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Research article

Climatic conditions and landscape diversity predict plant–bee interactions and pollen deposition in bee-pollinated plants

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Climate change, landscape homogenization, and the decline of beneficial insects threaten pollination services to wild plants and crops. Understanding how pollination potential (i.e. the capacity of ecosystems to support pollination of plants) is affected by climate change and landscape homogenization is fundamental for our ability to predict how such anthropogenic stressors affect plant biodiversity. Models of pollinator potential are improved when based on pairwise plant–pollinator interactions and pollinator's plant preferences. However, whether the sum of predicted pairwise interactions with a plant within a habitat (a proxy for pollination potential) relates to pollen deposition on flowering plants has not yet been investigated. We sampled plant–bee interactions in 68 Scandinavian plant communities in landscapes of varying land-cover heterogeneity along a latitudinal temperature gradient of 4–8°C, and estimated pollen deposition as the number of pollen grains on flowers of the bee-pollinated plants *Lotus corniculatus* and *Vicia cracca*. We show that plant–bee interactions, and the pollination potential for these bee-pollinated plants increase with landscape diversity, annual mean temperature, and plant abundance, and decrease with distances to sand-dominated soils. Furthermore, the pollen deposition in flowers increased with the predicted pollination potential, which was driven by landscape diversity and plant abundance. Our study illustrates that the pollination potential, and thus pollen deposition, for wild plants can be mapped based on spatial models of plant–bee interactions that incorporate pollinator-specific plant preferences. Maps of pollination potential can be used to guide conservation and restoration planning.

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Introduction

Globally, insect diversity is decreasing at an alarming rate due to environmental stressors such as climate change and the homogenization of landscapes (Maxwell et al. 2016, Wagner et al. 2021). Such widespread changes in the insect fauna will reduce the stability of the functioning of natural and human-modified ecosystems (Cardoso et al. 2020). Pollination is a key ecosystem function and service, fundamental for the maintenance of wild plant biodiversity (Ollerton et al. 2011, Wei et al. 2021) and crop production (Klein et al. 2007, Reilly et al. 2020). Climate change can induce temporal and spatial mismatches in plant and pollinator co-occurrences (Hegland et al. 2009) thus affecting plant–pollinator interactions and the potential for plant pollination within an area (Kudo and Ida 2013), if not buffered through functional redundancy of plants or pollinators (Benadi et al. 2014). Landscape homogenization often entails a loss of floral and nesting resource diversity and reduces the resilience of plant–pollinator networks (Librán-Embid et al. 2021, Gómez-Martínez et al. 2022) and potentially the stability of pollination service delivery. Indeed, plant–bee interactions involving bumblebees, which are important pollinators in temperate regions (Maia et al. 2019), increase with increasing landscape diversity (Sydenham et al. 2022b). Pollination potential can be defined as an area's capacity to sustain pollinators and thereby plant pollination. Maps showing the predicted effects of climate and landscape diversity on pollination potential can help identify areas for conservation or restoration (Brudvig 2011) and can be an important asset for guiding agricultural practices for better crop pollination and for minimizing negative impacts on local biodiversity (Nogué et al. 2016, Remme et al. 2018).

Despite our knowledge of the potential impacts of climatic and landscape factors on pollination potential, predicting how plant–pollinator interactions and pollination are affected by climate change and habitat loss remains an important challenge in pollination ecology (Tylianakis and Morris 2017, Knight et al. 2018). Our ability to predict plant–pollinator interactions and pollination is complicated by pollinators often showing guild-specific responses to climate and landscape conditions (Sydenham et al. 2022b, Steffan-Dewenter et al. 2002) and guild-specific (or trait-specific) differences in plant preferences (Pichler et al. 2020). Pollination potential has been mapped as the expected abundance of pollinators that will be able to reach and pollinate plants in a field (Lonsdorf et al. 2009, Lonsdorf et al. 2011, Zulian et al. 2013). Newer versions of pollination potential models combine expert opinion-based habitat-suitability classifications of high-resolution land use maps (used in Lonsdorf et al. 2009) with coarse scale (e.g. 1-km resolution) species distribution models, allowing predictions to be made along continuous environmental gradients (Perennes et al. 2021). Pollinator species differ in their plant preferences due, in part,

to constraints imposed by morphology or phenology, which are important predictors of interactions in plant–pollinator networks (Olesen et al. 2011, Pichler et al. 2020). However, different plant preferences are typically not accounted for in models of pollination potential (Remme et al. 2018). While climatic conditions and landscape diversity contribute to the occurrence of plant–bee interactions, plant preferences of pollinators have recently been shown to be more important when predicting plant–pollinator interactions (Sydenham et al. 2022a, b). Accounting for plant preferences will therefore likely improve models and maps of pollination potential. However, the spatially replicated data on plant–pollinator interactions required to model plant–pollinator interactions across climate and landscape diversity gradients are costly and time consuming to collect (Poisot et al. 2021, Strydom et al. 2021). Indeed, spatial prediction models of pairwise plant–pollinator interactions have so far been limited to single landscapes (e.g. ca 50 × 50 km in Sydenham et al. 2022a) or to modelling of interaction partners for a few plant taxa such as Anthemideae, Cichorieae, Loteae, and Trifolieae (Sydenham et al. 2022b). To date, no studies have investigated if models using spatially replicated data of complex interactions between plants and pollinators that differ in their preferences can be used to produce ecologically meaningful predictions of pollination potential along gradients of climatic conditions and landscape diversity, and if such predictions correspond to actual plant pollination.

Currently available models of pollination potential often map pollinator abundance or diversity because these variables are assumed to be correlated with pollen deposition (Nogué et al. 2016). This assumption rests on pollinator abundance (Herbertsson et al. 2021) and plant–pollinator interaction frequency (Vázquez et al. 2005) being positively related to plant reproduction. Models of pollination potential are typically validated in terms of their ability to predict local pollinator abundance or diversity (Nogué et al. 2016, Perennes et al. 2021); or, more recently, plant–bee interaction probabilities (Sydenham et al. 2022a, b). However, increasing pollinator abundance or flower visitation frequency do not always guarantee an increase in pollination (reviewed by Cariveau et al. 2020, Tobajas et al. 2024). Prior to interpreting the predicted pollination potential as being indicative of plant pollination success, we first need to know if predictions of pollination potential correspond to spatial patterns of pollen deposition in flowers. Hence, models of pollination potential should provide information on how the pollen deposition in flowers varies across landscapes, encapsulating effects of climate and landscape diversity on pollinator distributions.

In the current study, we approach this question using data from 68 Scandinavian plant–bee interaction networks in semi-natural plant communities in landscapes of varying heterogeneity, sampled along a temperature gradient, to test if the models of pollination potential that account for plant preferences can be related to pollen deposition in bee-pollinated

plants (Fig. 1a–e). We first model pairwise plant–bee interactions to test if temperature and landscape diversity contribute to predicting plant–bee interactions (or pollination potential) and if their effects are modulated by bee guilds. We focus on two guilds, solitary bees and social bumblebees, because bumblebees are the dominant visitors to legumes and other typically bee-pollinated plants in our region (Maia et al. 2019) but have declined in abundance in European landscapes (Goulson et al. 2008), and bee-pollinated plants are particularly prone to be pollen limited (Bennett et al. 2020). Based on previous studies from the same region (Sydenham et al. 2022a, b) we expected the number of visits by bumblebees to increase with landscape diversity within 1 km radii surrounding sites, and visits by solitary bees which are more reliant on local habitat conditions (Steffan-Dewenter et al. 2002) to increase with annual mean temperature. Furthermore, we expected plant–bee interactions to decrease with the distance to deposits of sandy soils, because areas on sandy soils provide good nest site conditions for ground-nesting bees, and plant diversity is often higher than on richer soils. Indeed, the distance to sandy soils have previously been shown to be an important

predictor of bee occurrences, and plant–bee interactions, in our region (Sydenham et al 2022a, c). We then used data on pollen deposition collected at 27 sites in southeastern Norway (Fig. 1f–h) to test if the amount of pollen deposited on two bee-pollinated plants, *Lotus corniculatus* and *Viccia cracca*, corresponded to the predicted pollination potential. To explore if our models of plant–bee interactions capture the directions and strength of environmental drivers of pollen deposition, we compared models of pollen deposition predicted by pollination potential to a model where pollen deposition was modelled directly from the hypothesized drivers of pollination potential (viz. annual mean temperature, landscape diversity, distance to sandy soils, and local plant abundances).

Material and methods

Plant–bee interaction surveys

We sampled plant–bee interactions in 68 semi-natural, forb-dominated, plant communities (Fig. 1a, see the Supporting
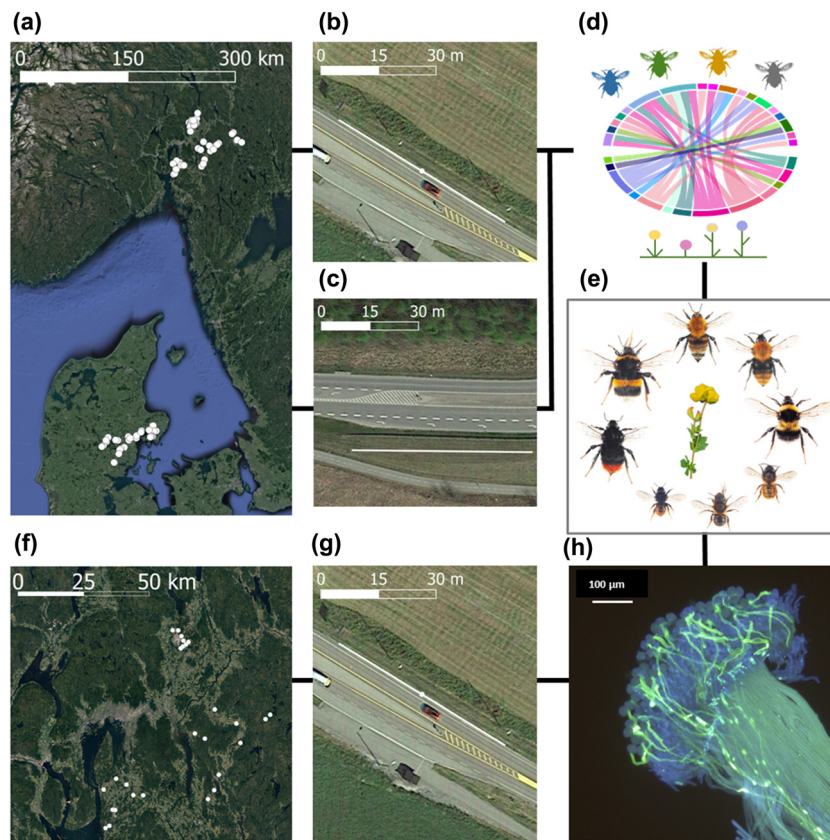
Figure 1. Graphical summary of study design. In study sites located in southeastern Norway (n = 41) and western Denmark (n = 27) (a), data on plant–bee interactions and local plant abundance were collected along 50 m transects placed along green linear features such as roadsides (b–c). Plant–bee interaction data were used to model and predict pairwise plant–bee interactions along gradients of annual mean temperature and landscape diversity (d). The site-specific *pollination potential* for the bee-pollinated model plants *Lotus corniculatus* (e) and *Vicia cracca* was calculated as the sum of interaction probabilities with the plant across all bee species in a site. In 27 of the Norwegian study sites (f), wilted flowers of the model plants *L. corniculatus* (e) and *V. cracca* were collected along the transects (g). We tested if the number of pollen grains on flowers of the model plants (h) increased with the site-specific *pollination potential*. Satellite imagery from Map data ©2022 Google via QGIS 2021.

information for details on study site locations). We focused on wild bees because they are considered central pollinators for many plant species (Willmer et al. 2017), because bee-pollinated plants are frequently pollen limited (Bennett et al. 2020), and because wild bee abundance is related to increased seed-set in many wild plants (Herbertsson et al. 2021). Furthermore, wild bees are also often the focus of pollination service models (Remme et al. 2018). We used linear, open landscape features such as roadsides as a model system and established one 50×2 m transect for our surveys in each site (Fig. 1b–c). To cover the main flowering period, we sampled plant–bee interactions once in May, June, and July at each site (Fig. 1d–e). To standardize sampling times across sites and countries, timing of the first sampling was determined by the peak flowering of *Taraxacum officinale*. All flower-visiting bees were collected from flowers and stored in 96% EtOH prior to identification. Species within the *Bombus* sensu stricto subgenus are cryptic and cannot be reliably identified manually (Carolan et al. 2012). Specimens within the *Bombus* sensu stricto subgenus were treated as one morpho-species. Each transect observation lasted 30 min, adding 30 s per collected specimen, to account for handling time. Sampling only took place on days with temperatures > 15°C, local wind speed < 5 m/s, with little to no cloud cover, and no rain, to standardize sampling conditions between networks.

Vegetation surveys

In late June to early July 2021, we sampled the plant communities by placing ten 1 m² vegetation plots regularly along each transect. In each 1 m² vegetation plot, we recorded the occurrence of bee-pollinated plant species, regardless of life stage, within four 0.25 m² subplots. Conducting vegetation surveys separately from plant–pollinator interaction surveys was necessary for us to be able to sample plant–bee interactions at all 68 sites within the same time periods. Despite being long after the flowering period of the earliest flowering plants, such as *Tussilago farfara*, these plants were recorded during our survey. Our approach allowed us to obtain estimates of plant abundances (i.e. number of plots, or subplots occupied by a plant), from just one survey per site, regardless of plant phenologies. Such single-survey estimates of plant abundances have previously been shown to be an important predictor of plant–bee interactions in our region (Sydenham et al. 2022a).

Pollen deposition surveys

We sampled wilted flowers from two legumes, *Vicia cracca* and *Lotus corniculatus,* along the transects in Norway (Fig. 1f–g) in July 2021, and counted the number of pollen grains deposited on stigmas as a measure of total pollen deposition (Alonso et al. 2012). Flower sampling was conducted independently from surveys of plant–pollinator interactions. These legumes were selected because they are mainly bee pollinated (Tyler et al. 2021) and had been found in at least 10 sites during the vegetation surveys. *Vicia cracca* and *L. corniculatus* occurred at 26 and 25 sites, respectively. We collected one flower from

10–15 individuals per species per site. Flowers were fixed with 4% formaldehyde alcohol acetic acid and stored at 4°C until further processing. The protocols to prepare gynoecia for microscopy were modified from Bedinger (2010). Entire flowers were softened in 5M NaOH for 24 h. After softening, the NaOH was removed by pipetting and gently washed out with ddH$_2$O five times. Then, several drops of 0.001 g/ml aniline blue fluorochrome (ABF) in 0.1M K$_2$HPO$_4$ pH 10 buffer were dropped on microscope slides. Gynoecia were carefully removed from flowers with tweezers, immersed in ABF on the microscope slides, covered with aluminum foil, and left for 1 h. Following staining, squashing, and mounting, we counted the number of pollen grains using a fluorescence microscope (Fig. 1h). Using pollen counts to estimate pollination services has two main advantages compared to pollen supplementation experiments where one contrasts the seed-set of flowers that have received supplementary pollen with non-manipulated flowers: 1) pollen counts provide estimates of the contribution of pollinators to the pre-zygotic phase of plant reproduction (Alonso, et al. 2012), without being confounded by other factors that might affect seed production (Ashman et al. 2004); and 2) hand-pollinating flowers risks damaging plant tissues, particularly on zygomorphic flowers where the stigma is concealed, which may affect seed set of hand-pollinated plants (Hegland and Totland 2008).

Predicting plant–bee interactions and pollination potential

We used the MetaComNet framework (Sydenham et al. 2022a) with a binomial GLMM to model the probability of occurrences of plant–bee interactions within sites, for all non-parasitic bee species observed across the 68 study sites. Parasitic species were excluded because their population dynamics and occurrences are indirectly related to landscape conditions via the response of their hosts. We used GLMMs instead of random forest models which were used in Sydenham et al. (2022a), because GLMs perform comparably well when modelling plant–bee interactions (Sydenham et al. 2022b) but allow for a more direct interpretation of predictor effects. We used the presence, or absence, of plant–bee interactions within sites as the response variable in the model. We included all plant species within a site that had been recorded during the vegetation surveys and from which bees had been collected at least once during the bee surveys, thereby excluding plants that flowered outside our sampling period. We included three groups of predictor variables in the model: spatial environmental predictors, plant species traits, and bee species traits (Table 1), and site identity as a random intercept term.

Spatial environmental predictors

Temperature is an important climatic driver of plant–bee interactions in our study region (Sydenham et al. 2022b). We therefore used the annual mean temperature at sampling locations, obtained from the WorldClim database (Fick and Hijmans 2017). As a proxy for landscape homogenization (or its inverse, landscape diversity), we followed Sydenham et al.

Table 1. Predictor variables used to model the occurrence of pairwise plant–bee interactions across 68 Scandinavian plant–bee networks.

Predictor	Class	Note
Environmental predictors		
Annual mean temperature	Numeric	Annual mean temperature mapped at a spatial resolution of 30 arc seconds (approx. 1 km at equator)
Landscape diversity	Numeric	Shannon landscape diversity within 1 km of a study site
Distance to sandy soils	Numeric	Distance (m) from site to nearest area mapped as having sand-dominated soils
Plant traits		
Plant abundance within site	Numeric	Number of 1 m² plots, out of 10, in a site where plant species was recorded. Range (min = 1, max = 10)
Plant peak flowering time	Numeric	Mean Julian day from all dates where wild bees were recorded to visit the plant species
Plant flowering duration	Numeric	Standard deviation in Julian days of all dates where wild bees were recorded to visit the plant species
Plant pollinator association score (Plant DCA1–4)	Numeric	Plant species scores on axes 1–4 from the detrended correspondence analysis (DCA) on number of plant genera within plant families that a bee species has been reported to visit, using data obtained from the literature
Pollinator trait		
Wild bee regional bee commonness	Numeric	Number of 10 km grid cells where the species has been recorded in the wider study region
Wild bee social status	Factor	Two levels: solitary and facultatively social versus eusocial *Bombus*
Wild bee phenology	Factor	Four levels: (1) active from April to July; (2) active from May to August; (3) active from June to August; (4) active from April to August.
Wild bee plant preference (Bee DCA1–4)	Numeric	Bee species scores on axes 1–4 from the detrended correspondence analysis (DCA) on number of plant genera within plant families that a bee species has been reported to visit, using data obtained from the literature

(2022b) and calculated the Shannon landscape diversity within circular buffers with radii of 1 km surrounding each site from a European 10 m resolution land cover map (Venter and Sydenham 2021). As a proxy for availability of high-quality nesting substrates for ground nesting bees, which account for the majority of bee species in our region, we included the geographic distance to sand-dominated geological deposits, estimated as the distance to the nearest spatial polygon classified as having a high or moderately high infiltration capacity in Norway (Geological Survey of Norway 2011) or explicitly classified as being sand-dominated in Denmark (Landbrugsstyrelsen 2019). We did not include specific predictors for cavity nesting bees, because we expected the availability of nesting substrates for this group to correspond with landscape diversity.

Plant species traits

Abundance-based processes are known to be important predictors of plant–pollinator interactions (Gómez-Martínez et al. 2022). As a proxy for site-specific plant abundance, we used the number of 1 m² vegetation plots in which a species occurred. Plants not recorded during the vegetation survey but on which bees had been observed were assigned a plant abundance value of 1, corresponding to the lowest value recorded for plants during the plant surveys. To account for forbidden links due to phenological mismatches (Olesen et al. 2011), we included the mean Julian day on which bees were observed on the plant across all sites as a proxy for plant peak flowering time. As a proxy for flowering time duration, we included the standard deviation of Julian days on which interactions between the plant and bees had been observed. As in Sydenham et al. (2022a, b), we used pre-existing data on plant and bee associations (Rasmussen et al.

2021) to derive plant–bee association scores for both plants and bees. We assembled a matrix with information on the number of plant genera for each of 62 plant families that 281 bee species from Denmark and Norway are known to visit (Rasmussen et al. 2021, Wood et al. 2021). We used a detrended correspondence analysis (DCA) in the 'vegan' package in R (Oksanen et al. 2022) to ordinate the plant family–bee species matrix and used the plant family and bee species DCA scores along the four axes returned by the *decorana()* function (DCAs 1–4), resulting in four scores for each plant species from our surveys (Plant DCA1–4). The DCA scores separated plant species according to differences in which bee species they are known to interact with.

Bee traits

Bee species that are widely distributed, and regionally common, are more likely than rarer species to interact with plants locally (Sydenham et al. 2022a, b). We included the number of 10 km grids within a spatial extent (Longitude = [7°58′12″, 13°50′24″], Latitude = [54°22′12″, 61°48′36″]) slightly exceeding that of our study region (Longitude = [9°28′12″, 12°20′24″], Latitude = [55°52′12″, 60°19′12″]) where bee species sampled during our study had been previously recorded (GBIF 2024) as a proxy for regional commonness (Sydenham et al. 2022a, b). We assigned each bee species a categorical trait with two levels to distinguish between eusocial bumblebees and solitary or facultatively social bees. We used data from the European bee fauna (Scheuchl and Willner 2016) to assign each bee species a phenological trait which was a categorical variable with four levels: 'spring–mid-summer' indicating activity from April to July; 'early–late summer' indicating activity from May to August; 'mid–late summer' indicating activity from June to August; and 'entire summer' indicating activity from April to

August. Although the phenology of species varies across climatic gradients the relative phenological difference among species is likely to be fairly constant. As for plants, each bee species was assigned a floral preference score (Bee DCA1–4), extracted from the DCA analysis.

Following R syntax, our plant–bee interaction model was formulated according to Eq. 1:

$$\begin{aligned} \mathrm{glmer}(&\text{Interaction occurrence} \sim \text{Bee Social status}\\ &\times \text{Annual mean temperature} + \text{Bee Social status}\\ &\times \text{Landscape Shannon diversity} + \text{Plant abundance}\\ &+ \text{BeeDCA1} \times \text{PlantDCA1} + \text{BeeDCA2} \times \text{PlantDCA2}\\ &+ \text{BeeDCA3} \times \text{PlantDCA3} + \text{BeeDCA4} \times \text{PlantDCA4}\\ &+ \text{Bee Phenology} \times \text{Plant Phenology}\\ &+ \text{square root}\big(\text{Distance to Sandy soils}\big)\\ &+ \text{Regional Commonness}\\ &+ \big(1|\text{Site identity}\big), \text{family} = \text{binomial}) \end{aligned} \quad (1)$$

We included interaction terms between bee social status and annual mean temperature and landscape Shannon diversity because we had previously found bumblebees and solitary bees to show guild-specific responses along these environmental gradients (Sydenham et al. 2022a). For plant and bee DCA scores we included interaction terms between combinations of related axes (e.g. BeeDCA1 × PlantDCA1, but not BeeDCA1 × PlantDCA2, also as in Sydenham et al. 2022a, b). We included an interaction term between bee and plant phenologies to allow our models to identify forbidden links (Olesen et al. 2011). BeeDCA2 and PlantDCA2 were excluded from the models because their interaction did not contribute significantly to the likelihood of the model (p = 0.092). The square root transformed distance to sandy soils was included as its contribution was close to significant (p = 0.056).

Correlation coefficients between continuous predictor variables suggested no issues with multicollinearity (Pearson r < 0.6). Not accounting for all spatially correlated environmental conditions that may affect plant–pollinator interactions could result in inflated p-values and, more importantly in our model, producing spatially biased predictions. Noise, turbulence, dust, and pollution which are related to traffic volume along roads may for instance affect plant–pollinator interactions (Phillips et al. 2021). We tested if model residuals were spatially correlated to assess if such not-accounted-for spatially correlated environmental conditions resulted in our model producing spatially biased predictions. For each site we calculated the mean Pearson standardized residual across all plant–bee interactions and used the *Moran.I* function in the 'ape' package (Paradis and Schliep 2019) to test if residuals were spatially correlated. To visually assess potential spatial autocorrelation we used the *spline.correlog* function in 'ncf' (Bjornstad 2022) to estimate and plot the

Morans' I correlation of residuals along geographic distances. The Pearson residuals were not spatially correlated (global Moran I: observed = 0.05, expected = −0.01, SD = 0.05, p-value = 0.19) and the confidence interval around the estimated Morans' I correlation broadly overlapped with zero along the geographic distances covered by our site-by-site comparisons (Supporting information).

To assess model performance and to calculate site-specific pollination potential, we used a leave-one-out cross-validation, where we iteratively removed data from one site, fitted the model to data from the remaining sites, and predicted the probability of plant–bee interactions for all plant species at the site in the left-out data (as in Sydenham et al. 2022b). We then used a binomial GLM and likelihood ratio based pseudo-R^2 to assess the relationship between the logit-transformed predicted probability of interactions and the presence or absence of interactions. Using the withheld data, we used the sum of predicted probabilities of interactions across all bee species for each plant at a site to obtain a site-specific measure of pollination potential for individual plant species (Sydenham et al. 2022a). We used linear regressions to assess how the square root transformed, site-specific pollination potential for *L. corniculatus* and *V. cracca* corresponded to the spatial environmental predictors: annual mean temperature, landscape diversity, distance to sandy soils, and plant abundance, including plant species as a categorical variable.

Estimation of pollen deposition

We used Zero-inflated negative binomial GLMMs from the 'glmmTMB' package in R (Mollie et al. 2017) to test if the predicted pollination potential corresponded to the number of pollen grains on flowers of *L. corniculatus* and *V. cracca*. We used zero-inflated models because they yielded satisfactory QQ-DHARMa residual plots (Hartig 2022) with no under-dispersion (dispersion = 1.01), whereas residuals from Poisson and negative binomial GLMMs were skewed and slightly under-dispersed (dispersion = 0.38, and 0.65, respectively). Site was included as a random intercept term to account for repeated measures from the same sites. We first fit models that included an interaction term between plant species identity and the predicted pollination potential.

Following R syntax, our pollen deposition model as a function of the predicted pollination potential was formulated according to Eq. 2:

$$\begin{aligned} \mathrm{glmmTMB}\big(&\text{Pollen grains on stigma}\\ &\sim \text{Predicted pollination potential}\\ &\times \text{Plant species} + \big(1|\text{Site identity}\big), \text{ziformula}\\ &=\sim 1, \text{family} = \text{nbinom1}\big) \end{aligned} \quad (2)$$

We then used likelihood ratio tests to carry out a backward simplification of the model until all the remaining variables were statistically significant (p ≤ 0.05).

We tested if pollen deposition on the stigmas of wild plants varied with our hypothesized drivers of plant–bee interaction frequencies: annual mean temperature, landscape diversity, plant abundance, and distance to sandy soils. We fitted a zero-inflated negative binomial GLMM with the number of pollen grains on *L. corniculatus* or *V. cracca* as response variable and with the four spatially variable predictors: annual mean temperature, landscape diversity within 1000 m radii, distances to sandy soils, and plant abundance as explanatory variables. We used a sequential backward elimination of variables until the likelihood ratio of all remaining variables was statistically significant.

Following R syntax, our pollen deposition model as a function of environmental predictors was formulated according to Eq. 3:

$$glmmTMB\big(Pollen\,grains\,on\,stigma \sim Plant\,abundance$$
$$+ Landscape\,Shannon\,diversity$$
$$+ Annual\,mean\,temperature \qquad (3)$$
$$+ Plant\,species + square\,root\big(Distance\,to\,Sandy\,soils\big)$$
$$+ \big(1|Site\,identity\big), ziformula = \sim 1, family = nbinom1\big)$$

To produce maps of pollination delivery in southeastern Norway, we used the zero inflated GLMMs together with the 'terra' package in R (Hijmans 2023a) to predict the number of pollen grains deposited on *L. corniculatus* as a function of either the predicted pollination potential or the environmental covariates that significantly contributed to explaining the geographic variation in the amount of pollen deposited on flowers. This allowed us to compare maps of pollination delivery generated using the predicted pollination potential to maps generated using environmental predictors directly.

All analyses were run using R ver. 4.2.2 with Rstudio on a x86_64-pc-linux-gnu (64-bit) platform (www.r-project.org). The 'vegan' package (Oksanen et al. 2022) was used for DCA analyses. We used the 'car' package (Fox and Weisberg 2019) for logit(x) transformations. The 'raster' package (Hijmans 2023b) was used to download annual mean temperature data for Scandinavia. The 'terra' package (Hijmans 2023a) was used for raster analyses. R^2 values were calculated with 'MuMIn' (Bartoń 2022). AUC values were calculated using 'pROC' (Robin et al. 2011). Zero-inflated models were fitted using package 'glmmTMB' (Brooks et al. 2017). The 'effects' package (Fox and Weisberg 2019) was used for plotting. The 'DHARMa' package was used for residual analyses (Hartig 2022).

Results

We collected a total of 1835 bee specimens comprising 79 species (Supporting information). Bees were observed visiting a suite of 93 plant species distributed across the 68 sites. Our data were very sparse and consisted of 953 unique occurrences of site–plant–bee interactions and 84 999 absences. The top five plant taxa in terms of number of bee species they interacted with across sites (Supporting information) were *Taraxacum* spp. (31 species), *Hieracium* spp. (17 species), *L. corniculatus* (17 species), *V. cracca* (15 species), and *Trifolium pratense* (15 species). The top five bee taxa were *Bombus pascuorum* (41 plant species), *Bombus* sensu stricto (40 plant species), *B. lapidarius* (34 plant species), *B. pratorum* (27 plant species), and *Seladonia tumulorum* (21 plant species).

The occurrence of plant–solitary bee interactions within sites increased with annual mean temperature but not for interactions involving the eusocial bumblebees (Supporting information). By contrast, interactions involving bumblebees increased with landscape diversity while solitary bee interactions showed no response to this variable (Supporting information). Plant–bee interaction probabilities increased with plant abundance and decreased with distance to sandy soils, independent of bee social status (Supporting information). The leave-one-out cross-validations showed that the occurrence of plant–bee interactions in left-out data were positively related to the predicted probability of plant–bee interactions when considering all 93 plant species as well as for *L. corniculatus* and *V. cracca* combined or alone (Table 2). Still, compared to validations when all 93 plant species were included, predictions were less accurate when validating on *L. corniculatus* and *V. cracca* combined or for *L. corniculatus* alone where predictions overestimated interaction frequencies (slope: logit(x) < 1) or *V. cracca* where predictions underestimated interaction occurrence frequencies (slope: logit(x) > 1) (Table 2).

Across all sites, the pollination potential of *L. corniculatus* and *V. cracca* increased with annual mean temperature (Fig. 2a), landscape diversity (Fig. 2b), and plant abundance (Fig. 2c), but decreased with the distance to sandy soils (Fig. 2f). Of these spatial predictors, landscape diversity (t = 27.5) and plant abundance (t = 27.1) were the most important, followed by distance to sandy soils (t = −17.4). However, while these spatial variables were significant in explaining occurrences of specific plant–bee interactions, their contributions to model likelihood-ratios were modest (all X^2 < 18) compared to those of plant–bee association traits (e.g. BeeDCA1 × PlantDCA1: X^2 = 368), plant–bee phenologies (Bee phenology × Plant phenology: X^2 = 131), and the regional commonness (Regional commonness: X^2 = 310) of bees which had considerably higher likelihood ratios (Supporting information).

The number of pollen grains on stigmas increased with the predicted pollination potential (Fig. 3a, Supporting information). This increase did not differ between *V. cracca* and *L. corniculatus*, indicated by the non-significant interaction term between predicted pollination potential and plant species ($\chi^2 = 0.03$, p = 0.864) which was dropped from the model. Of the spatial predictors used when modelling plant–bee interactions, annual mean temperature

Table 2. Leave-one-out cross validations of the relationship between the presence or absence of interactions between plants growing in a site and the 79 bee species distributed across sites, and the predicted probability that an interaction would occur. The predicted interaction probability was logit(x) transformed in all models so that slopes above or below 1 indicates that the predicted interaction probability under- or overestimated the occurrence of interactions. The goodness of fit of the relationships is shown using proportion variance explained (pseudo-R^2) and area under the receiver operator curve (AUC).

Model	Slope	SE	P	R^2	AUC
All 93 plant taxa					
Intercept	−0.10	0.09	0.254	0.20	0.85
Predicted interaction prob.	0.97	0.02	< 0.001		
Lotus corniculatus and *Vicia cracca*					
Intercept	−0.51	0.25	0.040	0.22	0.86
Predicted interaction prob.	0.88	0.07	< 0.001		
L. corniculatus					
Intercept	−0.90	0.36	0.01	0.15	0.81
Predicted interaction prob.	0.67	0.09	< 0.001		
V. cracca					
Intercept	0.07	0.35	0.836	0.32	0.92
Predicted interaction prob.	1.19	0.12	< 0.001		

(Fig. 3b), landscape diversity (Fig. 3c), and plant abundance (Fig. 3d) were indirectly associated with an increase in the number of pollen grains, while we found no relationship with distance to sandy soils (Fig. 3e). The mean number of pollen grains per stigma differed between plants, so that *L. corniculatus* had fewer pollen grains deposited per stigma (z-value = −8.62), compared to *V. cracca* (Supporting information).
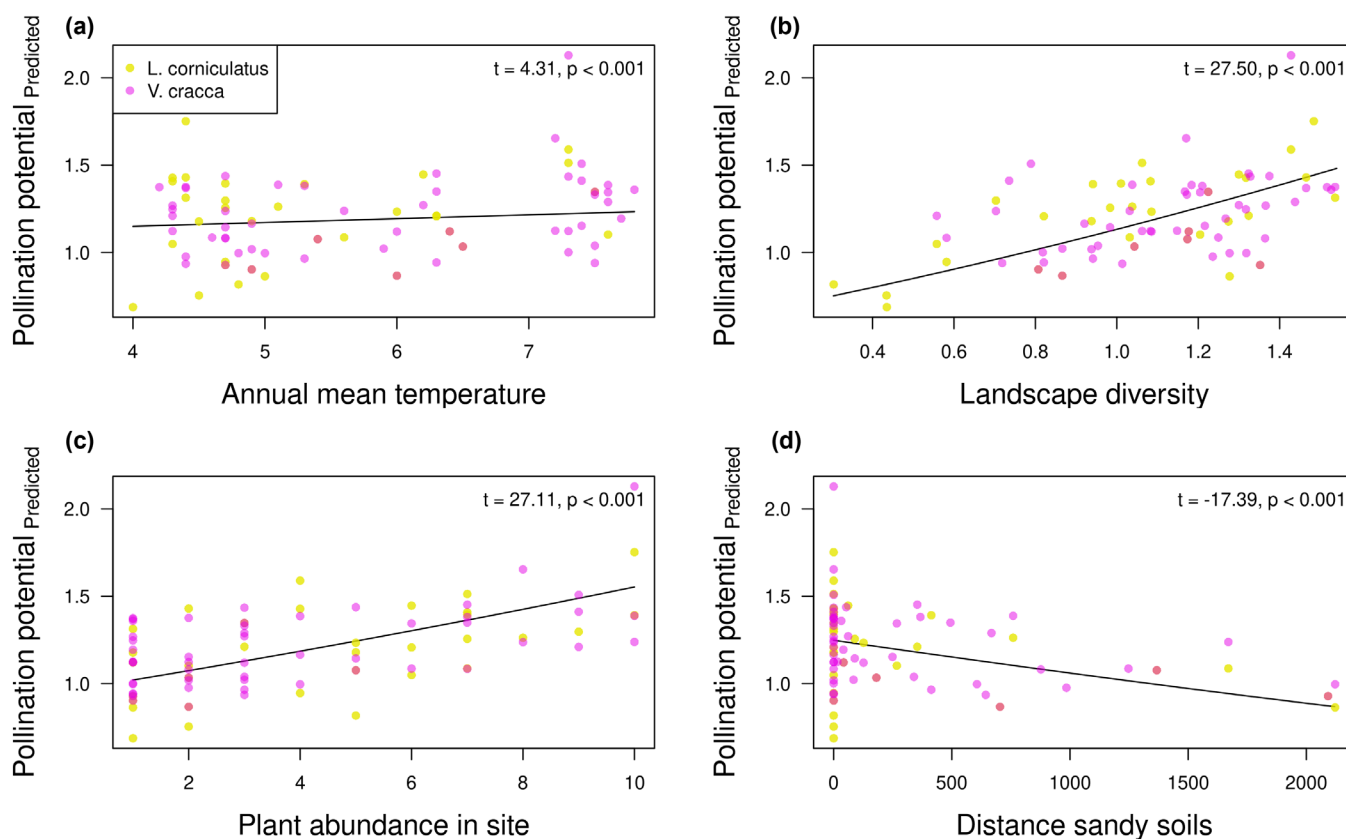

Figure 2. Spatial drivers of pollination potential, calculated as the sum of interaction probabilities across all bee species for a plant in a site (Table 2). The predicted pollination potential for bee-pollinated plants increased with annual mean temperature (a), landscape diversity (b), and plant abundance (c) and decreased with distances to sandy soils (d), varying systematically with the spatial predictors used to model pairwise plant–bee interactions (Supporting information). Pollination potential was calculated for *Lotus corniculatus* and *Vicia cracca* as the sum of predicted interaction probabilities across all 79 bee species within sites where the plants occurred. Excluding the outlier with a predicted pollination potential of 2.13 for *V. cracca* did not change the significance of the effect sizes (ann. mean temp: t-value = 4.22, landscape H: t-value = 28.06, plant abundance: t-value = 26.71, distance sandy soils: t-value = −18.08).

Discussion

Our findings illustrate that plant preferences of pollinators and guild-specific responses to environmental conditions, such as temperature and landscape diversity, can be included in models of pollination potential for predicting the pollen deposition in natural plant communities. This way, models of pairwise interactions allow linking ecosystem functions such as pollination to the drivers of species distributions and the assembly of ecological networks (Fig. 4).

In northern Europe, cold-adapted bumblebees (*Bombus* spp.) are central components of plant–pollinator networks (Maia et al. 2019) and large-bodied furry bees such as bumblebees are particularly efficient pollinators of many plants (Földesi et al. 2021). However, climate change at northern latitudes is expected to shift the composition of pollinator communities with a decrease in bumblebee abundance and an increase in the (typically more thermophilic) solitary bees (Hoiss et al. 2012, Sydenham et al. 2015, 2022b). While rising temperatures are resulting in range contractions for many species of bumblebees (Kerr et al. 2015, Jackson et al. 2022), it is not clear how such changes in the pollinator community will affect the pollination potential for typical bee-pollinated plants such as legumes and vetches, which may often be pollen limited (Bennett et al. 2020). Our findings suggest that negative effects on plant pollination from climate-driven bumblebee declines may be partly offset by positive effects from increasing visitation rates by solitary bees. That

temperature-associated increases in interaction frequency between solitary bees and plants may be greater than the reduction in interactions with bumblebees is in line with findings from another recent study conducted in the same region (Sydenham et al. 2022b). Intermediate rises in temperatures might therefore increase local pollination potential, if range expansions of solitary bees are more pronounced than the range contractions of bumblebees.

The homogenization of landscapes in northern Europe – with forest plantations, cereal fields, or urban areas dominating entire landscapes – reduces the population growth rates of pollinators such as bumblebees (Schweiger et al. 2022) and thereby plant–pollinator interaction frequencies. Bee species differ in their responses to habitat loss (Bommarco et al. 2010), and at the spatial scale at which landscape conditions assert the strongest effects (Steffan-Dewenter et al. 2002). Our findings corroborate recent findings that plant–bee interactions involving bumblebees increase with landscape diversity within a 1000 m radius, while solitary bees seem to not respond to landscape conditions at this spatial scale (Sydenham et al. 2022b). One potential explanation is that solitary bees respond to landscape conditions at smaller spatial scales than bumblebees because of their shorter foraging ranges (Steffan-Dewenter et al. 2002, Greenleaf et al. 2007). Another, non-exclusive, explanation is that because the distribution of high-quality habitat patches will change during the season, bumblebees rely on ecological conditions at larger spatial and longer temporal scales for the landscape to provide
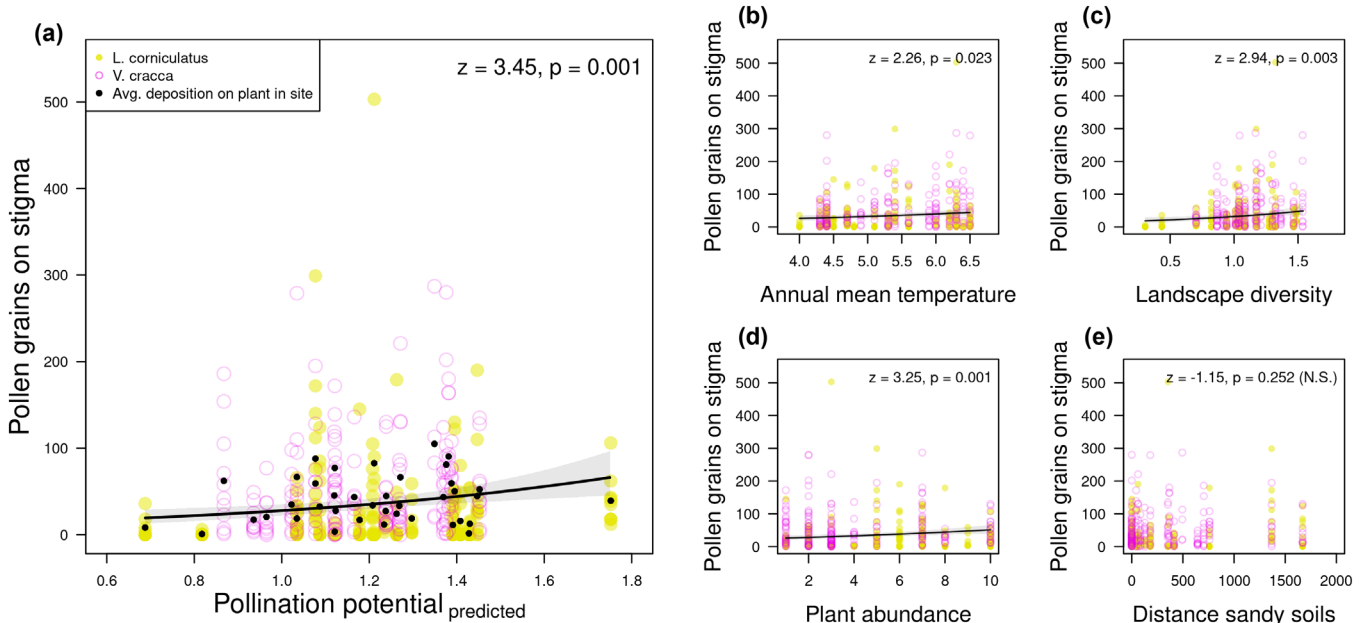

Figure 3. Pollination potential: predicted pollen deposition. The number of pollen grains deposited on stigmas of *Lotus corniculatus* and *Vicia cracca* within habitats increased with the predicted pollination potential ((a), Supporting information). Pollination potential was calculated as the sum of probabilities of pairwise interaction between 79 wild bee species and the target plant within sites (Fig. 2, Table 2). Yellow and purple points show number of pollen grains on individual flowers for each species. Black points show the average number of pollen grains on flowers of each plant species in a site. The number of pollen grains on stigmas was also positively related to the environmental drivers of plant–bee interactions (Supporting information): annual mean temperature (b); landscape diversity (c); and plant abundance (d); but not did not decrease significantly with distance to sandy soils (e). Regression lines, confidence intervals, z-values, and p-values are from zero-inflated negative binomial GLMMs.
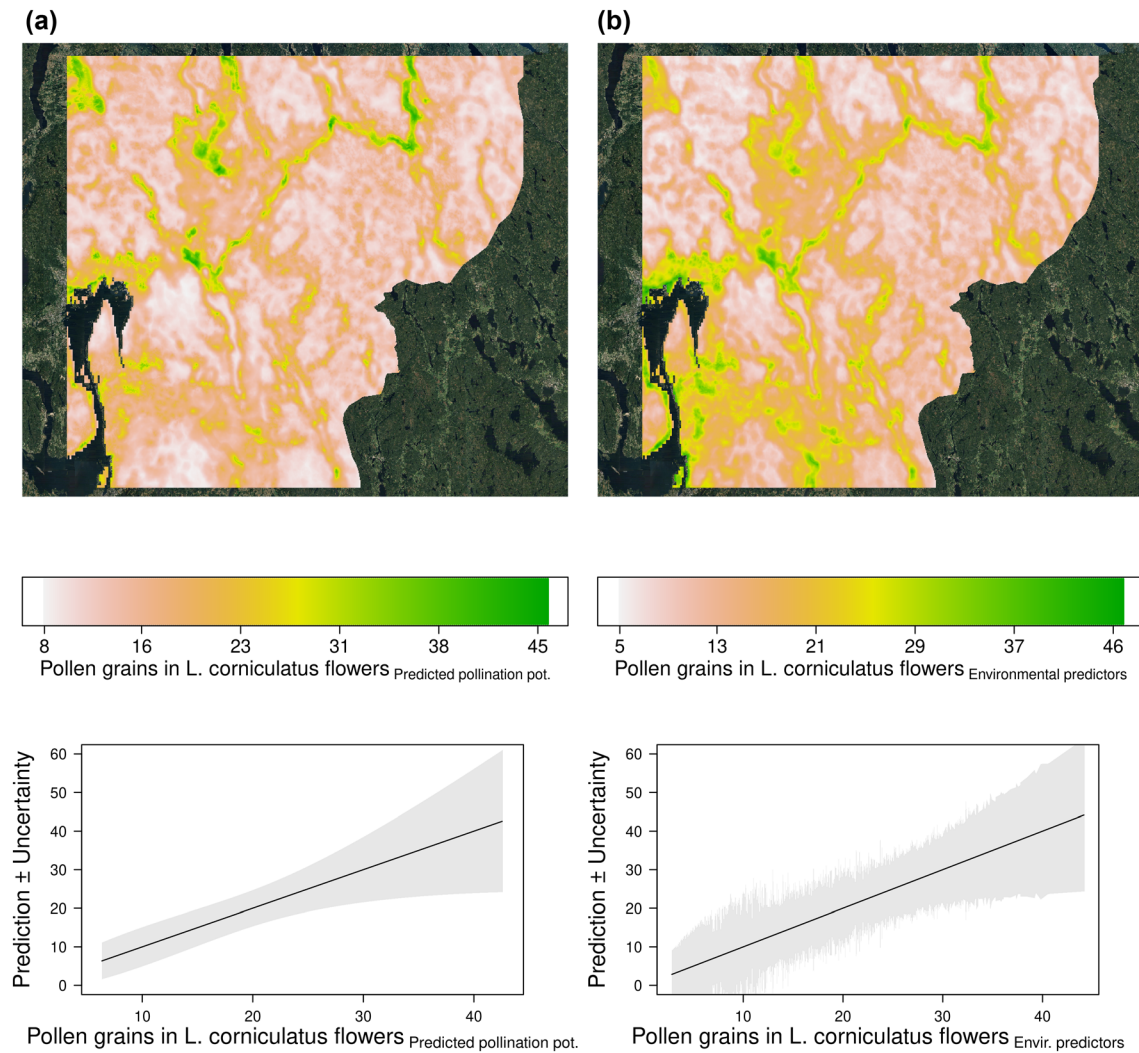
Figure 4. Spatial predictions of pollen deposition showing the predicted number of pollen grains on flowers of *Lotus corniculatus* from models of pollination potential (a) and from models of pollen grain counts as a function of the environmental predictors: annual mean temperature and landscape diversity (b). Plant abundances were held constant at an intermediate value (5) when making predictions. For both models the uncertainty (95% CIs) around predictions and how it increases proportionately with predicted pollen deposition is shown in subplots in the bottom panel.

sufficient and continuous floral resources. By contrast, habitat conditions at more local and shorter temporal scales may be sufficient to sustain solitary bees which typically have shorter spatial ranges and activity periods than bumblebees. Although plant–bee interactions involving solitary bees did not respond to landscape diversity, we found that interactions with bumblebees, pollination potential, and pollen deposition increased with landscape diversity, supporting the hypothesis that bumblebees are key pollinators of bee-pollinated plants in our region (Földesi et al. 2021). Consequently, our data support the findings of others (Gómez-Martínez et al. 2022) that maintaining or restoring landscape diversity is required to sustain diverse communities of flower visitors and thereby the structural resilience of plant–pollinator interactions.

Plant abundance was an important predictor of pollination potential and pollen deposition in our study, which is in line with previous studies showing that abundance-based processes are important contributors to plant–pollinator interactions (Gómez-Martínez et al. 2022, Sydenham et al. 2022a, b). Flower density explains why visitation frequencies vary not only across habitats but also within habitats, and bumblebees, for example, are attracted to plots with a high density of tubular flowers (Hegland and Boeke 2006). Conserving pollination services to plants is therefore likely to require that local plant populations are of an adequate size for them to attract pollinators.

Predictions from models such as ours are only applicable within the environmental conditions encountered while sampling data (Meyer and Pebesma 2021). Our data did not cover the boreal or alpine climate zones where climate change-associated increases in temperature are most likely to assert their strongest effects on bumblebees (Rasmont et al. 2015, Martinet et al. 2021). To predict how climate change is likely to affect plant–bee interactions and

the pollination potential of wild plants in boreal and alpine areas will therefore require tailored data collected for that purpose. Our findings should therefore not be extrapolated to non-temperate regions. Similarly, the amount of pollen deposited per visit is known to vary substantially between bee species (King et al. 2013, Földesi et al. 2021) but we did not have data to account for inter-specific differences in how much pollen different bee species can be expected to deliver per visit in our models. It may therefore be that models of pollination potential can be further improved by weighting the predicted probabilities of pairwise plant–pollinator interactions by the species-specific amount of deposited pollen expected per visit. Moreover, because we did not sub-sample the 50 m transects when surveying plant–bee interactions, we could not account for detection errors which might have improved the prediction accuracy of our models (Graham and Weinstein 2018). However, despite not accounting for inter-specific differences in pollen deposition rates, or detection errors, our model produced spatial prediction maps of pollination delivery broadly similar to those obtained when modelling the number of pollen grains per flower as a function of the spatial environmental predictors directly (Fig. 4).

Conclusions

Our study showed that it is possible to predict pollination potential from spatial models of plant–bee interactions and that the predicted pollination potential from such models corresponded to the number of pollen grains deposited on individual flowers of legumes. Pollination potential and pollen deposition on *L. corniculatus* and *V. cracca* increased with plant abundance, annual mean temperature, and landscape diversity. Our findings therefore suggest that conservation efforts aimed at preserving plant–bee interactions and pollination service delivery should therefore target habitats where plant abundances are sufficiently large to attract wild bee foragers and where the surrounding landscape is heterogenous enough to sustain populations of bumblebees. Spatial models, such as the ones presented in our study, can be used to map pollination potential and to direct pollination-oriented conservation and restoration efforts.

Author contributions

Markus A. K. Sydenham: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Yoko L. Dupont**: Data curation (equal); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anders Nielsen**: Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Jens M. Olesen**: Funding acquisition (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Henning B. Madsen**: Data curation (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Astrid B. Skrindo**: Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Claus Rasmussen**: Funding acquisition (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Megan S. Nowell**: Data curation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Zander S. Venter**: Data curation (supporting); Funding acquisition (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Stein Joar Hegland**: Funding acquisition (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anders G. Helle**: Data curation (supporting); Investigation (supporting); Writing – review and editing (supporting). **Daniel I. J. Skoog**: Data curation (supporting); Investigation (supporting). **Marianne S. Torvanger**: Data curation (supporting); Investigation (supporting). **Kaj-Andreas Hanevik**: Data curation (supporting); Investigation (supporting). **Sven Emil Hinderaker**: Data curation (supporting); Investigation (supporting). **Thorstein Paulsen**: Data curation (supporting); Investigation (supporting). **Katrine Eldegard**: Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Trond Reitan**: Funding acquisition (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Graciela M. Rusch**: Funding acquisition (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s1rn8pkgt (Sydenham et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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