



## Research Paper

# Priority maps for pollinator habitat enhancement schemes in semi-natural grasslands

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## HIGHLIGHTS

- Bee species richness in semi-natural grasslands is predicted at 20 m resolution.
- Prediction maps supplement current assessment criteria of semi-natural grassland.
- Prediction maps identify semi-natural grasslands for pollinator conservation.

## ARTICLE INFO

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## ABSTRACT

Conserving semi-natural grasslands, a threatened habitat type in European landscapes, is increasingly recognized as a measure to conserve pollinators. Our aim was to test if (a) prediction maps of solitary bee species richness could be used to rank semi-natural grasslands in terms of their potential for supporting wild bees, and (b) if such predictions extend current assessment criteria that determine which grasslands are eligible for being listed under habitat conservation schemes. We sampled wild bee communities in 52 semi-natural grasslands in southeast Norway. We conducted an across-year validation, using data from 2019 (32 sites) to model bee species richness, and used data from 2020 (20 sites) to validate predictions. We then conducted a leave-one-out cross-validation, iteratively using data from 51 sites to parameterize our model, and validating predictions on the withheld site. Finally, we used data from all 52 sites to update the model and tested if predicted species richness within the 1075 grasslands in our region was reflected in current assessment criteria scores assigned to those grasslands. Models from across-year, and leave-one-out cross-validations, predicted 39%, and 43% of bee species richness in semi-natural grasslands, respectively. Model predictions and current criteria of semi-natural grassland quality were not strongly related ( $R^2_{\text{adjusted}} = 0.01$ ), suggesting that prediction models can add a valuable extra dimension when prioritizing between semi-natural grassland for pollinator habitat conservation. Our findings illustrate how spatial prediction models can provide management authorities with a valuable tool for prioritizing where to direct habitat enhancement schemes in order to improve conservation effectiveness.

## 1. Introduction

Semi-natural grasslands are valued because they provide habitats for a wide array of plant and animal species and for their aesthetic and cultural value (Habel et al., 2013; Feurdean et al., 2018; Bengtsson et al., 2019). Since the 1950s, with the industrialization of agriculture and silviculture, the extent of semi-natural grasslands in rural landscapes has

declined across Europe and approximately half of the 53 described grassland types are considered threatened at the European scale (Jansen et al., 2016). Even in countries where agricultural intensification has been less pronounced, such as in Norway, mowed semi-natural grasslands (or hay meadows) are considered a critically endangered habitat type with forest encroachment and regrowth as the main threats (Norwegian Biodiversity Information Centre, 2018). In many countries,

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considerable efforts are invested in mapping, managing, and restoring existing semi-natural grasslands (Rydgren et al., 2010; Ruprecht et al., 2010; Auestad et al., 2015), and to create new ones (Fagan et al., 2008). The conservation of semi-natural grasslands is a central part of both national and international agri-environmental schemes (Uthes & Matzdorf, 2012; McCracken et al., 2015; Norwegian Ministries, 2018).

Semi-natural grasslands are important resources for wild pollinators. Since the widespread decline in the diversity of pollinating insects (Biesmeijer et al., 2006; Potts et al., 2010; Nieto et al., 2014) is tightly linked to changes in agricultural practices during the past century (Ollerton et al., 2014), there is currently a renewed interest in conserving and restoring important pollinator habitats, in particular semi-natural grasslands (Woodcock et al., 2014; Garrido et al., 2019; Bartual, et al., 2019). Indeed, managing remnant semi-natural grasslands is an integral part of national and international pollinator conservation strategies and an increased focus on the effects of conservation action effects on non-plant taxa has emerged the last decade (e.g. Berg et al., 2019). Nevertheless, current assessments of the ecological state of grasslands are often based on floral diversity and the occurrence of light-demanding plants such as *Arnica montana* (Öster et al., 2008).

In Norway, hay meadows (semi-natural grasslands hereafter) are eligible for receiving management funds if they are assessed to be of national (grade A) or regional (grade B) importance. The assessments of conservation importance are mainly based on the vascular plant species richness and occurrence of threatened plant species coupled with the size, management history and successional state of the grasslands (Norwegian Environment Agency, 2007, 2015, see Appendix S1). While insect-pollinated plant diversity is an important determinant of pollinator diversity in grasslands (e.g. Bartual et al., 2019), it remains unclear if the current conservation evaluation criteria based on the plant community are sufficient for assessing their value for pollinating insects. If not, new tools are needed for identifying semi-natural grasslands where habitat enhancement schemes – and increased floral diversity – will contribute the most towards conserving pollinating insects.

Insect pollinators include a diverse range of taxa with wasps (Hymenoptera), butterflies (Lepidoptera), flies (Diptera) and beetles (Coleoptera) being the most dominant orders. Among the pollinating insects, bees are regarded as the most important taxa because of their foraging behavior, their abundance and the diversity of plants with which they interact (Ollerton, 2017). Moreover, because bees are central place foragers, they respond strongly to changes in landscape and habitat conditions, an effect that is more apparent for solitary bees than for bumble bees even at local spatial scales (Steffan-Dewenter et al., 2002). By comparison, hoverflies, that are not central place foragers, do not show as marked declines in abundance as the distances to semi-natural habitat patches increases (Jauker et al., 2009). Because solitary bees show strong responses to environmental gradients, and because the species richness of solitary bees is correlated with the species richness of other pollinating insects, such as butterflies (Franzén & Nilsson, 2008), bees are suitable bioindicators for the broader insect community in farmlands (Goulson and Nicholls, 2016). Solitary bee species richness is therefore likely to be a useful proxy of the general habitat quality of semi-natural grasslands for pollinating insects.

To target bee-habitat enhancement schemes by increasing floral diversity in semi-natural grasslands, we need to identify grasslands where other environmental factors do not constrain bee diversity, so that the potential effect on solitary bee species richness will be greatest. In addition to local food (floral) resources, bee diversity depends on a series of environmental conditions (Sydenham et al., 2015). In central and northern Europe, solitary bee species richness increases with temperature and conversely declines with elevation and latitude (Hoiss et al., 2012; Sydenham et al., 2015). Also, habitat size is positively related to bee species richness (Taki et al., 2018; Sydenham et al., 2022). Increases in bee species richness with habitat area may result from habitat area being positively related to floral diversity (Krauss et al., 2004), or from larger patches being more likely to contain suitable nesting sites such as

patches of exposed soil, or both. Finally, nesting resources are an important but often overlooked determinant of local bee diversity in grasslands (Murray et al., 2012), and the proximity to suitable nesting sites will influence if bees can reach and forage on the flowers. Isolating the effect of nest-site limitation, from that of floral diversity, can be difficult if nest-site conditions and floral diversity are correlated (Roulston & Goodell, 2011). However, Sydenham et al. (2022) showed that a model of solitary bee species richness that included distances to nesting substrates as predictor variables, predicted variation in observed bee species richness that was not accounted for by plant species richness. Thus, we expect that habitat enhancement schemes on semi-natural grasslands (i.e. aiming at increasing flower diversity) will have most positive effect on pollinator diversity on grasslands that are i) located at low elevations and latitudes, ii) of sufficient size to support viable populations of bees, and iii) in close proximity to suitable nesting substrates.

The aim of this study was to test if we could use environmental conditions that are not altered by management to predict the diversity of solitary bees occurring in semi-natural grasslands. If so, such predictions could be used to identify areas where enhancing the quality of semi-natural grasslands would have the highest potential to sustain bee communities. We build on the model by Sydenham et al. (2022), a spatially explicit prediction model of solitary bee diversity parameterized using data from semi-natural grasslands, climate and distance to nesting suitable locations. The model was tested by predicting solitary bee species richness and the occurrence of threatened species in other open vegetation habitat types (power line clearings, road sides and urban green spaces). In the current study we implement the model from Sydenham et al. (2022) and provide a concrete example of how such models can be used to more effectively target pollinator habitat enhancement schemes of a threatened habitat type (mowed semi-natural grasslands). Specifically we:

- Validate the prediction model in a two-step process. We first conducted an across-year validation, to test if the model from Sydenham et al. (2022), parameterized using data from 32 grasslands sampled in 2019, predicted solitary bee species richness sampled in 20 new grasslands in 2020. We then combined the data from Sydenham et al. (2022) with the data sampled in 2020 and conducted a leave-one-out cross-validation to test if models parameterized using data from 51 sites (i.e. 52 - site x), could predict bee species richness in withheld sites (i.e. the x<sup>th</sup> site). We further tested if the prediction model was spatially or temporally biased by assessing if the residual variation from the leave-one-out cross-validations varied systematically with the predictor variables included in the model (e.g. sampling year). We then recalibrated the prediction model using data from all 52 sites, i.e. from both years.
- Show how such prediction models can be used in combination with current semi-natural grassland conservation value criteria, in order to obtain synergies between ongoing semi-natural grassland conservation actions and pollinator habitat enhancement schemes. To this end, we tested if semi-natural grasslands considered to be of 'national importance' or 'regional importance' according to the current criteria for the allocation of habitat conservation schemes, had a higher predicted solitary bee species richness than grasslands of 'local importance'.
- Finally, we provide examples of how current priority setting criteria can be combined with spatial predictions of solitary bee species richness to rank semi-natural grasslands to target habitat conservation actions.

## 2. Methods

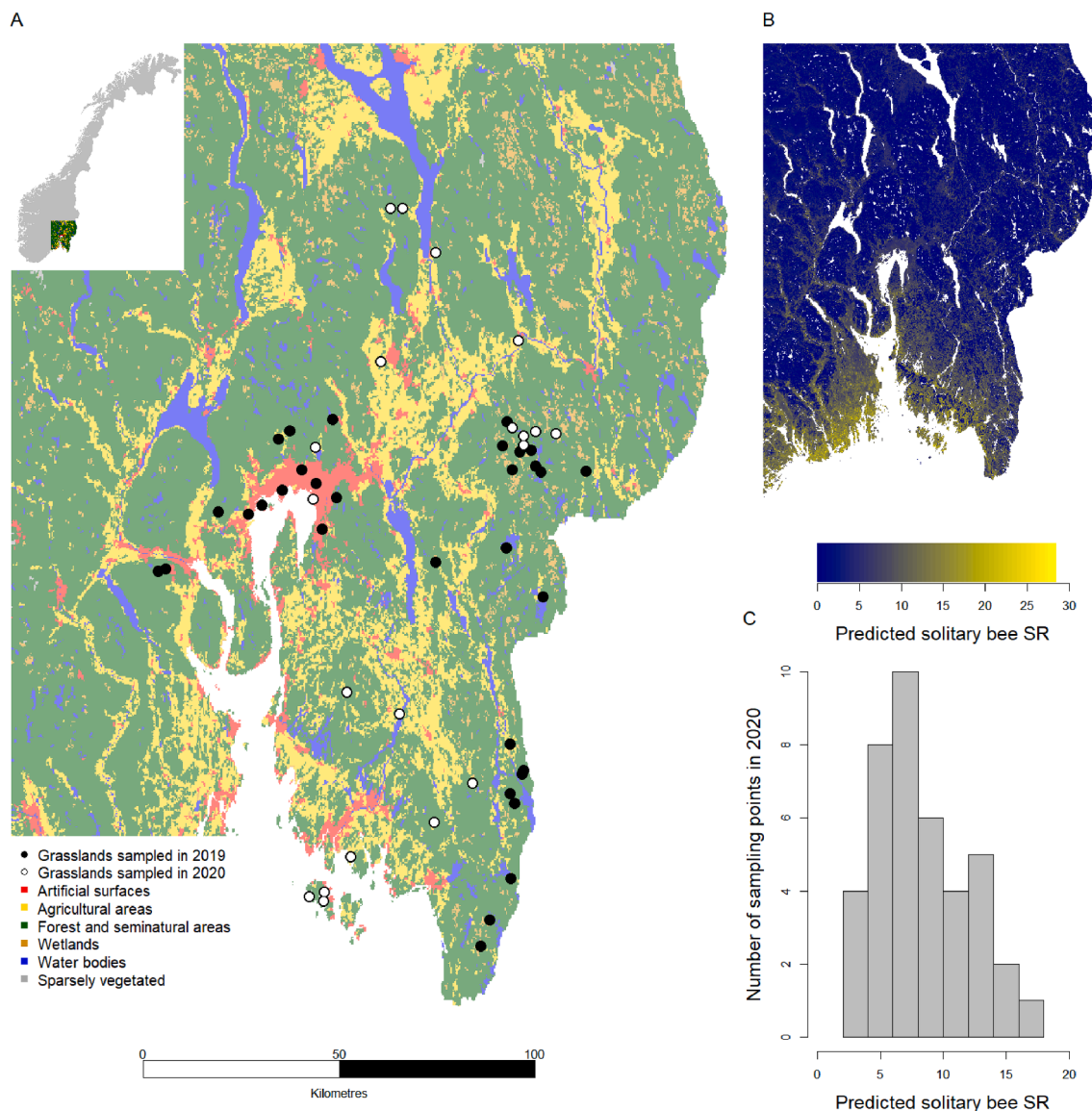
### 2.1. Modelling solitary bee species richness

To predict solitary bee species richness, we used data from a

standardized wild bee survey conducted in semi-natural grasslands distributed across southeast Norway in 2019 (Fig. 1A, Sydenham et al., 2022). We obtained information on the location, and type of the semi-natural grassland from the Norwegian Environment Agency's online database (www.naturbase.no), where habitat types are stored as georeferenced polygons. Because our aim was to predict bee diversity across the entire southeast Norway (i.e. the counties of Oslo, Viken and Innlandet, Fig. 1A), and that logistic constraints limited the sample size for this task, we ensured that the selected study sites were widely distributed so that they covered the main environmental gradients expected to drive wild bee diversity within the region (climatic conditions, habitat availability and distances to potential nesting substrates). We treated semi-natural grasslands located <200 m apart (i.e. within the typical foraging range of solitary bees) as belonging to a single site so that our final dataset consisted of 32 study sites (Fig. 1A).

In 2019, we sampled the wild bee communities in the 32 semi-natural grasslands (study sites) with three pan-trap triples (pan F hereafter) mounted on fence-poles and spaced at least 20 m apart. Each pan-trap consisted of three bowls, coated with fluorescent yellow, white, or

blue spray paint (Sparvar Leuchtfarbe, Germany). We used pan-traps to sample bee communities because this approach allowed us to sample all sites across a large area within a short timeframe, thus ensuring that the phenology of bee species would not interfere with the comparison site-level estimates of bee diversity. Although the efficiency of pan-traps vary among insect taxa, pan-traps are an efficient method for sampling solitary bee communities and provide species accumulation curves that are similar to those obtained from expert-based transect walks (O'Connor et al., 2019). All sites were surveyed once in May and June, and twice in July. Sampling was conducted during periods with four consecutive days with temperatures > 15 °C, little wind, and few clouds, allowing us to sample all 32 sites during the same sampling round. In the first sampling round, traps were installed on either 13th or 14th of May 2019. In the second, third and fourth (final) sampling rounds, traps were deployed on June 21/22, July 9/10/11, and July 23/24. In the fourth sampling round, one trap was tampered with at two sites. We therefore re-deployed the two traps on July 26 to ensure that all traps within all sites had the same number of sampling events throughout the season. During sampling events, pan traps were filled with water and a drop of



**Fig. 1.** (A) The distribution of semi-natural grasslands where wild bee communities were surveyed in 2019 and 2020 in southeast Norway. (B) The predicted solitary bee species richness (SR) throughout the study region, based on a prediction model built using the bee survey data from 2019 (Sydenham et al., 2022). (C) The distribution of predicted solitary bee species richness values across the 40 sample points (pan traps) distributed among the 20 semi-natural grasslands surveyed in 2020.

detergent and were left on site for 48 h before being collected. Sampled wild bees were stored in ethanol for later pinning and identification.

In Sydenham et al. (2022), we built a model that predicted solitary bee species richness at a 20 m resolution as a function of climate related variables (i.e. elevation, and latitude), habitat size, and distance to suitable nesting substrates; i.e. distance to soil types with a high infiltration capacity (i.e. sand dominated sediment types) and distance to old forests (forest stands with a minimum age of 80 years). Data on elevation was extracted from a 50 m digital elevation model (Norwegian Mapping Authority, 2016). Habitat size was estimated as the sum of the probabilities that the raster pixel where a trap was located and its eight neighboring cells were characterized by grassland vegetation, i.e. with dominance of herbaceous vegetation, with probabilities obtained from a random forest (Breiman, 2001) prediction model (see Sydenham et al., 2022). We used a 60 by 60 m grid because at larger radii habitat area was strongly correlated with elevation (Sydenham et al., 2022). An added benefit of using the smaller grid was that this allowed producing maps with a fine spatial resolution that have greater utility for individual land owners. Information on soil sediment infiltration capacity and forest stand ages were obtained from Geological Survey of Norway (2011) and Gjertsen & Nilsen (2012), respectively. Because our data included three traps per site, we used a Poisson GLMM with site identity as a random intercept term to account for non-independence between data points from the same site. We used this model, from Sydenham et al. (2022), on solitary bee species richness to produce a prediction map of the expected solitary bees richness within 20 m raster cells across southeastern Norway.

### 3. Model validation and re-calibration

In 2020, we selected 20 new study sites (semi-natural grasslands) within the same region as those sampled in Sydenham et al. (2022) in 2019 (Fig. 1A). The selection of sites in 2020, was based on the solitary bee species richness model produced from the data sampled in 2019 (Fig. 1B) so that the 20 new semi-natural grasslands spanned the gradient of the solitary bee species richness values predicted from the model from 2019 (Fig. 1C). In order to reduce operational costs related to field and laboratory work we reduced the number of pan traps (triplets) per site from three (as in 2019) to two. During spring 2020, we installed two pan traps, in each of the 20 semi-natural grasslands. During each sampling round, we deployed pan traps on half of the sites on day 1, the other half on day 2, and then collected traps on day 3 and 4. We deployed traps on May 13th and 14th, May 25th and 26th, June 14th and 15th, and July 16th and 17th, and thus obtained samples from all sites covering the same period as sampled in 2019, albeit with one less sampling round in July.

We conducted a two-step validation of the predicted solitary bee species richness (Fig. 1). We first conducted an across-year validation and used a Poisson GLMM, with site identity as a random effect ( $n = 20$ ), to test if the species richness of solitary bees sampled in traps in 2020 increased proportionately with the predicted solitary bee species richness of 2019 for those trap locations. Because of the log-link in the Poisson models, we log-transformed the predicted solitary bee species richness in order to straighten the regression curve. If species detectability is low, predictive performance on the bee species richness, sampled within individual traps could be influenced by random noise. We therefore used a linear regression model to test if the  $\log(y + 1)$  transformed average solitary bee species sampled across traps within sites in 2020 matched the  $\log(x + 1)$  transformed average predicted solitary bee species richness for the trap locations. We used linear models because of the non-integer response variable. Secondly, we used a leave-one-out cross validation to recalibrate the prediction model, using all available data from the two years of sampling. We used a Poisson GLMM to refit the model used to produce the prediction map (Fig. 1B) by including data from all sites sampled in both 2019 and 2020. We first attempted to specify site identity as a random effect nested

within sampling year, but DHARMA residual plots revealed that such a model did not fit the data well. We therefore included sampling year as a fixed effect term together with the variables used to produce the original prediction model. Fixed effects were: Elevation, Northern coordinates, Habitat size,  $\log(\text{distance to sandy sediments} + 1)$ ,  $\log(\text{Distance to old forests} + 1)$ , and sampling year as a categorical variable with two levels. Site identity was included as a random intercept term, with three pan-traps per site in 2019 and two pan-traps per site in 2020. We used Bayesian Information Criteria (BIC) to compare four different specifications of the model. In the most complex model, we allowed sampling year to interact with the other fixed effect terms (BIC = 657.6). In the three subsequent models, Habitat area was either left untransformed (BIC = 655.8), square root transformed (BIC = 655.7), or  $1/x$  transformed as in the original model formulation (BIC = 656.6). Models with Habitat area left untransformed or square root transformed yielded the lowest, and similar BIC values. We therefore proceeded with the model where Habitat area was untransformed. We iteratively fitted the Poisson GLMM to data from 51 of the 52 sites and used the resulting models to predict solitary bee species richness for the pan-traps in the held-out site. We log-transformed the predicted solitary bee species richness and used site identity ( $n = 51$ ) as a random effect. We used linear mixed effect models with site identity as a random effect term, and likelihood-ratio-tests to test if residual variation between observed and predicted solitary bee species richness varied systematically with the environmental predictors and sampling year. For site-level validations, we used a linear regression model to test if the  $\log(y + 1)$  transformed average solitary bee species richness per site corresponded with the  $\log(x + 1)$  transformed average predicted solitary bee species richness for the site (trap locations) and a linear regression on the residual variation from the model against sampling year to test if differences in the number of traps per site and distribution of sampling rounds across the season between the two years, led to biases in the model predictions.

We produced an updated prediction map based on the full model, parameterized using data from all 52 sites. We produced one map where year was held constant at 2019 and another where year was held constant at 2020 and used the average pixel values from these two maps as input into the new and updated map. To test if conservation importance (national, regional or local) of semi-natural grasslands corresponded to predicted bee species richness, we extracted the highest predicted solitary bee species richness for pixels within seminatural grassland polygon for each of the 1075 polygons in the study region. We used a linear regression to test if the  $\log(\text{max predicted solitary bee species richness})$  differed systematically among semi-natural grasslands of national, regional and local conservation value.

To illustrate how prediction maps can be used to target semi-natural grasslands for conservation management we assembled a data frame containing: (1) the unique semi-natural grassland identifier, from the Norwegian Environment Agency's data base; (2) the highest predicted solitary bee species richness for pixels found within the semi-natural grassland polygon; (3) the area, in square metres, of the semi-natural grassland polygon; (4) and the conservation status or value of the semi-natural grassland (i.e. of national, regional or local importance). We rescaled the two variables 'max predicted value' and 'log(grassland area)' between zero and one, and calculated the Euclidean distance for all semi-natural grasslands to the ideal grassland (for which 'max predicted value' and 'log(grassland area)' both equaled one). This approach allowed ranking grasslands in terms of the combination of their predicted solitary bee species richness and the area that was classified as semi-natural grassland at the time when the semi-natural grassland was surveyed and mapped. For grasslands with a large area in particular, large parts of what was once grassland is now overgrown by trees. However, small populations of grasslands associated, and often insect-pollinated, plants can persist in within coniferous forests for several decades after a grassland is converted into forest (Milberg et al., 2019), possibly reflecting an extinction-debt (Tilman et al., 1994). Grasslands with a large area, and a high predicted maximum value for solitary bees,

therefore provide an opportunity for efficiently restoring large habitats for pollinators and at the same time conserving large seminatural grasslands.

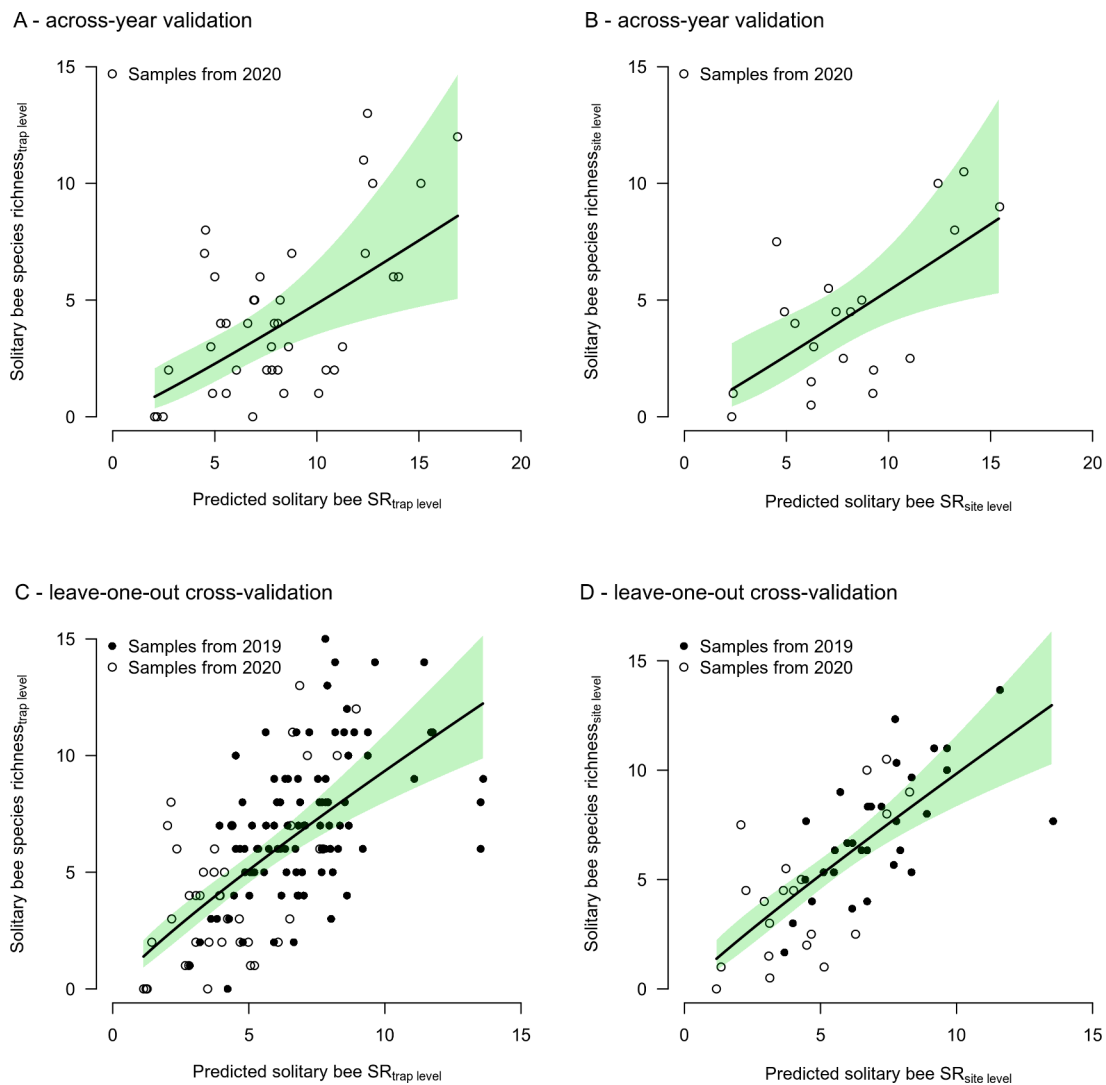
We used lme4 in R (Bates et al., 2015) to fit mixed models, the DHARMA package in R (Hartig, 2016) to ensure that residuals met model assumptions, and the MuMIn package in R (Barton, 2018) to calculate the variance explained by the fixed effect term, i.e. the predicted solitary bee species richness, alone ( $R^2_m$ ) and the variance explained by the fixed effect term and the random effect term, i.e. the site identity ( $R^2_c$ ). All analyses were conducted in R (R Core Team, 2020) with the raster package (Hijmans, 2018) for handling raster map data.

#### 4. Results

From the 32 sites surveyed in 2019, with three traps per site, we sampled a total of 1395 solitary bee specimens comprising a total of 83 species with an average of 7.2 species per trap (min = 0, max = 16). From the 20 sites surveyed in 2020, with two traps per site, we sampled 489 solitary bee specimens and 46 species, with an average of 4.4

species per trap (min = 0, max = 13).

For the across-year validations, the model predicted 39% of the variation in solitary bee species richness sampled in pan traps in the semi-natural grasslands surveyed in 2020 (Fig. 2A, Table 1). At the site level, the model predicted 39% of the variation in average bee species richness per trap (Fig. 2B, Table 1). The leave-one-out cross-validation showed that the model predicted 43% of the variation in solitary bee species richness sampled in pan traps in the semi-natural grasslands in the held-out-samples (Fig. 2C, Table 1). We found no relationships between the residual variation in observed solitary bee species richness (Fig. S1) and elevation ( $df = 1$ ,  $\chi^2 = 0.77$ ,  $p = 0.38$ ), northern coordinates ( $df = 1$ ,  $\chi^2 = 0.003$ ,  $p = 0.96$ ), habitat area ( $df = 1$ ,  $\chi^2 = 0.50$ ,  $p = 0.48$ ), distance to sandy soils ( $df = 1$ ,  $\chi^2 = 0.29$ ,  $p = 0.59$ ) or old forests ( $df = 1$ ,  $\chi^2 = 0.04$ ,  $p = 0.83$ ), or sampling year ( $df = 1$ ,  $\chi^2 = 2.20$ ,  $p = 0.14$ ). At the site level, i.e. when averaging data from traps within the semi-natural grasslands, the model predicted 53% of the variation in bee species richness (Fig. 2D, Table 1). The increase in variation explained when aggregating predictions from the trap to the site level, suggests that a considerable amount of the non-explained variation from



**Fig. 2.** Solitary bee species richness (SR) sampled from semi-natural grasslands (sites) in southeast Norway was positively related to the predicted solitary bee species richness. Plots A-B show results from validations of the original prediction model, parameterized using the 2019 data. Plots C-D show results from the leave-one-out cross validations where the prediction model was iteratively refit to data from all but one site and then used to predict solitary bee species richness within pan-traps from the missing site. Plots A, and C show validations at the individual trap level. Plots B, and D shows the average species richness of solitary bees sampled within semi-natural grassland sites (i.e. across individual traps) and their relationships to the mean predicted solitary species richness for the trap locations within the sites. Black lines show the fitted relationships and green shaded areas show the 95% confidence intervals for the regression slopes. See Table 1 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 1**

Observed solitary bee species richness per pan trap in withheld sites (semi-natural grasslands), as well as the average species richness per trap per site, were positively related to the predicted species richness of solitary bees. Model outputs are shown together with the variance explained by fixed effects alone ( $R^2_m$ ) and that explained by fixed effects and random effects combined ( $R^2_c$ ). Poisson GLMMs were used to fit models for solitary bee species richness within traps, while linear regression models were used to fit models to the  $\log(y + 1)$  average species richness across traps within sites. The predicted solitary bee species richness was log-transformed for Poisson GLMMs and  $\log(x + 1)$  transformed for linear regression models.

| Across-year validations  |         |          |       |         |         |         |  |
|--|---------|----------|-------|---------|---------|---------|--|
| Solitary bee species richness per trap <sub>Across-year validation</sub>                 |         |          |       |         |         |         |  |
| Fixed effects  | $\beta$ | SE       | z     | p       | $R^2_m$ | $R^2_c$ |  |
| Intercept  | -0.94   | 0.66     | -1.42 | 0.157   | 0.39    | 0.72    |  |
| Predicted solitary bee SR  | 1.09    | 0.31     | 3.54  | <0.001  |         |         |  |
| Random effects (n = 136)   | Groups  | $\sigma$ | SD    |         |         |         |  |
| Site ID  | 20      | 0.27     | 0.52  |         |         |         |  |
| Average solitary bee species richness per trap <sub>Across-year validation</sub>         |         |          |       |         |         |         |  |
| Fixed effects  | $\beta$ | SE       | t     | P       | $R^2_m$ | $R^2_c$ |  |
| Intercept  | -0.62   | 0.63     | -0.99 | 0.335   | 0.39    | NA      |  |
| Predicted solitary bee SR <sub>average per site</sub>                                    | 0.99    | 0.29     | 3.43  | 0.003   |         |         |  |
| Leave-one-out cross-validations  |         |          |       |         |         |         |  |
| Solitary bee species richness per trap <sub>Leave-one-out cross-validation</sub>         |         |          |       |         |         |         |  |
| Fixed effects  | $\beta$ | SE       | z     | p       | $R^2_m$ | $R^2_c$ |  |
| Intercept  | 0.22    | 0.22     | 0.99  | 0.321   | 0.43    | 0.60    |  |
| Predicted solitary bee SR  | 0.87    | 0.12     | 7.33  | < 0.001 |         |         |  |
| Random effects (n = 136)   | Groups  | $\sigma$ | SD    |         |         |         |  |
| Site ID  | 52      | 0.07     | 0.26  |         |         |         |  |
| Average solitary bee species richness per trap <sub>Leave-one-out cross-validation</sub> |         |          |       |         |         |         |  |
| Fixed effects  | $\beta$ | SE       | t     | P       | $R^2_m$ | $R^2_c$ |  |
| Intercept  | -0.17   | 0.27     | -0.62 | 0.537   | 0.53    | NA      |  |
| Predicted solitary bee SR <sub>average per site</sub>                                    | 1.06    | 0.14     | 7.52  | < 0.001 |         |         |  |

the trap-level validation was due to random noise between traps, within sites. An alternative explanation could be that data from a single trap was not enough to accurately capture bee-environment relationships, but this does seem to be the case since regression slopes and effect sizes from trap and site-level validations did not differ significantly (Table 1, Fig. 2C-D). We found no relationship between the residual variation in average species richness per site and sampling year (t-value = -0.58, p = 0.57).

The final model, that included data from all 52 semi-natural grasslands explained 61% of the variation in solitary bee species richness per trap, of which 55% was explained by the predictor variables (Table 2). As in the original model (Sydenham et al., 2022), species richness per trap decreased with latitude, elevation, and distances to nesting

**Table 2**

Predictor variable importance for the of solitary bee species richness within semi-natural grasslands in southeast Norway. Effect sizes (z-value) and likelihood ratio test statistics for each predictor variable, and the variance explained by fixed effects alone ( $R^2_m$ ) and by fixed effects and random effects ( $R^2_c$ ) are presented. The model was fit using a Poisson GLMM using Site identity (n = 52) as random effect across the 136 pan trap triplets from which bees were sampled.

| Solitary Bee SR                     | Z     | Df | $\chi^2$ | p       | $R^2_m$ | $R^2_c$ |
|-------------------------------------|-------|----|----------|---------|---------|---------|
| Northern coordinates                | -3.27 | 1  | 8.4      | 0.004   | 0.55    | 0.61    |
| Elevation                           | -2.24 | 1  | 5.5      | 0.019   |         |         |
| Habitat area                        | 3.21  | 1  | 8.95     | 0.003   |         |         |
| $\log(\text{Dist sandy soils} + 1)$ | -3.80 | 1  | 11.4     | 0.001   |         |         |
| $\log(\text{Dist old forest} + 1)$  | -2.05 | 1  | 3.85     | 0.050   |         |         |
| Year (2020 vs. 2019)                | -6.23 | 1  | 31.33    | < 0.001 |         |         |

substrates, and increased with habitat area. There were significantly fewer bees per trap in 2020 compared to 2019.

Using the predicted solitary bee species richness to identify semi-natural grasslands of potential importance to bee conservation supplemented current assessment criteria (Table 3). The predicted solitary bee species richness was on average slightly higher for semi-natural grasslands assessed to be of national (priority level 'A') and regional (priority level 'B') importance, and thus eligible to receive habitat enhancement funds, than for grasslands of local (priority level 'C') importance (Table 3). However, differences between priority levels were very small and priority level only explained 1% of the variation in the predicted solitary bee species richness.

The entire region covered by our prediction map included 1075, registered, semi-natural grasslands (Fig. 3A-B). Combining information from prediction models with information on semi-natural grassland area provides an efficient means for ranking grasslands in terms of their conservation value by focusing on either nationally important (Fig. 3C), or regionally important grasslands (Fig. 3D). As exemplified in Fig. 3E-F, such semi-natural grasslands are particularly threatened by forest regrowth because of land use abandonment (Norwegian Biodiversity Information Centre, 2018), so that the area currently managed to conserve the semi-natural grassland is often smaller than what was mapped during the time the area was surveyed.

**5. Discussion**

Due to important competing targets for funding biodiversity enhancing measures, there is a need to ensure that pollinator habitat enhancement schemes are implemented where they will have the greatest impact. In Norway, for instance, the sector-wide implementation of the national pollinator conservation strategy is to be conducted within existing budgets (Norwegian Ministries, 2019). Just within our study region there were a total of 1075 semi-natural grasslands which need external funding for their maintenance (Fig. 3A), illustrating how thinly funds would be distributed if all semi-natural grasslands were to receive an equal share of the available funds. Our findings suggest that prediction models combined with other valuation criteria (area and nature type conservation value) can be an efficient approach for prioritizing where to allocate additional, pollinator-habitat-enhancement-oriented funds in order to target semi-natural grasslands with a high potential for sustaining diverse bee communities, while simultaneously improving the conservation status of an endangered nature type (Fig. 3D-F).

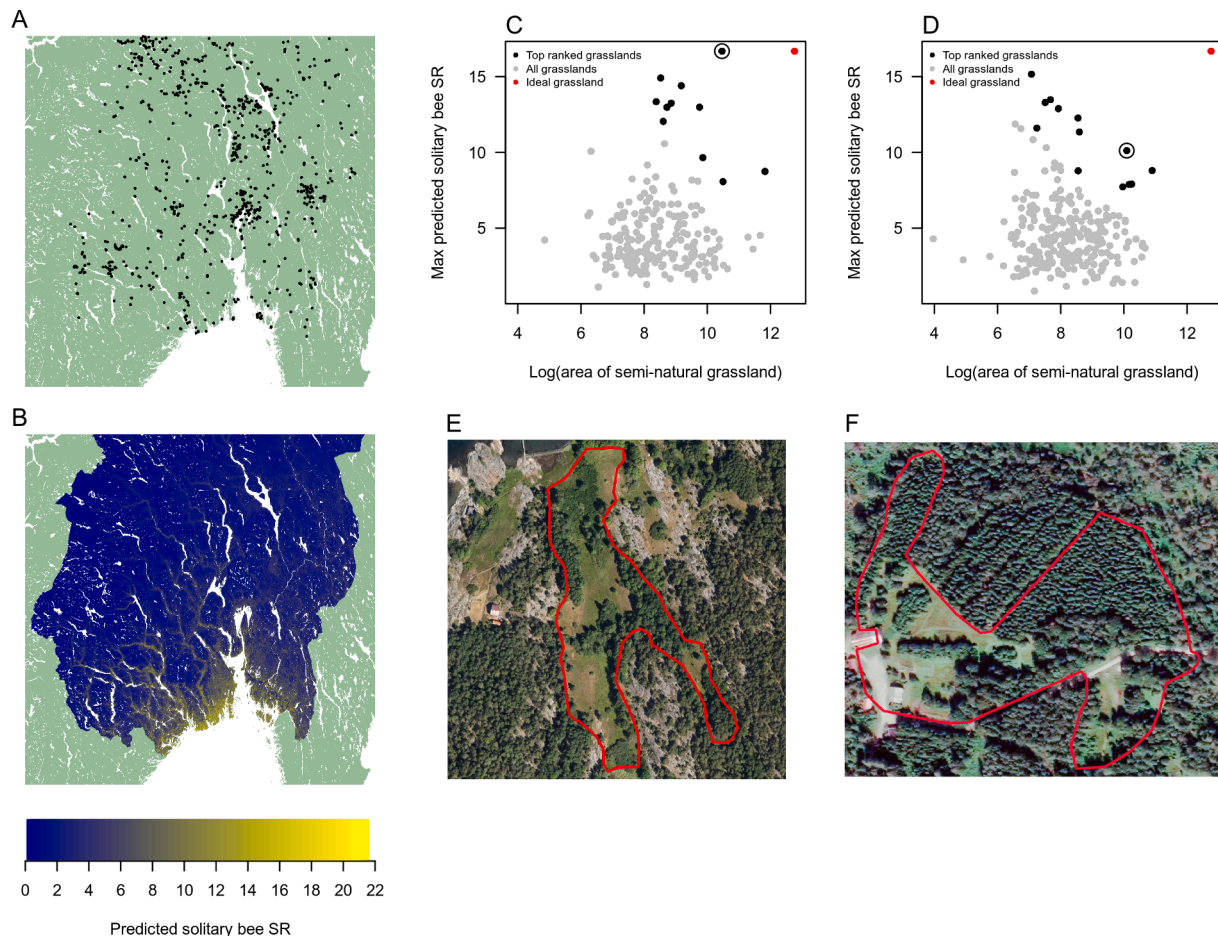
The focus of our study was to identify locations where conservation management of existing semi-natural grasslands is most likely to contribute towards pollinator conservation. However, semi-natural grasslands are of conservation value for more reasons than pollinator conservation. In addition to providing habitat for insects and threatened plant species, semi-natural grasslands provide provisioning, regulating and cultural ecosystem services (Bengtsson et al., 2019). Restoring or improving habitat conditions for wild bees in semi-natural grasslands might therefore come at the cost of other contributions of biodiversity to

**Table 3**

Maximum predicted solitary bee species richness in semi-natural grasslands was only weakly related to their assigned conservation priorities, defined by plant community based assessment criteria currently used by the management authorities. Model outputs from the linear regression analysis are shown together with the raw ( $R^2$ ) and adjusted ( $R^2_{adj}$ ) variance explained.

| Log(Predicted solitary bee species richness) |         |      |       |        |       |             |
|--|---------|------|-------|--------|-------|-------------|
| Fixed effects                                | $\beta$ | SE   | t     | p      | $R^2$ | $R^2_{adj}$ |
| Intercept (Priority level A)                 | 1.44    | 0.03 | 50.81 | <0.001 | 0.01  | 0.01        |
| Priority level B                             | -0.02   | 0.04 | -0.44 | 0.664  |       |             |
| Priority level C                             | -0.12   | 0.04 | -2.79 | 0.005  |       |             |

F-statistic: 4.48 on 2 and 1072 DF, model p-value = 0.011.



**Fig. 3.** Illustration of how semi-natural grasslands can be ranked according to their potential for hosting diverse pollinator communities (i.e. their predicted solitary bee species richness coupled with habitat size). (A) overview of all 1075 semi-natural grasslands within the study region. (B) The predicted solitary bee species richness within 20 m raster pixels for the entire region. (C) Nationally (D) and regionally important semi-natural grasslands ranked according to their size (area) and the highest predicted species richness of solitary bees. Semi-natural grasslands suggested to be prioritized seminatural grasslands, i.e. those that fall within the lower 5% percentile in terms of the Euclidean distance to the ideal grassland (maximum area and predicted solitary bee species richness), are colored in black. The two highest ranked semi-natural grasslands of (A) national and (B) regional importance are highlighted by a buffer circle and satellite images of the two semi-natural grasslands are shown in plot E and plot F, respectively. Note that large parts of the semi-natural grasslands in E-F have been overgrown by trees since they were mapped. Satellite imagery from Map data ©2021 Google via QGIS 2021.

people (Brondizio et al., 2019). Thus, resolving potential conservation conflicts – and identifying conservation synergies – at the locality-level is of utmost importance (Redpath et al., 2013). Prior to giving incentives to land owners to increase the size of the semi-natural grassland by e.g. cutting down trees within the locality (Fig. 3E-F), as often suggested in conservation plans for the grasslands in our region (e.g. <http://faktaark.naturbase.no/?id=BN00069612> for the grassland in Fig. 3C), environmental managers should assess if doing so will substantially reduce other values associated with the locality such as the presence of old hollow trees or trees that provide important foraging resources for bees. However, it seems to rarely be the case that ecosystem services related to wild bees are in conflict with other ecosystem services, such as carbon sequestration and the aesthetic valuation, associated with extensive grasslands (Le Clerc'h et al., 2019). A notable exception is tree planting and afforestation in open habitats which are promoted as a climate mitigation measure (Norwegian Environment Agency, 2020), but are in obvious conflict with the objectives of conserving semi-natural grasslands as habitat for pollinators. Prediction models showing where bee species diversity can potentially be high, can help resolve these conflicts by avoiding setting restrictions to other land-uses, when the likelihood of successful pollinator enhancement measures is low. Semi-natural grasslands that are of national or regional importance and where wild bee habitat enhancement

is likely to be successful should on the other hand be prioritized for habitat enhancement schemes (habitat and pollinator-specific), allowing managers to improve conditions for wild bees while at the same time improving the conservation value of highly valued semi-natural grasslands. Although the species richness of bees can be expected to saturate as habitat size increases, targeting large semi-natural grasslands should still be recommended because the population size of rare bees increases with floral resource levels (Larsson & Franzén, 2007). Large semi-natural grasslands are therefore more likely to be able to sustain viable populations of threatened bees, than small grasslands. Our findings illustrate how prediction models of bee diversity can be used to identify parcels containing semi-natural grasslands that are assessed to be of national or regional importance and where wild bee habitat enhancement is likely to be successful (Fig. 3).

Producing priority maps for pollinator habitat enhancement schemes in semi-natural grasslands requires access to georeferenced information on environmental conditions needed to predict pollinator diversity at relevant spatial resolutions. Ideally, such data should be available and standardized across national borders to allow comparative studies across biogeographic gradients. The multi-level filtering hypothesis (Keddy, 1992; Sydenham et al., 2015), i.e. that species composition is determined through a series of environmental filters, can act as a guide to the type of environmental variables that are needed to model bee

diversity. Since the effect of pollinator habitat enhancements schemes depend on environmental conditions (e.g. Scheper et al., 2013; Krimmer et al., 2019) and that we have just recently begun our attempts at making priority maps for where to implement wild bee habitat enhancement (e.g. Bellamy et al., 2017; Sydenham et al., 2020), there is a need for assessing the types of maps with environmental data at the level of resolution and accuracy required to identify conditions that limit wild bee diversity in semi-natural grasslands.

Current, readily available climate maps are at resolutions of c. 1000 m (e.g. Fick et al., 2017), which is too coarse to capture steep temperature gradients along elevation gradients as well as micro-climatic conditions including those in urban areas (Venter et al., 2020), and which are relevant for wild bee distributions. While latitude and elevation can serve as useful proxies for climatic conditions (e.g. Hoiss et al., 2012; Sydenham et al., 2015), such proxies may slightly underestimate the species richness of bees at high latitudes that fall within warm micro-habitat patches. We therefore expect that the influence of climatic conditions on bee diversity along latitudinal gradients can be more accurately modelled using downscaled climate maps.

In addition to climate associated variables, habitat size and landscape context are important determinants of bee diversity (e.g. Steffan-Dewenter et al., 2002; Rotchés-Ribalta et al., 2018). We used existing data to produce maps showing the probability that raster pixels and their surrounding pixels consist of semi-natural grassland (Sydenham et al., 2022). Although this approach provides data on a reasonably high spatial resolution (20 m) the thematic resolution is low and areas predicted to be potential bee habitat (i.e. open habitats, in early-successional stages) could range from sparsely vegetated areas to fully developed grasslands. Indeed, using land use maps with a high thematic resolution improves predictions of bee distributions (Marshall et al., 2021). We acknowledge that downscaled climate maps coupled with thematic high-resolution land use maps would likely have increased the prediction accuracy of our spatial modelling. Further, differences in foraging range between bee species (Greenleaf et al., 2007) might result in species-, or size-specific responses to the distance to potential nesting substrates, a significant predictor of wild bee diversity in the region of our study (Sydenham et al., 2022). Hence, factoring in such trait-specific responses might further improve model prediction. Nevertheless, we regard that the ability of the map to predict 52% of the average species richness in semi-natural grasslands and to detect the regionally most important semi-natural grasslands for wild bees as a valuable contribution towards improving both the effectiveness and efficiency of pollinator habitat enhancement measures. Our findings thus illustrate how ecological models could be used to optimize pollinator habitat enhancement schemes by informing management authorities about where to allocate funds for semi-natural grassland management aiming to achieve the greatest effect for pollinators.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2022.104354>.

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