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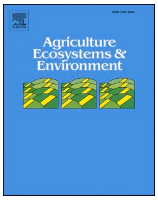

Wild bee responses to cropland landscape complexity are temporally-variable and taxon-specific: Evidence from a highly replicated pseudo-experiment

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ABSTRACT

Wild bees may benefit from the restoration of natural areas in agricultural regions. The abundance and diversity of wild bee species responds to the amount of nesting and foraging habitat, but it is less clear how the distribution of these resources (e.g., the landscape complexity) may affect bees. We implemented a pseudo-experiment to disentangle the effects of three components of landscape complexity for wild bees in a Canadian Prairie cropland region. We used an algorithm to identify 146 sites that minimized correlations in indices of patch richness (i.e., the diversity in land cover types) and contagion (i.e., their degree of interspersion), and that collectively captured a cross-section of landscape contexts that differed in the relative proportion of cropland to other non-crop land covers. We trapped bees at these locations repeatedly over time (1119 unique collection events; equivalent to 10,471 trap-days over two consecutive years), identifying 22,493 bees of 213 taxa, in order to model trends for bees at different times of the season. We found that increasing patch richness may support a greater number of bee taxa, but individual bee taxa varied considerably in their response to components of landscape complexity. The effect on the total abundance of wild bees was temporally-variable, with the amount of cropland positively associated with abundance earlier in the season when mass-flowering crops are in bloom, and negatively later in the season when semi-natural areas are likely to provide the most forage. The response of bee abundance to contagion also varied temporally, and demonstrated a “humped” effect later in the growing season, suggesting there is an optimum in the complementary resources provided by adjacent habitat types. Our study shows that increasing the amount or diversity of non-crop land covers in this region is not likely to have a consistent effect for the majority of species across the season. We argue that modifying croplands to support wild bees is likely to be a complex task, requiring study of the functional responses to landscape of bee species present in the region, and their interactions with the phenological variability in resources.

1. Introduction

Land use change for agriculture has been recognized as a major cause of biodiversity decline, impacting both terrestrial and freshwater habitats (Dalu et al., 2017; Kleijn et al., 2009; Tubiello et al., 2015). Recent assessments of biodiversity loss have called for more than 20% of working landscapes to be reserved for nature (Garibaldi et al., 2020). In croplands, biodiversity objectives may be achieved by retaining or restoring habitat, such as semi-natural vegetation, or restricting field expansion into existing natural or semi-natural areas (Corlett, 2016; Galpern and Gavin, 2020).

Wild bees are in decline globally (Koh et al., 2016; Zattara and Aizen, 2021), and their status in agriculturally-intensive regions has been the subject of many biodiversity studies. Research in croplands has often focused on how changing landscape composition (i.e. the relative areas of different land covers) can support bee populations (Kennedy et al., 2013; Landis, 2017; Martin et al., 2019; Senapathi et al., 2017). Studies generally agree that increasing the amount of floral and nesting resources and diversifying land covers is likely to support a larger and more diverse wild bee community by providing nesting and foraging niches that match the needs of more species (Carrié et al., 2012; Kennedy et al., 2010). However, the benefit of making landscapes more

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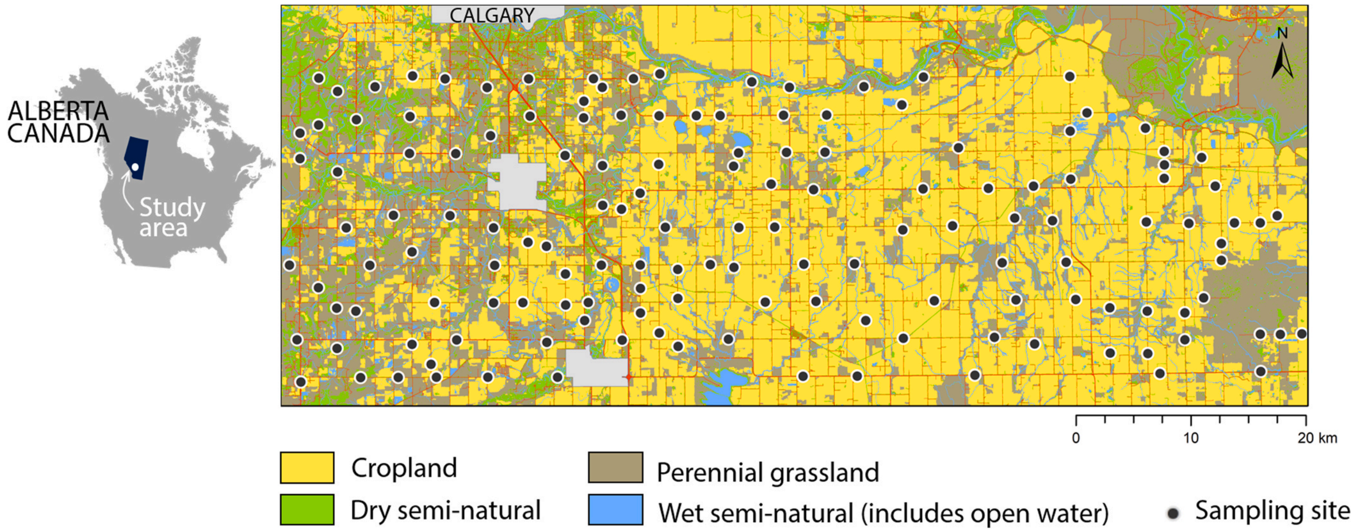

Fig. 1. The 80 × 40 km study area near Calgary, Alberta, Canada is dominated by annual cropland and perennial grassland (typically pasture). Much of the remaining land cover is semi-natural vegetation classified here in terms of its association with dry or wet locations, a distinction that may be functional for both bees and farmers. Circles are wild bee trapping sites (N = 146) on the vegetated verges of low-traffic roads and tracks (red lines). This map is visualized, here, at a coarse resolution that may have obscured fine-scale heterogeneity near each site.

complex in the spatial distribution of resources has been less clear. For example, increasing the amount of non-crop or semi-natural habitat, or improving the quality of existing habitat have been associated with higher bee diversity and abundance (e.g., Bukovinszky et al., 2017; Carrié et al., 2018; Hopfenmüller et al., 2014; Olynyk et al., 2021; Steckel et al., 2014). Diversity in the types of non-crop habitat have also been positively associated with bee diversity (e.g., Aguirre-Gutiérrez et al., 2015; Kennedy et al., 2010; Martins et al., 2015; Senapathi et al., 2017). Similarly, differences in the proximity of different types of habitat, sometimes characterized as a higher density of edges between different types of land cover, or alternatively, as the amount of aggregation of high-quality habitat, have been linked to higher bee diversity and abundance (e.g., Hopfenmüller et al., 2014; Senapathi et al., 2017). However, trends across arthropod groups have varied considerably (Martin et al., 2019). Edges (i.e., areas of transition between fields and non-crop land covers) may have less soil disturbance than inside cultivated fields, and support floral and nesting resources that are found in neither of the land covers, and therefore meet the niche requirements for many ground-nesting bees. Adjacent but contrasting land covers may also provide complementary resources, allowing bees to access both at less energetic expense; for example, exposed soil that provides a nesting substrate in proximity to a grassland hosting multiple species of wildflower. In this regard, it has been hypothesized that there should be an intermediate optimum in abundance that depends on the relative fraction of land covers providing complementary resources and the degree to which those covers interface (Martin et al., 2019). In landscapes where one land cover dominates, access to the others may require bees to fly further, implying that there is a particular configuration of these covers that may provide complementary resources at lower cost.

An important complication in recent findings is that the response of bee species to landscape gradients may depend on functional traits such as social or solitary life history, degree of floral specialization, nesting site preference, or dispersal and overwintering behaviour (Coutinho et al., 2018; Main et al., 2019; Martin et al., 2019; Martins et al., 2015). Therefore, changes to landscape conditions may favour some species and disadvantage others, making directional predictions for the entire bee community challenging, and complicating the conservation of multiple species simultaneously. For example, replacing cropland land covers that are dominant in shrubby vegetation with grasses and forbs may favour ground-nesting species that require exposed soil substrates, but support fewer cavity-nesting species.

Although habitat heterogeneity in cropland-dominated landscapes is likely to be a driver of bee abundance and diversity (Carrié et al., 2018; Kennedy et al., 2013), the relative importance of diversity in resource types, their proximity and interspersion and the relative proportion of cropland to other non-crop land covers remains uncertain. Studies have been challenged to separate these relationships for any arthropod, in part because the variables are often correlated across cropland sampling sites (Duflot et al., 2017; Martin et al., 2019). The phenology of bees presents another challenge (Neumüller et al., 2020) because species may be active for only a few weeks each year (e.g., Stemkovski et al., 2020). Further, differences in the flowering periods of plants favoured by different bee taxa (e.g., Kudo and Ida, 2013), and the presence of mass-flowering crops (e.g., Galpern et al., 2017), suggest that sampling throughout the flight season, and perhaps across years, may be necessary to confidently assess bee-landscape relationships. Finally, landscape conditions are typically measured from land cover data that broadly describe vegetation and land use. These may not be aligned with the resource needs of wild bee taxa (Fahrig et al., 2011) nor with how land managers may choose to implement changes. Thus, adjustments to how land cover is classified may improve interpretability.

Here, we addressed these challenges by using a pseudo-experimental design (Fahrig et al., 2011; Pasher et al., 2013), highly replicated across space and time, to investigate contrasting strategies for supporting wild bee communities in agricultural landscapes. Our design was intended to disentangle the contributions made by resource type diversity and interspersion, while controlling for the relative proportion of cropland. We sampled to capture a broad range of landscape conditions across the season, and with sufficient effort to model the responses of individual bee species. We also adopted a simplified functional representation of landscape in an attempt to describe its habitat value for wild bees (Fahrig et al., 2011) balancing functionality for land-use decision--makers who may implement these findings.

We tested three predictions motivated by the findings of earlier studies. The first, related to diversity in resources, was that more bee taxa (P1a), and a greater aggregate number of bees of any taxa (P1b), will be supported when a greater number of land cover classes are present. A second prediction, related to landscape complementation, was that landscapes where patches of land cover are complex in shape or distribution, such that they are interspersed and their edges interface more often, will lead to higher bee diversity (P2a) and total bee abundance (P2b). Finally, to assess taxon-specific responses and the

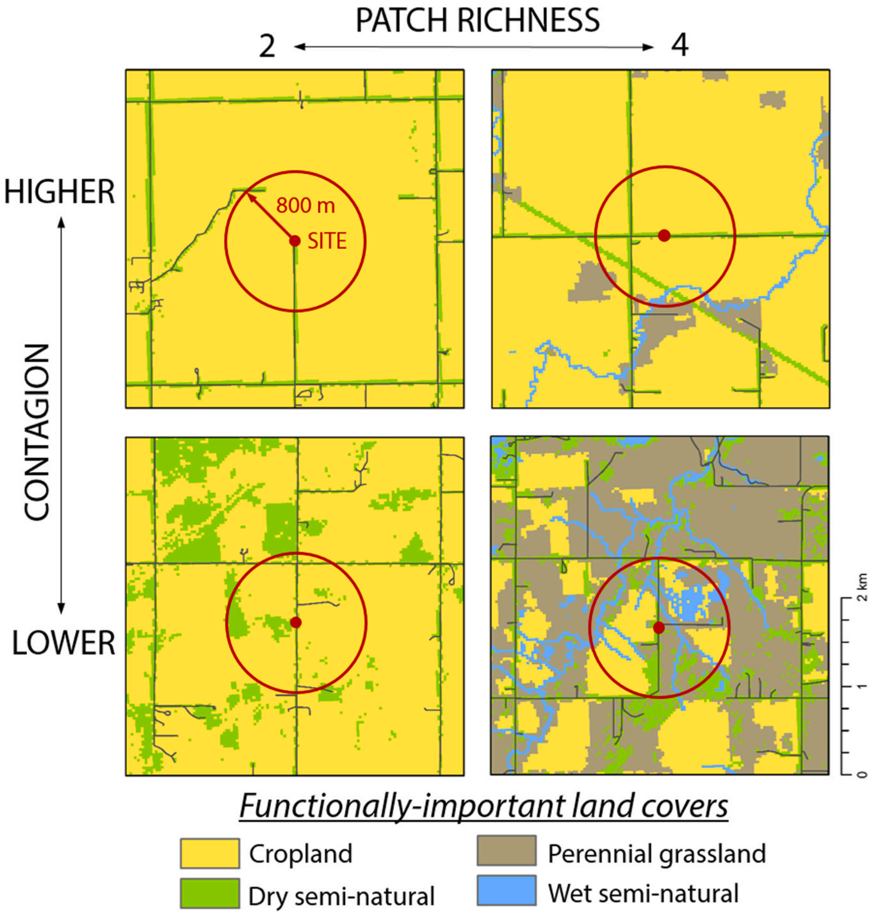

Fig. 2. The experimental design illustrated using four contrasting sites that were sampled in this study. All sampling sites were algorithmically-selected to test the independent contributions of patch richness and contagion landscape metrics. These variables were measured on a thematic map reclassified to represent land covers considered to be functionally important for wild bees (see Fig. 1). Patch richness is a count of the number of land cover classes within 800 m of the sampling site, while contagion describes their interspersion (or dispersion). At most sites in this study contagion captures the interspersion of cropland with one or more of the three other land cover classes (i.e. top row; bottom left).

possibility of applying landscape changes that support multiple species, we also asked if changes to these aspects of complexity were associated with parallel directional changes in abundance across the majority of bee species. We predicted that a higher richness of land cover classes, or more edge interface among different classes, should both correspond to numerical increases for more than half of the taxa sampled (P3).

We tested these predictions in the Canadian prairies by trapping bees at cropland locations algorithmically determined to provide contrasts between land cover diversity and interspersion, and by sampling longitudinally across the flight season in two consecutive years.

2. Materials and methods

2.1. Land cover diversity and interspersion

The study was conducted in Southern Alberta, Canada (50.663°N, 113.483°W; Fig. 1), an agriculturally intensive region where annual grain cropping and pasture are the dominant land uses. Wheat, barley and canola, a mass-flowering crop are the most frequently planted. Non-agricultural land covers are sparsely distributed and found in association with field edges, roadside verges and water features where they host native and introduced grasses, wildflowers, shrubs and less commonly trees.

We developed a functional map of the landscape (i.e. one that describes bee habitat) for measuring land cover amounts, land cover diversity and land cover interspersion. Spatial data for all major classes of land cover, some of which were available in high-resolution vector formats, were rasterized at 30 m resolution for a focal region (80 km x 40 km study area) and clustered into four new classes (Table S1; Fig. 1). Agricultural land covers were reclassified as: (1) cropland or (2) perennial grasslands. Two non-agricultural classes were used to contrast dry and wet semi-natural sites as follows: (3) roadside verges, field margins, shrub and forest patches were classified as dry semi-natural; (4) wetlands, permanent and intermittent stream courses were classified as wet semi-natural. These four classes were intended to capture distinctive vegetation and soil disturbance regimes in the region that may be functionally important for wild bee populations (i.e., the classes differ in the availability and continuity of flowers, or in tillage frequency and soil condition that could affect ground-nesting species). Additional thematic subdivisions in land cover were not used, as these were determined to capture isolated, small footprint land covers that are rare in this grassland landscape, one that has few trees to create structural complexity in habitat. Roads are the predominant non-crop human footprint and have verges that overlap considerably in vegetation and substrate conditions with the semi-natural grasslands found in fields (P. Galpern, unpublished data). We opted for four classes to represent the most distinctive functional contrasts in habitat for bees, and to create a schema that may also be functional for farmers who will make the land use decisions that affect bee populations. Farmers in this region who may apply findings from this study will be familiar with the contrast between wet and dry semi-natural land covers and perennial grasslands and treat these classes differently in practice. For example, wet semi-natural sites typically require drainage before they can be converted to cropland, dry semi-natural sites may require some clearance of woody vegetation before conversion, and perennial grasslands may be least costly to cultivate or restore.

We used patch richness, a count of land cover classes, to measure land cover diversity (i.e. 1, 2, 3 or 4). The interspersion (or dispersion) among land cover classes was measured using contagion (0–100%), an index that is inversely related to the density of edges among patches of different classes, where 0% indicates that the patch classes are maximally disaggregated, and 100% that they are maximally aggregated. The index was calculated as follows:

$$CONTAGION = \left[1 + \sum_{i=1}^{m}\sum_{k=1}^{m}\left[(P_i)\left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}}\right)\right]\left[\ln P_i\left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}}\right)\right]\right] \times 100$$

where P_i gives the proportion of the landscape occupied by patch class i, g_{jk} is the number of adjacencies between pixel of patch classes i and k, and m is the number of patch classes (McGarigal et al., 2012). We also measured cropland area to capture the dominance of cropland at the site, as it is likely to be inversely proportional to the amount of non-crop resources available to bees given the frequent soil disturbance and short-lived forage provided by this land cover (Galpern et al., 2020; Galpern and Gavin, 2020). It was therefore used as a covariate to model the effect that resources provided by semi-natural areas may have on the diversity and abundance of bees. While mass-flowering crops (particularly canola; *Brassica napus*) that provide short-lived nectar resources for some bee species are frequently planted (Galpern et al., 2017; bloom varies annually; approx. June 24 to July 20), their distribution is relatively even across the study area (Agriculture and Agri-Food Canada, 2015), implying the use of cropland area as a metric is likely to have consistent performance spatially as a negative correlate of resources provided by non-crop land covers. We calculated landscape metrics using Fragstats (McGarigal et al., 2012) from the functional land cover map at a radius of 800 m of each site. This distance represents the largest dimension of an average field in the region and is therefore a scale at which most land use changes are likely to occur (Galpern and Gavin, 2020). It is also a radius that represents a compromise between the typical foraging distance from the nest of bumble bees (about 1500 m depending on the species), the largest bees in our study, and smaller-bodied species (about 200–1500 m). It therefore provides an assessment of the landscape conditions most likely to affect a bee provisioning a nest near to the sampling site (Osborne et al., 2008; Zurbuchen et al., 2010).

2.2. Experimental design

Sampling was designed to test the independent and interactive contributions of land cover diversity (patch richness) and the interspersion/dispersion of land covers (contagion) to bee abundance and diversity (Fig. 2). A site selection algorithm in R (R Core Team, 2020) was developed for this purpose that: (1) reduced correlation between the patch richness and contagion metrics across sites (as suggested by Fahrig et al., 2011); (2) captured the full range of values for these metrics in the study area; and, (3) ensured sampling locations were located to maximize their separation. We used random locations ($N = 10{,}000$) to seed the algorithm, positioned along low-traffic roads and tracks that present a network of sampling opportunities across the study area (i.e., traps can be left undisturbed on vegetated roadside verges, approximately 2 m from the roadway; Galpern et al., 2017). We then reduced the location list to a set of candidate sites by grouping their contagion values into six bins, and, if one existed, selecting a location with each patch richness (i.e. 1, 2, 3 or 4) from each bin. The algorithm then repeated this selection process until the total number of candidate sites was 150. Where multiple sites with the same combinations were available for selection, the preferred site was the one with the largest distance from its nearest neighbour retained in previous steps.

2.3. Wild bees

We deployed blue vane traps (attractive to many bee species; Packer and Darla-West, 2021), filled with the non-toxic preservative propylene glycol at ground-level in vegetated roadside verges at the selected sites, continuously from mid-June to late-August in 2015 and 2016. In both years there were few bee species in flight nor flowers in bloom prior to the start of June, given the cold northern climate of the study area. A mid-June start to our sampling, therefore, excludes bee species with the earliest flight seasons. A GPS unit was used to ensure accurate trap placement. We removed samples from traps up to 6 times a year to capture the variation in bee abundance across the flight season. Bees were washed, pinned, and identified to species by a bee taxonomic expert using available keys (Table S2). If species identification remained ambiguous after referring to these resources, the taxonomist developed a morphospecies concept using a consistent set of characters, after the specimens were first identified to subgenus or genus. Voucher specimens are placed in the Invertebrate Section of the Museum of Zoology, Department of Biological Sciences, University of Calgary.

We calculated bee species richness, as well as Shannon diversity and Simpson diversity, and sample completeness at each site using the iNEXT package in R (Hsieh et al., 2016), assuming morphospecies represented unique taxa. We used the sample completeness metric as an alternative to rarefaction and extrapolation of data prior to calculating diversity, by ensuring sites met a minimum threshold in completeness (Chao and Jost, 2012). Shannon and Simpson metrics were used to gauge diversity while accounting for taxon relative abundance, with the Simpson metric placing the greatest emphasis on the diversity of common species. We separated bumble bees (genus *Bombus)* by caste (queens and workers), and excluded honey bees (*Apis mellifera*) from analyses as their distribution depends on colony placement. Diversity metrics were based on data from all collection events at each site, while abundance of bees was tallied by taxon, collection event and site. When a bee taxon in the study was not observed in a given collection event, we recorded abundance as a zero to represent its absence. The middle day of year for each collection event was converted to accumulated growing degree-days ($T_{\text{base}} = 5\ ^\circ\text{C}$) to create a phenological variable comparable across the study area and sampling years. This was done by cross-referencing growing degree-day data from the nearest weather station to each site (5 in study area; Alberta Agriculture and Forestry, 2018).

2.4. Statistical models

We modelled the association between wild bee diversity or abundance and landscape metrics using generalized additive models (GAMs) with the mgcv package in R (Wood, 2017a) due to their flexibility as a regression approach for handling random effects, spatiotemporal effects and variable selection (Wood, 2017b), and to model potential non-linearity in bee-landscape relationships (e.g., Martin et al., 2019). Landscape was represented in all models using patch richness, contagion, cropland area and their pairwise interactions, after centering and scaling to unit variance to permit comparison of effect sizes. All models also included a spatial smooth consisting of a tensor-product between sampling site easting and northing coordinates, intended to improve conditional independence among sites, minimize residual spatial autocorrelation, and control for the variance of unmodeled spatially-correlated environmental variables.

We built separate models for each measure of species diversity. We modelled abundance in two ways. Total abundance (i.e. the count of bees summed across taxa) was used to find the aggregate response of the entire bee community. Two mean bee abundance by taxon models (one for *Bombus* and another for non-*Bombus* taxa) explored the individual response of each taxon in a single mixed model to find a mean trend for all taxa and the variability among taxa. The *Bombus* model separated taxa by caste to model the distinctive phenological signatures in abundance of queens and workers (Galpern et al., 2017) corresponding to their eusocial life histories (not present among the non-*Bombus* taxa). All abundance models estimated a random intercept by site to capture unmodelled variance in abundance that may affect all taxa at a site and included year as a fixed factor to capture differences among sampling years. The abundance models also used a temporal smooth for growing degree-days and its interaction with the landscape variables to identify

Table 1

Significance of terms in Gaussian GAMs of bee diversity. Implied null hypotheses (H_o interpretation) are provided for P-values. Effective degrees of freedom (EDF) indicate the degree of non-linearity of a term after penalization, with one-dimensional terms approaching linearity at EDF ≈ 1, and two-dimensional terms approaching planarity at EDF ≈ 2. Shrinkage penalties on smooth terms allow the term to be removed from the model if there is no evidence of a relationship (EDF ≈ 0).

Term	**Term type**	**Shrinkage**	**H_o interpretation**	**(a) Species richness**		**(b) Shannon diversity**		**(c) Simpson diversity**	
				EDF	**P**	**EDF**	**P**	**EDF**	**P**
INTERCEPT	Parametric	NO	intercept = 0		**< 0.01**		**< 0.01**		**< 0.01**
PATCH RICHNESS	Smooth	YES	no effect	**0.90**	**< 0.01**	**0.81**	**0.02**	0.00	0.67
CONTAGION	Smooth	YES	no effect	0.00	0.98	0.57	0.12	0.00	0.25
CROPLAND AREA	Smooth	YES	no effect	0.00	0.85	0.00	0.64	**0.49**	**0.05**
EASTING × NORTHING	Smooth	YES	no effect; no interaction	**7.64**	**< 0.01**	**5.90**	**< 0.01**	**1.67**	**< 0.01**
CONTAGION × CROPLAND AREA	Smooth	YES	no interaction	0.00	0.72	0.00	0.52	0.00	0.26
PATCH RICHNESS × CROPLAND AREA	Smooth	YES	no interaction	0.00	0.93	0.28	0.29	3.19	0.01
PATCH RICHNESS × CONTAGION	Smooth	YES	no interaction	0.00	0.97	0.00	0.60	0.00	0.50

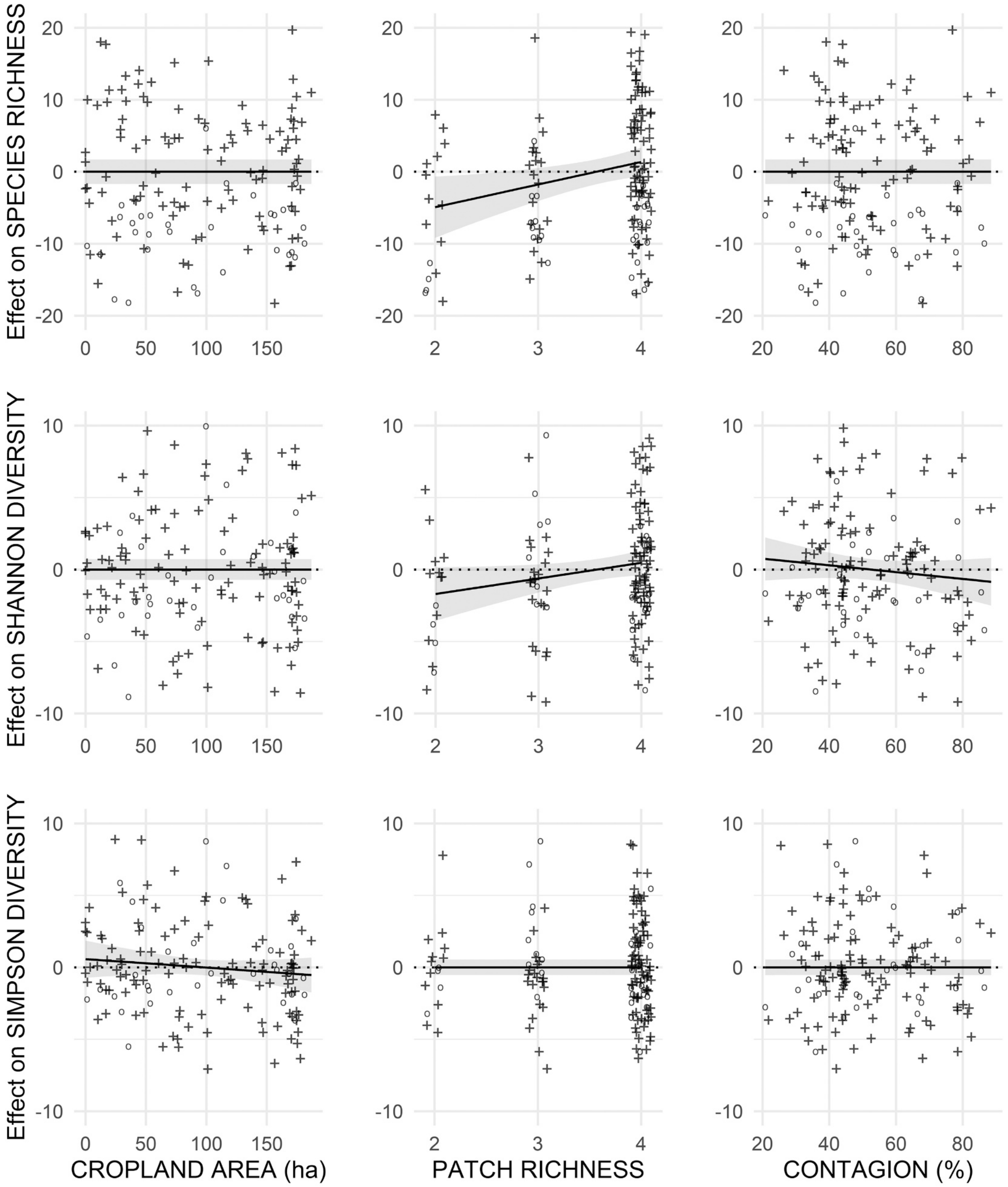

Fig. 3. Effects of landscape variables on bee diversity and their 95% confidence regions (shaded). Partial residuals are plotted, and are symbolized by sample completeness (SC) for estimating diversity metrics (+ indicates SC > 80%; o indicates SC ≤ 80%).

Table 2
Model comparison criteria for the three bee diversity models (a-c) and three bee abundance models (e-f) in this study. The full model provides the best explanation of the response variable using all model selection criteria in all sets of models. Sample size (N) used to build models represents the number of: sites in diversity models (a-c); site-time combinations in total bee abundance models, where abundance may sometimes equal zero (d); and, site-time-taxon combinations in mean bee abundance models, where abundance may sometimes equal zero (e-f). Dev. is an abbreviation for deviance and Res. is an abbreviation for residual.

							Analysis of variance†				
Model	**R^2_{adj}**	**Dev. explain (%)**	**AIC**	**ΔAIC**	**AIC_c**	**ΔAIC_c**	**Res. DF**	**Res. dev.**	**ΔDF**	**ΔDev.**	**P (>Chi)**
(a) Species richness (N = 146)											
— intercept only	0.00	0.00	1135	23	1135	21	145	19824			
— no landscape effects[1]	0.18	0.22	1116	4	1118	4	134	15431	-11	-4393	< 0.001
— full	0.21	0.25	1112		1114		132	14794	-1	-637	0.018
(b) Shannon diversity (N = 146)											
— intercept only	0.00	0.00	881	17	881	14	145	3480			
— no landscape effects	0.13	0.17	870	5	871	4	135	2891	-10	-589	0.001
— full	0.18	0.22	865		867		132	2700	-3	-191	0.025
(c) Simpson diversity (N = 146)											
— intercept only	0.00	0.00	786	10	786	9	145	1812			
— no landscape effects	0.04	0.05	782	6	782	5	143	1713	-2	-100	0.020
— full	0.12	0.16	776		777		136	1530	-7	-183	0.019
(d) Total bee abundance (N = 1119)											
— intercept only	0.00	0.00	8996	785	8996	726	1118	8992			
— no landscape effects	0.36	0.57	8349	139	8385	115	966	8085	-152	-907	< 0.001
— full	0.5	0.65	8211		8270		923	7875	-43	-211	< 0.001
(e) Mean abundance by taxon (non-*Bombus*; N = 42760)											
— intercept only	0.00	0.00	46044	9915	46044	9906	42759	46040			
— no landscape effects	0.1	0.51	37479	1351	37483	1346	42447	36937	-312	-9102	< 0.001
— full	0.16	0.57	36128		36137		42239	35253	-208	-1684	< 0.001
(f) Mean abundance by taxon (*Bombus*; N = 17550)											
— intercept only	0.00	0.00	25323	6059	25323	6049	17549	25319			
— no landscape effects	0.26	0.55	19680	415	19684	410	17322	19289	-227	-6030	< 0.001
— full	0.32	0.59	19264		19275		17206	18673	-116	-616	< 0.001

[1] *No landscape effects* models have all terms in the full model excluding CROPLAND AREA, CONTAGION, PATCH RICHNESS and their interactions. They therefore demonstrate the variance explained by a spatial smooth, and in abundance model sets, additionally the variance explained by random site intercepts and temporal smooths without landscape interactions.
†Provides comparison to the simpler model in the row above, in each model set.

time of year dependence in the response of bees to landscape, and the mean abundance by taxon models additionally allowed the temporal smooth to vary randomly by taxon (a factor smooth; Wood, 2017a). The latter models also fitted all landscape variables and their interactions as a mean across taxa (smooth fixed effects) as well as randomly for each taxon (linear slopes and intercepts using a random effect smoother; Wood, 2017a). Many taxa were collected at a small number of sites and were excluded from the mean abundance models to avoid excessive zeroes. Which taxa to exclude was determined from the taxon-site distribution by manually identifying a threshold that reduced the number of zeroes and the inclusion of morphospecies, while maximizing the number of taxa (reported in Results).

We set the initial number of knots on smooth landscape terms at 3 (patch richness), 5 (cropland area, contagion) and 7 (growing degree days). Smoothness estimation, using restricted maximum likelihood, was employed to avoid overfitting and can result in one-dimensional smooths being reduced to lines (i.e. effective degrees of freedom, EDF ≈ 1). Further, smooth landscape terms and spatial smooths used thin-plate spline shrinkage which achieves term selection by adding an extra penalty, enabling terms to be effectively removed from the model during fitting if they make no contribution (Marra and Wood, 2011; EDF ≈ 0). We modelled bee diversity metrics as Gaussian distributed with an identity link function and abundance counts as negative-binomial distributed with a log link function, using the total deployed hours of each trapping event as an offset. We tested the importance of landscape by comparing two additional models for each response variable, one with only an intercept, and a second with all terms except those based on landscape variables. Residuals were checked for normality and non-constant variance using the gratia package for R (Simpson, 2021) and were mapped to assess remaining spatial autocorrelation among sites. To confirm the absence of spatial autocorrelation, the significance of Mantel's I of residuals was calculated at 15 distance lags and tested using randomization (N = 100) with the ncf package for R (Bjørnstad, 2016).

3. Results

We sampled at 146 of 150 selected sites (four were not sampled due to the absence of suitable road verges) with a mean (± sd) nearest-neighbour distance of 2.7 ± 0.1 km (Fig. 1). The sites that were selected provided support across the full range of possible values for the two focal landscape metrics (Fig. S1) with mean and standard deviations as follows: patch richness (3.6 ± 0.7); contagion (52.4 ± 16.2%); cropland area (97 ± 60 ha). Patch richness and contagion of sampled sites were not strongly correlated using Spearman's r ($r = -0.44$), nor were patch richness with cropland area ($r = 0.50$) and contagion with cropland area ($r = 0.66$). The locations of 43 site-years (22%) were adjacent to fields planted in canola at the time of sampling. All other sites were adjacent to cereal fields. The selected sites also captured a broad range of functional land covers within an 800 m radius (mean ± sd, range): perennial grassland area (68.4 ± 44.5 ha, 0.1–164.0 ha); dry semi-natural area (28.9 ± 24.9 ha, 3.9–132.2 ha); and, wet semi-natural area (9.8 ± 8.4 ha, 0.1–45.4 ha).

There were 1119 collection events at 199 site-years for a total deployment of 10,471 trap-days (mean of 52 trap-days per site-year). We collected bees at 53 sites in both years and with consistent effort across years (570 events at 101 sites in 2015, and 549 events at 98 sites in 2016). We recorded a total of 22,493 bees of 213 taxa, with 1417 of these specimens representing 91 morphospecies, and the remainder assigned to species (Table S3).

3.1. Wild bee diversity

Patch richness was positively associated with species richness and Shannon diversity (Table 1; Fig. 3), supporting the prediction that greater richness in land cover composition supports more taxa (P1a).

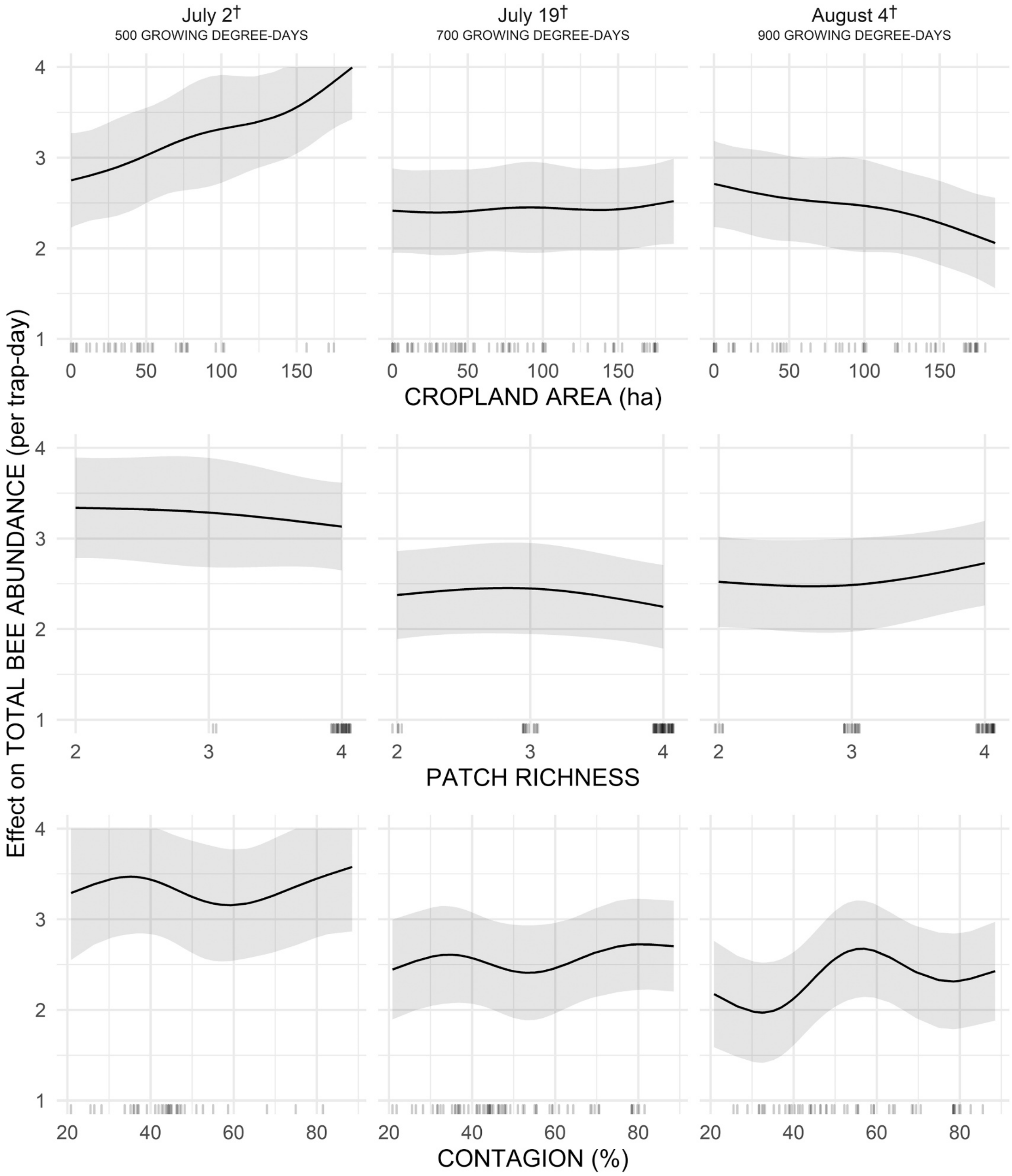

Fig. 4. Effects of landscape variables on total bee abundance during early-, mid- and late- season (left, middle and right columns respectively). Predicted mean fits and their 95% confidence regions (shaded) are plotted on the scale of the linear predictor. Effects of contagion (especially bottom right) are consistent with an optimum (i.e. hump shape). Markers on the horizontal axis provide conservative estimates of the distribution of the data supporting each of these curves (sites sampled within 10 growing degree days). Approximate dates are indicated with †.

There was some evidence for a negative relationship between cropland area and Simpson diversity (Table 1; Fig. 3), showing less cropland area (and therefore more semi-natural area) can support a higher diversity of bees, after discounting the presence of rare species (a property of Simpson diversity). However, there was no statistically significant evidence that variation in land cover interspersion affects bee diversity (P2a). Mean sample completeness for estimating the diversity metrics was 85%. Refitting these models while omitting sites with sample completeness below 80% (Fig. 3, circles; 32 sites removed) revealed identical trends and no changes to term significance (results not presented). Spatial smooths revealed parallel geographic trends in species richness and Shannon diversity metrics, with a lower diversity region covering the western half of the study area (Fig. S2, a, b), a pattern that was simplified in the Simpson diversity model (Fig. S2, c). Full models that included landscape effects explained more variance than the nested simpler models, and had the lowest AIC$_c$ (Table 2, a, b), with residuals showing no pattern that might indicate spatial clustering of the response (Fig. S3), nor evidence of spatial autocorrelation in the analysis of Mantel’s I statistic (results not shown).

3.2. *Wild bee abundance*

Results supported the prediction that the total number of bees is associated with land cover diversity and interspersion, however the strength and form of that relationship depended on the time of the year (Fig. 4; Table 2, d; Table 3), demonstrating that landscape changes could boost pollination services and bee populations, but not consistently across the season. Cropland area was positively associated with total bee

Table 3

Significance of terms in negative-binomial GAMs of bee abundance. Models of (a) total bee abundance demonstrate seasonally-dependent associations with landscape variables (i.e. interactions with growing degree-days; also see Fig. 4). Modelling of the mean abundance per taxon (b, c) also finds seasonally-dependent associations with landscape, but the conditional smooths are essentially flat (see Figs. S5, S6). However, these models find taxon-specific responses to landscape variables in both (b) non-*Bombus* and (c) *Bombus* taxon groups. Smooth terms are used for both non-linear predictors and linear random effects. Implied null hypotheses for P-values (H_o interpretation) are provided to aid interpretation. See Table 1 for interpretation of EDF.

Term	Term type	Shrinkage	H_o interpretation	(a) Total abundance		(b) Mean abundance by taxon (non-*Bombus*)		(c) Mean abundance by taxon (*Bombus*)	
				EDF	P	EDF	P	EDF	P
INTERCEPT	parametric	NO	intercept = 0		**< 0.01**		**< 0.01**		**< 0.01**
YEAR (2016)	parametric	NO	no effect		**< 0.01**		**< 0.01**		**< 0.01**
EASTING × NORTHING	smooth	YES	no effect; no interaction	0.00	0.78	**1.92**	**< 0.01**	1.03	0.29
PATCH RICHNESS	smooth	YES	no effect	0.00	0.87	0.01	0.43	0.00	1.00
× CONTAGION	smooth	YES	no interaction	0.08	0.32	0.00	0.98	0.00	0.70
× CROPLAND AREA	smooth	YES	no interaction	0.00	0.72	0.00	0.98	0.00	0.95
CROPLAND AREA	smooth	YES	no effect	0.00	0.86	0.00	1.00	0.75	0.07
× CONTAGION	smooth	YES	no interaction	0.00	0.57	0.00	0.97	0.01	0.46
CONTAGION	smooth	YES	no effect	0.67	0.08	0.00	0.98	0.00	0.18
GROWING DEGREE-DAYS	smooth	NO	no effect	**5.25**	**< 0.01**	**4.19**	**< 0.01**	3.88	0.10
× PATCH RICHNESS	smooth	YES	no interaction	**2.67**	**< 0.01**	**0.79**	**0.02**	**3.44**	**< 0.01**
× CROPLAND AREA	smooth	YES	no interaction	**4.61**	**< 0.01**	**6.83**	**< 0.01**	0.31	0.21
× CONTAGION	smooth	YES	no interaction	0.11	0.24	0.00	1.00	4.14	< 0.01
× CROPLAND AREA × PATCH RICHNESS	smooth	YES	no interaction	**3.43**	**0.04**	**11.52**	**< 0.01**	**11.75**	**< 0.01**
× CROPLAND AREA × CONTAGION	smooth	YES	no interaction	**7.66**	**< 0.01**	0.80	0.21	0.00	0.77
× PATCH RICHNESS × CONTAGION	smooth	YES	no interaction	0.00	0.83	**5.49**	**< 0.01**	0.00	0.41
INTERCEPT (by SITE)	random linear	NO	$\sigma_{intercepts} = 0$	**120.68**	**< 0.01**	**122.13**	**< 0.01**	**115.55**	**< 0.01**
GROWING DEGREE-DAYS (by TAXON)	smooth	NO	no effect			111.95	0.07	59.19	0.07
INTERCEPT (by TAXON)	random	NO	$\sigma_{intercepts} = 0$			**12.59**	**< 0.01**	**4.80**	**< 0.01**
PATCH RICHNESS (by TAXON)	random	NO	$\sigma_{slopes} = 0$			19.09	0.03	0.13	0.41
× CONTAGION	random	NO	$\sigma_{interactions} = 0$			8.12	0.24	2.29	0.14
× CROPLAND AREA	random	NO	$\sigma_{interactions} = 0$			**15.53**	**< 0.01**	0.01	0.71
CROPLAND AREA (by TAXON)	random	NO	$\sigma_{slopes} = 0$			**35.40**	**< 0.01**	**16.08**	**< 0.01**
× CONTAGION	random	NO	$\sigma_{interactions} = 0$			**26.00**	**< 0.01**	**9.96**	**0.04**
CONTAGION (by TAXON)	random	NO	$\sigma_{slopes} = 0$			**27.40**	**< 0.01**	**9.97**	**< 0.01**

abundance earlier in the season, with the relationship trending negative later in the year (Fig. 4, top row). Patch richness had an essentially flat relationship when plotted across the season, showing that while there is a significantly non-linear relationship, the effect of diversity in land covers on total abundance is weak (P1b; Fig. 4, middle row; Table 3). Contagion had a significant non-linear association with total abundance demonstrating a "hump" that is consistent with an intermediate optimum in land cover interspersion (P2b). Sites also differed in the total number of bees they collected (i.e. random intercept by site; Table 3, a), although there was no spatial pattern observed (easting x northing; Table 3, a), indicating that unmeasured local environmental conditions at each site may be chiefly driving these differences. Total abundance also varied predictably over time, with more bees collected earlier in the flight season (Fig. S4).

Mean abundance by taxon models included bee taxa (or for *Bombus,* taxon-caste combinations) collected at more than 20 sites and 3% of sampling events (Tables S3, S4), values that were chosen by inspecting the taxon-site distribution (Fig. S7). A total of 21,400 bees in 51 taxa were analyzed in these two models (12,841 non-*Bombus* bees in 39 taxa and 7319 *Bombus* bees in 12 species).

Both of the mean abundance by taxon models demonstrated taxon-specific responses to land cover diversity and interspersion variables (Table 2, e, f; Table 3, b, c). There were weak non-linear trends but no support for the prediction of a positive trend in the majority of non-*Bombus* taxa (P3; Fig. S5). *Bombus* taxa demonstrated weakly negative linear association with cropland area across taxa in the first half of the season (Fig. S6, top left, top middle), suggesting that taxon-caste combinations have a positive numerical response to semi-natural land, on average at this time of year. Taxon-specific associations with abundance in both taxonomic groups were strongest with cropland area as measured by the standard deviation of the standardized random slopes ($\beta_{CROPLAND\ AREA}$), and contagion was of secondary importance ($\beta_{CONTAGION}$; Figs. 5 and 6; Table 3, b, c). Patch richness effects on abundance were only different among non-*Bombus* taxa, and had the smallest standard deviation in random slopes ($\beta_{PATCH\ RICHESS}$; Fig. 5; Table 3, b), suggesting a lower relative importance of land cover diversity compared to land cover interspersion.

The mean abundance by taxon for non-*Bombus* bees varied across the season, and along a linear geographical gradient, with southeastern sites recording more individuals on average of a given taxon than northwestern sites (Table 3, b; Fig. S2, d). Neither spatial nor temporal pattern was evident in the mean response by taxon of *Bombus* bees (Table 3, c). No abundance model residuals had a pattern that might indicate spatial autocorrelation (Fig. S3), nor was there evidence of spatial autocorrelation in the analysis of Mantel's I statistic.

4. Discussion

Our highly replicated study found evidence for a temporally-variable and a taxon-specific abundance response by wild bees across a broad gradient of conditions in annual cropped landscapes (Table 3). Modelling showed that the total number of bees responds to variability in land cover diversity and land cover interspersion, but the strength and direction of the response varies across the summer (Fig. 4; Table 3, a). Individual taxa responded both negatively and positively to landscape variables (Figs. 5, 6), an effect that could explain seasonal variability in the total bee response because taxa vary in the timing of their flight periods. This finding echoes earlier studies that have demonstrated contrasting responses to landscape conditions by different bee taxa and by functional groupings of bees (Denning and Foster, 2018; Hopfenmüller et al., 2014).

We did not find, as others have predicted, a coordinated increase in abundance across the wild bee species present in this study area associated with greater availability and diversity in resource-containing habitats. Existing landscape variation, either associated with types of land cover (i.e., patch richness) or the interspersion of different patch

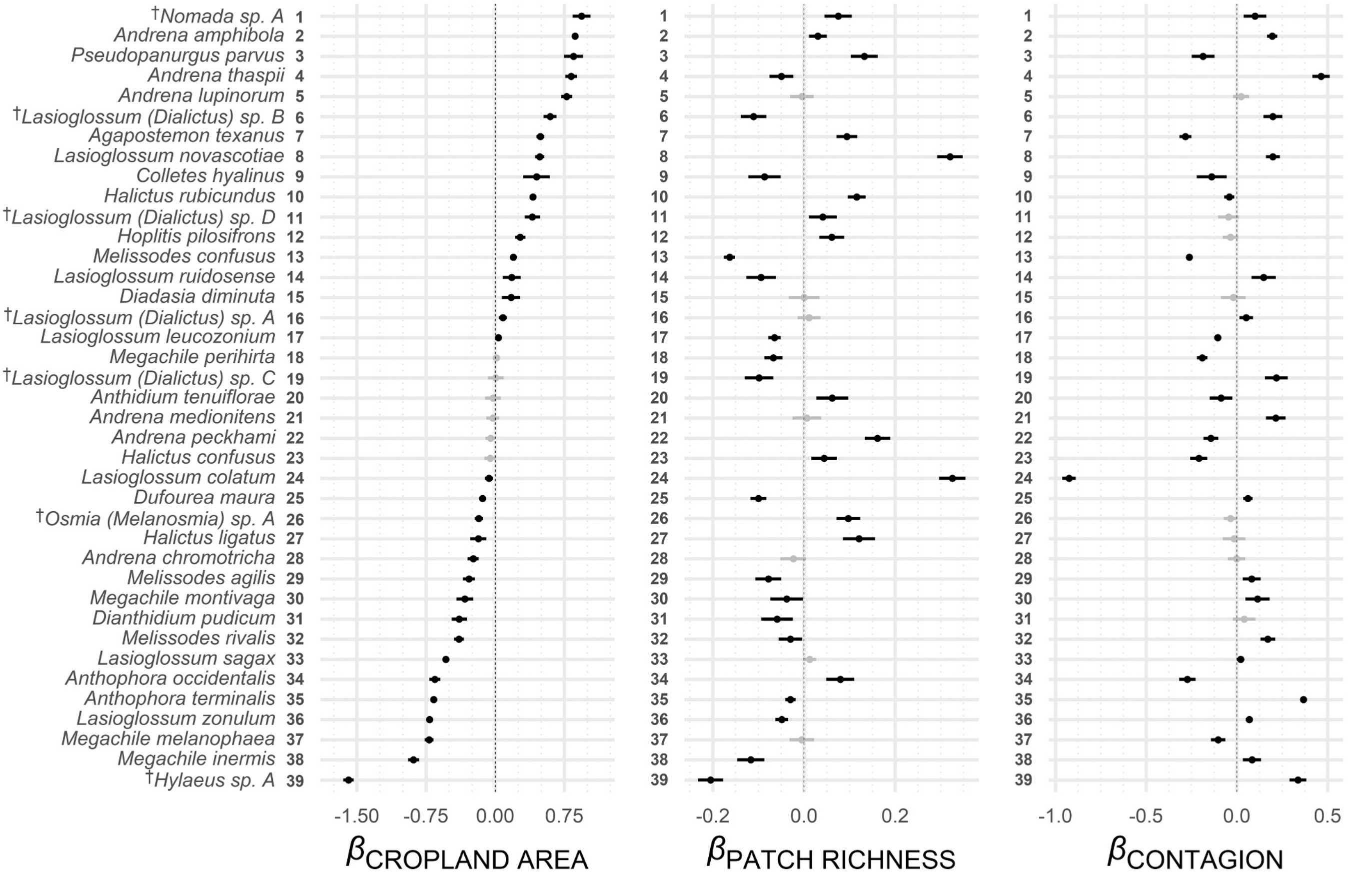

Fig. 5. Random slopes for landscape variables by taxon in the non-*Bombus* mean abundance model indicate the response to patch richness and contagion is taxon-specific. Slopes are for standardized variables permitting comparison among terms, and are shown with their mean and 95% confidence intervals. Grey symbols show slopes with intervals that include zero. Morphospecies are indicated with †.

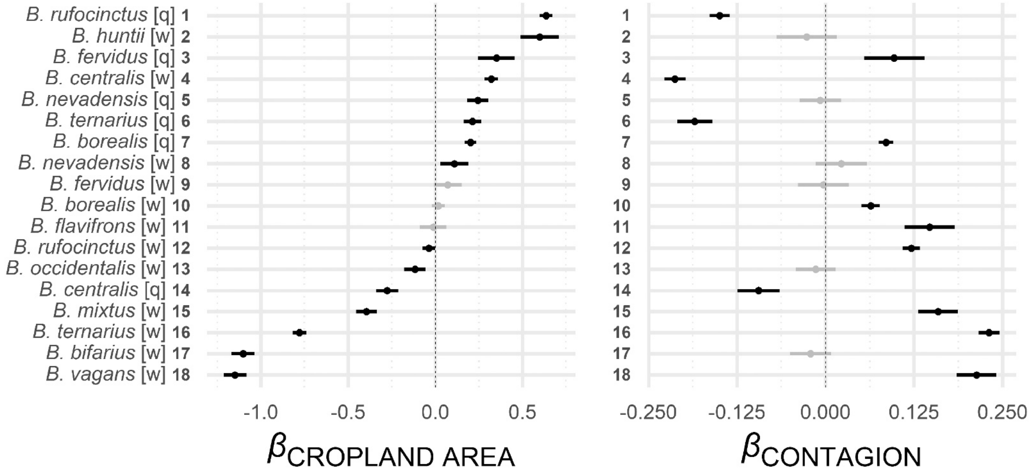

Fig. 6. Random slopes for landscape variables by taxon in the *Bombus* mean abundance model indicate the response to contagion is taxon-specific. Slopes are for standardized variables permitting comparison among terms, and are shown with their mean and 95% confidence intervals. Grey symbols show slopes with intervals that include zero. (q = queens; w = workers).

types (i.e., contagion) did not correspond to a positive mean trend across taxa (Table 3). Cropland area (i.e., an indicator of absence of semi-natural area) had both a positive and negative effect on total bee abundance. This variable is useful as an indicator of the availability of resources for bees in prairie croplands, because virtually all non-crop areas are likely to provide foraging and nesting resources for bees, while crop areas have frequently-disturbed nesting substrates and, in the case of mass-flowering crops, provide foraging resources for only part of the season. Others studies have often reported that semi-natural area is positively associated with bee abundance (Kennedy et al., 2013; Senapathi et al., 2017). However, it is possible that the results of other studies also reflect the particular assemblage of taxa present, and they may have insufficient replication of sampling over time to demonstrate that this response is variable. In our study, an early-season positive relationship with cropland area could be driven by mass-flowering canola crops (Fig. 4, top left) found at about a quarter of the sites, with a negative relationship later in the season reflecting the importance of semi-natural areas as the only remaining sources of bee forage after bloom ends (Fig. 4, top right).

Our findings concur with the consensus (e.g., Kennedy et al., 2013; Senapathi et al., 2017) that diversifying the composition of landscapes will attract a broader diversity of bees, and is consistent with the hypothesis that this broadens the diversity of floral resources and nesting substrates and therefore supports a greater number of habitat specialist taxa. However, for land cover interspersion, we did not find the predicted directional relationship with bee abundance. Rather, we found a "humped" one (e.g., most distinctive later in summer; Fig. 4, bottom right), a pattern that has been hypothesized for other groups of arthropods (e.g., Martin et al., 2019). We expected that configurations of habitat which place contrasting resources in closer proximity (e.g. suitable nesting substrate near continuously-available floral resources) would support larger populations because bees would able to access both within a smaller radius (i.e., landscape complementation; Dunning et al., 1992). However, the humped response to the contagion variable, revealed after controlling for the total amount of resources (cropland area), suggests there may be a tradeoff between the complementation that adjacent resources provide and the degree to which these resources are fragmented. In other words, our study shows that for a constant amount of habitat, there is an optimum in bee abundance occurring where habitat types interface at an intermediate level. However, this "hump" was a small one, suggesting that land use decision-makers who inadvertently increase contagion or interspersion beyond its optimum are unlikely to substantively depress bee populations.

Our study therefore affirms that bee responses to cropland conditions are complex (e.g., Denning and Foster, 2018). Importantly, our results show that the taxonomic make-up of bee communities and seasonal trends across the landscape make it challenging to produce simple prescriptions for wild bees. Predicting how landscape changes will affect wild bee abundance or pollination services may, therefore, require detailed knowledge of specific plant-pollinator interactions and wildflower or mass-flowering crop phenology and its potential for variability among years, in addition to the functional definitions of habitat like those we used here (Fahrig et al., 2011). Examining functionally important traits of bee taxa, such as their nesting site preference and floral specialization will also be critical for predicting how the bee community may respond to changes in land cover diversity and linterspersion. We did not do this, here, because such trait data for most bee taxa is either not available or highly uncertain, in part because many taxa in this region remain poorly known (e.g., 91 of 213 bee taxa in this study could not be confidently assessed to species by an expert using current keys). Investment in developing functional trait databases for more of the region's bee fauna is an essential next step to be able to generalize beyond the taxa studied, and make better predictions regarding bee community responses to landscape changes (de Bello et al., 2021). Put in the context of other factors, however, any simple change that could be implemented by a farmer is likely to have a relatively small impact on bees, as we found that landscape metrics explained only a small amount of deviance in any model ($< 10\%$ difference between full and no landscape effects models; Table 2).

Our pseudo-experiment is among the most highly replicated studies attempted for bees in a single cropland region, with repeated sampling of landscape conditions over space (146 sites) and time (~6 samples per site-year; 199 site-years). This approach selected sampling locations from among naturally occurring landscape conditions and used an algorithm to minimize the correlation between land cover diversity and interspersion at the sites sampled. Although selecting sites in this manner has the advantage of reflecting real-world landscape conditions, the approach is limited in that it cannot be used to infer causality. A caution, likely to apply to many landscape pseudo-experiments, is that the sites will have a non-zero correlation in the variables of interest (Fahrig et al., 2011). For example, in this study the contagion variable was somewhat correlated with cropland area at the sites sampled (Fig. S1; Spearman's $r = 0.66$) implying that our confidence should be lower when inferring an independent effect of either variable on bee diversity or abundance.

We found that total bee abundance varies across the flight season (Fig. S4), a result that may impact farmers seeking pollination services if there is a mismatch between peak abundance and the timing of crop bloom. Wild bee diversity and mean taxon abundance for non-*Bombus* bees also varied spatially over an 80 × 40 km region (Fig. S2). Future studies should therefore ensure replication over space and time to correctly estimate and control for spatiotemporal trends such as these.

Additionally, site-to-site variability in the abundance models explained a significant proportion of variance (Table 3), justifying its inclusion as a control. Modelling site-specific variability may have also acted as a control for the scale of our analysis (landscapes were defined at a radius of 800 m from the trapping location). Including this term allowed unmodelled variability caused by fine-scale features near the trap to be represented in the model. Choosing this radius was important given our objective to compare differences in landscape complexity in a way that is functional for farmers (i.e., most fields on the Canadian prairies are rectangular with dimensions that are multiples of 800 m; Galpern and Gavin, 2020).

4.1. *Significance*

Our study shows that diversifying land cover in croplands or increasing the complexity of fields by allowing succession of semi-natural vegetation may not have a unified benefit for the entire wild bee community, nor have a consistent effect across the entire season. For example, if landscape changes are intended to boost pollination services, they may not recruit a larger number of wild bees to the vicinity of a pollen-limited crop at the time of bloom. Where bee conservation in croplands is an objective, increasing land cover diversity may support a greater diversity of bee taxa, but the numerical response of individual species may vary considerably. An important finding is that the response of many taxa is significantly associated with these landscape metrics, suggesting that simple changes to landscape complexity have the potential to increase populations of target species known to pollinate crops effectively, or contribute to the recovery of species known to be at-risk in croplands. Caution is also warranted as changes intended to boost some taxa may also negatively affect others. Ultimately this study affirms that understanding functional traits, such as floral and nesting specializations of different species and how these may interact with the timing of foraging resources will be essential to ensure croplands are designed to support bee communities.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107652.

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