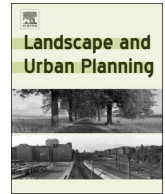




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Research Paper

When context matters: Spatial prediction models of environmental conditions can identify target areas for wild bee habitat management interventions

M.A.K. Sydenham^{a,b,*}, S.R. Moe^a, K. Eldegard^a^a Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway^b Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway

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ABSTRACT

Prioritizing where to implement management interventions is critical because managers have limited budgets and the effect of habitat enhancement depends on site-specific environmental conditions. Field experiments can identify the conditions where habitat enhancement is most effective, but are typically of limited extent and thus not sufficient for producing spatial predictions that can guide management efforts. We tested if we could produce spatial predictions maps – showing where management interventions to enhance bee habitat would be most successful – by combining spatial predictions of plant community composition (i.e., environmental conditions) obtained from field surveys with a field experiment, in which we quantified the effect of three types of management interventions on bee species richness. Using information from digital maps, we predicted plant species composition within power line clearings across southeast Norway. The intervention type, which involved cutting and removal of the woody vegetation, resulted in the largest increase in bee species richness, but the enhanced bee species richness was limited to clearings with forb-dominated vegetation. Importantly, the estimated effects on bee species richness did not differ between models using the predicted, *versus* the empirically observed, plant species composition as predictor, making it possible to produce spatial predictions of the increase in bee richness from implementing different management interventions. *Synthesis and applications:* Combining field surveys with data from field experiments can be used to produce high-resolution maps showing where wild bee habitat enhancement is likely to have the greatest effect. Such maps can inform decisions about where to allocate costly management interventions.

1. Introduction

The effect of habitat management interventions on species and populations depend on site-specific environmental conditions (Batáry, Báldi, Kleijn, & Tschamtké, 2010; McCracken et al., 2015). Tools that enable managers to decide on type of habitat interventions and to prioritize where to implement different interventions are critical, because managers operate with a limited budget. Field experiments in which habitat conditions are manipulated can reveal causal relationships between habitat interventions and population and species level ecological responses. However, field experiments are costly to implement, and consequently, they are typically limited in spatial and temporal extent, and limited to the organisms and environmental conditions that occur in the experimental plots. The limited sample size and extent of experiments can restrict our ability to produce valid spatial predictions of the environmental conditions (e.g. local plant species

composition) that influence the effectiveness of management interventions. Field experiments alone may therefore not be sufficient for producing spatial predictions that can guide habitat management efforts for species of conservation concern.

The conservation of wild bees (Hymenoptera: Anthophila) is gaining widespread attention and multiple countries have recently adopted national strategies for preserving this ecologically important taxon (Senapathi, Goddard, Kunin, & Baldock, 2017; Norwegian Ministries, 2018). Bees constitute a large and ecologically diverse taxon (Michener, 2007; Westrich, 1996) and the reported declines in their diversity (e.g. Biesmeijer et al., 2006; Potts et al., 2010) is therefore likely the result of multiple drivers, each calling for different management strategies. Some threats, such as habitat fragmentation (Carrié et al., 2017), habitat loss (Larsson & Franzén, 2007; Steffan-Dewenter, Munzenberg, Burger, Thies, & Tschamtké, 2002), and competition from managed bees (Herbertsson, Lindström, Rundlöf, Bommarco, & Smith, 2016)

* Corresponding author at: Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway.

E-mail addresses: markus.sydenham@nina.no (M.A.K. Sydenham), stein.moe@nmbu.no (S.R. Moe), katrine.eldegard@nmbu.no (K. Eldegard).<https://doi.org/10.1016/j.landurbplan.2019.103673>

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impact wild bee diversity by restricting the access to, and amount of limiting resources. Improving habitat conditions by increasing the amount of floral or nesting resources within the landscape is therefore central to conserving wild bee diversity.

In agricultural landscapes, agri-environmental schemes that improve the quality of existing habitats are promising instruments to promote wild bee diversity (Batáry, Dicks, Kleijn, & Sutherland, 2015; Hopwood, 2008). In silvicultural landscapes, power line clearings can contain diverse plant communities (Eldegard, Eytayo, Lie, & Moe, 2017; Eldegard, Totland, & Moe, 2015) and provide a promising possibility for creating and maintaining early successional habitats for wild bees (Russell, Ikerd, & Droege, 2005; Russell, Russell, Kaplan, Mian, & Kornbluth, 2018; Sydenham, Moe, Totland, & Eldegard, 2015; Wagner, Ascher, & Bricker, 2014). Although bee habitat management aimed at improving habitat resource availability and diversity generally increases bee diversity (Tonietto & Larkin, 2018), the effectiveness of such habitat interventions depends to a large extent on the environmental context (Batáry et al., 2010; Sydenham, Moe, Stanescu-Yadav, Totland, & Eldegard, 2016) and the experience level of land users and managers [typically land owners, (McCracken et al., 2015)]. Habitat interventions should therefore target sites where their effectiveness is greatest, since funding agencies typically operate on a limited budget (Batáry et al., 2015).

Identifying locations where the environmental conditions make habitat management most effective requires field experiments where the effect of management interventions are tested under different environmental conditions. The relevant environmental conditions may differ between regions and habitat types. In agricultural landscapes, relevant environmental gradients include the amount of resources in the surrounding landscape, both source habitats, from which bees can colonize restored habitats (Batáry et al., 2010; Scheper et al., 2013) and the amount of floral resources (Scheper et al., 2015). In power line clearings transecting forest, a thick layer of woody debris – with a stem diameter too small to be of value for cavity nesting bees – typically cover the ground after manual clearing of the woody vegetation. Sydenham et al. (2016) found that removing the debris, and thereby exposing the bare ground, increased bee species richness, but the effect size increased along a gradient from dwarf shrub to forb dominated plant communities. However useful data from field experiments are, such experiments are costly to operate and therefore typically run on a limited number of sites, making it difficult to predict the effect of management beyond the experimental sites. Predicting the effectiveness of habitat management actions is particularly difficult if important factors that influence the effectiveness cannot be extracted directly from for example land use maps, but depend on local environmental conditions, such as the composition of plants found within the site (Sydenham et al., 2016), or within neighbouring habitat patches (Scheper et al., 2015).

Field experiments documenting that the effectiveness of habitat management vary with environmental conditions are of little practical use if the effectiveness cannot be predicted at spatial scales relevant to managers. A potential solution would be to obtain spatial predictions of the effectiveness of habitat management by combining field experiment data with field survey data. With field experiments we here mean on-site manipulations of habitat conditions with the aim of testing the effect of habitat management interventions on for example bee diversity. With field survey data we mean data collected in the field, along environmental gradients but without the use of experimental manipulation of habitat. If plant composition can be predicted using data from field surveys, then these predictions could potentially be used in combination with the results from field experiments to predict the effect of management measures for bees across the entire region covered by the field survey data. Within our region, the gradient in forb species richness corresponds to a vegetation gradient ranging from dwarf shrub dominated to forb dominated which generally seems to drive bee diversity within power line clearings in our region (Sydenham

et al., 2015). We build upon the work of Sydenham et al. (2016) to test if we could predict the plant community composition within power line clearings and further produce spatial predictions of the effectiveness of removing the woody debris following maintenance clearing for bee species richness.

In this study, we tested if we could combine field survey data of plant communities with data from a large-scale field experiment investigating different habitat enhancement measures to increase plant and bee species richness, to produce spatial predictions of the effectiveness of habitat enhancement measures within power line clearings in SE Norway. Specifically, we tested if: (1) the plant community composition followed the same gradient (from dwarf shrub dominated to forb/shrub dominated) within the 19 sites where the field experiments had been conducted, as within the 51 sites where we had conducted vegetation surveys; (2) the plant species composition shifted from dwarf shrub dominance to forb and shrub dominance along gradients of elevation, terrain ruggedness, solar irradiance, precipitation during the growing season, the density of the surrounding forests, the amount of mires surrounding the sites, site specific productivity, and soil infiltration capacity; (3) the estimated site-specific effectiveness of wild bee habitat management differed between models that were based on the predicted plant community composition and models that were based on empirical data; and (4) if we would be able to identify locations for cost-effective wild bee habitat interventions.

2. Methods

2.1. Plant data collection

In Dataset_{survey}, vegetation inventories were conducted in 51 sites in power line clearings in SE Norway in 2009 and 2010 (Fig. 1A). We recorded the percentage cover of all plant species within four rectangular (5 × 1 m) plant plots placed along the centre of the power line clearing, with a distance of 50 m between neighbouring plots. Each plant plot consisted of five 1 m² subplots. If a species was present in a subplot, but had < 1% cover, it was recorded as 1%. Species that could not be readily identified to species were identified to the genus level. In Dataset_{exp}, field data on understorey vegetation was recorded in another 19 sites in power line clearings in 2013 (Fig. 1A). Each site consisted of three experimental plots; 30 m long and 40–80 m wide, depending on the width of the power line clearing. The experimental plots were located at least 20 m apart. The tree-layer vegetation within the three experimental plots at each site had been subjected to one of three treatments; (a) left Uncut, (b) Cut and left on the ground, or (c) cut and the resulting debris removed (Cut-remove) from the experimental plot [see Sydenham et al. (2016) for details on the experimental set-up]. We recorded the percentage cover of all plant species within nine 1 m² subplots placed in a regular grid pattern within a 10 × 10 m square in the centre of each treatment plot.

2.2. Bee data collection

In Dataset_{exp}, solitary bees had been sampled using three flight interception traps ('window traps') within each experimental plot in 2013 (see Sydenham et al. (2016)). The traps were installed immediately after snowmelt, emptied once per month, and operated throughout the summer before removal in August/September. Given that the individuals were free to move between the habitat treatment plots, we interpret a higher species richness or abundance of bees in one treatment type over the others as a preference for that treatment type by the bees within the local community. Assuming that bees seek to optimize the reward from their activities, the magnitude of this effect (or preference) should be positively related to the potential for increasing the fecundity and fitness (population-level effects) and diversity (species and community-level effects) of the bees within an area.

During the wild bee sampling, wind knocked over some traps and

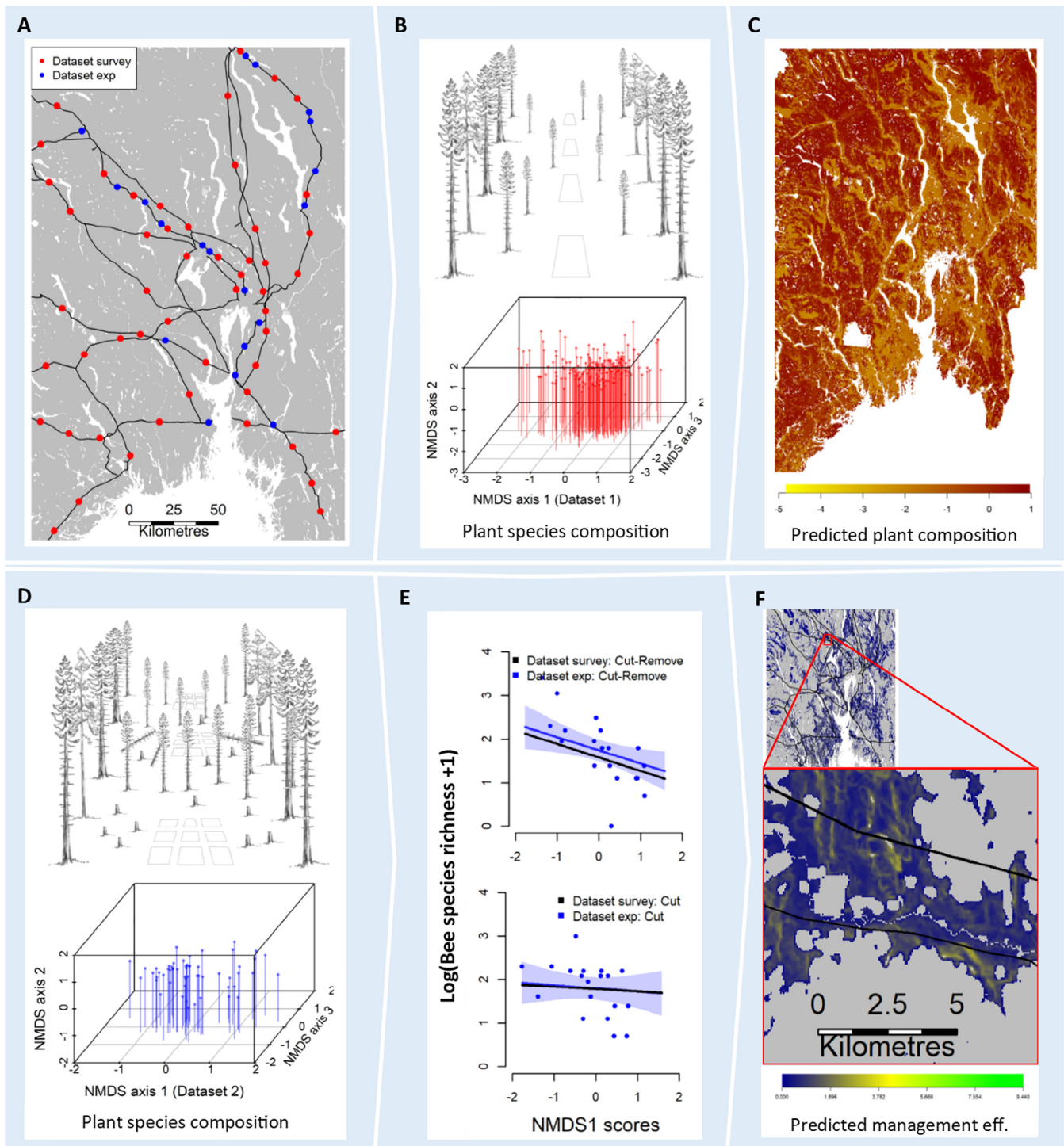


Fig. 1. Graphical summary of the project workflow. (A) The location of study sites within the regional power line grid in SE Norway. (B) Dataset_{survey} consisted of vegetation surveys conducted in four 5 m² plots, located 50 m apart within the 51 study sites (n = 204). We sorted the 204 plots along three NMDS axes of species turnover and (C) predicted the plant species turnover (plot scores on NMDS axis 1) throughout the region. The colour gradient (yellow-red) visualizes the predicted shift from forb to dwarf shrub dominated plant communities. (D) Dataset_{exp} consisted of vegetation surveys conducted in three sets of nine 1 m² plots, spaced at varying distances within the 19 study sites (n = 57). In each set, the nine 1 m² plots were each placed in an experimental unit where the trees had been either: cut, cut and removed or left uncut. We sampled wild bees within each treatment unit. (E) We modelled the species richness of bees as a response of elevation and an interaction between treatment unit type, and NMDS1 scores and compared the slopes between models using the predicted and empirical NMDS1 scores. (F) We predicted the effect of the ‘cut and remove’ treatment compared to the standard maintenance clearing (i.e. ‘cut’) across the entire region, allowing managers to identify where the effectiveness of removing woody debris is likely to be greatest (bright colours on the map). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

consequently the total number of successful collection rounds within treatment plots, ranged from nine to twelve. We therefore standardized the sampling intensity by using the expected abundance of each species within a site given nine trapping rounds. When calculating the standardized species richness per treatment plot we only included species with an expected abundance of at least one individual in one out of nine traps (see [Supplementary material Appendix S1](#) for details on the standardization procedure).

2.3. Environmental variables from digital maps

In order to produce spatial predictions of plant species compositions, we assembled a raster-stack containing environmental variables for use in the predictive modelling process (see [Supplementary material Appendix S2](#) for a detailed protocol). We selected environmental variables that we expected would be related to the growing conditions for plants; sites on low productive soils or at high elevations were dominated by dwarf shrubs whereas sites on high productive soils or at low elevations were dominated by forbs ([Eldegard et al., 2017](#)). The raster-stack contained raster layers with a resolution of 50×50 m for: elevation obtained from [The Norwegian Mapping Authority \(2016\)](#); terrain ruggedness [TRI, ([Hijmans et al., 2016](#))] calculated from the elevation map; monthly mean solar irradiance (IRR) and mean monthly Precipitation (Prec) for each month between May and August obtained from the WorldClim database ([Fick & Hijmans, 2017](#)). We included three raster layers to represent local soil conditions: soil infiltration potential obtained from the [Survey \(2011\)](#); Site specific productivity extracted from the AR50 land use maps obtained from the [Norwegian Institute of Bioeconomy Research \[NIBIO\] \(2007\)](#); and the proportionate area occupied by wetlands within 250 m of each 50 m^2 raster cell. We used a 250 m radius because solitary bee species richness is strongly correlated with the amount of habitat within the landscape at this spatial scale ([Steffan-Dewenter et al., 2002](#)). We calculated the mean tree cover density (TCD) within 250 m of each 50 m^2 raster cell as we expected a high TCD might prevent plant colonisations. We obtained maps on the WET and TCD from [Copernicus Land Monitoring Services \(2018\)](#). The distance to semi-natural grasslands ([Norwegian Environment Agency, 2011](#)) was included as it might influence the colonization potential of plants. Finally, we downloaded spatial data on the stately managed power line grid ([The Norwegian Water Resources and Energy Directorate, 2015](#)). We used the number of sets of pylons with aerial lines within each power line clearing as a proxy for the width of the power line clearing, as previous studies have found power line width to be an important driver of local plant diversity ([Eldegard et al., 2017](#)). Single sets of pylons and aerial lines has a width of 18 m for the high voltage 300 and 420 kV power lines, and the recommended clearing width is 10 m on each side ([Rasjonell Elektrisk Nettvirksomhet AS, 2013](#)), which amounts to a total width of 38 m for single-set clearings. The majority of the regional and distributional power lines in our study region are single-set clearings, but some stretches of the grid has double sets of pylons and aerial lines, and a total width of nearly 80 m.

2.4. Statistical analyses

We used the vegetation survey dataset $\text{Dataset}_{\text{survey}}$ to build predictive models for plant composition ([Fig. 1B, C](#)), and the data from the field experiment $\text{Dataset}_{\text{exp}}$ to validate the predictions (Tests 1 and 2). Thereafter, we tested if the context-dependent effectiveness of habitat interventions on wild bee species richness and abundance was estimated equally well with predicted plant species composition as with the empirical plant species composition (Test 3; [Fig. 1E](#)). Finally, we predicted the context-dependent effectiveness of wild bee habitat interventions within the entire power line grid (Test 4; [Fig. 1F](#)).

We estimated gradients in plant species compositional turnover for both datasets. For $\text{Dataset}_{\text{survey}}$ we used presence/absence data for the

plant taxa ($n = 133$) in each 5 m^2 plot to model differences in plant species composition. We used a non-metric dimensional scaling (NMDS), specified with centring, PC rotation, half-change scaling and step across, to place the 204 plant plots in a three-dimensional space ([Fig. 1B](#)), according to their Jaccard's dissimilarity in plant species composition ([Oksanen et al., 2013](#)). For $\text{Dataset}_{\text{exp}}$, (139 plant taxa) we used an NMDS, with the same specifications as for $\text{Dataset}_{\text{survey}}$, to place the 57 experimental plots in a three-dimensional space ([Fig. 1D](#)).

To test if we had obtained similar gradients in plant species composition for both datasets (Test 1), we tested if the species weighted scores along the NMDS axes from $\text{Dataset}_{\text{survey}}$ and $\text{Dataset}_{\text{exp}}$ corresponded similarly to the functional traits of plants. We first used the function `tnrs` in the `taxize` R package ([Chamberlain & Szocs, 2013](#)) to update the species names for all the recorded plant taxa in both datasets and removed taxa that had only been identified to genera – or for which we could not find accepted species names – resulting in 123, and 139 plant taxa for $\text{Dataset}_{\text{survey}}$ and $\text{Dataset}_{\text{exp}}$, respectively. For both datasets, we used linear regressions to test if the species NMDS scores were related to: the growth form of plants (Dwarf Shrub, Shrub, and Forb); the Ellenberg moisture tolerance; the Nitrogen-tolerance; and the woodiness of plants. The traits of plants were downloaded using the R package `TR8` ([Bocci, 2015](#)) sourcing traits from the `Ecoflora` ([Fitter & Peat, 1994](#)), `Catminat` ([Julve, 1998](#)), and `PLANTS` ([Green, 2009](#)) databases. The woodiness trait contained 15 factor levels, with multiple variations of “semi-woody”. We simplified this trait by renaming all “semi-woody” categories into a single category (i.e. “Semi-woody”). Species that had only been identified to genera or for which we could not retrieve information on specific traits were omitted from the tests. The tests included: 123 and 139 species for growth form; 108 and 107 species for both moisture and nitrogen tolerance; and 111 and 109 species for woodiness, for $\text{Dataset}_{\text{survey}}$ and $\text{Dataset}_{\text{exp}}$, respectively.

To test if the plant species composition shifted from dwarf shrub to forb-dominated along the environmental gradients (Test 2), we built a predictive model for the plant composition (NMDS scores) within power line clearings. We fitted linear mixed effect models (LMM) with the plant plot scores ($n = 204$) from the three NMDS axes from $\text{Dataset}_{\text{survey}}$ as the response variables and with site identities as random effects ($n = 51$). Mixed effect models were fitted using the `lme4` package ([Bates, Maechler, Bolker, & Walker, 2015](#)). We extracted environmental conditions for each plant plot from the environmental raster stack and checked for potential collinearity between variable pairs (Pearson correlation coefficient $r > 0.6$). We used elevation as the only proxy for climatic conditions as it was highly correlated to the monthly estimates of solar irradiance and temperature ($r > 0.7$). For each NMDS axis, we first built a full model containing all environmental variables with a p -value ≤ 0.1 . We reduced the full model by sequentially removing variables until all remaining variables were statistically significant ($p \leq 0.05$) and plotted the estimated regression slopes against the raw data to evaluate if the explanatory variables should be transformed (by e.g. adding a logarithmic term or a second order polynomial term, see [Table 1](#) for the variables and their transformations in the final models). We used likelihood ratio tests to evaluate if transforming the variables improved model fit and plotted the fitted values against the Pearson residuals to ensure that residuals were uniformly distributed. We calculated the marginal (i.e. variance accounted for by the fixed effects) and conditional variance (i.e. the variance accounted for by the fixed effects and the random effects) explained (R^2) by the models ([Barton, 2016](#)). We used the model formulas from the final models, combined with the raster maps of the environmental conditions to predict the NMDS axes scores across the entire region.

We used the 57 vegetation plot scores along the $\text{NMDS}_{\text{Dataset}_{\text{exp}}}$ axes to validate the predicted $\text{NMDS}_{\text{Dataset}_{\text{survey}}}$ scores ([Fig. 1C](#)) by fitting a LMM for each NMDS axis, using the empirical $\text{NMDS}_{\text{Dataset}_{\text{exp}}}$ scores as the response variable and the corresponding, predicted, $\text{NMDS}_{\text{Dataset}_{\text{survey}}}$ scores as a fixed effect variable. We included site identities ($n = 19$) and treatment plot types ($n = 3$) as random

Table 1

Plant species composition within power line clearings (NMDS axes scores from Dataset_{survey}, Fig. 1A, B) was related to local growing conditions, topography and elevation. Changes along NMDS1 reflected a shift from dwarf-shrub to forb dominated plant communities (Fig. 2). PWL width = Power line width (single versus double set of pylons and aerial lines). The variance explained by each model is provided both for the fixed effects alone (R^2_{Marginal}) and for the fixed effects and random effects ($R^2_{\text{Conditional}}$).

Plant community composition (NMDS axis 1 scores)					
Fixed effects	Estimate	SE	t	R^2_{Marginal}	$R^2_{\text{Conditional}}$
Intercept	0.25	0.11	2.27	0.43	0.73
Productivity	-6.58	0.97	-6.76		
Productivity ²	-3.41	1.01	-3.39		
Terrain ruggedness	-0.05	0.02	-2.99		
Random effects		Variance	SD		
Site (n = 51)	Intercept	0.22	0.47		
	Residual	0.19	0.44		
Plant community composition (NMDS axis 2 scores)					
Fixed effects	Estimate	SE	t	R^2_{Marginal}	$R^2_{\text{Conditional}}$
Intercept	0.00	0.04	0.00	0.33	0.56
MASL	-0.24	0.04	-5.77		
Shade	-0.08	0.04	-2.02		
Terrain ruggedness	0.12	0.04	3.01		
Random effects		Variance	SD		
Site (n = 51)	Intercept	0.06	0.24		
	Residual	0.11	0.33		
Plant community composition (NMDS axis 3 scores)					
Fixed effects	Estimate	SE	t	R^2_{Marginal}	$R^2_{\text{Conditional}}$
Intercept	0.06	0.05	1.12	0.03	0.22
PWL width	-0.16	0.08	-1.97		
Random effects		Variance	SD		
Site (n = 51)	Intercept	0.04	0.20		
	Residual	0.17	0.41		

intercept terms to account for site specific and treatment specific variations in NMDS scores.

To test if we could use the predicted plant species composition to model the site-specific effectiveness of wild bee habitat enhancement (Test 3), we ran six models with either the predicted NMDS1_{Dataseurvey} or the true NMDS1_{Dataseexp} scores as a fixed effect term. In the first two models, we used the standardized bee species richness as the response variables. In the third and fourth models, we used the standardized bee abundances as response variables. In the fifth and sixth models we ran the models on bee abundances but excluded Ericaceae specialists (*Andrena fuscipes*, *A. lapponica*, and *Colletes succinctus*), as these species differ in their foraging habitats from the remaining solitary bee species within our study system, and prefer habitats dominated by dwarf shrubs (particularly Ericaceae) which are typically characterized by having a low diversity of forbs (Sydenham et al., 2015). In all six models, we used site identity as a random effect, and log(y + 1) transformed the response variable to achieve normally distributed residuals.

We tested if the regression slopes differed between models using the NMDS1_{Dataseurvey} versus the NMDS1_{Dataseexp} scores. We first created a new data frame that included a dummy variable for the Dataset identity (DatasetID). We then refitted a LMM using the same response variables as in the original models and the site identity as a random intercept and used likelihood ratio tests to test if the interactions DatasetID_{Dataseurvey} or DatasetID_{Dataseexp} × NMDS1_{Dataseurvey} or DatasetID_{Dataseexp} × Cutting regime, and DatasetID_{Dataseurvey} or DatasetID_{Dataseexp} × Elevation were statistically significant.

We predicted the context-dependent effectiveness of wild bee

habitat management within the entire power line grid by using the bee species richness model obtained by NMDS1_{Dataseurvey} in combination with treatment type and elevation (Test 4). We predicted the expected number of bee species given each of the three experimental treatments: Cut and Remove; Cut; and Uncut and back-transformed these predictions onto the measurement scale. We then subtracted the predicted number of species given Cut and Remove from the predicted number of species given Cut and Uncut, since Cut and Remove has been shown to attract more bees to the treatment plots, than the other treatments (Sydenham et al., 2016). All analyses were conducted using R (R Core Team, 2018).

3. Results

We were able to identify the same gradient in plant species composition in both Dataset_{survey} and Dataset_{exp} (Fig. 2A–F). The NMDS-analysis separated the 204 plant plots from Dataset_{survey} along three NMDS axes (Fig. 1B, stress = 0.14, linear fit $R^2 = 0.92$). NMDS1_{Dataseurvey} separated sites according to the dominance by plants, such as forbs and shrubs that depended on fertile soils (Fig. 2A–C). The NMDS analysis of the plant plots from Dataset_{exp} (Fig. 1D, stress = 0.12, linear fit $R^2 = 0.92$) yielded a primary gradient (NMDS1) with the same interpretation as the ones retrieved from Dataset_{survey} (Fig. 2D–F). By contrast, the plant scores along NMDS2 and NMDS3 were less clearly related to the functional traits of plants in both Dataset_{survey} (Appendix S3 Figs. S1A–L) and Dataset_{exp} (Appendix S4 Figs. S2A–L).

Our model predicted a shift towards forb dominated plant communities (Table 1, i.e. decrease in NMDS1_{Dataseurvey} scores) as the site productivity index (df = 2, $\chi^2 = 46.9$, $p < 0.001$) and terrain ruggedness increased (df = 1, $\chi^2 = 9.0$, $p = 0.003$). The predicted NMDS1_{Dataseurvey} was related to scores along NMDS1_{Dataseexp} (Table 2, df = 1, $\chi^2 = 16.1$, $p < 0.001$). Scores along NMDS2_{Dataseurvey} decreased with elevation (df = 1, $\chi^2 = 26.7$, $p < 0.001$) and the shade index (df = 1, $\chi^2 = 4.1$, $p = 0.042$) and increased with terrain ruggedness (df = 1, $\chi^2 = 8.9$, $p = 0.003$). Scores along NMDS3_{Dataseurvey} were related to the width (i.e. single or double set of aerial lines) of the power line clearing (df = 1, $\chi^2 = 3.9$, $p = 0.049$) so that plots within wide clearings had lower NMDS scores than plots within narrow ones. However, this relationship was rather weak ($t = -1.97$). While the predicted NMDS scores along NMDS2 was not related to the values from the corresponding NMDS axes obtained from Dataset_{exp} (df = 1, $\chi^2 = 2.4$, $p = 0.12$) scores along NMDS3 were (df = 1, $\chi^2 = 8.1$, $p = 0.01$, Appendix S5 Table S1).

The predicted NMDS1_{Dataseurvey} scores captured the context dependent effectiveness of the three cutting regimes on solitary bee species richness (Table 3, Fig. 4). The term NMDS1_{Dataseexp} × Treatment (df = 2, $\chi^2 = 7.4$, $p = 0.025$) showed that as the NMDS1_{Dataseexp} scores of the treatment plot increased, the number of species sampled in the Cut-Remove treatment plots decreased at a higher rate than within the two other treatment categories (Cut and Uncut). Substituting the NMDS1_{Dataseexp} variable, with the NMDS1_{Predicted} variable resulted in a model for solitary bee species richness with similar regression slopes as when running the model with the NMDS1_{Dataseexp} (Fig. 4, Table 3). We found a similar context dependent effect when running the models on solitary bee abundance (Appendix S6, Table S2). However, neither the NMDS1_{Dataseexp} × Treatment (df = 2, $\chi^2 = 4.9$, $p = 0.087$) nor the NMDS1_{Predicted} × Treatment (df = 2, $\chi^2 = 3.3$, $p = 0.19$) terms were statistically significant. When the Ericaceae specialists were excluded, the NMDS1_{Dataseexp} × Treatment interaction (df = 2, $\chi^2 = 6.9$, $p = 0.033$) showed that the number of individuals attracted to the Cut-Remove treatment plots decreased from a higher initial abundance and at a higher rate than in the other two treatment categories when the NMDS1_{Dataseexp} score increased. A similar trend was found when substituting the NMDS1_{Dataseexp} variable with the NMDS1_{Predicted} variable, but in this case the NMDS1_{Predicted} × Treatment interaction was not statistically significant (df = 2, $\chi^2 = 4.7$, $p = 0.094$). Elevation was

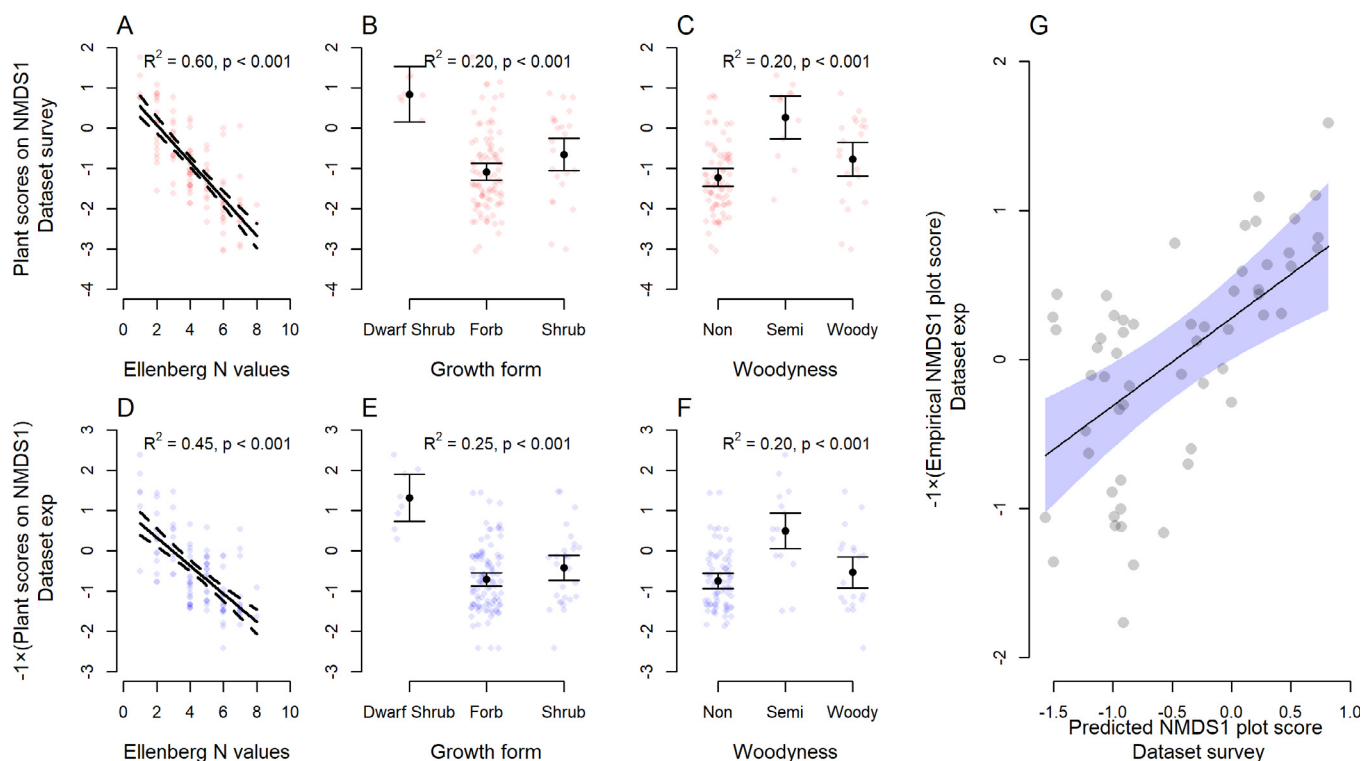


Fig. 2. The first NMDS axis in Dataset_{survey} and Dataset_{exp} separated sites along a gradient in site productivity. Plant scores on NMDS1_{Dataset_{survey}}, were (A) negatively correlated to the nutrient dependencies of plants and plants with low scores were typically (B) forbs and (C) non-woody. (D–F) Plant scores on NMDS1_{Dataset_{exp}} showed similar relationships to species traits. (G) The predicted NMDS1_{Dataset_{survey}} plot scores, were correlated with the empirical NMDS1_{Dataset_{exp}} scores. NMDS1_{Dataset_{exp}} axis scores were multiplying by minus 1 to align them with the NMDS1 scores from Dataset_{survey}.

Table 2

Validation of the prediction from Dataset_{survey} (Fig. 1C). The predicted plant community composition, i.e. scores along NMDS1, was compared to the corresponding NMDS1 scores obtained from the plant plots in Dataset_{exp}. The model was fitted using a linear mixed effects model with Site and Treatment (i.e., type of habitat enhancement) as random intercepts.

Fixed effects	Estimate	SE	t	R ² _{Marginal}	R ² _{Conditional}
Intercept	-0.28	0.14	-2.01	0.32	0.79
NMDS1 _{Predicted from dataset_{survey}}	-0.59	0.13	-4.39		
Random effects		Variance	SD		
Site (n = 19)	Intercept	0.23	0.48		
Treatment (n = 3)	Intercept	< 0.01	0.06		
	Residual	0.10	0.32		

retained in all models ($P < 0.05$); species richness and abundance decreased with elevation (Tables 3 and S2, Fig. 4). There were only slight differences in the parameter estimates when using the predicted NMDS1 scores compared to when we used the NMDS1 scores from Dataset_{exp} to model the context dependent effect of the cutting regimes on bee species richness and abundance. These differences were not large enough for the estimated relationships to differ significantly between the two sets of models (Table 4). The most similar parameter estimates were obtained for the models with $\log(\text{species richness} + 1)$ as a response variable (Fig. 4). We therefore used the $\log(\text{species richness} + 1)$ model, with the predicted NMDS1_{Dataset_{survey}} scores to predict the effectiveness of wild bee habitat management within power line clearings across the entire region (Figs. 3 and 4).

4. Discussion

In order to achieve the goals of the national pollinator strategies (Norwegian Ministries, 2018; Senapathi et al., 2017) and conserve wild bees in intensively managed landscapes, the quality of existing potential habitat patches will have to be improved. The fact that the effectiveness of habitat improvement schemes on bee diversity depends on the environmental context (Scheper et al., 2013; Sydenham et al., 2016) calls for decision-making tools for optimizing the effectiveness of wild bee habitat management. Our findings demonstrate how combining spatial predictions of site-specific environmental conditions (i.e., plant species composition), obtained from field surveys, with the causative power obtained from field experiments, can identify areas where habitat improvement schemes will be most effective (Figs. 1 and 4).

The effectiveness of the Cut-Remove intervention (Figs. 3 and 4) increased with site productivity (decreasing NMDS1 scores). This context dependent effect (difference between Cut-Remove and Cut) was slightly underestimated (lower intercept in Fig. 3D) when using the predicted NMDS1 scores (from Dataset_{survey}), as compared to the empirical NMDS1 scores (from Dataset_{exp}). Our proposed management map is therefore likely to be slightly conservative. However, we believe that most managers would view this as a beneficial attribute of a management tool. In mountainous regions and at high latitudes, productive soils are generally scarce and confined to lowland areas. These productive areas are typically used for agriculture, and have lost important wild bee habitats, such as semi-natural grasslands (Öckinger & Smith, 2007), due to agricultural intensification (Fjellstad & Dramstad, 1999; Ollerton, Erenler, Edwards, & Crockett, 2014). Large semi-natural elements in these landscapes mainly consist of production forests which, except in the earliest successional stages after logging (Rubene, Schroeder, & Ranius, 2015; Taki et al., 2013), are of little habitat value for wild bees. In such landscapes, power line clearings provide continuous stretches of land in early-mid successional stages (Eldegard

Table 3

The context dependent effectiveness of different habitat enhancement types (Cut-Remove, Cut, or Uncut) on the species richness of wild bees was modelled equally well by the predicted plant species compositions (NMDS1 scores from Dataset_{survey}, Fig. 1C) as by the NMDS1 scores obtained from field data collection of plant community composition within the treatment (Cut-Remove, Cut, or Uncut) plots (from Dataset_{exp}, Fig. 1D).

Effectiveness of habitat enhancement						
Fixed effects	Estimate	SE	t	R ² _{Marginal}	R ² _{Conditional}	
Intercept (Uncut)	1.40	0.13	10.88	0.40	0.74	
NMDS1 _{Predicted}	-0.02	0.12	-0.15			
Cut-Remove	0.33	0.12	2.74			
Cut	0.40	0.12	3.31			
Elevation	-0.32	0.11	-2.86			
NMDS1 _{predicted} × Cut-Remove	-0.27	0.12	-2.34			
NMDS1 _{predicted} × Cut	-0.11	0.13	-0.84			
Random effects		Variance	SD			
Site (n = 19)						
Intercept		0.18	0.42			
Residual		0.14	0.37			
Effectiveness of habitat enhancement						
Fixed effects	Estimate	SE	t	R ² _{Marginal}	R ² _{Conditional}	
Intercept (Uncut)	1.40	0.12	11.59	0.45	0.73	
NMDS1 _{Datasetexp}	-0.01	0.12	-0.04			
Cut-Remove	0.35	0.12	2.95			
Cut	0.38	0.12	3.09			
Elevation	-0.32	0.10	-3.07			
NMDS1 _{Datasetexp} × Cut-Remove	-0.32	0.12	-2.66			
NMDS1 _{Datasetexp} × Cut	-0.14	0.13	-1.10			
Random effects		Variance	SD			
Site (n = 19)						
Intercept		0.14	0.37			
Residual		0.14	0.37			

Table 4

The estimated context dependent effectiveness of wild bee habitat management (NMDS1 score × Treatment interaction term) did not differ between models using the predicted (Dataset_{survey}) or the locally measured (Dataset_{exp}) environmental context. Results from likelihood ratio tests.

Log(Bee species richness + 1)	D.f.	χ ²	P
DatasetID × Elevation	1	0.005	0.94
DataSetID × NMDS1score × Treatment	2	0.083	0.96
Log(Bee abundance + 1)			
DatasetID × Elevation	1	0.008	0.93
DataSetID × NMDS1score × Treatment	2	0.120	0.94
Log(Bee abundance Excl. Ericacea specialists + 1)			
DatasetID × Elevation	1	0.001	0.98
DataSetID × NMDS1score × Treatment	2	0.144	0.93

et al., 2017), and are of potential high value for pollinating insects such as wild bees (Hill & Bartomeus, 2016; Russell et al., 2005; Sydenham et al., 2015). Power line clearings in these productive areas may be of particularly high importance to bees if they are managed correctly through e.g. integrated vegetation management (Russell et al., 2018) or by exposing the ground by removing woody debris after maintenance clearing (Sydenham et al., 2016). Our findings demonstrate how spatial prediction maps can be used to identify priority areas within the power line grid (Fig. 1) where wild bee habitat enhancement is likely to have the greatest effect.

When evaluating the effectiveness of habitat management one should bear in mind that the effect of restoring or improving habitats can be delayed if the restored habitat patch is isolated from potential source habitats. In agricultural landscapes, for example, the effectiveness of habitat management has been shown to be greatest if the landscape contains source habitats from which bees can recolonize improved habitat patches (Batáry et al., 2010; Scheper et al., 2013). However, even in intensively managed landscapes, wild bee communities in restored habitat patches may ‘mature’ over time as less-mobile,

habitat specialists find their way and colonize the restored habitat patch (Kremen & M’Gonigle, 2015). Thus, habitat management schemes should define the goal of implementing management actions. If the aim is to secure the long-term viability of bee populations at a regional scale, then it might be a reasonable strategy to restore isolated habitat fragments, so that they may act as stepping stones between existing semi-natural habitat patches (Menz et al., 2011). Such a management plan might include areas where the immediate effect of habitat restoration is modest. By contrast, if the aim is to rapidly bolster bee populations, or for a landowner to direct her efforts to the area(s) where they will have the largest local effect of bee diversity, then management plans should target areas where the immediate effect is predicted to be greatest. In these cases, the modelling approach we have used here may provide a valuable guide for obtaining the desired effects of habitat management in a cost-efficient way.

Predicting the effectiveness of habitat management may be easiest in ecosystems with relatively steep environmental gradients. In boreal forests the gradient from low productive soils, dominated by dwarf shrubs, to intermediate to high productive soils dominated by forbs and shrubs (Eldegard et al., 2017) is fairly distinct and not strongly associated with specific plant species. It may be more difficult to predict factors that determine the management effectiveness in agricultural landscapes, such as the diversity of late flowering forbs in the surrounding landscape (Scheper et al., 2015), because forb diversity in grasslands depends on both local environmental conditions and on the management history of neighbouring areas (Gustavsson, Lennartsson, & Emanuelsson, 2007; Winsa, Bommarco, Lindborg, Marini, & Öckinger, 2015). Obtaining valid predictions in agricultural landscapes may therefore require more extensive field surveys than within power line clearings. Our spatial predictions should therefore not be used outside power line clearings, or in other regions, unless these predictions can be validated using independent empirical data from e.g. species occurrence records. Online repositories of species occurrence records such as the Global Biodiversity Information Facility ([GBIF], Edwards, Lane, & Nielsen, 2000) contain numerous recordings of species occurrences and

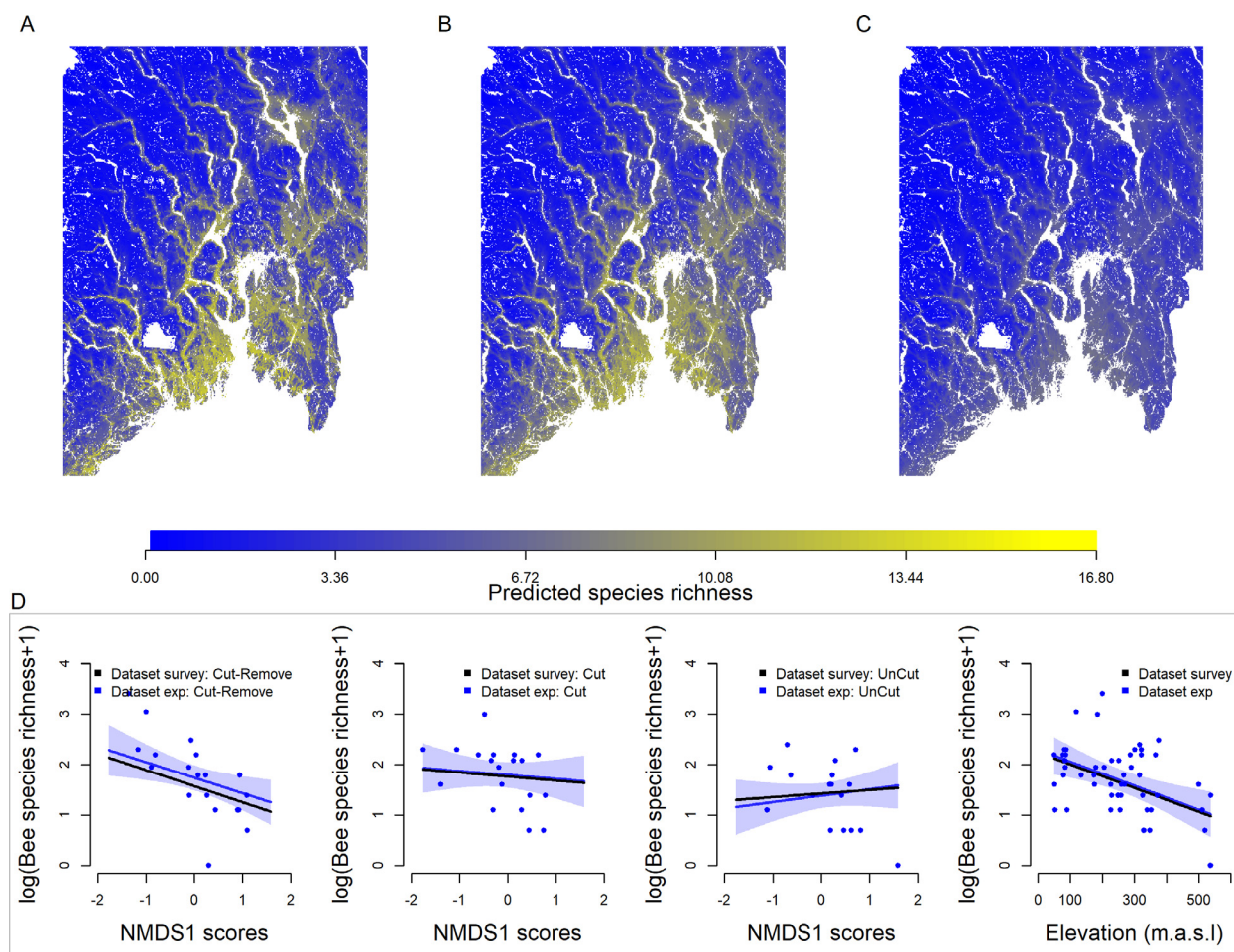


Fig. 3. The predicted bee species richness in plots managed by (A) ‘Cut-Remove’, (B) ‘Cut’, and (C) ‘Uncut’. (D) The effectiveness of ‘Cut-Remove’ was greatest in productive sites (low NMDS1 scores) and species richness decreased with elevation. The predicted species richness (A–C) from the model was back-transformed from the log-scale before plotted on the maps. The colour gradient (blue–yellow) visualize the predicted gradient in bee species richness given the three habitat management intervention types. Note that the estimated relationships between $\log(\text{Bee species richness} + 1)$ and NMDS1 scores are nearly parallel when using the NMDS scores from $\text{Dataset}_{\text{survey}}$ and $\text{Dataset}_{\text{exp}}$ but that the intercept is slightly lower when using the predicted NMDS1 scores from $\text{Dataset}_{\text{survey}}$ (treatment ‘Cut-Remove’). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the development of predictive modelling techniques, using species occurrence data from for example GBIF, is a rapidly developing field of research and models are constantly being refined (D’Amen, Rahbek, Zimmermann, & Guisan, 2017).

In contrast to local scale environmental conditions such as forb diversity, other determinants of the effectiveness of wild bee habitat management in agricultural landscapes, such as the amount of semi-natural grasslands in the surrounding landscape (Batáry et al., 2010) can be obtained from land use maps. Whenever possible, ecologists should aim to specify their ecological models so that they can predict across the landscape. In addition to providing managers with tangible predictions that they can use when deciding where to allocate management efforts, such predictions will also allow other ecologists to compare the predictions to their own models and thus potentially strengthen our understanding of fundamental ecological processes (Houlahan, McKinney, Anderson, & McGill, 2017).

5. Conclusions

Managers often operate with a limited budget for implementing conservation schemes and consequently they need tools for identifying areas where habitat improvement measures will be most efficient. One such tool is spatial prediction maps with a relevant resolution – like the one we have produced for bees in this study. Such maps can be used to

prioritize where to implement costly management interventions. Moreover, by providing predictions of the expected effect of any habitat improvement, it will be possible to validate the predictions in future studies (Houlahan et al., 2017) and further refine ongoing management schemes.

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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.2019.103673>.

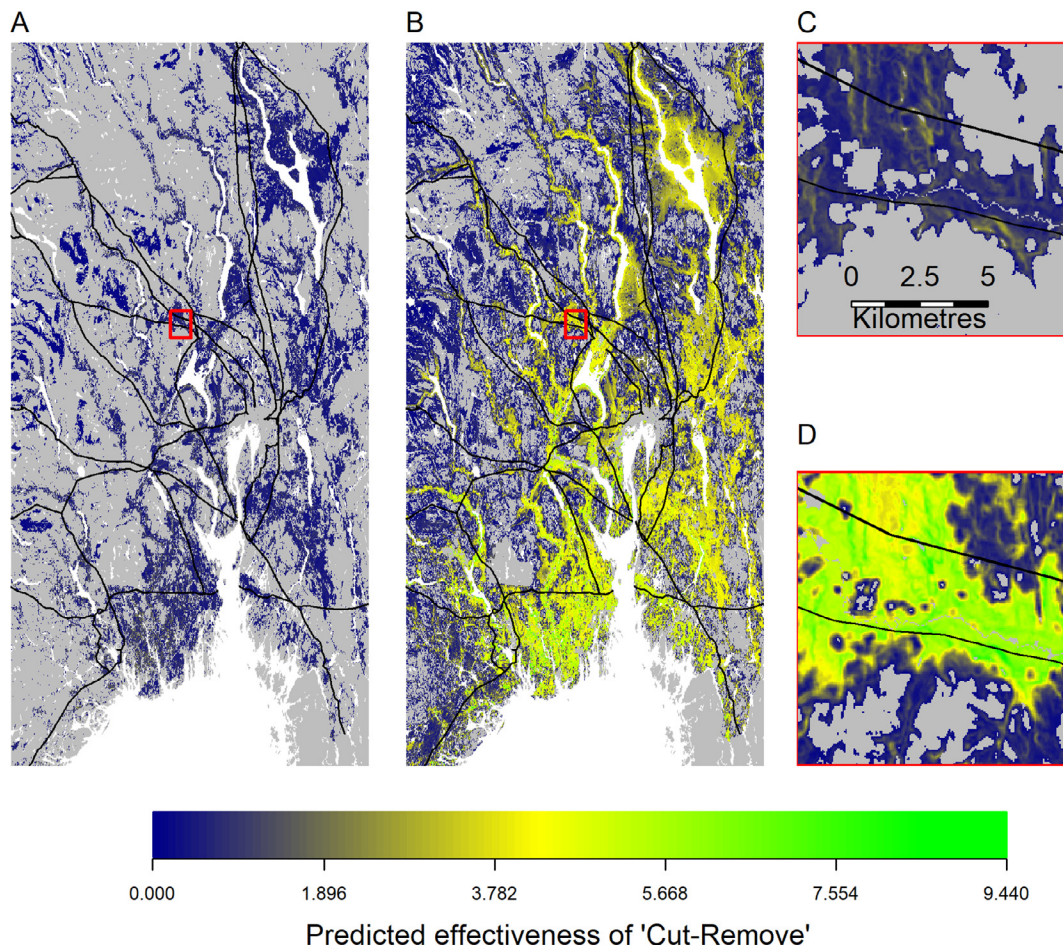


Fig. 4. The predicted difference in bee species richness between power line clearings subjected to: the (A) 'Cut-Remove' vs. 'Cut' treatments; and (B) the 'Cut-Remove' vs. 'Uncut' treatments. The effectiveness is illustrated by the colour gradient, with an increasing positive effect size (i.e., increased species richness) along the blue-green colour gradient. Subplots show the expected increase in species richness gained from the 'Cut-Remove' treatment compared to (C) 'Cut' and (D) 'Uncut', at fine spatial scales. Only areas where the 'Cut-Remove' treatment had a higher predicted species richness are shown in colour. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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