

Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands

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Evidence for declining populations of both wild and managed bees has raised concern about a potential global pollination crisis. Strategies to mitigate bee loss generally aim to enhance floral resources. However, we do not really know whether loss of preferred floral resources is the key driver of bee decline because accurate assessment of host plant preferences is difficult, particularly for species that have become rare. Here we examine whether population trends of wild bees in The Netherlands can be explained by trends in host plants, and how this relates to other factors such as climate change. We determined host plant preference of bee species using pollen loads on specimens in entomological collections that were collected before the onset of their decline, and used atlas data to quantify population trends of bee species and their host plants. We show that decline of preferred host plant species was one of two main factors associated with bee decline. Bee body size, the other main factor, was negatively related to population trend, which, because larger bee species have larger pollen requirements than smaller species, may also point toward food limitation as a key factor driving wild bee loss. Diet breadth and other potential factors such as length of flight period or climate change sensitivity were not important in explaining twentieth century bee population trends. These results highlight the species-specific nature of wild bee decline and indicate that mitigation strategies will only be effective if they target the specific host plants of declining species.

bee decline | land use change | floral resources | pollen preference | crop pollination

Pollinating insects such as bees play an essential role in the pollination of wild plants (1) and crops (2). However, reported population declines in both wild and managed bees (3–5) have raised concerns about loss of pollination services and triggered interest in identifying the underlying causes for bee decline (6). Land use change and agricultural intensification are major drivers of biodiversity loss in general (7, 8) and are considered the most important environmental drivers of loss of wild bee diversity in particular (6, 9). It is generally believed that these drivers affect bees, which depend on floral resources in both their larval and adult life stages, through repercussions on the availability of floral resources in contemporary anthropogenic landscapes (9–11), but, so far, scientific evidence that loss of floral resources is driving bee decline is lacking. Nevertheless, current strategies to mitigate bee decline focus primarily on enhancing floral resources (12). To prioritize and develop effective mitigation strategies, it is essential to identify the mechanisms underlying bee population trends and assess whether these are mediated by floral resources.

Although bees as a group are declining, individual species show more variable responses, with some species declining sharply while others remain stable or even increase under current land use change and agricultural intensification (3, 4, 13).

These differential responses can be used to disentangle the effects of floral resource availability from those of other potential factors affecting bee population trends. The proportion of the floral resources in contemporary anthropogenic landscapes that can be used for forage by a bee species depends on its diet breadth and host plant preference, and it may be expected that species that have declined have a narrower diet breadth and prefer host plants that have declined (14, 15). However, diet breadth and host plant preference of bee species is difficult to assess. Presently observed host plant use does not necessarily reflect actual preference, as preferred host plants may have gone locally extinct and bees that have declined may have become restricted in their food choice in their remaining habitats (15). In addition, if host plant use is measured for more individuals of abundant, widespread species than for rare ones, an apparent link between diet breadth and population trend may simply arise as a sampling artifact (16). Furthermore, the relationship between host plant use and population trend may be confounded by species' rarity prior to the onset of major environmental changes (17), as rarity in itself increases susceptibility to stochastic events (18) and has been shown to be one of the most important factors predicting population decline in various taxa (19–21). Surprisingly, to our knowledge, none of the studies that have so far examined the relationship between diet breadth and/or host plant preference and bee population trends have taken species' initial rarity into account (e.g., refs. 3, 4, 15, and 22). Other factors, such as body size (4, 23), phenology (4, 22), and

Significance

Growing concern about bee declines and associated loss of pollination services has increased the urgency to identify the underlying causes. So far, the identification of the key drivers of decline of bee populations has largely been based on speculation. We assessed the relative importance of a range of proposed factors responsible for wild bee decline and show that loss of preferred host plant species is one of the main factors associated with the decline of bee populations in The Netherlands. Interestingly, species foraging on crop plant families have stable or increasing populations. These results indicate that mitigation strategies for loss of wild bees will only be effective if they target the specific host plants of declining bee species.

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sensitivity to climate change (4, 24, 25) may be associated with bee decline as well, and, to date, the relative importance of diet breadth and pollen host plant preference in explaining bee population trends remains unclear.

Here we solve this problem by analyzing historical pollen preferences of wild bees (15). Bees are generally more selective in their choice of food plants when foraging for pollen (source of protein and minerals for both larvae and adults) than nectar (source of energy) (26, 27). Distributional changes in plant species from which pollen is collected therefore probably exerts a larger influence on bee populations than changes in nectar plants. We investigate whether and to what extent loss of preferred floral resources drives bee population trends in The Netherlands, one of the most human-modified and intensively farmed countries in the world. Over the course of the twentieth century, agriculture has intensified in The Netherlands (Fig. S1) and the area of seminatural habitat preferred by bees has diminished to only one-fifth of the area at the beginning of the twentieth century (Fig. S2). More than half of the bee species are currently on the national Red List (28). As such, this country is a particularly suitable study area to identify critical factors associated with bee population decline.

We assessed pollen host plant use of bee species independently from their population trends by analyzing pollen loads on the bodies of bee specimens that were collected before 1950 (15), before the onset of agricultural intensification in The Netherlands. Altogether, our analysis included trend and trait data of 57 bee species in 10 genera and 4 subfamilies (Table S1). We calculated population trend indices for bee species and their host plants (period 1902–1949 vs. 1975–1999) using extensive national species distribution datasets (13, 29). Linear mixed models, with bee subfamily as a random factor to account for phylogeny, and a multi-model inference approach were used to examine the relationship between bee population trends and pollen host plant use, simultaneously taking into account differences in species' rarity before the onset of agricultural intensification and other factors that have been proposed to explain bee population trends.

Results and Discussion

Model averaging across our set of candidate models ($\Delta AIC_c < 4$) (30) revealed that population change of pollen host plants (full-model averaged standardized regression coefficient $\beta = 0.54$; relative variable importance $\omega_p = 1.00$), body size ($\beta = -0.60$; $\omega_p = 1.00$), and range size before 1950 ($\beta = 0.20$; $\omega_p = 0.72$) were the most important factors associated with bee population trends (Table 1). A model with just these three predictors best explained wild bee population change between the periods 1902–1949 and 1975–1999. It suggests that bee population trends were positively

related with host plant change index (Fig. 1A) and initial range size (Fig. 1C) and negatively related with body size (Fig. 1B). This model explained 50% of the variation in bee population responses and had a probability of 0.37 of being the best model among the seven models in the candidate set. Analysis of bee trends based on a more extensive dataset that also included more recent bee records [period 1900–1989 vs. 1990–2011 (13)] produced similar results (Table S2).

Our data do not enable us to distinguish whether the observed link between population trends of bees and their preferred host plants results from plant declines causing bee declines or vice versa. However, circumstantial evidence argues in favor of the proposition that it is primarily the loss of preferred host plants that is causing bee decline. First, distribution changes of plants in The Netherlands do not differ among insect-pollinated, wind- or water-pollinated, and self-pollinating plants (3), which reflects that loss of plant diversity in The Netherlands is mainly driven by abiotic factors associated with land use change, such as eutrophication, desiccation, and acidification (31, 32). Second, most insect-pollinated plants are pollinated by a diverse array of both generalist and specialist pollinators (33), which makes them fairly robust to the loss of a subset of pollinators. Bee losses may, for instance, have been compensated for by the increase of other important groups of pollinators such as hoverflies. Hoverflies, whose larvae do not depend on floral resources, have not been negatively affected by land use change and have even increased in The Netherlands over the last decades (3). Finally, a recent study on plant–pollinator networks in grasslands shows that land use intensity primarily drives loss of host plants, and that loss of host plants subsequently drives bee decline, whereas the reciprocal effects are not pronounced (34).

Length of flight period ($\beta = 0.004$; $\omega_p = 0.15$) and the degree of phenological advancement of the flight periods of bees between 1902–1949 and 1975–1999 (climate change sensitivity) ($\beta = 0.001$; $\omega_p = 0.10$) had little value in explaining bee population trends (Table 1). Mean daily temperatures during the activity period of bees (April–September) have increased in The Netherlands between 1906 and 2012 (Fig. S3). However, the extent to which bees advanced their flight periods in response to these rising temperatures did not contribute to explaining differences in bee population trends. This may indicate that bee species did not suffer from phenological mismatches with their host plants (35).

Surprisingly, diet breadth, i.e., the number of different pollen host plants used by a bee species, was also only of minor importance in explaining bee population trends ($\beta = 0.03$; $\omega_p = 0.25$, Table 1). Species that use only a narrow array of food resources are generally expected to be more vulnerable to decline under environmental change (36). However, our results

Table 1. Model selection and model averaging results for candidate models explaining bee population trends

Predictor	Model							β	95% CI	ω_p
	1	2	3	4	5	6	7			
Change of host plants	0.54	0.53	0.55	0.53	0.53	0.54	0.58	0.54	0.29–0.79	1.00
Body size	–0.63	–0.62	–0.51	–0.51	–0.64	–0.63	–0.49	–0.60	–0.89 to –0.31	1.00
Range size before 1950	0.29	0.25			0.30	0.28		0.20	–0.14–0.54	0.72
Diet breadth		0.11		0.18				0.03	–0.14–0.21	0.25
Length of flight period					–0.02		0.11	0.00	–0.11–0.12	0.15
Phenological advancement						0.01		0.00	–0.07–0.08	0.10
ΔAIC_c	0.00	1.89	2.21	2.56	2.58	2.60	3.93			
ω_m	0.37	0.14	0.12	0.10	0.10	0.10	0.05			

Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (ΔAIC_c). Explanatory variables were standardized by centering and dividing by 2 SDs. Akaike model weights (ω_m) indicate the probability that a model is the best approximating model given the set of models considered. For each predictor, the parameter estimate for each candidate model is given, along with its model averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ω_p). Confidence intervals not overlapping zero are indicated in bold.

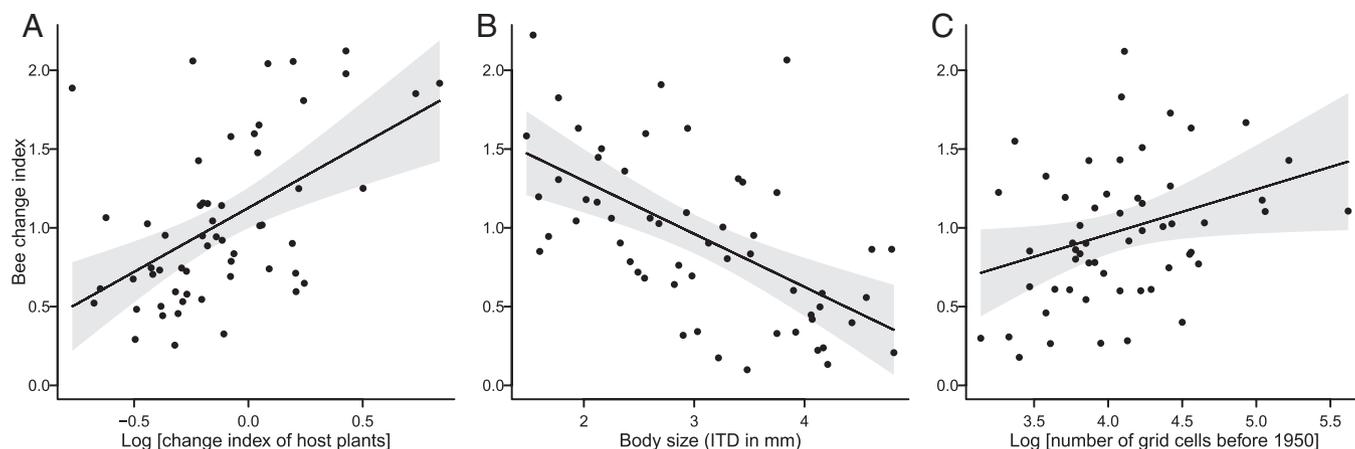


Fig. 1. Relationship between bee population trends and body size, change index of pollen host plants, and initial rarity of bee species. Partial regression plots based on the best model in the candidate set for (A) log-transformed weighted mean change index of pollen host plants in bee species' pollen diets, (B) body size measured as the intertegular distance (ITD), and (C) log-transformed number of occupied 5×5 km grid cells before 1950. Note that a bee change index of 1 indicates no change. Plotted points represent partial residuals. Shaded areas indicate 95% confidence bands.

indicate that bee species that use a low number of host plant species are not necessarily susceptible to decline, as long as their preferred host plants are not declining. Likewise, the more generalist species may be expected to decline if their most important host plants decline. Even the most generalist bee species are restricted in their range of host plants and have distinct preferences for certain pollen taxa (37). Bees may produce lower-quality offspring when larvae are reared on pollen of less-preferred host plants (38) or may fail to produce offspring altogether (39). Declining bee species therefore most likely suffered from reduced fitness as a consequence of the loss of their preferred host plant species.

The extent to which bee species' preferred host plants declined appeared to be associated with phenology. The population change of pollen host plants was negatively correlated with the timing of the beginning of the flight period of bee species ($r = -0.53$, $P < 0.001$; Fig. 2A), suggesting that particularly the late-flowering host plants have declined over the past century. In addition, an inventory of landscape-wide floral resource availability in 16 Dutch agricultural landscapes in 2012 showed that late-season floral resource availability is significantly lower than early-season resource availability (paired t test, $t_{15} = 8.30$, $P < 0.001$; Fig. 2B). In contemporary intensively used agricultural landscapes, mass-flowering crops (e.g., *Brassica napus*), flowering trees and shrubs (e.g., *Salix* spp., *Prunus* spp.), and flowering herbs in improved grasslands and field margins (e.g., *Taraxacum* spp., *Cardamine pratensis*, *Ranunculus* spp.) still provide ample early-season floral resources. However, later in the season, the availability of floral resources is strongly reduced because shrubs and trees have ceased flowering, grasslands have been grazed or cut for silage, and field margins have been mown. Taken together, these results suggest that floral resources are particularly limiting for bees that emerge later in the season.

The observed negative relationship between bee body size and population trend may result from the decline of the large-bodied bumblebee species, which as a group have experienced particular strong declines in Europe (13, 40). Yet, body size remained a key factor ($\beta = -0.39$; $\omega P = 0.93$) even when the 10 bumblebee species were excluded from the analysis, suggesting that the negative relationship with body size does not only reflect the decline of the bumblebees. Alternatively, the effect of body size may be linked to loss of floral resources as driving factor for wild bee decline. Large bee species may be more susceptible to land use change than smaller ones (4, 23) because of their larger pollen quantity requirements (41). In homogenous, intensively

farmed landscapes, declining floral resources may cause fewer problems for small species to find sufficient food for offspring production than for large species, despite the larger foraging ranges of large species (42).

To identify whether bee decline was associated with preference for specific plant families, we calculated for each plant family the mean trend index of bees that relied for at least 10% of their pollen diet on that particular plant family (Fig. 3). On average, bee species that preferentially collected pollen from plant species belonging to the Rosaceae family significantly increased while bees feeding on plants in the Fabaceae family decreased. This pattern remained when threshold values of 20% or 30% were used (Fig. S4). The declines in Fabaceae species can be attributed to the loss of Fabaceae-rich seminatural grasslands (14), but also to the drastic decrease of the agricultural use of Fabaceae as fodder and cover crops during the twentieth century (Fig. S5). Our findings shed new light on the consequences of reported losses of wild bees for crop pollination. Bees that preferentially collect pollen from Rosaceae, Brassicaceae, and Asteraceae species, which contain major insect-pollinated crops such as apple, strawberry, oil-seed rape, and sunflower, have remained stable or actually increased. Delivery of crop pollination services by wild bees may therefore be under less threat from land use change pressures than conservation of wild bee diversity.

Because it is impossible to experimentally examine causes of large-scale population declines, it is difficult to establish causal relationships between drivers and population trends. The robust linkage of bee population trends, through historical host plant preferences, to plant population trends that was found in this study therefore probably represents the best possible evidence for key factors causing bee population decline in intensively farmed landscapes for some time to come. These insights will help us develop more effective ways to mitigate loss of species that are threatened in their existence as well as promote bees important for delivery of crop pollination services.

Methods

Examined Bee Species. In The Netherlands, 357 wild bee species are found. A total of 256 species actively collect and transport pollen to provision their offspring. The remaining bees are cleptoparasitic bees that lay their eggs in brood cells of host bees and do not forage for pollen themselves. We focused our sampling efforts on bee species that use multiple host plant species ("polylectic bee species"), which constitute 70% of the pollen-collecting bee species in The Netherlands (13). We used the number of 5×5 km grid cells occupied before 1950, obtained from the national bee distribution database

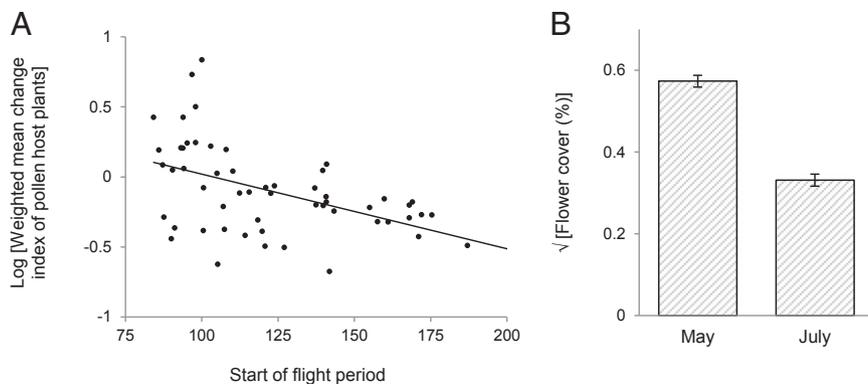


Fig. 2. Seasonal pattern of pollen host plant change and floral resource availability. (A) Relationship between the beginning of the flight period of bee species (number of days after 31 December) and the log-transformed weighted mean change index of pollen host plants in their pollen diets. (B) Mean estimated spring and summer floral resource availability (square root transformed flower cover) in 16 agricultural landscapes (1 km radius) in The Netherlands in 2012. Error bars represent SEM adjusted for paired observations.

(13), to assess species' rarity before the onset of major environmental change, and only included species if they were common (present in at least one-hundred-fifty 5×5 km grid cells), fairly common (70–149 grid cells), or only moderately rare (20–69 grid cells) before 1950. Bee species from the genus *Hylaeus* were excluded because female bees of these species transport pollen internally in their crops rather than externally on their bodies, which makes nondestructive sampling of pollen difficult. This resulted in a total of 75 bee species for which we aimed to determine pollen host plant use (see *Pollen Host Plant Use*).

Bee Population Trends. Relative bee population trends were determined using the national bee distribution database of European Invertebrate Survey (EIS) - The Netherlands (13). This database contains 186,147 records of bees collected and observed in The Netherlands between 1809 and 2011. Relative change indices for the focal bee species were calculated as the ratio between the number of occupied 5×5 km grid cells in the period 1902–1949 (26,749 records) and the number of occupied grid cells in the period 1975–1999 (45,447 records), divided by the average of the change ratio of all focal bee species. Relative change indices thus reflect bee species' performance between the two periods relative to the average performance of all of the species considered. We only used data of grid cells that were inventoried in both periods (total of 568 cells) and, to avoid potential bias arising from the much larger proportions of field observations in the database in recent years

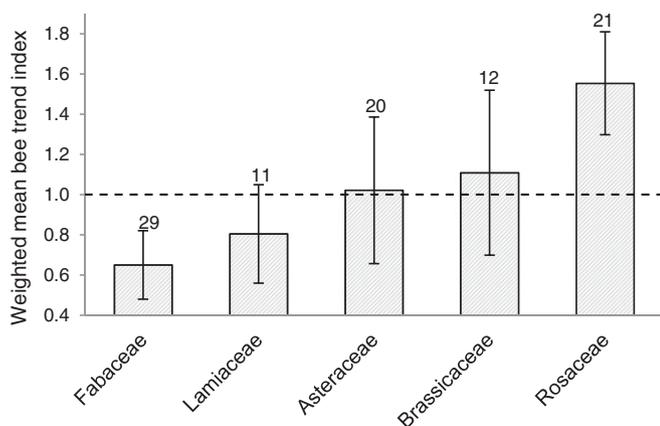


Fig. 3. Weighted mean population trends of bee species visiting the most frequently used host plant families. Mean population trends, weighted by the percentage pollen contribution of the host plant families to bee species' diets, are based on bee species that relied for at least 10% of their pollen diet on a particular plant family. Results are shown for plant families that made up at least 10% of the pollen diets of at least 10 bee species. Error bars indicate weighted 95% confidence intervals. Numbers above bars indicate sample size.

(which are mainly restricted to common and easily recognizable species), only included records from natural history collections. Sampling intensity differed between periods, which, as the probability that a species is recorded depends on sampling intensity, may introduce bias when comparing grid cells between both periods. Therefore, using the total number of bee records per period as a proxy for sampling intensity, we corrected for differences in sampling intensity between periods by multiplying the number of grid cells each species occupied in 1975–1999 with the quotient of the total number of bee records in 1902–1949 divided by the total number of bee records in the 1975–1999 period (13). The rationale behind comparing the 1902–1949 and 1975–1999 periods is that these periods form the basis for the national Red List of vascular plant species (29) (see *Pollen Host Plant Use*) and contrast a period of low-intensity farming with a period of intensive agriculture and reduced availability of seminatural bee habitat (Figs. S1 and S2). However, to assess whether the results of our study were robust to the chosen time periods, we also analyzed the drivers of wild bee decline using bee trends based on the periods used by Reemer et al. (13) [1900–1989 (77,920 records) vs. 1990–2011 (68,491 records)], total of 858 grid cells. Using trends based on these time periods produced results similar (Table S2) to the results reported in the main text (Table 1).

Pollen Host Plant Use. Pollen loads of female bees of the selected species were sampled in the entomological collections of the Natural History Museums of Amsterdam, Leiden, Leeuwarden, Rotterdam, Tilburg, Wageningen, and Brussels (Belgium). Samples were only taken from specimens that were collected before 1950 (between 1870 and 1950) and that had pollen in the pollen-carrying bodily structures (scopa or corbicula). Samples of pollen from each pollen load were mounted in glycerine jelly containing basic fuchsin to stain the pollen grains. Identification was done using a light microscope at $400\times$ magnification with the assistance of a reference pollen collection of ~ 130 species and reference documents (43). Pollen grains were identified to the lowest possible taxonomic level, mostly to genus (67%). For each sample, we estimated the percentage contribution of each pollen taxon, with pollen taxa contributing $<5\%$ not being considered as they may result from contamination. To avoid potential bias resulting from several samples collected at the same location at the same date, duplicate samples were randomly excluded from the dataset.

We could not reliably determine pollen host plant use for 18 of the selected 75 species because of insufficient numbers of pollen samples ($n < 15$) in museum collections, and these species were omitted from further analyses. The mean number of pollen samples per species of the final set of 57 bee species was 28.9 (min = 15, max = 63). These 57 species (Table S1) represent 40% of the pollen-collecting bee species that were observed in at least twenty 5×5 km grid cells in The Netherlands before 1950. The majority of the specimens of these species were collected at locations in The Netherlands, but a limited number (7%) were collected at Belgian locations near the Dutch–Belgian border. Out of the total number of 1,646 specimens, broadly equal numbers of specimens were collected in the southern and northern part of the study area (respectively 863 and 783). In total, we identified 170 different pollen taxa in the pollen loads of the 57 focal bee species.

Following Kleijn and Raemakers (15), we quantified pollen host plant preference for each bee species as the percentage contribution of each

pollen taxon to the total pollen load sampled from all specimens of the bee species. Population changes of pollen host plants during the twentieth century were based on the frequency of occurrence of plant species in 1×1 km grid cells in the periods 1902–1949 (1.7 million records) and 1975–1999 (3.5 million records) (29, 44). We calculated relative change indices of host plants as the ratio between the number of occupied grid cells in the period 1902–1949 and the number of occupied grid cells in the period 1975–1999, divided by the average of the change ratio of all identified bee host plants. Change indices were based on a selection of 7,374 grid cells with multiple observations within the grid cell across both periods (nearly 25% of the land surface of The Netherlands), corrected for temporal differences in sampling intensity (29). For pollen taxa that could only be identified to genus or family level, we used distribution data of the common plant species in the respective genus or family to calculate a weighted average change index for these pollen taxa (15). Next, for each bee species, we calculated the weighted mean population change index of the host plants in its pollen diet (CI_{diet}) as

$$CI_{diet} = \frac{\sum_{i=1}^n PC_i \times CI_i}{\sum_{i=1}^n PC_i}$$

with PC_i representing the percentage contribution of pollen taxon i to the total observed pollen load of the bee species, CI_i the relative change index of pollen taxon i , and n the total number of pollen taxa observed in the pollen loads of the bee species. Pollen diet breadth, i.e., the number of pollen taxa in the pollen diets of bee species, was determined after sample-based rarefaction to 15 samples using EstimateS software (45).

Other Factors Associated With Bee Decline. For each bee species, we assessed its initial rarity, body size, phenology, and response to climate change. First, as rarity in itself may be an important cause of population decline (18) and may confound any observed relationship between bee traits and population trends (17), we quantified species' rarity before the onset of major land use changes in The Netherlands as the number of 5×5 km grid cells before 1950.

Second, we measured bee body size as the intertegular distance (ITD). The ITD is the distance between the two insertion points of the wings, which is a reliable estimator of bee body size (46). For all species, except *Bombus* species, we measured the ITD of 10 female specimens. For *Bombus* species, we measured the ITD of 20 worker bees to account for larger intraspecific variation in body size in these species.

Third, we determined the start and length of the flight periods of bees using the national bee distribution database of EIS - The Netherlands (13). For both the 1902–1949 and 1975–1999 periods, we used the records in the bee database (mean number of records per species 1902–1949 = 92; 1975–1999 = 374) to calculate the 10th and 90th percentile of the recording day (1 January = 1) for each bee species and defined the 10th percentile as the start, and the number of days between the 10th and 90th percentiles as the length of the flight period of bee species (4). Seven species had become too rare (less than 40 records) to reliably determine their flight periods in the period 1975–1999. For these species, we predicted the start and length of the flight period using the linear relationships between the other species' start of flight period ($Start_{1975-1999} = 0.896 \times Start_{1902-1949} + 14.629$, $F_{1,49} = 484.1$, $P < 0.001$, $R^2 = 0.91$) and end of flight period in 1902–1949 and 1975–1999 ($End_{1975-1999} = 0.920 \times End_{1902-1949} + 15.929$, $F_{1,49} = 421.7$, $P < 0.001$, $R^2 = 0.90$). We quantified the influence of climate change by calculating the phenological advancement of bee species' flight periods between both periods ($Start_{1975-1999} - Start_{1902-1949}$).

Although nesting ecology may be expected to be an important factor underlying differential responses of bee species to land use change (11, 47), still little is known about the nesting requirements of most bee species, and nesting ecology is difficult to quantify. Rough categorical classifications of bee species' nesting ecology (e.g., nesting above ground vs. nesting below ground) oversimplify the broad array of nesting habitats, substrates, and construction materials used by different bee species (48) and probably obscures any relationship between bee species' nesting ecology and population response to land use change. Possibly as a consequence, previous analyses did not find any relationship between nesting ecology and population

trends of species (4). We therefore chose not to include any categorical measure of nesting ecology in our analysis.

Floral Resource Availability in Contemporary Agricultural Landscapes. In 2012, we used a stratified sampling approach to estimate spring and summer floral resource availability in 16 agricultural landscapes (1 km radius) in The Netherlands. Flower inventories were conducted in habitats in seven main land use classes: seminatural habitats (e.g., forest edges, wooded banks), cultivated grasslands, nonflowering crop fields (e.g., maize fields, wheat fields), flowering crop fields (oilseed rape fields), uncultivated field boundaries (field boundaries, ditch banks, road verges), nonflowering perennial habitats (forest interiors), and gardens. Flower inventories were performed twice: once in May and once in July. For each of the land use classes, we estimated percentage cover of flowering forbs in randomly selected plots (100 m²), evenly spread out over the study landscapes (grand total of 48 plots). We used GIS to calculate the area of land use classes in the 1-km-radius study landscapes, and calculated the estimated total landscape-wide floral resource availability (% cover) in May and July in each landscape as: (mean flower cover land use class A \times proportion of land use class A in the study landscape + mean flower cover land use class B \times proportion of land use class B in the study landscape + ...)/100.

Data Analysis. We used linear mixed models and an information theoretic approach to assess to what extent the explanatory variables were related to bee population trends. We constructed a set of linear mixed models containing all possible combinations of the different predictors, including an intercept only model. As phylogenetic analyses are controversial (49) and phylogenetic trees for bees are continuously challenged (50), we did not use phylogenetic regression but instead included bee subfamily as a random factor to account for potential nonindependence of trends and traits among closely related bee species (4). The variables "range size before 1950" and "change of host plants" were log-transformed to reduce positive skew. We excluded start of flight period (correlated with change of host plants, $r = -0.53$, $P < 0.001$) from the set of predictors to avoid multicollinearity. A multimodel inference approach that used start of the flight period instead of change in host plants showed that the highest-ranking model that included start of flight period ($AIC_c = 90.3$, Akaike model weight $\omega_m = 0.016$) was 62 times less likely to be the best model than the highest-ranking model that included change in host plants ($AIC_c = 82.0$, $\omega_m = 0.984$).

We ranked the 64 possible models according to their Akaike information criterion corrected for small sample size (AIC_c) (Table S3) and restricted our candidate model set to models with $\Delta AIC_c < 4$ (30). For each model in the candidate set, we calculated the Akaike model weight (ω_m), which reflects the probability that a model is the best approximating model given the set of candidate models considered (30). Marginal R^2 values (the variance explained by the fixed effects variables) of models were calculated following Nakagawa and Schielzeth (51). To account for model selection uncertainty, we calculated full-model averaged parameter estimates [including zero when predictors were not included in a particular model (52)] for each predictor in the candidate model set. The relative importance (ω_p) of a predictor was based on the sum of the Akaike weights across all models in the candidate model set that included the predictor (30). All analyses were performed using R (53), using the packages lme4 (54) and MuMIn (55).

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