



Research Paper

High resolution prediction maps of solitary bee diversity can guide conservation measures

M.A.K. Sydenham^{a,*}, Z.S. Venter^a, K. Eldegard^b, S.R. Moe^b, M. Steinert^b, A. Staverløkk^c, S. Dahle^c, D.I.J. Skoog^b, K.A. Hanevik^b, A. Skrindo^a, G.M. Rusch^c

^a Norwegian Institute for Nature Research - NINA, Sognsveien 68, NO-0855 Oslo, Norway

^b Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Høgskoleveien 12, NO-1432 Ås, Norway

^c Norwegian Institute for Nature Research - NINA, Høgskoleringen 9, NO-7034 Trondheim, Norway



HIGHLIGHTS

- Abiotic environmental conditions predict bee species richness across ecosystems.
- Prediction maps can improve the efficiency of habitat enhancements schemes.
- Prediction maps can also guide threatened species mapping surveys.

ARTICLE INFO

Keywords:

Wild bees
Pollinators
Biodiversity conservation
Habitat management
Spatial predictions

ABSTRACT

Wild bees are key ecosystem components making their decline a cause for concern. An effective measure to increase wild bee diversity is to enhance plant diversity. However, the effect on bee diversity of augmenting plant diversity depends on site-specific environmental conditions. We aimed to make spatial predictions of where: (a) environmental conditions maximize bee diversity, so that such areas can be prioritized for augmenting plant diversity; and (b) populations of threatened wild bee species are most likely to occur. We surveyed bee communities in traditionally managed hay meadows in SE Norway and modelled bee diversity as a function of climate, habitat area, and distance to nesting substrates. We used independent data to validate our predictions and found that plant *and* predicted bee species richness together explained 76% and 69% of the variation in observed solitary bee species richness in forested and agricultural ecosystems, respectively. In urban areas, the predicted bee species richness alone explained 31% of the variation in observed solitary bee species richness. Using data from online species occurrence records, we found that – compared to species of lower conservation concern – threatened solitary bee species were more typically recorded in areas with a high predicted solitary bee species richness. We show that spatial predictions of bee diversity can identify sites where augmenting plant diversity is likely to be most effective. Maps of predicted bee diversity can guide species surveys and monitoring projects and increase the chances of locating populations of threatened bees.

1. Introduction

Insects are instrumental to the functioning of most terrestrial ecosystems, increasing the need to reverse ongoing declines in insect biomass (Hallmann et al., 2017), abundance (Hallmann et al., 2019) and species diversity (Seibold et al., 2019). One of the many ways insects contribute to ecosystem functioning is by mediating the sexual

reproduction of approximately 87.5% of the 300 000 species of flowering plants worldwide (Ollerton et al., 2011). In most sub-alpine ecosystems, bees (Hymenoptera: Anthophila) constitute one of the most important groups of insect pollinators (Ollerton, 2017). Declines in pollinator diversity has been linked to changes in land use practices and the resulting degradation and loss of pollinator habitats during the past century (Biesmeijer et al., 2006; Ollerton, 2017; Potts et al., 2010). For

* Corresponding author.

E-mail addresses: markus.sydenham@nina.no (M.A.K. Sydenham), zander.venter@nina.no (Z.S. Venter), katrine.eldegard@nmbu.no (K. Eldegard), stein.moe@nmbu.no (S.R. Moe), Mari.Steinert@fhi.no (M. Steinert), arnstein.staverlokk@nina.no (A. Staverløkk), sondre.dahle@nina.no (S. Dahle), daniel@danielskoog.se (D.I.J. Skoog), astrid.skrindo@nina.no (A. Skrindo), graciela.rusch@nina.no (G.M. Rusch).

<https://doi.org/10.1016/j.landurbplan.2021.104267>

Received 16 April 2020; Received in revised form 31 August 2021; Accepted 29 September 2021

Available online 9 October 2021

0169-2046/© 2021 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

bees in particular, shrinking distributions (Nieto et al., 2017) and even extinction rates (Ollerton et al., 2014) are related to agricultural intensification. Due to their role as pollinators, bees have gained the wider public's attention, resulting in an increased interest in enhancing bee diversity and the development of regional (e.g. European Commission, 2018) and national strategies for conserving wild pollinators (Norwegian Ministries, 2018; Senapathi, Goddard, Kunin, Baldock, & Wright, 2017).

Mapping distributions of threatened species and establishing new or restoring degraded habitats for wild bees are key components of national (Norwegian Ministries, 2018; Senapathi, Goddard, Kunin, Baldock, & Wright, 2017) and international (IPBES 2016) pollinator conservation strategies. Bee diversity increases with floral resource diversity (e.g. Potts et al., 2004), hence establishment of flower-rich patches that provide pollen and nectar for wild bees (Carvell et al., 2007) is a common approach to promote wild bees in intensively managed landscapes (IPBES 2016). Such habitat enhancement schemes generally increase bee diversity (Tonietto et al., 2018), but their effect depends on the surrounding landscape context and are greatest when implemented in areas with an initially low plant diversity (Batáry et al., 2011; Batáry et al., 2010; Carvell et al., 2011; Marja et al., 2019). Prior to sowing in forbs, or otherwise improving habitat conditions, managers should therefore conduct surveys to determine if habitat enhancement schemes will improve on the current conditions. With ongoing declines in multiple insect taxa (Seibold et al., 2019), which are likely to require tax-specific mitigation actions, we need tools that can: (a) reduce the number of potential sites where vegetation surveys and potentially habitat enhancement schemes should be implemented by: (a) identifying sites where habitat enhancement efforts are likely to support diverse bee communities; and (b) increase the odds of locating populations of threatened species in surveys and monitoring schemes.

To optimize the effect of habitat enhancement efforts on wild bee diversity, one should target areas where environmental conditions do not constrain bee diversity. Most bee species are thermophilic with peaking diversity in xeric, mid-latitude regions (Orr et al. 2020). In central and northern Europe, bee diversity therefore declines with elevation (Hoiss et al., 2012) and latitude (Sydenham et al., 2015). Because bees are central place foragers, local bee species richness depends on nesting sites and floral resources co-occurring within bee foraging ranges, if not in the same patch (Westrich, 1996) and richness increases with habitat area often within just a few hundred metres (e.g. Steffan-Dewenter et al., 2002). Indeed, habitat area is a central determinant of bee diversity (Krauss et al., 2009, Jauker et al., 2013). While the majority of wild bees in Norway nest in the ground, and rare species typically prefer sandy soils, approximately 30% of the solitary bees in Norway nest in cavities, typically in dead wood (Scheuchl and Willner, 2016), a substrate associated with mature to old forests. Because of the complex habitat requirements of bees, identifying where climatic conditions, habitat area, and nesting conditions are optimal can guide managers towards locations where habitat enhancement measures – such as augmenting floral diversity – is most likely to result in species rich bee communities.

Wildlife-habitat relationship modelling (e.g. species distribution models, niche models) has been shown to be a promising tool for identifying areas where environmental conditions suggest habitat enhancement will contribute the most to conserving biodiversity in both marine (e.g. Zellmer et al., 2019) and terrestrial systems (e.g. Sydenham et al., 2020). Prediction models may also increase the efficiency of bee surveys projects, and have been used to predict bee distributions and associated pollination services to crops (e.g. Lonsdorf et al., 2009) and modelling trends in bee abundances at large spatial scales (Koh et al., 2016). So far pollinator habitat maps have largely been based on expert-based scoring of the suitability of land-use classes (e.g. Lonsdorf et al., 2009; Zulian et al., 2013), but Sydenham et al. (2020) in their study in power line clearings, showed that data-parameterized-predictions of plant diversity – based on field surveys – can identify sites where habitat

enhancement measures would have the greatest effect on bee diversity. Efficient prediction maps should be based on easily interpretable metrics of bee diversity (e.g. species richness) that respond strongly to environmental conditions at small spatial scales. Focusing on guilds of bees that show strong responses to environmental conditions is likely to provide more accurate predictions of habitat quality than if habitat generalists are included (Marshall et al., 2015). Modelling total species richness of wild bees within communities (i.e. (social) bumble bees and solitary bees), may therefore lead to suboptimal predictions compared to models restricted to solitary bee species richness, because solitary bees typically have short foraging ranges (Zurbuchen et al. 2010) and show stronger responses to landscape conditions at finer spatial scales than bumble bees (e.g. Steffan-Dewenter et al., 2002).

The aim of this study was to test if we could predict bee diversity based on climatic conditions, habitat area, and nest substrate quality. Availability of floral resources within foraging ranges is also critical for bee species occurrences, but floral resources are typically managed and subjected to considerable spatial and temporal variability. We therefore expected that indicators of climatic and nesting conditions, as well as the area of suitable habitats (i.e. bio-physical factors not immediately affected by management) would allow identifying areas where (a) increasing floral diversity would be most likely to provide resources for the most species in different ecosystems, and (b) where threatened species (i.e. Henriksen & Hilmo 2015) are most likely to occur. Specifically, we assessed if: (1) focusing on solitary bee species richness or Shannon diversity rendered models with a higher explanatory power than if all wild bees were included; (2) predictions from the best model explained variation in bee species richness in forested, agricultural and urban ecosystems not accounted for by local floral resource diversity; and (3) if our model correctly identified sites where threatened species typically occur and could thus be used to guide threatened species mapping projects.

2. Methods

2.1. Site selection and wild bee sampling

We surveyed wild bee communities in 32 seminatural grasslands in SE Norway (Fig. 1A-B), selected to represent gradients of latitude, elevation, landscape composition, and proximity to sandy sediments and to mature forests. Five grasslands were located in urban, three in agricultural, and 24 in predominantly forested landscapes, according to the 2012 Corine Land Cover classification scheme from the European Environment Agency (EEA). The seminatural grasslands in our survey consisted of localities registered as traditionally managed hay meadows in the Norwegian environment agency's database (www.naturbase.no), typically due to their flora and the presence of certain indicator plants such as *Arnica montana* (Öster et al., 2008). Seminatural grasslands can host diverse bee communities but also display a considerable bee species turnover related to local and landscape characteristics (Murray et al., 2012) and thus constitute a suitable model system for making spatial predictions of bee diversity.

We installed three pan-trap clusters in each seminatural grassland. Each cluster consisted of three fluorescent coloured pan traps (yellow, blue, white) mounted on a wooden fencepole. The pan-trap clusters were placed in sun exposed parts of the grassland and at least 20 m apart to reduce trap overlap (Droege et al., 2010) and allow for building prediction models with a 20 m spatial resolution, without two traps falling within the same mapping unit/grid cell. We used the pan-traps to sample bees four times from May to August at each location. During each sampling event, traps were installed and left active (filled with water and a drop of detergent) for 48 h. Sampling was only conducted when weather conditions allowed sampling bees from all 32 seminatural grasslands within a period of four days (See Appendix S1 for details). From each trap location, we tallied the species richness of solitary bees and bumble bees (Wild Bee SR), the species richness of just solitary bees

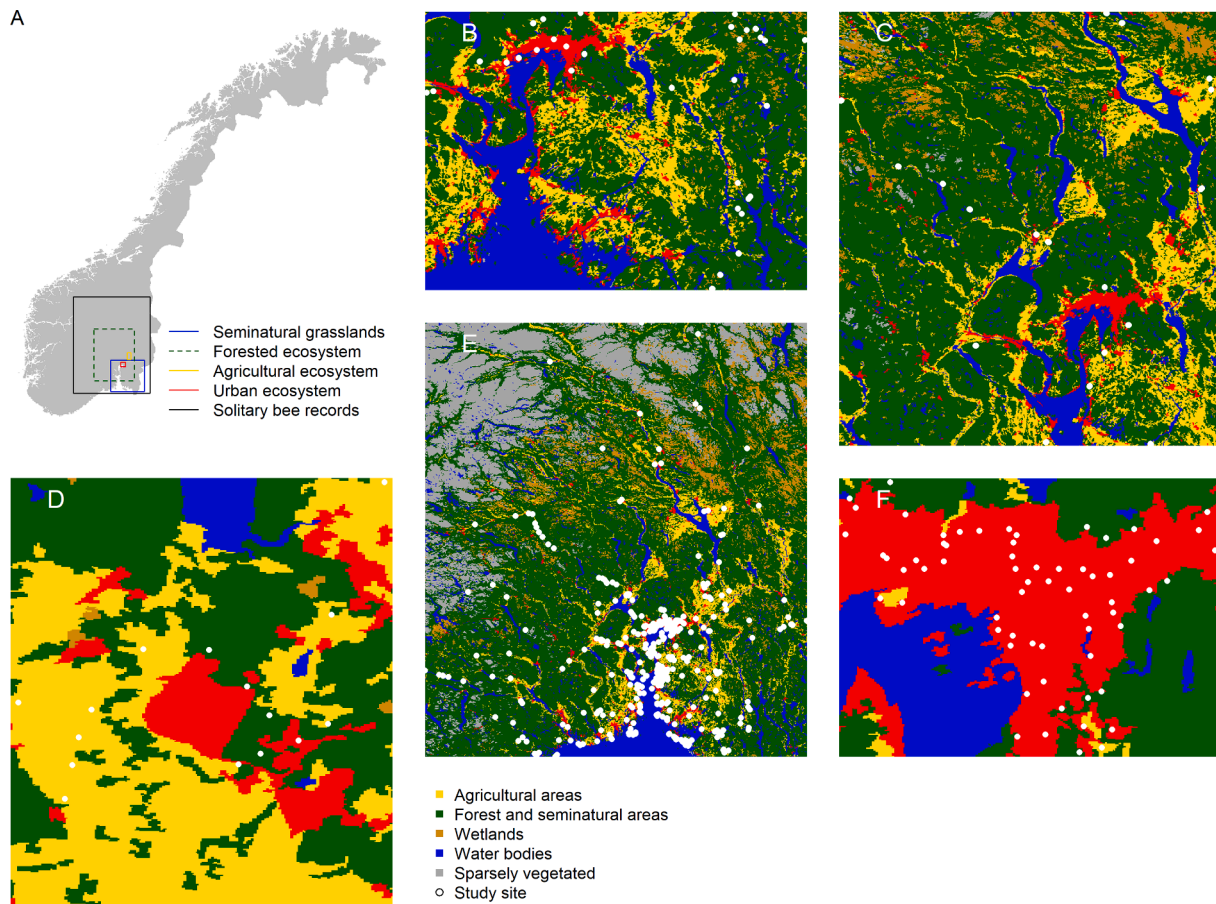


Fig. 1. (A) Map of SE Norway showing the extent of the five datasets used in this study. Data from the seminalural grasslands were used to parameterize our prediction model, which was then used to predict the diversity of bees sampled within the four other datasets. Locations of (B) 32 sites in seminalural grasslands; (C) 19 sites within forested ecosystems where wild bees were sampled in power line clearings; (D) 16 sites representing an agricultural ecosystem where wild bees were sampled along roadsides; (E) solitary bee species occurrence records downloaded from online repositories; (F) 65 study sites in urban ecosystems. The maps in B-F were drawn using Corine Land Cover classes (2012) obtained from the European Environment Agency and show the dominant land cover class within 100 m grid cells.

(Solitary Bee SR), and calculated the Shannon diversity of wild bees (Wild Bee H) and of solitary bees (Solitary Bee H).

2.2. Bee and plant diversity in forested, agricultural and urban ecosystems

The dataset from forested landscapes was collected as part of a field experiment investigating the effect of management practices on wild bee diversity in 19 power line clearings (sites) transecting forests in SE Norway (Steinert et al., 2020) [Fig. 1A,C]. Wild bees were surveyed using three flight interception traps installed in three experimental treatment plots where the woody vegetation had either been left unmanipulated (uncut); cut, leaving residue on the ground (cut); or cut, removing residue from the treatment plot (cut & remove). Bees were sampled continuously from spring to autumn in 2013 and in 2015. Distance between sites ranged from 5 to 200 km, and the elevation from 49 to 537 m.a.s.l. The plant community within each treatment plot was surveyed in nine 1 m² sub-plots in June/July 2013 and 2015. We tallied the species richness (SR) of forbs; the Wild Bee SR_{forest}; and the Solitary Bee SR_{forest} sampled in each treatment plot per year.

The dataset from agricultural landscapes was collected as part of a project investigating how quaternary geological sediments were related to bee diversity (Hanevik, 2018), and plant-bee interactions (Skoog, 2018) in roadsides (n = 16 sites) in SE Norway in collaboration with the Norwegian public roads administration (Fig. 1A,D). At each site, flower visiting bees were sampled using butterfly nets along a transect in roadsides. Distance between sites ranged from 1 to 27 km, and elevation

from 142 to 217 m.a.s.l. Each site was surveyed once in the first half of July and once in the first half of August 2017. During each survey, flower visiting bees observed along the transect were collected simultaneously by two collectors for the duration of one hour. Surveys were conducted between 11AM and 5PM under sunny weather conditions, with little wind and temperatures > 15 °C. Following each bee survey, plant species composition was recorded within six 1 m² subplots placed along the roadside, of which three were placed near the road and the other three, 3 m from the road. We tallied plant SR per site as well as the Wild Bee SR_{agricultural}, and the Solitary Bee SR_{agricultural}.

The dataset from urban landscapes was collected as part of a project investigating how urbanization influences bee diversity in Oslo, SE Norway (Fig. 1A,F). Wild bees were surveyed using pan-trap clusters similar to the ones we used to sample bees in seminalural grasslands. A total of 97 sites (urban green spaces) were surveyed once, for 48 h, with one pan-trap cluster per site, between July 21 and August 10. We standardized the dataset by (i) excluding data from sites where traps had been tampered with, and (ii) only including data that had been collected on days where at least five sites had been sampled (see Appendix S1 for details on how the dataset was standardized). The final dataset consisted of data from 65 sites with traps deployed between July 21 and August 4, 2017, with the occurrence of plants in bloom recorded along three transects with a width of 40 cm and a length of 20 m per site. Distances between sites ranged from 157 m to 19 km, and sites were distributed along an elevational gradient (range = 5–479 m.a.s.l.). We tallied Plant SR, Wild Bee SR_{Urban}, and Solitary Bee SR_{Urban}.

2.3. Occurrence records for threatened, near threatened and species of least concern

We extracted all (12651) bee occurrence records for Norway, observed between 2010 and 2019, with a minimum coordinate precision of 20 m, from the Norwegian Biodiversity Information Centre's Species maps (www.artskart.no, downloaded on December 2, 2019). We excluded 3763 records already included in the forested ecosystem dataset. We created two separate datasets: Wild Bee_{occurrences} contained records of both bumble bees and solitary bees; Solitary Bee_{occurrences} only included solitary bees. To reduce pseudo-replication, data points (species record) belonging to any one of the three red list status categories: Threatened species (i.e. VU, EN, and CR); Least concern (LC) species; and Near threatened (NT) species (Henriksen and Hilmo, 2015), were always separated by at least 250 m. Wild Bee_{occurrences}, consisted of 1504 records, of which 206, 65, and 1233 were of threatened, NT, and LC species, respectively. Solitary Bee_{occurrences} consisted of 470 records of which 44, 12, and 414 were of threatened, NT, and LC species, respectively (Fig. 1A,E).

2.4. Environmental predictors of bee diversity

We assembled a dataset containing environmental variables associated with climatic conditions, area of potential habitat, and distances to high quality nesting resources, estimated within 20 m × 20 m grid cells.

2.4.1. Climatic condition

We included latitude and elevation as proxies for climatic conditions. We obtained information on elevation from a 50-m resolution digital elevation model (Norwegian Mapping Authority 2016).

2.4.2. Habitat area

As a proxy for the area of bee habitat in and around potential habitats, we estimated the amount of early successional habitats at different radii around 20 m grid cells throughout the study region. We used maps of the proportion of sealed surfaces within 100 m of grid cells (Urban100m) as we expected this to be negatively related to habitat availability in urban areas. We used maps of the tree cover density within 100 m of grid cells (TCD100m) as a proxy for forest encroachment around and inside grid cells. Urban100m and TCD100m were obtained from the Copernicus Land Monitoring Services (2018). To estimate the amount of ruderals, grasslands and other early successional habitats surrounding grid cells, we built a supervised random forest model (Breiman, 2001) to predict the probability of grid cells being in an early successional state. We used a binary vector where TRUE was indicative of an area being in early succession and FALSE being indicative of non-bee habitat, as the response variable in the model. TRUE and FALSE values were obtained by using 3000 manually digitized points - sampled randomly across the study region - that were visually classified using very high resolution satellite imagery available through Collect Earth Online (<https://collect.earth/>). TRUE values were: roadsides; forest clear-cuts; and other early successional or ruderal areas. FALSE values were: sealed surfaces; dense forests; waterbodies; buildings; roads; tilled land; and industrial sites. Because the randomly distributed points resulted in very few TRUE values (Appendix S2, Fig. S2.2), we supplemented the TRUE values with: (a) 4584 occurrences of *Lotus corniculatus*, an indicator of early successional habitats (Wagner et al., 2019), recorded between 2010 and 2019, downloaded from the global information biodiversity facility (GBIF); and (b) 823 occurrences from 21 solitary bee species (from www.artskart.artsdatabanken.no), selected because they depend on early successional habitats for nesting sites (i.e. nest below ground) and/or floral resources. We used a wide range of variables to predict the probability of grid cells being potential bee habitat, i.e. in an early successional stage at a 20 m resolution. The model produced an overall accuracy of 92%, predicting bee habitat correctly in 91% of cases and non-bee habitat correctly in 95% of cases

(see Appendix S2 for details on the random forest model).

Visual inspection revealed that some grid cells on tilled land were misclassified as early successional habitats by our model. We therefore used a map of tilled land areas to reset values for grid cells located on tilled land to zero. We obtained the tilled land area map by rasterizing a vector based land use map (Björðal and Bjørkelo, 2006) and: (a) excluding grid cells that were misclassified as tilled land but were covered by seminatural nature types registered within the Norwegian Environment Agency's (2011) database; and (b) removing the outermost pixels from the tilled land areas to ensure that field margins would not be counted as tilled land. After having corrected the bee habitat map, we calculated the sum of the predicted probabilities of pixels containing bee habitat within 20 m (9 grid cells), and 40 m (25 grid cells) and within circular buffers with 100 m and 250 m radii surrounding each grid cell (Habitat₂₀, Habitat₄₀, Habitat_{100m}, and Habitat_{250m} hereafter). We used Habitat₂₀ in our models because Habitat_{250m} was strongly correlated with elevation ($\rho = -0.69$), and sensitivity analysis showed that Habitat₂₀ was more strongly correlated with the four bee diversity indices than Habitat_{40m}, and Habitat_{100m} (Steffan-Dewenter et al., 2002).

2.4.3. Nest site conditions

As a proxy for the availability of nesting sites for ground nesting bees, we included the geographic distance to geological sediments with a high or very high infiltration capacity, typically composed of or containing large amounts of sand (DistSand), obtained from Geological Survey of Norway (2011). As proxies for the availability of nesting sites for wood nesting bees, we calculated the geographic distances to the nearest (i) mature forest (forests aged > 80 yr; DistMatForest) and (ii) young forest (age 40 to 80 yr; DistYngForest). Maps of forest ages were obtained from the SatSkog database (Gjertsen and Nilsen, 2012). As a proxy for habitat quality, we included the predicted probability that the habitat was in early succession from the random forest model (Habitat_{focal}). We used Spearman rank correlations to assess the potential for multicollinearity between variable pairs, i.e. if the $|\rho|$ between variables pairs was > 0.7 (Dormann et al., 2013). While the $|\rho|$ was < 0.5 for the majority of variable pairs, Habitat_{focal} and Habitat₂₀ were strongly correlated ($\rho = 0.83$). However, we included both variables since the variable selection procedure would later on select the most important one. Urban100m was correlated, although not critically, with elevation ($\rho = -0.63$) and distance to mature forests ($\rho = 0.61$). Correlations between latitude and other variables were consistently below 0.5 suggesting that spatial autocorrelation would not be of significant influence.

2.5. Statistical analyses

2.5.1. Building and comparing models for predicting wild bee diversity

We used the data that from seminatural grasslands to model wild bee diversity. For each of: Wild Bee SR, Wild Bee H, Solitary Bee SR, and Solitary Bee H, we first fitted a full model that included all the environmental variables we hypothesized might influence the abiotic habitat conditions for bees: Latitude; Elevation; Urban_{100m}; TCD_{100m}; BeeHabitat_{20m}; DistSand; DistMatForest; DistYngForest; and BeeHabitat_{focal}. We $\log(x + 1)$ transformed the DistSand, DistMatForest, and DistYngForest, because we expected bee diversity to follow a distance decay function with distance to nesting habitats. We $1/(x)$ transformed BeeHabitat_{20m} because we expected bee diversity to increase asymptotically with habitat area. We included site identity as a random effect to account for the multiple samples per site (three traps per site). We then conducted a sequential backward elimination of variables until all remaining variables in the final models were statistically significant ($p \leq 0.05$). We used likelihood ratio tests to assess contribution of variables and their statistical significance. We used Poisson generalized linear mixed effects models (GLMMs) from the lme4 package (Bates et al., 2015) in R (R Core Team 2017) to model Wild Bee SR and Solitary Bee

SR, and linear mixed effect models (LMMs) to model Wild Bee and Solitary Bee H (Shannon diversity) and used residual plots to assess the goodness of fit of the models to the data. For the GLMMs we used the residuals obtained using the DHARMA package in R (Hartig, 2016), and regular residual plots for the LMMs. The residual distribution for the LMMs had heavy tails. We therefore used the inverse hyperbolic sine transformation to normalize the residual distribution for models on the Shannon diversity indices. We assessed each of the four, final, models by comparing the variance explained by the fixed effect terms (the R^2_{marginal}) in the models. The R^2_{delta} associated with each model was calculated using the MuMIN package (Barton and Barton, 2019). We used the model that performed the best (highest R^2 values) to predict the diversity of bees within 20 m grids across SE Norway.

2.5.2. Do prediction models and plant diversity explain patterns of bee diversity?

We extracted the bee diversity values - predicted from the seminatural grassland model - for each study site in the Forested, Agricultural and Urban datasets. Spearman rank correlations showed that predicted bee diversity was not confounded with plant species richness in the forested ($\rho = 0.21$), agricultural ($\rho = 0.19$) or urban ($\rho = 0.23$) study systems, allowing us to assess the additive effect of each variable on bee diversity. Within each system we tested if the variation in Wild bee SR and Solitary Bee SR between sites could be explained by the additive effect of predicted Solitary bee SR and flowering plant SR. We expected that the degree to which bee diversity would be limited by e.g. nest site availability would depend on the availability of floral resources. We therefore compared models where bee diversity was assumed to increase exponentially (untransformed), linearly ($\log(x)$), or asymptotically ($1/x$) with the predicted solitary bee SR.

We fitted two models, of varying complexity, to the Wild Bee SR_{Forests} and Solitary Bee SR_{Forests}. In the simple model, we only included data ($n = 38$), collected from the ‘cut & remove’ treatment plots as these plots were the most reminiscent of grasslands. These models were fitted using GLMMs with the predicted bee diversity and the surveyed forb species richness as fixed effects, and site identity ($n = 19$) and year ($n = 2$) as random intercept terms. In the complex models, we included data collected from all treatment plots ($n = 114$) with site identity ($n = 19$) and year ($n = 2$) as random intercept terms and a random intercept and slope for Forb SR on the treatment type ($n = 3$) because the relationship between bee diversity and forb SR in this system depends on treatment type (Steinert et al., 2020). Including the random slope allowed us to test if the expected increase of bee diversity with forb SR was significant after accounting for treatment specific effects that were not modelled by our prediction models. For each of the four resulting models we calculated the conditional and marginal R^2_{delta} values and used likelihood ratio tests to assess the statistical significance of the fixed effect terms.

For the datasets collected in agricultural landscapes (along roadsides) and in urban landscapes, we tested if the Wild Bee SR or Solitary Bee SR could be explained by the predicted bee diversity alone and in combination with the surveyed Plant SR. For the urban dataset we included sampling date as a random effect. The models for the agricultural system were fitted using Poisson GLMs whereas the models for the urban system were fitted using Poisson GLMMs. We used the R^2_{delta} to estimate the variation explained by our models, and likelihood ratio tests to test the statistical significance of the explanatory variables in our models. We used DHARMA residual plots (Hartig, 2016) to ensure that residual distributions were reasonable for the Poisson models described above.

2.5.3. Do prediction models identify sites where threatened bee species typically occur?

We tested if threatened wild bees (critically endangered ‘CR’, endangered ‘EN’, or vulnerable ‘VU’ in Henriksen and Hilmo 2015) occurred more often than bees of low conservation concern (least concern ‘LC’, or near threatened ‘NT’) in areas where our models

predicted a high bee diversity. We used the Wild Bee_{occurrence} and Solitary Bee_{occurrence} to extract the predicted bee diversity for each location where species had been recorded. To test if both the typical values and the distribution of predicted bee diversity values differed between threatened, near threatened and least concern bees we used the R package quantreg (Koenker et al., 2019) to fit quantile regressions, on the 25th, 50th and 75th quantiles on the predicted bee diversity. Furthermore, we used binomial GLMs with cloglog links to test if the proportion of 20 m grid cells with Wild Bee and Solitary Bee species occurrence records increased with predicted bee diversity and if the increase differed between red list categories. For the GLMs only threatened and LC species records were included due to few records of NT species.

3. Results

Our traps in seminatural grasslands collected 2278 wild bees, comprising 99 species, nearly half of the bee species recorded in Norway. Bumble bees accounted for 16 species and 883 specimens, and solitary and primitively eusocial bees accounted for 83 species and 1395 specimens. Wild Bee SR ranged from 2 to 19 (mean 10.64), while Solitary Bee SR ranged from 0 to 16 (mean 7.18) per trap.

The Solitary Bee SR model explained the largest amount of variation (Table 1). Solitary Bee SR decreased with latitude and elevation, and increased with the amount of potential bee habitat within 20 m of trap locations (Fig. 2). Solitary Bee SR further decreased with distances to high quality nesting substrates. The models for Wild Bee SR and Wild Bee H were qualitatively similar to the model for Solitary Bee SR, but did not include elevation as a regional level environmental filter (Table 1). Because the model for solitary bee SR explained the most variation, we proceeded with this model for predicting bee diversity across the study region (Fig. 2).

Predicted Solitary Bee SR was positively related to the observed species richness of solitary bees sampled in forested, agricultural and the urban ecosystems (Fig. 3, Table 2, Table S1.1). Predicted Solitary Bee SR

Table 1

Comparisons of models using different indices of bee diversity showed that using Solitary Bee SR as response variable provided the best model (highest R^2_m) for explaining wild bee diversity within seminatural grasslands in SE Norway. For each model the likelihood ratio test statistics and associated variance explained are summarized in the table. Variance explained by fixed effects alone and by fixed effects and random effects are shown for each model as R^2_m and R^2_c , respectively. Models for Wild Bee SR and Solitary Bee SR were fit using Poisson GLMMs, whereas models for Wild Bee H’ and Solitary Bee H’ were fit using LMMs with the response transformed using the inverse hyperbolic sine transformation. All models were fit using Site identity ($n = 32$) as random effect across the 96 pan-trap clusters from which bees were sampled.

	Df	χ^2	p	R^2_m	R^2_c
Wild Bee SR					
scale(Latitude)	1	11.30	0.001	0.27	0.37
1/(BeeHabitat ₂₀)	1	4.94	0.026		
log(DistSand + 1)	1	10.18	0.001		
Wild Bee H’	Df	χ^2	p	R^2_m	R^2_c
scale(Latitude)	1	8.60	0.003	0.27	0.44
1/(BeeHabitat ₂₀)	1	8.15	0.004		
log(DistSand + 1)	1	4.77	0.029		
log(DistMatForest + 1)	1	9.09	0.002		
Solitary Bee SR	Df	χ^2	p	R^2_m	R^2_c
scale(Latitude)	1	9.93	0.002	0.40	0.42
scale(Elevation)	1	4.27	0.037		
1/(BeeHabitat ₂₀)	1	7.31	0.007		
log(DistSand + 1)	1	13.54	< 0.001		
log(DistMatForest + 1)	1	8.70	0.003		
Solitary Bee H’	Df	χ^2	p	R^2_m	R^2_c
scale(Latitude)	1	8.03	0.005	0.35	0.51
scale(Elevation)	1	5.89	0.015		
1/(BeeHabitat ₂₀)	1	5.20	0.023		
log(DistSand + 1)	1	4.98	0.026		
log(DistMatForest + 1)		9.81	0.002		

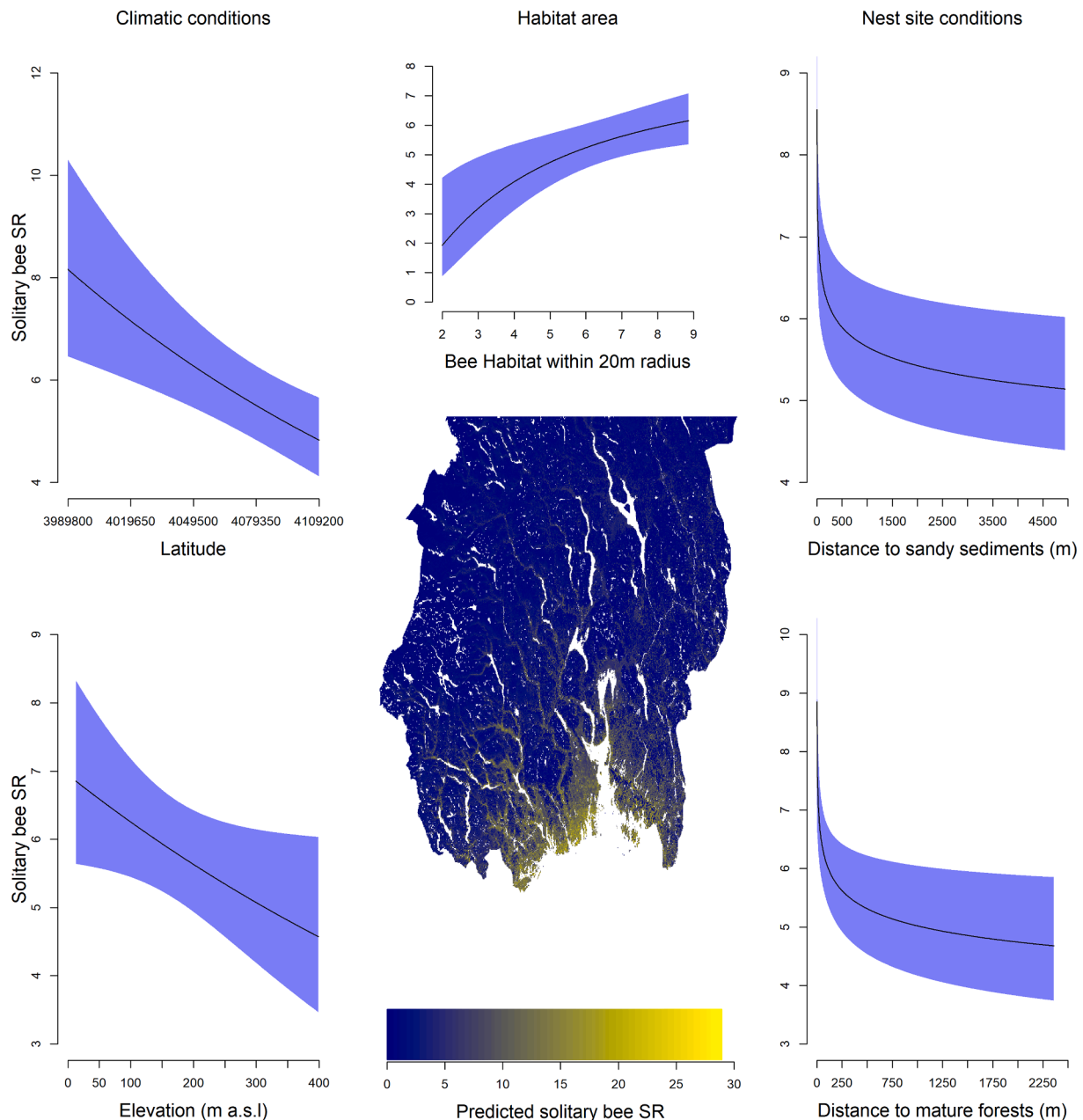


Fig. 2. The direction and drivers of the species richness (SR) of solitary bees within seminatural grasslands in SE Norway. Species richness decreased with latitude and elevation, both related to cooler climatic conditions. In contrast, species richness of solitary bees increased with increasing amounts of early successional habitat patches within 20 m of the seminatural grasslands, and with the proximity to sandy sediments and mature forests, surrogates for nesting habitat quality. See [Table 1](#) for test statistics. The model for solitary bee species richness was used to predict bee diversity across the entire study region.

alone explained 40%, and 23% of the variation in Solitary Bee SR_{Forest} in the simple and complex model, respectively, and 56% of the variation in the Solitary Bee $SR_{Agriculture}$. Predicted Solitary Bee SR and Forb SR captured different parts of the gradient in observed Solitary Bee SR_{Forest} . While the estimated Solitary Bee SR_{Forest} followed a saturation curve and increased from 2 to 10 species along the gradient in predicted Solitary Bee SR ([Fig. 3A](#)), it increased from 4 to 25 species with Forb SR gradient ([Fig. 3B](#)). In contrast, we found a near linear increase in Solitary Bee $SR_{Agriculture}$ along both the predicted Solitary Bee SR ([Fig. 3C](#)) and plant species richness ([Fig. 3D](#)). Solitary Bee SR_{Urban} increased with predicted Solitary Bee SR, which explained 31% of the variation ([Table 2](#)), while plant species richness did not contribute significantly in the urban system. Model results were qualitatively similar to those described above when using the predicted Solitary Bee SR to explain patterns of Wild Bee SR in the different ecosystems. A notable exception was that the

predicted Solitary Bee SR was not related to Wild Bee SR_{Urban} ([Table S1.2](#)).

Threatened solitary bee species were more frequently recorded in areas with high predicted Solitary Bee SR, compared to species of lower conservation status (i.e. NT and LC). Threatened solitary bee species had significantly higher 25th, 50th and 75th quantile values of predicted Solitary Bee SR compared to LC species ([Fig. 4A](#), [Table 3](#)). For NT solitary bee species, the distributions of predicted Solitary Bee SR values were not distinguishable from those of LC species. The proportion of 20 m raster pixels with records of Solitary Bee $occurrence$ increased with predicted Solitary Bee SR ([Fig. 4B](#)), with a slightly stronger increase for threatened solitary bees ($z = 1.997$) than LC bees (Red List status \times log (Pred. Solitary Bee SR + 1); $df = 1$, $\chi^2 = 4.09$, $p = 0.043$). When observations of bumble bees were included, the estimated quantile values were lower for all Red List categories quantiles ([Table S1.3](#)), and

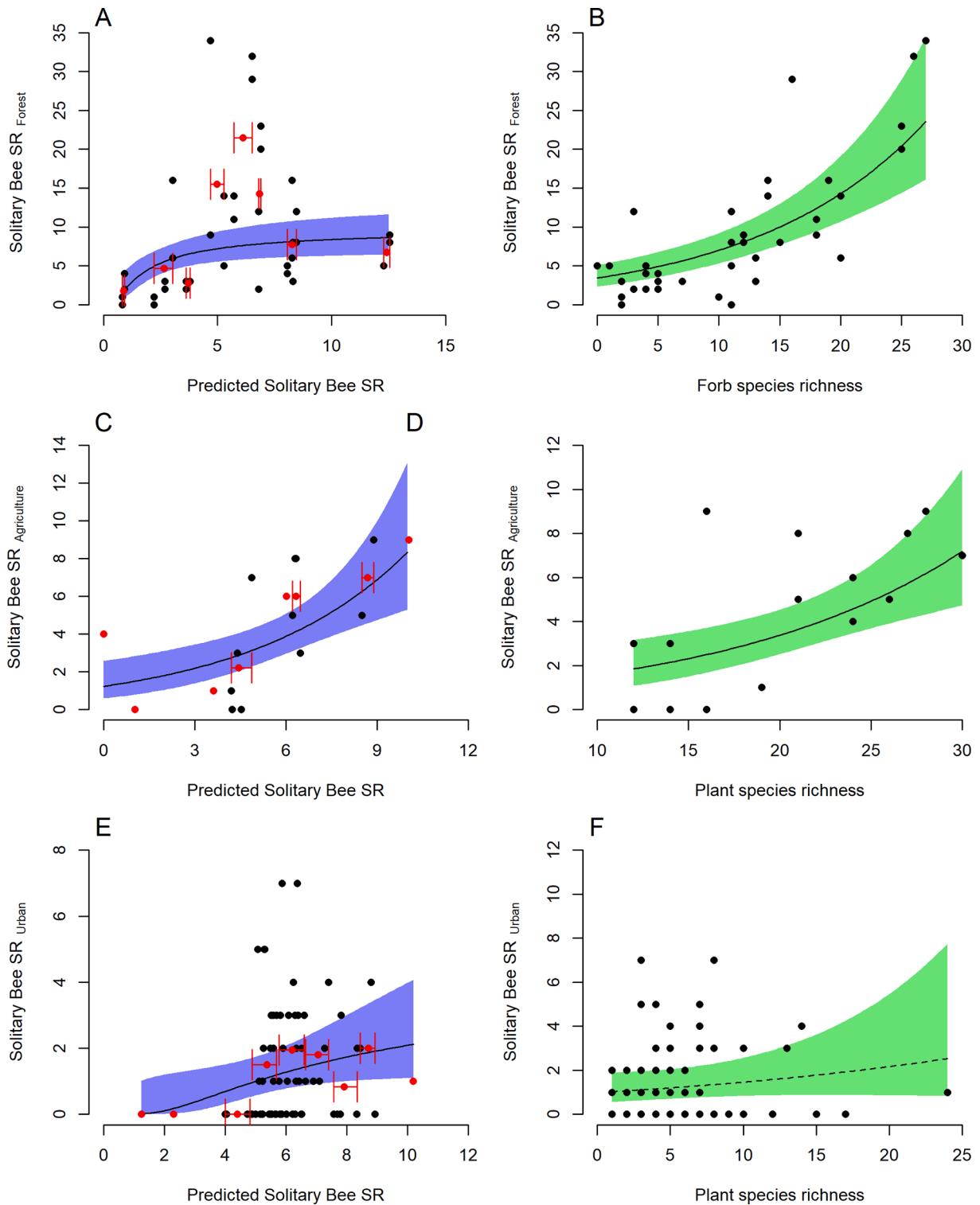


Fig. 3. Observed solitary bee species richness in different ecosystems in response to the additive influence of: predicted solitary bee species richness, predicted from climatic, landscape conditions, and distances to potential nesting sites; and local plant diversity, recorded through extensive surveys. Effects plots are shown for (A-B) forested ecosystems; (C-D) agricultural ecosystems; and (E-F) an urban ecosystem. Shaded areas show the 95% confidence intervals for the estimated relationships (blue for predicted Solitary Bee SR, green for plant and forb species richness). Note that in A, a large part of the residual variation in the interval 5–8 along the x-axis is accounted for by forb species richness, shown in B. The dashed line in F shows the non-significant relationship between Solitary Bee SR_{Urban} and plant species richness (not included in the final model for that ecosystem). Black points show raw data values, red points show the mean solitary bee species richness within 10 bins along the calibrated predicted solitary bee species richness. The interval width (red whiskers) of the 10 bins were defined using the cut (x,10) function in R. See [Table 3](#) for test statistics. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Comparison of the explanatory power of models combining predicted solitary bee SR (extracted from grassland ecosystem models) and surveyed plant SR to explain wild bee diversity in forested (power line clearings), agricultural and urban ecosystems. Likelihood ratio test statistics and associated variance explained. Two models, differing in their random effects structure, were fit for the forested ecosystem; (i) the simple model only included data from treatment plots where trees had been cut and the debris removed; (ii) the complex model included data from all treatment types (i.e. unmanipulated, trees cut, and trees cut and residues removed). Plant species richness was not statistically significant in the model for Urban bee species richness ($\chi^2 = 2.11$, $p = 0.15$), and was therefore not included in the final model. See Table S1.1 for full model outputs.

Model	Df	χ^2	p	R^2_m	R^2_c
Solitary Bee SR _{Forest} – simple model					
1/(Predicted Solitary Bee SR)	1	12.21	0.001	0.76	0.88
Forb SR	1	16.42	< 0.001		
Solitary Bee SR _{Forest} – Complex model					
log(Predicted Solitary Bee SR + 1)	1	12.54	< 0.001	0.35	0.78
log(Forb SR + 1)	1	6.40	0.011		
Solitary Bee SR _{Agricultural ecosystem}					
Predicted Solitary Bee SR	1	13.50	< 0.001	0.69	–
Plant SR	1	12.07	0.001		
Solitary Bee SR _{Urban ecosystem}					
1/(Predicted Solitary Bee SR)	1	6.45	0.011	0.31	0.52
Plant SR	1	–	–		

threatened species tended to have lower 25th, 50th and 75th quantiles than LC species. The proportion of 20 m pixels containing Wild Bee_{occurrence} records increased with predicted Solitary Bee SR. However, this increase differed between Red List categories with a weaker increase for threatened wild bees ($z = -4.08$, $p < 0.001$) than for LC bees (Red List status $\times \log(\text{Pred. Solitary Bee SR} + 1)$; $df = 1$, $\chi^2 = 15.77$, $p < 0.001$).

4. Discussion

Two key goals of pollinator conservation strategies (e.g. Norwegian Ministries, 2018) are to: (a) bolster wild bee populations by improving habitat quality; and (b) improve the knowledge base of the distribution of populations of threatened species through species mapping surveys. Our findings show that prediction maps can identify habitat patches

where climatic conditions, potential habitat area, and nesting substrates are unlikely to limit bee diversity so that habitat enhancement is likely to be effective (Fig. 5). Potential management actions at such sites could be: altering the mowing regime to promote forbs; or sowing in forbs if plant diversity is low; or removing non-native species that reduce floral diversity. Targeting surveys towards areas with a high predicted solitary bee species richness is likely to increase the odds of discovering populations of threatened species (Fig. 4A-B). Prediction maps – such as the one presented here – are therefore likely to provide a valuable tool for environment agencies and planning authorities aiming to implement pollinator conservation. Indeed, developing prediction models of bee habitat quality (or species richness) is an integrated goal of some national pollinator conservation strategies (Senapathi et al., 2017).

Although different sampling methods and periods were used to survey the bee communities in the forested (window traps – season wide sampling), agricultural (transect walks – in mid and late summer), and urban ecosystems (pan-traps – late summer), the predicted solitary bee species richness was positively related to the sampled species richness in all three systems, despite the fact that these predictions were based on data drawn exclusively from pan-traps. However, the shape of the relationship and variation explained differed between systems (Fig. 3). In the forested systems (power line clearings), the relationship between the sampled and predicted solitary bee species richness levelled off at a predicted value of about eight species (Fig. 3A). Non-linear relationships can indicate that bee diversity is limited by factors not accounted for in the prediction model. In the forest systems, forb richness appeared to be the strongest limiting factor for bee diversity (Fig. 3B), revealing a large potential for promoting wild bee diversity by augmenting forb richness in open canopy habitats in forest ecosystems. The effect of augmenting forb richness in this system is likely to be greatest at sites with a predicted solitary bee species richness above five and where prediction models of floral diversity (e.g. Sydenham et al., 2020) suggest that soil conditions are optimal for establishing flower rich patches.

In agricultural systems (roadsides), predicted solitary bee species richness and plant diversity appeared to be equally important, and both showed near-linear relationships with the sampled solitary bee species richness (Fig. 3C,D). Since the study sites were situated at approximately

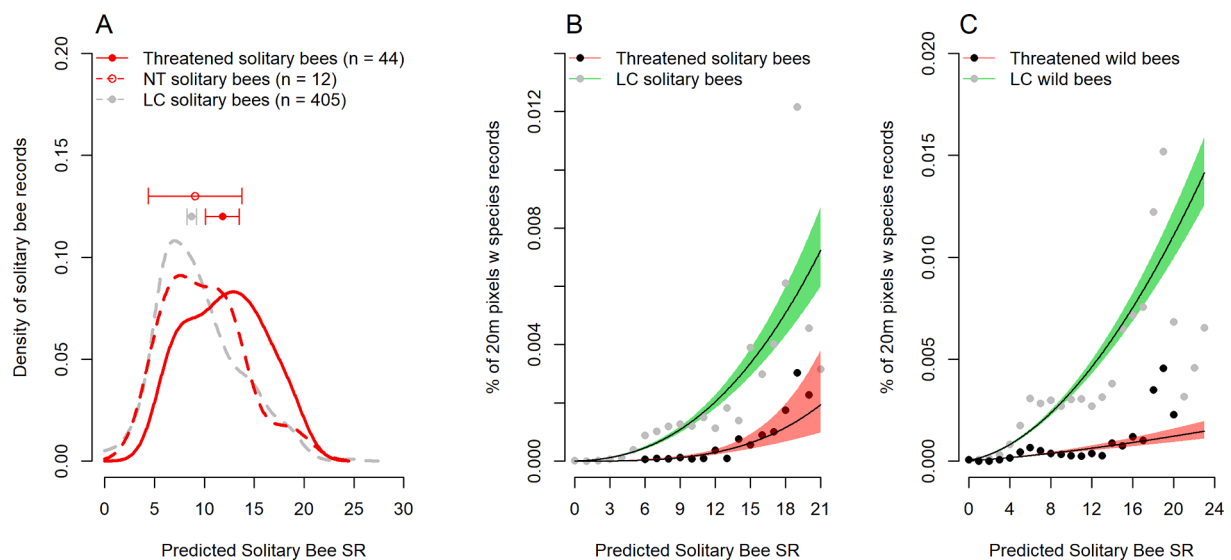


Fig. 4. Solitary bee species listed as threatened on the Norwegian red list (Henriksen & Hilmo, 2015) have typically been recorded from areas where our model predicted a higher Solitary Bee SR than common (LC) and near threatened (NT) species. (A) Density distribution of predicted Solitary Bee SR values for threatened, LC and NT. Points and confidence intervals show the median (typical) $\pm 2 \times SE$ values for each category. See Table 3 for summary statistics from the quantile regression analyses. (B-C) Effects plot from binomial GLM on the proportion of 20 m pixels with (B) solitary bee species and (C) all wild bee species records (here shown as percent to reduce the number of decimals) as a function of the interaction between red list status and predicted Solitary Bee SR. NT species were not included due to the low number of records of solitary (n = 12) and wild (n = 13) bees. Note that one outlier ([y, x] = [0.046, 25]) is excluded from the plots in B and C but was included in the analyses as its inclusion did not affect model outputs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Threatened solitary bee species are more frequently recorded at locations with high predicted solitary bee species richness, compared to species of low red list status (i.e. least concern (LC)) and near threatened (NT). The table shows the estimated 25th, 50th and 75th quantiles for the predicted solitary bee SR for each of the three categories of threatened species; vulnerable (VU), endangered (EN) and critically endangered (CR) (Henriksen & Hilmo, 2015) and the associated quantile regression test statistics.

Solitary bee occurrences	25th quantile	Pred. Solitary Bee SR	SE	t	p
IUCN LC species (intercept)	6.43	0.17	36.97	<	0.001
IUCN NT species	6.60	1.11	0.15	0.880	
IUCN Threatened species	8.99	0.88	2.91	0.004	
Solitary bee occurrences 50th quantile					
IUCN LCes (intercept)	8.73	0.24	36.32	<	0.001
IUCN NT species	9.06	2.35	0.14	0.890	
IUCN Threatened species	11.82	0.85	3.64	<	0.001
Solitary bee occurrences 75th quantile					
IUCN LC species (intercept)	11.80	0.40	29.71	<	0.001
IUCN NT species	12.62	0.81	1.01	0.315	
IUCN Threatened species	14.98	0.81	3.93	<	0.001

the same latitude and elevation, there was no influence of climatic conditions within this system. The predicted bee species richness in the agricultural system thereby reflected the importance of habitat size and distances to nesting substrates on bee diversity within roadsides (Fig. 2). These findings are in line with previous findings documenting the importance of nesting substrates and floral richness for bee diversity in roadsides (Hopwood, 2008). However, since traffic volume is negatively related to bee abundance along roadsides (Phillips et al., 2019) wild bee habitat enhancement schemes should target roadsides in regions with modest to low traffic volumes. Combining data on traffic volumes with prediction maps of bee diversity can aid identification of roadsides where increasing plant species richness will have the greatest effect on bee diversity in agricultural landscapes.

Urban ecosystems can contain high quality wild bee habitats (Baldock et al., 2015; Theodorou et al., 2020), such as botanical gardens and cemeteries (Baldock et al., 2019), that have been maintained for centuries. A potential explanation for the poorer performance of the prediction model in the urban system (31% variance explained, Table 3) may be that the resolution of the model, or the data used to parameterize the model was too coarse to capture the fine-grained nature of bee habitats in urban settings (Baldock et al., 2019). The area of impervious surface is often assumed to be negatively related to habitat area and has been shown to be negatively correlated with wild bee species richness in urban areas (Fortel et al 2014; Geslin et al 2016; Glaum et al 2017). That our model was built using mainly non-urban data likely explains why the urbanization variable did not contribute significantly to our prediction models (Table 1). Despite this, and as shown in Fig. 5 our model still distinguished between impervious surfaces such as roads, and open green spaces. Because plant species richness did not explain the residual variation, as it did in the agricultural and forested systems, we assessed if accounting for habitat heterogeneity in the urban system would improve model predictions. We calculated the weighted sum of predicted values for cells within typical foraging ranges (240 m) within a Gaussian filter ($\sigma = 80$) according to their distance to the focal cell. Substituting the predicted solitary bee species richness with the calibrated predictions improved the amount of variation in solitary bee species richness_{Urban} explained by the model ($df = 1$, $\chi^2 = 15.4$, $p < 0.001$, $R^2_m = 0.46$, $R^2_c = 0.63$, Fig. S1.1). An alternative approach could be to use models where areas with different environmental conditions

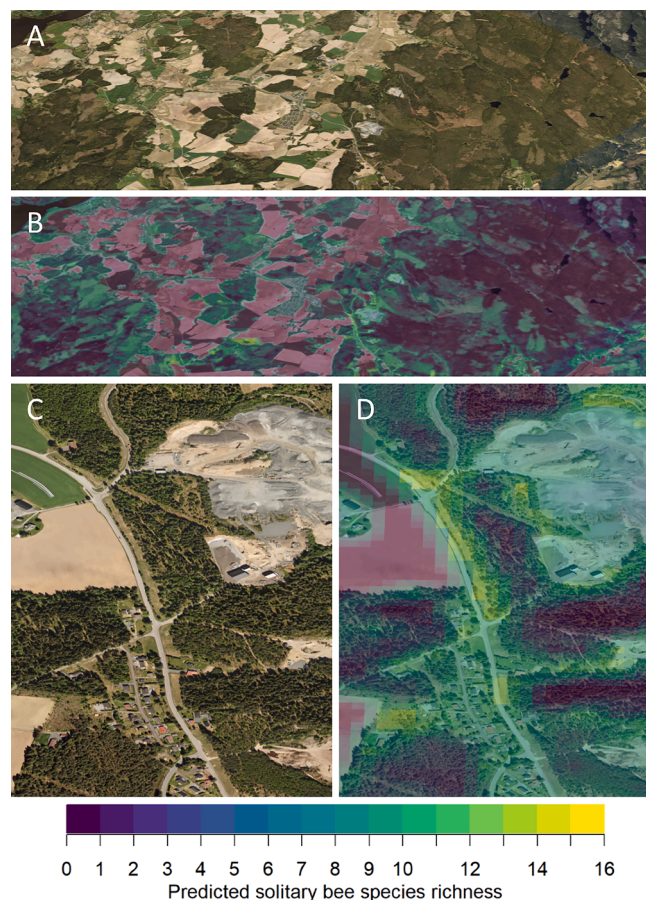


Fig. 5. Example of how prediction models can be used to identify sites with potential for bee conservation measures. (A) Ortho-image of a typical agricultural landscape in southeast Norway with agricultural land surrounded by forests. (B) The prediction model showing how potentially valuable bee habitats (bright coloured pixels) are distributed in the landscape. (C,D) One of the areas highlighted (yellow in D) by the model as having a high predicted species richness of solitary bees (>14) consists of an early successional area situated next to a road, nearby a sandpit. Such areas could be prioritized for instance for removal of invasive species that may outcompete the local flora, and for enhancing the diversity of insect pollinated plants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

are assigned a score, based on expert opinion, which are then used to calculate the expected habitat suitability of pixels within the raster map (e.g. Lonsdorf et al., 2009). This approach enables production of maps with a very high spatial resolution – for example, the resolution of land cover maps – without using empirical data to parameterize the model. Such expert-based models have been shown to predict approximately 40% of the variation in bee species richness in urban systems (e.g. Davis et al., 2017). Yet, these models entail a higher degree of subjectivity in parameterizing the models. Using a statistical modelling approach like we did has at least two benefits: we can formally test the influence of different variables and estimate the marginal contribution of each variable, while accounting for the effect of other variables. However, the spatial resolution of the prediction maps will be coarse if one does not sample bee communities from all potential habitat types.

Knowledge of the distribution of threatened species is a prerequisite for accurate Red List assessments and knowledge-based management. Since threatened bee species often have limited or highly fragmented distributions, and occur in low densities, targeted surveys are required to monitor and discover populations of threatened bee species. However, species mapping projects often discover few, if any, new

populations of threatened species and there is a need for tools that can make such projects more cost-efficient (pers. comm. Øystein Røskog, Oslo & Viken County Managers Office, Norway). Our finding that threatened solitary bee species were disproportionately more likely to be recorded in areas with a high predicted solitary bee species richness (Fig. 4A, C, Table 3), presents a promising avenue for using species richness prediction models for improving the cost-efficiency of threatened bee species mapping projects. For threatened bee species that specialize on a few plant species, a potential protocol could be to focus survey efforts to locations with a high predicted Solitary Bee SR at – or nearby – known occurrences of the host plants. Occurrences of host plants can be extracted from online species occurrence repositories (e.g. GBIF) where data on plant species occurrences is often richer than for many insect taxa.

Our prediction map was based on a model of solitary bee species richness built according to the hypothesis that multi-level filters constrain bee diversity (Sydenham et al., 2015). When using species richness as the response variable, species-specific, or functional trait specific responses, to environmental filters might be overlooked because e.g. nesting guild (Williams et al., 2010) and tongue length guild (Moretti et al., 2009) are important predictors of bee responses to environmental conditions. However, null model analyses (Appendix S1) suggested that solitary bee species richness was not biased against ground nesting, wood nesting, long or short tongued bee species richness in our system (Table S1.4). In contrast, solitary bee species richness was biased against bumble bee species richness (Table S1.4), likely because solitary bee species richness was related to environmental gradients not – or to a lesser extent – affecting bumble bees. Such gradients include climatic conditions, like elevation, to which solitary bee species richness responds more strongly than bumble bee species richness (e.g. Hoiss et al., 2012). Solitary bees also have shorter foraging ranges than bumble bees and therefore respond to environmental conditions at smaller spatial scales (Steffan-Dewenter et al., 2002). Additionally, bumble bees are less efficiently sampled with pan traps than solitary bees (O'Connor et al., 2019). Including bumble bees in the response variable may therefore have introduced statistical noise into the relationships between the wild bee species richness and the explanatory variables. Because of the bias against bumble bee species richness from solitary bee species richness, our model should not be used for devising conservation schemes for bumble bees.

Limitations and caveats Although our model predicted a considerable amount of variation in bee diversity in different ecosystems, it performed best in the agricultural system. This may partly be because the gradient in soil substrates and mowing regimes are more similar between the roadsides in the agricultural system and seminatural grasslands, compared to seminatural grasslands and urban green spaces or power line clearings in forested systems. Additionally, since urban sites were largely concentrated at locations with intermediate predicted species richness values, and only sampled once, one would expect a considerable amount of random noise within these data, as seen in the spread of solitary bee species richness around the average values (Fig. 3E). Moreover, in the urban system potential nesting sites may be more widely distributed than geological survey maps would suggest as sandy substrates can be found in and around playgrounds and parks. Nevertheless, without detailed maps of potential nesting sites in urban areas, prioritizing areas with naturally occurring sand deposits for bee habitat augmentation is a reasonable alternative. In addition to the resolution of predictor variables, the model formulation used sets some limitations to its applicability, that need to be considered when the tool is used for conservation planning. Because our model predicts bee diversity as an additive response of environmental conditions, values of intermediate predicted solitary bee species richness (i.e. 6–8) can be achieved with a larger number of unique combinations of predictor variable states than what is possible for achieving high values (>10) of predicted solitary bee species richness. As more data become available additive prediction models should therefore be updated by including of

interaction terms between predictor variables, thereby setting conditions for the estimated effect of individual variables such as bee habitat area and distance to sandy soils. Areas where the majority of parameterized environmental conditions are optimal should be prioritized for habitat enhancement because our model is additive and threatened solitary bees have typically been found at locations with a predicted value of > 10 (Fig. 4). Although our model reduces the number of potential sites for habitat enhancement schemes it does not provide information on local floral diversity. Sites selected by using the model will therefore need to be surveyed, allowing managers to identify the subset of these sites most in need of habitat enhancement (e.g. with the lowest floral diversity).

Conclusion and management implications Our findings demonstrate that prediction maps can reliably be used to identify areas where climatic conditions, habitat area, and nesting substrates do not limit solitary bees. Focusing habitat enhancement schemes, such as augmenting plant species richness if this is low, on sites with a high predicted bee species richness, will likely improve their effectiveness. Prediction models can also identify environmental conditions that limit bee diversity and guide habitat improvement measures, like establishment of nest sites for bees, in addition to augmenting plant species richness. Prediction maps similar to those produced here can be used to guide field surveys, and improve the effectiveness of inventories aimed at mapping threatened and rare species. Since our model was parameterized using data collected in early successional habitats, our prediction maps should be interpreted as reflecting the potential for supporting wild bees if vegetation is kept in an early succession and plant species richness is increased. Prediction maps provide managers with a tangible summary of the expected distributions of bee diversity, and ecologists with the opportunity to refine and improve the models as environmental maps with higher resolution, or other data become available. Because predictions maps are based on correlations, we encourage that managers supplement such models with well replicated control-treatment field experiments to identify where they are most useful, prior to large scale implementations.

CRediT authorship contribution statement

M.A.K. Sydenham: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Z.S. Venter:** Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **K. Eldegard:** Data curation, Funding acquisition, Resources, Writing – original draft, Writing – review & editing. **S.R. Moe:** Funding acquisition, Resources, Writing – original draft, Writing – review & editing. **M. Steinert:** Resources, Writing – review & editing. **A. Staverløkk:** Methodology, Resources. **S. Dahle:** Data curation, Resources, Writing – review & editing. **D.I.J. Skoog:** Data curation, Methodology, Resources, Writing – review & editing. **K.A. Hanevik:** Data curation, Methodology, Resources, Writing – review & editing. **A. Skrindo:** Funding acquisition, Methodology, Writing – review & editing. **G.M. Rusch:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – original draft, Writing – review & editing.

Acknowledgements

We thank Mikaela E.G.P. Olsen, Solveig Haug, Jonas Lystrup Andresen, and April McKay for operating the traps installed in the seminatural grasslands. Insect sampling and analyses of data from seminatural grasslands was funded by the Norwegian Agricultural Agency (Klima- og Miljøprogrammet: POLLILAND, grant number 2018/72806). Statnett SF funded operational costs related to the field work in power line clearings in the forested ecosystem. The Norwegian Public Roads Administration funded the collection of data along roadsides in

the agricultural ecosystem. Data collection at urban green spaces in Oslo was funded from the Strategic Institute (SIS) programme of the Research Council of Norway (grant no. 160022/F40) for the URBAN SIS project. We thank Øystein Røsoek at the county managers office Oslo/Viken for helpful discussions on the management implications of our study. We thank two anonymous reviewers and Associate editor Christopher Lepczyk for the thorough reviews and insightful comments on earlier versions of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2021.104267>.

References

- Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., ... Memmott, J. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, 282(1803), 20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., ... Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature ecology & evolution*, 3(3), 363–373.
- Barton, K., & Barton, M. K. (2019). Package 'MuMIn'. R package version, 1(6).
- Batáry, P., Báldi, A., Sárospataki, M., Kohler, F., Verhulst, J., Knop, E., ... Kleijn, D. (2010). Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems & Environment*, 136(1–2), 35–39.
- Batáry, P., Baldi, A., Kleijn, D., & Tschardt, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 278(1713), 1894–1902.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., ... Bolker, M. B. (2015). Package 'lme4'. *Convergence*, 12(1), 2.
- Biesmeijer, J. C., Roberts, S. P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., ... Settele, J. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313(5785), 351–354.
- Björkdal, I., & Björkelo, K. (2006). AR5 klassifikasjonssystem: Klassifikasjon av arealressurser. Håndbok fra Skog og landskap. [Norwegian].
- Breiman, L. (2001). Random forests. *Machine Learning*, 45(1), 5–32.
- Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D., & Nowakowski, M. (2007). Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44(1), 29–40.
- Carvell, C., Osborne, J. L., Bourke, A. F. G., Freeman, S. N., Pywell, R. F., & Heard, M. S. (2011). Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecological Applications*, 21(5), 1760–1771.
- Copernicus Land Monitoring Services (2018). Pan-European High Resolution Layers. Url: <https://land.copernicus.eu/pan-european/high-resolution-layers/> Accessed: 14 December 2018.
- Davis, A. Y., Lonsdorf, E. V., Shierk, C. R., Matteson, K. C., Taylor, J. R., Lovell, S. T., & Minor, E. S. (2017). Enhancing pollination supply in an urban ecosystem through landscape modifications. *Landscape and Urban Planning*, 162, 157–166.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46.
- Droege, S., Tepedino, V. J., LeBuhn, G., Link, W., Mincley, R. L., Chen, Q., & Conrad, C. (2010). Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conservation and Diversity*, 3(1), 15–23.
- European commission. (2018) The EU approach to tackle pollinator decline. Last updated: 07.08.2019. Url: https://ec.europa.eu/environment/nature/conservation/species/pollinators/index_en.htm Accessed 4 March 2020.
- Fortel, L., Henry, M., Guilbaud, L., Guirao, A. L., Kuhlmann, M., Mouret, H., ... Smith, M. A. (2014). Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PloS One*, 9(8), e104679.
- Geological Survey of Norway. (2011). Løsmasser WMS. Last updated: 13.06.2018. Url: <https://kartkatalog.geonorge.no/metadata/norges-geologiske-undersokelse/losmasser-wms/aa780848-5de8-4562-8f35-3d5c80ea8b48/> Accessed 14 December 2018.
- Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., ... Dajoz, I. (2016). The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecology and Evolution*, 6(18), 6599–6615.
- Gjertsen, A. K., & Nilsen, J. E. (2012). SAT-SKOG. Rapport fra Skog og landskap: Et skogkart basert på tolking av satellitbilder.
- Glaum, P., Simao, M.-C., Vaidya, C., Fitch, G., & Iuliano, B. (2017). Big city Bombus: Using natural history and land-use history to find significant environmental drivers in bumble-bee declines in urban development. *Royal Society Open Science*, 4(5), 170156. <https://doi.org/10.1098/rsos.170156>
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., ... Lamb, E. G. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PloS One*, 12(10), e0185809.
- Hallmann, C. A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., ... Jongejans, E. (2019). Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity*.
- Hanevik, K. A. (2018). The influence of nest-site limitation on the species richness and abundance of bees: Linking biodiversity and geology (Master's thesis, [KA Hanevik]).
- Hartig, F. (2016). Package "DHARMA": Residual diagnostics for hierarchical (multi-level/mixed) regression models. *An R package*.
- Henriksen, S., & Hilmo, O. (2015). *The 2015 Norwegian red list for species*. Norway: Norwegian Biodiversity Information Centre.
- Hoiss, B., Krauss, J., Potts, S. G., Roberts, S., & Steffan-Dewenter, I. (2012). Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4447–4456.
- Hopwood, J. L. (2008). The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*, 141(10), 2632–2640.
- Jauker, B., Krauss, J., Jauker, F., & Steffan-Dewenter, I. (2013). Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology*, 28(1), 107–120.
- Koenker, R., Portnoy, S., Ng, P. T., Zeileis, A., Grosjean, P., & Ripley, B. D. (2019). Package 'quantreg'. An R package.
- Koh, I., Lonsdorf, E. V., Williams, N. M., Brittain, C., Isaacs, R., Gibbs, J., & Ricketts, T. H. (2016). Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences*, 113(1), 140–145.
- Krauss, J., Alfert, T., & Steffan-Dewenter, I. (2009). Habitat area but not habitat age determines wild bee richness in limestone quarries. *Journal of Applied Ecology*, 46(1), 194–202.
- Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., & Greenleaf, S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, 103(9), 1589–1600.
- Marja, R., Kleijn, D., Tschardt, T., Klein, A.-M., Frank, T., Batáry, P., & Knops, J. (2019). Effectiveness of agri-environmental management on pollinators is moderated more by ecological contrast than by landscape structure or land-use intensity. *Ecology Letters*, 22(9), 1493–1500.
- Marshall, L., Carvalho, L. G., Aguirre-Gutiérrez, J., Bos, M., Groot, G. A., Kleijn, D., ... Biesmeijer, J. C. (2015). Testing projected wild bee distributions in agricultural habitats: Predictive power depends on species traits and habitat type. *Ecology and Evolution*, 5(19), 4426–4436.
- Moretti, M., De Bello, F., Roberts, S. P., & Potts, S. G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology*, 78(1), 98–108.
- Murray, T. E., Fitzpatrick, Ú., Byrne, A., Fealy, R., Brown, M. J. F., Paxton, R. J., & Steffan-Dewenter, I. (2012). Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology*, 49(5), 998–1008.
- Nieto, A., Roberts, S. P., Kemp, J., Rasmont, P., Kuhlmann, M., Criado, M. G., ... & De Meulemeester, T. (2017). European red list of bees.
- Norwegian Environment Agency. (2011). Viktige naturtyper. Last updated: 07.12.2018. url: <https://kartkatalog.geonorge.no/metadata/miljodirektoratet/viktige-naturtyper/d776ff93-104d-4aa5-a8d9-276df01eb51c/> Accessed 14 December 2018.
- Norwegian Mapping Authority. (2016). Høyde DTM 50 (UTM33) WMS. Last updated: 22.10.2018. url: <https://kartkatalog.geonorge.no/metadata/kartverket/hoyde-dtm-50-utm33-wms/12d9e00f-0232-489f-9810-3bccf54914ed/> Accessed: 14 December 2018.
- Norwegian Ministries. (2018). *National pollinator strategy a strategy for viable populations of wild bees and other pollinating insects*. Oslo: Norwegian Government Security and Service Organisation.
- O'Connor, R. S., Kunin, W. E., Garratt, M. P., Potts, S. G., Roy, H. E., Andrews, C., Jones, C. M., Peyton, J. M., Savage, J., Harvey, M. C., & Morris, R. K. (2019). Monitoring insect pollinators and flower visitation: The effectiveness and feasibility of different survey methods. *Methods in Ecology and Evolution*, 10(12), 2129–2140.
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120(3), 321–326.
- Ollerton, J., Erenler, H., Edwards, M., & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, 346(6215), 1360–1362.
- Ollerton, J. (2017). Pollinator diversity: Distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 353–376.
- Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C. D., & Ascher, J. S. (2020). Global patterns and drivers of bee distribution. *Current Biology*, 31, 1–8.
- IPBES. (2016). In *The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production* (p. 552 pages.). Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
- Phillips, B. B., Gaston, K. J., Bullock, J. M., & Osborne, J. L. (2019). Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. *Journal of Applied Ecology*, 56(10), 2316–2327.
- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., & Willmer, P. G. (2004). Nectar resource diversity organises flower-visitor community structure. *Entomologia experimentalis et applicata*, 113(2), 103–107.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345–353.

- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R foundation for statistical computing. <https://www.R-project.org/>.
- Scheuchl, E., & Willner, W. (2016). *Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt*. Quelle & Meyer Verlag.
- Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., ... Linsenmair, K. E. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674.
- Senapathi, D., Goddard, M. A., Kunin, W. E., Baldock, K. C. R., & Wright, G. (2017). Landscape impacts on pollinator communities in temperate systems: Evidence and knowledge gaps. *Functional Ecology*, *31*(1), 26–37.
- Skoog, D. I. J. (2018). *The influence of nesting resources on bee-flower interactions, revealed through functional traits, network structure and geology* (Master's thesis. Ås): Norwegian University of Life Sciences.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tschardtke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*(5), 1421–1432.
- Steinert, M., Sydenham, M. A. K., Eldegard, K., & Moe, S. R. (2020). Conservation of solitary bees in power-line clearings: Sustained increase in habitat quality through woody debris removal. *Global Ecology and Conservation*, *21*, e00823. <https://doi.org/10.1016/j.gecco.2019.e00823>
- Sydenham, M. A. K., Moe, S. R., Totland, Ø., & Eldegard, K. (2015). Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? *Ecography*, *38*(2), 140–153.
- Sydenham, M. A. K., Moe, S. R., & Eldegard, K. (2020). When context matters: Spatial prediction models of environmental conditions can identify target areas for wild bee habitat management interventions. *Landscape and Urban Planning*, *193*, 103673. <https://doi.org/10.1016/j.landurbplan.2019.103673>
- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., ... Paxton, R. J. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*, *11*(1). <https://doi.org/10.1038/s41467-020-14496-6>
- Tonietto, R. K., Larkin, D. J., & Diamond, S. (2018). Habitat restoration benefits wild bees: A meta-analysis. *Journal of Applied Ecology*, *55*(2), 582–590.
- Wagner, M., Fagan, K. C., Jefferson, R. G., Marrs, R. H., Mortimer, S. R., Bullock, J. M., & Pywell, R. F. (2019). Species indicators for naturally-regenerating and old calcareous grasslands in southern England. *Ecological Indicators*, *101*, 804–812.
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In *Linnean Society Symposium Series* (pp. 1–16). Academic Press Limited.
- Williams, N. M., Crone, E. E., Roulston, T'ai. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, *143*(10), 2280–2291.
- Zellmer, A. J., Claisse, J. T., Williams, C. M., Schwab, S., & Pondella, D. J. (2019). Predicting optimal sites for ecosystem restoration using stacked-species distribution modeling. *Frontiers in Marine Science*, *6*, 3.
- Zulian, G., Maes, J., & Paracchini, M. L. (2013). Linking land cover data and crop yields for mapping and assessment of pollination services in Europe. *Land*, *2*, 472–492.
- Zurbuchen, A., Landert, L., Kläiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*(3), 669–676.
- Öster, M., Persson, K., & Eriksson, O. (2008). Validation of plant diversity indicators in semi-natural grasslands. *Agriculture, Ecosystems & Environment*, *125*, 65–72.