy density of high strata, whereas wind-pollinated species decreased with canopy density of both low and high strata. We conclude that habitat and vegetation structure are important factors driving the distribution of pollination modes.

Keywords—Pollination mode, Vascular plants, (Semi-)natural habitats, Vegetation structure, Growth form, Spatial distribution

INTRODUCTION

Pollination is a critical event in the reproduction of flowering plants (Shivanna & Tandon 2014). Insect pollination (allogamy), wind pollination (allogamy) and self pollination (autogamy) account for the majority of plant species in temperate areas (Kühn et al. 2006). The importance of animal pollination for plant species is well documented, particularly regarding insect pollinations (Ollerton et al. 2011; Briggs et al. 2019), while the importance of wind and self pollination are less reported. Although, at the global scale, most flowering plants (around 80%) depend on

insect pollination, wind pollination is still essential for the reproduction of approximately 12% plants (Ollerton et al. 2011; Rodger et al. 2021). In addition, most insect or wind-pollinated plants are also auto-fertile (potentially self-pollinated), and 9% flowering plants are mainly auto-fertility (Rodger et al. 2021). However, it is not clear whether this pattern of occurrence in pollination modes (insect >> wind > self) is consistent across different semi-natural habitats at the local scale. We hypothesize that the occurrence of pollination modes varies across semi-natural habitats, because they also differ in their use intensity, their biotic and abiotic conditions (Culley et al. 2002; Kühn et

al. 2006; Rech et al. 2016). In addition, differences in pollinator abundance and diversity between habitats may affect the occurrence of pollination modes (Taki et al. 2011; Winfree et al. 2011).

Until now, many studies have shown that environmental conditions, including temperature, wind speed, humidity and precipitation, influence the spatial patterns in pollination modes. For example, the occurrence of insect and wind pollination varies with proportions of distinct habitat types (Kühn et al. 2006), temperature, precipitation and plant richness (Kühn et al. 2006; Hoiss et al. 2012; Rech et al. 2016). Self pollination is considered to provide reproductive assurance (Schoen et al. 1996; Kalisz et al. 2004; Rech et al. 2018), particularly in poor environments (e.g. pollinators or mates are absent; Baker 1955).

Furthermore, the effect of 3D vegetation structure, which means the canopy densities of different vegetation strata, is likely to be an important factor driving the variation in richness of pollination modes in different communities. Although some studies suggest vegetation structure (openness of a habitat) might be an important driver (Culley et al. 2002; Kühn et al. 2006; Varassin & Sazima 2012; Rech et al. 2016), it remains unclear how the occurrence of pollination modes changes with the density of vegetation.

Vegetation structure is suggested to be highly influential for insect pollinator diversity (Aguirre-Gutiérrez et al. 2017) due to the different microclimatic conditions it can represent, e.g. temperature, light and moisture (Luskin & Potts 2011; Varassin & Sazima 2012; Frenne et al. 2013). In addition, vegetation structure may affect the availability of nesting and feeding resources of pollinators (Grundel et al. 2010; Berg et al. 2011; Montero-Castaño & Vilà 2012; Varassin & Sazima 2012). It is unclear to what extent vegetation structure may be a more important explanatory factor to understand the richness of pollination modes than habitat classifications. However, pollination modes are non-randomly distributed among plant growth forms and types. Grasses are only wind-pollinated, whereas the frequency of insect and wind pollination among woody species and herbs may also be different. This in turn may determine the relationship with habitat type and vegetation structure, with wind pollination more effective in open, windy habitats and insect

pollination more effective in insect-rich areas (Rech et al. 2016).

In this study, we address two questions: (i) What is the distribution of the composition of insect, wind and self pollination across Dutch (semi-)natural habitats, and whether this distribution varies between woody plants, grasses and herbs? We expect a higher proportion of insect pollination in open habitats while a higher proportion of wind pollination in grassland and forested habitats. (ii) Is there a correlation between 3D vegetation structure and the occurrence of each pollination mode within (semi-)natural habitats, and does this vary for woody plants, grasses, and herbs? We expect that the richness of insect-pollinated plants will increase with herb layers while wind-pollinated species will either increase with grassland or forest habitats, and these relationships may vary between woody plants, grasses and herbs. Finally, we assessed the interaction between habitat type and 3D vegetation as determinants of pollination mode occurrence.

MATERIALS AND METHODS

HABITAT TYPES

To derive a complete national dataset from which habitat types could be obtained, we extracted 175 different habitat types at the country scale from three national sources: *Informatiemodel natuurbeheer* (Inter Provinciaal Overleg 2016), *basisregistratie gewaspercelen* (Ministerie van Economische Zaken (EZK) 2015), and *bestand bodemgebruik* (Centraal Bureau voor de Statistiek (CBS) 2012) using ESRI ArcGIS Desktop 10.2 (<https://desktop.arcgis.com/en/>). These 175 classes were aggregated into 15 habitat types, within which 7 are natural or semi-natural habitats, at a resolution of 10 × 10 m. However, as most vegetation plots were sampled in natural or semi-natural areas, we retained plots in 7 natural and semi-natural habitat types to further compare the distribution of plants pollinated by three different modes. The following habitats are included in this study: Dune (coastal dune habitats), Heather (heathlands with shrubs and woody elements managed as nature but often through sheep grazing), River swamp (swamps and marshlands along the rivers and streams, mosaic of open and woody elements), Semi-natural forest (forests with

primarily nature function), Semi-natural grassland (grasslands with primarily nature function but often managed extensively through grazing), Swamp peat (marshes and swamps in both peaty inland areas and brackish coastal areas) and Production forest (forests with both a production and nature function). The data of habitat types was rescaled to 100×100 m, and only grid cells with 100% of a single habitat type were kept to make sure habitat types precisely matched the vegetation plots.

VEGETATION STRUCTURE DATA

LIDAR data were used to analyse the vegetation structure across the Netherlands. We used four different strata of vegetation heights (0.5-2, 2-5, 5-10 and 10-20 m) and calculated the canopy density of each stratum in each grid cell with 100×100 resolution. It means a grid cell with dense forests will have a high value in the 10-20 m category and probably in the 5-10 m as well and may have low values in the 0.5-2 m layer representing the herb and shrub layers. The data was calculated from nationwide LIDAR data in the Netherlands (<http://www.ahn.nl>) collected from

2007 to 2012. For a full description of the vegetation structure calculation, see (Aguirre-Gutiérrez et al. 2017).

PLANT COMMUNITY DATA

We obtained vegetation plot data representing vascular plant species composition across the Netherlands from 2010-2017 to match with the habitat and vegetation structure data. The vegetation data originate from the Dutch Vegetation Database (Hennekens 2018). Following Večeřa (Večeřa et al. 2021), plots without georeferenced information or without sample size (i.e. the size of each sampled plot) or sample size $< 1 \text{ m}^2$ or $> 1,000 \text{ m}^2$ were excluded from this study. Based on these criteria, the dataset comprised 1,249 native species in 53,011 plots located in 33,289 grid cells with 1 ha area. These plots were assigned to grid cells of 100 m^2 to match with the habitat and vegetation structure data. The final filtered dataset, matched with the habitat types and vegetation structure data, contained 904 species in 11,937 georeferenced plots with sample sizes ranging from 1 to $1,000 \text{ m}^2$ (Fig. 1). These ranges reflect the sample sizes traditionally used

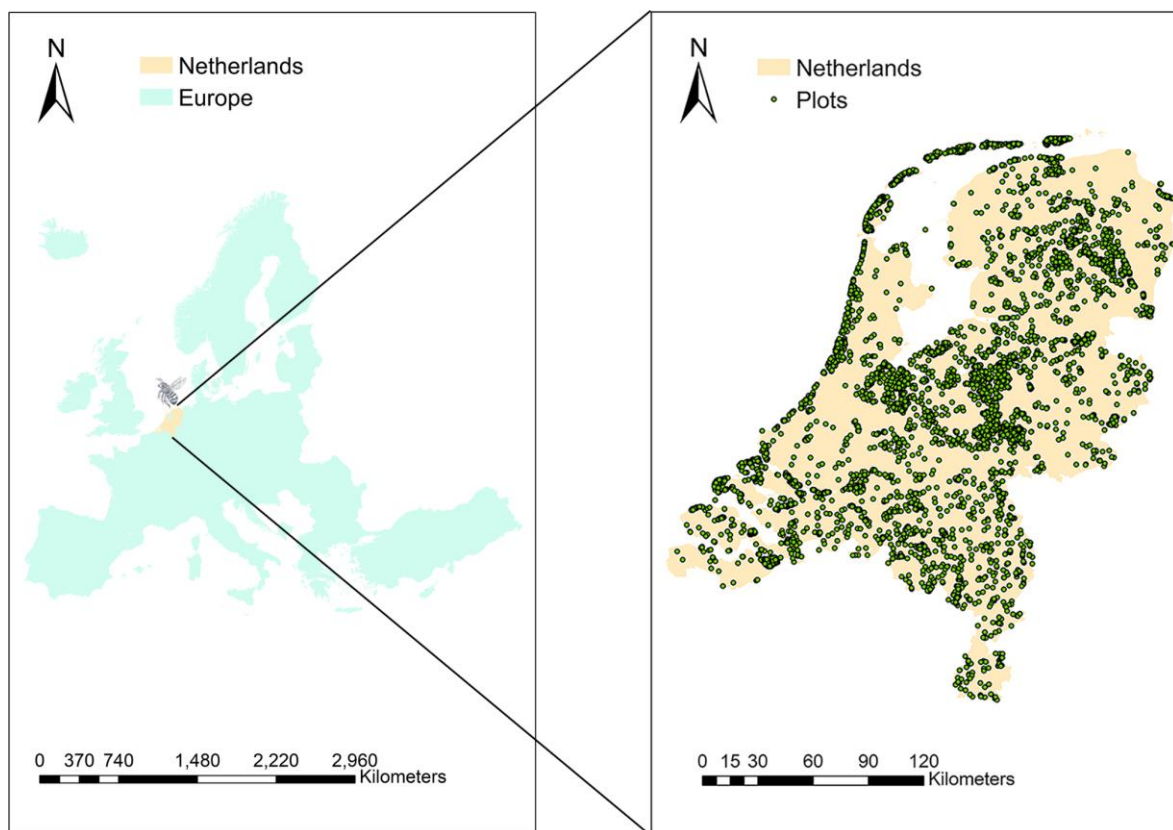


Figure 1. The distribution of 11,937 plots with coordinates and sample sizes between $1\text{-}1000 \text{ m}^2$ and matched with the habitat types map. Map projection: EPSG:28992, Amersfoort / RD New.

by the European phytosociology (Westhoff et al. 1978) to capture plant species in ecosystems from grassland to forest, and the datasets have been used in other studies (Hämmerle et al. 2018; Večeřa et al. 2021).

POLLINATION MODES AND GROWTH FORMS

Data of pollination modes were collected from Biobase (CSB 2003), which includes pollination modes of all Dutch vascular plants. Pollination modes were classified into insect pollination, wind pollination and self-pollination, and all plants were adapted to a binary classification in consideration of each of three pollination modes (Table 1). Further, specialization in pollination mode (named specialized insect pollination, specialized wind pollination and specialized self pollination) was assigned to plants that exhibit only one pollination mode. Pollination modes were attributed to every plant species observed in each plot. However, pollination modes are non-randomly distributed among plant growth forms and types. Grasses are only wind-pollinated, whereas the frequency of insect and wind pollination among woody species and herbs may also be different. This in turn may determine the relationship with habitat type and vegetation structure. Moreover, the effectiveness of pollination also depends on the type of plant. A woody plant species pollinated by wind is less likely to be affected by the cover of upper vegetation layer in a habitat, whereas for a herb or grass, wind pollination may be hampered by high vegetation surrounding it. Thus, we obtained data of growth forms, which includes herbs, grasses (grasses here refer to all grass-like plants in the families Poaceae (grasses), Juncaceae (rushes) and Cyperaceae (sedges)) and woody species, from Biobase (CSB 2003). The numbers of plant species pollinated by different modes in different growth form groups were in Table 1.

PERCENTAGE OF SPECIES WITH DIFFERENT POLLINATION MODES IN ALL GRID CELLS AND 7 (SEMI-)NATURAL HABITATS

In each grid cell, we first calculated the number of species pollinated by different modes in each plot within the grid cell. Second, since there might be more than one plot in each grid cell, we calculated the average number of species pollinated by different modes based on all plots in each grid cell. Third, averaged richness of species pollinated by different pollination modes were calculated based on richness of different pollination modes in all grid cells in each habitat type. The Euclidean distances between habitats were calculated by functions of `acom` and `dist` from package `compositions` (version 2.0-1) (van den Boogaart & Tolosana-Delgado 2008) and `hclust` function with the `ward.D2` method was used to get clusters of seven habitat types by the package `stats` (version 4.1.2) (R Core Team 2013). Since there are only 3 pollination modes, within which either wind or self pollination counted a lower proportion than the other two pollination modes in all habitat types, the maximum number of clusters was limited to 3 (i.e. the proportion of animal pollination = the proportion of wind pollination or self pollination, the proportion of animal pollination > the proportion of wind pollination or self pollination, the proportion of animal pollination < the proportion of wind pollination or self pollination). The number of clusters were obtained based on three criteria: (1) if (the minimum proportion of animal pollination - the maximum proportion of wind pollination or self pollination) > 0.5, we only kept 1 cluster, (2) if -0.5 <= (the minimum proportion of animal pollination - the maximum proportion of wind or self pollination) <= 0.5, we kept 2 clusters, (3) if -0.5 < (the minimum proportion of animal pollination - the maximum proportion of wind or self pollination), we kept 2 clusters, we kept 3 clusters.

Table 1. The number of species with different pollination modes and growth forms.

Pollination_mode	Herb	Grass	Woody (Tree/Shrub)
Insect	526	0	79 (17/62)
Wind	66	173	48 (41/7)
Self	387	7	23 (3/20)
Specialized insect	159	0	51 (10/41)
Specialized wind	22	166	42 (37/5)
Specialized self	14	0	0

A ternary plot (Hamilton & Ferry 2018) was used to compare which species group accounts for a higher percentage in each grid cell and habitat type.

DRIVERS OF 3D VEGETATION STRUCTURE ON THE DIVERSITY OF SPECIES POLLINATED BY DIFFERENT MODES

We assessed bivariate correlations among four variables of vegetation structure (canopy densities of 0.5-2, 2-5, 5-10 and 10-20 m vegetation strata) and found none of them with high correlations (Pearson's correlation coefficients $> |.7|$, (Dormann et al. 2013)). We further assessed multivariate correlations among predictors using VIFs (Variance inflation factors). We interpret our results using a conventional cutoff for VIF of 10.0. Finally, four variables were included in the final set of variables used during the modelling step.

We used a generalized linear mixed model with a poisson distribution to assess whether and how 3D vegetation structure drives the diversity of species pollinated by different pollination modes at a landscape level. Canopy densities of 0.5-2, 2-5, 5-10 and 10-20 m vegetation strata were taken as fixed effects. Since more than one plot may fall in the same 100×100 m grid cell and vegetation plots in our datasets were of different sizes, we used grid cell identity and sample size as random factors. All analyses were conducted in R (version 4.1.0) (R Core Team 2013) with the package *glmmTMB* (version 1.1.2.2) (Magnusson et al. 2017; Brooks et al. 2017).

We compared the importance of vegetation structure on driving the occurrence of pollination modes to habitat type to make this study comparable to peer-reviewed papers emphasizing the effect of habitat (e.g. (Kühn et al. 2006)). Since we only want to know the influential effects of vegetation structure and habitat on the richness of all plants pollinated by different modes in a community, analysis was conducted based on all plants instead of different plant types. We first constructed a full generalized linear mixed model (m1) with a poisson distribution. This model includes habitat type (a categorical variable including dune, heather, semi-natural grassland, river swamp, swamp peat, semi-natural forest and production forest) and four vegetation structure variables (canopy densities of 0.5-2, 2-5, 5-10 and 10-20 m vegetation strata) as fixed effects. Interactions between habitat type and vegetation

structure were included. Grid cell identity and sample size were maintained as random effects. Second, we constructed three other generalized linear mixed models by excluding interactions between habitat and vegetation structure (m2), removing canopy densities of four vegetation strata (m3) and habitat type (m4) from the full model each time, and each of these three models was compared to the full model (m1) by ANOVA. A model with a significantly larger AIC (Akaike information criterion) value than the full model (m1) means the excluded interaction or removed variable is significantly important.

RESULTS

DISTRIBUTION OF POLLINATION MODES COMPOSITION ACROSS DUTCH (SEMI-)NATURAL HABITATS

Across all (semi-)natural habitats in the Netherlands, insect-pollinated species (35%) and wind-pollinated species (38%) were more common than self-pollinated species (27%) (Appendix IV). Wind-pollinated species were more common in heather (49%) and production forest (43%) (Fig. 2A). Insect-pollinated species were more common in dune (40%) and river swamp (42%) (Fig. 2A). There was much variation between the different plots within habitat types (Appendix V A). For plants specially pollinated by one mode, wind pollination was most common in all habitats (Appendix VI A, Appendix VII A).

When splitting plants into different groups of growth type, insect pollination was the most common pollination mode across (semi-)natural habitats for woody species and herbs (Fig. 2B-C, Appendix V B-C). However, the insect pollination of woody species in dune, river swamp and swamp peat were more common than in other habitat types, whereas insect pollination of herbs in dunes was more common than in other habitats. Wind pollination was the most common pollination mode across (semi-)natural habitats for grasses (Fig. 2D, Appendix V D).

THE DISTRIBUTION OF POLLINATION MODES RELATED TO 3D VEGETATION STRUCTURE

In our final generalized linear mixed model with 904 plant species, we included canopy densities of 4 vegetation strata as fixed effects. Grid identity and sample sizes were taken as random effects.

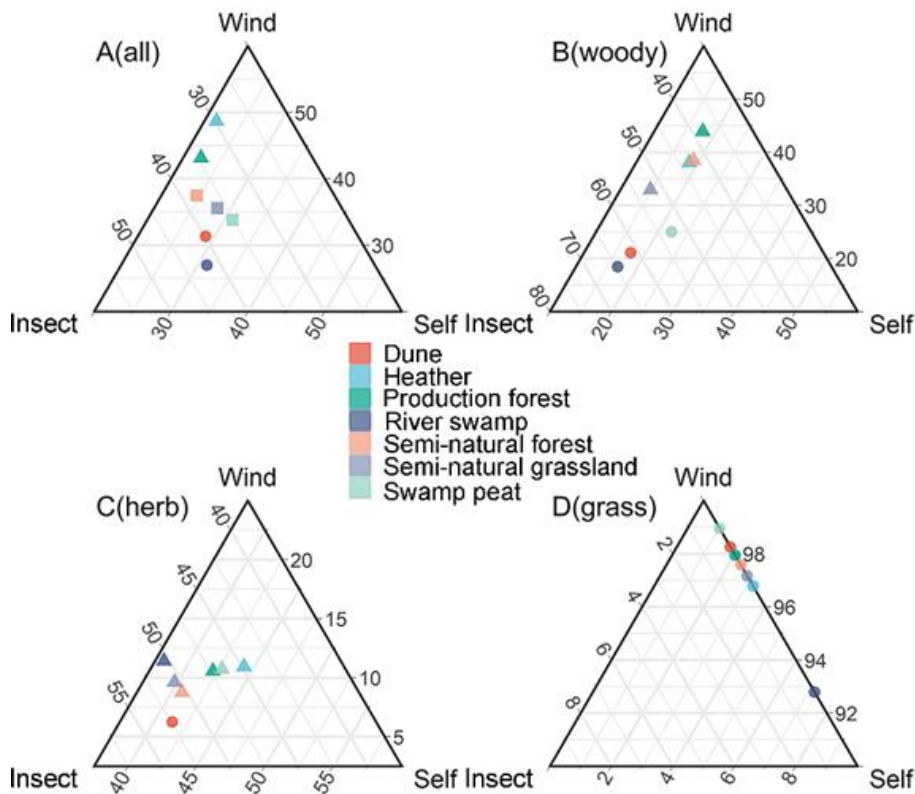


Figure 2. Percentages of species with different pollination modes in each of seven habitat types for (A) all plants, (B) woody species, (C) herbs and (D) grasses. In this ternary graph, different colours indicate different habitat types and different shapes mean statistically different clusters (cluster analysis by compositions). The average number of species in each habitat type can be found in Appendix I.

Our model showed that of 904 plant species, insect and self-pollinated species showed similar patterns and increased with denser herb and shrub (strata < 5 m) layers (Fig. 3A, Appendix VIII), whereas they decreased if the canopy density of high strata (> 5 m) increased. Wind-pollinated plants, on the other hand, decreased with denser canopy of low strata. Specialized insect-pollinated plants also increased with canopy density of low vegetation strata (< 5 m) but decreased with canopy density of high vegetation strata (Fig. 3B, Appendix XII).

For woody species, only wind-pollinated plants decreased with denser vegetation canopy of low strata (< 2 m height) (Fig. 4A, Appendix IX). Grasses, no matter if they are wind or self-pollinated, decreased with denser canopy density (Fig. 4E, Appendix X). For herbs, insect and self-pollinated species showed similar patterns. Both decreased with denser vegetation layers between 5 and 20 m (Fig. 4C, Appendix XI), whereas insect-pollinated plants increased with canopy density of low strata (< 5 m). Wind-pollinated herbs decreased with denser 0.5-2 m and 10-20 m vegetation.

Woody plants only had two specialized pollination modes (i.e. insect and wind) (Fig. 4B,

Appendix XIII). Insect-pollinated woody plants increased with denser canopy of low strata (< 5 m) but decreased with denser tree layer (> 10 m). In contrast, wind-pollinated plants increased with canopy density of strata above 2 m but decreased with canopy density of strata below 2 m. Wind-pollination was the only specialized pollination mode of grasses (Fig. 4F, Appendix XIV), which decreased with the canopy density of high strata (> 5 m). Although there were three specialized pollination modes of herbs (Fig. 4D, Appendix XV), only insect-pollinated species showed significant patterns. Those species increased with canopy density of strata from 2 to 5 m but decreased with denser canopies of other vegetation strata.

When comparing the influence of vegetation structure on the occurrence of pollination mode to habitat type, we found that although habitat type was more important than vegetation structure, both had a strong influence on the occurrence of the different pollination modes and that their relationship was not independent since removing either of habitat or vegetation structure or their interactions will make the AIC value higher (Table 2, Appendix XVI- XVII).

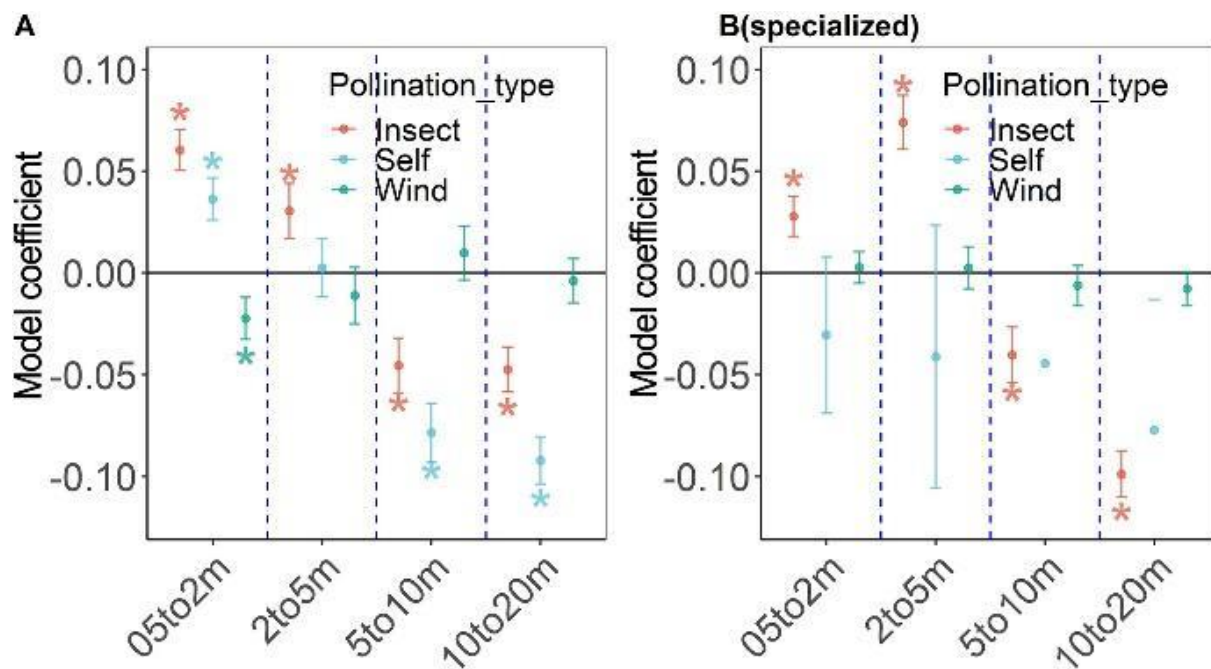


Figure 3. Model coefficients from the generalized linear mixed model (GLMM) of species richness in relation to canopy densities of four vegetation strata. Analysis was conducted within (A) three groups of insect pollination, wind pollination and self pollination and (B) three groups of specialized insect pollination, specialized wind pollination and specialized self pollination. 0.5to2m means the canopy density of 0.5-2 m vegetation strata. 2to5m means the canopy density of 2-5 m vegetation strata. 5to10m means the canopy density of 5-10 m vegetation strata. 10to20m means the canopy density of 10-20 m vegetation strata. Y axes indicate coefficients of predictors, which are also listed in Appendix II.

DISCUSSION

THE DISTRIBUTION OF POLLINATION MODES COMPOSITION ACROSS DUTCH (SEMI-)NATURAL HABITATS

The pattern of pollination modes over the whole Netherlands is different from that found in Germany (Kühn et al. 2006), where less wind and self pollination were found. More wind-pollinated plants in the Netherlands might be due to flatter landscapes as indicated in previous studies (Kühn et al. 2006; Rech et al. 2016). However, the finer scale used in our study may also explain part of the difference.

We further detected different distributions of three pollination modes in seven (semi-)natural habitat types, and the distributions were different between woody plants, herbs and grasses. Insect pollination is more common in dunes and river swamp habitats, while wind pollination is more common in open heathland, probably because of the high proportion of grasses, and production forest, which is less diverse in plants and insect pollinators than semi-natural forest (Aubin et al. 2008; Taki et al. 2011). Our study supports the hypothesis of Rech et al. (2016) that higher plant

diversity in a habitat contributes to higher insect pollination, as the Dutch dunes and river swamps have more plant species, while heathland and forest are often dominated by (dwarf) shrubs and trees. Fewer insect pollinators may contribute to a failure of insect pollination in forests (Winfree et al. 2011; Hanula et al. 2016).

Within plant types, pollination modes showed different distributions among habitats. Woody species largely mirrored the pattern of all plants with insect pollination being more common in dunes and river swamp, but also in swamp peat habitats. Most woody species in these habitats are shrubs, which are insect-pollinated, whereas the main big trees in production forest (and semi-natural forest) tend to be wind-pollinated (Regal 1982). Grasses are a main feature of semi-natural grassland and heathland and are wind-pollinated. This may explain the higher frequency of wind pollination in these habitats compared to dunes, river swamp and swamp peat. Herbs show quite different patterns compared to all plants. Insect pollination is the most common pollination mode of herbs across all (semi-)natural habitats, particularly in dunes.

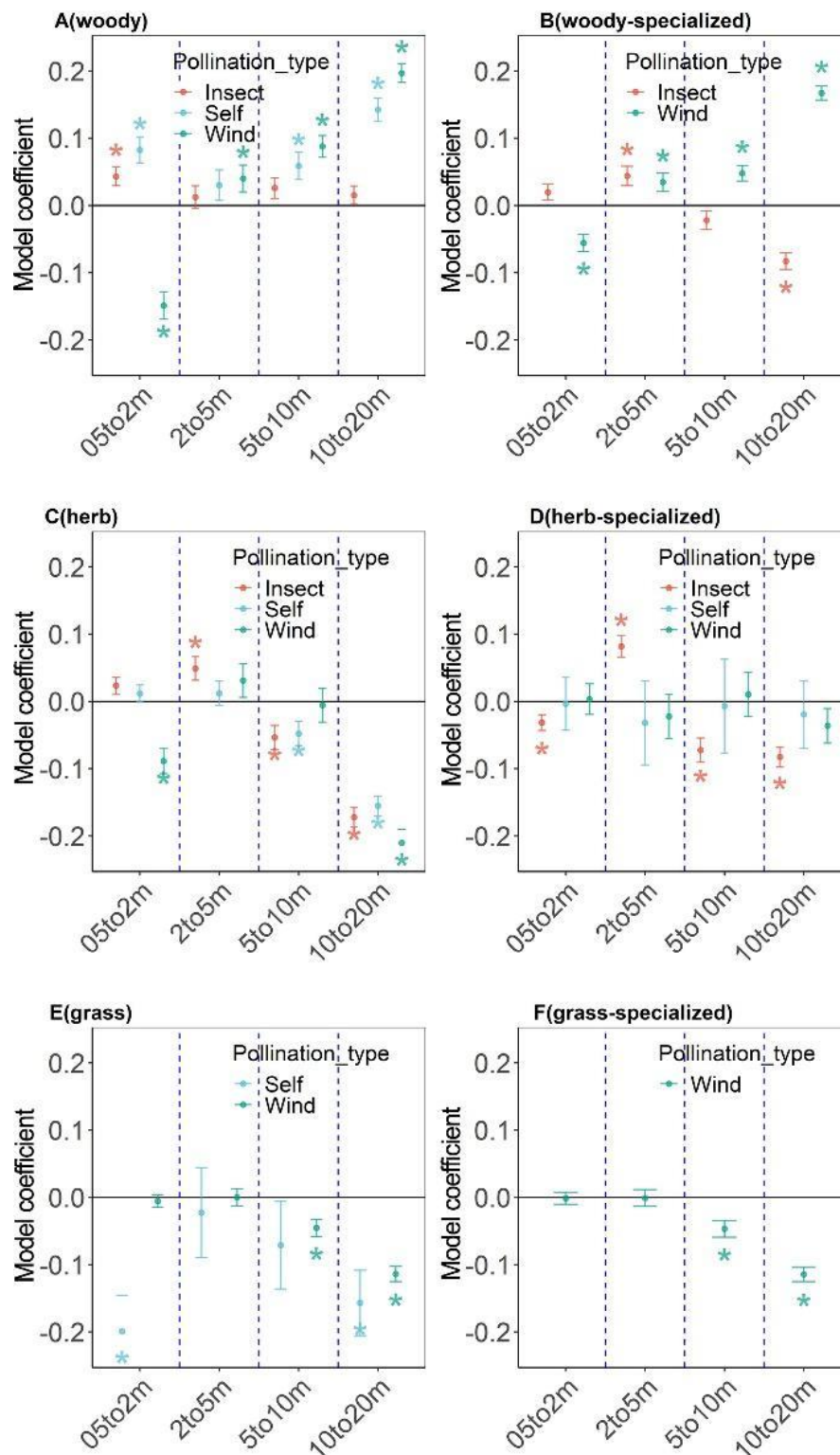


Figure 4. Model coefficients from the generalized linear mixed model (GLMM) of species richness in relation to canopy densities of four vegetation strata. A-B, for woody species with analysis conducted (A) within three groups of insect pollination, wind pollination and self pollination and (B) within three groups of specialized insect pollination, specialized wind pollination and specialized self pollination. C-D, for herbs with analysis conducted (C) within three groups of insect pollination, wind pollination and self pollination and (D) within three groups of specialized insect pollination, specialized wind pollination and specialized self pollination. E-F, for grasses with analysis conducted (E) within three groups of insect pollination, wind pollination and self pollination and (F) within three groups of specialized insect pollination, specialized wind pollination and specialized self pollination. 0.5to2m means the canopy density of 0.5- 2 m vegetation strata. 2to5m means the canopy density of 2-5 m vegetation strata. 5to10m means the canopy density of 5-10 m vegetation strata. 10to20m means the canopy density of 10- 20 m vegetation strata. Y axes indicate coefficients of predictors, which are also listed in Appendix II.

Table 2. Comparisons between each individual model (m2-m4) and the full model (m1). m1: richness ~ canopy densities of 0.5-2 m vegetation * habitat type + canopy densities of 2-5 m vegetation * habitat type + canopy densities of 5-10 m vegetation * habitat type + canopy densities of 10-20 m vegetation * habitat type. m2: richness ~ canopy densities of 0.5-2 m vegetation + canopy densities of 2-5 m vegetation + canopy densities of 5-10 m vegetation + canopy densities of 10-20 m vegetation + habitat type. m3: richness ~ habitat type. m4: richness ~ canopy densities of 0.5-2 m vegetation + canopy densities of 2-5 m vegetation + canopy densities of 5-10 m vegetation + canopy densities of 10-20 m vegetation.

Specialized	Pollination mode	Model	AIC	P.Value (compare to m1)	Significance
	Insect	m1	61097.08	-	*
-	Insect	m2	61171.36	0	*
-	Insect	m3	61279.10	0	*
-	Insect	m4	62543.69	0	*
	Self	m1	55183.43	-	*
-	Self	m2	55243.16	0	*
-	Self	m3	55323.67	0	*
-	Self	m4	56447.58	0	*
-	Wind	m1	56167.93	-	*
-	Wind	m2	56273.08	0	*
-	Wind	m3	56289.06	0	*
-	Wind	m4	57366.12	0	*
Specialized	Insect	m1	26532.72	-	*
Specialized	Insect	m2	26533.91	0.002	*
Specialized	Insect	m3	26627.18	0	*
Specialized	Insect	m4	26664.11	0	*
Specialized	Self	m1	2687.69	-	
Specialized	Self	m2	2640.07	1	
Specialized	Self	m3	2633.05	1	
Specialized	Self	m4	2629.68	1	
Specialized	Wind	m1	51872.57	-	*
Specialized	Wind	m2	51928.90	0	*
Specialized	Wind	m3	51934.45	0	*
Specialized	Wind	m4	52878.98	0	*

3D VEGETATION STRUCTURE IS CORRELATED WITH THE OCCURRENCE OF POLLINATION MODES

According to previously published studies, pollination mode can be explained by wind speed, temperature, humidity, precipitation, plant richness and openness of habitats. In this study, we found that plants using insect pollination increased with denser vegetation in low strata and decreased with denser vegetation in high strata. This is in line with previous findings. For example, dense canopies in high strata may cause a lower temperature underneath, which decreases nectar production by understory plants and affects pollinator foraging (Polatto et al. 2014; Hanula et al. 2016; Rech et al. 2016) and limits pollinator flight ability and activity (Hodkinson 2005). In fact, forest understories are often poor in plant species (Rech et al. 2016).

Wind pollination decreased with increasing canopy density in the 0.5-2 m vegetation stratum, probably because wind-pollinated species benefit from more open vegetation for pollen dispersal (Culley et al. 2002; see also Kühn et al. 2006; Rech et al. 2016). Rech et al. (2016) hypothesize that wind pollination is facilitated by open vegetation as denser vegetation in high strata might mechanically restrict pollen dispersal.

We found that woody species, herbs and grasses differ in their correlation with 3D vegetation structure. Compared to all plants, woody species pollinated by wind have positive correlations with canopy densities of 2-20 m vegetation. Most of these species are trees, for which wind pollination is less affected by surrounding vegetation. This result is different from (Rech et al. 2016), where wind pollination is more frequent in open fields probably due to more diverse species composition in lower latitude. Insect pollination only increased with canopy density of 0.5-2 m vegetation, which reflects mostly shrubs common in relatively open habitats. However, occurrences of plants that are obligate insect-pollinated increased with canopy density of 2-5 m vegetation but decreased with canopy density of 10-20 m vegetation, probably due to lower abundance and diversity of insect pollinators in forested areas and better wind pollination conditions in opener habitats. Grasses decreased with canopy density of 5-20 m vegetation, probably (as argued above) due to

lower effectiveness of wind pollination (the main pollination mode of grasses) in forests (Culley et al. 2002; Davis et al. 2004; Saunders 2018). Similarly, wind-pollinated herbs also showed negative relationships with canopy densities of both low and high strata, probably because of surrounding shrubs and trees limiting wind pollination. Compared to all plants, herbs pollinated by insects did not show a significant response to the canopy density of 0.5-2 meters. Furthermore, strict insect pollination decreased with the canopy density of 0.5-2 meters probably because too open habitats are suitable for wind pollination instead of insect pollination (Culley et al. 2002).

THE IMPORTANCE OF VEGETATION STRUCTURE ON DRIVING THE OCCURRENCE OF POLLINATION MODES COMPARED TO HABITAT TYPE

Overall, we found that insect pollination occurs more frequently in habitats covered by herbs or shrubs than in habitats with dense tree layers. These habitats are often related to dune, river swamp and swamp peat (Appendix III, Appendix XVIII). However, swamp peat has few insect-pollinated species. It means other environmental conditions, e.g. temperature, moisture, light, feeding resources in different habitats are also important factors driving the richness of different pollination modes (Regal 1982; Culley et al. 2002). However, the occurrence of wind pollination in habitats largely depends on different plant types. More wind-pollinated trees occur in habitats with a higher proportion of tree layers, which are corresponding to diverse wind-pollinated species in production forest or semi-natural forest, while grasses occur in open habitats. Our results also showed that although habitat type is important, which was also shown by Kühn et al. (2006), both habitat and vegetation structure are important factors driving the occurrence of different pollination modes and they are not independent. We suggest future studies identifying the effect of land use on pollination mode should not only focus on habitat type, but also vegetation structure and its interactions with habitat type.

CONCLUSION

We show that compositions of pollination modes are different across (semi-)natural habitats. In conclusion, insect pollination is more common in opener habitats, while wind pollination is more common in forested habitats. Within open

habitats, wind pollination is more common in habitats with a higher proportion of grasses. This pattern is slightly different for woody species, herbs and grasses due to different dominating modes for each plant group. For each pollination mode, its occurrence is related to vegetation structure. More insect pollination occurs in habitats covered by herbs or shrubs but not by large trees, whereas the occurrence of wind pollination in habitats with different vegetation structures depends on plant types. More wind-pollinated trees occur in habitats with denser upper layer trees, but grasses are more likely to occur in open habitats. For woody and herb species, specialized insect-pollination has a different response to vegetation structure compared to insect-pollination due to its high dependence on pollinators. Our study reveals that 3D vegetation structure might affect plant richness by affecting pollination modes. Thus, the conservation and management of plant species richness may actually require a different focus depending on pollination modes.

ACKNOWLEDGEMENTS

We thank Jesús Aguirre-Gutiérrez for the processing of the lidar data used in this paper. Kaixuan received the funding from the China Scholarship Council (Grant No. 201806320120). URL: <https://www.chinesescholarshipcouncil.com/>. LM was supported by a F.R.S.-FNRS fellowship “Chargé de recherches”.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. The average number of species in each habitat type.

Appendix II. Estimates from GLMMs.

Appendix III. Canopy densities of four vegetation strata in each habitat type.

Appendix IV. Percentages of species with different pollination modes in each of seven habitat types.

Appendix V. Percentages of species with different pollination modes in all grid cells for (A) all plants, (B) woody species, (C) herbs and (D) grasses.

Appendix VI. Percentages of species with different specialized pollination modes in each of seven habitat types for (A) all plants, (B) woody species, (C) herbs and (D) grasses.

Appendix VII. Percentages of species with different specialized pollination modes in all grid cells for (A) all plants, (B) woody species, (C) herbs and (D) grasses.

Appendix VIII. Responses of richness of all plants with different pollination modes to vegetation structure.

Appendix IX. Responses of richness of woody plants with different pollination modes to vegetation structure.

Appendix X. Responses of richness of grasses with different pollination modes to vegetation structure.

Appendix XI. Responses of richness of herbs with different pollination modes to vegetation structure.

Appendix XII. Responses of richness of all plants with different specialized pollination modes to vegetation structure.

Appendix XIII. Responses of richness of woody plants with different specialized pollination modes to vegetation structure.

Appendix XIV. Responses of richness of grasses with different specialized pollination modes to vegetation structure.

Appendix XV. Responses of richness of herbs with different specialized pollination modes to vegetation structure.

Appendix XVI. Responses of richness of plants with different pollination modes to each variable in the full mode.

Appendix XVII. Responses of richness of plants with different specialized pollination modes to each variable in the full mode.

REFERENCES

- Aguirre-Gutiérrez J, WallisDeVries MF, Marshall L, van't Zelfde M, Villalobos-Arámbula AR, Boekelo B, Bartholomeus H, Franzén M, Biesmeijer JC (2017) Butterflies show different functional and species diversity in relationship to vegetation structure and land use. *Global Ecology and Biogeography* 26:1126–1137.
- Aubin I, Messier C, Bouchard A (2008) Can plantations develop understory biological and physical attributes of naturally regenerated forests? *Biological Conservation* 141:2461–2476. <https://doi.org/10.1016/j.biocon.2008.07.007>.
- Baker HG (1955) Self-Compatibility and Establishment After 'Long-Distance' Dispersal. *Evolution* 9:347.
- Berg Å, Åhrné K, Öckinger E, Svensson R, Söderström B (2011) Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. *Biological Conservation* 144:2819–2831.
- Briggs H, Ayers CA, Armsworth PR, Brosi BJ (2019) Testing how antagonistic interactions impact the robustness of plant-pollinator networks. *Journal of Pollination Ecology* 25. [https://doi.org/10.26786/1920-7603\(2019\)540](https://doi.org/10.26786/1920-7603(2019)540)
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal* 9:378–400. Available

- online at: <https://www.research-collection.ethz.ch/handle/20.500.11850/239870>
- Centraal Bureau voor de Statistiek (CBS) (2012) Bestand Bodemgebruik Productbeschrijving.
- CSB (2003) Biobase 2003. Biodiversity Register. CBS. Voorburg/Heerlen.
- Culley TM, Weller SG, Sakai AK (2002) The evolution of wind pollination in angiosperms. *Trends in Ecology & Evolution* 17:361–369. [https://doi.org/10.1016/S0169-5347\(02\)02540-5](https://doi.org/10.1016/S0169-5347(02)02540-5).
- Davis HG, Taylor CM, Lambrinos JG, Strong DR (2004) Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proceedings of the National Academy of Sciences of the United States of America* 101:13804–13807. <https://doi.org/10.1073/pnas.0405230101>.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JR, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Frenne P de, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J, Decocq GM, Dierschke H, Eriksson O, Gilliam FS, Hédl R, Heinken T, Hermy M, Hommel P, Jenkins MA, Kelly DL, Kirby KJ, Mitchell FJ, Naaf T, Newman M, Peterken G, Petřík P, Schultz J, Sonnier G, van Calster H, Waller DM, Walther G-R, White PS, Woods KD, Wulf M, Graae BJ, Verheyen K (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America* 110:18561–18565.
- Grundel R, Jean RP, Frohnapple KJ, Glowacki GA, Scott PE, Pavlovic NB (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological applications: a publication of the Ecological Society of America* 20:1678–1692.
- Hamilton NE, Ferry M (2018) ggtern: Ternary Diagrams Using ggplot2. *Journal of Statistical Software* 87:1–17. [10.18637/jss.v087.c03](https://doi.org/10.18637/jss.v087.c03).
- Hämmerle AI, Wessely J, Baatar U-O, Essl F, Moser D, Jiménez-Alfaro B, Jandt U, Agrillo E, Stančić Z, Dirnböck T, Dullinger S (2018) A new method for jointly assessing effects of climate change and nitrogen deposition on habitats. *Biological Conservation* 228:52–61.
- Hanula JL, Ulyshen MD, Horn S (2016) Conserving Pollinators in North American Forests: A Review. *Natural Areas Journal* 36:427–439. <https://doi.org/10.3375/043.036.0409>
- Hennekens S (2018) Dutch Vegetation Database (LVD). v1.6. Alterra, Wageningen UR. Dataset/Samplingevent.
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489–513. <https://doi.org/10.1017/S1464793105006767>.
- Hoiss B, Gaviria J, Leingärtner A, Krauss J, Steffan-Dewenter I (2012) Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. *Diversity and Distributions* 19: 386–395. <https://doi.org/10.1111/j.1472-4642.2012.00941.x>.
- Inter Provinciaal Overleg (2016) Informatiemodel natuurbeheer (IMNAB): Index Natuur en Landschap.
- Kalisz S, Vogler DW, Hanley KM (2004) Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. *Nature* 430:884–887. <https://doi.org/10.1038/nature02776>.
- Kühn I, Bierman SM, Durka W, Klotz S (2006) Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. *The New Phytologist* 172:127–139.
- Luskin MS, Potts MD (2011) Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology* 12:540–551.
- Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Benthem K, Bolker B, Brooks M (2017) glmmTMB: Generalized Linear Mixed Models using Template Model Builder. R Package Version 0.2.0. Available online at: <https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf>.
- Ministerie van Economische Zaken (EZK) (2015) Basisregistratie Gewaspercelen (BRP).
- Montero-Castaño A, Vilà M (2012) Impact of landscape alteration and invasions on pollinators: a meta-analysis. *Journal of Ecology* 100:884–893. <https://doi.org/10.1111/j.1365-2745.2012.01968.x>
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- Polatto LP, Chaud-Netto J, Alves-Junior VV (2014) Influence of Abiotic Factors and Floral Resource Availability on Daily Foraging Activity of Bees. *Journal of Insect Behavior* 27:593–612. Available online at: <https://doi.org/10.1007/s10905-014-9452-6>
- R Core Team (2013) R: A language and environment for statistical computing.
- Rech AR, Dalgaard B, Sandel B, Sonne J, Svenning J-C, Holmes N, Ollerton J (2016) The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. *Plant Ecology & Diversity* 9:253–262.
- Rech AR, Jorge LR, Ollerton J, Sazima M (2018) Pollinator availability, mating system and variation in

- flower morphology in a tropical savanna tree. *Acta Botanica Brasiliica* 32:462–472. <https://doi.org/10.1590/0102-33062018abb0220>.
- Regal PJ (1982) Pollination by Wind and Animals: Ecology of Geographic Patterns. *Annual Review of Ecology, Evolution, and Systematics* 13:497–524.
- Rodger JG, Bennett JM, Razanajatovo M, Knight TM, van Kleunen M, Ashman T-L, Steets JA, Hui C, Arceo-Gómez G, Burd M, Burkle LA, Burns JH, Durka W, Freitas L, Kemp JE, Li J, Pauw A, Vamasi JC, Wolowski M, Xia J, Ellis AG (2021) Widespread vulnerability of flowering plant seed production to pollinator declines. *Sci. Adv.* 7:eabd3524.
- Saunders ME (2018) Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. *Insect Conservation and Diversity* 11:13–31. <https://doi.org/10.1111/icad.1224>.
- Schoen DJ, Morgan MT, Bataillon T. (1996) How does self-pollination evolve? Inferences from floral ecology and molecular genetic variation. *Philosophical Transactions of the Royal Society B* 351:1281–1290.
- Shivanna KR, Tandon R (2014) Pollination Ecology. In: Shivanna K (ed) *Reproductive ecology of flowering plants. A manual*. Springer, New York, pp 63–96.
- Taki H, Yamaura Y, Okabe K, Maeto K (2011) Plantation vs. natural forest: matrix quality determines pollinator abundance in crop fields. *Science Reports* 1:132. <https://doi.org/10.1038/srep00132>.
- van den Boogaart KG, Tolosana-Delgado R (2008) “compositions”: A unified R package to analyze compositional data. *Computers & Geosciences* 34:320–338.
- Varassin IG, Sazima M (2012) Spatial heterogeneity and the distribution of bromeliad pollinators in the Atlantic Forest. *Acta Oecologica* 43:104–112. <https://doi.org/10.1016/j.actao.2012.06.001>.
- Večeřa M, Axmanová I, Padullés Cubino J, Lososová Z, Divíšek J, Knollová I, Aćić S, Biurrun I, Boch S, Bonari G, Campos JA, Čarni A, Carranza ML, Casella L, Chiarucci A, Čušterevska R, Delbosc P, Dengler J, Fernández-González F, Gégout J-C, Jandt U, Jansen F, Jašková A, Jiménez-Alfaro B, Kuzemko A, Lebedeva M, Lenoir J, Lysenko T, Moeslund JE, Pielech R, Ruprecht E, Šibík J, Šilc U, Škvorc Ž, Swacha G, Tatarenko I, Vassilev K, Wohlgemuth T, Yamalov S, Chytrý M (2021) Mapping species richness of plant families in European vegetation. *Journal of Vegetation Science* 32.
- Westhoff V, Van der Maarel E, Whittaker RH (1978) *Classification of plant communities*. The Hague.
- Winfrey R, Bartomeus I, Cariveau DP (2011) Native Pollinators in Anthropogenic Habitats. *Annual Review of Ecology, Evolution, and Systematics* 42:1–22.