



Narrow anthropogenic linear corridors increase the abundance, diversity, and movement of bees in boreal forests

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ABSTRACT

Understanding how invertebrates respond to disturbance is important to maintaining biodiversity. In western Canadian boreal forests, anthropogenic linear corridors associated with energy exploration are a pervasive disturbance that affect many species. Trees and large shrubs are removed in a grid of narrow corridors, but the understory vegetation is generally maintained, mimicking early seral conditions. Little is known about how bees, an important group of pollinators, respond to linear corridors, with their response having important implications for plant-pollinator communities. Here, we investigated how bee abundance, diversity, species composition, and movement respond to these anthropogenic linear corridors, locally known as seismic lines. We compared bee abundance and diversity from pan traps on seismic lines (6 – 12 m wide) to traps placed 50 m into the adjacent forest interior, across 12 replicated sites. Malaise traps were used to measure bee movements on seismic lines relative to paired interior forests, but also with respect to flight direction relative to the orientation of seismic lines. Abundance and richness of bees were 3-times and 1.5-times higher, respectively, on seismic lines compared to the forest interior, with significant differences in species composition. Bees were more than twice as abundant and diverse in malaise traps that caught bees flying along seismic lines than any other combination of trap orientation and location. These results demonstrate that narrow anthropogenic linear corridors are locally increasing bee abundance and diversity in boreal forests, as well as use of these lines for movement. These results have major implications for boreal forest plant-pollinator communities.

1. Introduction

Habitat fragmentation is a major concern for many ecosystems (Fahrig, 2003; Haddad et al., 2015), including boreal forests (Schindler and Lee, 2010). Fragmentation affects both biodiversity and species interactions that underlie important ecosystem functions, such as pollination (Kevan et al., 1993). Relative to pollination services, the conservation of bee communities is important, as they contribute to pollination more than any other animal taxon (Hanula et al., 2016). Anthropogenic habitat fragmentation can alter both bee diversity and their movements. In northern Alberta's boreal forest, anthropogenic linear corridors associated with energy exploration represent one of the most common types of forest fragmentation (Lee and Boutin, 2006). These anthropogenic corridors are narrow, linear, clear-cuts through forests, called seismic lines, on which woody vegetation is removed, creating strips of early successional habitat that dissect natural forest communities (Fig. 1; Pattison et al., 2016). This results in higher sunlight exposure, increased temperatures, and higher windspeeds (Roberts

et al., 2018; Stern et al., 2018), but also makes it easier for organisms to move long distances given their linear structure. Similar to findings from other studies on corridor effects (Haddad et al., 2003), movements of organisms along seismic lines are known to increase for birds (St. Clair et al., 1998), wolves (Latham et al., 2011), invasive plants (Roberts et al., 2018), and butterflies (Riva et al., 2018b). However, there is little evidence showing how anthropogenic linear corridors, such as these, affect bees. In this study, we seek to understand how anthropogenic linear corridors affect the abundance, diversity, community composition, and movement of bees.

Bee diversity in temperate and boreal systems tends to be higher in early successional habitats compared to areas with higher forest cover (Odanaka and Rehan, 2020; Winfree et al., 2007). Butterflies respond similarly to seismic lines, likely due to a combination of increased floral resources, microclimate, and landscape structure (Riva et al., 2018a). Bees are known to respond to these types of changes in habitat (Knight et al., 2005; Rodríguez and Kouki, 2015). Given evidence for increased understory plant productivity on seismic lines (Dawe et al., 2017; Riva

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Fig. 1. An example of a ~5 m wide seismic line. Each site consisted of one transect running along the seismic line and another parallel transect 50 m into the adjacent forest interior. For each site, one set of pan traps was placed on a seismic line and one set was placed in the adjacent forest interior. For each transect at a subset of five sites, two malaise traps were placed in opposite orientations. One was oriented to catch bees flying along the seismic line and another placed to catch bees flying across the seismic line.

et al., 2020) and positive relationships to canopy openness (Nielsen et al., 2020), bees may select anthropogenic linear corridors simply due to increased resource availability. This may also be true for nesting habitat, as bees prefer open ground and woody debris for nesting, both of which are associated with these anthropogenic linear corridors where trees are cut, but the debris is left (Rodríguez and Kouki, 2015). Increased temperatures in these corridors may also modify habitat that is favorable for ground nesting bees and increase the foraging activity of bees (Potts and Willmer, 1997).

Anthropogenic linear corridors may also affect bee movement. Butterflies preferentially flew along seismic lines in a controlled release study (Riva et al., 2018b). There is evidence that bees increase their foraging range between resource patches using narrow strips of early successional forest habitat (Townsend and Levey, 2005). If this is true for seismic lines, there could be significant, landscape-scale implications for bee metacommunities. Increased connectivity between local flower and pollinator communities could lead to taxonomic homogenization and potential loss of species due to competition (Keith et al., 2009; Leibold et al., 2004) or disease (Keyghobadi et al., 2005). These changes could subsequently affect the plant and parasitoid communities, whose current patterns of diversity are partly a result of the current meta-community structure of bees (Aguilar et al., 2006; Roland and Taylor, 1997). Thus, it is of interest to understand how bees respond to anthropogenic linear corridors.

In this study, we hypothesize that these narrow anthropogenic linear disturbances (seismic lines) have a higher abundance and diversity of bees, and significantly different bee species composition, than the adjacent interior forest due to increased availability of floral and nesting resources. We also hypothesized that bees use these lines as movement corridors, preferentially travelling along them rather than across them, partly due to increased floral resources, but also due to ease of travel from loss of woody vegetation structure. The objectives of this study were to therefore investigate whether: 1) seismic lines affect the abundance, diversity, and species composition of bees, relative to adjacent interior forests; 2) changes in flower abundance, flower diversity, and/or canopy openness explain bee abundance, diversity, and community composition; and 3) bees travel along seismic lines more frequently than they travel across them and more than in forest interiors.

2. Methods

2.1. Study area and site selection

We conducted this study in the Richardson area of Alberta's Boreal forest, approximately 100 km north of Fort McMurray, Alberta (57° 32' 31.2" N, 111° 16' 55.2" W). This area has many seismic lines, ranging from 6 to 12 m in width, crisscrossing the landscape in a grid pattern at densities averaging at least 1.5 km/km² (Lee and Boutin, 2006), but locally as high as 20 km/km². The region is characterised by dry, sandy soils that are dominated by jack pine (*Pinus banksiana*) lichen woodlands and forests that are typified as having periodic low-intensity wildfires with dense jack pine regeneration (Filicetti and Nielsen, 2018).

We selected 12 seismic lines that were at least 300 m apart and never on the same line (different direction or intersected by another major feature). All sites were at least 50 m from any other disturbance (e.g. roads). Each site consisted of two 30 m transects, one placed along the center of a seismic line and another parallel transect 50 m into the adjacent forest interior randomly assigned to one side of the line. We chose 50 m as the adjacent forest distance due to space limitations, since in some places seismic lines were 100 m apart. Other studies have found differences between seismic line sites and interior forest sites as far as 25 m (Dabros et al., 2017; Dawe et al., 2017), but within the boreal forest region, most forest edge effects for larger disturbances, such as clearcuts, or for large natural openings like lakes do not reach further into the forest than 50 m (Harper et al., 2005, 2015), and thus locations 50 m from the corridors were considered as 'interior' forests for comparison.

2.2. Bee abundance and diversity

We used pan traps to measure the effect of seismic lines on bee abundance and diversity with a white, a blue, and a yellow trap used on each transect and combined for analysis. Pan traps of these colours are the most common, and often used together to account for differential effectiveness in capturing bee species (Moreira et al., 2016). Traps were 2/3 filled with water and a drop of unscented dish soap. We left traps out continuously for the main growing season, from May 5 to July 27, 2019, periodically collecting insects and resetting the traps with water and soap for a total of 305 unique samples and an average of 13 sample sessions. Individual sample length varied between 50 and in rare cases, 406 h; however, total sampling effort across the season was identical at all sites, with a mean sample length of 130 h. Traps were always set and collected within a few minutes of one another for each site consisting of a pair of transects (seismic line and interior forest).

Flower abundance and diversity were measured along each transect an average of 13 times, evenly distributed throughout the season, by estimating the number of flowers per 1% cover for each species that was flowering, and multiplying that by the percent cover of the species to estimate total abundance. This was done in ten 1-m radius quadrats for each 30-m transect and averaged for the transect.

2.3. Bee movement

We used malaise traps to measure the movement of bees. We used a malaise trap from the Natural History Book Service (NHBS) that has two large openings on opposite sides of the trap, allowing them to collect bees flying in either direction along a single axis. We set up two traps per transect, one oriented to catch bees flying along the seismic line, the other oriented to catch bees flying across the seismic line. We replicated this design in the corresponding paired interior forest transects. Traps were left out continuously for the same sampling dates as for pan traps, but we collected the insects periodically and reset the traps. Sample collections occurred between 48 and 358 h apart, but the total sampling effort over the whole season was the same at all sites with all insect samples combined for single composite value. Traps located at the same site were always set up and collected within a few minutes of one

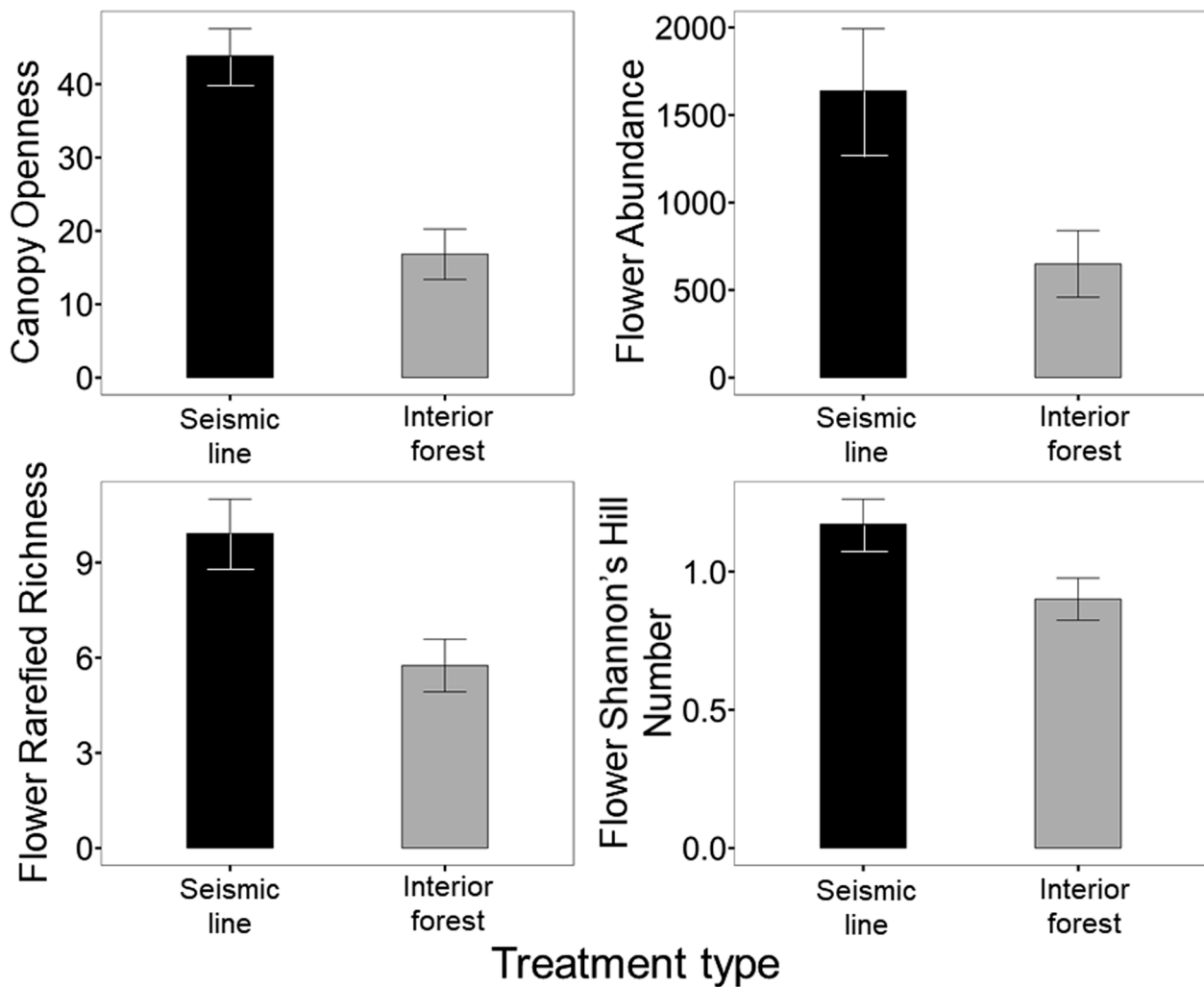


Fig. 2. Mean and standard error of canopy openness, flower abundance, flower rarefied richness, and flower Shannon's Hill number on seismic lines compared to forest interiors. All metrics are significantly different between seismic lines and interior forests ($p < 0.05$).

another. When a trap was damaged and required significant repairs, we stopped sampling for all traps at that site until a full set of malaise traps was available. We placed malaise traps at a subset of five sites (ten transects paired between seismic lines and adjacent forests) for logistical reasons. The sites selected were oriented in different directions, with approximately half running north–south and the other half running east–west. Thus, prevailing wind direction was not consistently related to orientation of “across” vs. “along” malaise traps across sites. We identified all bee specimens to species using taxonomic keys, and where no appropriate keys existed, to morpho-species (Andrus et al., n.d.-b, n.d.-a; Andrus and Droege, n.d.-b, n.d.-c, n.d.-a; Droege et al., n.d.; Griswold et al., n.d.; Larkin et al., n.d.).

We also measured canopy openness using a spherical densiometer. A single canopy openness measurement involved recording openness values in each cardinal direction and averaging the directions for a single value. Measurements were taken at three locations along each transect (both ends and the center) and again averaged to get an overall canopy openness for each transect. We took these measurements once at the end of the summer growing season.

We calculated species diversity of bees using rarefied species richness and Shannon's Hill number. Rarefied species richness, as opposed to raw richness, accounts for different sample sizes when comparing the number of species between sites (Simberloff, 1972). It is the mean number of species in a “re-sampled” sample of a standard size, where the sample size used for all sites is the lowest number of individuals sampled

at any site (Chao et al., 2014). Shannon's Hill number is a formulation of Shannon's diversity index that represents a sample's “effective number of species”, considering both the abundance and evenness of all observed species (Hill, 1973). It is the number of equally abundant species necessary to produce the observed value of diversity (Hill, 1973; Oksanen et al., 2018).

2.4. Statistical analysis

To assess the effect of seismic lines on bee abundance and diversity, we created three general linear mixed models (GLMM) with bee abundance, bee rarefied richness, and bee Shannon's Hill number as response variables. We used data from pan traps (season totals for each transect) as the response variables, rather than malaise traps, because pan traps catch more bees than malaise traps (Bartholomew and Prowell, 2005). Treatment type (seismic line or interior forest) was the only fixed effect, while site was included as a random effect. To test the effects of seismic lines on bee species composition, we ran a permutational multivariate analysis of variance (perMANOVA) using both Bray-Curtis (which considers species relative abundances) and Jaccard (which considers only species' presences/absences) distances to test the dissimilarity between seismic line and interior forest bee communities (McArdle and Anderson, 2001). We included treatment type and site as variables in both analyses. We also used a Nonmetric Multidimension Scaling (NMDS) analysis with Bray-Curtis distance to visualize differences between

seismic lines and interior forest communities.

We also ran a GLMM for each of canopy openness, flower abundance, flower rarefied richness, and flower Shannon's Hill number to test whether they differed between treatment type (seismic line vs. interior forest). For each of these models, we included treatment type as a fixed effect and site as a random effect.

To assess whether flower abundance, flower diversity, and/or canopy openness explained variation in bee abundance, diversity, or species composition between seismic lines and forest interiors, we ran GLMMs for bee abundance, rarefied richness, and Shannon's Hill number, and included flower abundance, flower diversity (either rarefied richness or Shannon's Hill number), and canopy openness as fixed effects in the models. We used rarefied richness of flowers in the bee abundance model so that rare species were given more weight, as some flower species attract a high number of bees, despite having low abundance. For the bee rarefied richness and Shannon's Hill number models, we used flower rarefied richness and flower Shannon's Hill number as the diversity metric, respectively. Site was added to these models as a random effect. To visualize these relationships, we created marginal plots showing how each explanatory variable in the final model affected the predicted value of the response variable, holding all other variables at their means. We also ran another set of perMANOVAs, as described above, but with canopy openness, flower abundance, and flower richness, instead of treatment type, but site was still included as a random effect.

To assess if bees preferentially travel along seismic lines more than they travel across them, we created another set of GLMMs with bee abundance, bee rarefied richness, and bee Shannon's Hill number in malaise traps as response variables. We included treatment type and trap orientation as fixed effects, as well as their interaction to account for differences in orientational movement between seismic line and interior forest transects. We again included site as a random effect in these models. For every GLMM, we simplified the fixed effects structure by systematically removing the least significant variable, starting with interactions, and evaluating the new model until only significant ($p < 0.05$) variables remained, or the removal of any remaining variables significantly increased the deviance of the model based on an analysis of variance (Crawley, 2005). The random effect was always kept in the models.

We fit each model to a Gaussian distribution and used a Shapiro-Wilk test on the final model's residuals to test for normality, as well as inspecting a fitted value versus residuals plot to confirm homogeneity of variances. When any of these assumptions was violated, we log transformed the response variables and retested the new models for normality and homogeneity of variances of residuals. We calculated two different R^2 values for each GLMM. Marginal R^2 describes the proportion of variance in the response variable explained by only the fixed effects of the model. Conditional R^2 describes the proportion of variance explained by the entire model including random effects (Bartoń and Barton, 2020; Nakagawa et al., 2017). Reporting both metrics allows for a more complete understanding of what conclusions can be drawn from the models (e.g. treatment vs. site effects). All statistical computing was completed using R and the tidyverse packages (R Core Team, 2020; Wickham et al., 2019). Other packages used for statistical analysis included vegan (Oksanen et al., 2018), glmmTMB (Magnusson et al., 2020), MuMIn (Bartoń and Barton, 2020), ecodist (Goslee and Urban, 2007), DHARMA (Hartig, 2018), and RVAideMemoire (Herve, 2019).

3. Results

3.1. Bee abundance and diversity

We collected and identified a total of 4,836 bees of 61 species from 305 pan trap samples, with a total of 39,687 h of trapping time between all samples (Appendix A). We collected and identified 777 bees of 47 species from 260 malaise trap samples, with a total of 34,243 h of

Table 1

Model structure for GLMMs (Gaussian distributions) showing how bee abundance and diversity from pan traps, canopy openness, flower abundance, and flower diversity differed on seismic lines compared to forest interiors (fixed effect). "Coef" represents the estimated effect of seismic lines (1) on each variable relative to the interior forest (0) from the GLMM. Site was included as a random effect in all models. Significant p-values are bolded.

| Response variable | Coef. | S.E. | p | Marginal R^2 | Conditional R^2 |
|------------------------------|---------|---------|---------|----------------|-------------------|
| Bee abundance | + | 32.071 | < 0.001 | 0.520 | 0.520 |
| Bee rarefied richness | + | 1.817 | < 0.001 | 0.596 | 0.596 |
| Bee Shannon's Hill number | + 0.558 | 0.893 | 0.949 | <0.001 | 0.385 |
| Log canopy openness | + 1.157 | 0.198 | < 0.001 | 0.555 | 0.630 |
| Flower abundance | + | 278.500 | < 0.001 | 0.223 | 0.594 |
| Flower rarefied richness | + 4.167 | 0.840 | < 0.001 | 0.307 | 0.713 |
| Flower Shannon's Hill number | + 0.271 | 0.109 | 0.013 | 0.198 | 0.260 |

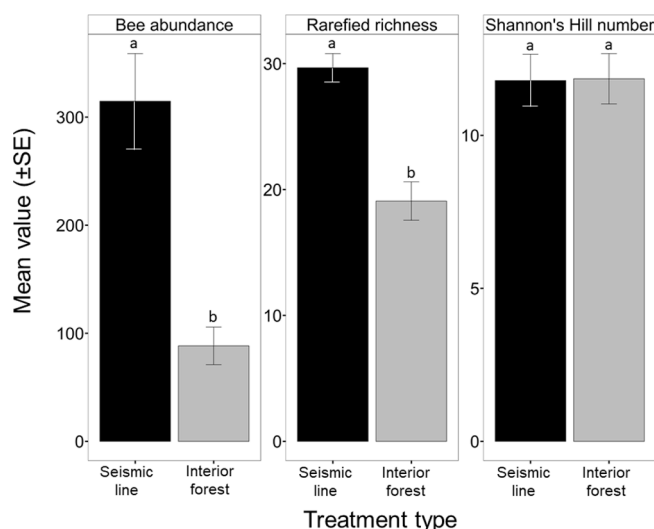


Fig. 3. Means and standard error of abundance, rarefied richness, and Shannon's Hill number of bees caught in pan traps on seismic lines and in the interior forest. Different letters indicate a significant effect of treatment type on each metric ($p < 0.05$).

trapping time between all samples (Appendix B).

Forest canopies were more than twice as open on seismic lines ($43.86\% \pm 3.71$) compared to interior forests ($16.81\% \pm 3.43$, $p < 0.001$). Mean flower abundance was also more than twice as high on seismic lines (1637.83 ± 354.96) than the interior forest (648.22 ± 190.2 , $p < 0.001$). Flower rarefied richness was 1.7-times higher on seismic lines (9.92 ± 1.08) compared to forest interiors (5.75 ± 0.83 , $p < 0.001$), while Shannon's Hill number of flowers on seismic lines (1.17 ± 0.09) was 1.3-times higher than the interior forest (0.90 ± 0.08 , $p = 0.013$, Fig. 2, Table 1).

Bee abundance in pan traps was more than 3-times higher on seismic lines (314.67 ± 44.07) compared to forest interiors (88.33 ± 17.38 , $p < 0.001$). Rarefied richness was 1.5-times higher on seismic lines (29.67 ± 1.13) compared to interior forest (19.08 ± 1.52 , $p < 0.001$), while Shannon's Hill number was nearly identical between seismic lines (11.79 ± 0.82) and interior forest transects (11.85 ± 0.82 , $p = 0.949$, Fig. 3, Table 1).

Species composition between seismic lines and the forest interior was

Table 2

Results of the perMANOVA analysis of bee species composition in pan traps including only treatment type and site using a) Bray-Curtis and b) Jaccard distances. Significant p-values are bolded.

| VARIABLE | DF | SS | MS | F | R ² | P |
|--|----|------|------|------|----------------|----------------|
| A. BRAY-CURTIS DISTANCE ESTIMATOR | | | | | | |
| TREATMENT TYPE | 1 | 1.18 | 1.18 | 8.82 | 0.27 | < 0.001 |
| SITE | 1 | 0.32 | 0.32 | 2.41 | 0.07 | 0.040 |
| RESIDUALS | 21 | 2.80 | 0.13 | | 0.65 | |
| TOTAL | 23 | 4.31 | | | 1.00 | |
| B. JACCARD DISTANCE ESTIMATOR | | | | | | |
| TREATMENT TYPE | 1 | 1.18 | 1.18 | 5.29 | 0.18 | < 0.001 |
| SITE | 1 | 0.40 | 0.40 | 1.81 | 0.06 | 0.040 |
| RESIDUALS | 21 | 4.71 | 0.22 | | 0.74 | |
| TOTAL | 23 | 8.41 | | | 1.00 | |

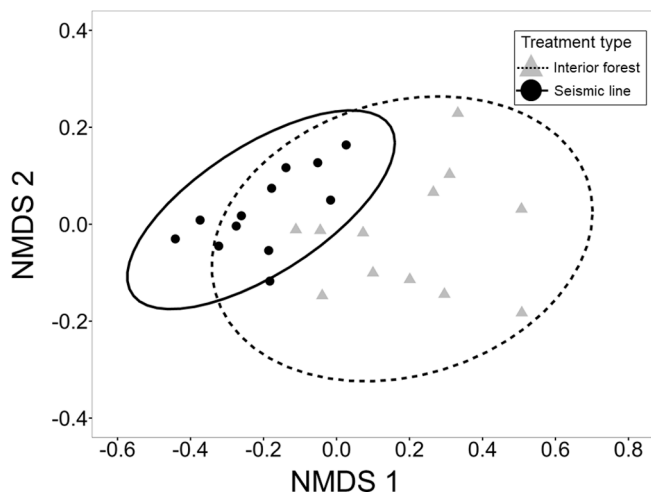


Fig. 4. NMDS of species composition for bees caught in pan traps using Bray-Curtis distance estimation. Grey triangles represent transects from the interior forest and black circles represent transects from seismic lines. The solid and dotted ellipses represent the distributions of seismic line and interior forest transects, respectively. Stress = 0.098.

significantly different in perMANOVA tests, for both the Jaccard ($p < 0.01$, $R^2 = 0.18$) and the Bray-Curtis distance estimators ($p < 0.01$, $R^2 = 0.27$, Table 2). The higher model fit for Bray-Curtis distances suggests that seismic lines affected not only bee presence/absence, but also their relative abundances. The NMDS (with Bray-Curtis distance) showed that bee communities on seismic lines were more similar to each other than were bee communities in interior forest transects. Communities on seismic lines also had moderately high separation from the forest interior on Axis 1 (Fig. 4).

For models including canopy openness, flower abundance, and flower diversity as fixed effects, bee abundance ($p < 0.001$) and rarefied richness ($p < 0.001$), but not Shannon's Hill number, were significantly and positively associated with increased canopy openness (Fig. 5A, 5D, Table 3). Bee abundance ($p = 0.002$) and rarefied richness ($p < 0.001$) were also positively associated with flower rarefied richness (Fig. 5C, 5E). Bee abundance also significantly decreased with increased flower abundance ($p = 0.028$, Fig. 5B, Table 3). No explanatory variable was significantly associated with bee Shannon's Hill number. Canopy openness also affected bee community composition in the perMANOVAs that included canopy openness, flower abundance, and flower rarefied richness ($p < 0.05$, Table 4) (see Table 5).

3.2. Bee movement

Malaise traps caught over 3-times more bees on seismic lines (59.10 ± 18.21) than the interior forest (18.60 ± 5.44 , $p < 0.05$), and traps oriented to catch bees flying along seismic lines caught over 3-times more bees (4.28 ± 1.42) than those oriented to catch bees flying across them (1.50 ± 0.29 , $p < 0.05$). Rarefied richness was twice as high on seismic lines (15.70 ± 2.77) compared to the interior forest (7.80 ± 1.62). However, this difference was not significant ($p = 0.261$). The same was true for Shannon's Hill number (9.80 ± 1.43 on seismic lines, 5.28 ± 0.83 in forest interiors, $p = 0.321$). Malaise traps oriented to catch bees flying along seismic lines caught more than twice as many bees as traps oriented in the same direction in forest interiors (56.70 ± 19.04 on seismic lines, 21.00 ± 4.37 in forest interiors, $p = 0.003$), had 1.7-times higher rarefied richness (14.90 ± 3.09 on seismic lines, 8.60 ± 1.42 in forest interiors, $p < 0.001$), and had over 1.5-times higher Shannon's Hill number (9.28 ± 1.61 on seismic lines, 5.80 ± 0.81 in forest interiors, $p < 0.001$). Treatment type (seismic line vs. forest interior) and orientation significantly interacted such that traps on seismic lines oriented to catch bees flying along the corridor caught a higher rarefied richness ($p = 0.019$) and Shannon's Hill number ($p = 0.013$) of bees. However, the interaction term was not significant for bee abundance, but there was evidence for an additive effect. Despite these results, bee abundances for each combination clearly show strong trends (see Fig. 6) suggesting an interaction between orientation and treatment type. We therefore used post-hoc pairwise comparisons with a Tukey adjustment for measures of bee abundance, rarefied richness, and Shannon's Hill number. Malaise traps on seismic lines oriented to catch bees flying along the corridors caught 1.3-time more bees (4.22 ± 0.32) than the next highest value (3.14 ± 0.32 , $p = 0.015$), and the "along corridors" value was significantly different than all other values. No other combination of treatment type and orientation were significantly different from one another. The same was true for rarefied richness, which had over twice as many species in traps travelling along seismic lines (21.20 ± 2.49) than the next highest value (10.20 ± 2.49 , $p = 0.008$). Shannon's Hill number also had twice as much diversity in traps travelling along seismic lines (21.20 ± 2.49) than the next highest value (10.20 ± 2.49 , $p = 0.008$). This demonstrated both numeric increases and compositional changes in bees moving along corridors as compared to across them or as compared to in any direction in forest interiors, supporting the hypothesis that corridors direct bee movements.

4. Discussion

We found that bees were over three times more abundant on seismic lines than in the interior forest, as well as having a higher rarefied richness, but not higher diversity. Bee species composition also significantly differed on seismic lines compared to the interior forest. Both bee abundance and rarefied richness were significantly and positively associated with canopy openness. Bee abundance was also slightly negatively associated with flower abundance and positively associated with flower rarefied richness, and bee rarefied richness was positively associated with flower rarefied richness. These results demonstrate that increases in bee richness were attributable, at least in part, to the more open canopy structure of seismic lines and the higher abundance and diversity of flowers present, suggesting an attractive effect of these anthropogenic linear corridors beyond changes in floral resource availability.

Increases in abundance and rarefied richness of bees on seismic lines is unsurprising, as there is substantial evidence of temperate and boreal pollinating insects positively responding to early successional habitats (Odanaka and Rehan, 2020; Rodríguez and Kouki, 2017). The fact that rarefied richness of bees was higher on seismic lines, but Shannon's Hill number was not, suggests that this effect is variable between species. Since Shannon's Hill number accounts for species evenness and puts less emphasis on rare species than does species richness, it appears that only

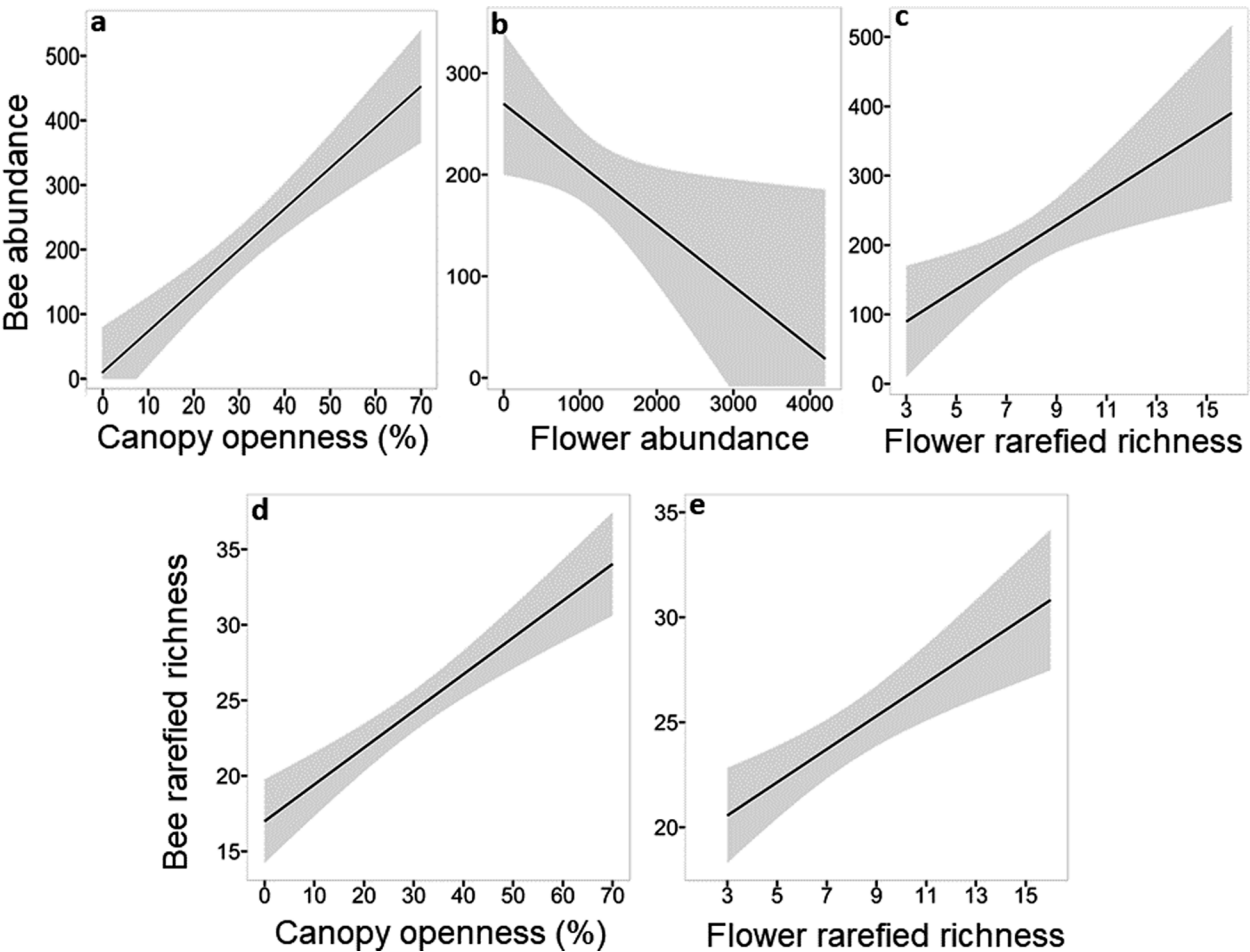


Fig. 5. Marginal plots showing the effects of explanatory variables (canopy openness, flower abundance, flower rarefied richness) on the predicted values response variables they significantly ($p < 0.05$) affected (bee abundance and rarefied richness), with all other variables held at their means (see Table 3). The black lines represent the predicted relationships and the grey bars represent a 95% confidence interval.

Table 3

Final model structure for GLMMs (Gaussian distribution) showing how bee abundance and diversity varies with canopy openness, flower abundance, and flower diversity. “Coef” represents estimated slope of the explanatory variable from the GLMM. Site was included as a random effect in all models. Significant p-values are bolded.

| Response variable | Explanatory variables | Coef. | S.E. | p | Marginal R ² | Conditional R ² |
|-------------------|--------------------------|---------|-------|-------------------|-------------------------|----------------------------|
| Abundance | Canopy openness | 6.333 | 1.033 | < 0.001 | 0.712 | 0.712 |
| | Flower abundance | − 0.060 | 0.027 | 0.028 | | |
| | Flower rarefied richness | 23.120 | 1.033 | 0.002 | | |
| Rarefied richness | Canopy openness | 0.244 | 0.040 | < 0.001 | 0.766 | 0.766 |
| | Flower richness | 0.789 | 0.191 | < 0.001 | | |
| | Shannon's Hill number | N/A | N/A | N/A | | |

some species are responding more strongly and positively to seismic lines than others (Hill, 1973). These results also show that bee community composition significantly differs between seismic line and interior forest transects, further suggesting that responses to seismic lines are highly variable between species.

Given the importance of floral resources to bee communities, it is also unsurprising that flower rarefied richness was positively related to bee abundance and rarefied richness (Gathmann and Tschardt, 2002; Westerfelt et al., 2018). We also found that flower abundance was weakly negatively correlated with bee abundance. This result may be because pan traps visually attract bees like flowers do, so when flower abundance increases, fewer bees are attracted to pan traps (Cane et al.,

2000; Cartar et al., 2019; Roulston et al., 2007). However, bee abundance appears to also change in response to the open canopy structure of seismic lines, or some related factor, in addition to changes in floral resource availability. This is also true for species composition, which was affected by canopy openness more than any other variable tested. One possible explanation is that these differences are driven by floral resources correlated with canopy openness that we did not measure, such as pollen and nectar quality, which are known to affect floral choice in *Bombus* (Somme et al., 2015). Another possibility is an increase in availability of suitable woody nesting habitats. In a temperate forest in Indiana, USA, the diversity of bees was positively associated with the presence of increased woody nesting materials (Grundel et al., 2010),

Table 4

Results of the perMANOVA analysis of bee species composition in pan traps including openness, flower abundance, flower rarefied richness and site using a) Bray-Curtis and b) Jaccard distances. Significant p-values are bolded.

| VARIABLE | DF | SS | MS | F | R ² | P |
|--|----|------|------|------|----------------|----------------|
| A. BRAY-CURTIS DISTANCE ESTIMATOR | | | | | | |
| CANOPY OPENNESS | 1 | 1.03 | 1.03 | 7.42 | 0.24 | < 0.001 |
| FLOWER ABUNDANCE | 1 | 0.27 | 0.27 | 1.97 | 0.06 | 0.080 |
| FLOWER RAREFIED RICHNESS | 1 | 0.14 | 0.14 | 1.04 | 0.03 | 0.356 |
| SITE | 1 | 0.21 | 0.21 | 1.53 | 0.05 | 0.150 |
| RESIDUALS | 19 | 2.64 | 0.14 | | 0.61 | |
| TOTAL | 23 | 4.31 | | | 1.00 | |
| B. JACCARD DISTANCE ESTIMATOR | | | | | | |
| CANOPY OPENNESS | 1 | 1.04 | 1.04 | 4.50 | 0.16 | < 0.001 |
| FLOWER ABUNDANCE | 1 | 0.36 | 0.36 | 1.57 | 0.06 | 0.091 |
| FLOWER RAREFIED RICHNESS | 1 | 0.21 | 0.21 | 0.92 | 0.03 | 0.500 |
| SITE | 1 | 0.31 | 0.31 | 1.33 | 0.05 | 0.172 |
| RESIDUALS | 19 | 4.38 | 0.23 | | 0.70 | |
| TOTAL | 23 | 6.31 | | | 1.00 | |

and in young boreal forest ecosystems, the abundance of the bee species *Megachile lapponica* and *Hylaeus annulatus*, both of which we observed in this study, increased with nesting material availability (Westerfelt et al., 2018). There also tends to be more coarse woody debris on seismic lines (Queiroz et al., 2019). Given the known nesting preferences of some solitary bees, such as the genera *Hylaeus*, *Megachile*, and *Hoplitis* in deadwood (Westerfelt et al., 2015), and the increased pollinator diversity associated with greater nesting resource availability in early successional forests (Rodríguez and Kouki, 2017), the observed increase in abundance and diversity of bees on seismic lines may be driven, at least in part, by an increased availability of woody nesting sites. Seismic lines also increase air and soil temperatures due to greater canopy openness (Stern et al., 2018; Tuff et al., 2016). Temperature is known to affect bee habitat selection, especially in ground nesting bees such as *Halictus* and *Osmia* (Everaars et al., 2011; Potts and Willmer, 1997). Temperature can also affect bee foraging, as the temperature for optimal foraging activity varies between species (Rader et al., 2013). Early successional habitats also have more bare, exposed soil, which creates favourable conditions for ground nesting bees (Rubene et al., 2015). Thus, increased temperature, sun-exposed soil, and woody debris on anthropogenic linear corridors could be improving nesting conditions and creating a preferred thermal habitat for bees.

We also caught three times more bees, and a more diverse composition, in malaise traps travelling along seismic lines than across them, and more on seismic lines than the interior forest. This suggests a highly diverse community of bees are flying along seismic lines more often than across them, and thus using these as corridors to enhance their

movement. This interpretation is consistent with the current understanding of how insects respond to corridors and other similar changes in landscape structure. For example, Riva et al (2018a) found that butterflies respond to seismic lines by preferentially moving along them. In addition, there is evidence that forest habitat corridors similar to seismic lines increase pollen transfer between flower patches (Townsend and Levey, 2005). This suggests that pollinating species, like bees, are travelling along these corridors in a similar manner to that observed on seismic lines, and perhaps preferentially pollinating flower patches located on these corridors. If bees are using seismic lines as efficient travel corridors, and subsequently increasing their dispersal and/or foraging range, previously separate plant-pollinator communities may begin to interact more frequently, and the metacommunity of small, relatively isolated local communities may begin to function more like a single, large community (Leibold et al., 2004). This could result in outbreeding depression in boreal bee or shrub populations at the landscape scale, making them more susceptible, for example, to disease (Keyghobadi et al., 2005). Additionally, this could result in taxonomic homogenization in the bee community, as well the plant and parasitoid communities they support (Keith et al., 2009; Roland and Taylor, 1997). The NMDS results support this hypothesis, as they show a homogenizing effect of the early seral conditions on seismic lines on bee communities despite increased diversity.

Increased movement of bees may also facilitate northward migration

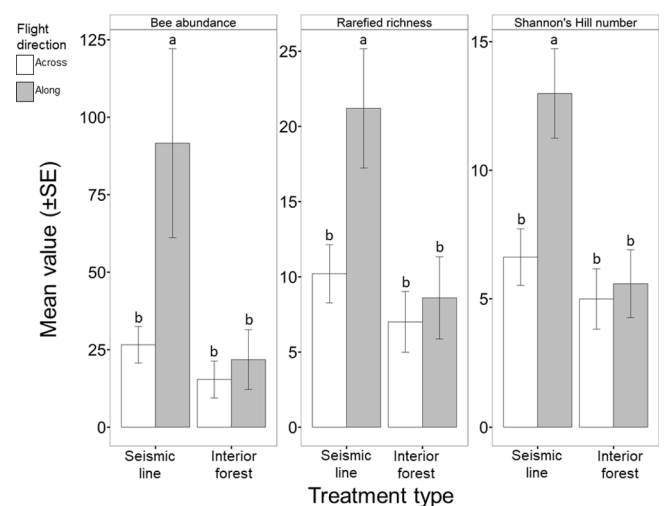


Fig. 6. Means and standard error of abundance, rarefied richness, and Shannon's Hill number of bees caught in malaise traps testing bee movement. Bar shading indicates flight direction relative to the seismic line. Different letters for each response variable indicate a significant difference ($p < 0.05$) from a pairwise comparison using a Tukey adjustment.

Table 5

Final model structure for GLMMs (Gaussian distributions) showing how bee abundance and diversity differed on seismic lines compared to in interior forests (treatment type) and in traps oriented to catch bees flying along seismic lines vs. across them (orientation). For treatment type, "Coef" describes the estimated effect of seismic lines (1) relative to forest interiors (0) from the GLMM. For orientation, "Coef" describes the estimated effect on bees caught in "along" traps (1) relative to "across" traps (0). Site was included as a random effect in all models. Significant p-values are bolded.

| Response variable | Explanatory variables | Coef. | S.E. | p | Marginal R ² | Conditional R ² |
|-----------------------|----------------------------|----------|-------|----------------|-------------------------|----------------------------|
| Abundance | Treatment type | + 1.047 | 0.236 | < 0.001 | 0.435 | 0.713 |
| | Orientation | + 0.712 | 0.236 | 0.003 | | |
| Rarefied richness | Treatment type | + 3.200 | 2.844 | 0.261 | 0.513 | 0.683 |
| | Orientation | + 11.000 | 2.844 | < 0.001 | | |
| | Treatment type:Orientation | + 9.400 | 4.022 | 0.019 | | |
| Shannon's Hill number | Treatment type | + 1.632 | 1.646 | 0.321 | 0.594 | 0.626 |
| | Orientation | + 6.367 | 1.646 | < 0.001 | | |
| | Treatment type:Orientation | + 5.772 | 2.328 | 0.013 | | |

due to climate change. Bee populations, especially *Bombus*, are undergoing declines in some locations due to warming global temperatures (Soroye et al., 2020). If bees are increasing their movement using anthropogenic linear corridors, and possibly increasing their dispersal range as a result, north–south oriented corridors may facilitate accelerated dispersal northward, allowing them to delay their exposure to warmer temperatures. Although the methods used here cannot differentiate between foraging movement and dispersal movement, increased range in either could have major consequences for the biodiversity of insect pollinator and flower communities and the populations that rely on them. Future work should investigate the spatial scale at which bees respond to seismic lines to elucidate if the effect of anthropogenic linear corridors on movement detected in this study is related to foraging, dispersal, or both.

Taken together, these results could mean that seismic lines are favouring open-habitat bee communities, creating more resource competition with forest interior specialists. Indeed, seismic lines may be drawing these early seral specialists out of interior forests, rather than increasing total abundance and diversity, which would cause the changes in species composition seen in this study. There is evidence that anthropogenic linear corridors do not increase bee diversity at a landscape scale (Dániel-Ferreira et al., 2020). Thus, seismic lines may introduce valuable early seral habitat for some bee species, while fragmenting preferred mature habitat for others. Future research should expand the spatial scale of this study to determine landscape level effects of seismic lines, as well as determine which species benefit most from these disturbances.

In summary, we found that the abundance and diversity of bees was more than twice as high on seismic lines compared to the interior forest, and species composition was significantly different between the two environments despite being only 50 m apart. The increase in bee abundance was explained by canopy openness, flower abundance, and flower rarefied richness, while canopy openness and flower diversity explained the increased bee diversity. We also found that malaise traps caught more bees on seismic lines and more bees travelling along or parallel to them, and there is evidence that bees are using seismic lines as travel corridors. These results suggest that narrow anthropogenic linear corridors associated with energy exploration either promote forest bee abundance, or attract bees out of interior forests, and provide evidence that bees also use these cut lines as travel corridors, which could have broader implications for pollinator community connectedness and function across the boreal forest.

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

See Table A1

Table A1

A list of bee species captured in pan traps with total seasonal abundances for each treatment type and overall total. Morphospecies are listed as "[Genus] spp."

| Family | Genus | Species | Seismic lines | Forest interiors | Total |
|--------------|----------------------|------------------------|---------------|------------------|-------------|
| Andrenidae | <i>Andrena</i> | <i>melanochroa</i> | 4 | 2 | 6 |
| Andrenidae | <i>Andrena</i> | <i>miranda</i> | 6 | 4 | 10 |
| Andrenidae | <i>Andrena</i> | <i>peckhami</i> | 23 | 1 | 24 |
| Andrenidae | <i>Andrena</i> | <i>thaspii</i> | 11 | 4 | 15 |
| Andrenidae | <i>Andrena</i> | <i>vicina</i> | 28 | 17 | 45 |
| Andrenidae | <i>Andrena</i> | <i>wellesleyana</i> | 7 | 0 | 7 |
| Apidae | <i>Anthophora</i> | <i>bomboides</i> | 45 | 9 | 54 |
| Apidae | <i>Bombus</i> | <i>bifarius</i> | 3 | 1 | 4 |
| Apidae | <i>Bombus</i> | <i>borealis</i> | 1 | 0 | 1 |
| Apidae | <i>Bombus</i> | <i>cryptarum</i> | 2 | 2 | 4 |
| Apidae | <i>Bombus</i> | <i>flavidus</i> | 4 | 4 | 8 |
| Apidae | <i>Bombus</i> | <i>flavifrons</i> | 1 | 1 | 2 |
| Apidae | <i>Bombus</i> | <i>frigidus</i> | 149 | 88 | 237 |
| Apidae | <i>Bombus</i> | <i>jonellus</i> | 1 | 0 | 1 |
| Apidae | <i>Bombus</i> | <i>melanopygus</i> | 8 | 6 | 14 |
| Apidae | <i>Bombus</i> | <i>perplexus</i> | 0 | 2 | 2 |
| Apidae | <i>Bombus</i> | <i>sandersoni</i> | 19 | 18 | 37 |
| Apidae | <i>Bombus</i> | <i>suckleyi</i> | 1 | 0 | 1 |
| Apidae | <i>Bombus</i> | <i>ternarius</i> | 131 | 60 | 191 |
| Apidae | <i>Bombus</i> | <i>terricola</i> | 6 | 2 | 8 |
| Apidae | <i>Bombus</i> | <i>vagans</i> | 41 | 25 | 66 |
| Apidae | <i>Melissodes</i> | <i>coreopsis</i> | 19 | 22 | 41 |
| Apidae | <i>Nomada</i> | <i>aquilarum</i> | 1 | 0 | 1 |
| Apidae | <i>Nomada</i> | <i>cuneata</i> | 3 | 1 | 4 |
| Apidae | <i>Nomada</i> | <i>lehighensis</i> | 1 | 0 | 1 |
| Apidae | <i>Nomada</i> | <i>perplexa</i> | 6 | 0 | 6 |
| Apidae | <i>Nomada</i> | <i>valida</i> | 0 | 1 | 1 |
| Apidae | <i>Protosmia</i> | <i>ribifloris</i> | 1 | 0 | 1 |
| Colletidae | <i>Colletes</i> | <i>Colletes</i> spp | 11 | 0 | 11 |
| Colletidae | <i>Hylaeus</i> | <i>annulatus</i> | 32 | 11 | 43 |
| Colletidae | <i>Hylaeus</i> | <i>basalis</i> | 98 | 26 | 124 |
| Halictidae | <i>Dufourea</i> | <i>Dufourea</i> spp | 1 | 0 | 1 |
| Halictidae | <i>Halictus</i> | <i>rubicundus</i> | 10 | 1 | 11 |
| Halictidae | <i>Lassioglossum</i> | <i>abundipunctum</i> | 87 | 47 | 134 |
| Halictidae | <i>Lassioglossum</i> | <i>athabascense</i> | 26 | 2 | 28 |
| Halictidae | <i>Lassioglossum</i> | <i>cressonii</i> | 253 | 98 | 351 |
| Halictidae | <i>Lassioglossum</i> | <i>egregium</i> | 2 | 3 | 5 |
| Halictidae | <i>Lassioglossum</i> | <i>leucozonium</i> | 10 | 3 | 13 |
| Halictidae | <i>Lassioglossum</i> | <i>parajorbesii</i> | 129 | 88 | 217 |
| Halictidae | <i>Lassioglossum</i> | <i>pavoninum</i> | 325 | 80 | 405 |
| Halictidae | <i>Lassioglossum</i> | <i>prasinogaster</i> | 9 | 2 | 11 |
| Halictidae | <i>Sphecodes</i> | <i>Sphecodes</i> spp 1 | 6 | 1 | 7 |
| Halictidae | <i>Sphecodes</i> | <i>Sphecodes</i> spp 2 | 3 | 0 | 3 |
| Halictidae | <i>Sphecodes</i> | <i>Sphecodes</i> spp 3 | 4 | 1 | 5 |
| Megachilidae | <i>Atoposmia</i> | <i>Atoposmia</i> spp | 1 | 1 | 2 |
| Megachilidae | <i>Coelioxys</i> | <i>sodalis</i> | 8 | 0 | 8 |
| Megachilidae | <i>Hoplitis</i> | <i>albifrons</i> | 172 | 9 | 181 |
| Megachilidae | <i>Hoplitis</i> | <i>spolata</i> | 6 | 2 | 8 |
| Megachilidae | <i>Hoplitis</i> | <i>truncata</i> | 8 | 3 | 11 |
| Megachilidae | <i>Megachile</i> | <i>addenda</i> | 5 | 0 | 5 |
| Megachilidae | <i>Megachile</i> | <i>gemula</i> | 2 | 0 | 2 |
| Megachilidae | <i>Megachile</i> | <i>lapponica</i> | 5 | 2 | 7 |
| Megachilidae | <i>Megachile</i> | <i>melanophaea</i> | 110 | 24 | 134 |
| Megachilidae | <i>Megachile</i> | <i>perihirta</i> | 42 | 9 | 51 |
| Megachilidae | <i>Osmia</i> | <i>bucephala</i> | 82 | 14 | 96 |
| Megachilidae | <i>Osmia</i> | <i>Osmia</i> spp 1 | 20 | 8 | 28 |
| Megachilidae | <i>Osmia</i> | <i>Osmia</i> spp 2 | 5 | 1 | 6 |
| Megachilidae | <i>Osmia</i> | <i>Osmia</i> spp 3 | 6 | 4 | 10 |
| Megachilidae | <i>Osmia</i> | <i>proxima</i> | 1156 | 254 | 1410 |
| Megachilidae | <i>Osmia</i> | <i>simillima</i> | 25 | 6 | 31 |
| Megachilidae | <i>Osmia</i> | <i>tarsata</i> | 595 | 90 | 685 |
| | | Total | 3776 | 1060 | 4836 |

Appendix B

See Table B1

Table B1

A list of bee species captured in malaise traps with total seasonal abundances for each treatment type and total overall. Morphospecies are listed as “[Genus] spp.”

| Family | Genus | Species | Seismic lines | Forest interiors | Total |
|--------------|----------------------|------------------------|---------------|------------------|------------|
| Andrenidae | <i>Andrena</i> | <i>melanochroa</i> | 2 | 0 | 2 |
| Andrenidae | <i>Andrena</i> | <i>miranda</i> | 11 | 1 | 12 |
| Andrenidae | <i>Andrena</i> | <i>peckhami</i> | 5 | 0 | 5 |
| Andrenidae | <i>Andrena</i> | <i>thaspia</i> | 7 | 2 | 9 |
| Andrenidae | <i>Andrena</i> | <i>vicina</i> | 18 | 2 | 20 |
| Andrenidae | <i>Andrena</i> | <i>wellesleyana</i> | 0 | 1 | 1 |
| Apidae | <i>Anthophora</i> | <i>bomboides</i> | 39 | 2 | 41 |
| Apidae | <i>Bombus</i> | <i>bifarius</i> | 0 | 1 | 1 |
| Apidae | <i>Bombus</i> | <i>cryptarum</i> | 0 | 1 | 1 |
| Apidae | <i>Bombus</i> | <i>flavidus</i> | 1 | 1 | 2 |
| Apidae | <i>Bombus</i> | <i>frigidus</i> | 7 | 3 | 10 |
| Apidae | <i>Bombus</i> | <i>melanopygus</i> | 0 | 1 | 1 |
| Apidae | <i>Bombus</i> | <i>sandersoni</i> | 6 | 8 | 14 |
| Apidae | <i>Bombus</i> | <i>ternarius</i> | 152 | 80 | 232 |
| Apidae | <i>Bombus</i> | <i>terricola</i> | 5 | 0 | 5 |
| Apidae | <i>Bombus</i> | <i>vagans</i> | 3 | 3 | 6 |
| Apidae | <i>Lassioglossum</i> | <i>wellesleyana</i> | 5 | 1 | 6 |
| Apidae | <i>Megachile</i> | <i>melanophaea</i> | 15 | 11 | 26 |
| Apidae | <i>Melissodes</i> | <i>coreopsis</i> | 44 | 6 | 50 |
| Apidae | <i>Nomada</i> | <i>bella</i> | 0 | 1 | 1 |
| Apidae | <i>Nomada</i> | <i>cuneata</i> | 1 | 0 | 1 |
| Apidae | <i>Nomada</i> | <i>lehighensis</i> | 1 | 0 | 1 |
| Colletidae | <i>Colletes</i> | <i>Colletes</i> spp | 16 | 4 | 20 |
| Colletidae | <i>Hylaeus</i> | <i>annulatus</i> | 2 | 1 | 3 |
| Colletidae | <i>Hylaeus</i> | <i>basalis</i> | 9 | 4 | 13 |
| Halictidae | <i>Halictus</i> | <i>rubicundus</i> | 3 | 0 | 3 |
| Halictidae | <i>Lassioglossum</i> | <i>abundipunctum</i> | 15 | 3 | 18 |
| Halictidae | <i>Lassioglossum</i> | <i>athabascense</i> | 6 | 3 | 9 |
| Halictidae | <i>Lassioglossum</i> | <i>cressonii</i> | 23 | 8 | 31 |
| Halictidae | <i>Lassioglossum</i> | <i>egregium</i> | 1 | 0 | 1 |
| Halictidae | <i>Lassioglossum</i> | <i>leucozonium</i> | 8 | 3 | 11 |
| Halictidae | <i>Lassioglossum</i> | <i>paraforbesii</i> | 31 | 6 | 37 |
| Halictidae | <i>Lassioglossum</i> | <i>pavoninum</i> | 15 | 7 | 22 |
| Halictidae | <i>Sphecodes</i> | <i>Sphecodes</i> spp 1 | 7 | 0 | 7 |
| Halictidae | <i>Sphecodes</i> | <i>Sphecodes</i> spp 2 | 4 | 0 | 4 |
| Megachilidae | <i>Coelioxys</i> | <i>sodalis</i> | 2 | 1 | 3 |
| Megachilidae | <i>Hoplitis</i> | <i>albifrons</i> | 15 | 0 | 15 |
| Megachilidae | <i>Hoplitis</i> | <i>spolata</i> | 3 | 0 | 3 |
| Megachilidae | <i>Hoplitis</i> | <i>truncata</i> | 2 | 1 | 3 |
| Megachilidae | <i>Megachile</i> | <i>lapponica</i> | 1 | 1 | 2 |
| Megachilidae | <i>Megachile</i> | <i>perihirta</i> | 12 | 2 | 14 |
| Megachilidae | <i>Osmia</i> | <i>bucephala</i> | 2 | 1 | 3 |
| Megachilidae | <i>Osmia</i> | <i>Osmia</i> spp 1 | 0 | 1 | 1 |
| Megachilidae | <i>Osmia</i> | <i>Osmia</i> spp 3 | 11 | 0 | 11 |
| Megachilidae | <i>Osmia</i> | <i>proxima</i> | 61 | 14 | 75 |
| Megachilidae | <i>Osmia</i> | <i>simillima</i> | 2 | 0 | 2 |
| Megachilidae | <i>Osmia</i> | <i>tarsata</i> | 18 | 1 | 19 |
| | | Total | 591 | 186 | 777 |

Appendix C

See Table C1

Table C1

A list of plant species observed with open flowers. Abundance values are the sums for all quadrats of the highest number of flowers observed in each quadrat at one time for each species.

| Order | Family | Genus | Species | Seismic lines | Forest interiors | Total |
|----------------|-----------------|-----------------------|-------------------------|---------------|------------------|---------------|
| Apiales | Araliaceae | <i>Aralia</i> | <i>nudicaulis</i> | 24 | 35 | 59 |
| Asparagales | Asparagaceae | <i>Maianthemum</i> | <i>canadense</i> | 7945 | 4060 | 12,005 |
| Asparagales | Orchidaceae | <i>Cypripedium</i> | <i>acaule</i> | 1 | 0 | 1 |
| Asterales | Asteraceae | <i>Aster</i> | <i>Aster</i> spp | 19 | 0 | 19 |
| Asterales | Asteraceae | <i>Solidago</i> | <i>Solidago</i> spp | 178 | 83 | 261 |
| Asterales | Asteraceae | <i>Taraxacum</i> | <i>officinale</i> | 1 | 0 | 1 |
| Asterales | Campanulaceae | <i>Campanula</i> | <i>rotundifolia</i> | 7 | 4 | 11 |
| Brassicales | Brassicaceae | <i>Arabidopsis</i> | <i>lyrata</i> | 2 | 0 | 2 |
| Caryophyllales | Caryophyllaceae | <i>Stellaria</i> | <i>longifolia</i> | 2 | 17 | 19 |
| Cornales | Cornaceae | <i>Cornus</i> | <i>canadensis</i> | 63 | 32 | 95 |
| Dipsacales | Caprifoliaceae | <i>Linnaea</i> | <i>borealis</i> | 332 | 132 | 464 |
| Ericales | Ericaceae | <i>Arctostaphylos</i> | <i>uva-ursi</i> | 3848 | 518 | 4366 |
| Ericales | Ericaceae | <i>Chamaedaphne</i> | <i>calyculata</i> | 87 | 0 | 87 |
| Ericales | Ericaceae | <i>Pyrola</i> | <i>asarifolia</i> | 7 | 20 | 27 |
| Ericales | Ericaceae | <i>Rhododendron</i> | <i>groenlandicum</i> | 85 | 0 | 85 |
| Ericales | Ericaceae | <i>Vaccinium</i> | <i>myrtilloides</i> | 7840 | 2758 | 10,598 |
| Ericales | Ericaceae | <i>Vaccinium</i> | <i>vitis-idaea</i> | 298 | 37 | 335 |
| Ericales | Primulaceae | <i>Trientalis</i> | <i>borealis</i> | 2 | 0 | 2 |
| Gentianales | Apocynaceae | <i>Apocynum</i> | <i>androsaemifolium</i> | 32 | 0 | 32 |
| Gentianales | Rubiaceae | <i>Galium</i> | <i>boreale</i> | 142 | 32 | 174 |
| Lamiales | Orobanchaceae | <i>Melampyrum</i> | <i>lineare</i> | 248 | 194 | 442 |
| Malvales | Cistaceae | <i>Hudsonia</i> | <i>tomentosa</i> | 2 | 0 | 2 |
| Myrtales | Onagraceae | <i>Chamaenerion</i> | <i>angustifolium</i> | 16 | 0 | 16 |
| Ranunculales | Ranunculaceae | <i>Thalictrum</i> | <i>venulosum</i> | 22 | 0 | 22 |
| Rosales | Rosaceae | <i>Amelanchier</i> | <i>alnifolia</i> | 55 | 5 | 60 |
| Rosales | Rosaceae | <i>Fragaria</i> | <i>virginiana</i> | 10 | 1 | 11 |
| Rosales | Rosaceae | <i>Prunus</i> | <i>pensylvanica</i> | 22 | 0 | 22 |
| Rosales | Rosaceae | <i>Rosa</i> | <i>acicularis</i> | 69 | 38 | 107 |
| Rosales | Rosaceae | <i>Rubus</i> | <i>idaeus</i> | 7 | 6 | 13 |
| Rosales | Rosaceae | <i>Sibbaldiopsis</i> | <i>tridentata</i> | 1 | 1 | 2 |
| Santalales | Santalaceae | <i>Geocaulon</i> | <i>lividum</i> | 2 | 3 | 5 |
| | | | Total | 21,369 | 7976 | 29,345 |

Appendix D

See Fig. D1

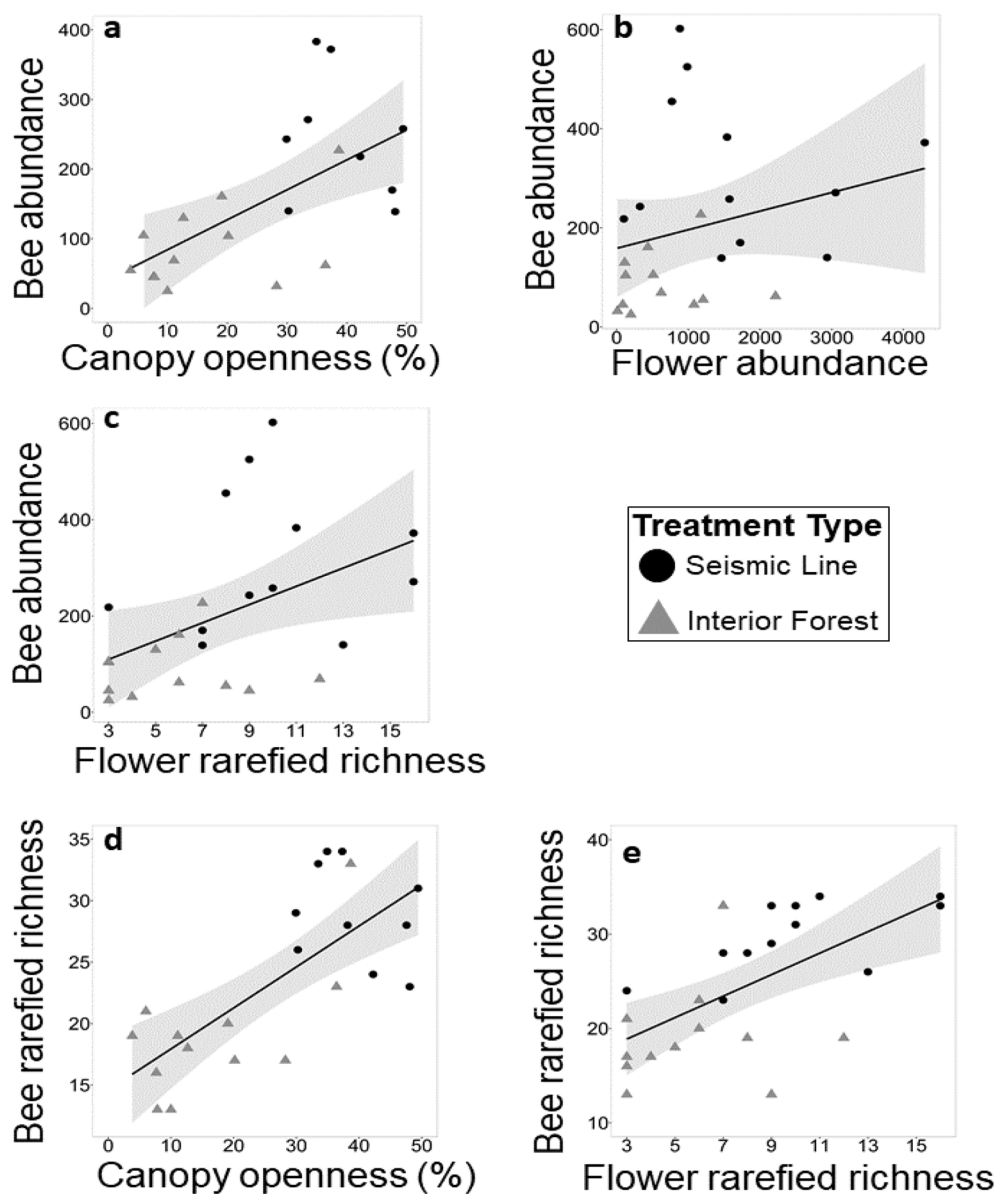


Fig. D1. Scatter plots showing the relationship between key explanatory variables (canopy openness, flower abundance, flower rarefied richness) and either bee abundance or rarefied richness. Grey bars represent a 95% confidence interval of a linear regression.

References

- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: Review and synthesis through a meta-analysis. *Ecol. Lett.* 9 (8), 968–980. <https://doi.org/10.1111/j.1461-0248.2006.00927.x>.
- Andrus, R., & Droege, S., n.d.-a. Draft Guide to the Female *Coelioxys* of Eastern North America. Discover Life. https://www.discoverlife.org/mp/20q?guide=Coelioxys_female.
- Andrus, R., & Droege, S., n.d.-b. Draft Guide to the Hoplitids of Eastern North America. Discover Life. <https://www.discoverlife.org/mp/20q?guide=Hoplitids>.
- Andrus, R., & Droege, S., n.d.-c. Guide to the Melissodes of Eastern North America. Discover Life. https://www.discoverlife.org/mp/20q?guide=Melissodes_female.
- Andrus, R., Droege, S., & Griswold, T., n.d.-a. Draft Guide to the Hylaeus of Eastern North America. Discover Life. https://www.discoverlife.org/mp/20q?guide=Hylaeus_female.
- Andrus, R., Droege, S., & Griswold, T., n.d.-b. Draft Guide to the Male *Osmia* of Eastern North America. Discover Life. https://www.discoverlife.org/mp/20q?guide=Osmia_male.
- Bartholomew, C.S., Prowell, D., 2005. Pan compared to malaise trapping for bees (Hymenoptera: Apoidea) in a longleaf pine savanna. *J. Kansas Entomol. Soc.* 78 (4), 390–392. <https://doi.org/10.2317/0409.24.1>.
- Bartoń, K., & Barton, K., 2020. MuMIn: Multi-Model Inference, Version 1.43.6. R Package Version 1.43.17. <https://cran.r-project.org/package=MuMIn>.
- Cane, J.H., Minkley, R.L., Kervin, L.J., 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *J. Kansas Entomol. Soc.* <https://doi.org/10.2307/25085973>.
- Cartar, R., Wonneck, M., & Evans, M., 2019. Passive traps can be poor samplers of bee abundance: sobering insights from pan traps in the rough fescue grasslands. 6th Joint Annual Meeting of the Entomological Societies of Alberta and Saskatchewan.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84 (1), 45–67. <https://doi.org/10.1890/13-0133.1>.
- Crawley, M.J., 2005. *Statistics: An Introduction Using R*. John Wiley and Sons Ltd.
- Dabrows, A., James Hammond, H.E., Pinno, J., Pinno, B., Langor, D., 2017. Edge influence of low-impact seismic lines for oil exploration on upland forest vegetation in northern Alberta (Canada). *For. Ecol. Manage.* 400, 278–288. <https://doi.org/10.1016/j.foreco.2017.06.030>.
- Daniel-Ferreira, J., Bommarco, R., Wissman, J., Öckinger, E., 2020. Linear infrastructure habitats increase landscape-scale diversity of plants but not of flower-visiting insects. *Sci. Rep.* 10 (1), 21374. <https://doi.org/10.1038/s41598-020-78090-y>.
- Dawe, C.A., Filicetti, A.T., Nielsen, S.E., 2017. Effects of linear disturbances and fire severity on velvet leaf blueberry abundance, vigor, and berry production in recently burned jack pine forests. *Forests* 8 (10). <https://doi.org/10.3390/f8100398>.
- Development Core Team, R., 2020. R: A Language and Environment for Statistical Computing. In R Foundation for Statistical Computing. <https://doi.org/10.1007/978-3-540-74686-7>.
- Droege, S., Gibbs, J., Ikerd, H., Griswold, T., Pascarella, J., & Pickering, J. (n.d.). Guide to the Lasiglossum of Eastern North America. Discover Life. <https://www.discoverlife.org/mp/20q?guide=Lasiglossum>.
- Everaars, J., Strohbach, M.W., Gruber, B., Dormann, C.F., 2011. Microsite conditions dominate habitat selection of the red mason bee (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. *Landscape Urban Plann.* 103 (1), 15–23. <https://doi.org/10.1016/j.landurbplan.2011.05.008>.
- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. In Annual Review of Ecology, Evolution, and Systematics (Vol. 34, Issue 1, pp. 487–515). Annual Reviews Inc. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>.
- Filicetti, A.T., Nielsen, S.E., 2018. Fire and forest recovery on seismic lines in sandy upland jack pine (*Pinus banksiana*) forests. *For. Ecol. Manage.* 421, 32–39. <https://doi.org/10.1016/j.foreco.2018.01.027>.
- Gathmann, A., Tschamtker, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71 (5), 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>.
- Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.* 22 (7), 1–19. <https://doi.org/10.18637/jss.v022.i07>.
- Griswold, T., Ikerd, H., Droege, S., & Pascarella, J. (n.d.). Draft Guide to the Female *Osmia* of Eastern North America. Discover Life. https://www.discoverlife.org/mp/20q?guide=Osmia_female.
- Grundel, R., Jean, R.P., Frohnapple, K.J., Glowacki, G.A., Scott, P.E., Pavlovic, N.B., 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecol. Appl.* 20 (6), 1678–1692. <https://doi.org/10.1890/08-1792.1>.
- Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S., Spira, T., 2003. Corridor use by diverse taxa. *Ecology* 84 (3), 609–615. [https://doi.org/10.1890/0012-9658\(2003\)084\[0609:CUBDT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0609:CUBDT]2.0.CO;2).
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1 (2), e1500052. <https://doi.org/10.1126/sciadv.1500052>.
- Hanula, J.L., Ulyshen, M.D., Horn, S., 2016. Conserving Pollinators in North American Forests: A Review. *Natural Areas J.* 36 (4), 427–439. <https://doi.org/10.3375/043.036.0409>.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Broszofski, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.A., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.A., 2005. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. *Conserv. Biol.* 19 (3), 768–782. <https://doi.org/10.1111/j.1523-1739.2005.00045.x>.
- Harper, K.A., Macdonald, S.E., Mayerhofer, M.S., Biswas, S.R., Esseen, P.A., Hylander, K., Stewart, K.J., Mallik, A.U., Drapeau, P., Jonsson, B.G., Lesieur, D., Kouki, J., Bergeron, Y., 2015. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. *J. Ecol.* 103 (3), 550–562. <https://doi.org/10.1111/1365-2745.12398>.
- Hartig, F., 2018. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.0. In <https://CRAN.R-project.org/package=DHARMA>. <https://cran.r-project.org/web/packages/DHARMA/DHARMA.pdf>.
- Herve, M., 2019. Testing and Plotting Procedures for Biostatistics “RVAideMemoire”. Cran. <https://cran.r-project.org/web/packages/RVAideMemoire/RVAideMemoire.pdf>.
- Hill, M.O., 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology* 54 (2), 427–432. <https://doi.org/10.2307/1934352>.
- Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E., Bullock, J.M., 2009. Taxonomic homogenization of woodland plant communities over 70 years. *Proc. Royal Soc. B Biol. Sci.* 276 (1672), 3539–3544. <https://doi.org/10.1098/rspb.2009.0938>.
- Kevan, P.G., Tikhmenev, E.A., Usui, M., 1993. Insects and plants in the pollination ecology of the boreal zone. *Ecol. Res.* 8 (3), 247–267. <https://doi.org/10.1007/BF02347185>.
- Keyghobadi, N., Roland, J., Strobeck, C., 2005. Genetic differentiation and gene flow among populations of the alpine butterfly, *Parnassius smintheus*, vary with landscape connectivity. *Mol. Ecol.* 14 (7), 1897–1909. <https://doi.org/10.1111/j.1365-294X.2005.02563.x>.
- Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, R.A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Mol. Ecol.* 14 (6), 1811–1820. <https://doi.org/10.1111/j.1365-294X.2005.02540.x>.
- Larkin, L., Andrus, R., & Droege, S. (n.d.). Guide to the *Andrena* of North America. Discover Life. https://www.discoverlife.org/mp/20q?guide=Andrena_female.
- Latham, A.D.M., Latham, M.C., Boyce, M.S., Boutin, S., 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecol. Appl.* 21 (8), 2854–2865. <https://doi.org/10.1890/11-0666.1>.
- Lee, P., Boutin, S., 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. *J. Environ. Manage.* 78 (3), 240–250. <https://doi.org/10.1016/j.jenvman.2005.03.016>.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecol. Lett.* 7 (7), 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>.
- Magnusson, A., Skaug, H.J., Nielsen, A., Berg, C.W., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Brooks, M.E., 2020. Package “glmmTMB”. Generalized Linear Mixed Models using Template Model Builder. CRAN 9 (2), 378–400.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology* 82 (1), 290–297. [https://doi.org/10.1890/0012-9658\(2001\)082\[0290:FMTCDD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0290:FMTCDD]2.0.CO;2).
- Moreira, E. F., Santos, R. L. da S., Penna, U. L., Angel-Coca, C., de Oliveira, F. F., & Viana, B. F. (2016). Are pan traps colors complementary to sample community of potential pollinator insects? *Journal of Insect Conservation*, 20(4), 583–596. <https://doi.org/10.1007/s10841-016-9890-x>.
- Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* 14 (134). <https://doi.org/10.1098/rsif.2017.0213>.
- Nielsen, S.E., Dennett, J.M., Bater, C.W., 2020. Predicting occurrence, abundance, and fruiting of a cultural keystone species to inform landscape values and priority sites for habitat enhancements. *Forests* 11 (7), 783. <https://doi.org/10.3390/f11070783>.
- Odanaka, K.A., Rehan, S.M., 2020. Wild bee distribution near forested landscapes is dependent on successional state. *Forest Ecosyst.* 7 (1). <https://doi.org/10.1186/s40663-020-00241-4>.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szocs, E., & Wagner, H. (2018). *Vegan: community ecology package*, version. R Package Version 2.5-6. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>.
- Pattison, C.A., Quinn, M.S., Dale, P., Catterall, C.P., 2016. The Landscape Impact of Linear Seismic Clearings for Oil and Gas Development in Boreal Forest. Northwest. <https://doi.org/10.3955/046.090.0312>.
- Potts, S.G., Willmer, P., 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecol. Entomol.* 22 (3), 319–328. <https://doi.org/10.1046/j.1365-2311.1997.00071.x>.
- Queiroz, G.L., McDermid, G.J., Castilla, G., Linke, J., Rahman, M.M., 2019. Mapping coarse woody debris with random forest classification of centimetric aerial imagery. *Forests* 10 (6). <https://doi.org/10.3390/f10060471>.
- Rader, R., Reilly, J., Bartomeus, I., Winfree, R., 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Glob. Change Biol.* 19 (10), 3103–3110. <https://doi.org/10.1111/gcb.12264>.
- Riva, F., Acorn, J.H., Nielsen, S.E., 2018a. Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests. *Biol. Conserv.* 217, 173–180. <https://doi.org/10.1016/j.biocon.2017.10.022>.
- Riva, F., Acorn, J.H., Nielsen, S.E., 2018b. Narrow anthropogenic corridors direct the movement of a generalist boreal butterfly. *Biol. Lett.* 14 (2). <https://doi.org/10.1098/rsbl.2017.0770>.

- Riva, F., Pinzon, J., Acorn, J.H., Nielsen, S.E., 2020. Composite Effects of Cutlines and Wildfire Result in Fire Refuges for Plants and Butterflies in Boreal Treed Peatlands. *Ecosystems* 23 (3), 485–497. <https://doi.org/10.1007/s10021-019-00417-2>.
- Roberts, D., Ciuti, S., Barber, Q.E., Willier, C., Nielsen, S.E., 2018. Accelerated seed dispersal along linear disturbances in the Canadian oil sands region. *Sci. Rep.* 8 (1) <https://doi.org/10.1038/s41598-018-22678-y>.
- Rodríguez, A., Kouki, J., 2015. Emulating natural disturbance in forest management enhances pollination services for dominant *Vaccinium* shrubs in boreal pine-dominated forests. *For. Ecol. Manage.* 350, 1–12. <https://doi.org/10.1016/j.foreco.2015.04.029>.
- Rodríguez, A., Kouki, J., 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecol. Appl.* 27 (2), 589–602. <https://doi.org/10.1002/eap.1468>.
- Roland, J., Taylor, P.D., 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386 (6626), 710–713. <https://doi.org/10.1038/386710a0>.
- Roulston, T.H., Smith, S.A., Brewster, A.L., 2007. Short communication: A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *J. Kansas Entomol. Soc.* [https://doi.org/10.2317/0022-8567\(2007\)80\[179:ACOPTA\]2.0.CO;2](https://doi.org/10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2).
- Rubene, D., Schroeder, M., Ranius, T., 2015. Diversity patterns of wild bees and wasps in managed boreal forests: Effects of spatial structure, local habitat and surrounding landscape. *Biol. Conserv.* 184, 201–208. <https://doi.org/10.1016/j.biocon.2015.01.029>.
- Schindler, D.W., Lee, P.G., 2010. Comprehensive conservation planning to protect biodiversity and ecosystem services in Canadian boreal regions under a warming climate and increasing exploitation. *Biol. Conserv.* 143 (7), 1571–1586. <https://doi.org/10.1016/j.biocon.2010.04.003>.
- Simberloff, D., 1972. Properties of the Rarefaction Diversity Measurement. *American Naturalist* 106 (949), 414–418. <https://doi.org/10.1086/282781>.
- Somme, L., Vanderplanck, M., Michez, D., Lombaerde, I., Moerman, R., Wathelet, B., Wattiez, R., Lognay, G., Jacquemart, A.L., 2015. Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie* 46 (1), 92–106. <https://doi.org/10.1007/s13592-014-0307-0>.
- Soroye, P., Newbold, T., Kerr, J., 2020. Climate change contributes to widespread declines among bumble bees across continents. *Science* 367 (6478), 685–688. <https://doi.org/10.1126/science.aax8591>.
- St. Clair, C. C., Bélisle, M., Desrochers, A., & Hannon, S., 1998. Winter responses of forest birds to habitat corridors and gaps. *Ecology and Society*, 2(2). <https://doi.org/10.5751/es-00068-020213>.
- Stern, E., Riva, F., Nielsen, S., 2018. Effects of Narrow Linear Disturbances on Light and Wind Patterns in Fragmented Boreal Forests in Northeastern Alberta. *Forests* 9 (8), 486. <https://doi.org/10.3390/f9080486>.
- Townsend, P.A., Levey, D.J., 2005. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* 86 (2), 466–475. <https://doi.org/10.1890/03-0607>.
- Tuff, K.T., Tuff, T., Davies, K.F., 2016. A framework for integrating thermal biology into fragmentation research. *Ecol. Lett.* 19 (4), 361–374. <https://doi.org/10.1111/ele.12579>.
- Westerfelt, P., Weslien, J., Widenfalk, O., 2018. Population patterns in relation to food and nesting resource for two cavity-nesting bee species in young boreal forest stands. *For. Ecol. Manage.* 430, 629–638. <https://doi.org/10.1016/j.foreco.2018.08.053>.
- Westerfelt, P., Widenfalk, O., Lindelöw, Å., Gustafsson, L., Weslien, J., 2015. Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conservat. Diversity* 8 (6), 493–504. <https://doi.org/10.1111/icad.12128>.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Yutani, H., 2019. Welcome to the Tidyverse. *J. Open Source Software*. <https://doi.org/10.21105/joss.01686>.
- Winfrey, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.* 21 (1), 213–223. <https://doi.org/10.1111/j.1523-1739.2006.00574.x>.