








RESEARCH ARTICLE

The contributions of flower strips to wild bee conservation in agricultural landscapes can be predicted using pollinator habitat suitability models

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Abstract

1. Sowing flower strips along field edges is a widely adopted method for conserving pollinating insects in agricultural landscapes. To maximize the effect of flower strips given limited resources, we need spatially explicit tools that can prioritize their placement, and for identifying plant species to include in seed mixtures.
2. We sampled bees and plant species as well as their interactions in a semi-controlled field experiment with roadside/field edge pairs with/without a sown flower strip at 31 sites in Norway and used a regional spatial model of solitary bee species richness to test if the effect of flower strips on bee species richness was predictable from the modelled solitary bee species richness.
3. We found that sites with flower strips were more bee species rich compared to sites without flower strips and that this effect was greatest in areas that the regional solitary bee species richness model had identified to be particularly important for bees. Spatial models revealed that even within small landscapes there were pronounced differences between field edges in the predicted effect of sowing flower strips.
4. Of the plant species that attracted the most bee species, the majority mainly attracted bumblebees and only few species also attracted solitary bees. Considering both the taxonomic diversity of bees and the species richness of bees attracted by plants we suggest that seed mixes containing *Hieracium* spp. such as *Hieracium umbellatum*, *Pilosella officinarum*, *Taraxacum* spp., *Trifolium repens*, *Lotus corniculatus*, *Stellaria graminea* and *Achillea millefolium* would provide resources for diverse bee communities in our region.

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5. Spatial prediction models of bee diversity can be used to identify locations where flower strips are likely to have the largest effect and can thereby provide managers with an important tool for prioritizing how funding for agri-environmental schemes such as flower strips should be allocated. Such flower strips should contain plant species that are attractive to both solitary and bumblebees, and do not need to be particularly plant species rich as long as the selected plants complement each other.

KEYWORDS

agri-environmental schemes, bees, flower strips, networks, pollinators, restoration, spatial

1 | INTRODUCTION

Agricultural intensification contributes to global declines in insect biodiversity (Raven & Wagner, 2021), including that of pollinators of wild and cultivated plants (IPBES, 2016). During the past century agricultural intensification has left European agricultural landscapes homogenous (Jongman, 2002; Stoate et al., 2009) and floristically impoverished (Baude et al., 2016; Carvell et al., 2006). This has led to reduced biodiversity in these landscapes (Carvalho et al., 2013; Ollerton et al., 2014), including a loss of pollinator diversity (Hemberger et al., 2021) with potential consequences for ecosystem service delivery (IPBES, 2016). Acknowledging the need to halt and reverse declines of wild pollinators (IPBES, 2016), several countries and intergovernmental organizations, such as the EU, have developed pollinator conservation strategies and initiatives (Norwegian Ministries, 2018; Stout & Dicks, 2022; Underwood et al., 2017).

Sowing flower strips along field edges of both pollinator dependent and independent crops has become a widely adopted agri-environmental scheme for enhancing resources for pollinating insects in agricultural landscapes (Albrecht et al., 2020; Haaland et al., 2011), hence supporting the delivery of crop pollination as an ecosystem service in the wider landscape (Feltham et al., 2015). Flower strips do not just attract pollinators from the wider landscape but have the potential to increase wild bee populations (Bommarco et al., 2021; Ganser et al., 2021) and species diversity in the landscape (Jönsson et al., 2015). However, and as for pollinator conservation schemes in forested ecosystems (Sydenham et al., 2020), there is mounting evidence that the effect of flower strips in agroecosystems depends on the capacity of the wider landscape to support pollinator diversity (Batáry et al., 2011; Carvell et al., 2011; Heard et al., 2007).

Also, because pollinators differ in their floral preferences (Mueller & Kuhlmann, 2008; Rasmussen et al., 2021; Wood et al., 2021), and phenology (Oertli et al., 2005; Rasmussen et al., 2016), the diversity of pollinators supported by flower strips will depend on their plant species composition (Burkle et al., 2020; M'Gonigle et al., 2017). Ideally, flower strips should consist of native plants from locally sourced seeds, to conserve local species and genomic plant diversity. However, sourcing local seeds of multiple plants is costly and flower strips in, for example, Norway are typically

sown using commercially available seed mixes consisting of both native and non-native species sourced from non-Norwegian seeds (Vold, 2020). To ensure that funding allocated to agri-environmental schemes is spent cost-effectively, there is a need for tools that can help prioritize on which sites to sow flower strips, and which plant species to sow.

We used bee and plant species records collected in 31 sites with or without sown flower strips in agricultural landscapes in South-eastern Norway, together with a spatial prediction model of solitary bee species richness (Sydenham, Eldegard, Venter, et al., 2022) to assess: (1) if the local richness of bee-visited plants was enhanced by the presence of flower strips in field edges; and (2) if the species richness of wild bees increased with flower strips and whether this effect increased with higher values of predicted bee habitat suitability. Finally (3), we compare visitation rates by bees with the aim of identifying plant species with a disproportionately large contribution to support bee diversity. We use wild bees as a model system because of their efficiency as pollinators (Willmer et al., 2017) and because of their ecology as central place foragers (Westrich, 1996) with limited foraging ranges (Gathmann & Tschardt, 2002; Greenleaf et al., 2007; Zurbuchen et al., 2010), which makes them excellent indicators of habitat suitability, including the availability of floral resources.

2 | MATERIALS AND METHODS

We used a paired design of study sites located in Southeastern Norway consisting of a field edge and an adjacent vegetated roadside, with or without a sown flower strip in the field (Figure 1). During early spring (April) 2022, we used data from Vestfold/Telemark County Governor's office to identify sites where farmers had previously (in 2021 and sometimes also in 2020) sown a flower strip along the field edge. We included sites in our study if farmers were also planning to sow a flower strip along the same field edge in 2022. Species composition of the flower strips varied, but *Phacelia tanacetifolia*, *Trifolium pratense* and *Trifolium repens* were commonly used in the seed mixtures. We paired each flower strip site with a control site (i.e. study site without flower strip) with a road side of similar width, located between 1 and 5 km from the flower strip site. We

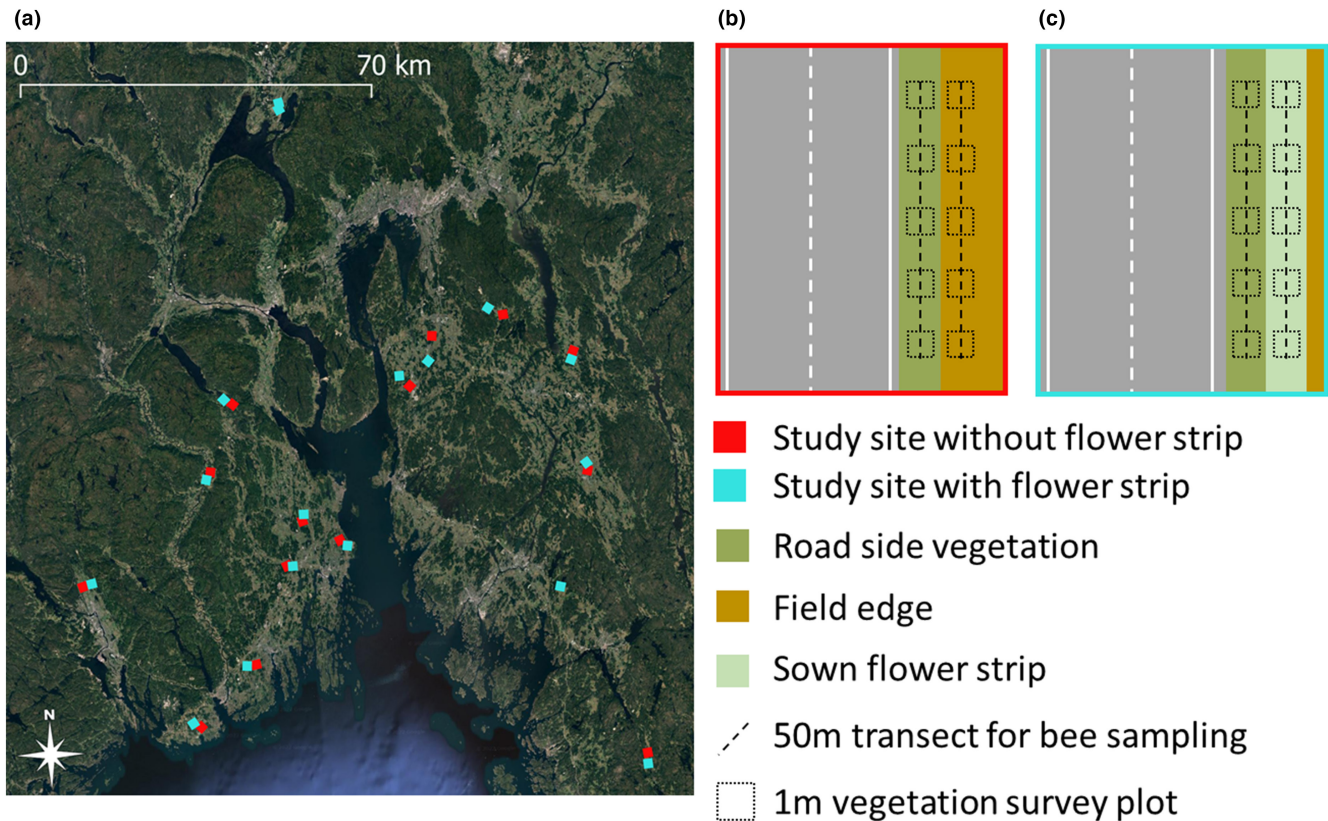


FIGURE 1 The Oslo fjord region showing the location of study sites in southeastern Norway (a). Each study site consisted of a road side and an adjacent field edge without (b) or with (c) a sown flower strip. Satellite imagery from Map data ©2023 Google via QGIS 2023.

considered our samples as independent, that is, that they sampled different bee communities, because distances of 1 km or greater are beyond the typical foraging range of most wild bees in our region (e.g. Kendall et al., 2022). At one of the intended control sites, the farmer did sow a flower strip in 2022 and for another site we did not find a suitable control site. Our resulting study design consisted of 17 flower strip sites with a vegetated roadside *and* a flower strip (Figure 1b), and 14 control sites with a vegetated roadside *and without* a flower strip (Figure 1c).

At each site we sampled wild flower-visiting bees with an entomological net by walking slowly for 20 min along two 50 m transects placed in the vegetated road- and field edge respectively (Figure 1). To account for handling time, we added 30 s sampling time per collected specimen. For our samples to cover seasonally distinct parts of the local bee communities (Oertli et al., 2005), we conducted three surveys during the summer of 2022: in late May (early summer), late June/early July (summer) and late July (late summer). Because of unstable weather we were only able to sample 25 of the 31 sites during the first survey. All flower-visiting bees collected were kept in 50 mL falcon tubes filled with 96% ethanol, labelled according to date, collector identification, site, habitat (roadside vs. field edge) and plant species. Collected bees were identified by the lead author. Voucher specimens are stored in the entomological collections at the Norwegian Institute for Nature Research in Oslo. In July, we placed five 1 m² square vegetation plots regularly along the

50 m transects with one plot per 10 m. In each 1 m² vegetation plot we recorded the occurrence of forb and shrub species in four 25 by 25 cm sub-plots. We recorded all species regardless of growth stage so that our single plant survey provided estimates of the relative frequency of plant flowering during and outside the survey period (as in Sydenham, Venter, Reitan, et al., 2022). No permits were required to conduct our fieldwork.

We compared species richness of bee-visited plants between transect types, that is, roadsides in flower strip sites, roadsides in control sites, field edges in flower strip sites and field edges in control sites. We included plant species that were visited by a bee at least once in at least one site (as in Sydenham, Venter, Reitan, et al., 2022). To test for statistical differences, we used linear mixed effects models (LMMs) with the $\log(y + 1)$ transformed average plant species richness as well as the standard deviation in plant species richness measured across the five 1 m² vegetation plots per transect as a proxy for transect-specific plant richness and density. Density was included to provide an assessment of whether plant species richness was more homogeneously distributed in the sown flower strips compared to the naturally vegetated road sides. We included site identity as a random effect. We used Poisson GLMs to test if plant species richness in sites with flower strips was higher than that of control sites without flower strips.

We tested if spatial prediction models of solitary bee species richness can be used to identify where flower strips are likely to

increase bee diversity the most. For each site we extracted the predicted solitary bee species richness from a region-wide pollinator habitat suitability model (Sydenham, Eldegard, Venter, et al., 2022). We compared the predicted values with the bee species richness observed in the 31 sites calculated using data collected during the second and third field surveys (hereafter *bee species richness*). We excluded social and clepto-parasitic bees when calculating species richness. We used Poisson GLMs to test if the observed species richness of wild, non-parasitic bees increased with the predicted solitary bee species richness, with the presence of a flower strip within the site, with plant species richness, and if including an interaction term between the predicted solitary bee species richness and the presence of flower strips significantly improved model fit. During the second and third surveys, the roadside had been cut in 10 sites prior to one of the two surveys. We therefore also tested if transect mowing explained residual variation. We used likelihood ratio tests to perform a backward elimination of variables.

We compared plant species regarding how many wild bee species they attracted on average. For this purpose, we used data on bee-flower interactions recorded in the 25 study sites with data from three surveys during the flowering season to be able to include early season records, thus avoiding the underestimation of the importance of early flowering species such as dandelions (*Taraxacum* spp.) for spring/early summer active bees. For each site, we used the number of plant species occurrence records in the 25 by 25 cm

sub-plots as a proxy for site plant abundance. Plant species were assigned an abundance value of zero if they had not been recorded in the site vegetation survey but had been observed interacting with bees. We used a Poisson GLMM to estimate the average number of wild bee species attracted to each plant species within a site after controlling for the effects of the abundance of the plant species. We included the site identity as a random intercept to account for unknown factors determining site-specific differences in the bee species richness observed on a plant.

All analyses were conducted using R (R Core Team, 2022). Mixed models were fit using lme4 (Bates et al., 2015) and model R^2 's were calculated using MuMIn (Bartoń, 2020). We used likelihood ratio tests to test our predictions (with $\alpha=0.05$) and DHARMA plots (Hartig, 2021) to assess residual distributions. We used the raster package in R (Hijmans, 2022) for handling spatial data. R code and data are available from Sydenham et al. (2023).

3 | RESULTS

Mean richness and its standard deviation of bee-visited plant species were lowest in field edges without flower strips compared to that of flower strips and roadsides, which did not differ substantially (Figure 2a,b, Table 1). Even though four species were exclusively found in flower strips (i.e. *Vicia faba*, *Trifolium incarnatum*, *Glebionis*

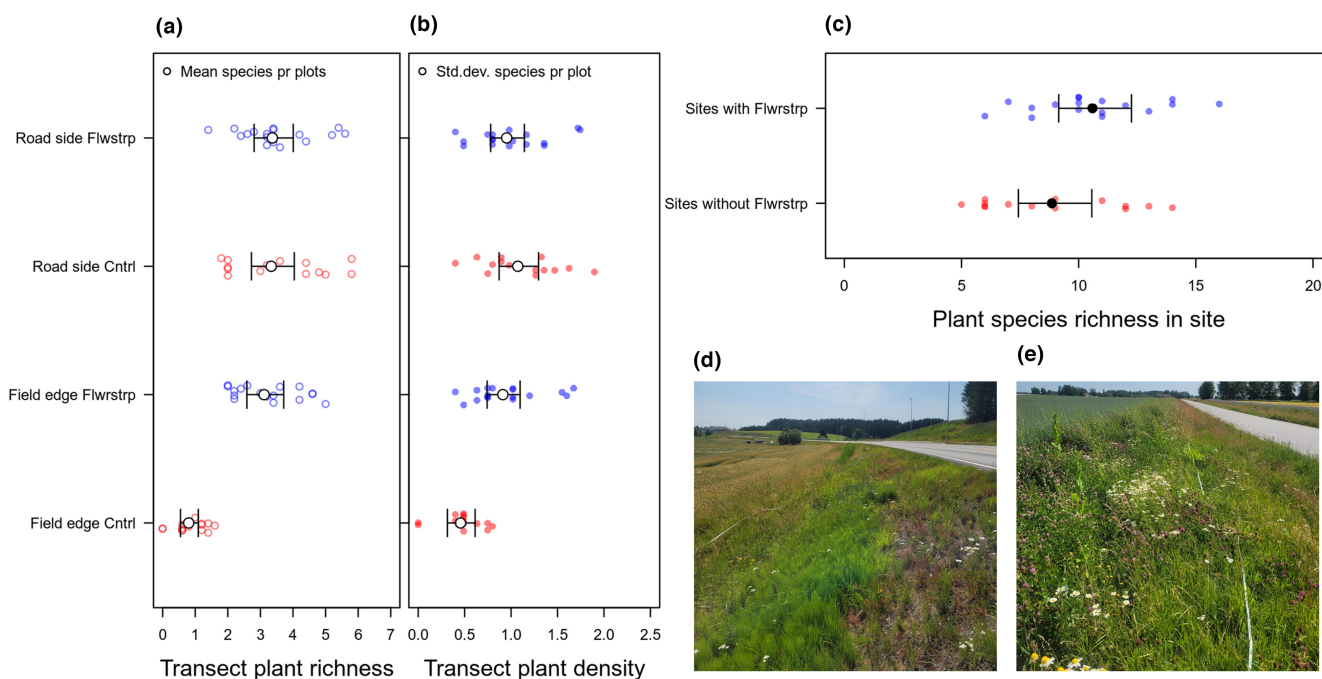


FIGURE 2 Effects of flower strips on the species richness and density of bee-visited plants along field edges and adjacent roadsides. Differences in (a) plant species richness, showing the expected mean species richness in plots across sites, and (b) density, showing the expected standard deviation of species richness in plots across sites, along 50m transects placed along field edges or roadsides, both with (Flwrstrp) or without (Cntrl) sown flower strips. (c) Comparison of the total species richness of bee-visited plants in study sites with (flower strip sites) or without (control sites) sown flower strips. Blue and red points show data from sites with and without flower strips respectively. (d) Example of study site with a plant species rich roadside but no flower strip. (e) Plant species rich study site with roadside and flower strip. Black points show estimated values from GLMs and whiskers show the corresponding 95% confidence intervals.

TABLE 1 Statistical model summaries from tests of research questions related to: how sown flower strips influenced bee-visited plant species richness and density (research question I); how the species richness of wild bees was affected by sown flower strips and if the magnitude of this effect is predictable from habitat suitability models (research question II); and how plant species within sites differ in their contribution to bee species richness, after controlling for their abundance (research question III).

Research question I					
Average plant species richness in plots	df	F	p	R ² _{marginal}	R ² _{conditional}
Fixed effects terms					
Transect type (four levels ^a)	3	39.3	<0.001	0.62	0.72
Random effects (62 observations)					
Site (n = 31)		0.020	0.142		
Residuals		0.060	0.244		
Std. dev. plant species richness in plots	df	F	p	R ² _{marginal}	R ² _{conditional}
Fixed effects terms					
Transect type (four levels ^a)	3	10.4	<0.001	0.32	0.39
Random effects (62 observations)					
Site (n = 31)		0.004	0.062		
Residuals		0.033	0.181		
Plant species richness in site	df	χ ²	p	R ² _{marginal}	R ² _{conditional}
Fixed effects terms					
Site treatment type (two levels ^b)	1	2.36	0.124	0.07	NA
Research question II					
Bee species richness	df	χ ²	p	R ² _{marginal}	R ² _{conditional}
Fixed effects terms					
Log ₁₀ (Predicted solitary bee species richness)	1	9.74	0.002	0.59	NA
Site treatment type (two levels ^b)	1	19.20	<0.001		
Research question III					
Bee plant-visitor richness	df	χ ²	p	R ² _{marginal}	R ² _{conditional}
Fixed effects terms					
Plant species identity (47 levels)	45	115.3	<0.001	0.44	0.49
Plant species abundance	1	55.57	<0.001		
Random effects (271 observations)					
Site (n = 25)		0.083	0.288		

^aFour levels: field edge with/without flower strip, roadside with/without flower strip.

^bTwo levels: flower strip site versus control site.

segetum and *Cichorium intybus*), sites with flower strips did not have higher total plant species richness than sites without flower strips (Figure 2c, Table 1).

We found that the pollinator habitat suitability model (Sydenham, Eldegard, Venter, et al., 2022; Sydenham, Venter, Eldegard, et al., 2022) correctly identified sites where flower strips increased bee diversity the most. We sampled a total of 42 species and 1272 individuals of non-parasitic wild bees. All species were native to Norway. Bee species richness increased with the predicted solitary bee species richness (Figure 3a, Table 1) and was higher in sites with flower strips than in control sites (Figure 3a,b). Backward elimination of variables showed that observed bee species richness was not related to: differences in plant species richness (df=1, $\chi^2=0.51$, $p=0.48$); whether or not the road side had been cut prior to the surveys (df=1, $\chi^2=0.72$, $p=0.40$); and or an interaction term between treatment type and the predicted solitary bee species richness (df=1, $\chi^2=2.08$, $p=0.15$). Mapping the difference between the expected bee species richness in field edges with and without flower strips as a function of the predicted solitary

bee species richness showed a considerable spatial variation in the effect one can expect from sowing flower strips (Figure 3c–e).

Our assessment of plant species in terms of their contributions to bee diversity revealed that while most plants attracted multiple species of bumblebees, only a subset of the plants attracted several solitary bee species. Of the 47 bee-visited plant species, *Glebionis segetum*, *Centaurea scabiosa* and *Ranunculus ficaria* on average attracted the most bee species per site (Figure 4a,b). However, because these species occurred in few sites only, it is uncertain whether these plants always support a high diversity of bee species. In terms of the number of unique interactions between bees and plants (Figure 4a) and the species richness of bee plant visitors (Figure 4b), species such as *Hieracium* spp., *Barbarea vulgaris*, *T. repens* and *Lotus corniculatus* attracted a broad suite of both bumblebees and solitary bees. *Hieracium* spp. was also visited by the nationally threatened (VU, Artsdatabanken, 2021) solitary bee *Dasygaster hirtipes* which is specialized in collecting pollen from yellow composites. However, some plants such as *Stellaria graminea* that were consistently visited by a small number

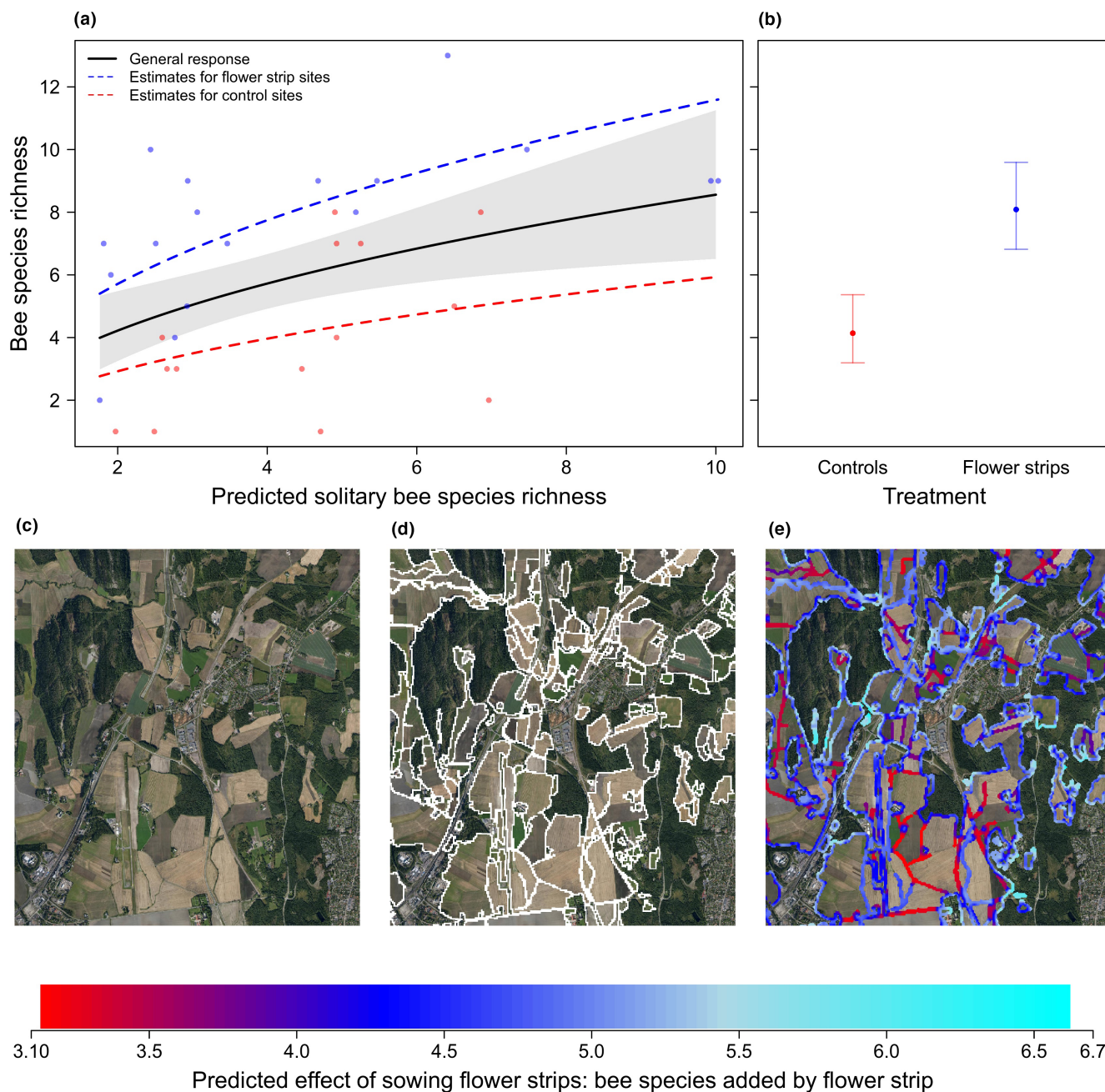


FIGURE 3 (a) Bee species richness increased with the predicted solitary bee species richness. Importantly, the expected difference in bee species richness between sites with flower strips compared to sites without flower strips increased as a function of the predicted solitary bee species richness. (b) Establishing flower strips increased bee species richness. (c) A typical Norwegian agricultural landscape dominated by coniferous forests and agricultural fields. (d) All field edges, identified from the Norwegian AR5 area resource map (Bjørndal & Bjørkelo, 2006). (e) Spatial variation in the predicted effect of sowing flower strips along field edges in the landscape. Field edges where effects are predicted to be large should be prioritized.

of bee species seem to indicate more specialized plant–bee interactions. The abundance of a plant species within a site was a strong predictor of the number of bee species it attracted (Figure 4c).

4 | DISCUSSION

Spatial models that predict richness of functional groups, such as pollinators, have been developed as tools to help identify priority

areas to target habitat enhancement measures, that is, where it is expected that these measures will have most effect (Sydenham et al., 2020). This study is, to our knowledge, the first to assess the ability of such models to predict the effectiveness of habitat enhancement measures using the establishment of flower strips in field edges. Our results show that: (1) flower strips increase the availability of floral resources in field edges by providing an important addition to the resources provided by flowers in adjacent roadsides; (2) flower strips increase bee species richness and pollinator habitat

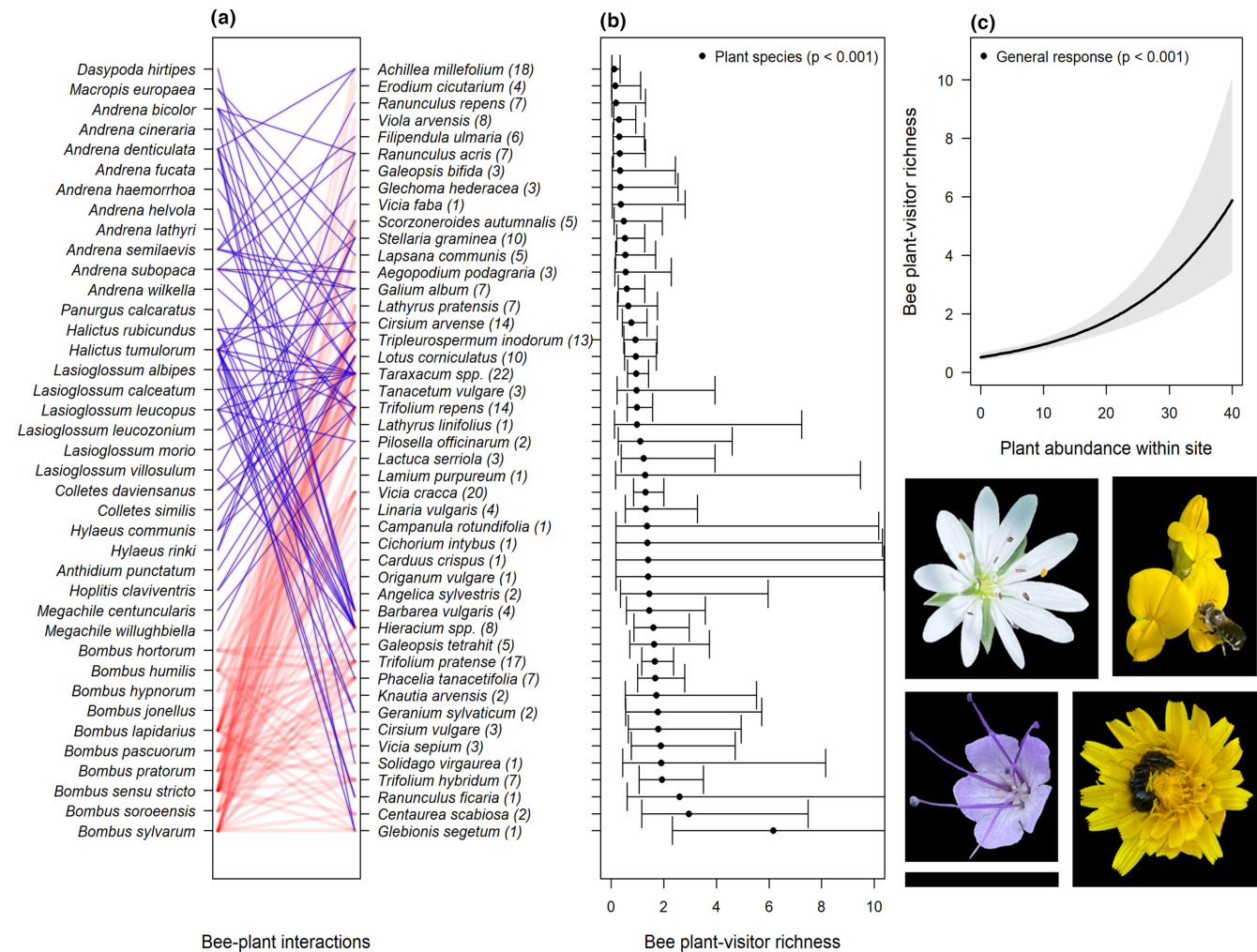


FIGURE 4 Assessment of the contribution of individual plant species for supporting diverse wild bee communities in sown flower strips, based on: (a) observed interactions between bee species and plant species; and (b) the expected number of wild bee species observed visiting a plant species within our study sites, after controlling for (c) the abundance of the plant species within the site. Numbers within parentheses show the number of observations (sites) per plant species. Darker lines are drawn for interactions with solitary bees (blue) than for bumblebees (red) in (a). Whiskers and polygons in (b, c) show 95% confidence intervals from a Poisson GLMM, p -values are from likelihood ratio tests. The inserted images show flowers of plants occurring in our study from top-left corner: *Stellaria graminea*, *Lotus corniculatus*, the non-native *Phacelia tanacetifolia* and a *Hieracium* spp.

suitability models can identify field edges where the effect of enhanced flower resources was largest; and (3) that a relatively small subset of the plants within field edges and roadsides are attractive to both solitary bees and bumblebees.

The dependency of the effectiveness of flower strips on the landscape context, that is, the area and proximity to other suitable nesting and flower resources (Sydenham, Eldegard, Venter, et al., 2022; Sydenham, Venter, Eldegard, et al., 2022), varies among pollinator taxa and appears to be greater for solitary bees than for bumblebees (Hellwig et al., 2022). This difference could be due to the smaller foraging ranges of solitary bees (Greenleaf et al., 2007), because solitary bees generally respond to habitat availability at smaller spatial scales than bumblebees (Steffan-Dewenter et al., 2002), or that solitary bees often have very specific nest site requirements (Hellwig et al., 2022). Indeed, bumblebee species richness often depends on landscape conditions measured at spatial scales of up to several

kilometres (Grüter & Hayes, 2022; Kallioniemi et al., 2017) and their response to floral plantings has previously been shown to depend on landscape conditions at 1000m (Heard et al., 2007). If bumblebees utilize the same foraging patches as solitary bees, targeting habitat enhancement schemes to benefit solitary bees should also support bumblebees, particularly if multiple flower strips can be added within the foraging range of bumblebees. The predicted solitary bee species richness may therefore be a useful indicator of flower strip effectiveness for promoting wild bee diversity within landscapes.

It is important to restrict the use of spatial models of flower strip effectiveness to landscapes where predictions can be trusted, or within their area of applicability (Meyer & Pebesma, 2021). The area of applicability of prediction models can be defined by the range of environmental conditions within which they have been trained, beyond which interpretation becomes spurious. The model of solitary bee species richness we used was built using data from

temperate and boreal lowlands in southeastern Norway, predicting the highest bee diversity in areas with comparatively warmer climates, that is, at low elevations and latitudes (Sydenham, Eldegard, Venter, et al., 2022; Sydenham, Venter, Eldegard, et al., 2022). While bee diversity generally increases with temperature in northern Europe (Hoiss et al., 2012), several bee species have a boreal and alpine distribution and are not found in the temperate lowlands. These include several species of bumblebees, in addition to some solitary bees such as *Osmia nigriventris* (Müller et al., 2019) that a model restricted to lowland areas would be biased against. Habitat enhancement models should therefore be tailored to the environmental conditions in which they will be applied.

Our study shows that plants commonly included in flower seed mixes are rarely used by solitary bees (Wood et al., 2017). Indeed, while the non-native *Phacelia tanacetifolia* on average attracted many species, these were almost exclusively bumblebees. In line with recent studies (e.g. Nichols et al., 2022), we found that only a few plant species, or taxonomic aggregations, attract a wide range of solitary bee species. Warzecha et al. (2018) for instance, found that four plant species provided resources for 81% of all recorded pollinator species in their study. In addition to providing enough plant species to cater for diverse bee communities, plant abundances should be evenly distributed among species to ensure a high nutritional diversity for bees (Klaus et al., 2021). To cater for diverse bee communities in our region our findings suggest that a seed mix containing for example: *Hieracium* spp. such as *Hieracium umbellatum*, *Pilosella officinarum*, *Taraxacum* spp., *Trifolium repens*, *Lotus corniculatus*, *Stellaria graminea* and *Achillea millefolium*, would provide abundant resources for both generalist and specialized bees, thereby supporting species rich bee communities. Some of the mentioned species may be costly to produce seeds from, in which case a strategy of managing the areas that promote these species would be preferable to including them in a seed mix (Nichols et al., 2019; Warzecha et al., 2018).

Our findings support those of others, indicating that flower strips increase both bee and plant species richness in field edges (Geppert et al., 2020). However, flower strips do not replace the need to conserve existing semi-natural habitat patches with a long continuity but should be viewed as a much-needed supplement in agricultural landscapes (von Königslöw et al., 2021). Spatial models can identify which manageable environmental conditions reduce the expected effect of flower strips at a farm, in our case too small areas of grassland habitat, or too long distances to old growth forest or sandy soil deposits (Sydenham, Eldegard, Venter, et al., 2022; Sydenham, Venter, Eldegard, et al., 2022). Spatial models can thus be used to inform farmers and authorities funding pollinator conservation schemes on what additional habitat enhancement schemes might be needed to increase the effectiveness of flower strips.

5 | CONCLUSIONS

Bee richness prediction models based on the availability of nesting substrate and the area of open habitats within flying distances

successfully identified sites where flower resource enhancement measures produce the largest response in wild bee richness. Seed mixes do not need to contain many plant species but should contain species that provide resources for a diverse bee community, including phenological spread of flowering, and ensure high nutritional diversity. While our specific results should not be extrapolated beyond the flora, fauna and climate region covered by our study, our findings suggest that spatial models of bee species diversity have the potential for making agri-environmental schemes more cost-effective in a broader sense. They may also contribute to making the decision process on funding allocation more transparent.

AUTHOR CONTRIBUTIONS

Markus A. K. Sydenham was involved in conceptualization, methodology, formal analysis, investigation, resources, data curation, writing—original draft, writing—review and editing, visualization, supervision, project administration and funding acquisition. Zander S. Venter was involved in formal analysis, investigation, data curation and writing—review and editing. Katrine Eldegard was involved in writing—original draft, writing—review and editing, supervision and funding acquisition. Marianne S. Torvanger was involved in validation, investigation, writing—original draft and writing—review and editing. Megan S. Nowell was involved in writing—original draft, writing—review and editing and visualization. Silke Hansen was involved in investigation, writing—original draft and writing—review and editing. John Ingar Øverland was involved in writing—original draft, writing—review and editing and funding acquisition. Yoko L. Dupont and Claus Rasmussen were involved in writing—original draft and writing—review and editing. Astrid B. Skringdo and Graciela M. Rusch were involved in methodology, writing—original draft, writing—review and editing and funding acquisition.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12283>.

DATA AVAILABILITY STATEMENT

Data and R code available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.280gb5mvp> (Sydenham et al., 2023).

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